



Effects of mixed tree species on springtails (Collembola) increase under reduced water availability

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Abstract Soil fauna are crucial for nutrient cycling and promoting plant growth. Plant species mixtures can enhance soil biodiversity and ecosystem functions, but their effects on soil fauna under changing water availability remain poorly understood. To address this gap, we combined a field experiment with a meta-analysis to examine how plant species mixtures influence springtail communities under varying water availability. In a field experiment in Ontario, Canada, we assessed springtail abundance, species richness, Simpson's diversity index, and community composition in pure and mixed stands of trembling aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*)

under ambient, reduced (− 25%), and increased (+ 25%) throughfall in young boreal forest. Tree mixtures enhanced springtail abundance and increased Simpson's diversity index from − 8.3% under ambient water to + 12.3% under reduced water. Springtail community compositions varied significantly among stand types, with shifts in community composition strongly correlated with fine-root biomass and soil water content. A meta-analysis revealed the effects of plant mixtures on springtail abundance were more positive in sites with less precipitation. On the basis of these results, converting plant mixtures to monocultures will significantly decrease springtail abundance and diversity in areas with less water.

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Introduction

Soil fauna are essential for terrestrial ecosystem functioning, contributing to key ecological processes including litter decomposition, plant growth, and nutrient dynamics (Barrios 2007; Bardgett and van der Putten 2014; Soong et al. 2016). Among the most-abundant organisms, springtails

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(Collembola, Hexapoda: Entognatha) are integral to soil food webs and nutrient dynamics, and their high sensitivity to environmental disturbances makes them valuable bio-indicators of soil health (George et al. 2017; Gruss et al. 2022; Joimel et al. 2022). Climate change is altering precipitation regimes and plant community composition, with cascading effects on soil biodiversity and ecosystem functions (Blankinship et al. 2011; Nielsen 2019; Ganault et al. 2021; Zhang et al. 2022b). However, how water availability and plant mixtures interact to influence springtail communities remains unexplored.

Recent quantitative syntheses demonstrated that increased precipitation generally enhances springtail abundance (Blankinship et al. 2011; Goncharov et al. 2023), whereas drought conditions tend to reduce it (Peng et al. 2022). Reduced precipitation can limit microbial activity, constrain microhabitat suitability, and restrict the diversity and quantity of detrital resources, thereby diminishing habitat quality and ultimately leading to declines in springtail abundance and richness (Maestre et al. 2015; Qu et al. 2023; Zhu et al. 2024). Additionally, altered precipitation can shift their community structure (Lindberg et al. 2002; Xu et al. 2012; A'Bear et al. 2013; Turnbull and Lindo 2015), driven by interspecific variation in tolerance and adaptive strategies to water stress (Escribano-Álvarez et al. 2021; Wang et al. 2022) and by changes in food resources. For instance, shifts in the ratio of fungal to bacterial biomass, driven by changes in soil moisture during drought, may affect the availability of food sources for springtails because many springtail species preferentially feed on fungi, while others utilize bacteria or detritus, potentially altering community composition (Zhou et al. 2020; Canarini et al. 2024).

Plant mixtures may shape springtail communities by enhancing resource availability and habitat complexity. Higher plant diversity in mixtures can increase inputs of litterfall, root production, microbial activity (Zheng et al. 2019; Podzikowski et al. 2023; Liu et al. 2024), and microhabitat heterogeneity (Pretzsch et al. 2016; Ullah et al. 2024). These factors collectively support higher density and diversity of soil fauna compared to monocultures (Madej et al. 2011; Li et al. 2021; Ma et al. 2023). For springtails, however, there are relatively few empirical studies on the impacts of plant mixtures (tree or litter), and studies have yielded inconsistent results (Zhang et al. 2022a). For example, in Brazil and Germany, springtail abundance or diversity did not differ significantly between pure and mixed stands (Salamon and Alpei 2009; Zagatto et al. 2019), whereas springtail abundance and richness were intermediate in mixed coniferous and deciduous forests compared to pure forests in France (Korboulewsky et al. 2021). In contrast, in a litterbag experiment in Japan, springtail abundance in litter mixtures (oak-sasa-pine mixture) was higher than in single-species litters after 1 year of decomposition (Kaneko and Salamanca

1999). These differing responses may, in part, be influenced by differences in water availability, which can mediate the effects of plant mixtures on springtail communities.

The effect of plant mixtures on soil springtails might change with altered water availability. The stress gradient hypothesis posits that in stressful environments, facilitation among plant species becomes more dominant than competition, suggesting that the effects of plant mixtures on food resources and their support for springtails could intensify under water stress (Maestre et al. 2009). Furthermore, compared to monocultures, the greater structural complexity and broader ecological niche provided by plant mixtures could harbor more water-tolerant springtail species (Yachi and Loreau 1999; Marx et al. 2012), therefore enhancing community resistance and maintaining better performance under conditions of reduced precipitation. In addition, plant diversity can amplify the benefits of water addition on plant productivity, as diverse communities are more capable of exploiting additional resources (Wright et al. 2015; Chen et al. 2021b), consequently increasing soil springtail abundance and diversity. Accordingly, we hypothesize that responses of springtails to tree species mixtures will mirror those previously observed for soil microbial communities (Chen et al. 2019), with stronger positive effects of mixtures emerging under conditions of reduced water availability.

Here, in a field experiment, we manipulated water availability to evaluate the influence of tree species mixtures (mixed *Pinus banksiana* Lamb. and *Populus tremuloides* Michx.) on springtail communities in the Canadian boreal forest. Moreover, to evaluate whether the responses of springtails to plant mixtures are consistent across larger scales and influenced by water availability, we performed a meta-analysis of empirical studies that examined the variation in plant mixture effects on springtail abundance and richness. We hypothesized that (1) plant species mixture promotes greater springtail abundance and species richness at both local and large scales due to enhanced litterfall and root inputs and increased soil microbial biomass; (2) the positive effects of plant mixtures on springtails are amplified under reduced water availability. Additionally, we expected springtail abundance and diversity to vary among stand types and across water availability treatments.

Materials and methods

Study site and experimental design

The field experiment was established in a 15-year-old, naturally regenerated boreal forest in northwestern Ontario, Canada (49.55° N, 90.12° W). The site lies within the Lake Nipigon Ecoregion (Ecoregion 3W) and is characterized by a mean annual temperature of 2.5 °C and an average annual

precipitation of 712 mm from 1970 to 2000 (Crins et al. 2009; Fick and Hijmans 2017). The soil on the upland sites is characterized by relatively deep glacial till soils, classified as Brunisolic. The study encompassed nine forest stands representing three overstorey types: pure conifer stands (*P. banksiana*), pure broadleaf stands (*P. remuloides*), and mixed stands with both species. Three replicates of each overstorey type were used, with stands exceeding 1 ha in area and separated by at least 1 km to limit spatial dependence among sites (Table 1) (Chen et al. 2019).

In 2016, water availability were manipulated within each forest stand using a split-plot design. Three 6 m × 6 m plots per stand were assigned to one of three treatments: ambient precipitation (control), a 25% reduction in throughfall, or a 25% increase in throughfall during the growing season (May–October). The 25% reduction approximates the median expected change in precipitation regimes for boreal forests under 21st-century climate scenarios (IPCC 2015). For the throughfall reduction treatment, four rain-exclusion structures (each 3 m × 3 m) were installed under the canopy in each plot. Each structure consisted of a metal frame supporting transparent acrylic troughs mounted at a 10° slope to facilitate water drainage. The shelters were elevated, with the higher end and the lower end positioned at 1.8 m and 1.35 m above the floor, allowing rainfall to be intercepted efficiently. Collected water was redirected to the corresponding water addition plots using two polyvinyl chloride (PVC) pipes (8 cm inner diameter), suspended approximately 5 cm above the floor surface to minimize surface disturbance of water washing. Each pipe was perforated with six openings of varying diameters (0.64–6.99 cm), spaced at 46 cm intervals, enabling even redistribution of water across the plot. For avoiding hydrological interference among treatments, a minimum buffer distance of 5 m was maintained between adjacent plots (Fig. S1) (Chen et al. 2019).

Sampling, extraction, and identification

Springtails were sampled in September 2020, 4 years after the manipulation experiment of water availability was initiated in 2016. Five litter subsamples were collected per plot

using a 10 cm × 10 cm quadrat and combined as a composite sample for the plot (Bruckner et al. 2000). Subsamples were collected > 1 m from each other. In total, 27 composite samples were collected, representing all combinations of water treatments and stand types. Samples were transported to the laboratory in paper bags.

Springtails were extracted from litter samples using Tullgren funnels over a 10-d period, with some preserved in 70% ethanol (Macfadyen 1961), as described for moisture-related studies (Nielsen et al. 2010). To minimize potential stress on moisture-sensitive species, we maintained a moderate temperature (40 °C) with good ventilation to allow gradual drying and promote behavioral movement rather than forced escape from desiccation (Bruckner 2024). Although we recognize that prolonged extraction may still affect some moisture-sensitive taxa, all samples were subjected to identical conditions to ensure comparability across treatments. Springtails were separated from other invertebrates, then were further morphotyped, counted, and identified using a compound microscope. Specimens were identified to species level when possible, or otherwise grouped into morphospecies using the most current taxonomic literature (Hopkin 1997; Fjellberg 2010; Turnbull and Stebaeva 2019). A comprehensive list of species is presented in Table 1.

In August 2018, stand structural characteristics were investigated by recording the species identity and measuring stem diameter (1.3 m height) for all trees and shrubs within each plot, and five mineral soil cores at a depth of 10 cm were randomly sampled. Freeze-dried soil samples (3.0 g) were used to analyze microbial phospholipid fatty acids (Frostegård and Bååth 1996; Quideau et al. 2016). The ratio of fungal to bacterial biomass (FB) was computed as the proportion of saprotrophic fungal PLFAs relative to the total bacterial PLFAs (Chen et al. 2019). From July 2017 to August 2018, litterfall was collected monthly using four litter traps randomly positioned within each plot to capture organic litter (Chen et al. 2017). Litterfall production was calculated as the dry mass of litter for a calendar year (Mg ha⁻¹ a⁻¹). Fine roots (diameter less than 2 mm) were sampled at 15 cm depth using a soil corer (6.6 cm diameter) in August 2019. Root samples were dried in an oven at 65 °C

Table 1 Stand characteristics (mean ± 1 SE, N=3) of pure and mixed stands of trembling aspen (*Populus*) and jack pine (*P. banksiana*) in northwestern Ontario, Canada (Chen et al. 2019)

Overstorey type	Stand basal area (m ² ha ⁻¹)	Tree species richness	Stand density (ind. ha ⁻¹)	Stand composition by basal area (%)			
				Jack pine	Trembling aspen	White birch	Other tree species
Mixed	1.39 (0.24)	4.33 (0.33)	9200 (1301)	48 (7)	28 (3)	15 (4)	4 (1)
Conifer	0.93 (0.33)	2.67 (0.33)	11,600 (4148)	98 (1)	1 (1)	1 (1)	1 (0)
Broadleaf	1.55 (0.35)	2.67 (0.33)	5933 (1790)	3 (2)	92 (2)	3 (2)	2 (1)

to a constant mass (g), then biomass was standardized to area (g m^{-2}) based on the cross-sectional area of soil corer. The volumetric soil water content was determined at the time of sampling using Decagon sensors (GS1, Decagon Devices Inc., Pullman, WA, USA) inserted 5 cm below the soil surface.

Statistical analyses

For springtail attributes, abundance was quantified as the number of individuals per square meter and richness as the total number of species per morphospecies per plot. Simpson's diversity index was calculated as $1-D$, where D is the probability that two randomly selected individuals belong to the same species; higher index values indicate greater diversity. Community composition was described as the abundance of each species or morphospecies recorded in each plot.

Linear mixed-effects models were applied with water treatment and stand type as fixed effects and plot ID as a random effect, to assess their influence on springtail attributes (abundance, richness, and Simpson's diversity index) and environmental variables including fine root biomass, litter production, ratio of fungal to bacterial biomass, and soil water content. The model was fitted using restricted maximum likelihood estimation (REML) implemented using lme4 package (Bates et al. 2014) in R version 4.5.0 (R Core Team 2025). Normality of residuals was examined for all response variables and environmental covariates using Shapiro–Wilk's test. Among these, only springtail abundance deviated significantly from normality and was thus log-transformed before analysis to meet model assumptions.

To evaluate the strength of tree diversity effects on springtail attributes, we calculated the response ratio (RR) as the observed value in mixtures divided by the expected value derived from monoculture performance. To account for species identity effects, we calculated the expected values as the weighted average of values corresponding to monocultures of the species present in the mixture, with weights based on their relative basal area within the mixture (Loreau and Hector 2001). To improve interpretability, we used the natural log-transformed response ratio (lnRR).

To assess whether the lnRR of the springtail attributes to tree species mixtures varied across water treatments, we applied a linear model incorporating water treatment (W) as a fixed effect. The effect of tree species mixtures was considered statistically significant at $\alpha=0.05$ when the 95% confidence intervals (CIs) for the estimated RR did not include zero. Pairwise differences between treatment groups were considered significant when their 95% CIs did not overlap with the mean value of the comparison group. A one-way (ANOVA) was used to test whether abundance, richness, and Simpson's diversity index for the springtails varied in

relation to fine root biomass, litterfall production, the fungal to bacterial biomass ratio, and soil water content.

To assess whether springtail community composition varied among stand types and water availability treatments, we used a permutational multivariate ANOVA (PERMANOVA) in the R package vegan (Anderson 2001). A Bray–Curtis dissimilarity matrix was applied to quantify species composition, and significance was determined based on 999 permutations. Community clusters were illustrated through non-metric multidimensional scaling (NMDS) with Bray–Curtis distances.

Meta-analysis

In a meta-analysis to summarize all available published evidence of the effects of plant species mixtures on springtail abundance and richness up to July 2024, data were collected and extracted using the criteria and search terms described by (Zhang et al. 2022a): (1) The effects of plant diversity on springtail abundance and richness could be isolated from other factors; (2) data for springtail abundance and richness could be retrieved directly from texts, tables, or figures using freely available Plot Digitizer version 2.0 (<https://plotdigitizer.com>). Overall, we collected 55 observations from 12 studies (Table S1), including 35 observations on springtail abundance from nine publications, and 20 observations on springtail richness from seven publications. Effect sizes of plant mixtures (lnRR) were calculated as the observed value in mixtures divided by the expected value derived from monoculture performance, and weighted by replication numbers.

It was then determined whether the plant mixture effect changes with mean annual precipitation (MAP) using a linear mixed-effect model with plant richness (R) and MAP as fixed factors and studies as the random factor:

$$Y = \beta_0 + \beta_1 R_i + \beta_2 MAP_{(j(k))} + \pi_k + \varepsilon_{(k(ij))}, \quad (1)$$

where the β terms are coefficients, π_k denotes the random effect with plot identity, and $\varepsilon_{(k(ij))}$ is the residual error. To ensure comparability across predictors and improve model interpretability, we standardized all continuous predictors by subtracting the mean and dividing by one standard deviation. Under this standardization, β_0 is the overall mean lnRR at the mean plant richness (R) and MAP (Chen et al. 2021a). Normality of residuals was examined using Shapiro–Wilk's test. To achieve the normality assumption, data for springtail richness were logarithmically transformed before analysis.

Results

Among the 924 individuals representing 21 distinct species or morphospecies that were identified (Table 2),

Table 2 Mean springtail abundance (individuals per plot; mean $\pm$ SD; N = 3) in each water manipulation treatment

Species	Broadleaf			Conifer			Mixed stand		
	Addition	Ambient	Reduced	Addition	Ambient	Reduced	Addition	Ambient	Reduced
<i>Entomobrya</i> sp.1	20.0 (3.0)	18.3 (4.5)	8.3 (6.0)	26.8 (13.8)	36.8 (23.3)	18.3 (4.5)	21.8 (14.3)	53.3 (24.0)	20.0 (20.0)
<i>Entomobrya</i> sp.2	3.3 (1.8)	11.8 (9.3)	0.0 (0.0)	6.8 (6.8)	30.0 (18.0)	15.0 (5.0)	11.8 (9.3)	8.3 (3.3)	6.8 (1.8)
<i>Entomobrya</i> sp.3	28.3 (9.3)	20.0 (3.0)	43.3 (10.3)	31.8 (20.5)	50.0 (20.3)	20.0 (13.3)	91.8 (11.8)	66.8 (51.8)	93.3 (58.0)
<i>Entomobrya</i> sp.4	3.3 (1.8)	11.8 (6.0)	0.0 (0.0)	0.0 (0.0)	5.0 (3.0)	1.8 (1.8)	5.0 (5.0)	0.0 (0.0)	0.0 (0.0)
<i>Entomobrya</i> sp.5	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	5.0 (3.0)	0.0 (0.0)	0.0 (0.0)	38.3 (16.0)	13.3 (3.3)	13.3 (6.8)
<i>Vertagopus</i> nr. <i>asiaticus</i>	1.8 (1.8)	0.0 (0.0)	0.0 (0.0)	3.3 (3.3)	5.0 (5.0)	1.8 (1.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Appendisotoma</i> nr. <i>abiskoensis</i>	6.8 (4.5)	0.0 (0.0)	0.0 (0.0)	5.0 (3.0)	20.0 (17.5)	15.0 (5.0)	6.8 (3.3)	20.0 (11.5)	23.3 (16.5)
<i>Folsomia</i> sp.1 (nr. <i>candida</i>)	3.3 (3.3)	1.8 (1.8)	3.3 (3.3)	23.3 (13.8)	13.3 (13.3)	20.0 (7.8)	15.0 (12.5)	15.0 (5.8)	33.3 (25.8)
<i>Folsomia</i> sp.2	3.3 (1.8)	3.3 (1.8)	3.3 (1.8)	11.8 (6.8)	1.8 (1.8)	13.3 (1.8)	6.8 (3.3)	0.0 (0.0)	8.3 (8.3)
<i>Isotoma</i> sp.1 (nr. <i>riparia</i>)	5.0 (3.0)	5.0 (3.0)	3.3 (1.8)	0.0 (0.0)	8.3 (4.5)	6.8 (4.5)	3.3 (3.3)	6.8 (4.5)	5.0 (5.0)
<i>Isotoma</i> sp.2 (nr. <i>viridis</i>)	1.8 (1.8)	3.3 (3.3)	0.0 (0.0)	3.3 (3.3)	13.3 (8.8)	10.0 (7.8)	0.0 (0.0)	5.0 (5.0)	16.8 (16.8)
<i>Isotoma</i> sp.3	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	5.0 (5.0)	15.0 (15.0)	3.3 (3.3)	25.0 (20.3)	11.8 (6.0)
<i>Lepidocyrtus</i> sp.1 (nr. <i>ruber</i>)	3.3 (3.3)	1.8 (1.8)	0.0 (0.0)	1.8 (1.8)	5.0 (3.0)	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	1.8 (1.8)
<i>Lepidocyrtus</i> sp.2 (nr. <i>cyaneus</i>)	1.8 (1.8)	0.0 (0.0)	3.3 (3.3)	0.0 (0.0)	1.8 (1.8)	5.0 (3.0)	0.0 (0.0)	8.3 (4.5)	6.8 (3.3)
<i>Tomocerus</i> nr. <i>minor</i>	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	1.8 (1.8)	3.3 (3.3)	3.3 (1.8)	1.8 (1.8)	1.8 (1.8)	3.3 (1.8)
<i>Arrhopalites</i> sp.	0.0 (0.0)	0.0 (0.0)	3.3 (3.3)	1.8 (1.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	0.0 (0.0)
<i>Sminthurinus</i> sp.1	0.0 (0.0)	3.3 (1.8)	0.0 (0.0)	5.0 (5.0)	8.3 (6.0)	15.0 (3.0)	6.8 (1.8)	5.0 (3.0)	5.0 (3.0)
<i>Sminthurinus</i> sp.2 (nr. <i>aureus</i>)	5.0 (5.0)	1.8 (1.8)	0.0 (0.0)	3.3 (3.3)	10.0 (5.0)	8.3 (1.8)	3.3 (1.8)	6.8 (3.3)	1.8 (1.8)
<i>Sminthurides</i> nr. <i>occultus</i>	3.3 (3.3)	3.3 (3.3)	3.3 (3.3)	0.0 (0.0)	1.8 (1.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
<i>Sphaeridia</i> nr. <i>pumilis</i>	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	8.3 (8.3)	6.8 (6.8)	6.8 (6.8)
<i>Onychiuridae</i> sp.	1.8 (1.8)	1.8 (1.8)	3.3 (1.8)	1.8 (1.8)	1.8 (1.8)	0.0 (0.0)	6.8 (4.5)	0.0 (0.0)	6.8 (4.5)

Entomobrya sp.1, *Entomobrya* sp.3, and *Folsomia* nr. *candida* were present across all experimental treatments. In contrast, other species were absent in a specific treatment: *Isotoma* nr. *riparia* was absent in *Pinus* monocultures under ambient precipitation; *Entomobrya* sp.2 and *Sminthurinus* nr. *aureus* were not detected in *Populus* monocultures with increased precipitation; and *Folsomia* sp.2 was not found in the *Pinus* + *Populus* mixture with reduced precipitation. Notably, *Sphaeridia* nr. *pumilis* was unique to the *Pinus* + *Populus* mixture.

Springtail abundance significantly varied among stand types ($P = 0.029$) but was unaffected by differences in water availability ($P = 0.989$, Fig. 1A, Table 3). Abundance was significantly higher in mixed stands (993 ind. m⁻², $P = 0.032$) and marginally higher in conifer stands (695 ind. m⁻², $P = 0.070$) compared to broadleaf stands (364 ind. m⁻²). Overall, richness did not vary with stand type ($P = 0.301$) or water treatment ($P = 0.566$) (Fig. 1B, Table 3). Simpson's diversity index ranged from 0.73 to 0.92 and was not affected by stand type ($P = 0.656$); however, a significant interaction between stand type and water treatment was detected ($P = 0.002$). In conifer stands, water addition led to a 21.0% increase in Simpson's diversity index ($P = 0.007$). However, a reduction in water decreased the diversity index by 18.5% in broadleaf stands ($P = 0.100$), but increased it by 20.4% in mixed stands ($P = 0.011$) (Fig. 1C, Table 3).

Hypotheses 1 and 2 were partially supported. With ambient water, the tree mixture did not significantly affect the abundance, richness, or Simpson's diversity index of springtails (Fig. 2). However, the tree mixture effects on Simpson's diversity index differed significantly across water treatments ($P = 0.012$), whereas no significant differences were observed for abundance ($P = 0.179$) or richness ($P = 0.089$) (Fig. 2, Table S2). Specifically, mixture effects on Simpson's diversity index significantly decreased with increasing water availability, although the tree mixture effects remained non-significant under both water reduction and water addition treatments. Under reduced water availability, the effect of tree mixtures on Simpson's diversity index was significantly enhanced, shifting from negative values under ambient (−8.3%) and water addition (−13.5%) treatments to a positive effect of 12.3% ($P = 0.029$ and 0.012, respectively, Fig. 2). In addition, although the effect of the water treatment was not significant, the influence of tree mixtures on springtail abundance varied with water treatments: marginally positive for ambient conditions, significantly positive for water addition, and negligible for water reduction.

The meta-analysis of previous studies showed that the species combinations did not significantly affect springtail abundance (9%, 95% CI = −5 to 23%, $P = 0.251$) or richness (11%, 95% CI = −1 to 4%, $P = 0.156$) (Fig. 3). The effect size of species mixtures on springtail abundance was

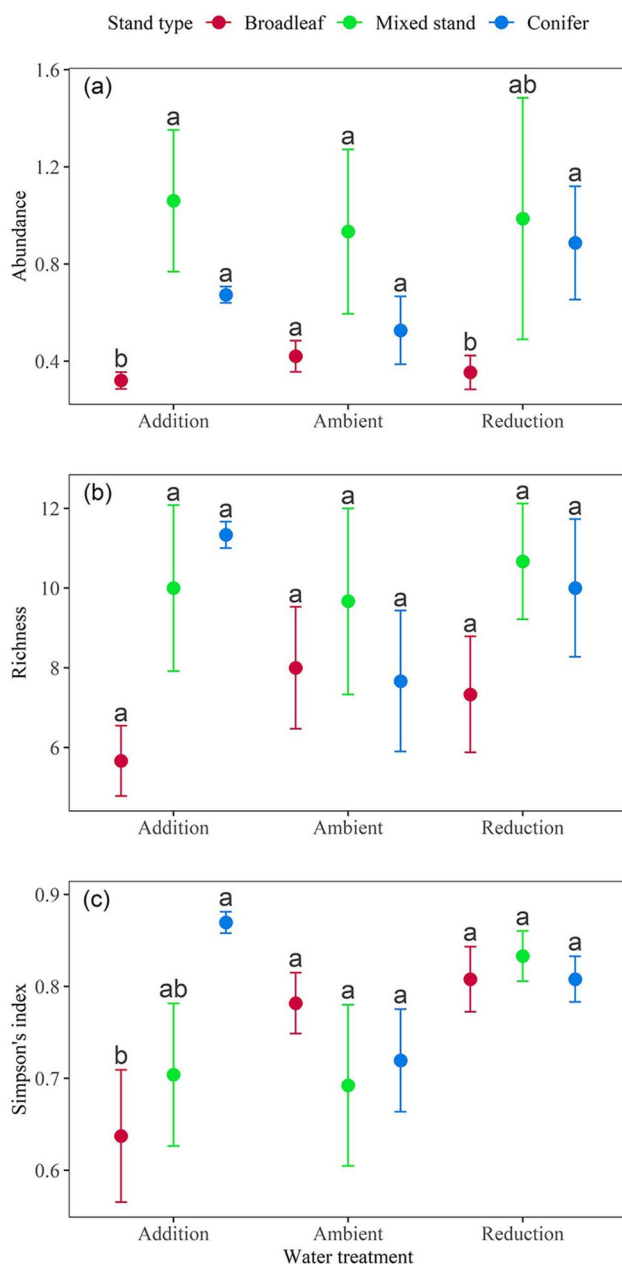


Fig. 1 Means ($\pm$ SD) for springtail attributes across stand types (broadleaf, mixed stand, conifer) and water treatments (25% addition, ambient, and 25% reduction). Significant differences among stand types within each water treatment are indicated by different letters (Tukey's HSD, $\alpha=0.05$)

significantly negatively correlated with MAP ($P=0.005$), but the effect size on springtail richness did not (Fig. 3, Table S3, $P=0.127$). Overall, species mixtures increased springtail abundance when water availability was low, but decreased it when water availability was high.

Soil springtail abundance and richness were positively correlated to litter production ($P=0.009$, $R^2=0.191$; $P=0.005$, $R^2=0.273$). While the Simpson's diversity index

Table 3 Statistical summary of the response of springtail attributes to water treatment and stand type

Source	df	P
Abundance ($R^2_{\text{marginal}}=0.511$, $R^2_{\text{conditional}}=0.686$)		
Water	2,12	0.989
Stand type	2,6	0.029
Water $\times$ Stand type	4,12	0.236
Richness ($R^2_{\text{marginal}}=0.288$, $R^2_{\text{conditional}}=0.722$)		
Water	2,12	0.566
Stand type	2,6	0.301
Water $\times$ Stand type	4,12	0.125
Simpson's diversity index ($R^2_{\text{marginal}}=0.385$, $R^2_{\text{conditional}}=0.827$)		
Water	2,12	0.005
Stand type	2,6	0.656
Water $\times$ Stand type	4,12	0.002
Community composition		
Water	2	0.185
Stand type	2	0.007
Water $\times$ Stand type	4	0.026

Marginal and conditional R^2 values are provided for mixed-effects models where applicable. $P<0.05$ is highlighted in bold

was negatively associated with fine root biomass ($P=0.047$, $R^2=0.149$). Springtail attributes were not associated with soil water content or the ratio of fungal to bacterial biomass (Fig. S2). PERMANOVA results indicated that the community composition of springtails varied significantly among stand types, but not among water treatments ($P=0.007$ and 0.185 , respectively). However, a significant interaction was observed, with the influence of stand type on community composition modulated by water availability ($P=0.026$) (Table 3, Fig. 4). Specifically, the Bray–Curtis dissimilarity index (BC) between springtail communities in conifer and mixed stands was 0.324, indicating moderate compositional differences. In contrast, communities in broadleaf stands showed greater dissimilarity compared to those in mixed and conifer stands, with BC values of 0.552 and 0.395, respectively. The BC between springtail communities in the ambient and reduced water conditions was relatively low (0.260), but moderate between ambient and increased water treatments (0.470) and between reduced and increased water treatments (0.465). In broadleaf stands, the springtail community was dominated by *Entomobrya* sp.3 (35.7%) and sp.1 (18.2%). In mixed-species stands, community composition was more evenly distributed, with four species contributing notably to overall abundance: *Entomobrya* sp.3 (32.4%), *Entomobrya* sp.1 (12.2%), *Entomobrya* sp.5 (8.4%), and *Folsomia* nr. *candida* (8.2%). Variation in community composition was significantly associated with soil water content ($R^2=0.269$, $P=0.021$) and fine-root biomass ($R^2=0.214$, $P=0.047$) (Table S4).

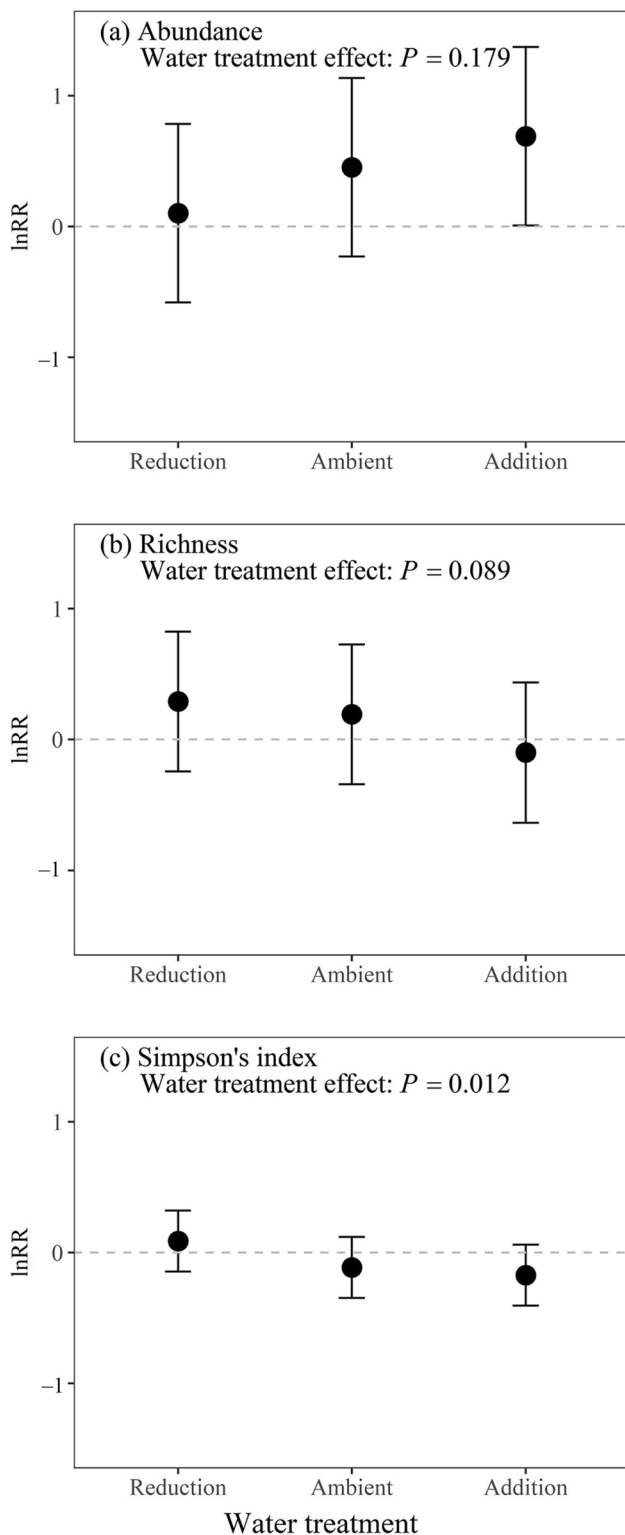


Fig. 2 Response ratio (lnRR) of springtail abundance, taxon richness, and Simpson's diversity index to the effects of tree mixtures. Estimates were presented as means $\pm$ 95% confidence intervals (CIs). Mixture effects were significant at $\alpha=0.05$ if the 95% CIs did not cover 0

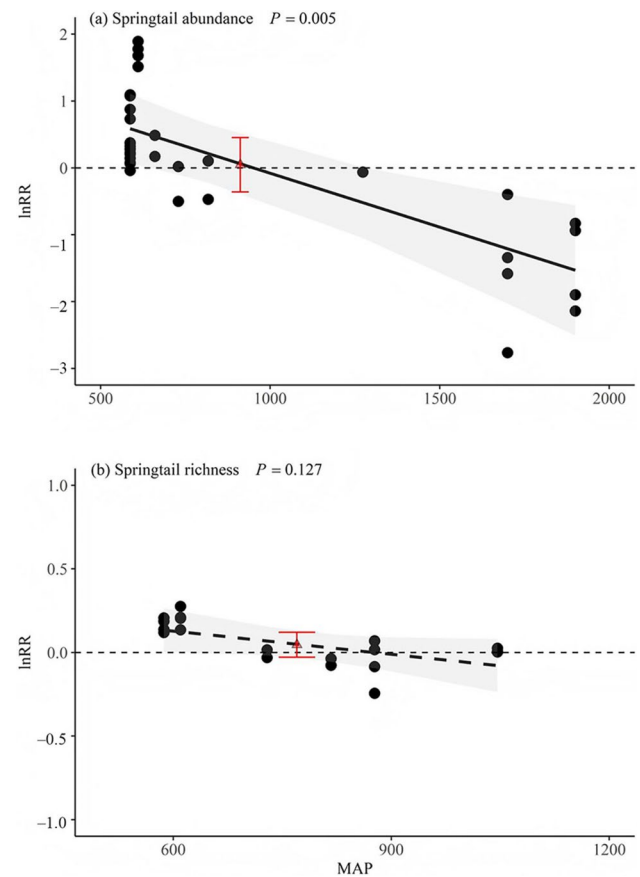


Fig. 3 Effects of plant mixtures on springtail abundance (A) and richness (B) in relation to mean annual precipitation (MAP). Red triangles: overall mean estimates; error bars: 95% confidence intervals. Mixture effects were significant at $\alpha=0.05$ if the 95% CIs did not cover 0

Discussion

We integrated a field experiment and a meta-analysis, providing the first evidence that the effects of plant mixture on Simpson's diversity index of springtails increased when water availability was reduced and that their abundance was more positively affected by plant mixtures in drier conditions across a broader gradient of water availability, suggesting a stronger link between plant species diversity and soil fauna in water-stressed environments. In addition, our findings demonstrate that tree species mixtures enhanced springtail abundance, whereas their influence on springtail richness appears negligible within natural boreal forest ecosystems. Furthermore, positive correlations between springtail abundance and richness with litter production were observed in the experiment.

As anticipated, stand type had a significant effect on springtail abundance and species richness, with higher values for mixed-species stands than broadleaf monocultures. These results align with previous findings (Korboulewsky

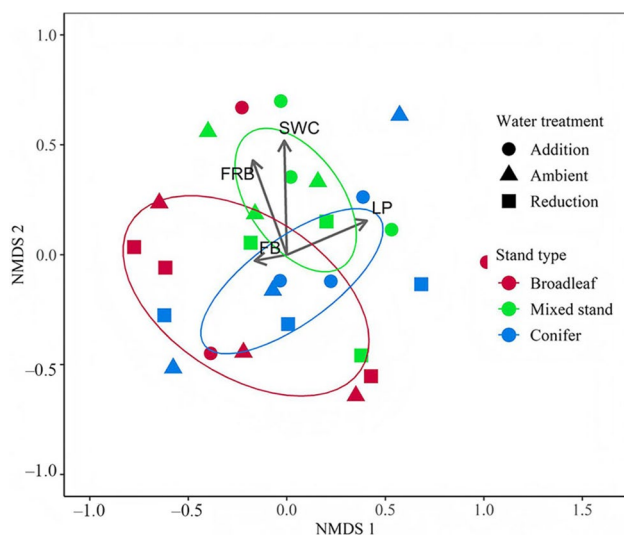


Fig. 4 NMDS ordination illustrating differences in springtail community composition across stand types and water treatments. The analysis, based on Bray–Curtis dissimilarity, yielded a final stress value of 0.23. Ellipses represent 95% CIs for the weighted centroids of each stand type. Vectors denote environmental variables including soil water content (SWC), the ratio of fungal to bacterial biomass (FB), litterfall production (LP), and annual fine-root biomass (FRB)

et al. 2016, 2021; Zhang et al. 2025) and indicate that adding coniferous litter to broadleaf stands can enhance habitat heterogeneity and resource availability for springtails (Santtonja et al. 2017; Sánchez-Galindo et al. 2021; Zhang et al. 2022a). Contrary to expectations and earlier studies (Lindberg et al. 2002; Kardol et al. 2011; Peguero et al. 2019; Wise and Lensing 2019; Goncharov et al. 2023), springtail abundance, richness or community composition had no significant response to altered water availability. The non-significant impact of altered precipitation suggests that a 25% change in water availability was insufficient to elicit measurable shifts in springtail abundance, richness or community structure, likely due to the inherent high variability of springtails in young natural boreal forests (Holmstrup et al. 2013; Bonfanti et al. 2022). The response may reflect the prevalence of drought-resilient species in boreal soils, many of which tolerate desiccation through strategies such as cryoprotective dehydration (Holmstrup 2014). These adaptations likely buffer against cold and moderate moisture changes, explaining the contrast with studies applying more severe drought or in less-buffered systems. However, Simpson's diversity index for springtails responded differently to water availability among stand types. Springtail diversity was enhanced by increased water availability in coniferous stands. While food and microhabitat are relatively abundant in the thick forest floor, water might be a limited resource for the springtail community because of the interception of precipitation by dense canopy in conifer stands. In contrast, the reduction of Simpson's diversity index with higher

water availability in broadleaf and mixed stands may reflect a combined effect of higher water and litter quality, leading to competitive exclusion where a few dominant species outcompete and suppress others in the community (Tilman 1982), thus promoting lower diversity for springtail species.

Overall, mixed stands harbored more evenly distributed communities, while broadleaf stands were dominated by a few species. Such patterns may reflect differential niche partitioning and functional redundancy in diverse plant communities, which could contribute to greater ecosystem stability under fluctuating conditions (Loreau and Hector 2001). Notably, the effect of stand type on springtail community composition was contingent upon water availability. Of the five environmental variables assessed, community variation was most strongly associated with soil moisture and fine root biomass, although the explanatory power of fine root biomass was relatively modest ($R^2 = 0.214$, $P = 0.047$). Springtail community composition was only weakly associated with microbial composition and litter production. Similar patterns have been reported for springtails and other soil mesofauna (Salamon and Alphei 2009; Wang et al. 2022).

Our regression analysis indicated that the abundance of springtails in litter was primarily associated with litterfall production (Fig. S2), which aligns with previous studies demonstrating that the diversity of species in mixed tree stands enhances plant-derived inputs to soil ecosystems (Zheng et al. 2019; Wan et al. 2023). The observed negative association between Simpson's diversity index and fine root biomass (Fig. S2) suggests that increased biomass allocation to belowground parts may be linked to reduced diversity of springtails in the litter, possibly due to diminished above-ground litter inputs. Furthermore, a lower Simpson's diversity index for mixed stands than the expected average for corresponding monocultures indicated that more resources in mixed stands may promote complex trophic interactions and increase interspecific competition (Hillebrand et al. 2008). Thus in our study, the relatively competitive *Entomobrya* species was dominant in mixed stands due to their generalist diet and high habitat flexibility.

Our first hypothesis—that plant mixtures promote higher springtail abundance and richness—was only partially supported. While tree species mixtures enhanced abundance, richness and Simpson's diversity index showed no significant change. Lack of tree mixture effects on springtail richness in our experiment indicates a mixture of only two tree species may not significantly enhance habitat heterogeneity or create sufficient additional ecological niches to support more springtail species. Alternatively, the absence of tree mixture effect on springtail species richness may be attributed to the relatively low diversity and structural complexity of the understorey in young mixed stands (Zhang et al. 2017). Similarly, non-significant responses of springtail abundance or richness

in the meta-analysis might result from the limited species richness in tree species mixtures and the relatively small number of studies included (Zhang et al. 2022a).

The second hypothesis—that tree mixture effects are amplified under reduced water availability—was partially supported. The effect size of tree mixtures on abundance or richness did not alter with water availability in our experiment. But importantly, across a broader range of water availability, the meta-analysis showed increased and positive effect sizes on abundance with reduced MAP, suggesting potential climate-modulated responses. These findings support the idea that water stress may amplify mixture benefits, possibly via interspecific facilitation. The increasing effects of tree mixtures on Simpson's diversity index (from -8.3% to $+12.3\%$) is further corroboration, indicating stronger diversity effects under stress. This finding parallels a recent study that reported enhanced microbial resistance to drought with increasing herbaceous species richness (Xi et al. 2023). The conditional effect aligns with the stress-gradient hypothesis and supports the context-dependent nature of the biodiversity-ecosystem functional relationships and emphasizes the importance of evaluating biotic interactions in multiple environmental scenarios (Maestre et al. 2009; Wright et al. 2021). At larger geoscales with substantial variation in precipitation, extremely water-limited conditions may enhance complementary rooting patterns and water-use strategies among tree species, thereby increasing soil moisture availability, food resources, and ultimately springtail abundance. However, the 25% reduction in water availability applied in this experiment was insufficient to clearly demonstrate enhanced abundance.

Our findings establish important links between above- and belowground diversity, highlighting the critical role of plant mixtures in sustaining soil biodiversity, particularly in drought-prone environments. However, we acknowledge that the relatively small number of studies included in the meta-analysis ($N=12$) may limit the generalization of our findings. Furthermore, the potential for publication bias should be considered, as studies with nonsignificant or null results are less likely to be published and thus be included in meta-analyses. In addition, limitations in taxonomic resolution may also have constrained the detection of species-specific responses of springtails. Nonetheless, our results suggest that tree-planting efforts aimed at biodiversity conservation should prioritize fostering mixed-stand forests that include both broadleaf and coniferous species to better enhance soil biodiversity and maintain ecosystem processes such as decomposition and nutrient cycling. With rising drought frequency and intensity in the future (IPCC 2023), plant-soil biodiversity interactions are likely to play a critical role in mediating ecosystem responses to climate change. Further study of the effects of species-rich tree mixtures on springtail

communities as climate changes is required to reveal consistent patterns and clarify underlying mechanisms.

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Data availability Data of this study are available from the corresponding author upon reasonable request.

Declarations

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

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