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Plant diversity increases the abundance and diversity of soil fauna: A *meta*-analysis

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ABSTRACT

Soil fauna communities are an important component of soil biodiversity, which is key to myriad terrestrial ecosystem processes. However, despite the current alarming loss of plant diversity, it remains unclear how plant diversity affects soil fauna 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 fauna communities.

1. 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 et al., 2015) and play important roles in litter decomposition through fragmentation, transformation, and feeding on microbes (Coleman et al., 2018; Kampichler and Bruckner, 2009; Soong et al., 2016). 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 (Partsch et al., 2006; Setala and Huhta, 1991; van Groenigen et al., 2014). Likewise, plants regulate soil fauna through resource inputs, root exudates, and microhabitat modifications (Hooper 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 et al., 2012), litterfall (Zheng et al., 2019), root productivity (Ma and Chen, 2016), and microbial biomass (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 (Cavard et al., 2011; Madej et al., 2011; Wardle, 2006). Thirdly, plant mixtures may alter soil water content and temperature (Bello et al., 2019; Liu et al., 2019), mediating the microclimate to be more favorable for fauna (Song 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 et al., 2016). However, original studies have reported divergent

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responses in the abundance and diversity of soil fauna to plant diversity (Korboulewsky et al., 2021; Schwarz et al., 2015). These divergent responses may have resulted not only from the differences in their responses between soil fauna groups (Kostenko et al., 2015), but also from 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 (Chen et al., 2019; Ravenek et al., 2014; Zhang et al., 2012). This is because species complementarity for resource use may increase (Barry et al., 2019), while functional redundancy decrease over time (Reich 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 et al., 2013; Wubs et al., 2019). Short-term experiments may conceal the delayed fauna responses that are driven by the accumulation of resources over time (Eisenhauer et al., 2011; Hedlund et al., 2003). 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 (Hisano et al., 2018; Paquette and Messier, 2011) and soil microorganisms (Chen et al., 2019). Diversity effects may vary with ecosystem type due to different growth rates and nutrient turnover (Schmid et al., 2009). Plant diversity effects may increase under stress since facilitation may be more common than competition among plants (Maestre et al., 2009), influencing food resources available for soil fauna (Taylor and Wolters, 2005; Wu 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 (Bello et al., 2019; Forrester et al., 2010).

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. Methods

2.1. 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 S1).

2.2. 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*, *Arancida*, 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 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 et al., 2019; Chen et al., 2021), 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. 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. Data analysis

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

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

where Xt is the observed value of soil fauna in mixtures, 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 1st and 99th percentile, as recommended (Zuur 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 (Ma and Chen, 2016; Pittelkow et al., 2015), 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:

$$lnRR = \beta_0 + \beta_1 \bullet \mathrm{R} + \beta_2 \bullet \mathrm{A} + \beta_3 \bullet \mathrm{R} \times \mathrm{A} + \beta_4 \bullet \mathrm{E} + \beta_5 \bullet \mathrm{S} + \pi_{\mathrm{study}} + \pi_{\mathrm{datatype}} + \varepsilon \tag{3}$$

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 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 et al., 2003).

Similar to previous studies (Chen and Chen, 2021; 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). 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 S3). 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.

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

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

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 Eq. (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 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 Eq. (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 S4).

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 S5). 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 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 1 and Table S6).

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, 2020).

3. 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 1, Fig. 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. 1A, Table 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. 1B, Table 1).

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. 1C, $P = 0.076$), but insignificantly with stand age (Fig. 1D, Table 1, $P = 0.397$).

On average, the mixture effects differ significantly between forests and grasslands for soil fauna abundance and diversity (Fig. 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. 3, $R^2 = 0.31$, $P < 0.001$).

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. 4). Specifically, both the abundance and diversity of *Arancida* increased in response to plant mixtures, but those of other groups did not (Fig. 4).

4. Discussion

Our *meta*-analysis provided new insights into the debate regarding

Table 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 (Eq. (3) in Methods). P values are in bold when < 0.05.

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		

Linear mixed-effects model fit tests used Satterthwaite approximations for denominator degrees of freedom (df).

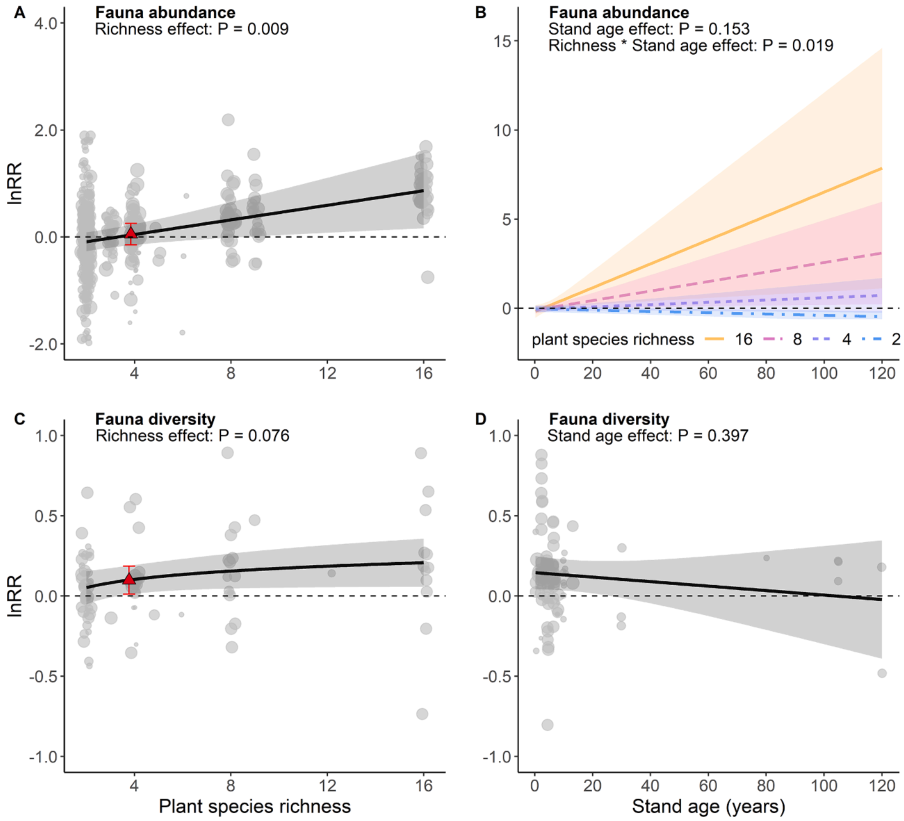

Fig. 1. Effects of plant mixtures on soil fauna abundance and diversity (A, C) in relation to plant species richness in mixtures, and (B, D) in relation to stand age and by species richness levels. Red triangles and error bars represent the overall mean and its 95% confidence intervals. Black and colored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

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 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 mixture. This finding indicates that fauna abundance and diversity responded to plant mixture similarly and suggests that increases in resource availability driven by plant mixtures could increase soil fauna diversity and fauna abundance (Storch 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 et al., 2016). Our results

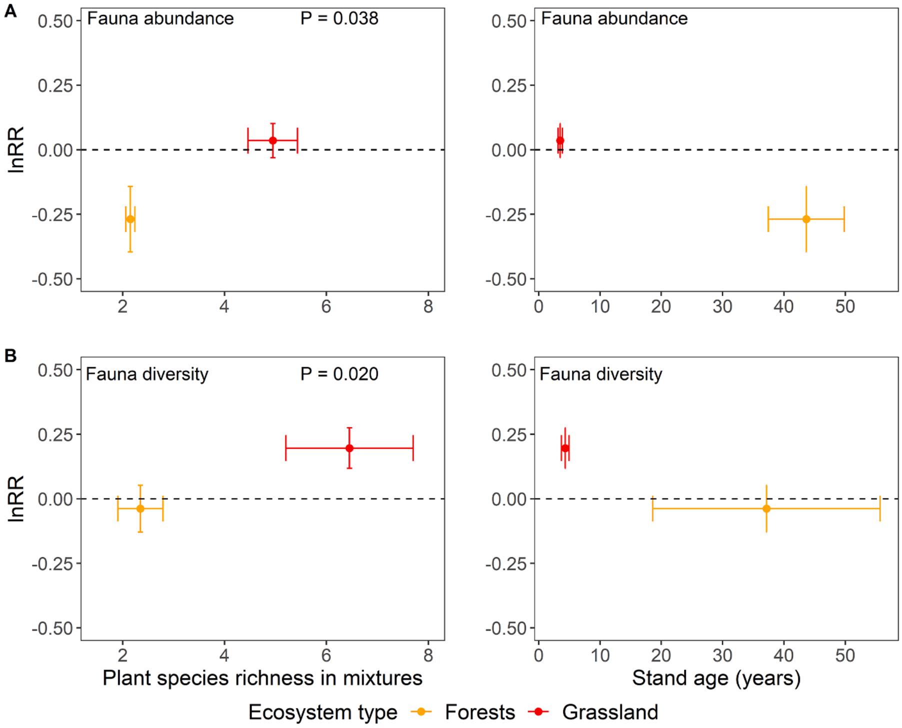

Fig. 2. Comparison of (A) soil fauna abundance and (B) diversity in plant species mixtures versus monocultures between forests and grasslands. Means and vertical and horizontal error bars represent means and 95% confidence intervals for plant mixture effects, species richness in mixtures, and stand age 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.

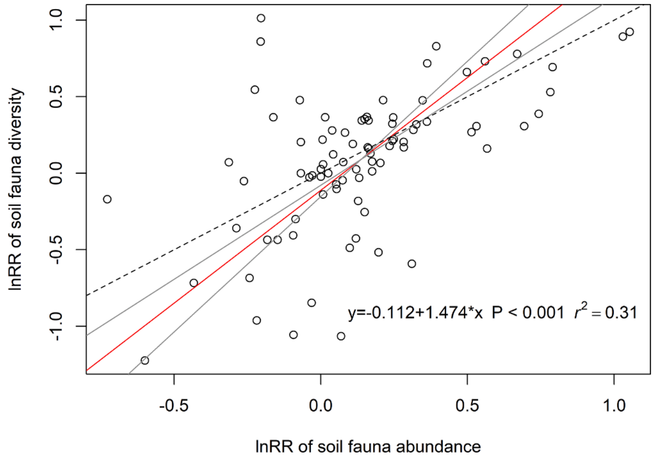

Fig. 3. Relationship between the log response ratios of soil fauna abundance and diversity. Fitted regression (red line) and 95% confidence region (grey lines) are presented. The dashed line represents the 45-degree line.

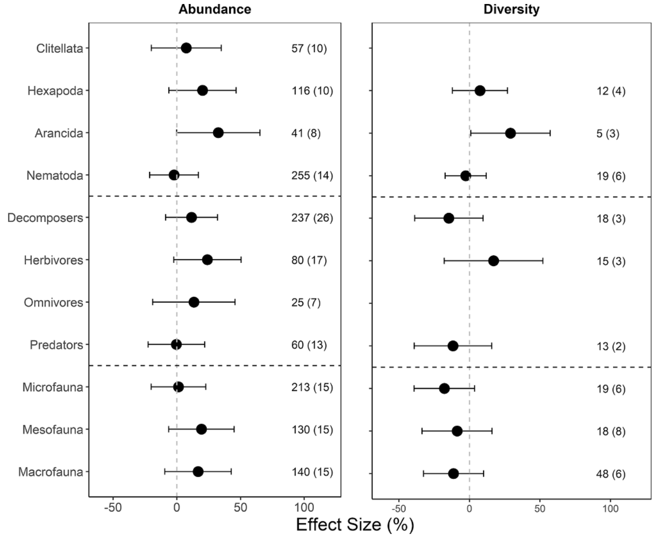

Fig. 4. Plant mixture effects on the abundance and diversity of soil fauna of different groups. Overall effect represents the increase or decrease (%) of soil fauna abundance and diversity compared to the corresponding mean for constituent monocultures at the mean species richness and mean stand age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

suggest that a positive diversity-productivity relationship (Zhang et al., 2012) may be propagated to belowground soil fauna communities. Driven by inter-specific plant interactions (Barry et al., 2019; Forrester and Bauhus, 2016), the increased amount and diversity of resources in high-richness plant communities (Ma et al., 2017; Peng et al., 2021; Zheng et al., 2019) 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 (Allan et al., 2013; Eisenhauer et al., 2011). It also suggests that the age effect on soil fauna is dependent on plant species richness in mixtures (Fig. S1) because of higher performance in species-rich communities over time compared to species-poor communities (Meyer 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 (Ma and Chen, 2016; Zhang et al., 2012) soil carbon (Chen et al., 2020), and soil microbial biomass to plant mixture effects (Chen et al., 2019).

We observed significantly larger effects of plant mixtures on fauna in grasslands than 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. 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 *Arancida*. 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 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 et al., 2019). The 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 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 with 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.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2022.115694.

References

Allan, E., Weisser, W.W., Fischer, M., Schulze, E.D., Weigelt, A., Roscher, C., Baade, J., Barnard, R.L., Bessler, H., Buchmann, N., Ebeling, A., Eisenhauer, N., Engels, C., Fergus, A.J., Gleixner, G., Gubsch, M., Halle, S., Klein, A.M., Kertscher, I., Kuu, A., Lange, M., Le Roux, X., Meyer, S.T., Migunova, V.D., Milcu, A., Niklaus, P.A., Oelmann, Y., Pasalic, E., Petermann, J.S., Poly, F., Rottstock, T., Sabais, A.C., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Steinbeiss, S., Schwichtenberg, G., Temperton, V., Tscharntke, T., Voigt, W., Wilcke, W., Wirth, C., Schmid, B., 2013. A comparison of the strength of biodiversity effects across multiple functions. Oecologia 173 (1), 223–237. https://doi.org/10.1007/s00442-012-2589-0.

Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y., Connolly, J., De Deyn, G.B., de Kroon, H., Isbell, F., Milcu, A., Roscher, C., Scherer-Lorenzen, M., Schmid, B., Weigelt, A., 2019. The Future of Complementarity: Disentangling Causes from Consequences. Trends Ecol. Evol. 34 (2), 167–180. https://doi.org/10.1016/j.tree.2018.10.013.

Bartoń, K., 2018. MuMIn: Multi-model inference. R Package Version 1 (42), 1.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Bedano, J.C., Ruf, A., 2010. Sensitivity of different taxonomic levels of soil Gamasina to land use and anthropogenic disturbances. Agric. For. Entomol. 12 (2), 203–212. https://doi.org/10.1111/j.1461-9563.2009.00470.x.

Bello, J., Hasselquist, N.J., Vallet, P., Kahmen, A., Perot, T., Korboulewsky, N., 2019. Complementary water uptake depth of Quercus petraea and Pinus sylvestris in mixed stands during an extreme drought. Plant Soil 437 (1–2), 93–115. https://doi.org/10.1007/s11104-019-03951-z.

Button, K.S., Ioannidis, J.P.A., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S.J., Munafò, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. Nat. Rev. Neurosci. 14 (5), 365–376. https://doi.org/10.1038/nrn3475.

Cavard, X., Macdonald, S.E., Bergeron, Y., Chen, H.Y.H., 2011. Importance of mixedwoods for biodiversity conservation: Evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environ. Rev. 19 (NA), 142–161. https://doi.org/10.1139/a11-004.

Chen, C., Chen, H.Y.H., Chen, X., Huang, Z., 2019. Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration. Nat. Commun. 10 (1), 1332. https://doi.org/10.1038/s41467-019-09258-y.

Chen, H.Y.H., Brassard, B.W., 2012. Intrinsic and Extrinsic Controls of Fine Root Life Span. Crit. Rev. Plant Sci. 32 (3), 151–161. https://doi.org/10.1080/07352689.2012.734742.

Chen, X., Chen, H.Y.H., 2021. Plant mixture balances terrestrial ecosystem C:N: P stoichiometry. Nat. Commun. 12 (1), 4562. https://doi.org/10.1038/s41467-021-24889-w.

Chen, X., Chen, H.Y.H., Chen, C., Ma, Z., Searle, E.B., Yu, Z., Huang, Z., 2020. Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. Biol. Rev. 95 (1), 167–183. https://doi.org/10.1111/brv.12554.

Chen, X.L., Chen, H.Y.H., Searle, E.B., Chen, C., Reich, P.B., 2021. Negative to positive shifts in diversity effects on soil nitrogen over time. Nat. Sustain. 4 (3), 225–U234. https://doi.org/10.1038/s41893-020-00641-y.

Cohen, J., Cohen, P., West, S.G., Aiken, L.S., 2003. Applied multiple regression/correlation analysis for the behavioral sciences, 3rd ed. Lawrence Erlbaum Associates Publishers.

Coleman, D.C., Callaham, M.A., Crossley Jr, D., 2018. Fundamentals of soil ecology. Academic Press. https://doi.org/10.1016/C2015-0-04083-7.

Eisenhauer, N., Milcu, A., Sabais, A.C.W., Bessler, H., Brenner, J., Engels, C., Klarner, B., Maraun, M., Partsch, S., Roscher, C., Schonert, F., Temperton, V.M., Thomisch, K., Weigelt, A., Weisser, W.W., Scheu, S., Hector, A., 2011. Plant diversity surpasses plant functional groups and plant productivity as driver of soil biota in the long term. PLoS ONE 6 (1), e16055. https://doi.org/10.1371/journal.pone.0016055.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity Relationships in Forests. Curr. For. Rep. 2 (1), 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Forrester, D.I., Theiveyanathan, S., Collopy, J.J., Marcar, N.E., 2010. Enhanced water use efficiency in a mixed Eucalyptus globulus and Acacia mearnsii plantation. For. Ecol. Manage. 259 (9), 1761–1770. https://doi.org/10.1016/j.foreco.2009.07.036.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The Meta-Analysis of Response Ratios in Experimental Ecology. Ecology 80 (4), 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:Tmaorr]2.0.Co;2.

Hedlund, K., Santa Regina, I., Van der Putten, W.H., Lepš, J., Díaz, T., Korthals, G.W., Lavorel, S., Brown, V.K., Gormsen, D., Mortimer, S.R., Rodríguez Barrueco, C., Roy, J., Smilauer, P., Smilauerová, M., Van Dijk, C., 2003. Plant species diversity, plant biomass and responses of the soil community on abandoned land across Europe: idiosyncracy or above-belowground time lags. Oikos 103 (1), 45–58. https://doi.org/10.1034/j.1600-0706.2003.12511.x.

Hisano, M., Searle, E.B., Chen, H.Y.H., 2018. Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. Biol. Rev. Camb. Philos. Soc. 93 (1), 439–456. https://doi.org/10.1111/brv.12351.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussard, L., Mark Dangerfield, J., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., Van Der Putten, W.H., De Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M., Wolters, V., 2000. Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks. Bioscience 50 (12), 1049–1061. https://doi.org/10.1641/0006-3568(2000)050[1049:Ibaabb]2.0.Co;2.

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evol. 19 (2), 101–108. https://doi.org/10.1016/j.tree.2003.10.013.

Kampichler, C., Bruckner, A., 2009. The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. Biol. Rev. Camb. Philos. Soc. 84 (3), 375–389. https://doi.org/10.1111/j.1469-185X.2009.00078.x.

Korboulewsky, N., Heiniger, C., De Danieli, S., Brun, J.J., 2021. Effect of tree mixture on Collembola diversity and community structure in temperate broadleaf and coniferous forests. For. Ecol. Manage. 482, 118876. https://doi.org/10.1016/j.foreco.2020.118876.

Korboulewsky, N., Perez, G., Chauvat, M., 2016. How tree diversity affects soil fauna diversity: A review. Soil Biol. Biochem. 94, 94–106. https://doi.org/10.1016/j.soilbio.2015.11.024.

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. Ecol. Evol. 5 (4), 836–847. https://doi.org/10.1002/ece3.1337.

Lawrence, A.P., Bowers, M.A., 2002. A test of the 'hot' mustard extraction method of sampling earthworms. Soil Biol. Biochem. 34 (4), 549–552. https://doi.org/10.1016/s0038-0717(01)00211-5.

Lee, K.E., Foster, R.C., 1991. Soil fauna and soil structure. Soil Res. 29 (6), 745–775. https://doi.org/10.1071/sr9910745.

Legendre, P., 1998. Model II regression user's guide. R edition, R Vignette, p. 14.

Liu, Y.u., Miao, H.-T., Chang, X., Wu, G.-L., 2019. Higher species diversity improves soil water infiltration capacity by increasing soil organic matter content in semiarid grasslands. Land Degrad. Dev. 30 (13), 1599–1606. https://doi.org/10.1002/ldr.3349.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412 (6842), 72–76. https://doi.org/10.1038/35083573.

Ma, Z., Chen, H.Y.H., 2016. Effects of species diversity on fine root productivity in diverse ecosystems: a global meta-analysis. Glob. Ecol. Biogeogr. 25 (11), 1387–1396. https://doi.org/10.1111/geb.12488.

Ma, Z., Chen, H.Y.H., Bellingham, P., 2017. Effects of species diversity on fine root productivity increase with stand development and associated mechanisms in a boreal forest. J. Ecol. 105 (1), 237–245. https://doi.org/10.1111/1365-2745.12667.

Maaß, S., Caruso, T., Rillig, M.C., 2015. Functional role of microarthropods in soil aggregation. Pedobiologia 58 (2–3), 59–63. https://doi.org/10.1016/j.pedobi.2015.03.001.

Madej, G., Barczyk, G., Gawenda, I., 2011. Importance of Microhabitats for Preservation of Species Diversity, on the Basis of Mesostigmatid Mites (Mesostigmata, Arachnida, Acari). Polish J. Environ. Stud. 20 (4).

Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J. Ecol. 97 (2), 199–205. https://doi.org/10.1111/j.1365-2745.2008.01476.x.

Meehan, M.L., Song, Z., Lumley, L.M., Cobb, T.P., Proctor, H., 2019. Soil mites as bioindicators of disturbance in the boreal forest in northern Alberta, Canada: Testing taxonomic sufficiency at multiple taxonomic levels. Ecol. Ind. 102, 349–365. https://doi.org/10.1016/j.ecolind.2019.02.043.

Meyer, S.T., Ebeling, A., Eisenhauer, N., Hertzog, L., Hillebrand, H., Milcu, A., Pompe, S., Abbas, M., Bessler, H., Buchmann, N., De Luca, E., Engels, C., Fischer, M., Gleixner, G., Hudewenz, A., Klein, A.M., Kroon, H., Leimer, S., Loranger, H., Mommer, L., Oelmann, Y., Ravenek, J.M., Roscher, C., Rottstock, T., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Schmid, B., Schulze, E.D., Staudler, A., Strecker, T., Temperton, V., Tscharntke, T., Vogel, A., Voigt, W., Weigelt, A., Wilcke, W., Weisser, W.W., 2016. Effects of biodiversity strengthen over time as ecosystem functioning declines at low and increases at high biodiversity. Ecosphere 7 (12), e01619. https://doi.org/10.1002/ecs2.1619.

Nielsen, U.N., 2019. Functional Roles of Soil Fauna. In: Nielsen, U.N. (Ed.), Soil Fauna Assemblages. Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge, pp. 42–85. https://doi.org/10.1017/9781108123518.003.

Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob. Ecol. Biogeogr. 20 (1), 170–180. https://doi.org/10.1111/j.1466-8238.2010.00592.x.

Partsch, S., Milcu, A., Scheu, S., 2006. Decomposers (Lumbricidae, Collembola) affect plant performance in model grasslands of different diversity. Ecology 87 (10), 2548–2558. https://doi.org/10.1890/0012-9658(2006)87[2548:dlcapp]2.0.co;2.

Peng, S., Chen, H.Y.H., Kerkhoff, A., 2021. Global responses of fine root biomass and traits to plant species mixtures in terrestrial ecosystems. Glob. Ecol. Biogeogr. 30 (1), 289–304. https://doi.org/10.1111/geb.13205.

Pittelkow, C.M., Liang, X., Linquist, B.A., van Groenigen, K.J., Lee, J., Lundy, M.E., van Gestel, N., Six, J., Venterea, R.T., van Kessel, C., 2015. Productivity limits and potentials of the principles of conservation agriculture. Nature 517 (7534), 365–368. https://doi.org/10.1038/nature13809.

R Core Team, 2020. R: a language and environment for statistical computing. Version 3.6.3. R Foundation for Statistical Computing.

Ravenek, J.M., Bessler, H., Engels, C., Scherer-Lorenzen, M., Gessler, A., Gockele, A., De Luca, E., Temperton, V.M., Ebeling, A., Roscher, C., Schmid, B., Weisser, W.W., Wirth, C., de Kroon, H., Weigelt, A., Mommer, L., 2014. Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. Oikos 123 (12), 1528–1536. https://doi.org/10.1111/oik.01502.

Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F., Eisenhauer, N., 2012. Impacts of biodiversity loss escalate through time as redundancy fades. Science 336 (6081), 589–592. https://doi.org/10.1126/science.1217909.

Schmid, B., Balvanera, P., Cardinale, B.J., Godbold, J., Pfisterer, A.B., Raffaelli, D., Solan, M., Srivastava, D.S., 2009. Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. In: Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), Biodiversity, Ecosystem Functioning, and Human Wellbeing. Oxford University Press, pp. 14–29. https://doi.org/10.1093/acprof:oso/9780199547951.003.0002.

Schwarz, B., Dietrich, C., Cesarz, S., Scherer-Lorenzen, M., Auge, H., Schulz, E., Eisenhauer, N., 2015. Non-significant tree diversity but significant identity effects on earthworm communities in three tree diversity experiments. Eur. J. Soil Biol. 67, 17–26. https://doi.org/10.1016/j.ejsobi.2015.01.001.

Setala, H., Huhta, V., 1991. Soil Fauna Increase Betula Pendula Growth: Laboratory Experiments With Coniferous Forest Floor. Ecology 72 (2), 665–671. https://doi.org/10.2307/2937206.

Song, M., Li, X., Jing, S., Lei, L., Wang, J., Wan, S., 2016. Responses of soil nematodes to water and nitrogen additions in an old-field grassland. Appl. Soil Ecol. 102, 53–60. https://doi.org/10.1016/j.apsoil.2016.02.011.

Soong, J.L., Vandegehuchte, M.L., Horton, A.J., Nielsen, U.N., Denef, K., Shaw, E.A., de Tomasel, C.M., Parton, W., Wall, D.H., Cotrufo, M.F., 2016. Soil microarthropods support ecosystem productivity and soil C accrual: Evidence from a litter decomposition study in the tallgrass prairie. Soil Biol. Biochem. 92, 230–238. https://doi.org/10.1016/j.soilbio.2015.10.014.

Storch, D., Bohdalková, E., Okie, J., Gravel, D., 2018. The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity-diversity relationship. Ecol. Lett. 21 (6), 920–937. https://doi.org/10.1111/ele.12941.

Taylor, A.R., Wolters, V., 2005. Responses of oribatid mite communities to summer drought: The influence of litter type and quality. Soil Biol. Biochem. 37 (11), 2117–2130. https://doi.org/10.1016/j.soilbio.2005.03.015.

Trabucco, A., Zomer, R., 2009. 2009. Global aridity index and global potential evapo-transpiration geospatial database, CGIAR Consortium for Spatial Information.

van Groenigen, J.W., Lubbers, I.M., Vos, H.M., Brown, G.G., De Deyn, G.B., van Groenigen, K.J., 2014. Earthworms increase plant production: a meta-analysis. Sci. Rep. 4, 6365. https://doi.org/10.1038/srep06365.

Wardle, D.A., 2005. How plant communities influence decomposer communities. In: Hopkins, D., Usher, M., Bardgett, R. (Eds.), Biological Diversity and Function in Soils. Ecological Reviews. Cambridge University Press, Cambridge, pp. 119–138. https://doi.org/10.1017/cbo9780511541926.008.

Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecol. Lett. 9 (7), 870–886. https://doi.org/10.1111/j.1461-0248.2006.00931.x.

Wu, T., Su, F., Han, H., Du, Y., Yu, C., Wan, S., 2014. Responses of soil microarthropods to warming and increased precipitation in a semiarid temperate steppe. Appl. Soil Ecol. 84, 200–207. https://doi.org/10.1016/j.apsoil.2014.07.003.

Wubs, E.R.J., Putten, W.H., Mortimer, S.R., Korthals, G.W., Duyts, H., Wagenaar, R., Bezemer, T.M., Suding, K., 2019. Single introductions of soil biota and plants generate long-term legacies in soil and plant community assembly. Ecol. Lett. 22 (7), 1145–1151. https://doi.org/10.1111/ele.13271.

Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. J. Ecol. 100 (3), 742–749. https://doi.org/10.1111/j.1365-2745.2011.01944.x.

Zheng, L.-T., Chen, H.Y.H., Yan, E.-R., Gilliam, F., 2019. Tree species diversity promotes litterfall productivity through crown complementarity in subtropical forests. J. Ecol. 107 (4), 1852–1861. https://doi.org/10.1111/1365-2745.13142.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1 (1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.