

# Metabarcoding reveals that mixed forests mitigate negative effects of non-native trees on canopy arthropod diversity

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## Abstract

Averting climate change-induced forest diebacks increasingly relies on tree species planted outside of their natural range and on the addition of non-native tree species to mixed-species forests. However, the consequences of such changes for associated biodiversity remain poorly understood, especially for the forest canopy as a largely understudied forest stratum. Here, we used flight interception traps and a metabarcoding approach to study the taxonomic and functional (trophic guilds) composition and taxon richness of canopy arthropods. We sampled 15 monospecific and mixed stands of native European beech, native Norway spruce—planted outside its natural range—and non-native Douglas fir in northwest Germany. We found that the diversity of arthropods was lower in non-native Douglas fir compared with native beech stands. Taxon richness of herbivores was reduced by both conifer species. Other functional guilds, however, were not affected by stand type. Arthropod composition differed strongly between native broadleaved beech and monospecific coniferous (native spruce or non-native Douglas fir) stands, with less pronounced differences between the native and non-native conifers. Beech–conifer mixtures consistently hosted intermediate arthropod diversity and community composition compared with the respective monospecific stands. Moreover, arthropod diversity had a positive relationship with the number of canopy microhabitats. Our study shows that considering arthropod taxa of multiple functional groups reveals the multifaceted impact of non-native tree species on forest canopy arthropod communities. Contrasting with previous studies that primarily focused on the forest floor, we found that native beech hosts a rich diversity of arthropods, compared with lower diversity and distinct communities in economically attractive, and especially in non-native, conifers with few canopy microhabitats. Broadleaf–conifer mixtures did not perform better than native beech stands, but mitigated the negative effects of conifers, making such mixtures a compromise to foster both forest-associated diversity and economic yield.

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**KEY WORDS**

DNA barcoding, forestry, genetic diversity, insects, invertebrates, multitaxon, OTUs, trophic guilds

## INTRODUCTION

Current global biodiversity loss destabilizes ecosystem resilience and functioning (Hautier et al., 2015; Oliver et al., 2015). Forest ecosystems are increasingly threatened by climate change-induced extreme weather events (Schlyter et al., 2006; Subramanian et al., 2019). In central Europe, large-scale forest diebacks during the last decades have required the development of new forest management strategies (Thorn et al., 2019). Temperate forests are at the same time important safeguards for biodiversity, harboring many specialized, and sometimes highly endangered species (Brokerhoff et al., 2017; Seibold et al., 2019). New management strategies should thus account for future climatic changes while simultaneously maintaining and promoting native forest biodiversity (Messier et al., 2022). In search of such resilient, economically attractive, and biodiversity-friendly forest management strategies, mixtures of fast-growing conifers and broadleaved trees are considered a promising approach as their phylogenetic differences result in functional complementarity in resource use, growth and performance (Felton et al., 2010, 2021; Haberstroh & Werner, 2022). Their impacts on forest biodiversity, however, are yet poorly understood.

In forests as well as in many other ecosystems, arthropods play essential roles in trophic interactions such as herbivory, decomposition, or predation (Wildermuth, Dönges, et al., 2023; Wildermuth, Fardiansah, et al., 2023; Yang & Gratton, 2014). Arthropod composition (taxonomic and functional) therefore strongly influences forest functioning and integrity (Schowalter, 2017). This makes arthropods a suitable organism group to examine and evaluate the effects of forest management on biodiversity (Maleque et al., 2006, 2009).

In previous studies, it has been shown that different functional groups of forest arthropods show varying responses to broadleaf-conifer mixtures. The abundance of monophagous herbivore pest species, for example, usually decreases in mixtures (Heiermann & Schütz, 2008; Jactel et al., 2017; Kaitaniemi et al., 2007). Generally, the response of herbivores is highly dependent on their dietary specialization as well as the tree species of the respective stand (Gossner, 2004; Leidinger et al., 2019). Consequently, the community composition of herbivorous arthropods can vary strongly among forest stand types, and their richness does not necessarily increase in mixed forest stands (Leidinger et al., 2021).

Generalist arthropod predators and omnivores were shown to have a considerably lower dependency on tree identity (Barsoum et al., 2014; Oxbrough et al., 2012; Roques et al., 2006). These trophic guilds are rather dependent on structural forest properties, such as canopy openness, which can result in equal or even higher abundance and diversity in coniferous stands compared with broadleaf-conifer mixtures (Barsoum et al., 2014; Kriegel et al., 2021; Oxbrough et al., 2016). Saproxylic arthropods, in comparison, are foremost dependent on the forest management type, as deadwood quantity and heterogeneity drive their abundance and richness (Felton et al., 2010; Seibold et al., 2016). Overall, mixtures of broadleaved and coniferous tree species often seem to mitigate differing tree species effects on arthropod communities, but do not necessarily promote their diversity when compared with monocultures (Kriegel et al., 2021; Oxbrough et al., 2012; Wang et al., 2019).

Besides planting broadleaf-conifer mixtures, admixing fast-growing, yet drought-tolerant non-native trees with few associated local pest species to native tree species might increase forest resilience and thus maintain productivity (Feng et al., 2022; Liang et al., 2016; Thurm & Pretzsch, 2016). However, the ecological consequences of planting non-native tree species are poorly understood and may possibly threaten local biodiversity and ecosystem functioning as many native forest-dwelling species are not adapted to these neophytes (Tallamy et al., 2021; Thomas et al., 2022). For instance, early successional stages of non-native trees and shrubs were found to host a strongly reduced community of herbivorous arthropods and their predators compared with native plant communities (Ballard et al., 2013; Burghardt et al., 2010). In contrast, in other studies, stands including non-native conifers promoted generalist predators compared with native trees (Kriegel et al., 2021; Matevski & Schuldt, 2021; Oxbrough et al., 2016). Oxbrough et al. (2016), however, reported that some arthropod predators decreased in non-native stands, which highlights the need for multitaxon studies (i.e., studies covering multiple orders and trophic guilds simultaneously) to develop a more general understanding of how non-native tree species impact forest arthropods (see also Wang et al., 2019).

Previous studies that investigated the effects of (non-native) conifer admixture on broadleaved forests largely used morphological arthropod identification (e.g., Gossner & Ammer, 2006; Matevski & Schuldt, 2021; Oxbrough et al., 2016). This reduces the arthropod groups to be

analyzed to those that are well studied and comparably easy to identify. This makes it almost impossible to gain a complete picture of forest arthropod diversity and composition (Smith et al., 2009; Waugh, 2007). Hence, species-level analyses of highly diverse, but difficult to identify, arthropod groups such as Diptera, Hymenoptera, and Sternorrhyncha, generally remain underrepresented (Hardy, 2018; Skevington & Dang, 2002). These groups, however, might show distinct patterns of forest-type dependencies compared with broadly studied groups such as Araneae, Coleoptera and Lepidoptera (e.g., Kriegel et al., 2021; Matevski & Schuldt, 2021; Oxbrough et al., 2012, 2016). Genetic barcoding is increasingly used to extend the knowledge of the diversity of highly diverse and understudied arthropod groups (Kress et al., 2015; Smith et al., 2009). Especially, the method of metabarcoding represents a promising tool for analyzing whole communities with unknown species composition (Ji et al., 2013; Steinke et al., 2022) without prior morphological identification (Barsoum et al., 2019; Liu et al., 2020; Yu et al., 2012).

Our study focuses on central Europe, where the fast-growing Norway spruce (*Picea abies* (L.) H.Karst.) constitutes the most important timber supply. However, many spruce monocultures that were planted outside of their natural range were negatively affected by recent droughts (Popkin, 2021). The fast-growing Northern American Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco) is considered a promising substitute for Norway spruce due to its higher resilience against droughts and native bark beetles (Thomas et al., 2022), and could be admixed with Central European beech trees (Thurm & Pretzsch, 2016). Here, we studied the richness and composition of canopy arthropods in broadleaf-conifer mixtures and pure stands of native European beech, native Norway spruce—planted outside its natural range—and non-native Douglas fir in Germany, using a metabarcoding approach. Past studies mostly focused on the ground stratum, although the forest canopy constitutes the major aboveground part of trees and hosts high abundances of arthropods that may react more sensitively to tree species identity than ground-dwelling taxa (Floren et al., 2022). We tested for differences in canopy arthropod diversity between monocultures and mixtures of the focal tree species. We further included forest structural properties (i.e., canopy openness, number of microhabitats, and tree species neighborhood diversity) to assess the degree to which such structural properties might explain stand type-specific arthropod diversity patterns.

We aimed to test the following hypotheses: (1) taxonomic and functional arthropod diversity is higher in stands containing native tree species compared with monocultures of non-native Douglas fir, which should be particularly evident for herbivores; (2) tree-species

mixtures of native beech and conifers host intermediate arthropod diversity compared with beech and conifer monoculture stands respectively; (3) arthropod composition differs between beech stands (pure stands and mixtures) and pure coniferous stands, but also between native spruce and non-native Douglas fir; and (4) structural habitat conditions imposed by the tree species, such as canopy openness and microhabitats, strongly contribute to explaining the observed diversity patterns; particularly for arthropod predators and omnivores.

## METHODS

### Sampling sites

We conducted the study in a managed temperate forest in the federal state of Lower Saxony, northwest Germany (51.666 N, 9.569 E; 300 m above sea level). The study area is characterized by spodic cryic cambisol soils (Foltran et al., 2023) and has a mean annual temperature of 8.9°C and mean annual precipitation of 837 mm (Matevski et al., 2021). Within this study area, we sampled three sites with a minimum distance of 2.6 km between sites, each of them comprising five different mature forest stands: pure stands of European beech (*Fagus sylvatica* L.), Norway spruce (*P. abies*), and Douglas fir (*P. menziesii*), and mixed stands of beech-Douglas fir and beech-spruce (see Appendix S1: Table S1 for coordinates of all plots). Each of the 15 plots covered 0.25 ha, with a minimum distance of 100 m between plots. Trees were 91 years old on average (see sites 1–3 in Matevski et al., 2021), with even age classes within plots and tree species.

### Arthropod data

Between the end of June and the end of July 2022, we placed three flight interception traps for 4 weeks in each plot. Each trap consisted of two crossed window panes of 50 × 24 cm, a round lid of 30 cm diameter, a funnel of 26.5 cm diameter and a bottle (1 L) containing 200 mL of 99.5% polypropylene glycol. The lid covered the trap to reduce the dilution of the polypropylene glycol by rain. The funnel was attached below the window panes, guiding falling arthropods into the bottle (see Appendix S1: Figure S1a). Flight interception traps are activity-based traps, sampling mostly flying arthropods that collide with the window panes (Knuff et al., 2019). We placed the traps into the tree canopy at an average height of 16 m, ranging from 10 to 24 m in height (averages per stand type from 15 to 18 m) and at least 10 m apart. The exact

height and position in the plot depended on the canopy height and the tree-species distributions, as we aimed to place traps in the low to middle canopy, covering exactly one tree species (monocultures) or even proportions of two tree species (mixtures). The latter was an approximation, as we needed to choose an anchor point in one tree species, but we placed the trap in such a way that it was surrounded by branches of both admixed species (see Appendix S1: Figure S1b). However, in all mixed plots we selected at least one anchor point in each tree species. After collection, we removed plant material from the samples and stored the samples in 96% undenatured, high-purity ethanol. Subsequent laboratory processing, sequencing (metabarcoding) and bioinformatics up until the first taxonomic assignment were performed by biome-id (Wilhelmshaven, Germany).

## Sample preparation

Samples were sieved and separated into two size fractions (small <6.5 mm and large >6.5 mm). Each size fraction was homogenized using an ULTRA-TURRAX Tube Drive (IKAWerke GmbH, Staufen, Germany) and then 2.5 mL of each fraction were mixed together. Ethanol was removed and the samples were incubated overnight with T1 buffer and proteinase K (Macherey Nagel, Düren, Germany). To clean the solution, lysates were centrifuged and DNA was extracted from 600 µL of the suspension using the NucleoSpin Tissue Kit (Macherey Nagel, Düren, Germany) according to the manufacturer's instructions.

## Next-generation sequencing (NGS) library preparation

The extracted DNA was then used as a template for the amplification of a 313-base pairs (bp) fragment of the cytochrome *c* oxidase subunit I (*COI*) gene. The following primers were used:

*COI* forward primer: 5'-GGWACWGGWTGAACW GTWTAYCCYCC-3' (Leray et al., 2013).

*COI* reverse primer: 5'-TAIACYTCIGGRTGICCR AARAAYCA-3' (Geller et al., 2013).

After modifying each primer to include 5' Illumina overhang adapters, the correct amplification of an amplicon was verified via electrophoresis on a 1.5% agarose gel. The polymerase chain reaction products were then purified using the NucleoMag NGS Clean-up kit (Macherey Nagel, Düren, Germany). Using a Nextera XT Index Kit (Illumina Inc., San Diego, CA, USA) protocol, dual indexes and Illumina sequencing adapters were attached

to the amplicons. Amplicons were then purified using the NucleoMag NGS Clean-up kit. Quantification of libraries was done on the Promega Quantifluor ONE dsDNA system (Promega, Mannheim, Germany). Equimolarly pooled libraries were then sequenced on an Illumina MiSeq system with a 2 × 250 bp paired-end read module. The total expected read counts for the Illumina MiSeq v.2 kit (2 × 250) were 24 million to 30 million paired-end reads, based on information provided by Illumina. In our MiSeq run we obtained for the 45 samples an average of 144,807 paired-end reads per sample.

## Bioinformatic analysis

Assembly of paired-end reads was performed using vsearch v. 2.18.0 (Rognes et al., 2016), with a minimum overlap of 100 base pairs. Using cutadapt (Martin, 2011), assembled reads were demultiplexed according to the sample-specific dual indexes. After filtering for uncalled base pairs ("N"), contigs were de-replicated with vsearch. De-replicated sequences were then aggregated to operational taxonomic units (OTUs), applying a 97% similarity threshold (Wang et al., 2019; Yu et al., 2012). OTUs are the standard basic unit when identifying arthropod diversity via metabarcoding (see e.g. Barsoum et al., 2019; Steinke et al., 2022; Yu et al., 2012). Chimera sequences were detected and removed using the UCHIME algorithm in vsearch (Edgar et al., 2011). Using the blastn algorithm (Camacho et al., 2008), all remaining OTUs were then taxonomically assigned based on a local version of the BOLD database of European Arthropods (status: July 2022). Furthermore, each OTU was assigned to a BOLD barcode identification number (BIN). BINs represent clusters of barcode sequences (in our case OTUs) of high similarity under consideration of available taxonomic identification (Ratnasingham & Hebert, 2013). One OTU could not be assigned to any BIN at the time of our analyses (Hymenoptera). We therefore considered it an own BIN and assigned a surrogate identity. For taxonomic analyses, only OTUs with species-level assignment were considered. OTUs without species assignment were double-checked by searching their BIN in the public BOLD data portal, using the BOLD API Web service (status: October 2022). As BINs are clusters of barcode sequences from various sources, multiple species assignments per BIN might occur. In such cases, we prioritized the names of museum specimens over those provided by other sources. No conflicts of differing species assignments between museums occurred. In the final dataset, no BIN was assigned to multiple species. Species-level assignments in our study have to be treated with caution, because many taxa may not resolve well on the used gene fragment. Therefore, we call the species assignments

henceforth “taxa” and we use “taxon richness” instead of “species richness.”

We applied the following quality criteria to OTUs, BINs and taxon data: First, we set the minimum overlap of OTU and matching reference to 300 (of 313) base pairs. Second, for analyses of BINs and taxa the minimum similarity threshold between OTU sequence and best match on the BOLD database was set to 97% (Barsoum et al., 2019). Third, we set the minimum number of reads per sample for OTUs, BINs, and taxa to three, five, and 10 each. As some BINs and taxa comprised multiple OTUs in single samples, we aggregated all reads of unique BINs and taxon identities per sample for their respective analyses. We analyzed the richness of OTUs, BINs, and taxa separately. However, functional and taxonomic groupings and analyses as described in the following are based on taxonomic assignments (taxon richness).

## Functional traits

We assigned all analyzed arthropod taxa to their feeding guilds following the definition of Rappa et al. (2022). We retrieved information on diets and feeding guilds at the family level for Coleoptera from Gossner (2004) and Rappa et al. (2022); for Diptera from Hughes et al. (2000), Woodcock et al. (2003), Ulyshen (2018), Mlynarek et al. (2018) and Vezsenyi et al. (2022); for Heteroptera from Gossner (2004), Sobek et al. (2009) and Röder et al. (2010); and for Hymenoptera from Archibald et al. (2018) and Tward et al. (2021). We classified Araneae, Neuroptera and Opiliones as carnivorous (Floren et al., 2022; Gossner & Ammer, 2006); Auchenorrhyncha, Lepidoptera, Orthoptera (only Caelifera were detected), Polyxenida, Sternorrhyncha and Thysanoptera as herbivorous (David, 1995; Floren et al., 2022; Moran & Southwood, 1982); Blattodea, Collembola and Julida as saprovorous (Floren et al., 2022; Rusek, 1998); and Dermaptera, Psocodea and Sarcoptiformes as omnivorous (Moran & Southwood, 1982; New, 1987; Velazco et al., 2021). We excluded two records of Trichoptera from the feeding guild analysis, as they are “tourists” and nonfeeding (Floren et al., 2022; Moran & Southwood, 1982). Finally, we calculated the taxon richness of eight orders (Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, and Psocodea) and all feeding guilds, and the functional group richness as the number of different feeding guilds per plot.

## Habitat structure

We used the following environmental properties to relate arthropod communities to stand characteristics: relative area potentially available (APA) of Douglas fir and Norway

spruce, tree neighborhood diversity (NDiv), canopy openness and number of tree microhabitats. All environmental properties were measured at the plot level. We included the APA to consider different mixture proportions in the plots. The APA reflects the exact proportion occupied by the canopies of each tree species per plot. It was calculated by rasterizing the plots and assigning each pixel to the closest tree canopy, with tree canopy radii estimated allometrically based on the diameter at breast height (dbh; Gspalzl et al., 2012). NDiv accounts for possible effects of taxonomic tree neighborhood heterogeneity. NDiv is spatially explicit and tree individual-based, as it reflects the number of monospecific and heterospecific neighbors bordering the APA of each tree. This avoids high diversity scores for plots with monospecific patches of different tree species (Glatthorn, 2021). NDiv values range between 0 (monospecific) and 1 (heterospecific). Canopy openness and microhabitats are important drivers of canopy-associated animal communities such as arthropods (Normann et al., 2016; Plewa et al., 2017; Vodka & Cizek, 2013). Canopy openness was measured on each plot in a 3 × 4 m grid with a 10 m distance between measurement points, using a Solariscope (SOL 300, Ing.-Büro Behling, Hermannsburg). Openness was averaged at the plot level. We counted tree microhabitats for all trees with a diameter at breast height ≥ 15 cm, considering all microhabitats following Larrieu et al. (2018).

## Statistical analyses

All statistical analyses were conducted with R 4.2.1 (R Core Team, 2022). Using a generalized linear-mixed-effects model (GLMM) approach, we built three models to analyze diversity patterns at plot scale. We did so because stand type and tree proportions naturally were highly correlated, but to examine our first two hypotheses, we were interested in the fine-scale impacts of exact tree proportions in addition to the categorical stand types. Also, tree proportions and environmental stand characteristics were correlated, but to test our fourth hypothesis, we were interested in identifying environmental characteristics that explain or add to the tree species identity effects. First, we tested for relationships between forest stand types as categorical fixed effects and all arthropod variables as response (OTUs, BINs, taxon richness (overall, per order, per trophic guild) and functional group richness). In this model, we also tested for relationships between the tree species where the trap was attached and arthropod responses, depending on whether the tree was admixed or in a monoculture. In a second model, we used the numerical tree species proportions as fixed effects. In a third model, we analyzed the environmental variables of canopy openness, number of

microhabitats and tree neighborhood diversity as fixed effects. We conducted all analyses with trap-level data and included plots nested in the three sites as random effects. All GLMMs were conducted using the R package *lme4*, applying a Poisson model family with log-link to account for the heteroscedastic data distribution of arthropod responses (Bates et al., 2014). As the number of microhabitats showed a strong positive skewedness, we log-transformed this predictor to avoid disproportionately high weighting for extreme values (Fink, 2009). We further checked all models for normal, homoscedastic residual distribution and for multicollinearity between co-variables (Fox & Weisberg, 2019). For the latter, we ensured that all variance inflation factors (VIFs) were  $\leq 5$ . Thereafter, we ran a stepwise model selection based on the Akaike information criterion (AIC). This approach identifies the models with the smallest global AIC and reduces them to the essential predictors (Burnham & Anderson, 2004). We applied Tukey honestly significant difference post hoc tests to the categorical stand type models, using the *multcomp* R package (Hothorn et al., 2008). We visualized all results using the *ggplot2* R package (Wickham, 2016).

To further investigate the influence of stand type on arthropod richness at the landscape scale (hypotheses one and two), we estimated the taxon richness for individual forest stands across plots, as well as for mixed stands (pooled) and monoculture stands (pooled) across stand types. Moreover, we estimated the taxon richness per tree species where the trap was attached, depending on whether the tree was admixed or in a monoculture. To do so, we used incidence-based rarefaction and short-range extrapolation (double sample size) as implemented in the *iNEXT* R package (Hsieh et al., 2016). This approach allows for richness comparisons among sites of unbalanced sample size (Hsieh et al., 2016). In a two-step analysis, we set the Hill number to  $q = 0$ , which is equivalent to taxon richness, and  $q = 1$ , which is the exponential Shannon diversity and reflects the effective number of common arthropods (Chao et al., 2014; Hsieh et al., 2016).

To investigate our third hypothesis, we analyzed the arthropod community composition of the five stand types with a three-dimensional nonmetric multidimensional scaling ordination (NMDS), using the *vegan* R package (Oksanen et al., 2022). We based the analysis on taxon presence-absence and applied the Raup-Crick dissimilarity index, which prevents the disproportionate influence of frequent taxa, while communities sharing rare species will be evaluated as more similar (Raup & Crick, 1979). We fitted the environmental properties post hoc to the ordination with a regression analysis, using the NMDS axes scores (“envfit” function). We assessed significant differences between stand types with an analysis of

similarity (ANOSIM,  $N = 9999$ ) and post hoc pairwise comparison (package *pairwiseAdonis*, Martinez Arbizu, 2017). We visualized the number of unique taxa per stand type using the *ggVennDiagram* package (Gao, 2022).

## RESULTS

The total sequence read number was 1,513,115 reads, which were aggregated to 4739 OTUs. After the removal of all OTUs with less than 300 overlapping base pairs with the reference ( $N = 356$ , 7.5%), the total OTU count was 4383 across all sites, which matched with 528 BINs and 443 taxon names on the species level. The results for OTUs, BINs and taxa were largely uniform (see Appendix S1: Tables S2–S4). Therefore, and because all taxonomic and functional analyses were based on taxon identity and richness, we only present results on the species level in the following. We further present only results based on the minimum threshold of five reads per sample. We decided to focus solely on this threshold as the results for the minimum thresholds of three, five and 10 did not differ substantially (Appendix S1: Tables S2–S10). Moreover, five reads per sample are considered a reliable minimum (Wang et al., 2019). Removal of all taxa that did not occur with a minimum of five reads in any sample, resulted in 312 analyzed arthropod taxa (Appendix S1: Table S11). The most taxon-rich order was Diptera (95 taxa), followed by Coleoptera (74 taxa) and Lepidoptera (43 taxa). Herbivorous arthropods were particularly taxon-rich (75 taxa, plus 27 palynivorous taxa), as were carnivores (75 taxa) and omnivores (71 taxa; Appendix S1: Table S11).

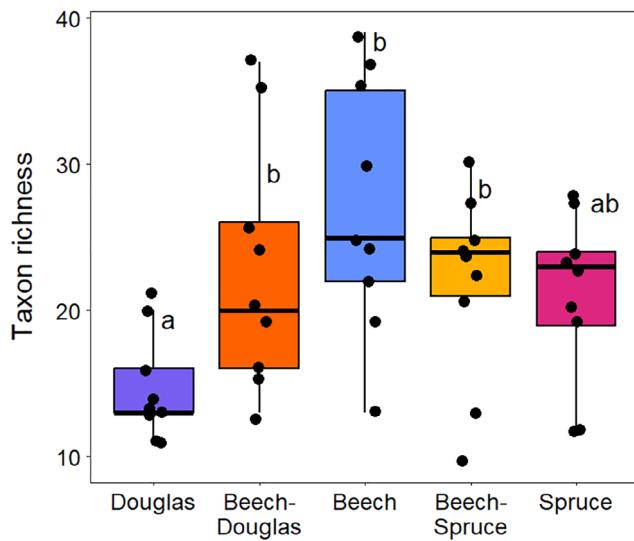
### Stand type effects

Pure and mixed beech stands hosted a significantly higher number of taxa compared with non-native Douglas fir stands ( $F = 5.39$ ;  $df = 4, 8$ ;  $p < 0.05$  for all comparisons; Figure 1). Furthermore, traps in beech trees, irrespective of whether they were growing within a pure or mixed stand, had significantly higher taxon richness than traps in pure Douglas fir stands ( $F = 4.3$ ;  $df = 4, 8$ ;  $p < 0.05$ ; Appendix S1: Figure S2a). We recorded 160 taxa (51.3% of all taxa) exclusively in pure and mixed beech stands, with 57 taxa (18.3%) recorded exclusively in pure beech stands. Pure spruce stands hosted 43 unique taxa (13.8%) and non-native Douglas fir hosted 24 unique taxa (7.7%; Appendix S1: Figure S3).

Taxon richness of Araneae, Hymenoptera, Neuroptera and Psocodea was not significantly influenced by stand type (Table 1; Appendix S1: Table S5). Coleoptera had

higher taxon richness in pure beech stands and beech-spruce mixtures compared with pure Douglas fir stands ( $F = 2.73$ ;  $df = 4, 8$ ;  $p < 0.05$ ; Figure 2a). Diptera had higher taxon richness in pure beech stands compared with pure Douglas fir stands ( $F = 3.66$ ;  $df = 4, 8$ ;  $p < 0.01$ ; Figure 2b). Hemiptera had the lowest taxon richness in pure Douglas fir stands compared with all other stand types ( $F = 3.19$ ;  $df = 4, 8$ ;  $p < 0.05$ ). For Lepidoptera, taxon richness was higher in pure beech than in monospecific conifer stands ( $F = 5.56$ ;  $df = 4, 8$ ;  $p < 0.005$ ; Table 1).

The only feeding guild with significant differences in taxon richness between stand types was the guild of herbivores, which had a higher taxon richness in pure beech stands compared with all other stand types ( $F = 10.87$ ;  $df = 4, 8$ ;  $p < 0.05$ , except beech versus beech-Douglas fir:  $p = 0.05$  [marginally significant]; Figure 2c). Furthermore, herbivore taxon richness was higher in beech-Douglas fir



**FIGURE 1** Boxplot of arthropod taxon richness per stand type at plot level. Significant differences are indicated by lowercase letters. Black dots are the observed values for each of the 45 traps.

**TABLE 1** Mean taxon richness of arthropod orders per stand  $\pm$  standard error.

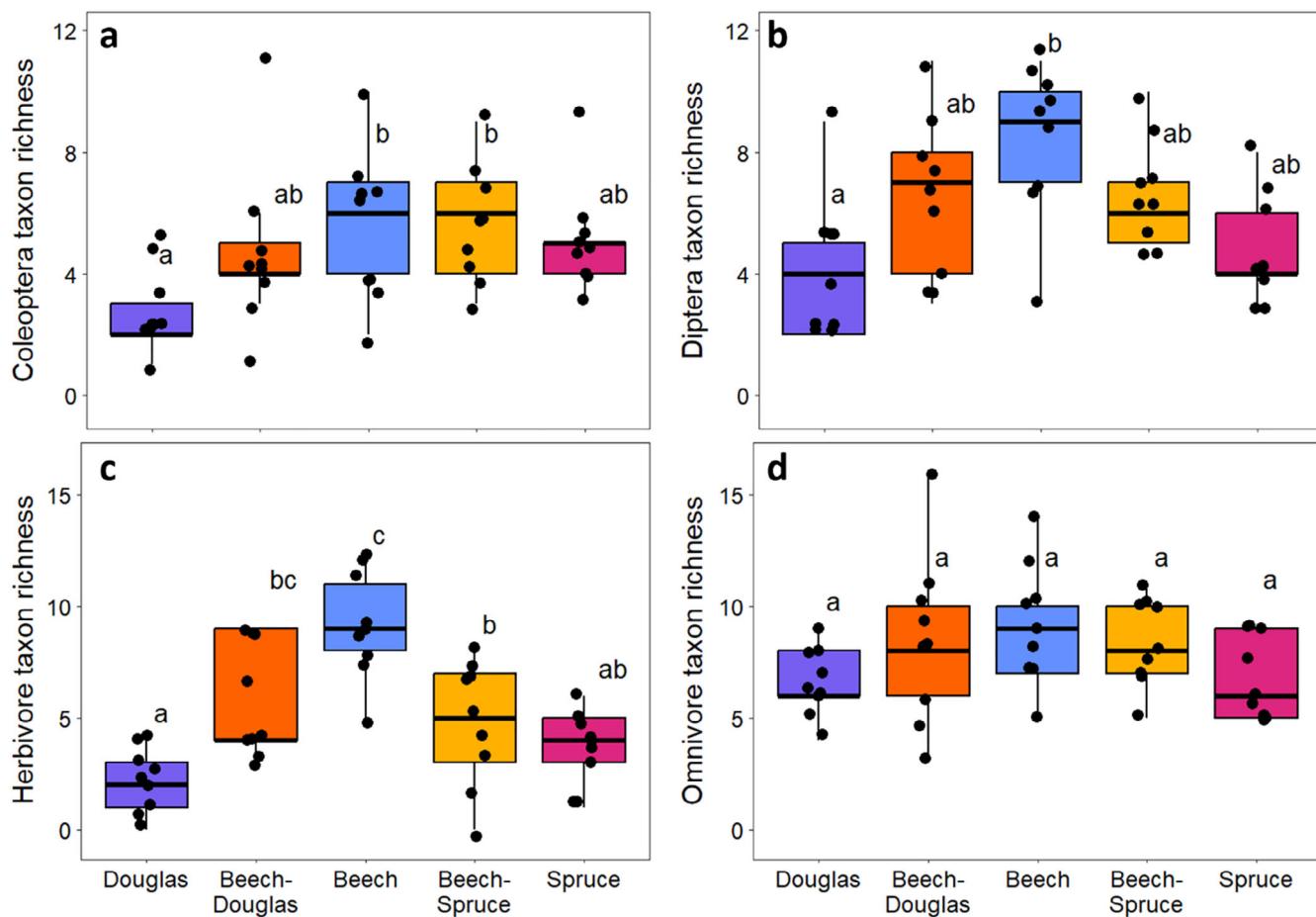
Arthropod order	Douglas fir	Beech-Douglas fir	Beech	Beech-spruce	Spruce
Araneae	$0.22 \pm 0.22$	$0.22 \pm 0.15$	$0.44 \pm 0.24$	$0.11 \pm 0.11$	$0.56 \pm 0.24$
Coleoptera	$2.67 \pm 0.47^a$	$4.67 \pm 0.91^{ab}$	$5.56 \pm 0.84^b$	$5.67 \pm 0.62^b$	$5.11 \pm 0.56^{ab}$
Diptera	$4 \pm 0.78^a$	$6.44 \pm 0.91^{ab}$	$8.56 \pm 0.85^b$	$6.67 \pm 0.6^{ab}$	$4.78 \pm 0.6^{ab}$
Hemiptera	$0.89 \pm 0.26^a$	$3 \pm 0.58^b$	$3.56 \pm 0.5^b$	$2.67 \pm 0.53^b$	$3.11 \pm 0.54^b$
Hymenoptera	$0.78 \pm 0.28$	$1.56 \pm 0.5$	$1.56 \pm 0.44$	$1.33 \pm 0.33$	$2.22 \pm 0.46$
Lepidoptera	$1 \pm 0.24^a$	$1.67 \pm 0.58^{ab}$	$3.78 \pm 0.49^b$	$1.67 \pm 0.44^{ab}$	$1.11 \pm 0.26^a$
Neuroptera	$0.67 \pm 0.17$	$1.44 \pm 0.29$	$1.22 \pm 0.32$	$1.44 \pm 0.24$	$1.11 \pm 0.48$
Psocodea	$3.22 \pm 0.49$	$2.89 \pm 0.56$	$1.67 \pm 0.29$	$1.44 \pm 0.38$	$2.11 \pm 0.39$

Note: Significance letters in superscript were received from Tukey's honestly significant difference post hoc tests of linear mixed-effects models.

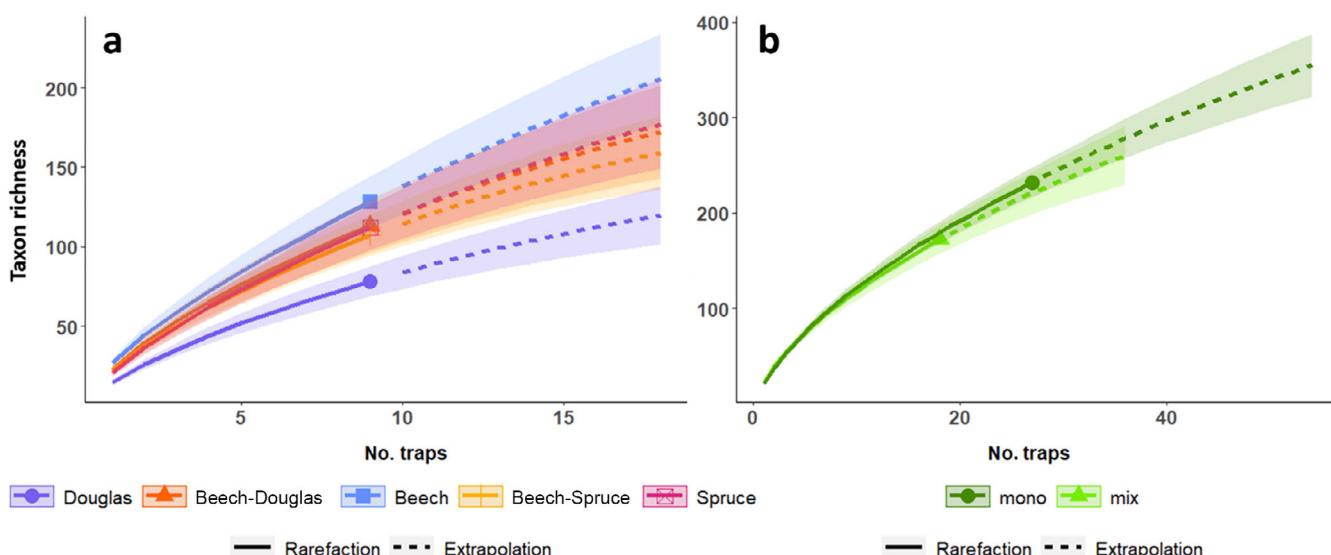
mixtures than in pure Douglas fir stands ( $p < 0.001$ ). Other guilds, especially omnivores, were more equally distributed between stands (Figure 2d; Appendix S1: Table S6). Functional group richness did not differ significantly between stand types ( $F = 0.4$ ;  $df = 4, 8$ ).

Taxon accumulation and extrapolation curves ( $q = 0$ ) at the stand level indicated lower arthropod richness in Douglas fir monocultures compared with the other stand types (Figure 3a). Extrapolated taxon richness in traps attached to beech trees in mixtures did not differ significantly from richness in beech monocultures but, as a trend, richness in mixtures was lower (Appendix S1: Figure S2b). No difference in taxon richness was found across stand types between monospecific and mixed forest stands (Figure 3b). Accumulation and extrapolation curves for common taxa ( $q = 1$ ) showed the same patterns (Appendix S1: Figure S5).

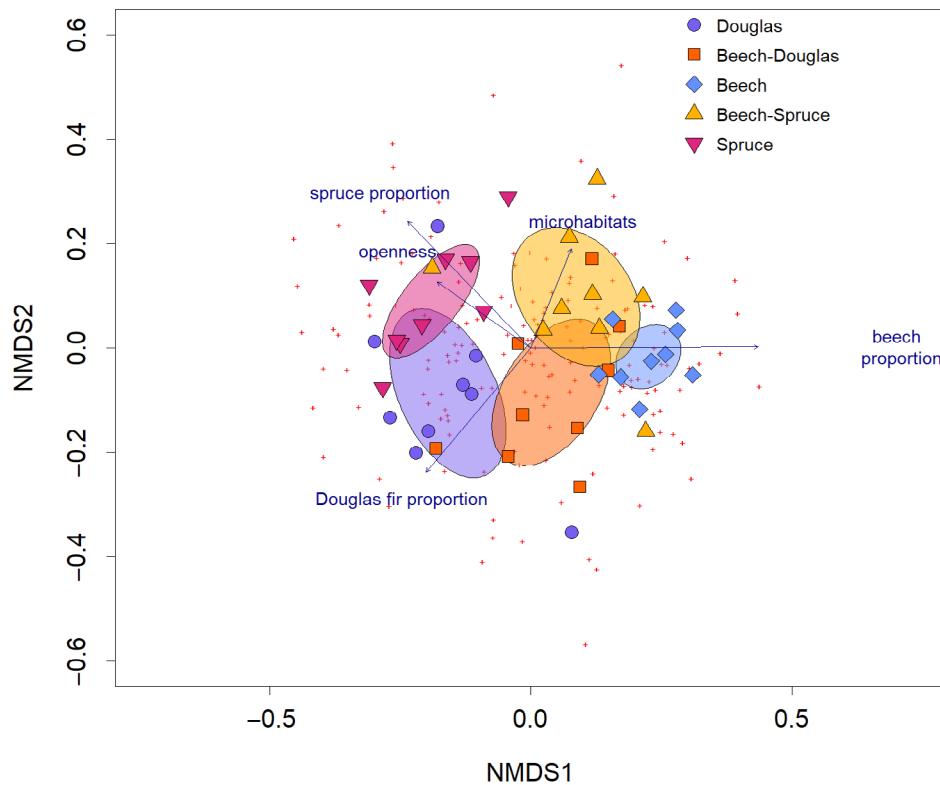
Stand type had a significant effect on community composition (ANOSIM  $R = 0.4$ ,  $p < 0.001$ ). The community composition differed significantly between pure conifer stands on the one hand and pure beech and mixture stands on the other hand ( $p < 0.05$  for all comparisons; Figure 4). Community compositions did not differ significantly between pure Douglas fir and pure spruce ( $p = 0.25$ ), and between the two respective conifer mixtures and pure beech ( $p = 0.31$ ; Appendix S1: Table S12). The ordination of NMDS axes 1 versus 2 and 3 showed very similar results. Comparing axes 2 versus 3 showed additional trends of community differentiation between the two conifers (Appendix S1: Figure S6). Only a few omnivorous Diptera taxa were recorded with high incidence frequency in all stand types (Appendix S1: Table S11). While beech stands were characterized by high incidence frequencies of omnivorous and herbivorous arthropod taxa (Coleoptera, e.g., *Orcheses fagi*; Hemiptera, e.g., *Phyllaphis fagi*; Lepidoptera, e.g., *Phyllonorycter maestingella*), Douglas fir stands only showed high incidence frequencies for omnivores such as



**FIGURE 2** Boxplots of taxon richness of (a) Coleoptera, (b) Diptera, (c) herbivores, and (d) omnivores per stand type at plot level. Significant differences are marked with lowercase letters. Black dots are the observed values for each of the 45 traps. See Appendix S1: Figure S4 for boxplots of all other arthropod orders and feeding guilds.



**FIGURE 3** Incidence-based rarefaction (solid lines) and short-range extrapolation (dashed lines) of taxon richness ( $q = 0$ ) for (a) individual forest stand types across plots and (b) monoculture stands and mixed culture stands across stand types, respectively. Colors and symbols indicate different stand types. Shaded areas represent 95% confidence bands.



**FIGURE 4** Nonmetric multidimensional scaling (NMDS) ordination of arthropod community composition per stand type. Stress <0.2. Red crosses represent arthropod taxa (species names can be found in Appendix S1: Table S11). Filled symbols represent the study plots and stand types. Ellipses show the standard deviation of stand type point scores. Blue arrows show significant correlations of environmental variables with axes scores (detailed statistical results in Appendix S1: Table S13).

Psocodea. Spruce stands further hosted high incidence frequencies of a carnivorous Hemiptera taxon, *Atractotomus magnicornis* (Appendix S1: Table S11). Canopy openness and coniferous proportions, especially spruce proportion, correlated with similar arthropod communities. The number of microhabitats did not correlate with similar arthropod communities as any single tree species proportion, but had a positive association with beech–spruce mixtures (Figure 4; Appendix S1: Table S13).

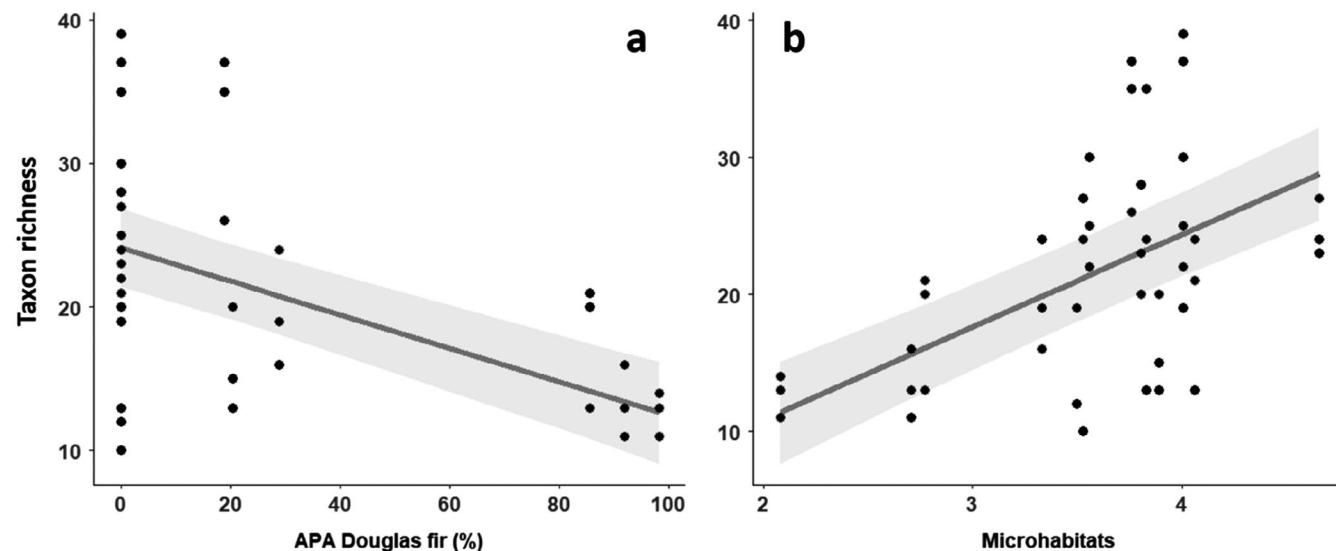
## Environmental effects

Douglas fir proportion and taxon richness of arthropods had a negative relationship (model estimate  $\pm$  standard error (SE):  $-0.22 \pm 0.05$ ;  $p < 0.001$ ; Figure 5a, Table 2). Tree neighborhood diversity (NDiv) and canopy openness had no significant effect on any arthropod response variable, but the number of microhabitats had a positive relationship with taxon richness ( $0.21 \pm 0.04$ ;  $p < 0.001$ ; Figure 5b, Table 2).

The only order without a significant relationship with any environmental property was Araneae. Taxon richness of Coleoptera, Diptera, Hemiptera and Lepidoptera had a negative relationship with the proportion of Douglas fir

( $-0.3 \pm 0.09$ ,  $-0.28 \pm 0.08$ ,  $-0.5 \pm 0.14$ ,  $-0.43 \pm 0.15$ ;  $p < 0.005$  for all orders; Appendix S1: Table S7). In contrast, the taxon richness of Psocodea increased with the increasing proportion of Douglas fir ( $0.24 \pm 0.1$ ;  $p < 0.005$ ). Taxon richness of Diptera and Lepidoptera had a negative relationship with the proportion of Norway spruce (model estimates:  $-0.2 \pm 0.08$ ,  $-0.41 \pm 0.14$ ;  $p < 0.05$ ). The log-transformed number of microhabitats had a positive relationship with the taxon richness of Coleoptera, Diptera, Hemiptera, Hymenoptera and Neuroptera (model estimates:  $0.23 \pm 0.08$ ,  $0.25 \pm 0.08$ ,  $0.42 \pm 0.11$ ,  $0.33 \pm 0.14$ ,  $0.31 \pm 0.16$ ;  $p < 0.05$  for all orders; Appendix S1: Table S8).

Taxon richness of fungivores, herbivores, parasitoids and omnivores decreased with the increasing proportion of Douglas fir (model estimates:  $-0.47 \pm 0.1$ ,  $-0.84 \pm 0.34$ ,  $-0.13 \pm 0.06$ ,  $-0.56 \pm 0.27$ ;  $p < 0.05$  for all orders; Appendix S1: Table S9). Taxon richness of herbivores further had a negative relationship with Norway spruce proportion ( $-0.33 \pm 0.09$ ;  $p < 0.001$ ). The number of microhabitats had a positive relationship with the taxon richness of herbivores and parasitoids (model estimates:  $0.42 \pm 0.1$ ,  $0.58 \pm 0.21$ ;  $p < 0.01$ ; Appendix S1: Table S10). Moreover, the taxon richness of herbivores had a negative relationship with canopy openness ( $-0.21 \pm 0.1$ ;  $p < 0.05$ ).



**FIGURE 5** Relationships between (a) Douglas fir proportion (area potentially available [APA]) and taxon richness and (b) number of microhabitats and taxon richness. Gray bands represent 95% confidence intervals.

**TABLE 2** Model summaries for arthropod taxon richness versus proportions of conifers (APA Norway spruce and APA Douglas fir) and environmental properties (only the number of microhabitats was selected for the final model according to the lowest global Akaike information criterion).

Fixed effect	Model estimate	SE	z value	p value
Tree proportions				
Intercept	3.03	0.1	30.79	<0.001
Spruce proportion	-0.09	0.05	-1.92	0.055 (ns)
Douglas fir proportion	-0.22	0.05	-4.42	<0.001
Environmental variables				
Intercept	3.03	0.11	27.24	<0.001
No. microhabitats (log-transformed)	0.21	0.04	4.98	<0.001

Abbreviations: APA, area potentially available; log, logarithm; ns, not significant; SE, standard error.

## DISCUSSION

Using a metabarcoding approach, we investigated the diversity of canopy arthropods across different taxa and functional groups in temperate forest stands of native European beech, native Norway spruce—planted outside of its natural range—and non-native Douglas fir in northwest Germany. We provide insights on how climate change-adapted forest management might alter arthropod communities in the largely understudied canopy stratum of such monoculture and mixture stands. Our study revealed an overall higher diversity of canopy arthropods in native broadleaf forest stands compared with non-native conifer stands. This is in contrast with the findings of previous studies, which focused on predatory, forest floor-dwelling arthropods and found no or even positive effects of non-native conifers compared with native broadleaves (Kriegel et al., 2021; Matevski

et al., 2021; Oxbrough et al., 2016). We therefore emphasize the need to consider arthropods of multiple functional groups (i.e., trophic guilds) and forest strata to gain a better understanding of how non-native trees affect forest arthropods. Tree species mixtures mitigated the negative effects of non-native tree species, but did not increase arthropod diversity. This is in line with recent findings that tree-species mixtures can buffer negative tree-species identity effects on associated biodiversity (Matevski & Schuldt, 2021; Schuldt et al., 2022; Wang et al., 2019).

## Native beech versus non-native conifers

Providing solid support for our first hypothesis, we found consistent and pronounced differences in arthropod taxon richness at plot and stand scale between European

beech stands (high richness) and non-native Douglas fir stands (low richness). This result was further supported by the negative relationship between the proportion of Douglas fir and arthropod diversity. Notably, past studies on predatory arthropods found contrasting patterns: arboreal spider diversity was higher in young, non-native Douglas fir stands than in stands of native trees (Matevski & Schuldt, 2021), as was the diversity of predatory arthropods in mature Douglas fir stands compared with native stands (Gossner et al., 2005; Kriegel et al., 2021). Other studies have reported a conspicuous shift in arthropod community composition, but no difference in arthropod diversity between non-native and native trees (Gossner & Ammer, 2006; Gossner & Simon, 2002; Oxbrough et al., 2012). However, other studies support our findings, as they found lower arthropod diversity and abundance in early successions of non-native versus native trees and shrubs (Ballard et al., 2013; Burghardt & Tallamy, 2013). Moreover, a metabarcoding study in subtropical forests found higher overall arthropod diversity in native forests compared with non-native trees (Wang et al., 2019). We propose two possible main explanations for these heterogenous results: (1) coverage of few and often contrasting functional groups in many previous studies; and (2) stratum-dependent differences between forest floor and tree canopy.

Herbivorous arthropods include many species that are highly specialized primary consumers of trees. In consequence, this guild might be more dependent on tree species identity than other trophic guilds, which are often less specialized (e.g., carnivores and omnivores). Such guilds with a more generalized resource use depend more strongly on structural elements and prey availability (Gossner & Ammer, 2006; Kriegel et al., 2021; Tallamy et al., 2021), which may explain why these groups are not negatively affected by (or even benefit from) stands of non-native trees (Gossner et al., 2005; Gossner & Ammer, 2006; Matevski & Schuldt, 2021). As expected, our multitaxon study revealed that the diversity of herbivores was the most negatively impacted by non-native Douglas fir. Particularly, host-specific herbivores might have difficulties adapting to the resources provided by non-native tree species, which leads to a reduction in the number of associated herbivores from the regional species pool (Burghardt et al., 2010). This pattern is quite universal and supported by a range of studies (e.g., Burghardt & Tallamy, 2013; Gossner & Ammer, 2006; Helden et al., 2012). Furthermore, Roques et al. (2006) reported that non-native Douglas fir in Europe is mostly utilized by polyphagous herbivores, while only a few specialist species are adapted to feed on this tree. We further observed a weak negative relationship between canopy openness and herbivore diversity. This finding contrasts previous

studies reporting positive effects of canopy gaps on the abundance and diversity of herbivorous arthropods (e.g., Achury et al., 2023; Ulyshen et al., 2005; see Zeller et al., 2023 for review). In our study, however, this was clearly linked to tree-species identity effects, as non-native Douglas fir stands have a conspicuously more open canopy than native beech stands (Matevski et al., 2021). Notably, the richness of the sparsely researched and diverse Diptera was reduced by both conifers, highlighting the advantages of comprehensive metabarcoding approaches (Wang et al., 2019).

Regarding the role of stratum-dependent arthropod diversity patterns, we underline that many past studies reporting no or even beneficial effects of non-native tree species on arthropod diversity investigated ground-dwelling predators (e.g., Kriegel et al., 2021; Oxbrough et al., 2016; Schuldt & Scherer-Lorenzen, 2014). Ground-dwelling predators, however, are more strongly shaped by structural stand properties such as canopy openness or herb complexity (Barsoum et al., 2014; Kriegel et al., 2021; Matevski et al., 2021), whereas canopy arthropods—and especially herbivorous canopy arthropods—are highly dependent on tree-species identity (Floren et al., 2022; Leidinger et al., 2019). The fact that we found no evidence for the negative effects of Douglas fir on the functional group richness of canopy arthropods might be due to the limited number of investigated traits (feeding guild).

## Native versus non-native conifers

Comparing non-native Douglas fir to Norway spruce revealed few differences in arthropod diversity. This is in accordance with previous studies in Europe, reporting similar levels of arthropod diversity in non-native and native conifer stands (Gossner & Ammer, 2006; Gossner & Simon, 2002; Matevski & Schuldt, 2021; Oxbrough et al., 2012, 2016). These similarities were explained by the comparable canopy structure and close phylogenetic relatedness of coniferous tree species (Matevski & Schuldt, 2021; Seifert et al., 2020; Vilà et al., 2015). In our study, however, Hemiptera showed significantly higher diversity in spruce than in Douglas fir stands. The order Hemiptera comprises many specialized herbivores, which, in the case of the suborders Auchenorrhyncha and Sternorrhyncha, were mostly neglected in research on Douglas fir in Europe so far. Yet, it is such specialized taxa that are the least adaptable to the introduction of non-native tree species (Roques et al., 2006). Our results indicate that Hemiptera especially rely on native conifer species. Notably, a previous study found extremely low numbers of canopy arthropods in non-native Douglas fir in winter, whereas native

spruce stands hosted a diverse and numerous community (Gossner & Utschick, 2004). The authors suggested that taller trees and increased canopy openness in Douglas fir might hamper the overwintering of native arthropods. This might have negative cascading effects on the abundance and richness of consumer species such as many insectivorous birds (Gossner & Utschick, 2004). In line with this and with our findings, Schuldt et al. (2022) found that bird abundance in summer is lower in Douglas fir stands than in native spruce and beech stands, respectively. Partly supporting our fourth hypothesis, another factor driving the observed differences between non-native Douglas fir and native spruce was the low number of microhabitats in Douglas fir stands in our study. Available microhabitats increased the diversity of arthropods in our study. Tree microhabitats are important drivers of arthropod assemblages (e.g., Cours et al., 2021; Sallé et al., 2021; Thorn et al., 2016). The reason for the low number of microhabitats in Douglas fir in our study remains unclear, but low diversity and abundance of associated canopy biota, such as birds and fungi, might be a reason for the lower numbers of microhabitats compared with native conifers (Schmid et al., 2014; Schuldt et al., 2022).

## Mixture effects and community composition

Tree species mixtures consistently hosted intermediate levels of arthropod diversity compared with the respective monospecific stands, supporting our second hypothesis. Therefore, we did not find higher arthropod diversity in the pooled mixtures at landscape scale compared with pooled monocultures. We further observed no differences between arthropod diversity in pure beech stands compared with arthropod diversity in traps that were attached to beech trees in mixtures. This is in line with previous studies on canopy arthropods and other forest-associated biota, which reported intermediate or unchanged diversity in mixtures compared with monospecific stands (Kriegel et al., 2021; Leidinger et al., 2019; Schuldt et al., 2022; Wang et al., 2019). However, other studies suggest positive effects of tree diversification on associated arthropods, as the combined communities add up to higher species numbers (Ampoorter et al., 2020; Schuldt et al., 2019; Sobek et al., 2009). A possible explanation for the lack of such an effect in our study might be that the isolation effects of trees in admixture with phylogenetically distant tree species reduce the number of associated specialist arthropods (Gossner et al., 2009; Seifert et al., 2020; Yguel et al., 2011). We conclude that

broadleaf-conifer mixtures do not necessarily promote associated diversity, but can buffer negative tree-species identity effects of economically attractive (non-native) conifers (Budde et al., 2011; Leidinger et al., 2021; Wildermuth, Dönges, et al., 2023). A recent study, however, showed that, over a 14 year-timespan, ground beetle diversity was increasing in temperate broadleaf-conifer mixtures, but decreasing in coniferous monocultures, indicating the positive long-term effects of such mixtures (Evans et al., 2022). Notably, in beech-Douglas fir mixtures of our study, the diversity of herbivorous arthropods was significantly higher than in pure Douglas fir stands, and the associated diversity of beech trees in mixed stands was similar to the diversity in pure beech stands. This supports findings that specialized herbivorous arthropods can already be substantially promoted by partial admixture of their native host trees to non-native tree species (Gossner et al., 2009; Hacker & Müller, 2009).

In support of our third hypothesis, arthropod taxon composition differed strongly between native broadleaved beech and monospecific coniferous stands, while differences between native and non-native conifers were less pronounced. This pattern accords with previous studies showing that dissimilarity in community composition of arthropods increases with phylogenetic distance among trees (Gossner et al., 2009; Seifert et al., 2020; Vilà et al., 2015). We further found that arthropod communities in monospecific Douglas fir stands were characterized by omnivorous taxa and lower numbers of rare taxa in general, with Douglas fir hosting less than half the number of unique taxa compared with native beech stands. This supports the finding of Roques et al. (2006) who reported that in Europe mostly polyphagous arthropods feed on non-native Douglas fir. Notably, arthropod communities in monospecific conifer stands were promoted by canopy openness, corroborating that stand structural properties are major drivers of arthropod communities in coniferous forests (Kriegel et al., 2021; Matevski & Schuldt, 2021; Wildermuth, Dönges, et al., 2023). This positive effect of openness in conifers on taxon richness and the above-reported negative effect of lacking microhabitats in Douglas fir on taxon richness support our fourth hypothesis that structural habitat conditions imposed by the tree species contribute to explaining observed diversity patterns. However, we did not observe the expected pronounced positive effect on predators and omnivores, as previously reported for ground-dwelling arthropod generalists (Kriegel et al., 2021; Wildermuth, Fardiansah, et al., 2023; Ziesche & Roth, 2008). This, once again, underlines that consideration of different forest strata is needed to better understand the effects of forest management on associated arthropod diversity.

## Conclusions

Our study shows that considering arthropod taxa of multiple functional groups reveals the multifaceted impact of non-native tree species on forest canopy arthropod communities. In contrast to previous studies that primarily focused on the forest floor and few trophic guilds, we found that native beech stands host a high diversity of canopy arthropods, compared with the negative effects of increasing conifer proportion and especially non-native Douglas fir monocultures. Broadleaf-conifer mixtures did not perform better than native beech stands, but mitigated the negative effects of conifers, making such mixtures a compromise to promote both forest-associated diversity and economic yield. Further, retention measures fostering microhabitat availability could promote canopy arthropod diversity.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Wildermuth, 2023) are available from GRO.data at <https://doi.org/10.25625/EVX6VK>.

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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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