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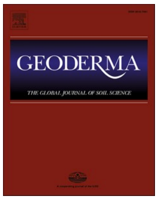

Functional traits in soil-living oribatid mites unveil trophic reorganization in belowground communities by introduced tree species

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ABSTRACT

Biodiversity loss and its potential threat on ecosystem functions call for a critical evaluation of human impacts on forest ecosystems. Management practices based on stand diversification offer a possible solution to biodiversity loss due to monoculture plantations, and these practices often involve planting introduced tree species. Although introduced non-native tree species may provide high economic returns, they may also form novel ecosystems and threaten local biodiversity, but this has been little studied. Here, we combined a taxonomic and trait-based approach and investigated communities of oribatid mites (Oribatida, Acari) across forest types of both native and introduced tree species in Northern Germany. Both trophic and life-history traits of oribatid mites were evaluated using native European beech (*Fagus sylvatica*) as reference, compared to native Norway spruce (*Picea abies*), introduced Douglas fir (*Pseudotsuga menziesii*) and beech-conifer mixtures. The abundance and diversity of oribatid mites were generally similar among monocultures of European beech, Norway spruce and Douglas fir. By contrast, species and trait compositions of oribatid mite communities were shifted to include more primary decomposers and more surface-living oribatid mites in Douglas fir, resulting in a trophic reorganization with less predators than in European beech forests. These results suggest that oribatid mites maintain a similar level of trait diversity regardless of forest type, but the changes in trophic guild composition and vertical distribution indicate greater availability of litter-based resources in Douglas fir than in European beech forests. The similar abundance and diversity of oribatid mite communities in Douglas fir mixed stands as in native European beech forests points to mixed forests as a promising management option for future forestry. Overall, our trait-based analyses provided insights into the changes of soil biota composition, revealing the impact of introduced tree species on the structure and functions of soil animal communities.

1. Introduction

A single tree species can support several orders of magnitude higher biodiversity, from canopy birds and ground beetles to soil invertebrates. Conserving these biota has become a pressing concern for sustainable forest management which requires to maintain the increasing societal

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demands for ecosystem goods and services (Hansen et al., 1991; Ammer, 2019). Exotic tree species have been introduced intentionally or unintentionally all around the world (Vitousek et al., 1997; Sapsford et al., 2020). Although these species may better cope with a changing climate and are preferred when providing greater economic returns (Mascaro et al., 2012; Glatthorn et al., 2023), introduced tree species may also form novel ecosystems and threaten biodiversity of native flora and fauna (Pejchar and Mooney, 2009; Schuldt et al., 2022). As an adaptive strategy, stand diversification better integrates introduced tree species into local forest management to maintain both timber production and biodiversity (Bolte et al., 2009; Ammer, 2016). Previous findings highlighted the positive effects of tree species mixtures on biodiversity, nutrient availability and forest productivity due to e.g., complementarity in light, water and nutrient use between tree species (Cremer et al., 2016; Ammer, 2019; Lwila et al., 2021). However, the effects of tree species mixtures on soil communities depend on environmental context (Ratcliffe et al., 2017; Lu and Scheu, 2021), may differ between native and introduced tree species (Korboulewsky et al., 2016), and are much better understood for aboveground than belowground biodiversity (Scheu, 2005; Bardgett and van der Putten, 2014).

Soil invertebrate communities differ from those above the ground by being constrained by the porous structure of the soil habitats (Ettema and Wardle, 2002; Ruamps et al., 2011), and more relying on detritus as food resources (Moore et al., 2004). Although tree biodiversity has been suggested to be of minor importance for soil biodiversity (Korboulewsky et al., 2016; Leidinger et al., 2021), tree identity may significantly modify the soil habitat and resource availability and thereby influence soil biodiversity (Sylvain and Buddle, 2010; Eissfeller et al., 2013). Litter characteristics are important for structuring soil animal communities and mixed forests comprising tree species of dissimilar traits may promote soil biodiversity (Hansen and Coleman, 1998; Kaneko and Salamanca, 1999). In Central Europe, the negative effects of introduced species such as Douglas fir on associated aboveground invertebrates were shown to be mitigated by planting mixed forests (Wildermuth et al., 2023). However, although soil animal communities were found to be resilient against changes in tree species and forest management intensity (Marian et al., 2020; Pollierer et al., 2021), soil invertebrates have been little studied in pure and mixed forests including native and introduced tree species. There is a particular lack of knowledge about changes in the functional diversity of soil animal communities due to changes in tree species composition, which is a major gap in our understanding of how forest ecosystems function (Bardgett and van der Putten, 2014; Weiss and Ray, 2019).

Trait-based approaches are a powerful tool for linking species traits to ecosystem functions. Functional traits are most heavily used by plant ecologists (Funk et al., 2017), but also have been adopted widely for investigating vertebrate and aboveground arthropod communities (McGill et al., 2006; Vandewalle et al., 2010). Trait-based analyses of soil invertebrates have provided insights into the functional response of belowground communities to biological invasions and the transformation of natural ecosystems by humans (Brousseau et al., 2019; Malloch et al., 2020). Soil invertebrates comprise multiple trophic levels, are vertically stratified along the soil profile, employ a range of reproductive strategies and are compartmentalized by body size, which relates to the complex architecture of soils (Scheu and Falca, 2000; Potapov, 2022; Maraun et al., 2023). These characteristics reflect the use of resources and habitat space as well as the variety of life-history strategies of soil invertebrates (McCary et al., 2021), providing the perspective to mechanistically understand their responses to environmental changes. However, trait-based approaches have rarely been used to investigate the response of soil invertebrates to introduced tree species. Generally, there is increasing interest in using multiple traits across trophic levels to better understand trait-environment relationships in soil animal ecology (Susanti et al., 2021; Auclerc et al., 2022; Chen et al., 2024).

Oribatid mites (Acari) are an abundant group of soil invertebrates in particular in forests (Wallwork, 1983; Maraun and Scheu, 2000). Globally, about 11,500 oribatid mite species have been described (Subías, 2004), with a remarkable fraction of the species (10 %) reproducing via parthenogenesis (Heethoff et al., 2009). This is at least ten times higher than the average of animal species (Norton and Palmer, 1991), and this high frequency of parthenogenetic reproduction is linked to resource availability and variability of environmental conditions (Scheu and Drossel, 2007; Maraun et al., 2019). Although utilizing only a fraction of the energy entering the soil, oribatid mites contribute to soil structure formation by producing discrete fecal pellets. Their feeding habits were primarily recognized as mycophagous and saprophagous (Seastedt and Crossley, 1984), but studies employing stable isotope analysis revealed high trophic diversity spanning three to four trophic levels (Schneider et al., 2004). Compared to other soil microarthropods, Oribatida have evolved a slow life-history strategy, with low fecundity and repeated reproduction (iteropary) during long adulthood (Norton, 1994; Pfingstl and Schatz, 2021). The slow life history likely reflects adaptation to low-quality food, which results in relatively stable densities over time in forest soils (Norton, 1994). Overall, due to their high functional diversity at multiple levels (trophic, reproduction, life history traits) and sensitivity to changes in soil conditions, oribatid mites are an interesting group for studying the impact of tree species composition on soil biodiversity and functions.

Here, we utilized both taxonomic and functional analyses to better understand the response of oribatid mite communities to pure and mixed coniferous forests, comparing pure stands of native European beech (*Fagus sylvatica* L.) with two important timber species, i.e., Norway spruce (*Picea abies* [L.] Karst.) and Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco.) as well as the mixtures of either of these conifers with European beech. European beech was chosen as reference due to its status as the climax species in lowland and lower montane regions in Central Europe (Leuschner et al., 2017). While native to Europe, Norway spruce has been planted outside of its native range, and Douglas fir was introduced from North America more than 150 years ago (Nicolescu et al., 2023). We hypothesized that (1) compared to European beech, the abundance as well as taxonomic and functional diversity of oribatid mites to be higher, and community and trait composition to be more shifted in Douglas fir than in Norway spruce forests. In addition, we hypothesized that (2) mixed stands have higher diversity and functions than monocultures, particularly in Douglas fir mixtures due to higher complementarity between tree species. (3) Trait community and trait based functional groups provide more mechanistic links between tree species composition and oribatid mite communities. Our hypotheses are connected by the overarching hypothesis that resource alteration caused by changes in tree species composition may affect the structure and functional organization of soil food webs. These changes may allow to uncover the functional consequences of different forest management practices as well as help to mechanistically understand the linkage between above- and belowground diversity in forests.

2. Methods

2.1. Study sites

The work was conducted in temperate forests at eight sites in Northern Germany (Fig. 1). At each site, plots of European beech (*F. sylvatica*, Beech), Douglas fir (*P. menziesii*, Douglas), Norway spruce (*P. abies*, Spruce), and conifer-beech mixtures (Douglas fir/European beech and Norway spruce/European beech, Do./Be. and Sp./Be. respectively) were established. Plot size was 2,500 m^2, mostly 50 m x 50 m. The studied stands were even-aged and state-owned forests. The distance between plots within a site ranged from 76 to 4600 m. The stands were dominated by mature trees of average age of 80 years. Focal tree species in pure stands comprised over 90 % of total basal area. In Douglas fir mixed stands, focal tree species comprised on average 34 % European beech and 58 % Douglas fir; in Norway spruce mixed stands,

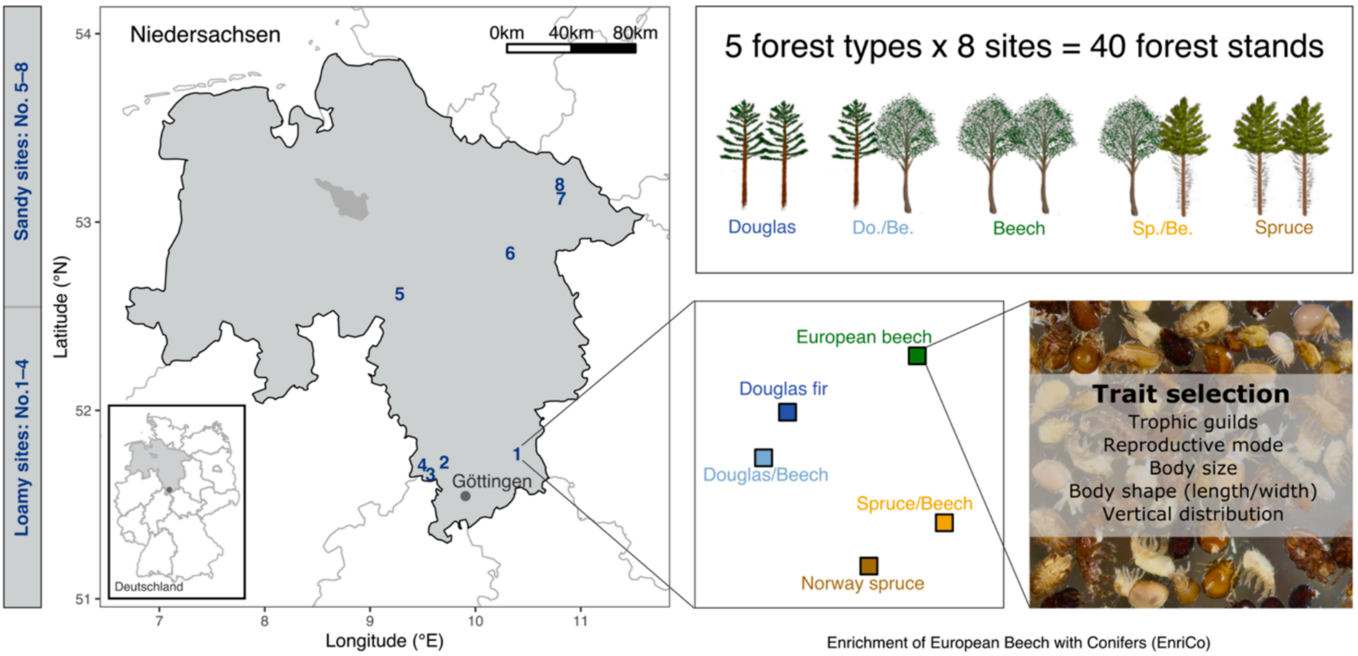

Fig. 1. Location of the sandy and loamy study sites in Lower Saxony, and distribution of the five forest types investigated at each site (monocultures of European beech, Douglas fir and Norway spruce as well as mixed stands of European beech either with Douglas fir [Do./Be.] or Norway spruce [Sp./Be.]).

focal tree species comprised on average 56 % European beech and 37 % Norway spruce (Ammer et al., 2020).

The eight sites covered a range of environmental conditions, with four loamy sites in the south (51.662°–51.770°) stocking on parent rock of either loess-influenced Triassic sandstone or mixtures of Paleozoic greywacke, sandstone, quartzite and phyllite, resulting in soil types of partly podzolic Cambisols and Luvisols. The mean annual precipitation at these sites is 821–1029 mm. The other four sandy sites in the north (52.621°–53.201°) were located on Podzols over parent material of out-washed sand, with a mean annual precipitation ranging from 672–746 mm. The distance between sites ranged from 5 to 190 km (Ammer et al., 2020). Site condition was included as an explanatory variable in data analyses because it was shown to strongly moderate the effects of forest type on soil decomposer communities (Lu and Scheu, 2021). More details on site characteristics and soil chemical properties are given in (Foltran et al., 2023).

2.2. Field sampling

Soil animals were sampled using a metal corer (Ø 5 cm) between November 2017 and January 2018, when soil animal density is high (Luxton, 1982; Migge et al., 1998). One soil core was taken close to the center of each plot and separated into litter (O_L), 0–5 and 5–10 cm soil depths. Considering the high abundance within each sample (Fig. S1) and our main interest of comparing different forest types, only one core was taken for animal identification per plot. Spatial patterns of soil oribatid mites were found to be autocorrelated at distances < 40 m (Minor, 2011). Therefore, our sampling allowed us to put efforts into investigating true replicates of forest types while fulfilling representative samples within plots. In total, 120 samples were analyzed (8 sites × 5 forest types × 3 depths). Soil cores were taken at an equidistance from trees of the same (pure stands) or different species (mixed stands). Neighborhood conifer proportions in mixed stands at 10 m radius of our sampling points agree well with the stand-level proportion of coniferous species (slope = 0.944, adjusted $R^2 = 0.997$ and slope = 0.916, adjusted $R^2 = 0.958$ for Douglas fir and Norway spruce, respectively). Soil arthropods were extracted using high-gradient heat extraction (Macfadyen, 1961). The extracted animals were collected in 50 % diethylene glycol and then transferred into 70 % ethanol for determination. We quantified the number of immature Oribatida and estimated their biomass based on their body length (supplementary method). Adult Oribatida were identified mostly to species level based on Weigmann (2006).

2.3. Environmental variables

To predict the community structure of oribatid mites, we measured root elements (C, N), litter mass, elements (C, N, P, K, Ca), bacteria, fungi and microbial biomass (C_{mic}) in organic layers (O_L, O_F). We primarily used variables from organic layers because the abundance and richness of oribatid mites decreased from litter to soil (see Fig. S1). These variables were measured by coordinated sampling in the framework of the Research Training Group 2300. In the first sampling campaign, fine roots (<2 mm) were collected from composite soil samples at an equidistance from neighboring trees; plots were split in four quadrats, and five samples were collected and pooled using a metal corer (Ø 8 cm, 0–10 cm in depth) in each of three quadrats. Fine root C and N concentrations were analyzed using an elemental analyzer (Vario MSA 2.7S, Sartorius Lab Instrument GmbH & Co. KG, Germany). In the second campaign, composite organic layer samples from four random points were taken using a metal frame (Ø 27 cm) and P, K, Ca concentration from O_L and O_F layers were determined by inductively coupled plasma-optical emission spectrometry (ICP-OES; Spectro Genesis, Spectro, Kleve, Germany) after pressure digestion with nitric acid (Foltran et al., 2023). In the third campaign, composite samples of three soil cores (Ø 5 cm) – spaced 5 m along a transect – were taken from each plot; from litter and 0–5 cm soil (mainly O_F) microbial biomass was measured by substrate-induced respiration and microbial guilds were determined by phospholipid fatty acids analysis (PLFA); litter mass was measured by drying litter at 50 °C for 48 h; C and N concentrations of litter were analyzed using an elemental analyzer as described in Lu and Scheu (2021). PLFA markers for microbial guilds included 18:2ω6,9 for fungi, and i15:0, a15:0, i16:0, i17:0, cy17:0, cy19:0, 16:1ω7 and 18:1ω7 for bacteria (Lu and Scheu, 2021). As abiotic variables, we included latitude and pH. Latitude was incorporated since it reflects variations in precipitation, soil types and temperature across study sites (Ammer et al., 2020; Schuldt et al., 2022). pH was measured using a ratio of sample to solution (1 M KCl) of 1:10 (wt:vol) for litter and 1:5 for O_F (Lu and Scheu, 2021).

2.4. Functional traits

(1) *Trophic guilds*. Based on bulk stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$), we differentiated four guilds, including primary decomposers, secondary decomposers, taxa that incorporate calcium, and predators/scavengers (Schneider et al., 2004; Fischer et al., 2010, 2014; Bluhm et al., 2016; Magilton et al., 2019). Primary decomposers are saprophagous and predominantly feed on litter; secondary decomposers are mainly mycophagous. Taxa with calcium cuticles comprised species with endophagous immature stages and included primary and secondary decomposers; it was included as separate guild for their different stoichiometry demands (Warnke et al., 2023). Predators/scavengers occupy high trophic levels and likely feed on microfauna.

(2) *Vertical distribution* reflects habitat use (Pande and Berthet, 1975; Mitchell, 1978). Depth distribution of each species was estimated by abundance-weighted mean of depths for each species in litter, 0–5 and 5–10 cm soil depth (mean of 2.5, −2.5, −7.5 cm, respectively). Higher values suggest more surface than soil dwelling taxa.

(3) *Body shape* reflects adaptation to spatial micro-niches or pore space in soil habitats and access to resources (Schaefer and Caruso, 2019), and was calculated as the ratio between body length and width. Body length was measured from the tip of the prodorsum to the posterior edge of the notogaster, and body width as the widest distance of the notogaster; the gnathosoma and apophysis were not included. Body size was collected from literature complemented with measurements in this study (Table S1). Oribatid mites included a spectrum of globular to elongated body shapes, ranging approximately from 1.2 (globular) to 3.5 (elongated) in this study.

(4) *Body size* is a master trait reflecting energy use and life history strategies (Peters, 1983). Larger oribatid mites produce larger faces, which is linked to comminution and breakdown of litter. Large body size also enables individuals to be more efficient in extracting energy from low-quality food (Brown and Maurer, 1986). Body size influences vertical distribution of oribatid mites, with larger species being restricted to surface layers (Pande and Berthet, 1975; Luxton, 1981a).

(5) *Reproductive mode* is a life-history trait that includes sexual and parthenogenetic reproduction. A high number of parthenogenetic species coexists with sexual species of oribatid mites in forest soils (Norton and Palmer, 1991). The prevalence of sexual reproduction in a community reflects resource limitation, with parthenogenetic species thriving in habitats with abundant resources, supporting large populations (Scheu and Drossel, 2007; Mumladze et al., 2015; Maraun et al., 2019). Sexual individuals accounted on average for 33.7 % (range from 0 to 80 %) of all individuals in studied forests.

Traits were chosen to reflect how oribatid mite species partition food and habitat, as well as life-history strategies (Table S1). The numerical traits, body shape and vertical distribution, are weakly correlated with body size ($|r| < 0.24$), thereby providing complementary information for trait-based analyses.

2.5. Calculation of functional diversity and community metabolism

All analyses were performed in R 4.0.3 (R Core Team, 2023). Distance-based functional diversity indices were computed using the FD package (Laliberté et al., 2014). Functional evenness and divergence were derived in a multidimensional trait space taking population abundance into account (Villéger et al., 2008). Functional evenness describes the regularity of the distribution of species within the functional space defined by multiple traits, while functional divergence quantifies the degree of trait dispersion from the centroid in functional space. In addition, total biomass and metabolic rate were also computed. Fresh body mass of oribatid mites was calculated from body length and width based on a power function (Lebrun, 1971; Newton and Proctor, 2013); community metabolism was calculated as the sum of individual metabolic rates with group-specific coefficients (Ehnes et al., 2011; Potapov et al., 2019; Supplementary methods). Functional richness was highly correlated with species number ($r = 0.72$) and therefore functional richness is not presented in the results.

2.6. Statistical analysis

Linear mixed-effects models (LMMs) were used to analyze the effects of forest type (European beech, Douglas fir, Norway spruce, and two conifer-beech mixtures), site condition (loamy and sandy sites) and their interactions on oribatid mite diversity. The response variables included abundance, biomass, community metabolism, richness, functional evenness and divergence as well as guild compositions and community weighted means of oribatid mites. The eight sites were included as random factor. Prior to analyses, the abundances of specimens per taxon from the same soil cores were summed up across sample depths, and data were log- or sqrt-transformed to meet model assumptions. The effects of site condition did not interact with forest type and therefore we focused on main effects of forest type. We used the *emmeans* function for estimating marginal means, and the *contrast* function to test the significance among forest types using European beech as reference (Lenth, 2019). Model residuals were plotted to validate normality and homoscedasticity assumptions.

Nonmetric multidimensional scaling (NMDS) and permutational multivariate analyses of variance (PERMANOVA) were used to analyze community structure of species and traits using Bray-Curtis dissimilarities. Community trait compositions were calculated using abundance weighted means of trait values. Numeric trait variables were standardized to the range of zero and one. For categorical traits, dummy variables were used in the analysis (0 or 1). Only species that occurred in more than one plot were included in species composition analyses. Community structure was not compared in each sample depth, because depth (litter and soil) did not significantly interact with forest type (PERMANOVA, $F_{4,58} = 1.19$, $P = 0.665$). For each soil core the number of individuals of each species present in 0–5 and 5–10 cm were summed up because low densities of oribatid mites in 5–10 cm depth (Fig. S1). Only adults of oribatid mites were included for trait and community analyses. Standardized environmental variables ($r < 0.8$) that predicted oribatid community structure were fitted in the NMDS using “envfit”. Further, multivariate homogeneity of dispersion (beta-diversity) between forest types was assessed using “betadisper” (Anderson et al., 2006). Beta and gamma diversity per forest type was analyzed using the abundance-based rarefaction and extrapolation functions of the iNEXT package. We used Hill number $q = 0$ for the effective number of all species including rare species (Hsieh et al., 2016). The package ‘nlme’ was used for LMMs (Pinheiro et al., 2019), and ‘vegan’ was used for NMDS (‘metaMDS’) and PERMANOVA (‘adonis2’ and “pairwise.adonis”).

3. Results

A total of 7,011 individuals of oribatid mites were recorded, belonging to 71 species. *Oppiella nova* (Oudemans, 1902), *Suctobelbella* spp. Jacot, 1937, *Oppiella subpectinata* (Oudemans, 1900) and *Tectocepheus velatus velatus* (Michael, 1880) were the most abundant oribatid mite taxa, together accounting for 49.4 % of the total individuals of adults. Thirteen species were singletons and eleven species were doubletons. Juveniles constituted 54.0 % of the total number and 28.8 % of the total fresh mass of oribatid mites. Total density of adult oribatid mites was on average $63.1 \times 10^3 \pm 13.1 \times 10^3$ (mean ± SE) m^{-2}, total fresh biomass averaged 755.0 ± 111.0 mg m^{-2} and community metabolism averaged 1.74 ± 0.22 J m^{-2} h^{-1} (Fig. 2). The average alpha species richness per sample was 13.4 ± 0.89. Total fresh biomass in Norway spruce was 2.14 times higher than that in European beech (509 $\pm$ 134 mg m^{-2}) (Table S2, Fig. 2).

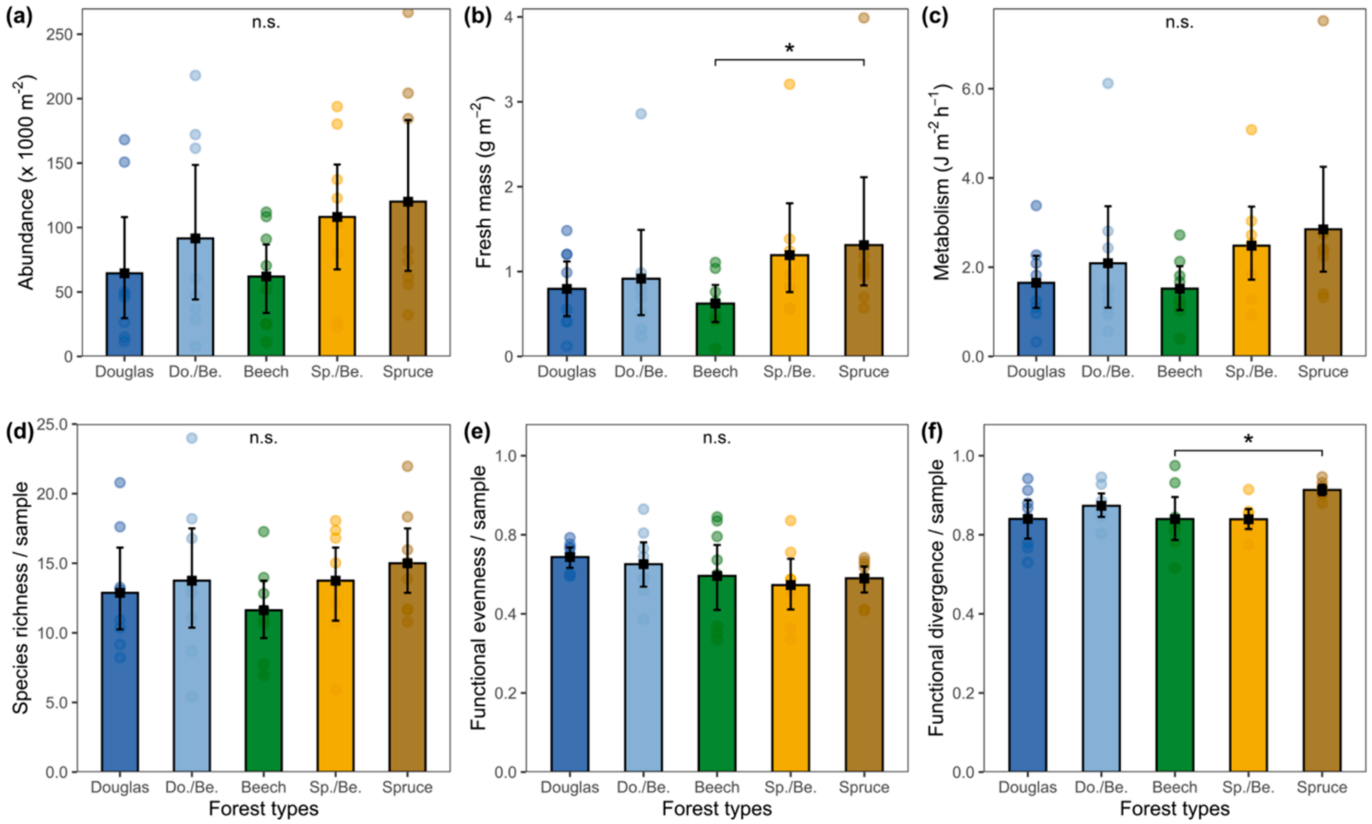

Fig. 2. Abundance (a), fresh biomass (b), metabolism (c), species richness (d), functional evenness (e) and functional divergence (f) of soil oribatid mite communities in five different forest types: European beech (Beech), Douglas fir (Douglas), Norway spruce (Spruce), and two conifer-beech mixtures (Do./Be. and Sp./Be.). Error bars represent 95 % confidence intervals. Significant differences between European beech and other forest types are denoted by asterisks at lines linking the respective forest types (* $P \leq 0.05$; n.s. $P > 0.05$).

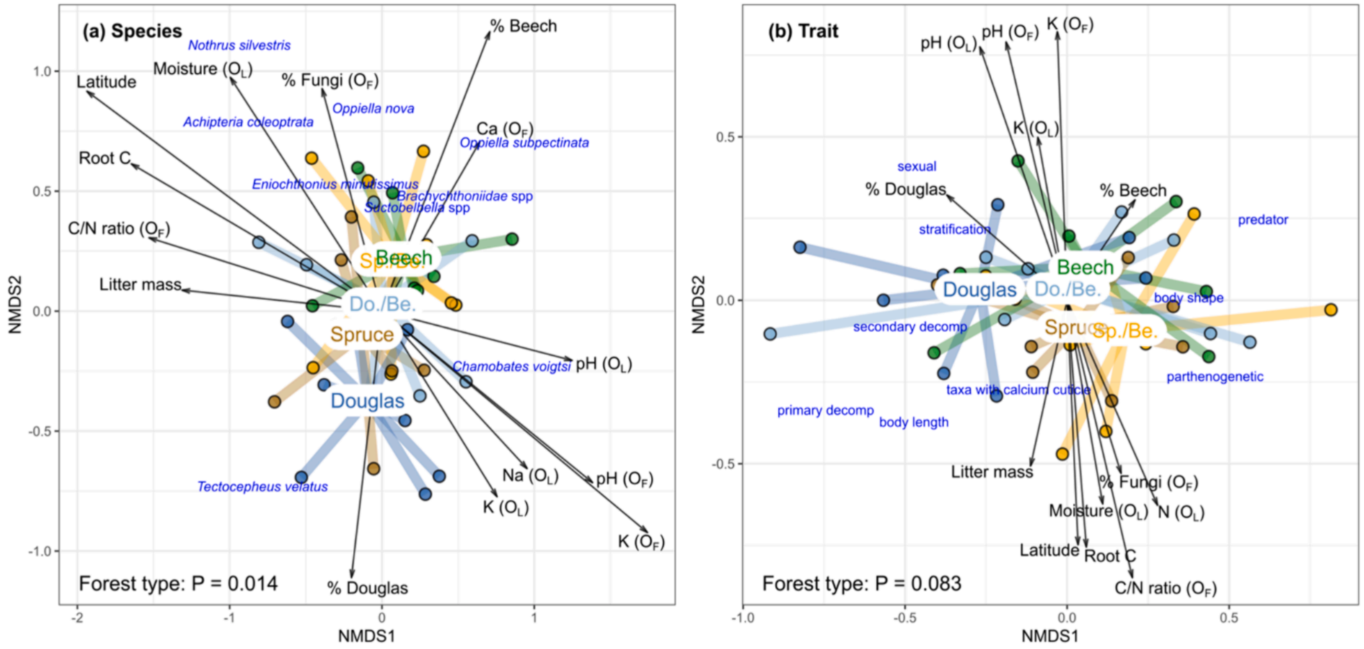

Fig. 3. Nonmetric multidimensional scaling (NMDS) of oribatid mite species (a) and trait composition (b) across five forest types, including European beech (Beech), Douglas fir (Douglas), Norway spruce (Spruce), and two conifer – beech mixtures (Do./Be. and Sp./Be.). The NMDS stress value for oribatid species is 0.27 and for trait composition 0.13 (k = 2). Environmental variables significantly correlating with the distribution of species and traits are indicated by arrows ($P \leq 0.05$). C, N, P, K, Na and Ca are concentrations of elements. Proportions of European beech (% Beech) and Douglas fir (% Douglas) are based on tree basal area at breast height. The nine most abundant taxa in (a) and all traits in (b) are given in blue.

On average, in monospecific and mixed stands of conifers 3.2 ± 0.3 oribatid mite species occurred per sample which were not found in European beech forests, and this was similar in Douglas fir and Norway spruce forests (Fig. S2). Further, functional divergence was 0.089 ± 0.039 higher in Norway spruce than in European beech forests (Fig. 2f). At a landscape scale, beta and gamma diversity were similar among forest types (Fig. S2).

Oribatid mite species and trait communities differed among forest types with the trait composition being only marginally affected (Table S3, Fig. 3; PERMANOVA, $F_{4,30} = 1.47$, $P = 0.014$ and $F_{4,30} = 1.71$, $P = 0.083$, respectively). Species composition in Douglas fir forests differed most from that in European beech forests ($P = 0.003$), with Norway spruce and mixed forests of Douglas fir and European beech being in between. Trait composition further separated Norway spruce and mixed stands of Norway spruce and European beech from Douglas fir forests along the second NMDS axis, with the difference being significant between Douglas fir and mixed Norway spruce forests ($P = 0.021$). Sample dissimilarly suggested no overdispersion in oribatid mite assemblages across forest types for both taxonomic and functional assemblages (betadisper, $Ps > 0.69$). Mixed forests generally had intermediate taxonomic and functional composition compared to the respective monocultures.

Site condition strongly affected species and trait composition of oribatid mites (PERMANOVA, $F_{1,30} = 2.88$, $P = 0.002$ and $F_{1,30} = 3.18$, $P = 0.033$, respectively). The differences in species composition between site conditions were mainly due to changes in latitude and litter nutrients (Fig. 3a). The concentrations of K and Na were highest in the litter of Douglas fir, while in beech fungi in 0–5 cm soil (mainly O_F) and litter Ca concentrations were highest (Table S4).

The abundance of the dominant taxa *Oppiella nova*, *Suctobelbella* spp. and *Oppiella subpectinata* was lower in Douglas fir than in European beech forests (Fig. 3a, 4). Guild composition and community weighted mean of oribatid mite traits varied with forest types (Figs. 5, S3). The proportion of predatory/scavenging oribatid mites was lower in Douglas fir (−31.4 %) than in European beech forests (Fig. 3b, 5a). The relative proportion of oribatid mites that incorporated Ca in their cuticle was on average 5.3 % higher in Norway spruce than in European beech forests (Table S5, Figs. 4, 5b), while the proportion of primary decomposers was higher in Norway spruce (+13.5 %) than in European beech forests (Fig. 5c). The proportion of sexually reproducing oribatid mites in European beech (33.7 %) was significantly higher than in mixtures of European beech and Norway spruce (17.5 %; Fig. 5d), and the vertical distribution of oribatid mites were more to the surface in Douglas fir than in European beech forests (Fig. 5f).

4. Discussion

We studied species and trait composition of oribatid mite communities in pure and mixed forests including native and introduced tree species. Shifts in species and trait composition rather than overall changes in aggregated diversity metrics best revealed functional changes in tree – decomposer relationships. This suggests that species and trait composition provide insights linking belowground communities with changes in tree species composition. Collectively, our data suggest that Douglas fir alters oribatid mite guild composition towards more primary decomposers and surface-living oribatid mites, indicating a shift towards the use of more litter-based resources. By contrast, tree mixtures diminished shifts in species and trait composition of oribatid mites compared to European beech forests, suggesting that stand diversification serves as a promising management practice mitigating potentially negative effects of planting introduced tree species such as Douglas fir.

4.1. Functional stability of soil oribatid mite assemblages

Rejecting our first hypothesis, metrics of diversity (e.g., species richness, density, biomass) did not significantly differ between Douglas fir and European beech forests. As species and trait diversity are major components of their functioning (Naeem et al., 1994), this suggests that the collective functions of oribatid mites are little compromised by

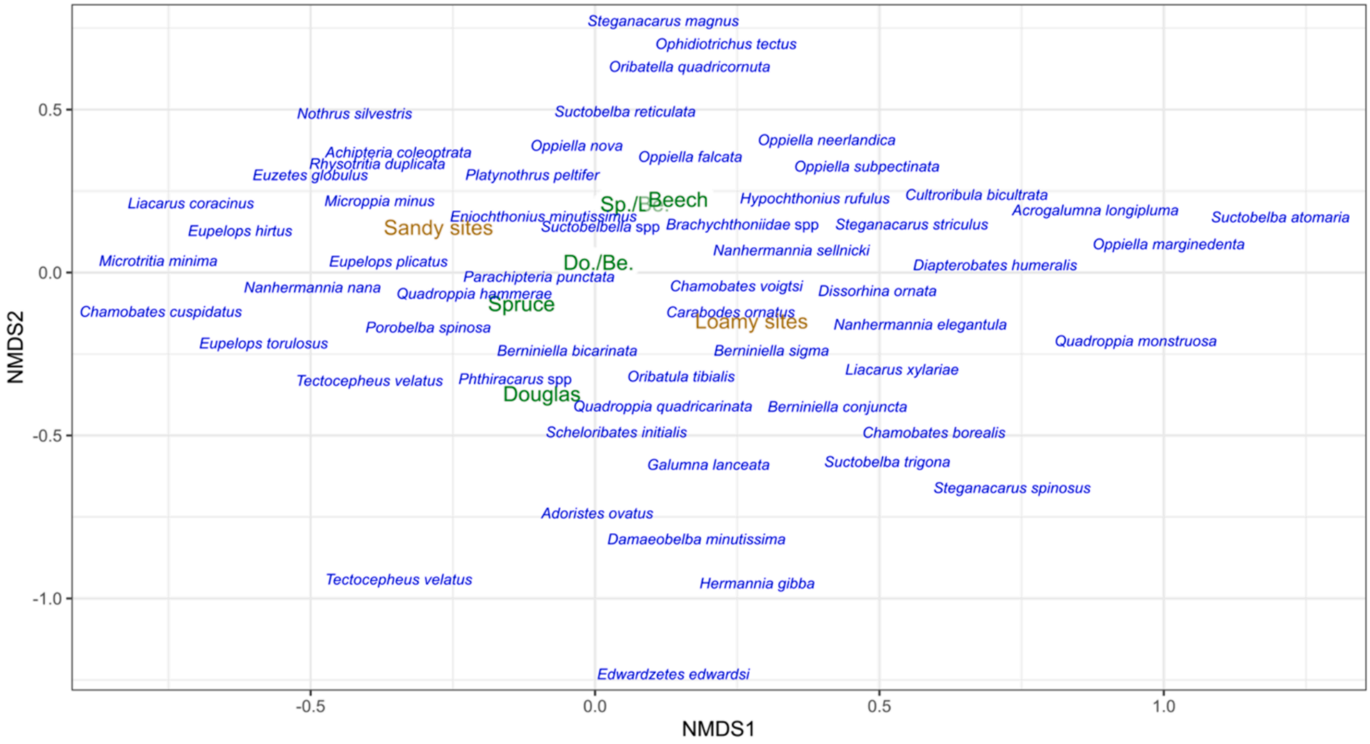

Fig. 4. Nonmetric multidimensional scaling (NMDS) of oribatid species across five forest types, including European beech (Beech), Douglas fir (Douglas), Norway spruce (Spruce) and two conifer – beech mixtures (Do./Be. and Sp./Be.) at sandy and loamy sites.

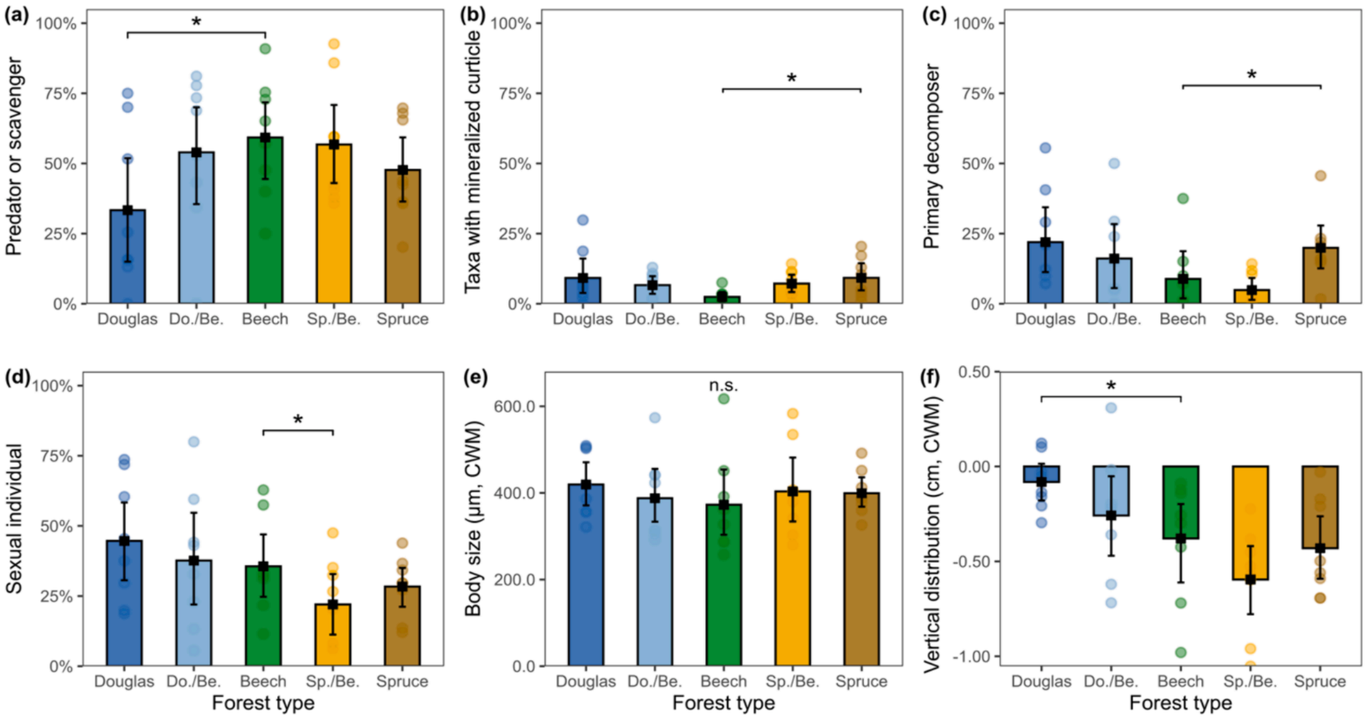

Fig. 5. Proportions of predator/scavenger oribatid mites (a), taxa that incorporate calcium (b), primary decomposer oribatid mites (c) and sexual reproducing individuals of oribatid mites (d) as well as community-weighted-mean (CWM) oribatid mite body size (e) and mean vertical distribution of oribatid mites (f) in five forest types, including European beech (Beech), Douglas fir (Douglas), Norway spruce (Spruce), and two conifer-beech mixtures (Do./Be. and Sp./Be.). Error bars represent 95 % confidence intervals. Significant differences between European beech and other forest types are denoted by asterisks at lines linking the respective forest types (* $P \leq 0.05$; n.s. $P > 0.05$).

planting Douglas fir despite their changes in functional composition. Further supporting this conclusion, species richness of oribatid mites was similar across all forest types from local to landscape scales. All trophic levels or guilds of oribatid mites were present across sites and the trophic diversity of oribatid mites, spanning over three trophic levels, likely contributed to the stability of diversity metrics across forest types (Schneider et al., 2004; Lu et al., 2022). The similar collective community attributes of oribatid mites among different forest types also suggest that the impact of forest types is not as strong as other disturbances such as clear-cutting or drought stress, which have been shown to reduce oribatid mite abundance and richness (Lindo and Visser, 2004). However, as a note of caution, the non-significant results may stem from low sampling intensity within plots, but previous studies also corroborated our finding that the total abundance and richness of oribatid mites are resistant to changes in tree species composition (Migge et al., 1998; Bluhm et al., 2016). Additionally, if species loss is constrained within certain thresholds, it may have little effect on functionality as long as a diversity of traits is maintained (Mori et al., 2013). Although there also are exceptions (Caruso et al., 2020), this may apply to oribatid mites as their diversity has been shown to be little affected by forest age or by planting non-native tree species (Migge et al., 1998; Sylvain and Buddle, 2010; Erdmann et al., 2012). Organic layers in forests provide a wide range of food resources and stable environmental conditions (Moore et al., 2004), and this likely contributes to high resistance of detritus-based food webs against environmental changes including the plantation of introduced tree species or mixtures (Sylvain and Buddle, 2010; Pollierer et al., 2021).

Mixed forests did not support higher abundance and diversity of oribatid mites also rejecting our second hypothesis. Although Douglas fir was introduced from North America, whereas Norway spruce is native, admixing of each of these conifer tree species to beech stands resulted in a community structure of oribatid mites similar to native beech stands, suggesting that it is the identity of tree functional groups (conifer vs. deciduous) structuring oribatid mite communities. Our sampling intensity within plots may underestimate local species diversity, and further studies are required to investigate biodiversity patterns at varying spatial scales as well as including other seasons (Luxton, 1981b; Chen et al., 2024). However, in agreement with our results, studies on spiders and ground beetles also found intermediate diversity in mixed stands compared to monocultures (Kriegel et al., 2021; Matevski et al., 2021). Recent studies suggest tree mixtures to contribute to higher beta and gamma diversity of larger organisms such as birds (Schuldt et al., 2022), whereas results of our study indicate that this does not apply to soil microarthropods. This is likely due to the small size, trophic diversity of oribatid mites and buffering conditions in soil, arguing for the need to also consider smaller scale habitats and heterogeneity for evaluating consequences of planting forests of introduced tree species and mixed forests.

4.2. Connecting oribatid mite guild structure with resource availability

We examined the impact of forest type on the trait composition of soil oribatid mites using a range of traits related to their resource and habitat use. Douglas fir forests were characterized by more primary decomposers and less predatory species, and shifted oribatid mite communities more than Norway spruce suggesting that the impact of tree species vary even within functional groups such as conifers. However, we did not identify any soil or litter characteristics correlating with these traits suggesting that the measured biotic and abiotic variables at bulk scale provide limited information on the structuring forces linking them with forest type (Maraun and Scheu, 2000). Further, high cover of understory vegetation in Douglas fir stands due to more open canopies (Glatthorn et al., 2023) may have contributed to the dissimilarity of oribatid mite traits between Douglas fir and European beech. Norway spruce monocultures were characterized by thick organic layers associated with high biomass and functional divergence of oribatid mites, suggesting more specialized niche exploitation of abundant species. These contrasting effects of tree species on different guilds of soil microarthropods resulted in the reorganization of the trophic structure of oribatid mite communities. As guilds of soil mites are associated with different food resources (Zhang et al., 2023), the shift in guild structure suggests changes in coniferous forests towards more litter-based resources, especially in Douglas fir. This is consistent with the relatively high abundance of saprotrophic fungi in Douglas fir (Likulunga et al., 2021; Lu and Scheu, 2021), supported further by the presence of more litter-inhabiting oribatid mites in Douglas fir compared to European beech.

Many ptychoid species have endophagous juveniles such as *Phthiracarus* spp., *Rhysotritia duplicata* and *Microtritia minima*, which are abundant in temperate forests (Luxton, 1981b). These juveniles often burrow in decaying needles and are more abundant in coniferous than in deciduous forests, suggesting that decaying coniferous needles including those of Douglas fir provide favorable food and habitat than decaying European beech leaves. Our study reveals that considering trophic guilds contributes to a mechanistic understanding of the linkages between resource availability and microarthropod communities in forests of native and introduced tree species. Further, oribatid mites include parthenogenetic and sexually reproducing species, with parthenogenesis being the dominant form in forest oribatid mite communities (Maraun et al., 2019). Results of our study indicated that the frequency of sexually reproducing oribatid mites varies among forest types and is higher in Douglas fir forests, especially at loamy sites (J.-Z. Lu, unpubl. data). This indicates more limited resource supply and more heterogeneous resource distribution in Douglas fir forests, conditions which have been suggested to favor sexual over parthenogenetic reproduction (Scheu and Drossel, 2007; Song et al., 2011).

Recent evidence highlights the significance of root-derived resources in structuring belowground communities in both temperate and tropical forests (Pollierer et al., 2007; Zhou et al., 2023). Shortage of root-derived resources in particular negatively impacts small oribatid mites such as *Oppiella nova* (Remén et al., 2008) and this species was also negatively affected by Douglas fir in our study. Douglas fir stands at northern sandy sites are characterized by lower microbial biomass and lower fine root biomass compared to European beech forests (Lu and Scheu, 2021; Lwila et al., 2021), and this likely was associated with reduced root-derived resources. These findings are consistent with previous studies indicating that in comparison to Norway spruce and European beech forests, Douglas fir forests shifted fungal communities from symbiotrophs towards more saprotrophs (Likulunga et al., 2021). Furthermore, more surface distributed oribatid mite assemblages indicate a shift towards litter-based resources in Douglas fir compared to European beech forests.

In contrast to earlier studies, which assumed oribatid mites to be of limited use for assessing changes in land use (Maraun and Scheu, 2000; Lindo and Visser, 2004), our findings together with others indicate that oribatid mites may in fact be sensitive indicators of environmental change in particular informative when considering their traits (Minor et al., 2017; Salazar-Fillippo et al., 2023). Although trait-based approaches require additional effort, they can be more powerful in identifying mechanisms responsible for effects of land-use changes on animal communities including those in soil (Zaitsev et al., 2002; Vandewalle et al., 2010; Minor et al., 2017). Incorporating multiple traits related to the use of habitat and resources allows linking changes in species composition to ecosystem-level processes such as resource availability. Overall, our study underscores the efficacy of trait-based approaches for analyzing the response of soil invertebrates to changes in forest tree species composition. Trait-based approaches in soil animal ecology therefore are a promising tool for the development of sustainable management practices for forest ecosystems.

5. Conclusions and management implications

The results suggest that the abundance, richness and community metabolism of oribatid mites are highly invariant across forest types, pointing to high resilience of soil animal communities. However, introduced Douglas fir shifted the taxonomic and functional composition of oribatid mite communities, but this was less pronounced in mixed beech forests than in pure Douglas fir forests. This suggests that, from a conservation perspective, mixtures of tree species are likely to mitigate potential impacts of introduced tree species on soil animal communities. The species and trait composition of oribatid mites emphasize the necessity to investigate oribatid mites at high taxonomic resolution to identify the response of oribatid mite communities to environmental change. Soil functional ecology, linking taxonomy and traits, promises a better understanding of tree-soil relationships. Functional analysis of soil oribatid mites highlights the importance of combining habitat use, life-history tactics and reproductive mode to better understand the assembly of soil animal communities, but also how environmental change alters the ecosystem-level consequences of shifts in soil animal community composition.

CRediT authorship contribution statement

Jing-Zhong Lu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christian Bluhm:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Estela Foltran:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation. **Carmen Alicia Rivera Pérez:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation. **Christian Ammer:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Tancredi Caruso:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Methodology. **Jonas Glatthorn:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Conceptualization. **Norbert Lamersdorf:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Andrea Polle:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Dorothee Sandmann:** Writing – review & editing, Validation, Resources, Methodology. **Ina Schaefer:** Writing – review & editing, Validation, Supervision, Resources, Methodology. **Andreas Schuldt:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition. **Mark Maraun:** Writing – review & editing, Validation, Supervision, Resources, Methodology. **Stefan Scheu:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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

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