PLANT DIVERSITY EFFECTS ON SOIL COLLEMBOLA IN BOREAL FOREST

By

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ABSTRACT

Collembola are one of the most abundant soil fauna in terrestrial ecosystems. They play essential roles in ecosystem processes like litter decomposition. Ongoing biodiversity loss across taxa harms the stability and resilience of ecosystems and therefore threatens our sustainable development. Recent evidence has shown that biodiversity loss negatively impacts ecosystem processes and functions such as productivity, soil microbes, and the production of fine roots. Despite the critical importance of soil Collembola, our understanding of the effects of plant diversity on soil Collembola remains uncertain. The purpose of this dissertation is first to summarize previous studies and reveal the general response of Collembola to plant species diversity across ecosystems. The second objective is to test whether tree mixtures affect the Collembola community in young boreal forests and if these mixture effects change with water conditions and stand ages.

In my first study, by conducting a meta-analysis of 623 paired observations of plant mixtures and corresponding monocultures from 40 studies, I examined the effects of plant mixtures on soil fauna abundance and diversity across global terrestrial ecosystems and summarized consistent responses of soil fauna to plant species diversity across soil depths, ecosystem types, and climate conditions. I found that the diversity of soil fauna was on average 10% greater in plant mixtures than expected from corresponding monocultures. In contrast, the abundance of fauna did not respond to plant mixtures. Importantly, plant mixture effects on both soil fauna abundance and diversity significantly increased with plant species richness in mixtures. Moreover, the effects of plant mixtures on soil fauna abundance increased over time in diverse species mixtures.

In my second study, I investigated whether the responses of soil Collembola abundance, richness, evenness, and composition to tree mixtures altered with water availability (25% rainfall addition, ambient, and 25% rainfall reduction). This study was conducted in a young boreal forest with pure and mixed jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) using a split-plot design. Forest floor Collembola were sampled and identified to species or morphospecies. Positive mixture effects were observed on soil Collembola abundance under water addition. Importantly, tree mixture effects on evenness increased from -16% under ambient water condition to +3% under water reduction. Only the evenness responded to altered precipitation with higher values in conifer stands under water addition and in mixed stands under water reduction, while the abundance and richness did not. With respect to the effects of stand types, the abundance and richness were highest in mixed stands and lowest in broadleaf stands, but the evenness did not differ with stand type. Community composition in mixed stands differed from broadleaf stands. Further, shifts in soil water content, litter production, and fine root biomass were positively associated with shifts in the abundance, richness, and community composition of Collembola, while soil temperature negatively affected the abundance and richness. I conclude that mixtures of tree species and altered precipitation can locally impact the abundance and diversity of Collembola in young boreal forests.

In my third study, I tested the interactive effects of stand types and stand ages on the Collembola community in 15-year-old and 41-year-old stands with pure and mixed jack pine and trembling aspen in the natural boreal forest. Consistent with my hypothesis, tree mixture effects on Collembola abundance and diversity increased with stand development from neutral in 15-year-old stands to positive in 41-year-old stands. Negative mixture effects were also observed on

the Simpson’s index in 15-year-old stands. Effects of stand types are also more pronounced in older stands. In 15-year-old stands, only evenness responded to stand type with lower values in mixed stands than in broadleaf stands, whereas in 41-year-old stands, abundance and richness were higher in conifer and mixed stands than in broadleaf stands. The findings provide the first evidence for mixture effects on Collembola, which vary in relation to stand development in natural boreal forests.

Overall, my study advances our understanding of the responses of the Collembola community to plant diversity in the context of global changes. It highlights the potential importance of plant diversity conservation. It provides us with the knowledge of effective forest management strategies to maintain a diverse and stable Collembola community and relative functions responding to ongoing diversity loss and climate change.

Keywords: plant diversity, tree mixture, altered precipitation, Collembola, stand age, boreal forest

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corresponding to stand types. Predictor variables included soil temperature (ST), soil water content (SWC), annual litterfall production (LP), fine root biomass (FRB), and soil microbial biomass (SMB).

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NOTE

This is a manuscript-based thesis. The chapters were written to suit the submission requirements of the targeted journals. Formatting and reference styles may differ. Since individual chapters reflect the joint contributions of myself and my academic supervisor, I use “we” instead of “I” for individual chapters.

Chapters:

2. Zhang, Y., Peng, S., Chen, X., & Chen, H. Y. (2022). Plant diversity increases the abundance and diversity of soil fauna: A meta-analysis. Geoderma, 411, 115694.

3. Zhang, Y., Chen, X., Peng, S., Chen, C., & Chen, H. Y. (2024). Tree mixture effects on Collembola evenness increased under reduced throughfall in a young boreal forest. (Submitted to Soil Biology and Biochemistry).

4. Zhang, Y., Peng, S., Gao, B., Chen, C., Chen, X., & Chen, H. Y. (2024). Increased positive tree species mixture effects on the abundance and richness of Collembola with stand development in natural boreal forests. (Preparing to submit to Forest Ecology and Management).

Chapter 1: GENERAL INTRODUCTION

Soil fauna are key components of ecological processes and functions, including soil structure maintenance, litter decomposition, and promoting plant growth via grazing on soil microbes and plant residuals (Forey, Coulibaly et al. 2015, Maaß, Caruso et al. 2015). Collembola, also known as springtails, are a group of small, wingless hexapods. They are among the most abundant groups of soil fauna and commonly inhabitant in soil and litter in terrestrial ecosystems (Hopkin 1997, Orgiazzi, Bardgett et al. 2016). There are 474 described extant and approximately 675 estimated Collembola species in Canada (Turnbull and Stebaeva 2019). Collembola are also known as bioindicators as they are sensitive to environmental changes thus indicating the health and quality of the environment (Machado, Oliveira Filho et al. 2019, Joimel, Chassain et al. 2022). They are significant components of soil communities. They contribute to animal biomass and participate in ecosystem processes like the formation of soil aggregates, litter decomposition, microbial activity regulation, nutrient cycling, and plant growth (Barrios 2007, Chapin, Matson et al. 2011, Soong, Vandegehuchte et al. 2016).

Ongoing biodiversity loss impacts ecosystem functions globally (Cardinale, Duffy et al. 2012, Leclère, Obersteiner et al. 2020). Great efforts have been made to explore the relationships between biodiversity and ecosystem functions in recent years. Most previous studies have studied the responses of aboveground and shown a general pattern that increasing plant species diversity promotes plant production (Liang, Crowther et al. 2016, Duffy, Godwin et al. 2017). However, how plant diversity affects soil fauna remains uncertain.

Increasing plant species diversity can increase aboveground litterfall, belowground root biomass and mortality (Ma and Chen 2018), and promote microbial activities (Lange, Eisenhauer et al. 2015, Chen, Chen et al. 2019). This may provide a greater amount and diversity of food resources and heterogeneity microhabitat structure for soil faunal communities, thus increasing the abundance and diversity and altering the community composition of soil fauna. However, experimental evidence for the relationship between plant and soil faunal community diversity is mixed. Positive effects of plant diversity (Scherber, Eisenhauer et al. 2010, Eisenhauer, Dobies et al. 2013), as well as nonsignificant (Salamon, Schaefer et al. 2004, Korboulewsky, Perez et al. 2016, Zagatto, Pereira et al. 2019), and even negative effects (Korboulewsky, Heiniger et al. 2021) on the abundance and diversity of soil fauna, have all been reported.

Altered precipitation regime is another alarming challenge for the sustainable development of forests (IPCC 2021). Evidence showed that dramatic rainfall patterns can negatively affect forest pocess such as tree growth (Gavinet, Ourcival et al. 2019, Mackay, Savoy et al. 2020). Different groups of soil fauna may vary in their responses to altered precipitation. Collembola, for example, are relatively vulnerable to water stress. It is suggested that biodiversity has the potential to mitigate the negative effects and enhance the positive effects of climate change on ecosystem functioning (Hisano, Searle et al. 2018). On the other hand, it is argued that plant diversity effects may increase with environmental stress (Maestre, Callaway et al. 2009).

The objective of this dissertation was to further improve our understanding of the responses of soil fauna to plant diversity. To achieve this, I first conducted a global meta-analysis to summarize the general pattern of plant mixture effects on the abundance and diversity of soil fauna and examined whether these effects would change with species richness in plant mixture, stand age, soil depth, climate conditions (mean annual temperatures and aridity indexes), and ecosystem types. Second, by rainfall manipulation, I investigated whether tree mixture effects on the abundance and diversity of the Collembola community changed with altered precipitation in young boreal forests. Third, I examined whether tree mixture effects on the abundance and diversity of the Collembola community increased with stand age. My study will advance our knowledge of the relationship between plant diversity and soil faunal community, and gain insights into the variation of plant diversity effects on soil fauna with altered context conditions.

Chapter 2: Plant diversity increases the abundance and diversity of soil fauna: a meta-analysis.

2.1 Abstract

Soil faunal communities are an important component of soil biodiversity, which is key to many terrestrial ecosystem processes. However, despite the current alarming loss of plant diversity, it remains unclear how plant diversity affects soil faunal communities. By synthesizing 623 paired observations of plant mixtures and corresponding monocultures from 40 studies, we examined the effects of plant mixtures on soil fauna abundance and diversity. Further, we investigated the dependence of mixture effects on species richness, stand age, climate conditions, and ecosystem types. We found that, on average, the diversity of soil fauna was 10% higher in plant mixtures than the average of corresponding monocultures, while the abundance of fauna did not differ significantly between the mixtures and the average of monocultures. The mixture effects on both soil fauna abundance and diversity increased with plant species richness in mixtures, which resulted in higher abundance and diversity of soil fauna in species-rich plant mixtures than the averages of their corresponding monocultures. Moreover, the effects of plant mixtures on soil fauna abundance increased over time in diverse species mixtures. After accounting for the effects of species richness in mixtures and stand age, the effects of plant mixtures on the abundance and diversity of soil fauna were consistent across soil depths, ecosystem types, and climate conditions. Our analysis highlights the potential importance of plant diversity conservation for the maintenance of soil faunal communities.

2.2 Introduction

Soil fauna are critical components of soil biodiversity and essential for the support of ecosystem functionality. They participate in the maintenance of soil structures through bioturbation (Lee and Foster 1991, Maaß, Caruso et al. 2015) and play important roles in litter decomposition through fragmentation, transformation, and feeding on microbes (Kampichler and Bruckner 2009, Soong, Vandegehuchte et al. 2016, Coleman, Callaham et al. 2018). Although parasites and herbivores feed on plants, most soil fauna promote plant growth by improving nutrient availability for plants and suppressing herbivores or other plant pests (Setala and Huhta 1991, Partsch, Milcu et al. 2006, van Groenigen, Lubbers et al. 2014). Likewise, plants regulate soil fauna through resource inputs, root exudates, and microhabitat modifications (Hooper, Bignell et al. 2000, Wardle 2005). However, despite the alarming loss of plant diversity due to anthropogenic disturbances, how plant diversity affects the abundance and diversity of soil fauna remains uncertain.

Plant species mixtures are likely to contain more abundant and diverse soil fauna than the average of the corresponding plant monocultures. Plant species mixture may affect soil fauna through several mechanisms. Firstly, increased aboveground productivity (Zhang, Chen et al. 2012), litterfall (Zheng, Chen et al. 2019), root productivity (Ma and Chen 2016), and microbial biomass (Chen, Chen et al. 2019) would provide more food resources and thus may support more abundant soil fauna in plant mixtures than the average of corresponding monocultures. Secondly, various types of resources in mixtures are likely to increase food diversity and microhabitat complexity, spatially and temporarily; thus, supporting a significant diversity of soil fauna, including rare species (Wardle 2006, Cavard, Macdonald et al. 2011, Madej, Barczyk et al. 2011). Thirdly, plant mixtures may alter soil water content and temperature (Bello, Hasselquist et al. 2019, Liu, Miao et al. 2019), mediating the microclimate to be more favorable for fauna (Song, Li et al. 2016). Consequently, we anticipated that the abundance and diversity of soil fauna would increase with species richness in plant mixtures.

A previous review reported that, on average, the abundance and diversity of earthworms and microarthropods did not differ between tree mixtures and monocultures in temperate forests (Korboulewsky, Perez et al. 2016). However, original studies have reported divergent responses in the abundance and diversity of soil fauna to plant diversity (Schwarz, Dietrich et al. 2015, Korboulewsky, Heiniger et al. 2021). These divergent responses may have resulted not only from the differences in their responses between soil fauna groups (Kostenko, Duyts et al. 2015), but also differences in plant species richness in mixtures, stand age, ecosystem types, and climate conditions. An improved understanding of the responses of soil fauna to plant mixtures associated with species richness in mixtures, stand age, ecosystem types, and climate conditions is urgently required for soil fauna conservation.

The effects of plant mixtures on soil fauna may also depend on experimental time. Evidence has shown that the magnitude of diversity effects on plant productivity, root biomass, and microbial biomass also increase over time (Zhang, Chen et al. 2012, Ravenek, Bessler et al. 2014, Chen, Chen et al. 2019). This is because species complementarity for resource use may increase (Barry, Mommer et al. 2019), while functional redundancy decrease over time (Reich, Tilman et al. 2012). As both plants and microbes drive the dynamics of fauna communities, we expected similar temporal responses of soil fauna to plant diversity. However, the temporally increasing diversity effects on soil fauna may lag behind plant productivity as fauna requires years to colonize experimental communities (Allan, Weisser et al. 2013, Wubs, van der Putten et al. 2019). Short-term experiments may conceal the delayed fauna responses that are driven by the accumulation of resources over time (Hedlund, Santa Regina et al. 2003, Eisenhauer, Milcu et al. 2011). Thus, we hypothesized that the mixture effects on soil fauna abundance and diversity would increase over time.

The positive effects of plant diversity may increase with the environmental stresses associated with ecosystem type and climate conditions, similar to the responses of plant productivity (Paquette and Messier 2011, Hisano, Searle et al. 2018) and soil microorganisms (Chen, Chen et al. 2019). Diversity effects may vary with ecosystem type due to different growth rates and nutrient turnover (Schmid, Balvanera et al. 2009). Plant diversity effects may increase under stress since facilitation may be more common than competition among plants (Maestre, Callaway et al. 2009), influencing food resources available for soil fauna (Taylor and Wolters 2005, Wu, Su et al. 2014). For example, when under dry conditions, plant mixtures may improve water use efficiencies due to increased facilitation, thereby increasing soil water availability and plant-derived resources for soil fauna (Forrester, Theiveyanathan et al. 2010, Bello, Hasselquist et al. 2019).

A synthesis may help to reveal general patterns and assess context-dependent diversity effects on soil fauna. By collecting 623 paired observations of plant mixtures and monocultures, we tested whether: (1) soil fauna abundance and diversity would be higher in plant mixtures than the average of corresponding monocultures; (2) the effects of plant mixtures would increase with plant richness in mixtures and over time; (3) the effects of plant mixtures on soil fauna vary with ecosystem type and climate conditions. We anticipated that: (1) the abundance and diversity of soil fauna would be higher in plant mixtures than corresponding monocultures; (2) the effects of plant mixtures would increase with species richness in mixtures and over time; (3) the positive plant diversity effects on fauna would increase with environmental stress.

2.3 Methods

2.3.1 Data collection

We searched peer-reviewed publications that investigated the effects of plant diversity on soil fauna abundance and diversity up to January 2021, using Web of Science and Google Scholar with several keyword combinations: (plant diversity OR richness OR tree diversity OR species diversity OR mixture OR polyculture) AND (soil fauna OR soil biota OR soil organism OR soil food webs OR soil biodiversity OR Collembola OR Mites OR Earthworm OR Nematodes OR Enchytraeids OR arthropod OR invertebrate OR microfauna OR mesofauna OR macrofauna OR decomposers OR trophic groups).

We selected studies that met the following criteria: (1) they were purposely designed to test the effects of plant diversity on the abundance and diversity of soil fauna; (2) they had at least one mixture treatment with corresponding monocultures; (3) they had the same soil and climate conditions and stand age in the mixtures and monocultures. When different studies included the same data, we recorded the data only once. When a study included plant mixtures of different numbers of species, we considered them to be distinct observations. Overall, we collected 623 observations from 40 publications that studied the plant diversity effects on soil fauna, 532 from 36 publications for fauna abundance, and 91 from 22 publications for fauna diversity (a list of the data sources is found in Table S2-1 and cited in Dataset References).

2.3.2 Data extraction

Data were extracted directly from texts, tables, or figures using Plot Digitizer version 2.0. For each study, we extracted the abundance (density or biomass) and diversity (richness) of soil fauna at each plant richness level, soil depth, and stand age. For studies that reported both density and biomass, we recorded only fauna density. For 13 of 40 publications that reported richness-level data, we derived one mean value of fauna attributes for each plant species richness level. For 27 publications that reported plot-level data, we derived each mean value of fauna attributes for each plant mixture combination of each plant species richness level. Besides taxon classification (*Clitellata*, *Nematoda*, *Hexapoda*, *Arachnida*, and others), soil fauna were categorized by trophic groups (herbivores, decomposers, omnivores, or predators) based on original studies and the relevant literature. We also classified soil fauna into groups based on body size: microfauna, mesofauna, and macrofauna (Coleman, Callaham et al. 2018, Nielsen 2019).

Further, we extracted plant species richness, the species ratio in plant mixtures, the soil sampling depth (the midpoint values of corresponding depth intervals) (Chen and Brassard 2012), stand age, ecosystem type (forest or grassland), geographical location (latitude and longitude), and mean annual temperature (MAT) from original or cited papers. When the MAT was unavailable, they were obtained from the WorldClim version 2 dataset (Fick and Hijmans 2017). The annual aridity index (AI) was calculated as the ratio of mean annual precipitation to mean annual potential evapotranspiration and derived from the Global Aridity and PET Database based on the site locations (Trabucco and Zomer 2009).

Similar to previous studies (Chen, Chen et al. 2019), we calculated the species ratios in plant mixtures based on the basal area or stem density of forests and coverage or sowing density of seeds in grasslands(Chen, Chen et al. 2021). Ten publications did not specify the species ratios of constituent plants in mixtures; thus, we assumed that the plant species in these studies were evenly distributed. For earthworm studies that used the mustard extraction method, the soil depth of extraction was assumed to be 25 cm (Lawrence and Bowers 2002). Stand age was recorded as the number of years between stand establishment or the experiment initiation and the sampling of soil fauna.

2.3.3 Data analysis

The effect size (lnRR, log-transformed response ratio) was used to evaluate the plant mixture effects on soil fauna (Hedges, Gurevitch et al. 1999). The lnRR was calculated as:

$$\ln RR = \ln\left(\frac{\mathrm{X_t}}{\mathrm{X_c}}\right) \tag{1}$$

where Xt is the observed value of soil fauna in mixtures, and Xc is the expected value. To account for the species compositional effect, Xc is calculated as the weighted mean values of soil fauna in monocultures of constituent species in mixtures (Loreau and Hector 2001). We dealt with outliers by percentile capping at the 1st and 99th percentile, as recommended (Zuur, Ieno et al. 2010).

Effect size estimates and subsequent inferences in the meta-analysis could be dependent on how the individual observations are weighted. Weightings based on sampling variance might assign extreme importance to only a few individual observations. Subsequently, the average lnRR would be mainly determined by a small number of studies. Similar to previous meta-analyses (Pittelkow, Liang et al. 2015, Ma and Chen 2016), we used the number of replications for weighting to estimate the effect size:

$$W_r = (N_c \times N_t)/(N_c + N_t) \tag{2}$$

where W_r is the weight for each observation, N_c and N_t are the numbers of replications in plant monocultures and the corresponding mixtures.

We tested whether the responses of soil fauna abundance and diversity to plant mixtures were affected by the plant species richness in mixtures (R), stand age (A), ecosystem type (E), and soil depth (S) using the following model:

$$lnRR = \beta_0 + \beta_1 \cdot R + \beta_2 \cdot A + \beta_3 \cdot R \times A + \beta_4 \cdot E + \beta_5 \cdot S$$

$$+\pi_{study} + \pi_{datatype} + \varepsilon \qquad (3)$$

where β_i are the coefficients to be estimated, π_{stduy} is the random effect factor of the 'study' accounting for the autocorrelation between observations within each study; $\pi_{datatype}$ is the random factor of datatypes (plot-level data vs. richness-level data); ε is the sampling error. We conducted the analysis using the restricted maximum likelihood estimation in the lme4 package (Bates, Maechler et al. 2014). We scaled all continuous predictors (observed values minus mean and divided by one standard deviation). When continuous predictors are scaled (minus mean and divided by one standard deviation), β_0 is the overall mean lnRR at the mean R, mean A and mean S (Cohen, Cohen et al. 2003).

Similar to previous studies (Chen and Chen 2021, Chen, Chen et al. 2021), to assess the linearity assumption between the lnRR and continuous predictors, we compared linear, log-linear, and quadratic functions with a continuous predictor as the only fixed factor and study as the random factor. To prevent overfitting (Johnson and Omland 2004), we selected the most parsimonious model with the lowest AIC value among all alternatives with the condition of retaining species richness and stand age, as they were the core hypotheses of our study. R, A, and ln(S) yielded the lowest Akaike information criterion (AIC) values for fauna abundance, whereas ln(R), A, and S yielded the lowest AIC values for fauna diversity (Table S2-2). Model selection was accomplished by using the 'dredge' function of the MuMIn package (Bartoń 2018). Among the best models (ΔAIC ≤ 2 are considered equivalent), we selected the models with the highest weight for interpretation (Table S2-3). All terms associated with ecosystem type and soil depth were excluded. The model selection led to equation (4) for soil fauna abundance and equation (5) for soil fauna diversity as the most parsimonious models, respectively.

$$lnRR = \beta_0 + \beta_1 \cdot R + \beta_2 \cdot A + \beta_3 \cdot R \times A + \pi_{study} + \pi_{datatype} + \varepsilon \tag{4}$$

$$lnRR = \beta_0 + \beta_1 \cdot \ln{(R)} + \beta_2 \cdot A + \pi_{study} + \pi_{datatype} + \varepsilon \tag{5}$$

For the studies (38 out of 40 studies) conducted in natural climates, we examined the effects of the aridity index and mean annual temperature on the effect size by substituting the ecosystem type in equation (3), respectively. All terms with the aridity index and mean annual temperature were excluded in the most parsimonious models. Similar to previous studies (Chen and Chen 2021, Chen, Chen et al. 2021), to better understand the effects of ecosystem type on effect size, we conducted an analysis with ecosystem type as the only fixed factor, 'study' and 'datatype' as random factors. Nevertheless, we graphically demonstrated the associations between ecosystem type, species richness in mixtures, and stand age.

For studies that classified soil fauna (38 out of 40 studies), we expanded equation (3) to test whether the responses of soil fauna to plant mixtures differed between faunal groups while simultaneously accounting for the variations in species richness in mixtures, stand age, and soil depth. We selected the most parsimonious model with the lowest AIC value among all alternatives with the condition of retaining species richness, stand age, and fauna groups (Table S2-4).

To test whether our results are biased by ten studies that did not report species ratios of constituent plants in mixtures, we conducted the same analysis using the data set excluding these ten studies. We compared the estimates and species-richness trends for the data sets with and without these ten studies and found that both data sets yield qualitatively similar estimates and trends (Table S2-5). Thus, we report results for the whole data set. The assumption of normality of all models was assessed based on the histograms of model residuals as recommended (Zuur, Ieno et al. 2010).

To graphically illustrate whether the effects of stand age on lnRR differed with species richness in mixtures, we calculated species richness-dependent stand age effects at species richness levels of 2, 4, 8, and 16, respectively. To better understand the relationship between responses of abundance and diversity to plant species mixtures, for 20 studies that reported the effects of plant mixtures on both abundance and diversity, we examined the lnRRs of soil fauna abundance and diversity by using Type II regression since either can be considered dependent or independent variable (Legendre 1998). Moreover, we selected the studies that reported the responses of both abundance and diversity. We compared the estimates from all data and the subset, and we found the estimates were qualitatively similar (Table 2-1 and Table S2-6).

To facilitate interpretation, we transform lnRR and its corresponding 95% confidence intervals (CIs) to percentages as: $\left(e^{\ln RR} - 1\right) \times 100\%$. If the 95% CIs did not cross zero, the mixture effects on soil fauna abundance and diversity were considered significant at $\alpha = 0.05$. All analyses were performed in R 3.6.3 (R Core Team 2023).

2.4 Results

On average, the abundance of soil fauna did not differ between plant mixtures and the average of constituent monocultures (5%, 95% CI = -15 – 25%, $P = 0.674$) (Table 2-1, Fig. 2-1). However, the effect size on soil fauna abundance increased significantly with species richness in mixtures, from negative (-9%) in two species mixtures to positive (184%) in 16 species mixtures (Fig. 2-1A, Table 2-1, $P = 0.009$). The mixture effect on fauna abundance, on average, did not increase with stand age ($P = 0.153$); however, the age-associated effect size interacted significantly with species richness in mixtures ($P = 0.019$), showing an increasingly positive plant mixture effect with stand age for species-rich plant communities (Fig. 2-1B, Table 2-1).

Table 2-1 The effects of plant mixtures, species richness in mixtures (R), and stand age (A) on the abundance and diversity of soil fauna. Akaike information criterion (AIC) values for the most parsimonious model and the full model (Equation (3) in Methods). P values are in bold when < 0.05. Linear mixed-effects model fit tests used Satterthwaite approximations for denominator degrees of freedom (df).

Source	The most parsimonious model						Full model
	Coefficient	Std. error	df	T	P	AIC	AIC
Fauna abundance							
(Intercept)	0.052	0.102	2	0.508	0.674	1151.2	1158.5
R	0.292	0.110	258	2.65	**0.009**		
A	0.189	0.132	182	1.434	0.153		
R × A	0.605	0.256	241	2.366	**0.019**		
Fauna diversity							
(Intercept)	0.099	0.045	17	2.218	**0.040**	71.2	80.4
R	0.057	0.032	88	1.797	0.076		
A	-0.036	0.042	70	-0.852	0.397		

The diversity of soil fauna was significantly higher in plant mixtures than the average of corresponding monocultures (mean effect size = 10%, CI = 0 – 19%, $P = 0.040$). The effect size on soil fauna diversity increased marginally with species richness in mixtures, from 5% in two species mixtures to 22% in 16 species mixtures (Fig. 2-1C, *P* = 0.076), but insignificantly with stand age (Fig. 2-1D, Table 1, *P* = 0.397).

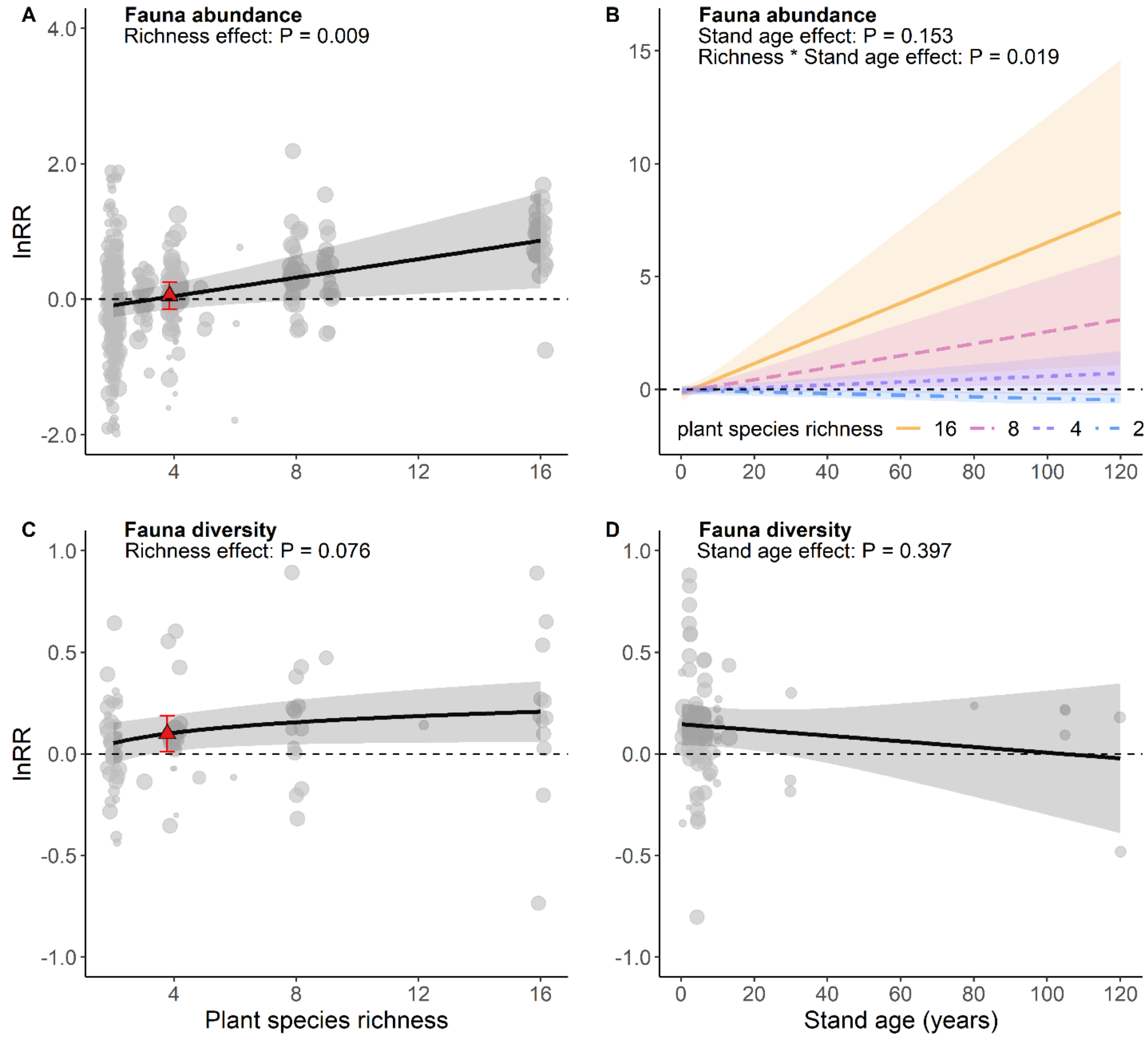

Figure 2-1: Effects of plant mixtures on soil fauna abundance and diversity (A, C) in relation to plant species richness in mixtures, and (B, D) in relation to stand age and by species richness levels. Red triangles and error bars represent the overall mean and its 95% confidence intervals. Black and colored lines represent the average and species richness-specific responses,

respectively, with 95% confidence intervals shaded in colors. The sizes of grey circles represent the relative weights of corresponding observations.

On average, the mixture effects differ significantly between forests and grasslands for soil fauna abundance and diversity (Fig. 2-2, $P = 0.038$ and 0.020, respectively). Both the species richness in mixtures and stand age differed strongly between the two ecosystem types ($P < 0.01$ in all cases). Across those studies simultaneously reporting the effects of plant mixtures of both soil fauna abundance and diversity, the effect sizes were strongly positively correlated (Fig. 2-3, $R^2 = 0.31$, $P < 0.001$).

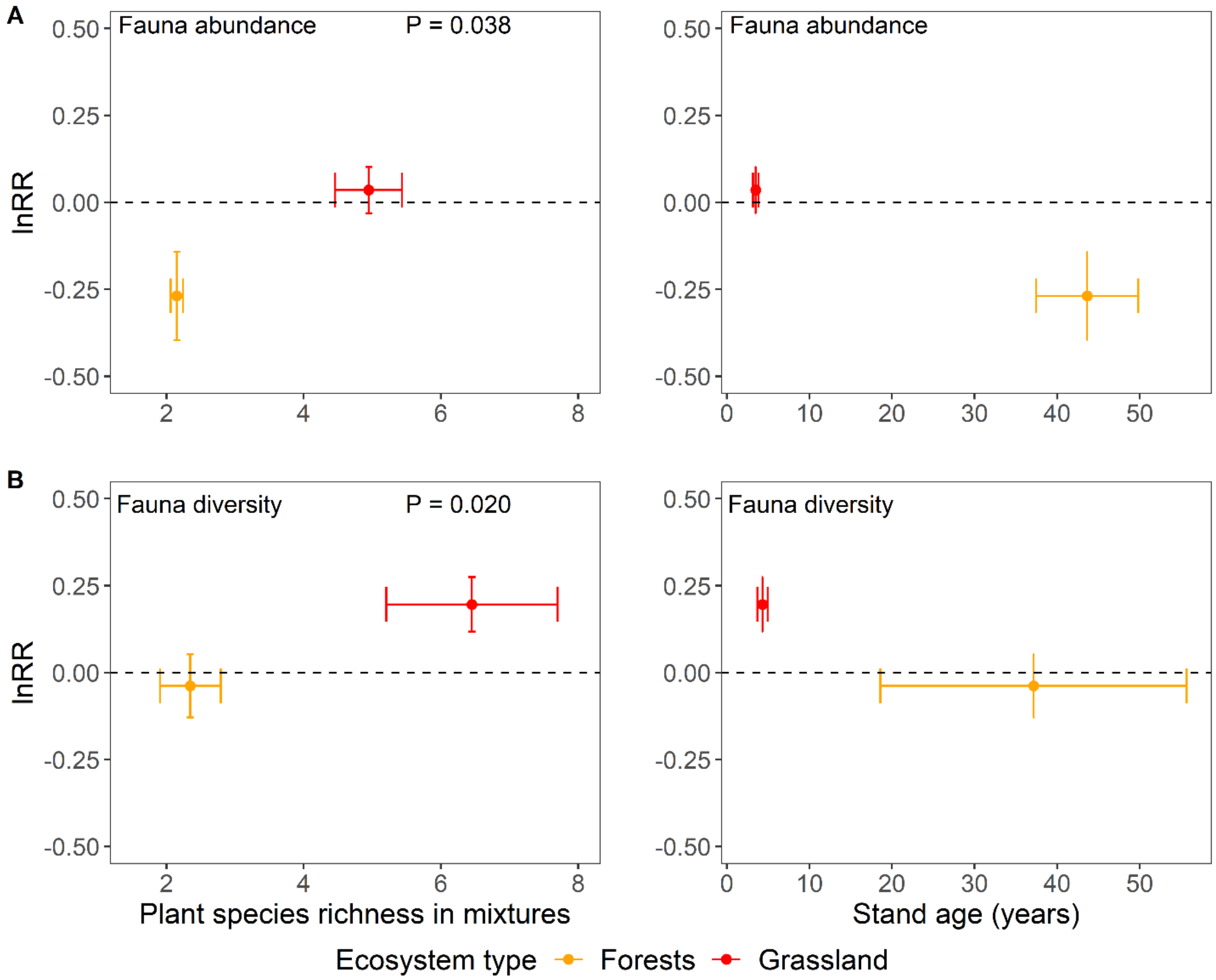

Figure 2-1: Comparison of soil fauna abundance and diversity in plant species mixtures versus monocultures between forests and grasslands. Means and vertical and horizontal error bars represent means and 95% confidence intervals for (A) plant mixture effects and species richness in mixtures, and (B) plant mixture effects and stand age in mixtures, respectively. P values, derived from the linear mixed model with ecosystem types as the only fixed factor and 'study' and 'datatype' as random factors, represent the significance of the differences in the natural log response ratios (lnRRs) between ecosystem types.

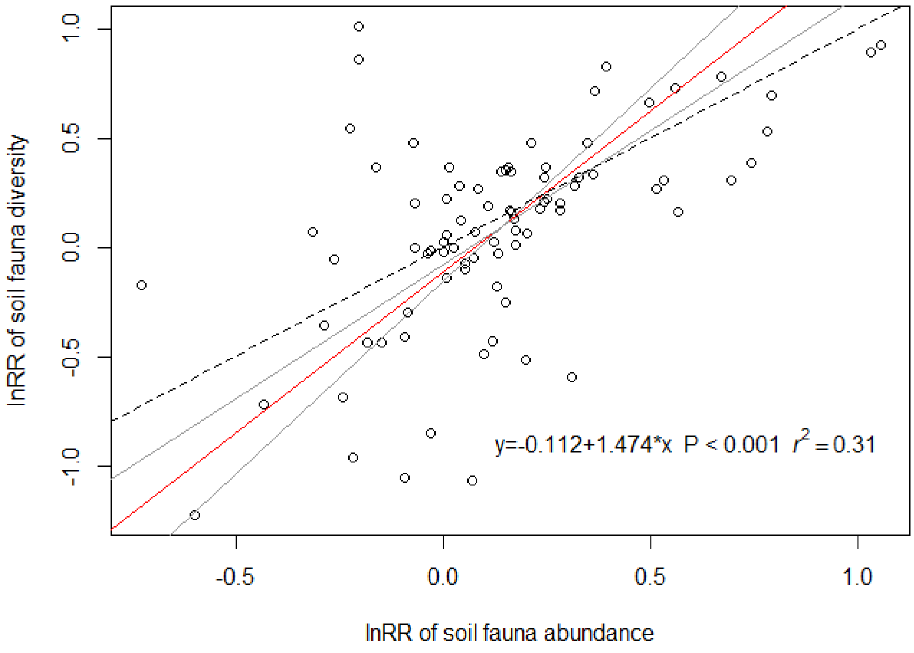

Figure 2-3 Relationship between the log response ratios of soil fauna abundance and diversity. Fitted regression (red line) and 95% confidence region (grey lines) are presented. The dashed line represents the 45-degree line.

For those studies that reported fauna by groups, the responses of fauna abundance and diversity to plant mixture were similar among trophic and body size groups but different among taxonomic groups (Fig. 2-4). Specifically, both the abundance and diversity of *Arachnida* increased in response to plant mixtures, but those of other groups did not (Fig. 2-4).

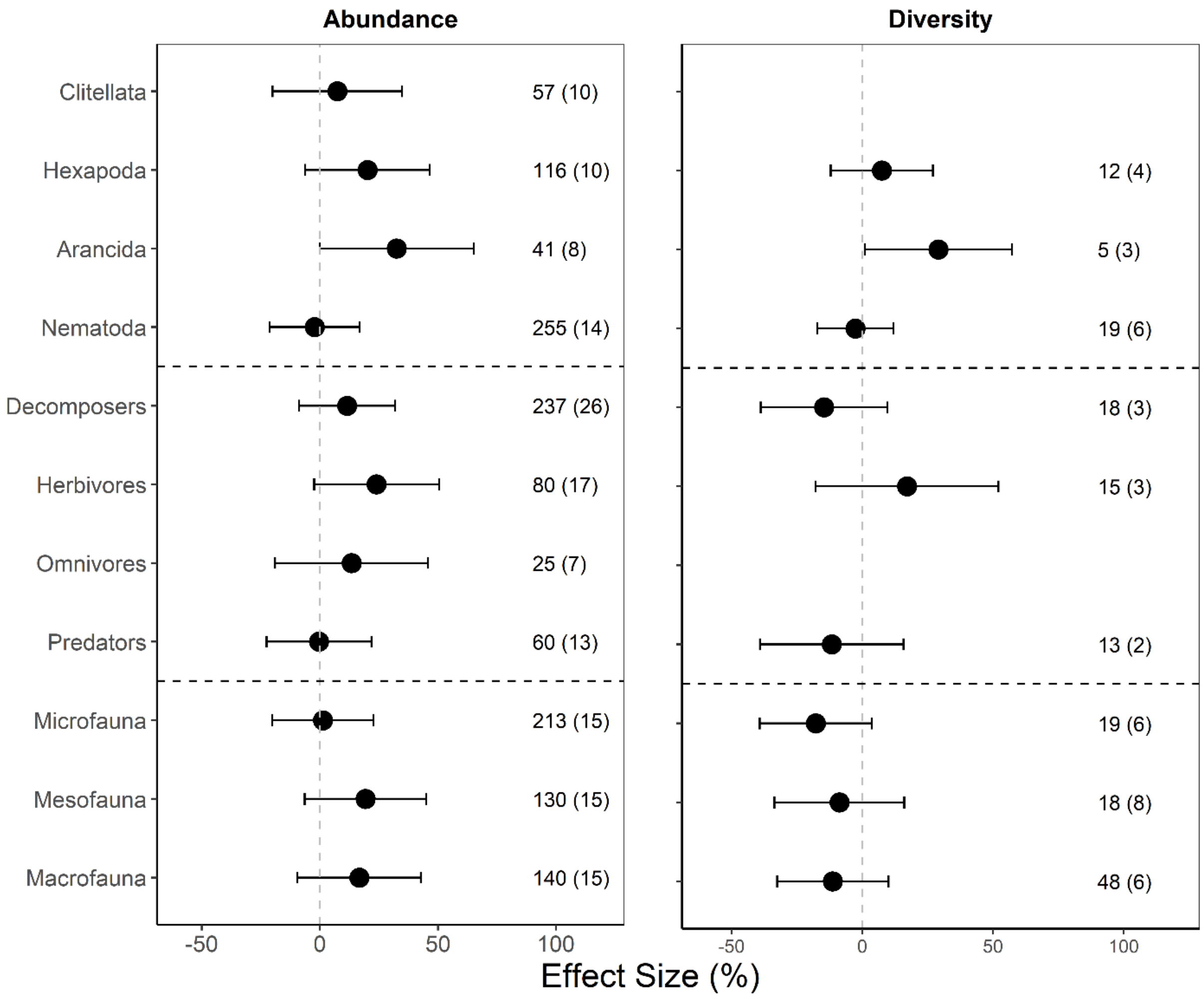

Figure 2-4 Plant mixture effects on the abundance and diversity of soil fauna of different groups. The overall effect represents the increase or decrease (%) of soil fauna abundance and diversity compared to the corresponding mean for constituent monocultures at the mean species richness and mean stand age in mixtures. For each fauna group, the value is derived from the expanded equation (3). Values are means and 95% confidence intervals of the percentage effects between the plant species mixtures and monocultures. The number of observations is shown beside each category, with the number of studies in parentheses.

2.5 Discussion

Our meta-analysis provided new insights into the debate regarding the relationship between plant diversity and soil fauna. Although we found no evidence of positive mixture effects on the abundance of soil fauna on average, we demonstrated that the effect size on abundance increased with plant species richness in mixtures and stand age in diverse species mixtures across wide ranges of climate conditions. Moreover, we found positive mixture effects on the diversity of soil fauna on average.

Our results revealed positive effects of plant species mixtures on fauna diversity, but we found no evidence of significant average mixture effects on fauna abundance. Our finding is consistent with our understanding that plant mixtures provide varied food resources and microhabitats for soil fauna than monocultures (Cavard, Macdonald et al. 2011). The lack of strong mixture effects on abundance may have resulted from the null effect of two species mixtures (327 out of 532 observations on abundance). The limited mixture effects on soil fauna abundance in two species mixtures might be attributable to a limited increase in plant-derived resources and strong top-down regulation. However, it is unclear whether the different responses in abundance and diversity resulted from different sampling efforts of original studies (types of mixtures, richness levels, ages, biomes, and others). Among the studies that simultaneously reported fauna abundance and diversity, we found a strong positive association between their responses to plant mixtures. This finding indicates that fauna abundance and diversity responded to plant mixtures similarly and suggests that increases in resource availability driven by plant mixtures could increase soil fauna diversity and fauna abundance (Storch, Bohdalkova et al. 2018).

Confirming our second hypothesis, we found significant increases in plant mixture effects on the abundance of soil fauna and a marginal increase in fauna diversity with species richness in mixtures. This extends the findings of a previous review that summarized studies comparing the abundance and diversity of earthworms, Collembola, and Oribatid mites in pure and mixed stands, and found that the majority of previous studies reported positive effects of increased tree richness on soil fauna in temperate forests (Korboulewsky, Perez et al. 2016). Our results suggest that a positive diversity-productivity relationship (Zhang, Chen et al. 2012) may be propagated to belowground soil faunal communities. Driven by inter-specific plant interactions (Forrester and Bauhus 2016, Barry, Mommer et al. 2019), the increased amount and diversity of resources in high-richness plant communities (Ma and Chen 2017, Zheng, Chen et al. 2019, Peng and Chen 2021) may support more soil fauna than low-richness plant communities.

Importantly, we found a pronounced positive effect of stand age on the abundance of fauna in species-rich plant communities. This interaction was likely due to the accumulation of plant-derived resources over time, and the latent responses of soil fauna abundance to plant diversity (Eisenhauer, Milcu et al. 2011, Allan, Weisser et al. 2013). It also suggests that the age effect on soil fauna is dependent on plant species richness in mixtures (Figure S2-1) because of higher performance in species-rich communities over time compared to species-poor communities (Meyer, Ebeling et al. 2016). The data was insufficient to draw any conclusions regarding changes in the diversity effects on soil fauna diversity over time. Additional long-term experiments with high richness levels are required to reveal changes in the mixture effects on soil fauna diversity with stand age. Overall, our study indicates that the lack of plant mixture effects on fauna in certain studies might be attributable to limited plant species richness and short experimental durations.

Despite the wide range of variations in soil depths, mean annual temperature and aridity index in our meta-data, the responses of soil fauna to plant mixtures did not differ with soil depths nor climatic conditions. This suggests that the responses of the abundance and diversity of soil fauna to plant mixtures are consistent across soil depths and climate conditions, similar to the responses of aboveground and belowground productivity (Zhang, Chen et al. 2012, Ma and

Chen 2016) soil carbon (Chen, Chen et al. 2020), and soil microbial biomass to plant mixture effects (Chen, Chen et al. 2019).

We observed significantly larger effects of plant mixtures on fauna in grasslands than in forests. Fauna diversity to plant mixtures responded positively to plant mixtures in grasslands. Meanwhile, fauna abundance responded negatively to plant mixtures in forests. However, once the species richness effects have been accounted for, there was no difference in the responses between grasslands and forests. The negative effects in forests are attributable to the limited scale of plant richness (average richness level = 2.15, Fig. 2-2A) in these studies for forests. Most original studies in forests (184 out of 199 observations) included only two plant species mixtures. To better understand the mixture effects on soil fauna in forests, future studies of plant mixture effects on soil fauna in forests should incorporate high plant richness levels.

For studies that classified soil fauna, we found that plant mixtures increased both the abundance and diversity of *Arachnida*. However, we did not find any difference in mixture effects on fauna abundance or diversity among trophic groups. This result probably reflects that few original studies have conducted high-resolution identification, and each trophic group was subject to few observations with little statistical power (Button, Ioannidis et al. 2013). Identification to the species level or the genus level is necessary to reveal underlying mechanisms of fauna responses to plant communities as coarse identification could cause information loss (Bedano and Ruf 2010, Meehan, Song et al. 2019). Further accumulation of fauna data of groups will be required to reveal variations of plant mixture effects with soil fauna among groups.

Our analysis focused on the variations in plant mixture effects on the abundance and diversity of soil fauna. Importantly, we found positive mixture effects on the diversity of soil fauna on average, but not on the abundance of soil fauna. The responses of both soil fauna abundance and diversity increased with the plant species richness in mixtures. Moreover, increased plant diversity effects on soil fauna abundance were more pronounced in old-growth stands. Our results indicate that the loss of plant diversity might cause declines in fauna abundance and diversity over time. Our findings suggest that ecosystem functions and services that rely on soil fauna, such as decomposition and soil formation, are likely being threatened by ongoing local plant species diversity loss. Future studies should incorporate high plant richness levels, long-term durations, and the high-resolution identification of soil fauna to elucidate the specific mechanisms of mixture effects on soil fauna.

Chapter 3: Tree mixture effects on Collembola evenness increased under reduced throughfall in a young boreal forest.

3.1 Abstract

Despite the essential role of soil Collembola in ecosystem functions and services, how soil Collembola respond to altered precipitation and tree mixtures in natural forests remains understudied. In this study, we evaluated the responses of soil Collembola abundance, richness, evenness, and composition to altered precipitation (25% water addition, ambient, and 25% water reduction) in pure and mixed jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) in a young boreal forest using a split-plot design. Forest floor Collembola were sampled and identified to taxonomic species or morphospecies. We found that abundance and richness were highest in mixed stands and lowest in broadleaf stands, but evenness did not differ with stand type. Neither abundance nor richness responded to altered precipitation, but the evenness increased in conifer stands under water addition and in mixed stands under water reduction. Tree mixture increased soil Collembola abundance under water addition, and tree mixture effects on evenness increased from -16% under ambient water to +3% under water reduction. Community composition in mixed stands differed from broadleaf stands. Furthermore, shifts in the community composition of Collembola were significantly associated with soil water content, litter production, and fine root biomass. Collembola abundance and richness increased with litter production and decreased with soil temperature, while evenness was decreased with fine root biomass. We conclude that mixtures of tree species and altered precipitation can locally impact the abundance and diversity of Collembola in young boreal forests.

3.2 Introduction

Collembola (Hexapoda: Entognatha), bioindicators within soil fauna, are one of the most abundant and essential components of soil fauna in terrestrial ecosystems (Orgiazzi, Bardgett et al. 2016, Joimel, Chassain et al. 2022). They contribute to ecosystem processes and functions such as litter decomposition, soil organic matter turnover, and plant growth (Barrios 2007, Chapin, Matson et al. 2011, Soong, Vandegehuchte et al. 2016). It is well established that altered precipitation regimes and biodiversity loss impact ecosystem functions and services. Evidence showed that altered precipitation regimes can affect the Collembola community and related ecosystem functions (Blankinship, Niklaus et al. 2011, Bardgett and van der Putten 2014, Nielsen 2019). However, the responses of Collembola to tree mixtures remain highly debated (Schwarz, Dietrich et al. 2015, Ganault, Nahmani et al. 2021, Zhang, Peng et al. 2022).

Changes in precipitation can strongly affect Collembola. Low water availability and associated unsustainable amount and diversity of food resources (soil microbes, litterfall, and root) could negatively affect the abundance and diversity of soil Collembola (Maestre, Delgado-Baquerizo et al. 2015, Ren, Chen et al. 2018, Zhou, Zhou et al. 2018). Recent meta-analyses have summarized a positive effect of increased precipitation and a negative effect of drought on Collembola density (Blankinship, Niklaus et al. 2011, A'Bear, Jones et al. 2014, Peng, Peñuelas et al. 2022, Goncharov, Leonov et al. 2023). Meanwhile, the community composition of Collembola can also be impacted by altered precipitation (Lindberg, Engtsson et al. 2002, Xu, Kuster et al. 2012, A'Bear, Boddy et al. 2013, Turnbull and Lindo 2015), which can result from varied tolerance and adaption strategy of Collembola species to water stress (Kærsgaard, Holmstrup et al. 2004, Holmstrup and Bayley 2013, Wang, Slotsbo et al. 2022) and shifted fungal: bacterial ratio (Maestre, Delgado-Baquerizo et al. 2015, Nielsen and Ball 2015, Zhou, Wang et al. 2020). However, it remains unknown whether responses of Collembola communities to increased or decreased precipitation may depend on forest overstory types.

Tree species diversity or mixtures may influence Collembola communities. High plant species diversity in tree mixtures can increase the quantity and diversity of food resources such as litterfall (Zheng, Chen et al. 2019), roots (Ma and Chen 2016), and microbes (Wen, Lei et al. 2014) and microhabitat heterogeneity, which in turn support a higher density and diversity of soil fauna than monocultures do (Hansen and Coleman 1998, Sulkava and Huhta 1998, Madej, Barczyk et al. 2011, Li, Shi et al. 2021, Zhang, Peng et al. 2022). Moreover, tree mixtures with dissimilar litter traits can benefit soil fauna. For example, the introduction of broadleaf species to coniferous stands can offset unfavorable conditions of habitats because of a lower C: N ratio and lignin content in the litter layer (Ammer, Weber et al. 2006, Korboulewsky, Perez et al. 2016). The community composition of soil fauna can also vary among pure and mixed stands of broadleaf and conifer species because of varying physical characteristics of litter, varying canopy structure, and different microbial compositions. Increased fungal: bacteria ratio in mixed stands can benefit fungal feeders, subsequently changing community structure (Wardle, Yeates et al. 2006, Salamon and Alphei 2009, Chen, Chen et al. 2019). Specifically, for Collembola, few empirical studies have reported the effects of tree or litter mixtures, and they do not show a general pattern. Nonsignificant differences in Collembola abundance and diversity between pure and mixed stands have been reported in Brazil and Germany (Salamon, Scheu et al. 2008, Salamon and Alphei 2009, Zagatto, Pereira et al. 2019), while intermediate richness and abundance of Collembola have been found in mixed stands compared to pure coniferous or deciduous stands in France (Korboulewsky, Heiniger et al. 2021). In a litterbag experiment in an oak-pine forest in Japan, Collembola were more abundant in litter mixtures (Sasa, oak, and pine) than in single litters after 1-year incubation (Kaneko and Salamanca 2002). These studies explored the responses of Collembola to mixtures but failed to separate diversity and identity effects. Some studies reported the dilution of one tree species to admixtures (Chauvat, Titsch et al. 2011, Hasegawa, Ota et al. 2014, Leidinger, Blaschke et al. 2021). No studies have examined true mixture effects on the Collembola community in natural forests.

Altered precipitation may change the effect of tree mixtures on soil Collembola. Mixture effects may increase under water stress since facilitation may be more common than competition (Maestre, Callaway et al. 2009). Compared to pure stands, greater complexity and a broader niche range of mixed stands could support more tolerant Collembola species for water stress (Yachi and Loreau 1999, Marx, Guhmann et al. 2012), therefore increasing the resistance of the Collembola community and having better performance under altered precipitation. Further, greater stability of plant productivity and microbes in tree mixtures (Jucker, Bouriaud et al. 2014, Gillespie, Fromin et al. 2020) can benefit the Collembola community. Accordingly, we hypothesize that the response of Collembola to altered precipitation in tree mixtures would mirror those of soil microbes in our previous study (Chen, Chen et al. 2019); i.e., positive effects of tree mixtures on Collembola are more pronounced under water addition and reduction.

In this study, we focus on the response of Collembola abundance, diversity, and community composition to altered precipitation (water addition and reduction) in pure and mixed jack pine (*Pinus banksiana Lamb.*) and trembling aspen (*Populus tremuloides Michx.*). We hypothesize that (1) water reduction has negative effects on the abundance and diversity of Collembola, whereas water addition has positive effects; (2) tree species mixture increases the abundance and diversity of Collembola; (3) the effects of tree mixtures are more pronounced under water addition and water reduction. Moreover, we expect the community compositions of Collembola to differ between stand types and water treatments.

3.3 Materials and Methods

3.3.1 Study site and experimental design

The study was conducted in a young boreal forest (49.55°N, 90.12°W), located about 150 km north of Lake Superior and about 100 km west of Lake Nipigon, Ontario, Canada. The study area falls in the 3W ecoregion and is characterized by warm summers and cold, snowy winters (Crins, Gray et al. 2009). The mean annual temperature is 2.5 °C with a mean annual precipitation of 712 mm across a temporal range of 1970 – 2000 (Fick and Hijmans 2017). The soil type is relatively deep glacial till of the Brunisolic order on the upland sites. The young boreal forest has been naturally regenerating for 15 years since the last stand-replacing fire. The dominant species of overstory tree species include *Pinus banksiana* Lamb., *Populus tremuloides* Michx. and *Betula papyrifera* Marshall, along with understory shrubs including *Alnus incana* (L.) Moench, *Prunus pensylvanica* L.f. and *Salix* spp.

Three overstory types were selected, including broadleaf stands dominated by *Populus tremuloides*, and conifer stands dominated by *Pinus banksiana* and their mixtures, each with three replicate stands. The nine stands (each with an area > 1 ha) were allocated with a distance of > 1 km to minimize spatial autocorrelation. Within each stand, three split-plot level water availability treatment plots (6 × 6 m) were established in 2016 (Chen, Chen et al. 2019): ambient, 25% throughfall reduction during the growing season (May to October), and 25% throughfall addition during the growing season, which are the medians of expected changes to water availability in Canadian boreal forests during the 21st century (Edenhofer 2015). We built four units of rain shelters covering an area of 3 × 3 m to reduce incoming throughfall under the canopy. The rain shelters consisted of metal support frames and U-shaped clear acrylic troughs. The U-shaped clear acrylic troughs had an orientation of a 10° angle vertically to ensure water flow, with the high end at 1.8 m above ground and the low end at 1.35 m above ground. The retained water from the water reduction treatment was funneled into two 8 cm (inner diameter) polyvinyl chloride (PVC) pipes in the water addition plots. The PVC pipes were about 5 cm above the soil surface to minimize the washing effect of increased water availability. The pipes had six holes of different diameters (0.64, 1.91, 3.18, 4.45, 5.72, and 6.99 cm) with a regular interval of 46 cm to distribute the collected water evenly over the water addition plot. The control treatment received ambient precipitation. Between treatments, a ≥5 m buffer zone was established (Chen, Chen et al. 2019).

To quantify stand characteristics, we identified all tree species and measured the diameter at breast height (DBH; 1.3 m above the root collar) of all trees and shrubs in each of the 27 plots at the end of the growing season of 2020. The volumetric soil water content and soil temperature were measured using Decagon sensors at a depth of 5 cm below the soil surface at the time of sampling.

3.3.2 Sampling, extraction, and identification

The sampling of soil Collembola took place in September 2020 from 27 plots (3 water treatments × 3 stand types × 3 replications). Five soil subsamples were randomly collected by hand using a 10 × 10 cm quadrat on the forest floor and were mixed as a composite sample in each plot (Bruckner, Barth et al. 2000). In total, 27 composite samples were collected. Samples were carried to the lab in punctured polyethylene bags stored in an ice-filled cooler.

Collembola were extracted from the soil samples into collecting cups (5 cm diameter) with 70% EtOH using the Tullgren funnel (15 cm diameter, from Bioquip company) under 25w bulbs in laboratory conditions for 10 days (Macfadyen 1961). Collembola were sorted from other organisms, morphotyped, and counted using a dissecting microscope, and then were further identified under a compound microscope (40X-2000X). For taxonomic identification, Collembolas were identified to taxonomic species where possible or to morphospecies (see Table 1 for full list) based on current literature (Hopkin 1997, Fjellberg 2007, Fjellberg 2010, Turnbull and Stebaeva 2019).

Soil microbial biomass was determined by phospholipid fatty acid analysis in August 2018 (Chen, Chen et al. 2019). The annual litterfall production was determined using litter traps from July 2017 to August 2018 (Chen, Brant et al. 2017). Fine root biomass was determined in August 2019. Fine roots (< 2 mm in diameter) were extracted from soil cores (6.6 cm diameter, 15 cm depth) and oven-dried to a constant mass at 65 °C and weight.

3.3.3 Statistical Analysis

For each plot, we quantified the abundance (number of individuals per m^2), richness (total number of species/morphospecies), and evenness (J, Pielou's index) for Collembola. Collembola community composition was defined as the assemblage of species/morphospecies and their relative abundance within each plot.

We used a linear mixed-effect model to test the effects of stand type and water treatment on the abundance and evenness of Collembola. For Collembola richness, we used a generalized linear model with the assumption of a Poisson distribution.

$$Y = \beta_0 + \beta_1 \cdot S_i + \beta_2 \cdot W_{j(k)} + \beta_3 \cdot S_i \times W_{j(k)} + \pi_k + \varepsilon_{l(ijk)} \qquad (1)$$

where βs are the coefficients, S_i (i = 1, 2, 3) is stand type (broadleaf, conifer, and mixedwood), $W_{j(k)}$ (j=1, 2, 3) is water treatment (25% water addition, ambient, and 25% water reduction) nested within each plot (k = 1, 2, …9), π_k is the random effect of plot, and $\varepsilon_{l(ijk)}$ is the sampling error. We conducted the analysis using the restricted maximum likelihood estimation in the lme4 package (Bates, Maechler et al. 2014). Assumptions of normality were examined by Shapiro-Wilk's test on residuals. The abundance of Collembola was reciprocally transformed to achieve normality.

To test the tree species mixture effect, we used a log-transformed response ratio (lnRR) to quantify the effects of species mixtures on Collembola abundance, species richness, and evenness:

$$\ln RR = \ln\left(\frac{\mathrm{X_t}}{\mathrm{X_c}}\right) \tag{2}$$

where Xt is the observed value of soil fauna in mixtures, and Xc is the expected value. To account for the species compositional effect, Xc was calculated as the weighted mean values of Collembola abundance, richness, and evenness in monocultures of constituent species in mixtures (Loreau and Hector 2001):

$$X_c = \sum(V_i \times P_i) \tag{3}$$

where V_i is the observed value of Collembola abundance, richness, and evenness in the monoculture of species i, and P_i is the proportion of species i basal area (m^2 ha $^{-1}$) in the corresponding mixture per split plot.

We tested whether the responses of Collembola abundance, richness, and evenness to tree species mixtures were affected by water treatment (W) using the following model:

$$lnRR = \beta_0 + \beta_1 \cdot W_i + \pi_j + \varepsilon_{k(ij)} \tag{4}$$

where βs are the coefficients, W_i is the water treatment (25% water addition, ambient, and 25% water reduction); π_j is the random effect of plot, and $\varepsilon_{k(ij)}$ is the sampling error. The mixed species effects were significant at $\alpha = 0.05$ if the 95% CIs of estimated lnRR did not cover

0. The difference between groups was significant if 95% CIs of their coefficients did not overlap another's mean.

To examine if the composition of the Collembola community varies with overstorey type and water treatments, we conducted a permutational multivariate analysis of variance tests (perMANOVA) (Anderson 2001). In perMANOVA, we employed the Bray-Curtis dissimilarity matrix to summarize species composition and used 999 permutations to determine statistical significance. We visualized the compositional data using nonmetric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity measure. Moreover, we used linear regression to examine the relationship of Collembola abundance, richness, and evenness relative to soil water content, soil temperature, litterfall production, fine root biomass, and microbial biomass. All analyses were performed using lme4 and vegan packages in R 4.3.0 (R Core Team 2023).

3.4 Results

In total, 924 individuals were identified out of 21 species/morphospecies (Table 3-1). Among all species, three species were present in all treatments (*Entombrya sp.1*, *Entombrya sp.3*, and *Folsomia* nr. *candida*), four species were absent in only one treatment (*Entombrya sp.2* and *Sminthurinus* nr. *aureus* were absent in *Populus* stands under water addition, *Isotoma* nr. *ripara* was absent in *Pinus* stands under ambient condition, *Folsomia sp.2* was absent in *Pinus* + *Populus* stands under water reduction), and one species was present only in *Pinus* + *Populus* stands (*Sphaeridia* nr. *pumilis*).

Table 3-1 Mean abundance (individuals/m^2; mean ± standard deviations; N=3) of Collembola species/morphospecies per treatment.

	Broadleaf			**Conifer**			**Mixedwood**		
	Addition	**Control**	**Reduction**	**Addition**	**Control**	**Reduction**	**Addition**	**Control**	**Reduction**
Order Entomobryomorpha									
***Entomobrya* sp. 1**	80 ± 12	73 ± 18	33 ± 24	107 ± 55	147 ± 93	73 ± 18	87 ± 57	213 ± 96	80 ± 80
***Entomobrya* sp. 2**	13 ± 7	47 ± 37	0 ± 0	27 ± 27	120 ± 72	60 ± 20	47 ± 37	33 ± 13	27 ± 7
***Entomobrya* sp. 3**	113 ± 37	80 ± 12	173 ± 41	127 ± 82	200 ± 81	80 ± 53	367 ± 47	267 ± 207	373 ± 232
***Entomobrya* sp. 4**	13 ± 7	47 ± 24	0 ± 0	0 ± 0	20 ± 12	7 ± 7	20 ± 20	0 ± 0	0 ± 0
***Entomobrya* sp. 5**	0 ± 0	0 ± 0	7 ± 7	20 ± 12	0 ± 0	0 ± 0	153 ± 64	53 ± 13	53 ± 27
Vertagopus* nr. *asiaticus	7 ± 7	0 ± 0	0 ± 0	13 ± 13	20 ± 20	7 ± 7	0 ± 0	0 ± 0	0 ± 0
Appendisotoma* nr. *abiskoensis	27 ± 18	0 ± 0	0 ± 0	20 ± 12	80 ± 70	60 ± 20	27 ± 13	80 ± 46	93 ± 66
***Folsomia* sp. 1 (nr. *candida*)**	13 ± 13	7 ± 7	13 ± 13	93 ± 55	53 ± 53	80 ± 31	60 ± 50	60 ± 23	133 ± 103
***Folsomia* sp. 2**	13 ± 7	13 ± 7	13 ± 7	47 ± 27	7 ± 7	53 ± 7	27 ± 13	0 ± 0	33 ± 33
***Isotoma* sp. 1 (nr. *riparia*)**	20 ± 12	20 ± 12	13 ± 7	0 ± 0	33 ± 18	27 ± 18	13 ± 13	27 ± 18	20 ± 20
***Isotoma* sp.2 (nr. *viridis*)**	7 ± 7	13 ± 13	0 ± 0	13 ± 13	53 ± 35	40 ± 31	0 ± 0	20 ± 20	67 ± 67
***Isotoma* sp. 3**	0 ± 0	0 ± 0	0 ± 0	0 ± 0	20 ± 20	60 ± 60	13 ± 13	100 ± 81	47 ± 24
***Lepidocyrtus* sp.1 (nr. *ruber*)**	13 ± 13	7 ± 7	0 ± 0	7 ± 7	20 ± 12	0 ± 0	0 ± 0	7 ± 7	7 ± 7
***Lepidocyrtus* sp.2 (nr. *cyaneus*)**	7 ± 7	0 ± 0	13 ± 13	0 ± 0	7 ± 7	20 ± 12	0 ± 0	33 ± 18	27 ± 13
Tomocerus* nr. *minor	0 ± 0	0 ± 0	7 ± 7	7 ± 7	13 ± 13	13 ± 7	7 ± 7	7 ± 7	13 ± 7
Order Symphypleona									
***Arrhopalites* sp.**	0 ± 0	0 ± 0	13 ± 13	7 ± 7	0 ± 0	0 ± 0	0 ± 0	7 ± 7	0 ± 0
***Sminthurinus* sp.1**	0 ± 0	13 ± 7	0 ± 0	20 ± 20	33 ± 24	60 ± 12	27 ± 7	20 ± 12	20 ± 12
***Sminthurinus* sp.2 (nr. *aureus*)**	20 ± 20	7 ± 7	0 ± 0	13 ± 13	40 ± 20	33 ± 7	13 ± 7	27 ± 13	7 ± 7
Sminthurides* nr. *occultus	13 ± 13	13 ± 13	13 ± 13	0 ± 0	7 ± 7	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Sphaeridia* nr. *pumilis	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	33 ± 33	27 ± 27	27 ± 27
Order Poduromorpha									
Onychiuridae sp.	7 ± 7	7 ± 7	13 ± 7	7 ± 7	7 ± 7	0 ± 0	27 ± 18	0 ± 0	27 ± 18

The abundance and richness of Collembola differed significantly with stand type (*P* = 0.029 and 0.051, respectively) but did not change significantly with water alteration (Table 3-2, Fig. 3-1). The abundance in mixed (993 ind.m^{-2}) and conifer stands (695 ind.m^{-2}) were higher than broadleaf stands (364 ind.m^{-2}) (*P* = 0.032 and 0.070, respectively). Under ambient water and addition, abundance was higher in mixed (933 and 1060 ind.m^{-2}) than broadleaf stands (420 and 320 ind.m^{-2}); Under water reduction, abundance were higher in both mixed (987 ind.m^{-2}) and conifer stands (887 ind.m^{-2}) than broadleaf stands (353 ind.m^{-2}) (Fig. 3-1). The richness was marginally higher in mixed stands with an average of 10.1 species) than in broadleaf stands with 7.0 mean species (*P* = 0.058). We observed a higher richness in conifer stands (mean = 11.3 species) and in mixed stands (mean = 10 species) than in broadleaf stands (7.7 mean species) under water addition (*P* = 0.059). Evenness ranged from 0.73 to 0.92 and did not vary significantly with stand types (*P* = 0.402) (Fig. 3-1, Table 3-2). However, the effects of water treatment on evenness were contingent on stand types. Water addition increased evenness by 14.7% (*P* = 0.016) in conifer but decreased it by 11.4% (*P* = 0.039) in broadleaf stands. Water reduction increased evenness by 18.2% (*P* = 0.006) in mixed stands (Fig. 3-1, Table 3-2).

Table 3-2 Effects of water treatment (W) and stand type (S) on Collembola abundance, richness, evenness, and community composition.

Source	df	*P*
Abundance ($R^2_{marginal}$ = 0.511, $R^2_{conditional}$ = 0.686)		
W	2,12	0.989
S	2,6	**0.029**
W × S	4,12	0.236
Richness (R^2 = 0.491)		
W	2,24	0.815
S	2,22	**0.051**
W × S	4,18	0.524
Evenness ($R^2_{marginal}$ = 0.444, $R^2_{conditional}$ = 0.820)		
W	2,12	**0.005**
S	2,6	0.402
W × S	4,12	**0.002**
Community composition		
W	2	0.152
S	2	**0.005**
W × S	4	**0.020**

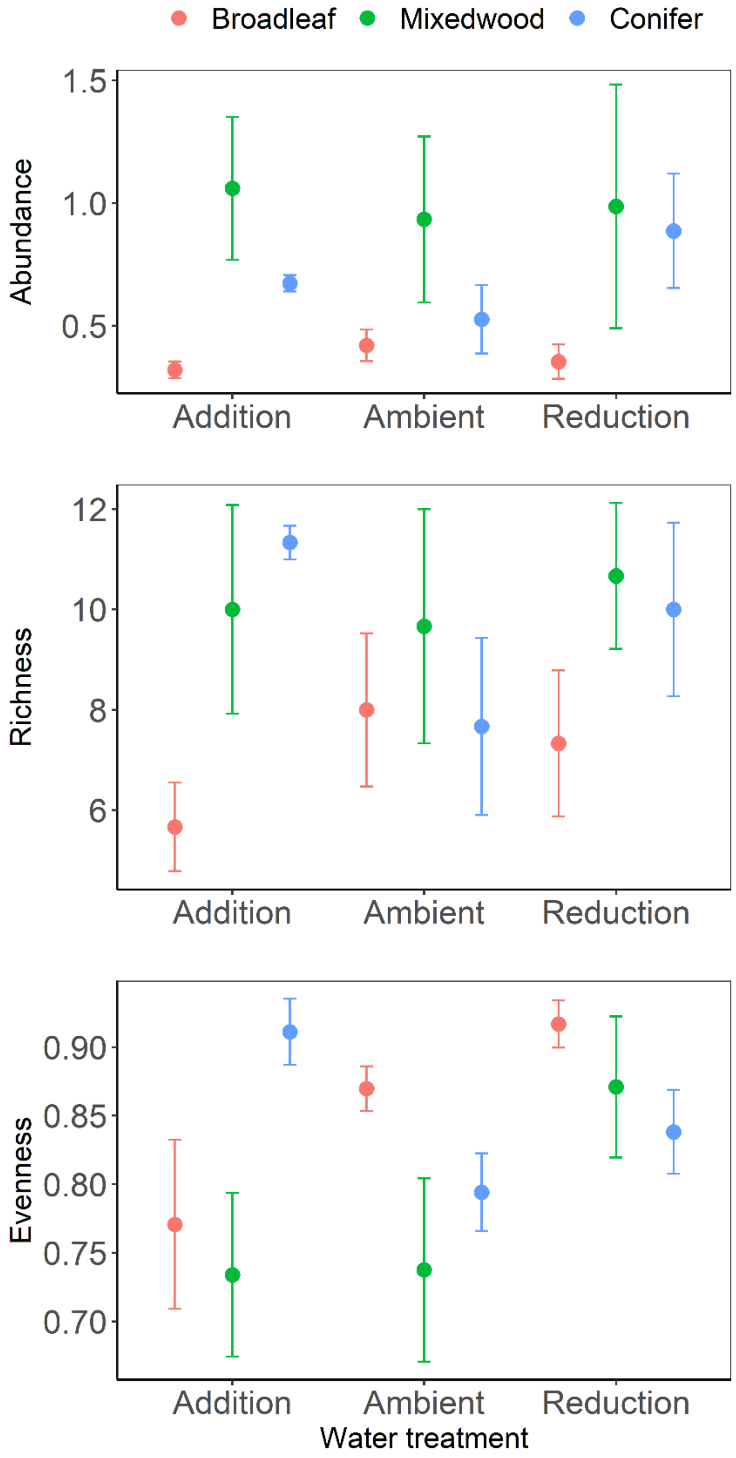

Figure 3-1 Collembola attributes (abundance, richness, and evenness) in relation to stand types and water treatments. Values are mean ± stand errors.

The mixture effects differed significantly between water treatments for evenness ($P < 0.001$), while abundance and richness did not ($P = 0.510$ and 0.089, respectively) (Fig. 3-2, Table 3-3). Mixture effects on abundance were significantly positive with water addition, marginally positive with ambient conditions, and nonsignificant with water reduction. Mixture effects on richness did not vary across water treatments. Mixture effects on evenness were significantly negative with ambient conditions and water addition, but non-significant with water reduction. Compared with the ambient conditions, water reduction significantly increased the mixture effects on evenness, from -16% to +3% (Fig. 3-2, $P = 0.001$).

Table 3-3 Effects (P values) of water treatments on the response ratio of Collembola abundance, richness, and evenness to species mixtures.

Attributes	df	F	*P*
Abundance	2,4	0.80	0.510
Richness	2,4	4.69	0.089
Evenness	2,4	71.71	**< 0.001**

Note: Linear mixed-effects model fit tests used Satterthwaite approximations for denominator degrees of freedom (df). *P* are significance of the model and $P < 0.05$ is highlighted in bold.

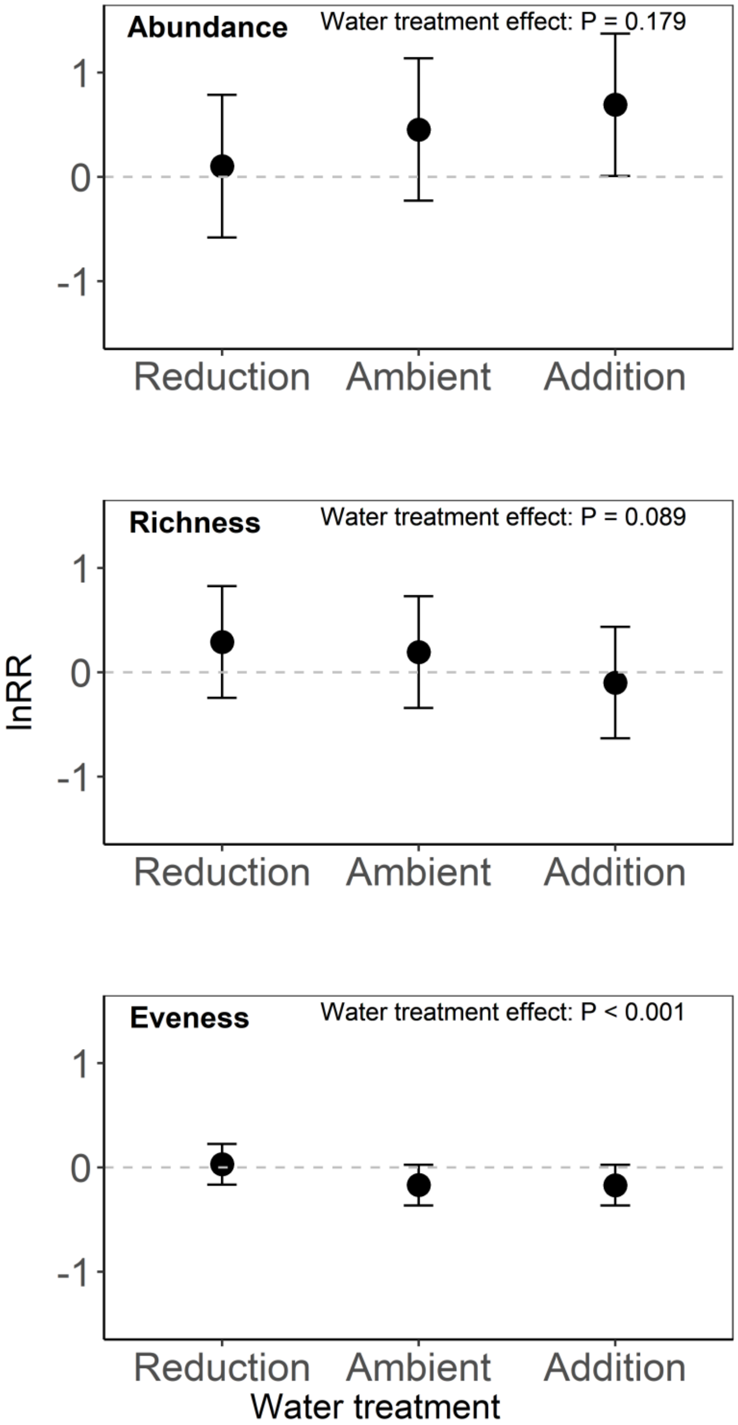

Figure 3-2: Plant mixture effects on Collembola abundance, richness, and evenness. For each Collembola attribute, the value is derived from Eq. (4). Values are mean ± 95% confidence intervals (CIs). The mixed species effects were significant at $\alpha = 0.05$ if the 95% CIs did not cover 0. The difference between groups was significant if 95% CIs of their coefficients did not overlap the another's mean.

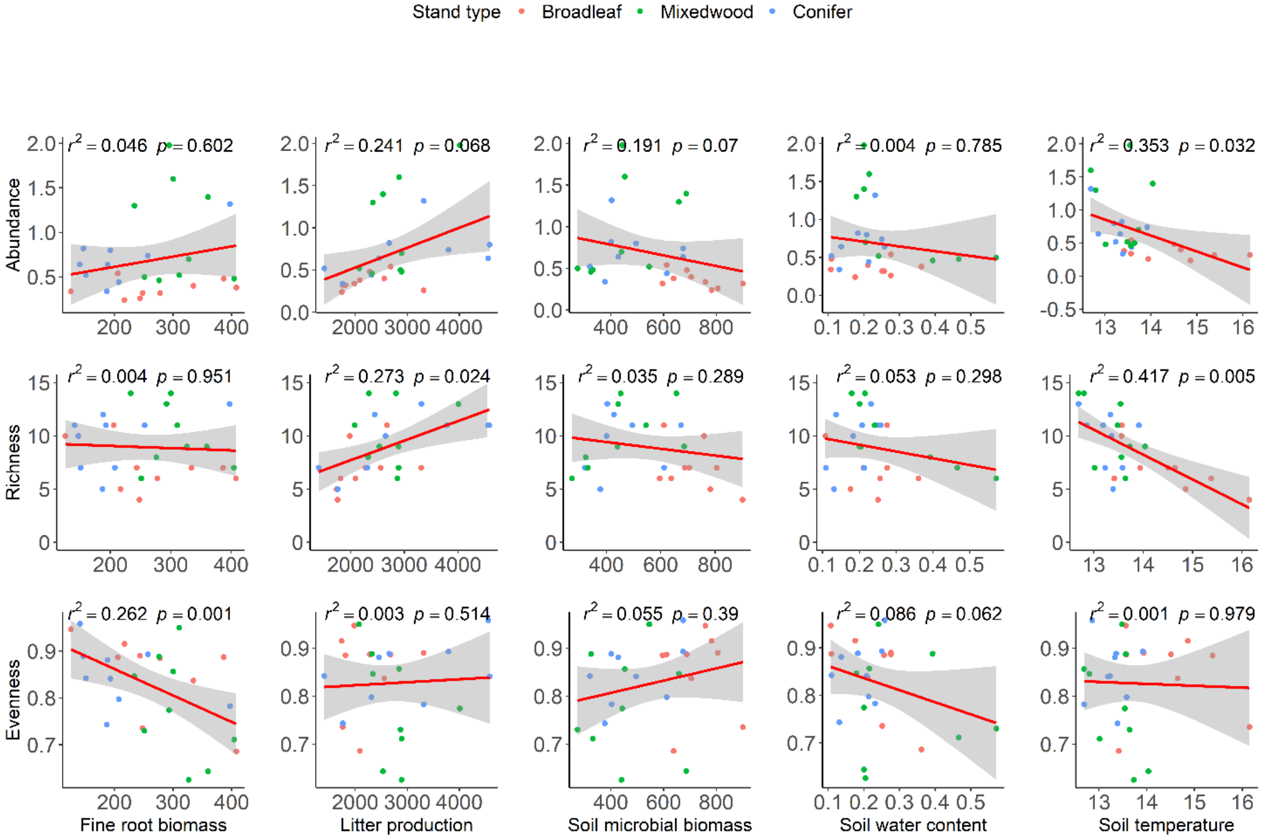

Figure 3-3: The abundance, richness, and evenness in relation to fine root biomass, litter production, soil microbial biomass, soil water content and soil temperature. Lines and shaded areas represent the fitted linear regressions and their 95% confidence intervals.

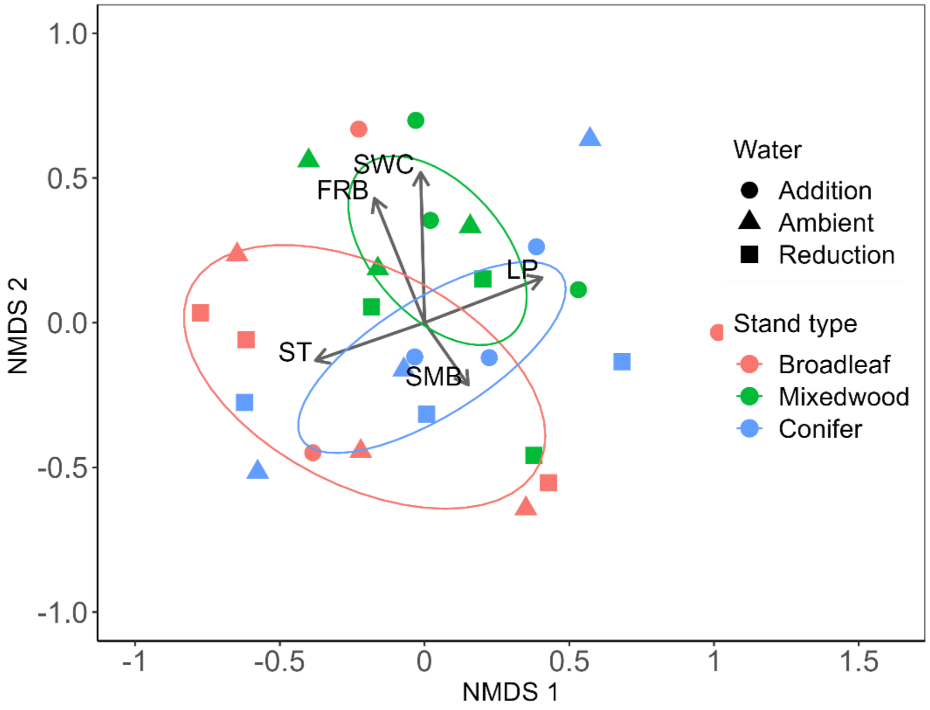

Figure 3-4: Nonmetric multidimensional scaling ordination of soil Collembola communities for different overstory types and water treatment combinations in relation to environmental characteristics. The best NMDS solution was attained at a stress of 0.23 based on Bray Curtis distance. Ellipses represent 95% confidence intervals (CIs) of the weighted averages of scores corresponding to stand types. Predictor variables included soil temperature (ST), soil water content (SWC), annual litterfall production (LP), fine root biomass (FRB), and soil microbial biomass (SMB).

Collembola abundance and richness increased with litter production and decreased with soil temperature, while evenness decreased with fine root biomass (Fig. 3-3). Collembola attributes were not related to soil water content (Fig. 3-3). The perMANOVA analysis revealed that Collembola community compositions differed significantly with stand types (F = 2.96, *P* = 0.005, R^2 = 0.205) but did not differ with water treatments (F = 0.776, *P* = 0.152, R^2 = 0.054).

Moreover, the effects of stand types on the Collembola community composition depended on water treatments (F = 0.855, $P = 0.034$, $R^2 = 0.118$) (Table 3-2, Fig. 3-4). Specifically, Bray-Curtis dissimilarity index (BC) was 0.324 for Collembola communities in conifer vs mixed stands. Collembola communities in broadleaf stands were distinct from those in conifer and mixed stands (BC = 0.395, 0.552, respectively). BC was low (BC = 0.260) for communities in stands under control vs water reduction, but medium for stands under control vs water addition (BC = 0.470) and water reduction vs water addition (BC = 0.465). Two *Entomobrya* species (*Entombrya* sp.1 and sp. 3) associated mixed stands while one *Sminthurinus* species dominated conifer stands. The Collembola community compositions revealed significant and positive correlations with soil water content ($R^2 = 0.269$, $P = 0.015$), fine root biomass ($R^2 = 0.214$, $P = 0.060$), and litter production ($R^2 = 0.189$, $P = 0.083$) (Table 3-4).

Table 3-4 Correlation of environmental variables to Collembola community

Variables	Collembola community			
	NMDS1	NMDS2	R^2	*P*
Fine root biomass	-0.3735	0.9276	0.2143	**0.060**
Litter production	0.9344	0.3564	0.1886	**0.083**
Soil microbial biomass	0.5751	-0.8181	0.0688	0.398
Soil water content	-0.0253	0.9997	0.2694	**0.015**
Soil temperature	-0.9453	-0.3161	0.1589	0.121

3.5 Discussion

Our study discovered a positive tree mixture effect on Collembola abundance and a neutral effect on Collembola richness in natural forests. This provided further evidence that tree communities with greater diversity may preserve soil ecosystem functions. Importantly, our results provided experimental evidence that tree mixture effects on richness and evenness increased with lower water availability, which indicated the essential role of water availability in moderating the relationships between plant diversity and ecosystem functions.

We found that water addition increased Collembola evenness in conifer but decreased evenness in broadleaf stands, indicating a critical role of stand type in moderating the effects of water availability on Collembola. This finding suggests that water addition could reduce water stress on rare species in conifer stands, promoting higher evenness. In contrast, the decrease of evenness with water addition in broadleaf stands might be attributable to higher water combined with more soil nutrients leading to competitive exclusion by a few competitive species dominating the community. In mixed stands, water reduction increased Collembola evenness whereas water addition did not, showing different responses from pure stands. This finding suggests that Collembola community structure in mixed stands is relatively more sensitive to low water availability than to wet conditions, compared to pure broadleaf or conifer stands. Contrary to most previous studies (Lindberg, Engtsson et al. 2002, Kardol, Reynolds et al. 2011, Peguero, Sol et al. 2019, Wise and Lensing 2019, Goncharov, Leonov et al. 2023), neither abundance nor richness responded to water treatments. This finding indicates changes of such magnitude (25%) in water availability did not impose notable impacts on Collembola abundance or richness in young natural boreal forests. Different from lab experiments, Collembola in natural boreal forests are more resilient, perhaps because they may be adapted well to cold and drought weather

(Holmstrup 2014). Alternatively, Collembola abundance and richness are more driven by litter productivity and soil temperature rather than by soil water content in cold boreal forests, as indicated by our regression analyses.

Our results reveal the first empirical evidence of a positive tree mixture effect on Collembola abundance in natural forests. In line with previous studies showing increased plant input in tree mixtures (Zhang, Chen et al. 2012, Zheng, Chen et al. 2019), our results suggest that Collembola abundance is primarily affected by litterfall production in natural forests, as indicated by our additional analysis. Furthermore, we observed lower evenness in mixed stands than the average of corresponding monocultures. This might be the result of increased competition among Collembola species for resources and more complex trophic interactions in tree mixtures compared to monocultures, resulting in certain species thriving or diminishing.

Contrasted with our previous meta-analysis (Zhang, Peng et al. 2022), we found tree mixture had negligible effects on Collembola richness suggesting plant mixture effects can depend on ecosystems. Tree mixture of two species may not provide additional niches for more species to coexist in young natural boreal forests. Alternatively, the lack of mixture effect on Collembola richness might have resulted from limited understorey diversity and density in young mixed stands (Zhang, Chen et al. 2016). Importantly, we found that water reduction increased the mixture effects on evenness, from -16% to +3%, providing empirical evidence that the mixture effect can be higher in harsher environments, perhaps due to interspecific facilitation (Maestre, Callaway et al. 2009). As expected, abundance and richness were significantly affected by the stand type with higher values in mixed than broadleaf stands. This finding agrees with previous studies (Cavard, Macdonald et al. 2011, Korboulewsky, Perez et al. 2016, Korboulewsky, Heiniger et al. 2021) and indicates that admixture of varied litter types can positively affect Collembola abundance and richness.

In contrast to our expectations and previous reports (Kardol, Reynolds et al. 2011, A'Bear, Jones et al. 2014, Turnbull and Lindo 2015), water treatment did not impact the Collembola community structure. The lack of differences between water treatments indicated that Collembola of high variability in community structure (Bonfanti, Hedde et al. 2022) in the young natural boreal forest were not sensitive to water in this range of altered precipitation. But importantly, water availability moderated the effects of stand types on the Collembola community. Among 5 abiotic factors we tested, the effects on the community composition were mainly driven by soil water content, fine root biomass, and litter production rather than soil microbial biomass and soil temperature. Similar responses have been observed for Collembola and other mesofauna species (Salamon and Alphei 2009, Holmstrup, Sørensen et al. 2013, Wang, Slotsbo et al. 2022). Community composition was also clearly affected by stand types. Indicated by the Bray dissimilarity distance, tree mixtures harbor dissimilar Collembola composition from broadleaf stands (BC = 0.552). In broadleaf stands, *Entombrya* sp. 3 (35.7%) and *Entombrya* sp. 1 (18.2%) dominated the community. In mixed stands, four species (*Entombrya* sp. 3: 32.4%; *Entombrya* sp.1: 12.2%; *Entombrya* sp. 5: 8.4%; *Folsomia* nr. *candida*: 8.2%) were relatively abundant.

In conclusion, our study provides the first evidence of a positive tree mixture effect on Collembola abundance in young boreal forests. Notably, we found that mixture effects on evenness increased under water reduction. Furthermore, our results suggest that stand type impacts Collembola abundance, richness, and community composition because of higher litter production, fine root biomass, and soil water content in mixed stands than in broadleaf or conifer stands. Moreover, water treatments moderated the effects of stand type on Collembola evenness and community composition. These results highlight the importance of water availability in regulating the Collembola community. Moreover, it shows that the maintenance of stand types and diversity in natural boreal forests is necessary for the Collembola community. Finally, we suggest that more studies on soil Collembola to tree mixtures of high species richness are needed in natural forests in the context of climate change. Further research should explicitly include high-resolution identification and functional classification of soil Collembola and environmental properties to resolve and understand the underlying mechanism.

Chapter 4: Increased positive tree species mixture effects on the abundance and richness of Collembola with stand age in natural boreal forests.

4.1 Abstract

Despite the essential role of Collembola in litter decomposition, the dynamics of Collembola in tree mixtures following stand development in natural forests remains unexplored. This study investigated the response of Collembola abundance, diversity, and community structure to stand type and stand age in pure and mixed jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) of 15-year-old and 41-year-old stands in natural boreal forest. We found that responses of Collembola to stand type depend on stand age. In 15-year-old stands, only evenness responded to stand type with lower values in mixed stands than in broadleaf stands. In 41-year-old stands, abundance and richness were higher in conifer and mixed stands than in broadleaf stands. We found a negative mixture effect on the Simpson's index in 15-year-old stands but a nonsignificant effect on it in 41-year-old stands. We also observed nonsignificant effects on the abundance and richness in 15-year-old stands but increased and positive mixture effects in 41-year-old stands. Our results provide the first evidence for changed mixture effects on Collembola with stand development in natural boreal forests.

4.2 Introduction

Collembola (Hexapoda: Entognatha) are among the most abundant groups of soil fauna in forest soils (Orgiazzi, Bardgett et al. 2016). Their density can reach 10^5 individuals per m^2 (Petersen and Luxton 1982). They play an important role in soil food webs and ecosystem processes like litter decomposition by grazing plant materials and soil fungi and simulating nutrient cycling (Sackett, Classen et al. 2010, Nielsen, Ayres et al. 2011, Frouz 2018). Tree mixing has been proposed as a sustainable forest management strategy as it can improve performance in ecosystem functioning and services like plant productivity and biodiversity conservation (Cavard, Macdonald et al. 2011, Mori, Lertzman et al. 2017, Feng, Schmid et al. 2022). However, the response of Collembola to tree species mixtures in natural forests of different ages remains understudied.

On the most abundant mesic sites in boreal forests, overstorey tree composition can be dominated by either conifers, broadleaves, or their mixtures (Taylor and Chen 2011). The abundance and diversity of Collembola may be higher in broadleaf stands compared to conifer stands, as Collembola has a preference for high-quality litter (lower C: N ratio) (Korboulewsky, Perez et al. 2016, Sánchez-Galindo, Sandmann et al. 2021). On the other hand, tree mixtures may have the most abundant and diverse Collembola community. It has been suggested that tree species mixtures have better performance in litterfall, root biomass, and microbial activities (Zheng, Chen et al. 2019, Beugnon, Du et al. 2021, Zeng, Xiang et al. 2021, Beugnon, Eisenhauer et al. 2023) than the average of monocultures due to species complementary and reduced inter-specific competition (Barry, Mommer et al. 2019), and therefore may support more abundant and diverse Collembola because of increased amount and diversity of food resources. Moreover, heterogeneous habitat structures in tree mixtures can provide additional niches for

Collembola (LaRue, Knott et al. 2023). Besides, conifer, broadleaf, and mixed stands may have dissimilar community compositions of Collembola because of varied soil pH, humus forms, and microbial composition, and varied canopy structures and understory plants (Lu and Scheu 2021, Martins da Silva, Bartz et al. 2023).

However, empirical studies have reported mixed results on the responses of Collembola abundance and diversity to tree mixtures (Kaneko and Salamanca 2002, Scheu, Albers et al. 2003, Salamon, Scheu et al. 2008, Salamon and Alphei 2009, Zagatto, Pereira et al. 2019, Korboulewsky, Heiniger et al. 2021). Notably, most studies did not compare tree mixtures to each monoculture of constituted species in mixtures, therefore confounding true tree species mixture effects. Furthermore, tree mixture effects on Collembola can change with stand development. Biodiversity effects on ecosystem functioning can shift over time due to increased species complementarity for resource use and decreased functional redundancy over time (Chen, Chen et al. 2021, Thakur, van der Putten et al. 2021, Wu, Bao et al. 2023). The abundance, diversity, and community structure of Collembola could change with stand development because of increased litterfall amount and fungal activity (Chen, Brant et al. 2017, Uri, Kukumägi et al. 2022). In addition, the short canopy with low leaf area index in young forests can result in high temperatures and low moisture content in the forest floor while the development of the canopy and increased root biomass following stand development (Geng, Ma et al. 2022) can ameliorate unfavorable conditions and create heterogeneous microhabitats for Collembola (Penone, Allan et al. 2019). Finally, some species only appear when required conditions and certain microhabitats, such as the litter layer, coarse woody debris, and mosses develop with stand development (Potapov, Korotkevich et al. 2018, Rousseau, Venier et al. 2018, Fujii, Cornelissen et al. 2023).

Therefore, the mixture effects on the abundance and diversity of Collembola are expected to increase with stand age.

Our study investigated the abundance, diversity, and community composition of Collembola in pure and mixed jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.) in post-fire boreal forests of two stand ages (15 and 41 years old). We hypothesize that: (1) tree mixture increases the abundance and diversity of Collembola; (2) tree mixture effects on Collembola are more pronounced in older stands. Also, we expect the community composition of Collembola to differ with stand types and stand ages.

4.3 Materials and methods

4.3.1 Study site and experimental design

The study was conducted in the central boreal forests of Canada, located north of Lake Superior and west of Lake Nipigon, Ontario, Canada (49°22′ N - 49°45′ N, 89°10′ W–89°56′ W). The study area falls in the 3W ecoregion and is characterized by warm summers and cold, snowy winters (Crins, Gray et al. 2009). The mean annual temperature is 2.5 °C with a mean annual precipitation of 712 mm across a temporal range of 1970–2000 (Fick and Hijmans 2017). The soil type is relatively deep glacial till of the Brunisolic order on the upland sites. The dominant overstory tree species include jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloides* Michx.). The common understory shrub species include pin cherry (*Prunus pensylvanica* L. fil), alder (*Alnus*), and beaked hazelnut (*Corylus cornuta* Marsh.).

We sampled pure and mixed *Populus tremuloides* Michx. (*Populus*) and *Pinus banksiana* Lamb. (*Pinus*) stands of two post-fire stand age classes: 15 and 41 years. We replicated each of the stand age classes and overstorey types three times. Stand ages were derived from fire records and verified by sampling dominant trees (Senici, Chen et al. 2010). A circular plot (400 m^2) was randomly established to represent each sample stand (Hart and Chen 2008). We used an ecological classification approach to ensure that all sample stands were similar based on topography and soil texture (Taylor 2000). We allocated all sites on mid-slope positions of well-drained glacial moraines with > 50 cm in thickness. The soil moisture regime class was confirmed by a soil profile examination, dug to the parent material, within each selected stand. The similarity of the sites was further validated through a comparison of the physical and chemical properties of soils; that is, the concentrations of total nitrogen and total carbon, cation exchange capacity, and soil texture composition of the mineral soil at a depth of 30 – 55 cm, following the method described by (Laganière, Paré et al. 2012). Stands were allocated several kilometers apart from each other to minimize neighborhood and unknown environmental influences that might be spatially correlated.

4.3.2 Sampling, extraction, and identification of Collembola

A circular plot (400 m^2) was randomly established to represent each sample stand. For each plot, ten subsamples of forest floor Collembola were randomly collected using a 10 × 10 cm quadrat and mixed as a composite sample (Bruckner, Barth et al. 2000) in October 2022. Samples were carried to the lab in punctured polyethylene bags in an ice-filled cooler. Collembola were extracted within 24 hours after sampling using the Tullgren funnel (Macfadyen 1961) with a mesh size of 2 mm for ten days (Crossley and Blair 1991) and stored in 70% ethanol. Collembola were identified to taxonomic species level or morphospecies (Dindal 1990, Hopkin 1997, Babenko, Stebaeva et al. 2019) and counted. Species richness was calculated as the number of species per sample. Abundance was estimated as individuals per m^2. Simpson's index was calculated as $S = 1 - \sum \left(\frac{n(n-1)}{N(N-1)}\right)$, where n represents the numbers of individuals of a particular species, N represents the total number of individuals of all species combined. Pielou's index was calculated as J = $\frac{-\sum p_i \cdot \ln p_i}{\ln S}$, where p_i is the proportional abundance of species i, S is the total number of species in the community. Collembola community composition was defined as the assemblage of species/morphospecies and their relative abundance within each plot.

4.3.3 Statistical Analysis

Generalized linear mixed-effects models were used to analyze the differences in Collembola attributes (abundance, species richness, Simpson's index, and evenness) among stand types and ages. The evenness was defined as following the gamma distribution. The richness and Simpson index of Collembola followed the normal distribution. The abundance was log-transformed to meet the assumption of normal distribution. Differences between stand ages and stand types in Collembola attributes were tested at the 5% probability level using a two-way analysis of variance (stand type × age) and posthoc Tukey HSD test.

To test tree mixture effects, a log-transformed response ratio ($\ln RR$) was employed to quantify the effects of tree species mixtures on Collembola abundance, richness, Simpson's index and evenness.

$$\ln RR = \ln\left(\frac{\mathrm{X_t}}{\mathrm{X_c}}\right) \tag{1}$$

where Xt and Xc are the observed value and the expected value of soil Collembola in mixtures. To account for the species compositional effect, Xc was calculated as the weighted mean values in monocultures of constituent species in mixtures (Loreau and Hector 2001):

$$X_c = \sum(V_i \times P_i) \tag{2}$$

where V_i is the observed value of Collembola abundance, richness, Simpson's index and evenness in the monoculture of species i, and P_i is the proportion of species i basal area ($\mathrm{m^2\ ha^{-}}$

^{1}) in the corresponding mixture per plot. We tested whether the responses of Collembola abundance, richness, Simpson's index and evenness to tree species mixtures were affected by Stand age using the linear mixed model.

Community composition was compared between stand types and ages using the Bray-Curtis dissimilarity matrix and performed by non-metric multidimensional scaling (NMDS) using the VEGAN package in R (Jari Oksanen, Kindt et al. 2015). PerMANOVA was conducted to determine statistical significance (Anderson 2001). Indicator analysis (IndVal) was performed for each species independently (Legendre and Legendre 2012). All analyses were performed in R 4.3.0 (R Core Team 2023).

4.4 Results

In total, 6620 individuals of Collembola were identified belonging to 39 species/morphospecies (Table 4-1). The abundance, richness, and evenness differed significantly between stand types and stand age classes ($P < 0.001$), while Simpson's index did not differ between stand types ($P = 0.193$) or age classes ($P = 0.875$). The abundance and richness were significantly higher in mixed stands (1023 ind.m^{-2} and 18 species) and conifer stands (600 ind.m^{-2} and 15 species) than broadleaf stands (107 ind.m^{-2} and 5 species) in 41-year-old stands, but there were no significant differences in 15-year-old stands (Fig. 4-1, Table 4-2). On average, the abundance and richness increased by 262% and 86% with stand age ($P < 0.001$) from 15-year-old to 41-year-old stands, while the evenness decreased by 8.6%.

Table 4-1 Mean abundance (individuals/m^2; mean ± standard deviations; N=3) of Collembola species/morphospecies per treatment.

	Broadleaf		**Mixedwood**		**Conifer**	
	15	**41**	**15**	**41**	**15**	**41**
Order Entomobryomorpha						
Entomobrya sp. 1	3 ± 3	3 ± 3	13 ± 3	3 ± 3	13 ± 7	0 ± 0
Entomobrya sp. 2	7 ± 7	7 ± 7	20 ± 9	33 ± 7	20 ± 6	7 ± 3
Entomobrya sp. 3	10 ± 6	0 ± 0	30 ± 30	57 ± 37	33 ± 0	13 ± 9
Entomobrya sp. 4	3 ± 3	13 ±13	0 ± 0	23 ± 9	17 ± 17	13 ± 13
Entomobrya sp. 5	0 ± 0	0 ± 0	0 ± 0	7 ± 7	0 ± 0	0 ± 0
Vertagopus* nr. *asiaticus	0 ± 0	0 ± 0	0 ± 0	37 ± 22	0 ± 0	33 ± 19
Vertagopus* nr. *laricis	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	13 ± 9
Desoria sp.1* (nr. *gelida)	13 ± 9	0 ± 0	10 ± 0	23 ± 3	3 ± 0	3 ± 3
Desoria sp.2	0 ± 0	0 ± 0	0 ± 3	90 ± 70	20 ± 20	20 ± 6
Appendisotoma* nr. *Abiskoensis	10 ± 10	17 ± 17	17 ± 7	110 ± 60	23 ± 12	70 ± 12
Folsomia sp.1* (nr. *candida)	0 ± 0	23 ± 19	3 ± 20	80 ± 40	0 ± 3	137 ± 78
Folsomia sp.2	0 ± 0	7 ± 3	7 ± 0	43 ± 30	7 ± 7	57 ± 38
Isotomurus sp.1* (nr. *palustris)	7 ± 7	0 ± 0	0 ± 0	0 ± 0	7 ± 0	0 ± 0
Isotoma sp.1* (nr. *riparia)	23 ± 3	0 ± 0	10 ± 0	57 ± 17	13 ± 6	7 ± 3
Isotoma sp.2* (nr. *viridia)	10 ± 10	0 ± 0	10 ± 0	30 ± 15	0 ± 0	27 ± 27
Isotoma sp.3	0 ± 0	7 ± 7	0 ± 7	0 ± 0	0 ± 0	10 ± 10
Isotoma sp.4	0 ± 0	7 ± 7	0 ± 0	7 ± 7	0 ± 0	0 ± 0
Isotoma sp. 5	0 ± 0	0 ± 0	0 ± 0	7 ± 7	0 ± 0	7 ± 7
Isotoma sp.6	0 ± 0	0 ± 0	0 ± 0	33 ± 15	0 ± 0	47 ± 18
Proisotoma sp.1* (nr. *notabilis)	0 ± 0	0 ± 0	0 ± 0	67 ± 62	0 ± 0	43 ± 9
Lepidocyrtus* nr. *cyaneus	0 ± 0	0 ± 0	3 ± 3	7 ± 7	3 ± 3	3 ± 3
Lepidocyrtus sp.2	0 ± 0	0 ± 0	0 ± 0	10 ± 6	0 ± 0	0 ± 0
Lepidocyrtus sp.3	3 ± 3	7 ± 7	10 ± 9	243 ± 127	7 ± 0	40 ± 21
Tomocerus* nr. *Minor	0 ± 0	0 ± 0	0 ± 3	7 ± 7	3 ± 0	7 ± 7
Order Symphypleona						
Dicyrtomina sp.1	0 ± 0	0 ± 0	0 ± 7	0 ± 0	7 ± 12	0 ± 0
Dicyrtomina sp.2	0 ± 0	0 ± 0	0 ± 3	0 ± 0	0 ± 0	3 ± 3
Sminthurinus sp.1	0 ± 0	3 ± 3	0 ± 0	10 ± 10	7 ± 7	0 ± 0
Sminthurinus sp.2* (nr. *aureus)	0 ± 0	0 ± 0	0 ± 0	10 ± 0	0 ± 0	3 ± 3
Sminthurinus sp.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	3 ± 3	3 ± 3
Sminthurinus sp.4	0 ± 0	3 ± 3	0 ± 3	0 ± 0	13 ± 10	10 ± 10
Sminthurus sp.1* (nr. *fitchi)	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	3 ± 3
Sminthurus sp.2	0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Sminthurides* nr. *occultus	0 ± 0	3 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Sphaeridia* nr. *pumilis	7 ± 7	0 ± 0	7 ± 0	0 ± 0	0 ± 0	3 ± 3
Bourletiella sp.1	0 ± 0	0 ± 0	0 ± 0	3 ± 3	0 ± 0	7 ± 7
Bourletiella sp.2	0 ± 0	0 ± 0	0 ± 7	0 ± 0	7 ± 7	0 ± 0
Bourletiella sp.3	0 ± 0	0 ± 0	0 ± 0	17 ± 17	0 ± 0	0 ± 0
Order Poduromorpha						
Pseudachorutinae *species*	3 ± 3	3 ± 3	0 ± 3	0 ± 0	3 ± 0	3 ± 3
Xenylla species	0 ± 0	0 ± 0	7 ± 3	7 ± 7	3 ± 12	7 ± 7

Table 4-3 Effects of stand type (T) and age (A) on Collembola abundance, richness, Simpson's index, and evenness

Source	df	Chi-square	*P*
Abundance			
T	2	34.81	**< 0.001**
A	1	21.00	**< 0.001**
T × A	2	9.40	**0.030**
Richness			
T	2	17.96	**< 0.001**
A	1	14.45	**< 0.001**
T × A	2	3.55	**0.032**
Simpson			
T	2	6.57	0.193
A	1	1.27	0.875
T × A	2	3.03	0.272
Evenness			
T	2	8.81	**0.013**
A	1	6.14	**0.012**
T × A	2	0.09	0.958

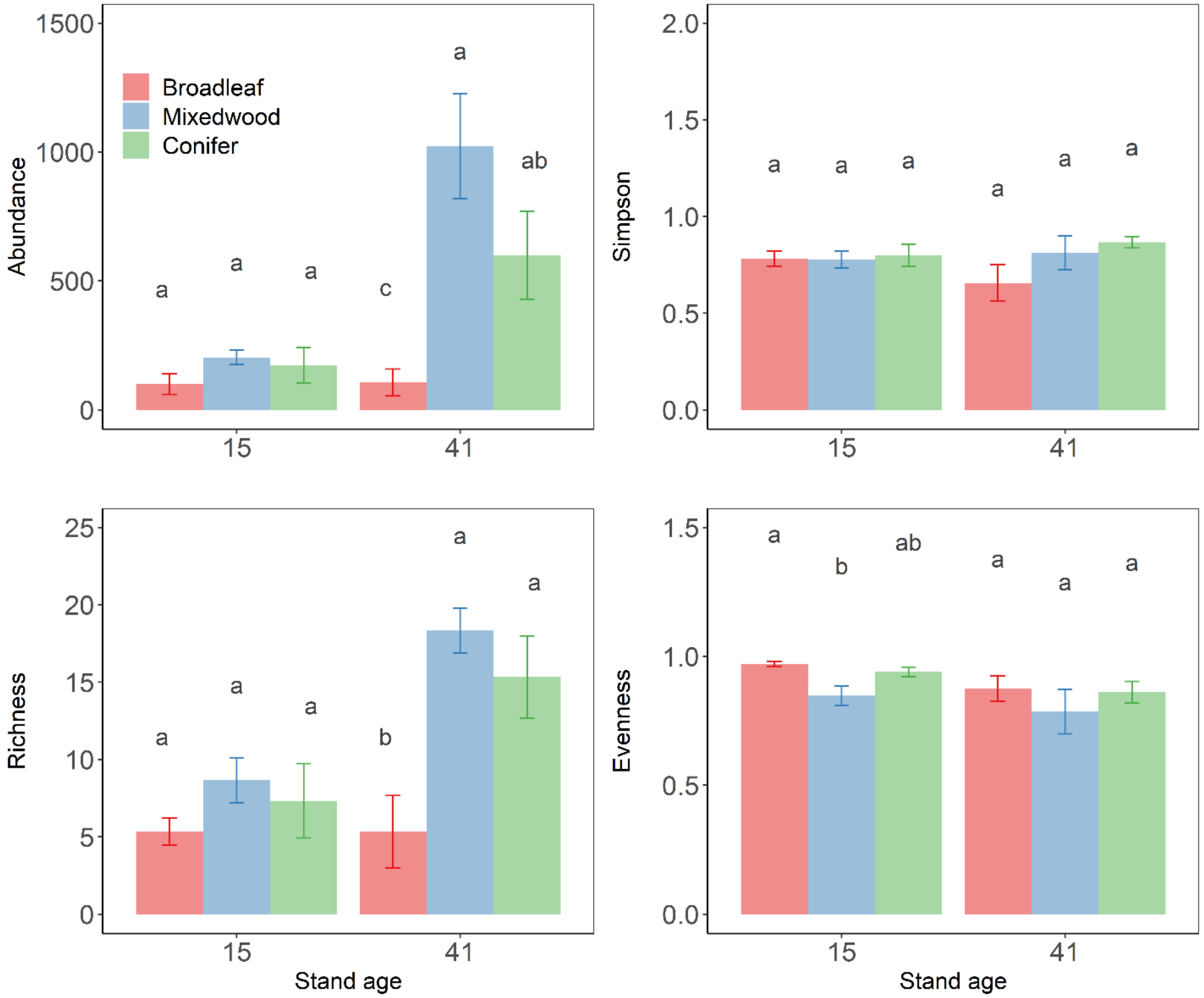

Figure 4-1: Collembola attributes (abundance, richness, Simpson's index, and evenness) in relation to stand types and stand ages. Error bars represent standard error. Different letters indicate a significant difference between stands within the same age category (α = 0.05).

Tree mixture effects on abundance and richness were significantly increased by stand age (*P* = 0.005 and 0.017) from neutral in 15-year-old stands to positive in 41-year-old stands (Table 4-4, Fig. 4-2). In 41-year-old stands, tree species mixture increased abundance and richness by 271% and 120%, respectively (Fig. 4-2). Meanwhile, in 15-year-old stands, tree mixture negatively affected Simpson's index. Evenness did not respond to tree mixture for both stand ages.

Table 4-3 Effects of stand age on the response ratio of Collembola abundance, richness, Simpson's index, and evenness to tree species mixtures

Attribute	Stand age		
	df	F	*P*
Abundance	1,2	219.04	**0.005**
Richness	1,2	56.58	**0.017**
Simpson's index	1,4	0.687	0.454
Evenness	1,2	0.089	0.794

Note: Linear mixed-effects model fit tests used Satterthwaite approximations for denominator degrees of freedom (df). *P* are significance of the model and *P* < 0.05 is highlighted in bold.

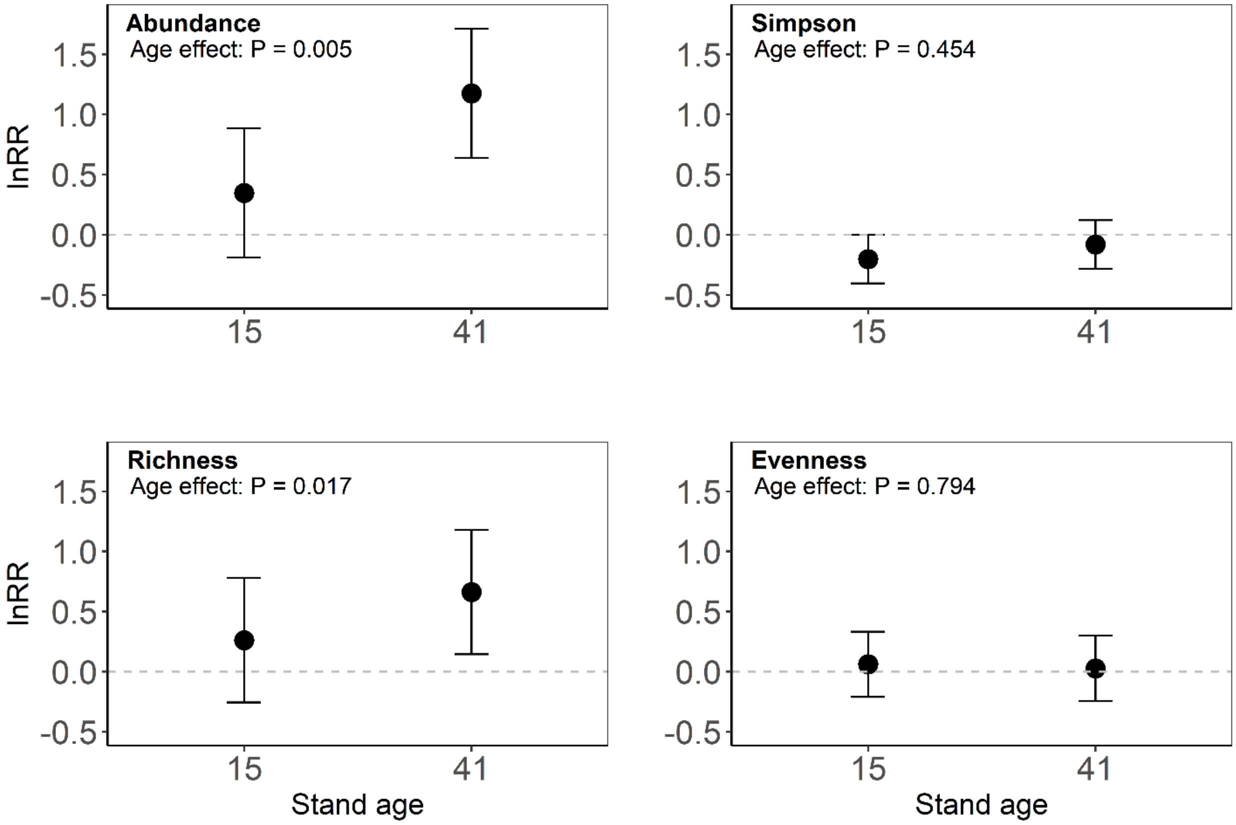

Figure 4-2: Tree mixture effects on Collembola abundance, richness, Simpson's index, and evenness. Values are mean ± 95% confidence intervals (CIs). The mixed species effects were

significant at α = 0.05 if the 95% CIs did not cover 0. The difference between groups was significant if 95% CIs of their coefficients did not overlap another's mean.

Collembola showed dissimilar community composition between stand types (*P* = 0.021) and ages (*P* = 0.002) (Fig. 4-3). High Bray-Curtis dissimilarity index (BC) ranging from 0.5-0.8 for Collembola communities between stand types and stand ages. The most dissimilar communities were in broadleaf stands from mixed stands (BC = 0.802). Collembola communities in 41-year-old stands also dissimilar from 15-year-old stands (BC = 0.727). Indicator analysis showed that six species (*Isotoma* sp. 6, *Folsomia* nr. *candida*, *Vertagopus* nr. *asiaticus*, *Appendisotoma* nr. *abiskoensis*, *Proisotoma* nr. *notabilis*, and *Lepidocyrtus* sp. 3) were strongly associated with stands of 41-year-old, while two species (*Entomobrya* sp. 2 and *Entomobrya* sp. 3) were associated with mixed stands.

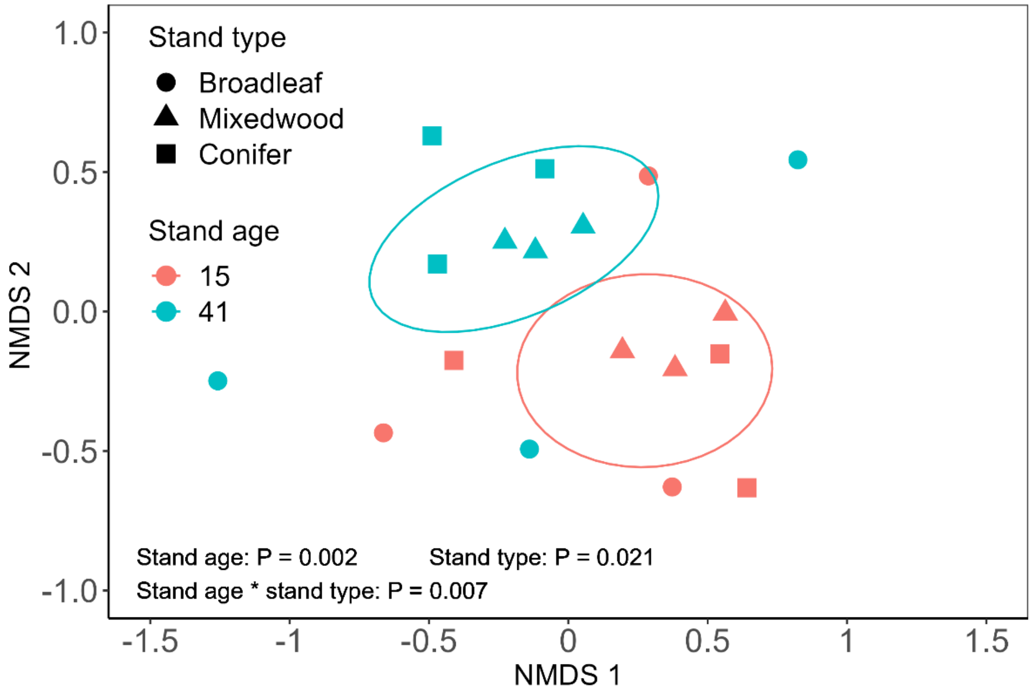

Figure 4-3: Nonmetric multidimensional scaling ordination of soil Collembola communities for different stand types and ages. The best NMDS solution was attained at a stress of 0.17. Ellipses represent 95% confidence intervals (CIs) of the weighted averages of scores corresponding to stand ages.

4.5 Discussion

To the best of our knowledge, we present the first study to show tree mixture effects on Collembola abundance and diversity in natural boreal forests of different ages. We observed positive tree species mixture effects on Collembola abundance and richness in 41-year-old stands but not in 15-year-old stands, showing increasing mixture effects with stand development. We found higher abundance, richness, and lower evenness in 41-year-old stands than in 15-year-old stands. In 41-year-old stands, the abundance and richness differed among stand types with higher values in conifer and mixed stands than broadleaf stands. Moreover, the Collembola community composition differed with stand types and stand ages.

Consistent with our first hypothesis, we observed significant and positive tree mixture effects on Collembola abundance and species richness in 41-year-old stands, suggesting that the amount and diversity of food and habitat resources increased under tree mixtures compared to corresponding monocultures. Our findings extends the previous findings of positive mixture effects on fine root biomass and litterfall production to Collembola abundance and species richness (Ma and Chen 2018, Wan, Joly et al. 2023). Nonsignificant mixture effects on the abundance and richness in younger stands may be a result of a high level of interspecific competition for fewer resources at the early stage of stand development compared to mid-aged stands (Anyomi, Neary et al. 2022). However, we observed negative mixture effects on Simpson's index in 15-year-old stands, which is due to the even distribution of species in young stands compared to mid-aged stands. Nonsignificant mixture effects on evenness at both stand ages indicated relatively stable species distribution in the communities. Importantly, our study revealed that tree mixture effects on Collembola abundance and richness increased with stand age. This pattern agrees with our previous findings that diversity effects on tree growth, fine roots, and soil nitrogen increase over time (Ma and Chen 2018, Taylor, Gao et al. 2020, Chen, Chen et al. 2021). However, mixture effects on Simpson's index and evenness did not show such a pattern.

As expected, the abundance, richness, and evenness of Collembola increased with stand age. Notably, the density of *Isotomidae* and *Lepidocyrtus* species significantly increased in the 51-year-old stands. It shows that increased resources and structural diversity in older stands can promote the Collembola community (Ouyang, Xiang et al. 2019, LaRue, Knott et al. 2023). It is plausibly attributable to increased living plant materials like mosses, understorey litter, fine root biomass, and increased canopy closure, and thus the resulting increased heterogeneity and niche specialization on the forest floor in older stands (Bartels and Chen 2010, Bokhorst, Wardle et al. 2014, Kumar, Chen et al. 2018, Geng, Ma et al. 2022).

Conifer and mixed stands had higher Collembola abundance and richness than broadleaf stands, indicating that Collembola favour acidic soils, humus forms, deep litter layers, and high fungal activity associated with coniferous trees in boreal forests. (Russell and Gergócs 2019) did not find differences in abundance and diversity of Collembola among mixed, deciduous, and coniferous stands in Germany, but species composition of Collembola differed strongly along a gradient from deciduous over mixed to coniferous stands. In our study, *Appendisotoma* nr. *abiskoensis* (12.9%), *Isotoma* nr. *riparia* (11.3%), and *Folsomia* nr. *candida* (11.3%) dominated communities in broadleaf stands; *Folsomia* nr. *candida* (18.1%), *Appendisotoma* nr. *Abiskoensis* (11.2%), and *Folsomia* sp.2 (9.1%) dominated conifer stands; *Lepidocyrtus* sp.3 (20.9%), *Appendisotoma* nr. *abiskoensis* (10.3%), and *Entomobrya* sp.3 (9.2%) dominated mixed stands. As indicated by indicator analysis, two species (*Entombrya* sp. 2 and *Entombrya* sp. 3) were associated with mixed stands showing mixed stands have more suitable habitat conditions for these species. As expected, the dominance structure of the Collembola altered with stand age. In 15-year-old stands, species were relatively evenly distributed. *Entombrya* sp. 3 (12.8%) and *Entombrya* sp.1 (9.6%) were relatively abundant, while in 41-year-old stands, *Lepidocyrtus* sp.3 (15.6%), *Folsomia* nr. *candida* (13.0%), and *Appendisotoma* nr. *abiskoensis* (10.6%) dominated Collembola communities. By indicator analysis, six species (*Isotoma* sp.6, *Folsomia* nr. *candida*, *Vertagopus* nr. *asiaticus*, *Appendisotoma* nr. *abiskoensis*, *Proisotoma* nr. *notabilis*, *Lepidocyrtus* sp.3) were indicators of mid-aged stands, suggesting that mid-aged stands can provide additional structural diversity for these species. Consistent with previous reports (Korboulewsky, Heiniger et al. 2021, Leidinger, Blaschke et al. 2021), dissimilar community compositions of Collembola among stand types and stand ages are possibly attributable to varied resources and habitat structure among treatments. Further causal studies on related factors are needed to reveal the underlying mechanism.

Overall, our study suggests that tree mixture effects on Collembola abundance and richness increased with stand development from neutral in 15-year-old stands to positive in 41-year-old stands in the natural boreal forest. Differences in Collembola attributes among stand types were more pronounced in older stands with higher abundance and richness in conifer and mixed stands than in broadleaf stands. We highlighted the importance of tree mixtures of mid-aged stands in maintaining abundant and diverse Collembola communities. Further, we addressed the varied overstorey types and stand ages in forest management are vital in terms of maintaining heterogeneous soil habitats and therefore conserving the Collembola community mosaic. Future research could contribute to the tree mixture effects of high species richness levels on the Collembola community and associated environmental factors in natural forests to serve the objectives of forest biodiversity conservation.

Chapter 5: GENERAL CONCLUSION

This dissertation shows evidence that plant mixtures have more diverse soil fauna than do monocultures, extending our understanding of the positive biodiversity-ecosystem functions relationships from aboveground productivity to the belowground soil faunal communities (Zhang, Chen et al. 2012). I found that the effects of plant mixtures on the Collembola community increased with water stress and stand age in boreal forests. A summary of the key findings of this dissertation is as follows:

1. By meta-analysis of 40 studies, I showed an overall positive relationship between plant species diversity and soil fauna diversity across varied climate conditions. It indicated more diverse food resources and microhabitats in plant mixtures. However, the effect sizes of species mixtures on both the abundance and diversity of soil fauna increased with species richness in plant mixtures and over time. This pattern was consistent across soil depth and ecosystem types. This study demonstrated that the positive biodiversity-production relationship can propagate to the belowground biota. We should incorporate plant mixture effects on soil fauna into biodiversity considerations and acknowledge that the above-mentioned factors moderate the magnitude and direction of mixture effects.

2. In my rainfall manipulation study, I found no significant mixture effects on the Collembola community under ambient water conditions. But, importantly, positive mixture effects on Collembola abundance were observed with water addition. Moreover, I found greater mixture effects on Collembola richness and evenness with water reduction. This study provides empirical evidence for the stress-gradient

hypothesis, indicating that facilitation has a greater effect than competition among species under environmental stress (Maestre, Callaway et al. 2009). I conclude that soil water content, litter production, and fine root biomass promote a thriving Collembola community.

3. In my last study in boreal forests of two stand ages, I found significant and positive tree mixture effects on Collembola abundance and species richness in 41-year-old stands, indicating that the amount and diversity of food and habitat resources increased for tree mixtures compared to corresponding monocultures. Moreover, tree species mixture effects on Collembola abundance and richness increased with stand development from neutral to positive. In 41-year-old stands, the abundance and richness differed among stand types with higher values in conifer and mixed stands than broadleaf stands. Moreover, Collembola community compositions differed with stand types and stand ages.

To sum up, I summarized inconsistent evidence of previous plant species diversity studies on soil fauna, then experimentally investigated the responses of Collembola to tree mixtures of different ages and varied water availability in boreal forests. This dissertation highlights the importance of plant diversity in conserving this part of the soil faunal community in the context of climate change. It provides suggestions on sustainable forest management and conservation strategies in terms of the soil faunal community. Broadleaf, conifer, and mixed stands of both young and mid-age are necessary to conserve varied fauna communities. In particular, tree mixtures with high species richness are necessary to maintain abundant, diverse, and stable Collembola communities in boreal forests. Additional research is needed on the effects of plant mixtures on soil fauna, particularly in forest ecosystems. Hence, future forest studies should incorporate higher tree species richness, long experimental duration, and high identification resolution of fauna communities to reveal specific underlying mechanisms. Functional indices of faunal communities are also suggested to understand the mixture effects on associated ecosystem functions.

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APPENDIX: SUPPLEMENTAL INFORMATION FOR CHAPTER 2

Table S2-1 The source for original studies that have examined plant diversity effects on the abundance and diversity of soil fauna in this meta-analysis.

NO.	Publication
1.	Cesarz, S., Ruess, L., Jacob, M., Jacob, A., Schaefer, M., Scheu, S., 2013. Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes. Soil Biology and Biochemistry 62, 36-45.
2.	Chapman, K., Whittaker, J.B., Heal, O.W., 1988. Metabolic and faunal activity in litters of tree mixtures compared with pure stands. Agriculture, Ecosystems & Environment 24, 33-40.
3.	De Deyn, G.B., Raaijmakers, C.E., van Ruijven, J., Berendse, F., van der Putten, W.H., 2004. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. Oikos 106, 576-586.
4.	de la Fuente, E.B., Suárez, S.A., Lenardis, A.E., Poggio, S.L., 2014. Intercropping sunflower and soybean in intensive farming systems: Evaluating yield advantage and effect on weed and insect assemblages. NJAS - Wageningen Journal of Life Sciences 70-71, 47-52.
5.	Díaz-Aguilar, I., Quideau, S.A., Proctor, H.C., Kishchuk, B.E., Spence, J.R., 2013. Influence of stand composition on predatory mite (Mesostigmata) assemblages from the forest floor in western Canadian boreal mixedwood forests. Forest Ecology and Management 309, 105-114.
6.	Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S.E., Meyer, R.J., Worm, K., Reich, P.B., 2013. Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. Proceedings of the National Academy of Sciences of the United States of America 110, 6889-6894.
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richness, tree functional type, and microenvironment for soil macrofauna communities in European forests. Oecologia 196(2), 455-468.

11. Huixin, L., Manqiang, L., Feng, H., Xiaoyun, C., Yuanqiu, H., 2002. Nematode abundance under different vegetations restored on degraded red soil. Acta Ecologica Sinica 22, 1882-1889.
12. Kostenko, O., Duyts, H., Grootemaat, S., De Deyn, G.B., Bezemer, T.M., 2015. Plant diversity and identity effects on predatory nematodes and their prey. Ecology and Evolution 5, 836-847.
13. Laossi, K.-R., Barot, S., Carvalho, D., Desjardins, T., Lavelle, P., Martins, M., Mitja, D., Carolina Rendeiro, A., Rousseau, G., Sarrazin, M., Velasquez, E., Grimaldi, M., 2008. Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures. Pedobiologia 51, 397-407.
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Table S2-2 Values of Akaike information criterion of species richness in mixtures (R), stand age (A), and soil depth (S) for fauna abundance and diversity (see Methods).

Attribute	R			A			S		
	X	Log(X)	$X+X^2$	X	Log(X)	$X+X^2$	X	Log(X)	$X+X^2$
Fauna abundance	**1153.3**	1153.4	1157.9	**1148.0**	1151.7	1147.1	1152.8	**1150.9**	1153.9
Fauna diversity	66.0	**65.4**	69.6	**67.1**	65.6	69.7	**66.5**	67.5	69.7

Note: Numbers in bold were selected into the full models. $\Delta\mathrm{AIC} \leq 2$ was considered equivalent.

Table S2-3 Values of Akaike information criterion for alternative models.

Alternative models	AIC	Weight
Fauna abundance		
$lnRR = \beta_0 + \beta_1 \cdot R + \beta_2 \cdot A + \beta_3 \cdot R \times A + \pi_{study} + \pi_{datatype} + \varepsilon$	1151.4	0.598
$lnRR = \beta_0 + \beta_1 \cdot R + \beta_2 \cdot A + \pi_{study} + \pi_{datatype} + \varepsilon$	1153.6	0.197
$lnRR = \beta_0 + \beta_1 \cdot R + \beta_2 \cdot A + \beta_3 \cdot \ln(S) + \beta_4 \cdot R \times A + \pi_{study} + \pi_{datatype} + \varepsilon$	1154.7	0.115
Fauna diversity		
$lnRR = \beta_0 + \beta_1 \cdot \ln(R) + \beta_2 \cdot A + \pi_{study} + \pi_{datatype} + \varepsilon$	72.2	0.528
$lnRR = \beta_0 + \beta_1 \cdot \ln(R) + \beta_2 \cdot A + \beta_3 \cdot \ln(R) \times A + \pi_{study} + \pi_{datatype} + \varepsilon$	73.9	0.219
$lnRR = \beta_0 + \beta_1 \cdot \ln(R) + \beta_2 \cdot A + \beta_3 \cdot \mathrm{E} + \pi_{study} + \pi_{datatype} + \varepsilon$	74.3	0.182

Note: Abbreviations for terms are the same as in Table S2-2.

Table S2-4 Akaike information criterion (AIC) values of the full model (equation 3 in the Methods) and the most parsimonious models for soil fauna abundance and diversity of different fauna groups (G). All terms associated with ecosystem type and soil depth were excluded.

Attributes	Groups	Full model	The most parsimonious model	
		AIC	AIC	Terms
Fauna abundance	Taxonomic	1020.3	1016.2	R + A + G + R × A
	Body size	1054.7	1050.3	R + A + G + R × A
	Trophic	853.6	847.8	R + A + G + R × A
Fauna diversity	Taxonomic	-12.0	-19.6	ln(R) + A + G
	Body size	79.3	73.4	ln(R) + A + G + ln(R) × A
	Trophic	62.8	56.4	ln(R) +A+ G + ln(R) × A

Note: Abbreviations for terms are the same as in Table S2-2.

Table S2-5 Effects (*P* values) of plant species richness (R) and stand age (A) on natural log response ratios (lnRRs) of soil fauna abundance and diversity across all studies (1) and in the dataset excluding studies that did not report species ratios of constituent plants in mixtures (2).

Attributes		Fauna abundance		Fauna diversity	
		1	2	1	2
Intercept	Estimate	0.052	0.042	0.099	0.124
	t value	0.508	0.446	2.218	2.398
	P	0.674	0.729	**0.040**	**0.034**
R	Estimate	0.292	0.146	0.057	0.057
	t value	2.650	2.390	1.797	1.646
	P	**0.009**	**0.018**	0.076	0.104
A	Estimate	0.189	0.233	-0.036	-0.045
	t value	1.434	1.874	-0.852	-0.779
	P	0.153	0.063	0.397	0.438
R × A	Estimate	0.605	0.400		
	t value	2.366	1.947		
	P	**0.019**	0.053		

Table S2-6 The effects of plant mixtures, species richness in mixtures (R), and stand age (A) on the abundance and diversity of soil fauna across 20 studies that reported both fauna abundance and diversity. Coefficient estimates did not differ from those reported in Table 2-1 with at $\boldsymbol{\alpha} = 0.05$.

Source	Coefficient	Std. error	df	T	P
Fauna abundance					
(Intercept)	0.131	0.212	1	0.617	0.619
R	0.133	0.159	79	0.840	**0**.404
A	0.225	0.323	78	0.697	0.488
R × A	0.266	0.457	78	0.581	0.563
Fauna diversity					
(Intercept)	0.104	0.051	13	2.018	0.065
R	0.059	0.035	80	1.696	0.094
A	-0.040	0.047	58	-0.860	0.393

Figure S2-1 Effects of plant mixtures on soil fauna abundance in relation to plant species richness and by stand age levels. Colored lines represent stand age-specific responses, respectively, with 95% confidence intervals shaded in colors.