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Litter quality, mycorrhizal association, and soil properties regulate effects of tree species on the soil fauna community

Yan Peng^{a, b,*}, Martin Holmstrup^c, Inger Kappel Schmidt^a, An De Schrijver^{d, e}, Stephanie Schelfhout^d, Petr Heděnec^a, Haifeng Zheng^a, Luciana Ruggiero Bachega^f, Kai Yue^b, Lars Vesterdal^a

^a Department of Geosciences and Natural Resource Management, University of Copenhagen, DK-1958 Frederiksberg C, Denmark

^b Key Laboratory for Humid Subtropical Eco-Geographical Processes of the Ministry of Education, School of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China

^c Section of Terrestrial Ecology, Department of Bioscience, Aarhus University, Vejlsøvej 25, DK-8600 Silkeborg, Denmark

^d Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium

e School of Bioscience and Industrial Technology, HOGENT University of Applied Sciences and Arts, Brusselsesteenweg 161, 9090 Melle, Belgium

^t Department of Environmental Science, Federal University of São Carlos (UFSCar), São Carlos, SP 13565-905, Brazil

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ABSTRACT

Forest management, including selection of appropriate tree species to mitigate climate change and sustain biodiversity, requires a better understanding of factors that affect the composition of soil fauna communities. These communities are an integral part of the soil ecosystem and play an essential role in forest ecosystem functioning related to carbon and nitrogen cycling. Here, by performing a field study across six common gardens in Denmark, we evaluated the effects of tree species identity and mycorrhizal association (i.e., arbuscular mycorrhiza (AM) and ectomycorrhiza (ECM)) on soil fauna (meso- and macrofauna) taxonomic and functional community composition by using diversity, abundance, and biomass as proxies. We found that (1) tree species identity and mycorrhizal association both showed significant effects on soil fauna communities, but the separation between community characteristics in AM and ECM tree species was not entirely consistent; (2) total soil fauna abundance, biomass, as well as taxonomic and functional diversity were generally significantly higher under AM tree species, as well as lime, with higher litter quality (high N and base cation and low lignin:N ratio); (3) tree species significantly influenced the properties of litter, forest floor, and soil, among which litter and/or forest floor N, P, Ca, and Mg concentrations, soil pH, and soil moisture predominantly affected soil fauna abundance, biomass, and taxonomic and functional diversity. Our results from this multisite common garden experiment provide strong and consistent evidence of positive effects of tree species with higher litter quality on soil fauna communities in general, which helps to better understand the effects of tree species selection on soil biodiversity and its functions related to forest soil carbon sequestration.

1. Introduction

Soil fauna communities are an integral part of terrestrial ecosystems, playing an essential role in ecosystem functioning, particularly in biogeochemical cycles with feedback on plant productivity, diversity, and succession (Bardgett and van der Putten, 2014; Hättenschwiler et al., 2005). Soil fauna affect carbon (C) and nutrient cycles (Lubbers et al., 2020), modify soil structure (Gong et al., 2019) and water holding

capacity (Hallam and Hodson, 2020), which in turn contribute to the provision of a wide range of ecosystem services (Barrios, 2007). Soil fauna communities were reported to be shaped by a hierarchy of factors such as habitat heterogeneity, environmental factors, as well as top-down and bottom-up ecological processes (Bardgett and van der Putten, 2014; Cesco et al., 2012; Hättenschwiler et al., 2005). Forest management practices determine tree species compositions that are closely related to soil fauna diversity and functionality (Farská et al.,

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^{*} Corresponding author at: Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark.

E-mail addresses: yape@ign.ku.dk, ypeng117@163.com (Y. Peng).

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2014) through direct effects on litter production and litter quality (Schelfhout et al., 2017) and indirect effects on soil properties and microclimatic factors (Mueller et al., 2016). However, our understanding of tree species effects on soil faunal community composition and the underlying mechanisms are still very limited.

Tree species identities represent a wide range of plant functional traits, such as litter nutrient concentration, that can strongly affect the quantity and quality of soil resources supporting soil fauna (Faucon et al., 2017; Peng et al., 2020; Wang et al., 2020). Several observational and experimental studies support that soil nutrient availability positively mediates the abundance and diversity of soil fauna communities (Mueller et al., 2012; Sayad et al., 2012). When the availability of soil nutrients increases, the abundance and diversity of soil fauna are expected to increase due to stimulated opportunities for niche differentiation in terms of more sources of energy and nutrients (Barbier et al., 2008; Wardle et al., 2006). Therefore, tree species that produce litter with higher quality (higher N concentration and lower C:N ratio) and quantity may facilitate the abundance and diversity of soil fauna. Although studies have suggested that tree species can shape soil fauna communities (Frouz et al., 2011; Sauvadet et al., 2017), the main links between tree species identity and soil fauna community remain elusive.

Two dominant types of mycorrhizal fungi, namely arbuscular mycorrhizal fungi (AM) and ectomycorrhizal fungi (ECM), can enhance the access of trees to soil nutrients by forming associations with the roots of most tree species (van der Heijden et al., 2015). Despite their similar functioning in stimulating nutrient uptake, AM fungi generally scavenge for inorganic nutrients such as nitrogen (N) and phosphorus (P) released by saprotrophic microbes, whereas ECM fungi scavenge for organically bound nutrients such as N in proteins and P in inositol phosphates that require extracellular enzymes for degradation (Phillips et al., 2013; Wooliver et al., 2019). This results in a general pattern of higher litter quality for AM tree species than ECM tree species (Lin et al., 2017). Mycorrhizal association has been found to be an important moderator for several ecosystem functions. For example, a recent study found that ECM tree species with low quality and thus slowly decomposing leaf litter generally lead to a higher C stock in the forest floor, while AM tree species with fast decomposing leaf litter have a higher C stock in the mineral soil (Peng et al., 2020). Mycorrhizal association was also found to have direct effects on microbial communities and their activities via litter quality and indirectly through effects on soil properties such as pH and C:N ratio (Heděnec et al., 2020). However, it has not been studied if mycorrhizal association may regulate the effects of tree species on the soil fauna community composition.

The forest floor and top mineral soil are the main habitats and sources of carbon and nutrients for soil fauna, and the extent to which the properties of forest floor and soil are affected by tree species can be an important moderator of soil fauna community composition (Reich et al., 2005; National Research Council, 2005). For example, microclimate such as moisture and temperature of forest floor and soil can vary significantly under different tree species (Berger and Berger, 2012), and as soil fauna groups are sensitive to these factors, they may affect their community composition (Brown et al., 2004; García-Palacios et al., 2013). Soil pH has since long been found to be significantly correlated with the soil fauna community composition (Hågvar, 1990; van Straalen and Verhoef, 1997), and it can also have a bottom-up effect on the soil fauna community by influencing the relative abundance and biomass of soil microbes and the activity of soil enzymes (Mulder et al., 2005; Sinsabaugh et al., 2008). Other abiotic conditions that favor the productivity and diversity of microbes that form the basis of the soil food web can also facilitate the abundance and diversity of soil fauna (Hassall et al., 2006). Leaf litter Ca concentration was found to increase the abundance of earthworms (Reich et al., 2005), and Mg has been identified as a key component of invertebrate diets (National Research Council, 2005), which suggest that both forest floor and soil Ca and Mg may be important factors for soil fauna communities. Despite these findings in previous studies, it is still unclear how and with which

relative importance, tree species-mediated soil properties control tree soil fauna community composition.

In this study, we evaluated the effects of tree species identity and mycorrhizal association on the composition of soil fauna communities using abundance, biomass, and diversity as proxies in six European tree species across six common garden sites in Denmark. The six tree species differed in mycorrhizal association (four ECM and two AM tree species), and have divergent effects on litter quality and food resource availability, soil C and N stock, and water balance (Christiansen et al., 2010; Vesterdal et al., 2008). The objectives of this study were (i) to assess the effect of tree species in terms of their identity and mycorrhizal association on the composition of soil fauna communities with regard to abundance, biomass, and taxonomic and functional diversity, and (ii) to quantify how leaf litter, forest floor, and soil properties under different tree species can explain tree species effects on soil fauna. We hypothesized that (1) soil fauna abundance, biomass, and diversity are higher under tree species that produce litter with higher quality; (2) mycorrhizal association influences soil fauna communities, with higher soil fauna abundance, biomass, and diversity under AM tree species than ECM tree species; and (3) the properties of leaf litter, forest floor, and soil are important moderators regulating tree species effects, with positive influences of nutrient concentrations, soil temperature, and soil moisture on soil fauna abundance, biomass, and diversity.

2. Materials and methods

2.1. Study sites

This study was carried out across six common gardens in Denmark (Fig. S1). Four common garden sites were planted on land previously forested with Fagus sylvatica (Odsherred, Vallø, Viemose, and Wedellsborg) and two planted on former cropland (Mattrup and Kragelund). The common gardens were established in 1961 (Vallø) or in 1973 (the other five sites), and six tree species were randomly planted in singlespecies plots of 0.25 ha in a block design within each site (Vesterdal et al., 2008). The planted six tree species were ash (Fraxinus excelsior L.), maple (Acer pseudoplatanus L.), lime (Tilia cordata L.), oak (Quercus robur L.), beech (Fagus sylvatica L.), and Norway spruce (Picea abies (L.) Karst). Ash and maple are associated with AM fungi, while lime, oak, beech, and Norway spruce with ECM fungi (Harley and Harley, 1987). Ash was missing in two of the six sites (Kragelund and Vallø) due to failed establishments. The mean annual precipitation ranged from 580 to 890 mm and mean annual temperature from 7.5 to 8.4 °C across the six sampling sites, with relatively similar lengths of growing season at all sites. The six common gardens studied here have been maintained in good order after establishment, and have been used as experimental sites for decades (Vesterdal et al., 2008).

2.2. Soil fauna sampling, identification, and quantification

We collected earthworms, other macrofauna and mesofauna (Table 1) with different methods. At each site for each tree species, we selected three (for earthworms) or five (for remaining soil fauna) subplots (blocks) that were sampled according to a randomized block design. In October 2009, earthworms were collected in three subplots of 0.25 m^2 using a wooden frame of $0.5 \times 0.5 \text{ m}$ per site in three steps: first, the litter layer was hand-sorted for capturing litter-dwelling specimens; second, a mustard solution (60 g mustard powder in 30 L water) was applied on the soil surface for collection of deep-burrowing specimens; and third, the mineral soil layer was hand-sorted for capturing surface soil dwelling specimens (see detailed description in (Schelfhout et al., 2017). We used the data on total earthworm abundance and biomass (dry weight). Fresh weight of earthworms was transformed to dry weight following (Petersen and Luxton, 1982).

In early November 2017, the macrofauna species (except earthworms) were extracted from five subplots per site of the litter and

Table 1

An overview of the identified soil fauna at different taxonomic and functional groups.

Taxonomic group				Functional group	Function description
Identified group	Meso- or macrofauna	Identified level	Class level		
Lumbricidae	Macrofauna	family	Clitellata	earthworm	Soil engineers
Diplopoda	Macrofauna	class	Diplopoda	saprophage	Feeding on dead organic matter, including dead plants, bodies, fungi, and
Isopoda	Macrofauna	order	Malacostraca	saprophage	bacteria
Collembola	Mesofauna	subclass	Collembola	saprophage	
Oribatida	Mesofauna	order	Arachnida	saprophage	
Araneae	Macrofauna	order	Arachnida	predator	Hunting and eating other animals
Chilopoda	Macrofauna	class	Chilopoda	predator	
Pseudoscorpions	Macrofauna	order	Arachnida	predator	
Mesostigmata	Mesofauna	order	Arachnida	predator	
Gastropoda	Macrofauna	class	Gastropoda	herbivore	Grazing on plants
Insecta	Macrofauna	class	Insecta	omnivore	Feeding on plant, dead organic matter, bacteria, fungi, insects etc.
Prostigmata	Mesofauna	suborder	Arachnida	omnivore	

fermentation layers of the forest floor (including Oi and Oe layers) using a wooden frame of 25 \times 25 cm with a minimum distance of 10 m from the border of plots. After collecting the upper forest floor sample, we concurrently collected five cores (0–10 cm) of mainly mineral soil origin consisting of the thin Oa layer of the forest floor and the top A layers for extraction of mesofauna. This was done using a cylindrical soil corer (6 cm diameter \times 10 cm depth). Forest floor samples were stored in black plastic bags and soil samples in closed plastic cylinders and were immediately transported to lab. Upon arrival to the laboratory, samples were stored at 5 °C until extraction. Samples under Norway spruce were collected only in three sites (Odsherred, Vallø, and Viemose). Therefore, the sample size (n) for Norway spruce was 15, for ash 20, for maple, lime, beach, and oak 30, for AM tree species 50, and for ECM tree species 105. In total, we obtained 155 samples of forest floor and mineral soil each.

Macrofauna (except earthworms) were extracted from the forest floor samples using a Tullgren funnel-type extractor for one week, collected in benzoic acid, and subsequently stored in 70% ethanol for later identification. Mesofauna samples from mineral soil were divided into the 0–5 cm top layer and the 5–10 cm bottom layer using a knife to meet the requirements of the apparatus. Mesofauna were then extracted from these samples using a high gradient extraction apparatus (Mac-Fadyen type), where the temperature in the upper compartment increased stepwise from 25 °C to 50 °C within 7 days while the temperature at lower compartment remained constant at 3 °C (Holmstrup et al., 2017). The collected mesofauna from 0 to 5 and 5-10 cm layers were then merged and stored in glycerol. We used a dissection microscope to identify macro- and mesofauna to broad taxonomic groups and counted the number of individuals of each group. The sorted macrofauna groups were then oven-dried at 65 °C for 72 h and weighed. Because the mesofauna was stored in glycerol we could not determine the dry biomass directly, and instead we estimated total biomass of each taxonomic group by multiplying abundance by mean dry mass as described by previous studies (Petersen and Luxton, 1982; Vestergård et al., 2015). As a result, soil fauna were sorted into 12 taxonomic groups at the family, order, subclass, or class level, namely Araneae, Chilopoda, Diplopoda, Lumbricidae, Gastropoda, Insecta, Isopoda, Pseudoscorpions, Collembola, Mesostigmata, Oribatida, and Prostigmata (Table 1). In addition, we assigned soil fauna into 5 functional groups, namely earthworms, herbivores, omnivores, predators, and saprophages according to their food preferences and ecological functions (Artz et al., 2010). Although earthworms belong to the saprophage group, we treated them as a distinct group because of (1) their functioning as ecosystem engineers (Eisenhauer, 2010), and (2) their biomass accounted for the majority of that of saprophages, which may mask the effects on the remaining saprophage fauna in our analyses. To aid the interpretation of results, we converted the results of abundance and biomass into the same unit area (m^{-2}) for all soil fauna.

2.3. Properties of foliar litter, forest floor, and soil

We used the data of properties of freshly fallen foliar litter, forest floor (i.e., the organic or fermentation layer), and soil (i.e., mineral soil layer) from previous studies conducted in the same study sites (Vesterdal et al., 2008). In summary, freshly fallen litter was collected in 2004-2005 using ten circular litter traps with a diameter of 31 cm installed along two line transects in each site. This foliar and non-foliar litter was oven-dried at 65 °C, sorted as foliar and non-foliar litter, and weighed. We only used the data on foliar litter. In September 2004 the forest floor was sampled in 15 points along three line transects within each site using a 25 \times 25 cm wooden frame before the starting of foliar litterfall for deciduous species. Foliar fractions of the collected forest floor were oven-dried to constant weight at 65 °C and weighed. The forest floor turnover rate (k value) was calculated according to previous studies (Hansen et al., 2009; Vesterdal et al., 2008). Litter and forest floor total C and N were determined using dry combustion (Dumas method) in a Leco CNS 2000 Analyzer. Total concentrations of Ca, Mg, and P were determined after microwave-assisted digestion in concentrated HNO3, and the digests were subsequently analyzed for total element contents by ICP-OES (Perkin Elmer Optima 3000XL). Aciddetergent lignin contents were determined by proximate analysis (van Soest and Robertson, 1985) using the Walloon Agricultural Research Centre, Gembloux, Belgium. Finally, the lignin:N ratio was calculated.

As to soil properties, in October 2009, three soil cores of 0–5 cm depth with a diameter of 3 cm were mixed into one composite sample in each plot. Soil samples were oven-dried to constant weight at 40 °C, and then sieved with a 2 mm mesh size. Soil pH was determined in a 1:5 soil/KCl solution (1 M) with a glass electrode (Ross Sure-flow 8172), and the concentrations of Mg and Ca were measured by flame atomic absorption spectrophotometry after extraction with BaCl₂ (0.1 M) (ISO 11260). In addition, soil moisture was measured using a point-scale dielectric sensor (ML3 ThetaProbe, Delta-T Devices, Cambridge, UK) and soil temperature using a digital pocket thermometer (UEi 300AC, UEi Test Instruments, Oregon, US) at the same time as soil fauna sampling at each plot in November 2017.

2.4. Statistical analysis

The effects of tree species identity and mycorrhizal association on the properties of litter, forest floor, and soil, as well as on the abundance and biomass of soil fauna across or within each taxonomic or functional group were assessed by linear mixed models with tree species identity or mycorrhizal association as fixed effect and site as a random effect using the *lmer* function of the *lme4* package in R (Bates et al., 2015). Data were tested for the assumptions of normality and homogeneity of variances and were log-transformed when necessary before statistical analyses. To evaluate tree species effects on the overall diversity of soil fauna, we

calculated Shannon-Wiener index (\dot{H}) and Pielou index (J) as proxies of diversity and evenness, respectively, for either taxonomic or functional group using the following equations:

$$H' = -\sum_{i=1}^{s} P_i ln P_i \tag{1}$$

$$J = \frac{H'}{\ln S}$$
(2)

where P_i is the proportion of individuals (all identified soil fauna across different layers) in the *i*th taxonomic or functional group, and *S* is the total number of identified taxonomic group at the class level or functional group. The effects of tree species identity and mycorrhizal association on soil fauna abundance, biomass, diversity, and evenness were then quantified using linear mixed models with site as a random effect. Differences among tree species identities and mycorrhizal associations were tested with Tukey post-hoc tests at p < 0.05 using the *glht* function of the *multcomp* package (Hothorn et al., 2008).

To assess how the properties of litter, forest floor, and soil as regulated by tree species may affect soil fauna community compositions, we used linear mixed-effect models with the independent variables litter, forest floor, or soil properties as fixed effects and site as a random effect. The effects of each independent variable on soil fauna abundance, biomass, taxonomic or functional diversity were assessed separately. To further evaluate the relative importance of the variables that showed significant effects on soil fauna communities, we then applied linear mixed-effect model selection using the glmulti package (Calcagno and de Mazancourt, 2010). The model selection was based on maximum likelihood estimation, and the importance of each predictor was calculated as the sum of Akaike weights for all models that included the predictor. A cutoff of 0.8 for Akaike weights was set to differentiate essential and non-essential predictor variables (Yue et al., 2021). Data were log transferred before analysis, and all the statistical analyses were performed in R version 4.0.3 (R Core Team, 2020).

3. Results

3.1. Abundance and biomass of meso-, macro-, and total fauna

Across all taxonomic groups, soil macrofauna and mesofauna ranged from 2 to 1150 and from 589 to 131,380 individuals m⁻², respectively, under different tree species, with total soil fauna abundance being significantly lower under AM trees than under ECM trees (Fig. 1a, Table 2). Ash and Norway spruce had the lowest and highest soil fauna abundance, respectively. Soil fauna abundance was highest under ECM tree species, but the abundance under lime did not differ from that under AM trees. Mesofauna accounted for 96.4–99.6% of total soil fauna abundance (Fig. 1b), but only 0.8–33.6% of total fauna biomass (Fig. 1d). Soil fauna biomass was highest under ash and lowest under Norway spruce (Fig. 1c). Soil fauna biomass under lime was significantly higher than under other ECM trees, indicating greater similarity with AM trees.

3.2. Abundance, biomass, and diversity of soil fauna taxonomic groups

The taxonomic groups, Oribatida, Collembola, and Insecta had larger relative abundances than other groups (Fig. 1b), whereas Gastropoda, Lumbricidae and Diplopoda accounted for the largest proportion of soil fauna biomass (Fig. 1d). The abundance and biomass of soil fauna within each taxonomic group were significantly affected by tree species identity and mycorrhizal association except for the abundance of Pseudoscorpions and Prostigmata and the biomass of Insecta (Fig. 2). Generally, there were similar responses of soil fauna abundance and biomass to tree species identity and mycorrhizal association, with higher values under the AM trees ash and maple for macrofauna taxonomic groups than the ECM tree species except for Araneae, Chilopoda, and Pseudoscorpions. However, an opposite pattern was observed for the abundance and biomass of all mesofauna groups. The diversity and evenness indices for soil fauna were significantly higher under AM than ECM tree species, and individual species of the two mycorrhizal associations clearly separated in taxonomic diversity (Fig. 3a).



Fig. 1. Soil fauna (a) abundance (number of individuals m^{-2}), (b) relative abundance, (c) biomass, and (d) relative biomass of the 12 taxonomic groups under different tree species across the six common gardens. Values are means, and n = 15 (Norway spruce), 20 (ash), 30 (maple, lime, beech, and oak), 50 (AM), or 105 (ECM). Different letters indicate significant differences in the total abundance or biomass among different tree species at p < 0.05.

Table 2

Effects of the properties of litter, forest floor, and soil on soil fauna abundance, biomass, taxonomic and functional diversity (Shannon-Wiener index, \hat{H}), and evenness (Pielou index, J) as assessed by the linear mixed-effect models. Data were log transferred before statistical analyses. Estimates and p value are given, and bold indicate significant effects.

Predictor	Index	Abundance (individual m^{-2})		Biomass (mg m ⁻²)		Taxonomic \acute{H}		Taxonomic J		Functional \acute{H}		Functional J	
		Estimate	р	Estimate	р	Estimate	р	Estimate	р	Estimate	р	Estimate	р
Litter	C (g kg ⁻¹)	7.5	0.007	-9.9	< 0.001	-2.5	< 0.001	-2.2	0.001	-0.5	0.545	-0.3	0.671
	N (g kg ⁻¹)	-1.4	<0.001	1.9	< 0.001	0.3	0.001	0.2	0.008	0.1	0.270	0.1	0.990
	P (g kg ⁻¹)	-0.5	0.161	1.2	0.001	0.1	0.202	0.1	0.758	-0.1	0.253	-0.2	0.072
	Lignin:N	0.9	<0.001	$^{-1.2}$	< 0.001	-0.3	< 0.001	-0.2	< 0.001	-0.1	0.812	0.1	0.575
	Ca (g kg ⁻¹)	-0.9	0.001	1.8	< 0.001	0.2	< 0.001	0.3	0.006	0.1	0.290	-0.1	0.842
	Mg (g kg $^{-1}$)	-0.9	0.003	1.6	< 0.001	0.2	< 0.001	0.2	0.023	0.2	0.036	0.1	0.546
Forest floor	k value (year ⁻¹)	-0.5	<0.001	0.9	< 0.001	0.1	< 0.001	0.1	0.028	0.1	0.126	-0.1	0.929
	C (g kg ⁻¹)	-0.1	0.922	$^{-1.0}$	0.112	0.1	0.850	0.2	0.293	-0.1	0.955	0.1	0.800
	N (g kg ⁻¹)	-0.9	0.200	-2.3	0.001	0.2	0.200	0.3	0.157	-0.1	0.816	-0.1	0.727
	P (g kg ⁻¹)	-0.6	0.125	1.2	< 0.001	0.1	0.751	-0.1	0.648	0.1	0.315	0.1	0.738
	Ca (g kg ⁻¹)	-0.6	0.087	0.8	0.009	0.1	0.215	0.1	0.535	0.1	0.435	-0.1	0.969
	Mg (g kg $^{-1}$)	-1.1	0.006	0.7	0.028	0.1	0.262	0.1	0.840	0.3	0.019	0.1	0.422
Soil	Temperature (°C)	2.9	0.078	1.1	0.399	-0.4	0.218	-0.3	0.439	1.4	0.001	0.8	0.038
	Moisture (%)	-1.8	< 0.001	1.4	< 0.001	0.2	0.001	0.2	0.011	0.1	0.024	0.1	0.752
	pН	-4.2	<0.001	6.2	< 0.001	0.7	< 0.001	0.6	0.002	0.4	0.145	-0.1	0.980
	Ca ($\mu g g^{-1} BaCl_2$)	-0.5	< 0.001	0.7	< 0.001	0.1	< 0.001	0.1	0.001	0.1	0.273	0.1	0.792
	Mg (μ g g ⁻¹ BaCl ₂)	-0.5	0.001	0.7	< 0.001	0.2	< 0.001	0.1	0.002	0.1	0.251	0.1	0.874



Fig. 2. Effects of tree species identity and mycorrhizal association on soil fauna abundance (number of individuals m^{-2}) and biomass (mg m^{-2}) within each taxonomic group across the six sampling sites. Values are means ± 1 standard error (SE), and n = 15 (Norway spruce), 20 (ash), 30 (maple, lime, beech, and oak), 50 (AM), or 105 (ECM). Asterisks indicate significant effects of tree species identity and mycorrhizal association, and different letters indicate significant (p < 0.05) differences among different tree species. *p < 0.05, **p < 0.01, ***p < 0.001.

3.3. Abundance, biomass, and diversity of soil fauna functional groups

Tree species identity and mycorrhizal association showed significant effects on soil fauna abundance and biomass within each functional group except for omnivores (Fig. 4). The abundance and biomass of earthworms and herbivores were both higher under the AM trees ash and maple than under the ECM tree species, but lime was again not consistently different from the AM species. An opposite pattern was found for predators, with higher abundance and biomass under ECM species and a ranking of ash, maple < lime, oak, beech < spruce. The abundance of saprophages was significantly lower under AM trees compared with ECM trees, while their biomass was higher under AM trees (Fig. 4). When subdivided according to body size, the response of

macrofauna biomass of different functional groups to tree species was similar to that of total soil fauna (Fig. S2a), but mesofauna biomass for all three identified groups were significantly lower under AM than under ECM tree species (Fig. S2b). Consistent with taxonomic diversity, the functional diversity and evenness indices were significantly higher under AM tree species across all sampling sites. The individual species were not perfectly separated according to mycorrhizal association as the AM species were not significantly different from the ECM species lime and beech (Fig. 3b).

3.4. Drivers of tree species effects on soil fauna communities

Results from the linear mixed-effect models showed that litter C



Fig. 3. Effects of tree species identity and mycorrhizal association on soil fauna diversity and evenness of the (a) taxonomic and (b) functional groups across the six sampling sites. Values are means ± 1 standard error (SE), and n = 15 (Norway spruce), 20 (ash), 30 (maple, lime, beech, and oak), 50 (AM), or 105 (ECM). Asterisks indicate significant effects of tree species identity and mycorrhizal association, and different letters indicate significant (p < 0.05) differences among different tree species. *p < 0.05, **p < 0.01, ***p < 0.001.



Fig. 4. Effects of tree species identity and mycorrhizal association on soil fauna abundance (number of individuals m^{-2}) and biomass (mg m^{-2}) within each functional group across the six sampling sites. Values are means ± 1 standard error (SE), and n = 15 (Norway spruce), 20 (ash), 30 (maple, lime, beech, and oak), 50 (AM), or 105 (ECM). Asterisks indicate significant effects of tree species identity and mycorrhizal association, and different letters indicate significant (p < 0.05) differences among different tree species. *p < 0.05, **p < 0.01, ***p < 0.001.

concentration and lignin:N ratio were significantly positively correlated with soil fauna abundance (individuals m^{-2}), but the concentrations of N, Ca, and Mg related negatively to soil fauna abundance (Table 2). Forest floor turnover rate, soil moisture, soil pH, and the concentrations of Ca and Mg in forest floor and soil were significantly negatively related to soil fauna abundance. Factors that were significantly related to soil fauna abundance were also significantly related to soil fauna biomass, however, the direction of effects was opposite. In addition, litter and forest floor P concentrations showed a positive association with soil fauna biomass. Soil fauna taxonomic \hat{H} and J showed similar responses to litter and soil variables as soil fauna biomass, but were only positively correlated with the turnover rate of forest floor. As to functional diversity, Mg concentrations of litter and forest floor, soil temperature, and soil moisture were positively correlated to functional \hat{H} , while functional J only showed a significantly positive relationship with soil moisture (Table 2).

When assessing the relative importance of different variables related

to abundance, biomass and diversity of soil fauna communities, soil pH, soil moisture, and the concentrations of litter and forest floor Mg were found to explain most of the variance in soil fauna abundance (Fig. 5a), while soil pH, forest floor P, N, and Mg concentrations, as well as litter Ca and P concentrations were the most important variables explaining variation in soil fauna biomass (Fig. 5b). Soil moisture and litter lignin:N ratio best explained variability in soil fauna taxonomic H and J (Fig. 5c, d). However, despite the observed significant relationships with soil fauna functional diversity, variables used in our model selection explained only a modest share of the variance (Fig. 5e).

4. Discussion

Mycorrhizal association of different tree species has recently been reported as an important factor affecting multiple forest ecosystem functions such as C and N cycling (Keller and Phillips, 2019; Peng et al., 2020). Our results showed that total soil fauna biomass, diversity and



Fig. 5. Model-averaged importance of the properties of litter, forest floor, and soil on soil fauna (a) abundance, (b) biomass, (c) taxonomic diversity, (d) taxonomic evenness, and (e) functional diversity as assessed using linear-mixed effect model selection method. Only variables that showed significant effects as shown in Table 2 were included in the model selection analyses.

evenness were significantly higher under AM tree species compared to ECM tree species. Mycorrhizal association effects on soil fauna communities may be attributed to the higher litter N concentration and lower lignin:N ratio (i.e., a higher litter quality) produced from AM trees compared with ECM trees (Lin et al., 2017). Other studies have shown that AM trees generally have higher litter quality, typified by e.g., higher concentrations of N and P and lower lignin:N ratio, than ECM trees (Phillips et al., 2013), which ensures a higher availability of nutrients such as Ca and Mg that are important for maintaining a large community of soil fauna (Yang et al., 2020). This mechanism was supported by our results that litter or forest floor N, P, Ca, and Mg concentrations and lignin:N ratio were the most important factors affecting soil fauna communities (Fig. 5). The higher litter quality in AM species appear to support bacterial growth while ECM support fungal growth (Heděnec et al., 2020). This may affect soil fauna since the bacterial energy channel has fast nutrient turnover, while the fungal energy channel supports slow nutrient turnover, and the resulting higher nutrient availability in AM species can promote higher abundance of soil fauna (Frouz et al., 2011). In addition, AM tree species have higher rates of decomposition than ECM tree species (Lin et al., 2017), which can

provide more accessible energy and nutrients for soil fauna and thus support a higher biomass and diversity.

Despite the significant effects of mycorrhizal association on soil fauna communities, it is noteworthy that lime as associated with ECM fungi, had a more similar soil fauna community composition to that under AM trees. This may be attributed to the high litter quality of lime, which is close to that of AM trees ash and maple (Table S1). Indeed, litter quality for the six tree species showed a general trend of ash \approx maple \approx lime > oak \approx beech > Norway spruce, which well explained the divergence of lime from other ECM trees. This result suggests that the effects of mycorrhizal association on soil fauna communities are not always consistent at tree species-specific level, and litter quality is presumably the main factor driving tree species effects on soil fauna communities. While several large-scale studies have reported higher litter quality in terms of higher nutrient and lower lignin concentrations in AM tree species (Lin et al., 2017; Peng et al., 2020), this pattern will likely be less consistent when examining litter quality for specific tree species. The sample sizes for AM vs. ECM tree species in our study were relatively small and not equal, which may bias our assessment of the effects of mycorrhizal association. Furthermore, only the ECM species included a

coniferous species. Thus, future experiments including as many tree species from different phylogenetic groups as possible and with balanced numbers of AM and ECM tree species are necessary to further confirm the findings from our study.

The total abundance of soil fauna was lower under the AM tree species ash and maple, but the opposite pattern was found for total biomass. This may be attributed soil fauna communities under ash and maple being characterized by relatively high abundances of macrofauna with larger biomass, in particular earthworms, whereas ECM trees hosted higher abundance of microarthropods with low biomass. The divergent effects of tree species among different taxonomic and functional groups can be explained by differences in food preferences, life history, propagation characteristics, and adaptability mechanisms (Staley et al., 2007). For example, in contrast to the overall pattern, the abundances of Diplopoda, Gastropoda, Lumbricidae, and Isopoda under ash and maple were significantly higher than under other tree species, which may be directly related to their food preferences. The abundance and biomass of meso- and macrofauna showed opposite responses to mycorrhizal association, with higher values under AM trees for macrofauna and under ECM trees for mesofauna, except for macrofauna predators (Fig. S2a). Two potential mechanisms may explain the contrasting responses of meso- and macrofauna to mycorrhizal association: (1) mesofauna may prefer to inhabit a thick forest floor, which is a dominant trait under ECM tree species where forest floors accumulate due to lower litter quality and slower decomposition (Fujii et al., 2020); and (2) high biomass of soil macrofauna under AM tree species may directly affect the community of soil mesofauna negatively (Pollierer et al., 2021). The higher biomass of macrofauna predators under ECM than AM tree species (Fig. S2a) may indicate that macrofauna predators are more likely to feed on soil fauna of smaller body size, because the pattern of macrofauna predator biomass was consistent with the abundance and biomass of mesofauna.

Properties of litter and forest floor, as the major food source and habitat, can affect the composition of soil fauna communities directly (food source) or indirectly via soil environment (habitat). In the present study, we found that tree species identity and mycorrhizal association significantly affected the properties of litter, forest floor, and soil (Table S1), which were in turn related to soil fauna abundance and biomass, as well as soil fauna diversity and evenness. The community composition of soil fauna has been found to be tightly linked to resource availability, vegetation composition, and abiotic environments in various ecosystems (Ding et al., 2017). Previous studies found that leaf litter quality was positively correlated with soil fauna diversity (Frouz et al., 2013; Hobbie et al., 2006), which agree with our findings that both soil taxonomic and functional diversity were higher under tree species that have higher litter quality. Soil fauna biomass was higher under ash, maple, and lime, whereas abundance was higher under the other tree species having lower litter quality. Soil fauna are probably more likely to feed on substrate with higher concentrations of nutrients, which has been reported in several nutrient addition experiments (Sun et al., 2017; Wang et al., 2016). In line with this we found that concentrations of N, P, Ca, and Mg in litter and forest floor were the most important predictors for soil fauna communities.

Tree species identity also had significant effects on soil properties (Table S1), among which soil pH appeared important for soil fauna communities. Soil pH covaries with many other soil properties such as base cation availability, soil organic matter, and nitrification, which can all be important factors affecting soil fauna communities (Mueller et al., 2012; Reich et al., 2005). For example, soil acidification would lead to loss of cations for earthworms such as Ca, but stimulates the mobilization of Al that is toxic for earthworms (Bowman et al., 2008; van Gestel and Hoogerwerf, 2001). Soil microclimate, as driven by tree species, is of great importance for soil fauna communities, because it not only directly determines environmental conditions, but also closely relates to food resource availability to soil fauna (Marcin et al., 2021; Meehan et al., 2020). For instance, high soil temperature and moisture would

facilitate microbial decomposition of plant litter, supporting food accessibility of soil fauna feeding on organic matter and microbes (García-Palacios et al., 2013; Hassall et al., 2006). In our study, moisture showed significant effects on almost all indices of soil fauna, but soil temperature was only important for functional *H*'. The limited importance of soil temperature on soil fauna communities found in our study may be attributed to that we only measured the instantaneous soil temperature at soil fauna sampling, which does not fully capture the annual variation. Overall, our results indicated that tree species across the six studied sites had significant effects on soil pH and moisture, and indirectly regulate soil fauna communities through these soil conditions.

The earthworm sampling as well as the litter and soil sampling were carried out in previous studies in the multisite common garden experiment (Schelfhout et al., 2017; Vesterdal et al., 2012), and these data sampled in different years were included in an integrated evaluation of soil fauna communities and their tree species-specific drivers. Given that tree species effects on soils develop slowly over time (De Schrijver et al., 2012; Ritter et al., 2003), it is likely that tree species differences in soil chemistry and earthworm communities would remain relatively stable or change slightly in the 8 years between sampling of earthworms and sampling of remaining soil fauna. As long as tree species differences in e. g., soil pH slowly widen with time, we also expect responses of earthworms to tree species to increase, and our earthworm response may therefore be slightly conservative in comparison with responses of remaining soil fauna. Bearing this in mind, we argue that the combined analysis of responses in soil properties, earthworms and other soil fauna from the multisite common garden experiment provides a solid evaluation of tree species effects on soil fauna communities.

5. Conclusions

Tree species, in terms of identity and mycorrhizal association, had substantial impacts on soil fauna abundance, biomass, and taxonomic and functional diversity and evenness. Total soil fauna biomass, taxonomic and functional diversity, and evenness were significantly higher under the AM tree species ash and maple that have higher litter quality compared with the ECM tree species, but total abundance showed the opposite pattern which was driven by a much higher number of mesofauna species under ECM species. The abundance and biomass of macrofauna were higher under AM tree species, but lower for mesofauna under AM tree species. Soil fauna communities were not perfectly separated by mycorrhizal association, which could particularly be attributed to the observation that soil fauna communities under lime were more similar to those under AM tree species. Driving factors in leaf litter, forest floor and soil in lime were also more similar to those of AM species. Among the variables that were significantly affected by tree species, the leaf litter and forest floor N, P, Ca, and Mg concentrations, as well as soil pH and moisture best explained the variation in soil fauna abundance, biomass, and diversity. Overall, the distinct results obtained across the unique multisite common garden experiment provide evidence of consistent tree species effects on soil fauna communities across the range of climatic and soil conditions represented by the six sites distributed over Denmark. The effects of tree species and their specific drivers on soil fauna found in our study provide useful information for evaluating the impact of tree species selection on soil biodiversity and its functions such as forest soil C sequestration and dynamics.

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.2021.115570.

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