


ARTICLE

Species diversity of forest floor biota in non-native Douglas-fir stands is similar to that of native stands

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Cultivation of non-native tree species is a promising option to adapt managed forests to climate change. However, consequences of non-native tree species on flora, fauna, and microorganisms that occur in forest ecosystems (forest associates) need to be considered when managing forests. We lack a solid understanding of how cultivating non-native tree species in pure stands and in mixture with native tree species impacts abundance and species diversity of forest associates. We compared abundance, alpha-, beta- and gamma-diversity of eight forest-floor-associated taxa that are relevant for ecosystem functioning (including fungi, plants, arthropods, and small mammals) between different forest ecosystems. We addressed pure stands of non-native coniferous Douglas-fir (*Pseudotsuga menziesii*) and two native species, broad-leaved European beech (*Fagus sylvatica*) and coniferous Norway spruce (*Picea abies*), as well as mixed stands of European beech with each conifer in two regions with differing site conditions in temperate Northwest Germany. Diversity indices revealed differences among species groups. Gamma-diversity and alpha-diversity of forest associates in Douglas-fir and spruce stands were usually higher than in beech stands. Estimates of species diversity of mixed stands are intermediate between estimates for the respective pure stands. Differences in the diversity between the two study regions were highly taxon specific with no clear support for a general trend toward a higher or lower species diversity of forest associates depending on site quality. Abundance values show a pattern similar to our diversity estimates, but with a higher statistical uncertainty. Non-native Douglas-fir stands provided habitats to support associated species communities of equally high or higher diversity than stands of native beech or spruce. Mixed stands of non-native and native tree species may be a management option to achieve different goals, that is, to provide habitats for species

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that are strictly associated with beech and to increase resilience to climate change. However, the overall diversity of forest-floor-associated biota is not improved by cultivating Douglas-fir or spruce in mixture with beech.

KEYWORDS

adaptive management, biodiversity, Douglas-fir, European beech, mixed forest, multidiversity, Norway spruce

INTRODUCTION

Climate change has a strong impact on the composition and functioning of forest ecosystems around the world. As climatic extremes are predicted to occur even more frequently and at higher intensities in the future (Pfleiderer et al., 2019), forest management needs to adopt measures to ensure that production forests continue to provide a broad range of ecosystem goods and services (Bolte et al., 2009).

Due to uncertainties regarding future global greenhouse gas emissions and imperfect knowledge of how forests will respond to a changing climate, predictions about forest ecosystem dynamics are highly uncertain (Lindner et al., 2014). Depending on the global greenhouse gas emissions, global change may proceed rapidly and at least on some sites cultivation of non-native species that are expected to be well adapted to future conditions is one of several adaptive management strategies that have the potential to maintain provision of forest services (Bolte et al., 2009). In the end, a reasonable mix of all available adaptive management measures may be the safest option to be best prepared for a range of scenarios and to increase options for action of forest managers in the future (Glatthorn et al., 2023). To enable informed silvicultural decisions, the response of the ecosystem to different adaptive management measures should be studied in detail.

The consequences of non-native tree species on the flora, fauna, and microorganisms (forest associates) are one of the aspects that need to be considered when managing forests. Many species groups in forests depend on trees as food source or as habitat. Cultivation of non-native species may lead to a reduction of insect diversity or abundance in forests due to a missing adaptation of native insect communities to the new potential host species and the environmental conditions it is creating (Tallamy, 2004). A promising option to reduce the side effects of promoting non-native species is the establishment of mixed stands together with native tree species (Brundu et al., 2020). Additionally, stands with a higher tree species diversity may increase diversity and abundance of forest associates due to a higher habitat heterogeneity (Brockerhoff et al., 2017).

In Central Europe, non-native Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is a popular choice to replace coniferous species such as Norway spruce (*Picea abies* (L.) Karst.), which has suffered greatly in Central Europe from large storm, drought, and insect calamities recently (Thonfeld et al., 2022). Within the geological period of the Pliocene, the genus *Pseudotsuga* was present in Central Europe but later went extinct (Kunzmann, 2014). Douglas-fir was introduced to Central Europe from its native distribution range in the Pacific Northwest of North America in the 20th century (van Loo & Dobrowolska, 2019). Even though Norway spruce is native to Central Europe, in the study region it was planted outside its natural range, which is in montane regions at higher elevations (Leuschner & Ellenberg, 2017).

However, we lack a solid understanding of how cultivating Douglas-fir and Norway spruce in pure and mixed stands together with beech influences the species composition of forest associates compared with more natural stands that are dominated by European beech. Due to its high competitive strength, European beech would dominate a large part of late successional forests in Europe without intervention by forest management (Bolte et al., 2007; Leuschner & Ellenberg, 2017). In the last remnants of primeval European beech forests in Eastern Europe, beech proportion is higher than 95% (Hobi et al., 2015). Therefore, beech stands are a good reference to study the influence of other tree species on regional ecosystems.

Besides the abundance of forest associates, small-scale (plot-level) alpha-diversity and large-scale (landscape-level) gamma-diversity and beta-diversity (spatial distinctness of community composition) of forest associates are relevant as they are closely related to many ecosystem processes such as net primary productivity, nutrient fluxes, and to forest management regimes (O'Connor et al., 2017; Pasari et al., 2013; Schall et al., 2018). As the long-term maintenance of these ecosystem processes and their dynamics is crucial for the integrity of forest ecosystems, abundance and species diversity of forest associates are important indicators for sustainable forest management.

Forest associates may have lower diversity in forest stands that are dominated by non-native tree species in

comparison to stands of native tree species (Oxbrough et al., 2016). Similarly, native tree species that are cultivated in stands outside their natural range (such as Norway spruce in most regions of Central Europe) may host species communities that are less abundant or diverse in comparison to locally adapted native species (Horák et al., 2019; Matevski & Schuldt, 2021). Reasons for this may be that some native forest associates are host specific, or that certain structural or functional characteristics of non-native tree species are unsuitable for some native species (Hunter, 1999). However, there are many examples of non-native tree species and tree species grown outside their natural range that provide habitats for abundant and diverse communities of associated species (Brockerhoff et al., 2008). An equally high diversity of forest associates in non-native and in native stands may occur, for example, if the diversity of forest associates is mainly driven by factors such as light conditions, stand age, or stand structure and not by direct species identity effects or if non-native species are embedded in a matrix of native forest types (Hunter, 1999).

Since there is no consistent picture of how cultivating non-native tree species affects flora and fauna (Ammer et al., 2018), it is necessary to provide a sound basis for decision-making. Such a picture needs to include stand types representing pure and mixed stands, differing site conditions, and should focus on diverse taxa of associated species. Therefore, our study design addresses the composition of eight different species groups that are associated with the forest floor (soil and root fungi, vascular plants, springtails, oribatid mites, small mammals, ground beetles, and spiders) in different stand types. By including species groups from different trophic levels that are relevant for multiple ecosystem processes such as nutrient cycling, litter decomposition, herbivory, and predation, and by covering stands with different site conditions, our results allow conclusions about the impacts of tree species choice on ecosystem functioning. Site conditions range from more favorable sites with higher precipitation, lower temperatures, and more loamy soils to less favorable sites with lower precipitation, higher temperatures, and more sandy soils. We implemented a study design that replicates five different stand types (the so-called quintets) of pure stands of beech, Douglas-fir, and Norway spruce as well as mixed stands of beech with each of the conifers. This study design enabled us to analyze differences between broad-leaved and coniferous tree species, between native and non-native tree species, and between mixed and pure stands. Thus, the aim of this study was to better understand the consequences of cultivating non-native Douglas-fir and native Norway spruce in pure stands and in mixture with native European beech on the abundance and diversity of forest associates in Central Europe. More specifically, we tested the following four hypotheses.

1. Species diversity and abundance of forest associates are lower in pure non-native Douglas-fir or native but not site-adapted Norway spruce stands than in native European beech stands.
2. Species diversity and abundance are higher in native Norway spruce stands than in stands of non-native Douglas-fir.
3. Species diversity and abundance of forest associates are higher in mixed than in pure stands.
4. Species diversity and abundance of forest associates are higher in stands with more favorable site conditions.

All hypotheses were tested for all species together and for a subset of species that are characteristic of forest ecosystems, to study whether the forest-typical character of the native stands was compromised by introduction of a non-native species.

METHODS

Study design and study area

The study was part of a research project with forest plots located in the German state of Lower Saxony, Northwest Germany on eight units (quintets) of five rectangular study plots 0.25 ha in size (40 plots in total) distributed across the entire study area. Plots are located in even-aged, state-owned forests (Ammer et al., 2020). Most plots are square-shaped with an edge length of 50 m, some have a rectangular shape. The climate of the study area is temperate (Table 1). Four of the eight quintets were established in the uplands of Lower Saxony (numbers 1–4, Table 1), in the Solling and Harz mountain ranges, and four quintets were established in the lowlands of Lower Saxony (numbers 5–8, Table 1). The plots in the uplands show more fertile growing conditions with a higher annual precipitation and soils with high clay content (Foltran et al., 2020).

Each quintet consists of plots in three pure and two mixed-species stands. On average, the stands have an age of 80 years (the overall range lies between 42 and 130 years, Table 1). Pure stands are dominated by either native broad-leaved European beech, non-native coniferous Douglas-fir, or native coniferous Norway spruce. The two mixed stands in each quintet are composed of beech with one of the conifers (beech–Douglas-fir and beech–spruce mixtures).

Plots were established in 2017. Seven of the 40 plots were relocated after windthrow in early 2018. Half of the studied forest associates (springtails, oribatid mites, and soil and root fungi) were sampled in 2017, and the other

TABLE 1 Stand structure and environmental characteristics of the research plots (mean, minimum, and maximum values). Each quintet (row) consists of five plots with different tree species compositions (pure European beech, Douglas-fir, and Norway spruce stands and mixtures of beech with each conifer). Left right arrows indicate the number of plots that were replaced after windthrow in January 2018 after half of the species groups were sampled. The data refer to the complete set of 40 + 7 plots.

No.	Quintet	Stem no. (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Age (years)	Mixture	Mixture	Mixture	Sand	Annual	Annual	Elevation
					proportion beech (mixed plots only)	proportion conifer (mixed plots only)	proportion other tree species (all plots)				
1	Harz (n = 5)	342 (236–504)	45.1 (31.6–56.2)	88 (51–101)	0.45 (0.32–0.59)	0.54 (0.41–0.67)	0.04 (0.00–0.11)	16	1029	7.6	511 (492–524)
2	Dassel (n = 5 ↔ 1)	394 (300–488)	37.0 (22.7–50.4)	72 (42–88)	0.81 (0.72–0.90)	0.15 (0.10–0.20)	0.03 (0.00–0.08)	26	822	8.6	426 (362–443)
3	Winnefeld (n = 5 ↔ 3)	269 (194–572)	34.1 (26.3–49.3)	72 (44–94)	0.79 (0.74–0.84)	0.21 (0.16–0.26)	0.05 (0.00–0.17)	20	824	8.9	374 (345–402)
4	Nienover (n = 5 ↔ 3)	411 (256–604)	38.3 (28.3–52.0)	70 (45–87)	0.61 (0.44–0.79)	0.33 (0.19–0.49)	0.07 (0.00–0.16)	20	876	9.0	343 (273–405)
5	Nienburg (n = 5)	325 (252–444)	33.0 (28.6–39.3)	78 (61–108)	0.66 (0.47–0.85)	0.33 (0.12–0.53)	0.06 (0.00–0.23)	80	733	9.7	92 (84–101)
6	Unterlüß (n = 5)	373 (252–552)	35.7 (27.2–50.2)	94 (70–122)	0.69 (0.66–0.72)	0.22 (0.20–0.23)	0.11 (0.07–0.18)	79	747	9.0	161 (149–167)
7	Göhrde_II (n = 5)	506 (396–744)	35.5 (34.5–37.8)	76 (54–111)	0.55 (0.39–0.72)	0.34 (0.28–0.40)	0.09 (0.01–0.21)	79	682	9.2	130 (117–140)
8	Göhrde_I (n = 5)	364 (264–436)	35.8 (24.3–44.8)	78 (58–130)	0.50 (0.35–0.65)	0.44 (0.24–0.65)	0.06 (0.00–0.11)	73	673	9.2	120 (113–126)
Total (n = 40 ↔ 7)		369 (194–744)	36.7 (22.7–56.2)	78 (42–130)	0.64 (0.32–0.90)	0.32 (0.10–0.67)	0.06 (0.00–0.23)	49	805 (673–1029)	8.9 (7.6–9.7)	270 (84–524)

half of the forest associates (small mammals, vascular plants, spiders, ground beetles) were sampled in 2018.

Sampling of species groups

Cover-abundance of plant species was visually estimated in May and June 2020 on 100-m² subplots according to Braun-Blanquet (1951).

Root and soil fungi were sampled between November and December 2017. All plots were separated into four equally sized subplots. Five soil cores (8-cm diameter and 10-cm depth) were taken and pooled into one sample in three of the four subplots (resulting in three replicates per plot). Samples were divided into two compartments: roots and soil. DNA of all samples and compartments was extracted, the fungal nuclear ribosomal internal transcribed spacer 2 region (ITS2) was amplified, and Illumina sequencing was applied as described previously (Likulunga et al., 2021; Rivera Pérez et al., 2022). We used a standardized pipeline for quality filtering the raw sequences, which were then clustered at 97% sequence identity into operational taxonomic units (OTUs). OTUs were assigned to taxa by database alignments using the UNITE database v8.3 (October 5, 2021; <https://plutof.ut.ee/#/doi/10.15156/BIO/1281567>) (Abarenkov et al., 2021) and the nt (nucleotide) database (December 8, 2021) at <https://www.ncbi.nlm.nih.gov/nucleotide/>. OTUs with nonfungal taxonomic assignment were removed from the dataset. Therefore, the OTUs in our dataset represent proxies for fungal “species” in the forest plots.

To estimate fungal biomass, three soil cores (5 cm in diameter) were sampled at 5-m distance between November 2017 and January 2018, and were separated into three depths including litter, 0–5 and 5–10 cm depth as described in the study by Lu and Scheu (2021). Fungal abundance was estimated by phospholipid fatty acid analysis using the marker of 18:2 ω 6,9 (Frostegård et al., 2011). Further, springtails and oribatid mites were sampled similarly down to 10-cm depth, and one core per plot was taken. Animals were extracted using high-gradient heat extraction (Macfadyen, 1961).

Small mammals were surveyed between July and September of 2018, 2019, and 2020. Grids of 64 Sherman traps spaced 10 m apart were established on each plot, and all plots within each quintet were surveyed concurrently for four nights once per year. Captured animals were identified to species and individually marked to identify recaptures.

Arthropods were collected using pitfall traps between March and September 2019. Twelve pitfall traps were installed in a regular grid in each plot and specimens were taken at three-week intervals as described by

Kriegel et al. (2021). Ground beetles and spiders from a subset of eight traps were identified to species level. On quintets one to four, ground beetles from all 12 traps were identified. Ground beetles and spiders from quintet six (Unterlüß) were excluded from the analysis as trap collection was not possible during some of the three-week intervals, resulting in biased samples.

Forest specialist species of spiders (Kielhorn, 2017), vascular plants (Schmidt et al., 2011), oribatid mites (Weigmann, 2006), and ground beetles (expert opinion, see *Acknowledgments*) were identified and results regarding the subset of forest specialist species are presented in Appendix S1.

Analysis

All analyses were done using the R software (v4.1.1., R Core Team, 2021).

Alpha-, beta-, and gamma-diversity and abundance of all taxonomic groups were analyzed: Contrasts between stand types and site conditions were estimated using the log-response ratio as a measure of effect size.

Abundance was estimated as effective abundance after accounting for sampling effort (e.g., trap count and trapping days per plot).

Alpha- (plot level) and gamma-diversity (landscape level) of stand types and plots with favorable or unfavorable site conditions were estimated by Hill numbers of order zero (species richness α^0D and γ^0D), one (Shannon diversity α^1D and γ^1D), and two (Simpson diversity α^2D and γ^2D) using the R package iNEXT (Chao et al., 2014).

Alpha-diversity was estimated using individual-based abundance data of each species, plot, and sampling campaign. Estimates were rarefied to the 10% quantile of the number of sampled individuals per plot and sampling campaign for each species group (Oksanen et al., 2020).

Gamma-diversity was estimated using incidence frequency data of each species group, treating the incidence of all species per plot across all sampling campaigns as one observation. Beta-diversity was estimated as the average pairwise Jaccard dissimilarity between plots using the same incidence data as for the estimation of gamma-diversity using the R package vegan.

Beta- and gamma-diversity were estimated for the five stand types (hypotheses 1, 2, 3) using subsets of 8 plots of the same stand type, and for site differences (hypothesis 4) using the subsets of 20 plots per study region (quintets 1–4 and quintets 5–8, Table 1).

Contrasts between the plot-level target variables (alpha-diversity and abundance) were estimated from generalized linear mixed effect models (GLMMs) that were fitted with the R package glmmTMB (Brooks et al., 2017)

using a Gaussian distribution and a log-link function. Fixed effects were estimated for the two covariables “stand type” (five categories specifying the tree species composition) and “site condition” (two categories specifying plots with favorable or unfavorable site conditions). A random effect of the intercept was included for the quintet-ID and, in case of multiple campaigns, for the campaign-ID as well. Distributional assumptions of the models were validated using the R package DHARMA (Hartig, 2021). Contrasts between stand types and site conditions were calculated using estimated marginal means with the R package emmeans (Lenth, 2021).

Contrasts between each stand type or site condition regarding beta- and gamma-diversity were estimated using the `escalc` function of the `metafor` R package (Viechtbauer, 2010).

Multitaxon effect sizes were estimated by averaging the log-response ratios of the individual species groups using `metafor` R package. A meta-analytical method to aggregate effect sizes was preferred over direct estimation of a multidiversity index for each plot as this would not have been possible for the seven plots that were relocated after storm damage in 2018.

RESULTS

Differences between pure conifer and pure beech stands

Overall, the dataset comprises 3123 soil fungi (OTU), 2307 root fungi (OTU), 92 vascular plant, 26 springtail, 71 oribatid mite, 7 small mammal, 84 ground beetle, and 130 spider species or OTUs. On average, we encountered 942.82 soil fungi (OTU), 417.8 root fungi (OTU), 13.75 vascular plant, 5.58 springtail, 13.25 oribatid mite, 2.47 small mammal, 9.09 ground beetle, and 9.93 spider species or OTUs per plot and point in time. The multitaxon gamma-diversity estimates (γ^0D , γ^1D , γ^2D) indicated approximately 20% higher diversity in the conifer stands than in the beech stands (Figure 1) with only a narrow range of other plausible values (CIs indicate approximately between 10% and 35% higher diversity in conifer stands). Conifer stands had at least ~10% higher gamma-diversity of vascular plants, spiders, and root fungi than beech stands, indicating a more diverse species composition for these taxa in conifer stands (Figure 2; Appendix S1: Figure S7). The estimates of the remaining forest associates also usually indicated higher gamma-diversity in conifer stands than in beech stands. However, in these cases, the confidence bands covered rather low values as well, indicating that differences between conifer and beech stands may be small (Figure 2;

Appendix S1: Figure S7). For all forest associates except springtails, a substantially greater gamma-diversity in beech than in conifer stands appeared highly unlikely.

Plot-level alpha-diversity showed a similar pattern of a mostly higher diversity of forest associates in the conifer stands (higher multitaxon alpha-diversity of ~10% in conifer stands). However, the confidence range of Shannon and Simpson diversity (α^1D and α^2D ; Appendix S1: Figure S7F,G) often included negligible differences between the stands or even a higher alpha-diversity in the beech stands.

We found only small differences in multitaxon beta-diversity, as well as the beta-diversity of most individual species groups, between conifer and beech stands (Figure 2).

Even though the estimated multitaxon difference in abundance between conifer and beech stands was rather large (~25% higher average abundance in conifer stands), uncertainty was high and smaller differences are plausible as well (confidence bands indicate between 5% lower and 60% higher abundance in conifer stands). The abundance estimates of most individual species groups also had large confidence bands, and therefore, differences in abundance between pure conifer and beech stands were indeterminate (Figure 2).

Contrast between a native and a non-native conifer

Diversity or abundance of some species groups was higher in stands of one of the conifer species compared with the other conifer species (Figure 3; Appendix S1: Figure S8). However, differences were mostly either negligible or indeterminate. There was no obvious general pattern indicating preference for one of the conifers over the other by the studied forest associates, while abundance estimates were too uncertain to clearly indicate any preference by a specific group for either of the conifers.

Mixing effects of native and non-native conifers with beech

Multitaxon gamma-diversity of the mixed stands was intermediate between the values of the pure conifer and beech stands (Figure 1). Regarding individual species groups, only the point estimates of gamma species richness (γ^0D) and Shannon diversity (γ^1D) of springtails, oribatid mites, and small mammals were somewhat greater in mixed Douglas-fir-beech stands than in pure stands of either species (Figure 3; Appendix S1:

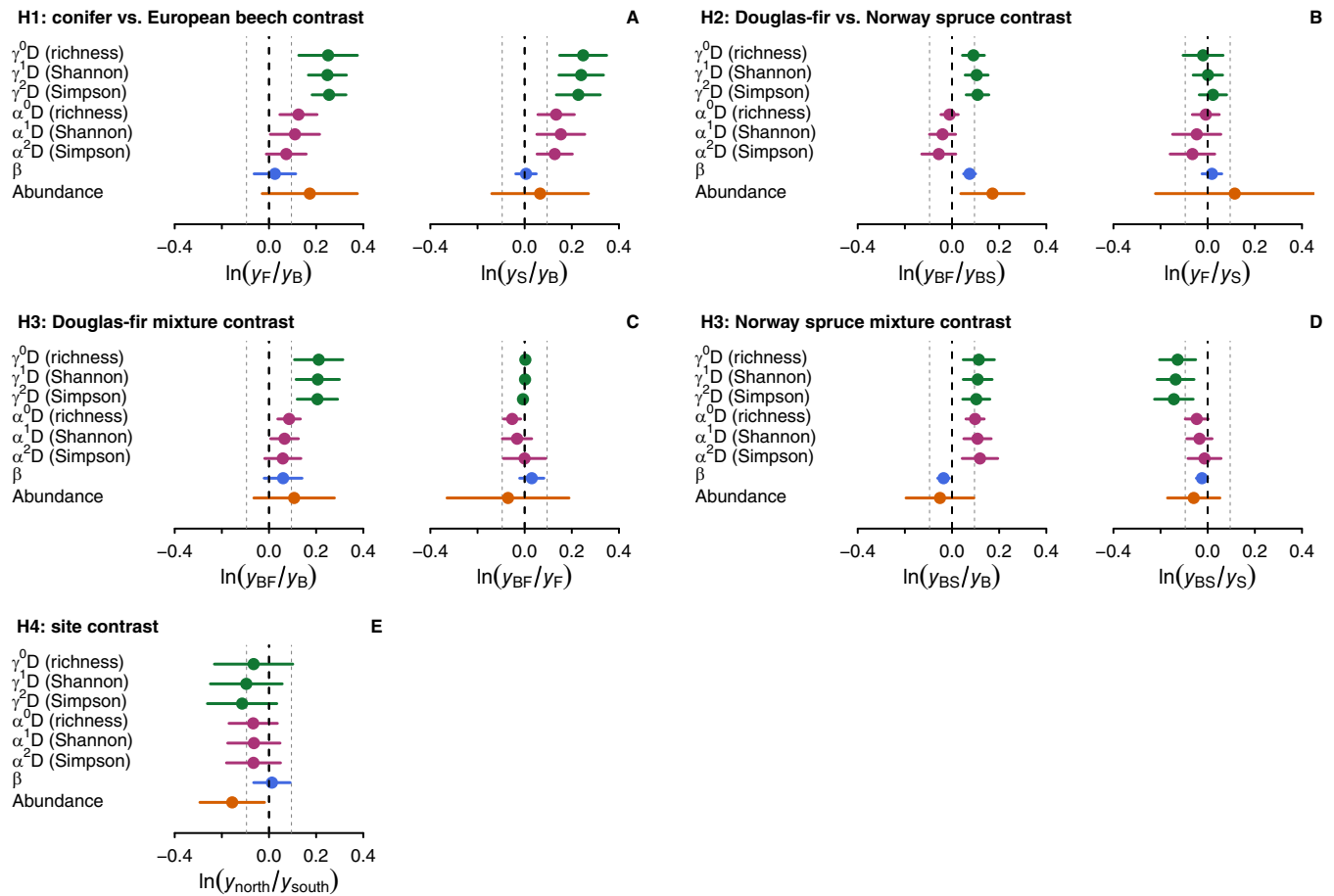


FIGURE 1 Multitaxon synthesis of relative differences of eight forest associates (soil and root fungi, vascular plants, springtails, oribatid mites, small mammals, ground beetles, and spiders) between different stand types and under different site conditions. The log-response ratio of the target variable y is used to quantify contrasts between stand types (pure stands of Douglas-fir F, Norway spruce S, and European beech B and mixed stands of European beech with each of the conifers, BF and BS, each group with $n = 8$, panels A–D) and regarding site conditions (more favorable southern sites and less favorable northern sites, each group with $n = 20$, panel E). Diversity is estimated via Hill numbers of order 0, 1, and 2 (species richness 0D , Shannon diversity 1D , and Simpson diversity 2D). Diversity is estimated at plot level (alpha-diversity α^0D , α^1D and α^2D , purple), across all plots of the same stand type (gamma-diversity γ^0D , γ^1D , γ^2D , green) and as average pairwise Jaccard dissimilarity between plots (beta-diversity β , blue). Abundance contrasts are colored in orange. Mean estimates of the log-response ratios (dots) and 95% CIs (whiskers) are presented. The black dashed 0-line represents no difference between stand types or site conditions. Greater absolute values of the log-response ratio than 0.095 (gray dashed lines) represent substantial differences where estimates of the more diverse or abundant category exceed estimates of the less diverse or abundant category by at least 10%.

Figure S8), indicating a potential positive mixing effect on species diversity of these forest associates. However, confidence bands were wide, and both no difference in species diversity or higher species diversity in pure Douglas-fir stands are equally likely.

Similarly, multitaxon alpha-diversity was not greater in any of the mixed stands than in the respective pure stands (Figures 4 and 5). This was also true for most individual species groups. However, Shannon and Simpson diversity (α^1D , α^2D) had a greater variability, indicating a higher uncertainty (e.g., springtails and vascular plants for both beech–conifer mixtures; Appendix S1: Figures S9 and S10).

Multitaxon beta-diversity and beta-diversity of most forest associates were equal in all stand types. Multitaxon

abundance of mixed stands was in-between the respective estimates of the pure stands. Regarding individual species groups, abundance contrasts between mixed and pure beech–conifer stands were uncertain due to wide confidence bands (Figures 4D and 5D).

Site differences

Differences in abundance, alpha-diversity, beta-diversity, and gamma-diversity between stands with less favorable site conditions in the north and more favorable site conditions in the south were highly taxon specific (Figure 6; Appendix S1: Figure S11). This resulted in high

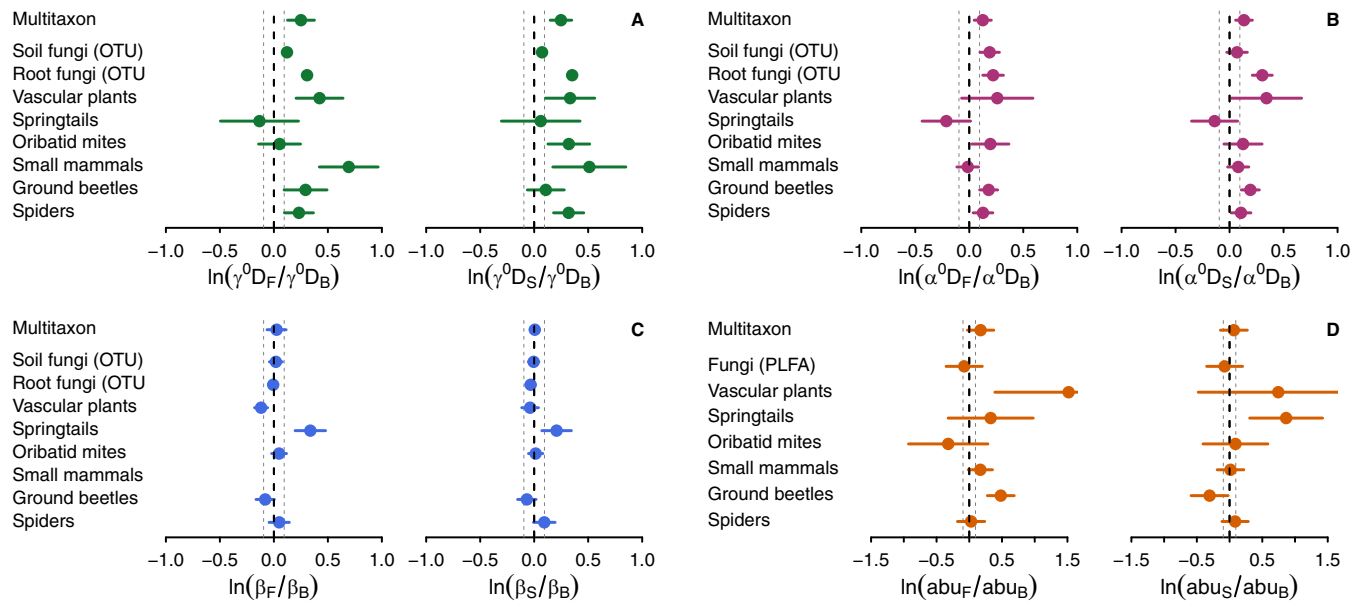


FIGURE 2 Relative difference in diversity and abundance of eight different forest associates between pure conifer and pure European beech stands. The log-response ratio of the target variable y quantifies contrasts regarding the species compositions of forest associates between Douglas-fir (F , $n = 8$) and Norway spruce (S , $n = 8$) stands in relation to European beech stands (B , $n = 8$) ($\ln(x_F/x_B)$ or $\ln(x_S/x_B)$). Negative values of the log-response ratio indicate support of hypothesis 1 (larger values in European beech stands), positive or neutral values are in opposition to hypothesis 1 (larger values in conifer stands). For a detailed description of the variables, see Figure 1. Note the different scale of the x -axes of the panels referring to abundances (D) or diversity (A–C). Results using other diversity indices to quantify alpha- and gamma-diversity (Shannon and Simpson) are reported in Appendix S1. OTU, operational taxonomic unit; PLFA, phospholipid fatty acid.

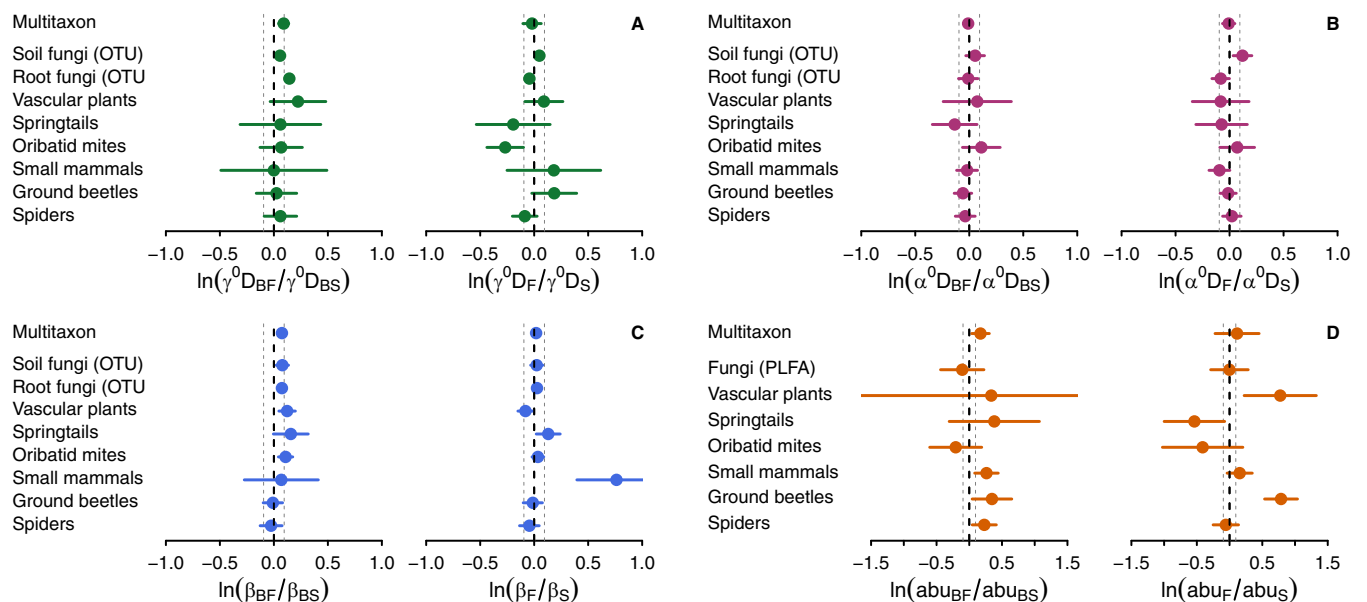


FIGURE 3 Relative difference in diversity and abundance of eight different forest associates between pure stands of Douglas-fir and Norway spruce and between stands of each conifer mixed with European beech. The log-response ratio of the target variable y is used to quantify contrasts regarding the species compositions of forest associates between pure or mixed Douglas-fir stands (F or BF , $n = 8$) in relation to pure or mixed Norway spruce stands (S or BS , $n = 8$) ($\ln(x_F/x_S)$ or $\ln(x_{BF}/x_{BS})$). Negative values of the log-response ratio indicate support of hypothesis 2 (larger values in native spruce than non-native Douglas-fir stands), positive or neutral values are in opposition to hypothesis 2 (equal or larger values in non-native Douglas-fir compared with native spruce). For a detailed description of the variables, see Figure 1. Note the different scale of the x -axes of the panels referring to abundances (D) or diversity (A–C). Results using other diversity indices to quantify alpha- and gamma-diversity (Shannon and Simpson) are reported in Appendix S1. OTU, operational taxonomic unit; PLFA, phospholipid fatty acid.

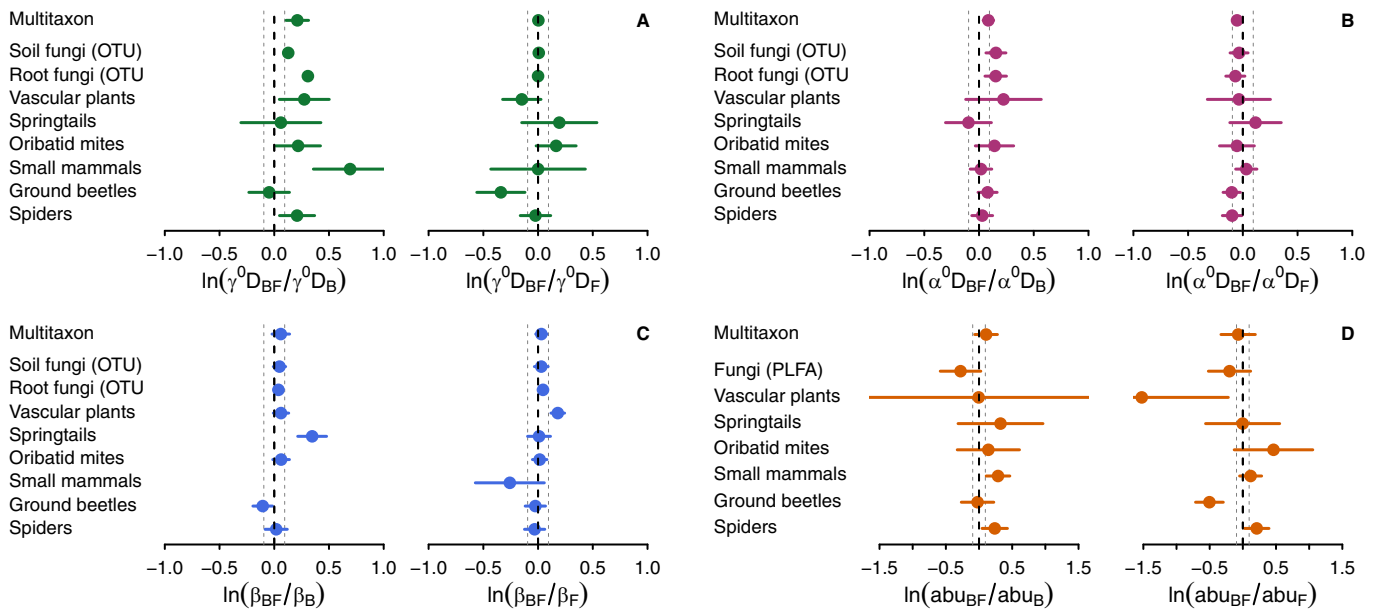


FIGURE 4 Relative difference in diversity and abundance of eight different forest associates between mixed and pure stands of European beech and Douglas-fir. The log-response ratio of the target variable y is used to quantify contrasts regarding the species compositions of forest associates between mixed European beech–Douglas-fir stands (BF, $n = 8$) and pure stands of both species (B or F, $n = 8$) ($\ln(x_{BF}/x_B)$ or $\ln(x_{BF}/x_F)$). Negative values of the log-response ratio indicate support of hypothesis 3 (larger values in mixed than in pure stands), positive or neutral values are in opposition to hypothesis 3 (equal or larger values in pure than in mixed stands). For a detailed description of the variables, see Figure 1. Note the different scale of the x-axes of the panels referring to abundances (D) or diversity (A–C). Results using other diversity indices to quantify alpha- and gamma-diversity (Shannon and Simpson) are reported in Appendix S1. OTU, operational taxonomic unit; PLFA, phospholipid fatty acid.

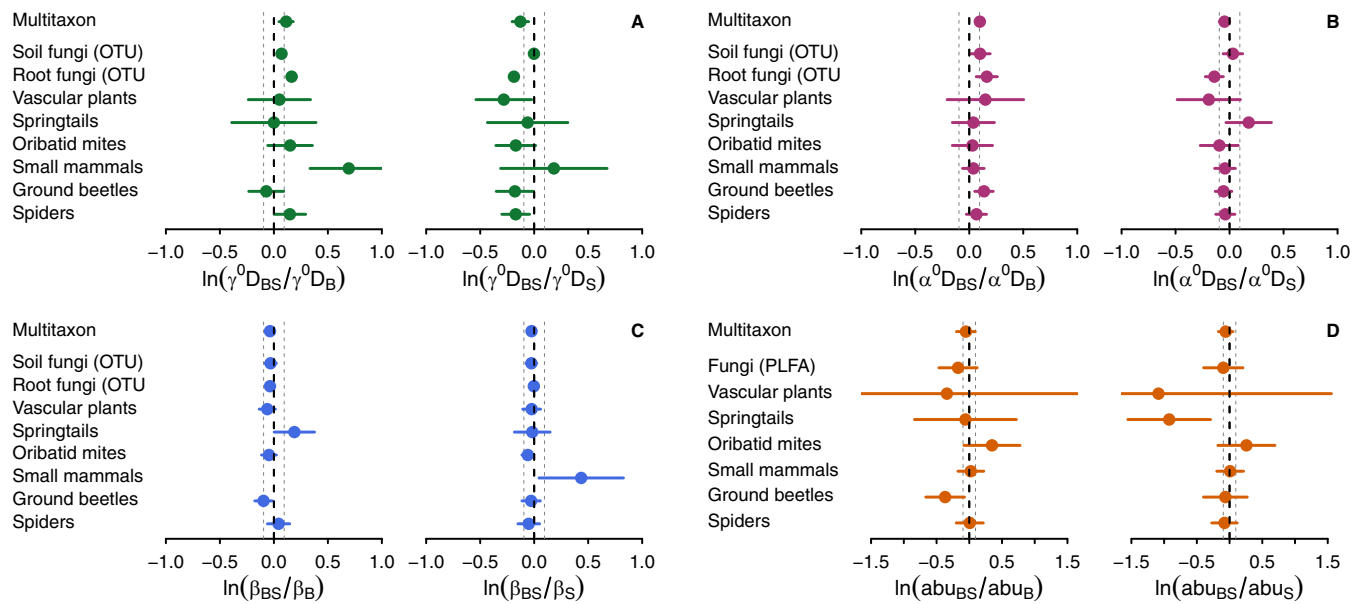


FIGURE 5 Relative difference in diversity and abundance of eight different forest associates between mixed and pure stands of European beech and Norway spruce. The log-response ratio of the target variable y is used to quantify contrasts regarding the species compositions of forest associates between mixed European beech–spruce stands (BS, $n = 8$) and pure stands of both species (B or S, $n = 8$) ($\ln(x_{BS}/x_B)$ or $\ln(x_{BS}/x_S)$). Negative values of the log-response ratio indicate support of hypothesis 3 (larger values in mixed than in pure stands), positive or neutral values are in opposition to hypothesis 3 (equal or larger values in pure than in mixed stands). For a detailed description of the variables, see Figure 1. Note the different scale of the x-axes of the panels referring to abundances (D) or diversity (A–C). Results using other diversity indices to quantify alpha- and gamma-diversity (Shannon and Simpson) are reported in Appendix S1. OTU, operational taxonomic unit; PLFA, phospholipid fatty acid.

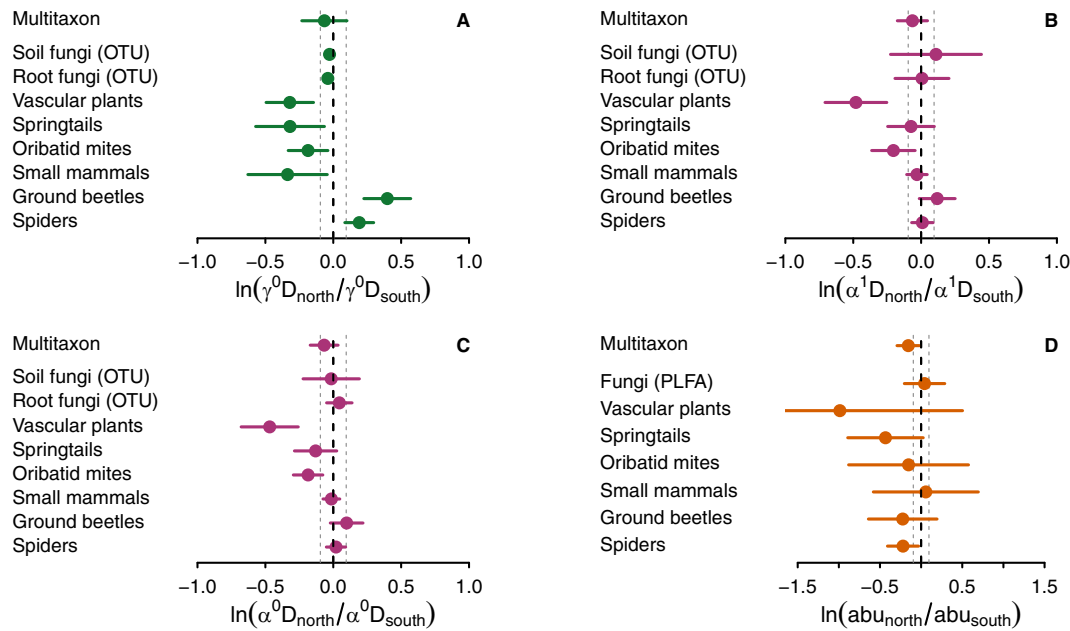


FIGURE 6 Relative difference in diversity and abundance of eight different forest associates between northern sites (less favorable site conditions) and southern sites (more favorable site conditions). The log-response ratio of the target variable y is used to quantify average contrasts across five stand types (pure stands of Douglas-fir, Norway spruce, and European beech and mixed stands of European beech with each of the conifers) regarding the species compositions of forest associates between northern ($n = 20$) and southern ($n = 20$) sites. Negative values of the log-response ratio indicate support of hypothesis 4 (larger values on sites with more favorable site conditions), positive or neutral values are in opposition to hypothesis 4 (equal or larger values on sites with less favorable site conditions). For a detailed description of the variables, see Figure 1. Note the different scale of the x-axes of the panels referring to abundances (D) or diversity (A–C). Results using other diversity indices to quantify alpha- and gamma-diversity (Shannon and Simpson) are reported in Appendix S1. OTU, operational taxonomic unit; PLFA, phospholipid fatty acid.

uncertainty in the multitaxon averages, without a clear indication of a higher multitaxon diversity or abundance in stands with favorable or unfavorable site conditions (Figure 1).

In particular, gamma-diversity of six out of eight forest associate groups differed between the two study regions (Figure 6; Appendix S1: Figure S11B,C). Spiders and ground beetles had a higher gamma-diversity in the northern sites, while root and soil fungi, vascular plants, springtails, and oribatid mites were more diverse in the south.

Estimates of alpha-diversity were more similar between the study regions. Even though vascular plants, oribatid mites, and springtails did have a different alpha-diversity in the northern and southern sites, these differences were mostly small and sometimes depended on the order of the diversity index (Figure 6; Appendix S1: Figure S11E,F).

Beta-diversity showed a taxon-specific pattern as well, with rather low differences between sites. Root fungi and small mammals had a slightly higher beta-diversity in the south while vascular plant and ground beetle beta-diversity was slightly higher in the north.

A high variance in abundance estimates prevents definite statements about patterns in these variables depending on site conditions.

Forest specialists

The multitaxon diversity and abundance estimates for the subset of forest-adapted species (Appendix S1: Figures S1–S6) had a higher uncertainty as a lower number of species groups was studied. Nevertheless, there was no clear difference between the observed patterns whether or not species more typical in open habitats were excluded.

DISCUSSION

Without forest management, European beech would most likely be the dominant tree species at all study sites. Douglas-fir and Norway spruce have been cultivated in Central Europe due to their high-quality timber since approximately 200 years ago (Douglas-fir, van Loo & Dobrowolska, 2019) or longer (Norway spruce, Klimo et al., 2000). Apparently, both conifers provide habitats of sufficient quality to support several forest-floor-associated communities with species diversity at least as high as in beech stands, despite limited time for these communities to adapt to the conditions created by these conifer species.

Communities of some forest associates even had higher alpha or gamma-diversity in Douglas-fir and spruce stands than in beech stands. As differences between conifer and beech stands varied between species groups and confidence bands are sometimes rather wide, there is some uncertainty about the size of this effect, in particular regarding abundance estimates. The results nevertheless present convincing evidence that communities of associated species in the soil and on the forest floor are at least not impoverished in species diversity and abundance in coniferous compared with beech stands. The results for the subset of forest specialist species (Appendix S1) are in line with these findings, which indicates that a higher or equal species diversity in conifer than in beech stands is not due to an increased number of species that are typical of more open, nonforest habitats. As the species diversity of communities is tightly linked to a multitude of processes (O'Connor et al., 2017), comparable diversity levels of multiple species groups indicate that ecosystem functioning is not impaired in any of the studied stand types.

Previous findings about diversity of associated species in conifer stands in relation to beech generally agree with this study, showing a similar diversity of forest associates in Norway spruce or Douglas-fir stands when compared with European beech stands (Budde, 2006; Heinrichs et al., 2019; Horák et al., 2019; Kambach et al., 2021; Pena et al., 2017; Salamon & Alphei, 2009; Schmidt & Weckesser, 2001). However, many studies report a higher diversity of forest associates in European beech than in conifer stands as well (Cassagne et al., 2004; Horák et al., 2019; Magura et al., 2003; Matevski & Schuldt, 2021; Ujházy et al., 2017). In some cases, this was potentially due to a comparison of old beech stands with young Norway spruce stands, making it hard to differentiate between the effects of species identity and stand age (Ujházy et al., 2017). Despite rather clear results for multiple species groups in this study, the variety of results in the scientific literature indicates that generalization across species groups, stand ages, management types, and site conditions remains difficult. This is emphasized by sometimes divergent results from studies that surveyed species compositions at multiple points in time or include different management systems (Steverding & Leuschner, 2002; Ujházy et al., 2017).

Minor differences in diversity between Douglas-fir, Norway spruce, and European beech stands for all species groups indicate that the non-native character of Douglas-fir does not reduce the species diversity or abundance of forest-floor-associated taxa. Comparisons of diversity between Douglas-fir and Norway spruce stands in the literature indicate that variability between conifer stands may be similar to variability between conifer and

beech stands. Several studies reported higher diversities in Douglas-fir stands than in Norway spruce (Buée et al., 2011; Goßner et al., 2005; Gossner et al., 2016). However, other studies did not find differences between Norway spruce and Douglas-fir (Ampoorter et al., 2015; Bertheau et al., 2009; Matevski & Schuldt, 2021). Some studies report differing diversities of arthropod and fungal communities in different situations, for example, depending on canopy stratum or point in time (Goßner & Ammer, 2006; Kubartová et al., 2009).

A range of studies across the world reported that the cultivation of a non-native species did not result in reduced diversity of plant and animal taxa (reviewed in Brockerhoff et al., 2008). However, there are studies that document lower species diversity in non-native compared with native stands of similar age and management type (e.g., Oxbrough et al., 2016; Schuldt & Scherer-Lorenzen, 2014). These differences are most striking when comparing stands of non-native tree species to native tree species that support rich species communities such as some oak species (Finch & Szumelda, 2007). In our study, the silvicultural regime applied to all stands aimed to establish mature forest stands that provide a broad range of ecosystem services in the long term. It seems as if the cultivation of non-native tree species does not necessarily prevent high species diversity of forest associates, at least on the forest floor.

Contrary to our expectations, we did not find higher diversity in mixed stands than in pure stands. For the studied species groups and species combinations, no increase in diversity of forest associates can be expected when tree species are planted in mixtures rather than monospecific stands. Most studies showing increasing species richness with an increasing number of tree species diversity (Fornoff et al., 2019; Matevski & Schuldt, 2021; Scherber et al., 2010; Sobek et al., 2009) encompass larger tree species gradients than two tree species. After all, the gradient of monospecific stands and two-species mixtures of this study may not have been enough to detect mixing effects on the diversity of forest associates. However, various mycorrhizal fungi show host specificity (Lang et al., 2011), and therefore, increased diversity might have been expected for root fungi in beech–conifer mixture. However, specialist fungi are often subordinate (Lang et al., 2011) and therefore small effects might have been masked by the multitude of generalist fungal species. Additionally, beech may have strong identity effects on the environment, for example, on soil pH and layer thickness, which may overpower mixing effects, at least for some species groups such as ground vegetation (Mölder et al., 2008).

Results regarding the different indices applied in this study to quantify species diversity (plot-level alpha-diversity,

landscape-level gamma-diversity of the forest types, and beta-diversity) were mostly similar, which indicates a high robustness of the results regarding weighting of relative abundances of species and the spatial scale of the analysis.

One underlying reason for the relatively small differences in species diversity we found between the studied stand types may be that environmental conditions are more relevant in shaping species diversity and abundance than the tree species composition itself. The impact of the studied conifers on environmental conditions in the stands may have been too small to cause dramatic changes in species diversity or abundance of the taxa we considered. However, it is important to keep in mind that despite their similar species diversity, specific species and species compositions of forest associates can show a strong response to the tree species composition, which was not studied here. For example, in Douglas-fir stands, the abundance of saprotrophic fungi was increased relative to mycorrhizal fungi as compared with beech forests (Likulunga et al., 2021), suggesting effects on functional biodiversity. Additionally, associated species in higher canopy strata that were not addressed by this study may show a stronger dependence on specific trees species, and therefore, their abundances and diversity may be more influenced by the tree species composition (Pedley et al., 2016; Wardhaugh, 2014).

Due to higher resource availability, we expected higher abundance across studied taxa at stands with more favorable site conditions in the south compared with the northern sites. As higher abundance is assumed to result in a higher diversity, we expected a higher diversity at the favorable compared with the unfavorable sites (“more individuals hypothesis,” Srivastava & Lawton, 1998). Even though there is a trend toward higher abundance of forest associates in stands with favorable site conditions, there is also high variability in abundance estimates. Compared with previous studies (Hotanen et al., 2006; Niedziakowska et al., 2010), the strength of the relationship between site quality and abundance in our study is rather low, which may be due to a wider gradient in site conditions in these studies. However, at least some forest associates had a higher (vascular plants, springtails, oribatid mites) diversity in stands with favorable site conditions, while others (spiders, ground beetles) were less diverse. Apparently, site conditions have a taxon-specific impact on the diversity of forest associates investigated here, independent of their rather variable abundance.

Results regarding differences between stand types were often similar across species groups. Nevertheless, none of the comparisons between stand types showed the same pattern across all species groups. Additionally, results regarding site differences were highly taxon specific. This demonstrates the importance of including

many taxa of different trophic levels when analyzing the impacts of external factors such as climate change, management regime, or tree species selection on the composition and functioning of ecosystems. If results are based on only a few indicator groups, important effects may be overlooked. Further research will show whether the findings of this study are confirmed when taking individual species into account as well as those species that spent a major part of their life cycle in upper canopy strata.

CONCLUSIONS

The species diversity of the forest associates we studied is tightly related to ecosystem processes such as nutrient cycling, decomposition of organic matter, predation, or seed dispersal (O'Connor et al., 2017). From the perspective of forest associates studied here, cultivation of Douglas-fir or Norway spruce seems to have no universal negative impact on species diversity in forests. Therefore, we conclude that the functioning of the studied communities is not impaired in any of the stand types by a reduced species diversity. However, studies from other regions that show different results need to be considered as well (Wohlgemuth et al., 2021). Additionally, forest management needs to take a holistic perspective on tree species choice, not only species diversity is of interest but also the composition of the assemblage. For example, the conifer stand types in this study have highly distinct species compositions from the beech stand (e.g., Kriegel et al., 2021; Likulunga et al., 2021). As the species assemblages in the conifer and beech stands are quite different, there is little potential for the conservation of beech-associated species assemblages in conifer stands. Depending on the management goals for a landscape, an appropriate mix of the different stand types including pure stands of native tree species and mixtures of native and non-native tree species may be a reasonable option. Such a combination would allow conifer species to be used for the provision of ecosystem goods such as timber while maintaining the high conservation value of pure native stands.

Mixed stands of the studied tree species may also be a good management option for reasons beyond the main focus of this study, for example, to increase productivity and thus carbon storage due to positive mixing effects. However, according to our results, such mixing effects do not generally lead to higher species diversity, at least for combinations of the three tree species and the forest associates studied here.

AUTHOR CONTRIBUTIONS

Jonas Glatthorn, Christian Ammer, Hannes Riebl, and Peter Schall designed the analysis. Jonas Glatthorn

analyzed the data. Jonas Glatthorn wrote the draft of the manuscript. Scott Appleby contributed to the writing; all other authors provided data and substantially contributed to revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw data used in this study are publicly available (Appleby, 2023; Lu et al., 2022; Lu & Scheu, 2022; Matevski & Kriegel, 2022; Rivera Pérez et al., 2021; Seinsche & Glatthorn, 2022).


ETHICS STATEMENT

Small mammal surveys were conducted in compliance with the German Animal Welfare Act under permit of the “Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit” permit number 33.9-42502-04-18/2790. All procedures involving animals were approved by the internal animal welfare committee of the University of Göttingen. Sampling of arthropod species that are protected by the German Federal Nature Conservation Act was done with an exception permit of the “Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten und Naturschutz.”

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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