

RESEARCH ARTICLE

Beneficial effects of native broadleaved forests on canopy beetle diversity are not reduced by admixture of non-native conifers

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Abstract

1. Biodiversity loss and vast forest diebacks due to climate change-induced disturbances require adapted forest management strategies that reconcile economic interests and conservation. Tree species selection, including admixture of fast-growing and drought-tolerant non-native species to native forests, is an increasingly considered approach. However, we lack data on how such mixtures affect native forest biodiversity, especially for the sparsely researched major above-ground part of trees, the canopy.
2. In 40 temperate forest plots in northwest Germany, we investigated how monocultures and admixtures of introduced fast-growing conifers (native Norway spruce planted outside its natural range and non-native Douglas fir) to native broadleaved European beech forests affect abundance, biomass, taxonomic and functional diversity and community composition of canopy beetles across trophic guilds. Diverse arthropod communities are vital contributors to forest health and resilience, and therefore valuable indicators to assess and evaluate forestry measures.
3. Monospecific stands of non-native Douglas fir reduced canopy beetle abundance and diversity compared to native European beech, exceeding the negative effects of Norway spruce. These effects were more pronounced for herbivorous beetles, while they were less strong for predators. Beetle communities in monospecific Norway spruce stands had low functional richness. European beech and mixtures with non-native Douglas fir had high dissimilarity between local communities (turnover, i.e. beta diversity) and high total beetle diversity at landscape scale (gamma diversity). Mixtures generally mitigated the negative effects of introduced conifers, including shifts in species community composition compared to native European beech.
4. *Synthesis and applications:* Monospecific stands of fast-growing non-native Douglas fir and native Norway spruce planted outside its natural occurrence showed undesirable effects such as low diversity and a shifted community

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composition of canopy beetles compared to native European beech. However, mixed stands mitigated negative effects and specifically admixed non-native Douglas fir did not reduce species turnover and landscape-scale beetle diversity. In line with recent studies on other forest taxa, we conclude that admixtures of introduced conifers to European beech forests, but not monospecific plantations, can potentially serve as a compromise between conservational and economic interests.

KEYWORDS

arthropods, Coleoptera, diversity partitioning, flight interception traps, indicator species, insects, managed forests, management adaptation

1 | INTRODUCTION

Global climate change and biodiversity loss pose unprecedented challenges to the resilience and functioning of forest ecosystems (Löf et al., 2019; Seibold et al., 2019), requiring research on the interface of forest management and biodiversity conservation (Deuffic et al., 2020; Staab et al., 2023). Widespread replacement of native forests with tree monocultures planted outside their natural range reduced forest biodiversity and resilience to disturbances (Jactel et al., 2017; Jaureguiberry et al., 2022; Wang et al., 2022). These plantation forests are increasingly hit by novel disturbance regimes, such as weather extremes, causing pest outbreaks and vast forest diebacks (Cours et al., 2022; Fuchs et al., 2022; Turner & Seidl, 2023). Whilst moderate forest disturbances and diebacks can increase habitat diversity and associated biodiversity (Cours et al., 2023; Viljur et al., 2022), large-scale forest diebacks are a major threat to temperate and boreal forests, decreasing economic yield (Fuchs et al., 2022), diversity of forest biota (Evans et al., 2017) and ultimately ecosystem services such as carbon sequestration (Messier et al., 2022). Therefore, adapted and more holistic forest management is needed, fostering biodiversity and multifunctionality under rising temperatures and the increasing frequency of extreme weather events (Löf et al., 2019).

Diversifying tree species in forests, particularly by planting broadleaf–conifer mixtures, is widely considered a promising solution, benefitting from complementarity in resource use, architecture and growth (Schwarz & Bauhus, 2019), while potentially hosting a diverse associated fauna (Ampoorter et al., 2020). The latter, however, remains disputed, with multiple studies reporting rather averaging than promoting impacts of mixed forests on the local diversity and abundance of different animal groups (Oxbrough et al., 2016; Schuldt et al., 2022; Wang et al., 2019). Yet, tree species bearing low biodiversity in monoculture consistently performed better in mixtures (Wang et al., 2019; Wildermuth, Seifert, et al., 2023). Notably, previous research was often hampered by focusing on local forest stands, while studies expanding their scope to regional scales detected higher landscape-scale diversity in mixed than in monospecific forests, resulting from a higher species turnover between

local communities (Leidinger et al., 2021; Wildermuth, Dönges, et al., 2023).

Such benefits of mixed forests might also allow for the integration of alternative, that is non-native tree species (Thomas et al., 2022; Thurm & Pretzsch, 2016). While drought-tolerant and fast-growing non-native tree species are economically a promising solution for climate change-adapted forest management (Fuchs et al., 2022), they can negatively affect native biodiversity and ecosystem functioning when planted in monocultures (Staab et al., 2023; Wang et al., 2019). When admixed with native tree species, such negative effects may be reduced, making mixtures a possible compromise between biodiversity conservation and economic interests (Thomas et al., 2022; Wildermuth, Seifert, et al., 2023). Still, such compromises might pose a threat to rare native forest biota, as their habitat requirements might be too specialized to adapt to novel forest types (Sánchez-Bayo & Wyckhuys, 2019).

Arthropod diversity is an important driver of forest functioning and resilience via provisioning of crucial ecosystem functions such as decomposition, predation, pollination and food resources for higher trophic levels (Leidinger et al., 2021; Maleque et al., 2009; Wildermuth, Fardiansah, et al., 2023). Particularly, beetles (Coleoptera) are hyperdiverse and highly abundant in forest ecosystems (Leidinger et al., 2021). They are further functionally highly diverse, that is cover various trophic guilds and broad interspecific variation in body size (Neff et al., 2022; Rappa et al., 2022; Ulrich, 2007). Therefore, including information on species-specific biomass can provide detailed insights into the effects of forest management on the functional structure of this diverse arthropod group (Rappa et al., 2022).

Past research showed that responses of forest arthropods to admixing broadleaved forest with (non-native) conifers depend strongly on the trophic guild and the investigated forest stratum (Glatthorn et al., 2023; Pedley et al., 2016; Wildermuth, Seifert, et al., 2023). On average, arthropods in the canopy are more dependent on tree species identity than ground-dwelling species because they are in direct contact with the specific crown architecture, resources and defence properties (Pedley et al., 2016; Wildermuth, Dönges, et al., 2023). Herbivores in the canopy, for

instance, were severely reduced in diversity and abundance by non-native trees, while showing intermediate diversity in mixed forest (Berthelot et al., 2023; Wildermuth, Seifert, et al., 2023). Omnivores and predators, however, were less affected by non-native tree presence—particularly on the forest floor (Glatthorn et al., 2023; Matevski & Schuldt, 2023; Oxbrough et al., 2016). Crucially, the canopy represents the major, yet understudied, above-ground part of trees (Floren et al., 2022).

Here, we studied temperate forests in Germany, Central Europe, where plantations of Norway spruce (*Picea abies* (L.) H.KARST.) dominate forestry for several 100 years (Fuchs et al., 2022; Nicolescu et al., 2023). Although native in high-mountain areas in Germany, Norway spruce does not naturally occur in central European lowland regions, and many of those planted monocultures died due to high vulnerability against drought-stress events and subsequent bark beetle infestations (Fuchs et al., 2022). Similarly, the naturally dominating tree species, European beech (*Fagus sylvatica* L.), showed local losses of vitality (Leuschner et al., 2023). Mixtures of Norway spruce and European beech and the partial introduction of non-native Northern American Douglas fir (*Pseudotsuga menziesii* (MIRBEL) FRANCO) are current strategies to halt the economical loss of managed forests (Fuchs et al., 2022; Thurm & Pretzsch, 2016). In German forestry, Douglas fir was introduced in the 19th century and can be found all over the country (Nicolescu et al., 2023), but regulated planting of non-native tree species and established native conifer plantations prevented major economic importance of Douglas fir (Thomas et al., 2022). To assess the compatibility of such novel tree species mixtures with biodiversity conservation, we investigated the canopy beetle community in 40 plots of monospecific and mixed stands of European beech, Norway spruce and Douglas fir. We assessed local beetle taxonomic and functional diversity within and across feeding guilds and the red list status, while controlling for the influence of the surrounding landscape composition (forest cover and tree species composition). We moreover investigated the beetle diversity at landscape scale and assessed the contributions of alpha and beta diversity to overall gamma diversity per forest stand type. Further, we analysed the beetle community composition and identified indicator species of each stand type.

We hypothesized that (i) overall canopy beetle diversity (taxonomic and functional), abundance and total biomass are reduced in monospecific stands of introduced conifers (Norway spruce and non-native Douglas fir) compared to monospecific and mixed native European beech stands. Specifically, we expected severe negative effects on herbivorous and threatened taxa and less severe effects on carnivorous and omnivorous taxa. Moreover, we hypothesized that (ii) mixed forest stands mitigate the negative effects of introduced conifers locally and promote arthropod diversity at the landscape scale, with higher beta diversity in mixtures compared to monocultures. Lastly, we hypothesized that (iii) canopy beetle communities differ strongly between broadleaved European beech and introduced coniferous stands, with more specialized indicator species occurring in European beech.

2 | MATERIALS AND METHODS

2.1 | Sampling sites

We conducted the study in temperate, even-aged production forests in the federal state of Lower Saxony, northwest Germany. The study area is characterized by mean annual temperatures ranging between 7.6 and 9.2°C and a mean annual precipitation varying between 670 and 1029 mm (Ammer et al., 2020). Plots were grouped into eight study sites, of which four were in the northern region of Lower Saxony and four were in the southern region (Figure 1). The northern and southern regions differed substantially in their abiotic conditions: the northern region was overall drier and warmer (mean = 8.5°C), with sandy, nutrient-poor soils (Foltran et al., 2023). The southern region was characterized by higher precipitation rates and lower temperatures (mean = 9.3°C), with loamy soils and higher levels of nutrient content (Foltran et al., 2023). Each of the eight sites comprised a quintet of plots, representing five different forest stands: monospecific European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and Douglas fir (*Pseudotsuga menziesii*), and mixtures of European beech–Douglas fir (beech–Douglas fir hereafter) and European beech–Norway spruce (beech–spruce hereafter; see Appendix S1: Table S1 for information on the exact mixture proportions per stand type). Each of the 40 rectangular plots measured 0.25 ha and had a minimum distance of 100 m to the next plot(s). All plots featured mature trees with an average age of 82 years (minimum: 46 years; maximum: 134 years), reflecting tree species-specific growth rates and harvesting ages. We extracted the relative forest cover and the share of the three target tree species (European beech, Norway spruce and Douglas fir) around our plots using tree species maps with 10 m resolution for Germany based on a combination of Sentinel-2 and Sentinel-1 time series and training data from the German National Forest Inventory (Blickensdörfer et al., 2022). For handling and analysing these spatial data, we used the R packages ‘terra’ (Hijmans, 2023) and ‘sf’ (Pebesma, 2018). We chose a 400 m radius because this radius was previously reported to strongly influence forest properties on local flying beetle communities (Janssen et al., 2009).

2.2 | Beetle sampling and trait information

Between mid-April and mid-August 2021, we placed three flight interception traps per plot. Traps were installed in the tree canopies at an average height of 17.5 m (standard deviation: ± 3.1 m). The minimum distance between traps was 10 m. In mixed stands, we aimed to keep similar distances to the admixed tree species by placing the traps between branches of both species, representing the interaction space in the best possible way (see Appendix S1: Figure S1). Each trap consisted of a round lid (30 cm in diameter), two crossed windowpanes (50 × 24 cm), a funnel (26.5 cm in diameter) and a bottle (1 L) with 200 mL of 50% polypropylene glycol. Flight interception traps are passive traps, sampling mostly flying arthropods colliding

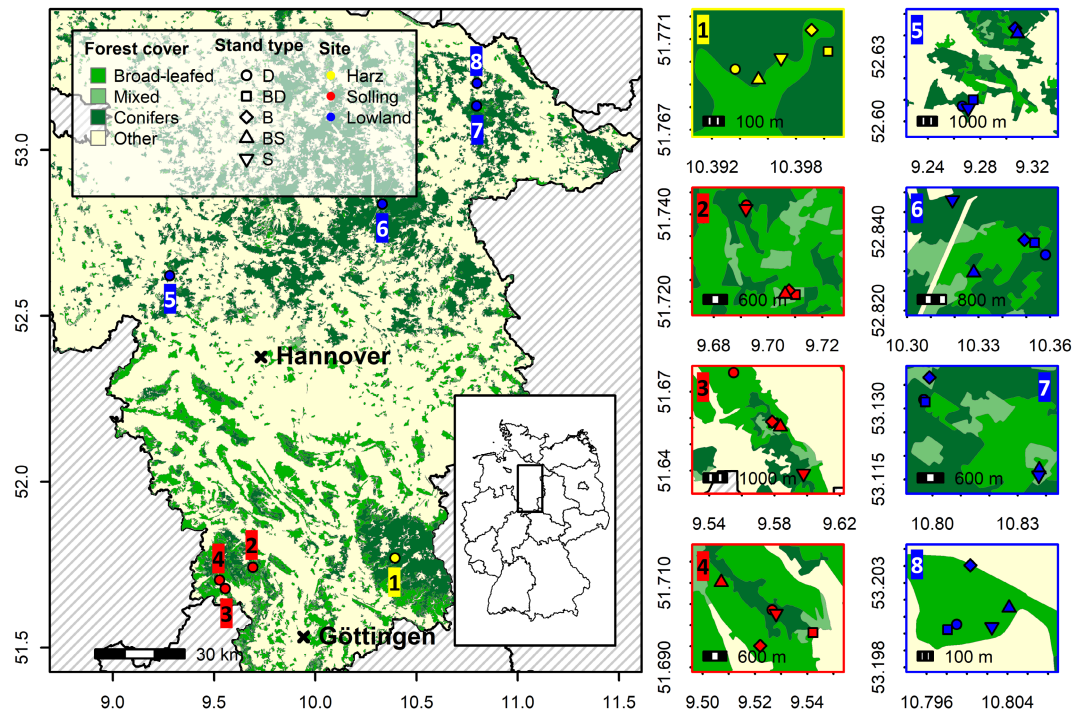


FIGURE 1 Map of the study area. Southern sites are in yellow and red, and northern sites are in blue. Symbols in the detailed site maps on the right indicate the stand types. D, Douglas fir, BD, Beech–Douglas fir; B, European beech; BS, Beech–Norway spruce; S, Norway spruce.

with the windowpanes (Knuff et al., 2019). We emptied each trap every 4 weeks, resulting in four samples per trap. The four samples per trap were pooled for later analyses, resulting in a total of 120 samples. Three samples needed to be excluded from further analysis due to sample loss in at least one of the four sampling periods (two traps in Douglas fir, one trap in European beech). After collection, samples were stored in 70% ethanol. Permissions to access the study plots and to sample canopy beetles were granted by the Niedersächsische Landesforsten (NLF) and the Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN), respectively. No ethical approval was required to conduct the study.

As far as possible, all sampled beetle individuals were morphologically identified to species level by taxonomic experts (W. Apfel, M. Hartmann, A. Kopetz and A. Weigel). In cases where species-level identification was not possible, beetles were assigned to the lowest identifiable taxonomic level, that is to family, tribe or genus. Short-term bark beetle calamities near some plots in the Harz Mountains led to extremely high abundance counts of bark beetles (>2000 individuals per trap; total number of individuals = 12,460). To avoid potential bias in general stand type comparisons due to these short-term influences, we excluded all Scolytinae (bark beetles) from our dataset and added a 'leave one out' statistical analysis, removing all plots in the Harz Mountains (see statistical methods). All taxa were assigned to the feeding guilds of carnivores, herbivores, myceto-detritivores and omnivores following Staab et al. (2023) and Rappa et al. (2022), with the latter providing guild assignments on family level (Appendix S1:

Table S2). These four guilds represent the main consumer types of beetles and thus their functional impact and reliance on specific resources as consumers (Staab et al., 2023).

We derived the mean body lengths of all taxa from Staab et al. (2023), Hagge et al. (2021) and Freude et al. (1964–1989). As biomass is an important ecosystem function of arthropod communities, reflecting both their impact as consumers as well as food source (Ballard et al., 2013), we calculated the mean body mass of all taxa following the length-based regression equation of Ulrich (2007). Finally, we assigned the current red list status (status of extinction risk) of each species following the red list of German invertebrates (Ries et al., 2021) to assess whether red-listed beetle species are associated with a particular stand type. We classified and pooled all species as red-listed, which were classified as near threatened, vulnerable, threatened and threatened to an unknown extent. This could potentially inform nature conservation and forest management.

2.3 | Statistical analyses

We conducted all statistical analyses in R v. 4.3.0 (R Core Team, 2023). We calculated the species richness (number of species), Shannon diversity and evenness per trap (samplings pooled) for each carnivores, herbivores, myceto-detritivores and omnivores, red-listed species and all beetles, using the package 'vegan' (Oksanen et al., 2022). Moreover, we calculated the rarefied species richness per trap for all beetles based on the smallest sample size ($n=11$ individuals). For

these species-based diversity indices, only specimens with species-level identifications were considered (4706 of 5416 sampled individuals). We further calculated the following functional diversity indices for all beetles ($n=5416$ individuals) based on the feeding guild and mean biomass of each taxon per trap (pooled), using the package 'FD' (Laliberté et al., 2014): functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve). These functional indices are important indicators of the functional impact of a community, reflecting on the diversity of functional characteristics (FRic), the relative abundance of extreme characteristics (FDiv) and whether all characteristics are evenly abundant and dissimilar to each other (FEve; Villéger et al., 2008; see Appendix S1 for further explanation).

2.3.1 | Comparison of local beetle responses

We analysed the following canopy beetle responses at trap level (pooled; $n=117$) in linear mixed-effects models (LMM), using the package 'nlme' (Pinheiro et al., 2021): abundance, species richness, Shannon diversity, evenness (overall, per feeding guild, red-listed species), biomass, rarefied species richness, FRic, FDiv and FEve (overall). We first ran a model with the landscape composition (forest cover and cover of the three target tree species) within a 400m radius around each plot as the predictors, with plot nested in site as random effect. We did this to identify possible influencing factors that are located outside the sampling plots, preselecting predictors for the main model while avoiding multicollinearity issues (see the description of the main model below). We checked the initial models for multicollinearity between predictors, ensuring that correlations between predictors were <0.7 and variance inflation factors (VIFs) were <3.5 , which is considered a strong indicator of low multicollinearity (Dormann et al., 2013; O'Brien, 2007). Thereafter, using the 'MASS' package (Ripley et al., 2013), we reduced the model stepwise to the smallest global second-order Akaike Information Criterion (AICc) and thus the most informative predictors (Burnham & Anderson, 2004). In the second model (the main model), we included the forest stand type of our plots and its interaction with the region (north and south), plus the landscape properties that were significant in the first model, with plot nested in site as random effect (Hypothesis 1). We included region as fixed effect because we wanted to test for the effects of the two different abiotic regimes. We only included those landscape properties in our initial main model, which had significant impacts according to the first model, because VIFs would have exceeded the threshold of 3.5 if we had included all predictors in the main model. While keeping stand type as our central predictor in all main models, we reduced the remaining predictors according to the smallest global AICc, achieving VIFs ≤ 2 in the final models. To ensure normal and homoscedastic residual distribution in both models, we transformed all count responses (abundance and species richness) with $\log(x+1)$. To identify significant differences between stand types and regions, we applied multiple

comparisons, using Tukey HSD post hoc tests with Holm's correction in the 'multcomp' package (Hothorn et al., 2008).

2.3.2 | Diversity rarefaction and extrapolation from local to regional scale

We analysed how canopy beetle diversity responded to forest stand type from the local level (trap) to the regional scale. Moreover, we estimated beetle diversity from local to regional scales for all pooled monospecific and mixed stands across sites (Hypothesis 2). These analyses were conducted with the 'iNEXT' package (Hsieh et al., 2022), using abundance-based rarefaction and short-range extrapolation (double sample size). Besides the Hill number $q=0$ (species richness), we also investigated $q=1$, which reflects the effective number of common beetles (exponential Shannon diversity) and $q=2$, reflecting the dominant species number (inverse Simpson diversity; Hsieh et al., 2022).

To further investigate how different stand types influence the importance of beetle beta diversity (species turnover between traps and species turnover between sites) relative to alpha diversity for the total gamma diversity, we implemented multiplicative diversity partitioning of species richness, using the 'vegan' package (*multipart* function, $N=999$). We used multiplicative partitioning to describe beta diversity as pure relative and independent differentiation of alpha diversity, with gamma diversity being the product of alpha and beta diversity at the plot level (Burghardt & Tallamy, 2015).

2.3.3 | Community composition, relative beta diversity and indicator species analysis

We investigated whether canopy beetle community composition at plot level is stand type specific (Hypothesis 3), using a nonmetric multidimensional scaling ordination (NMDS) in the 'vegan' package and an analysis of similarity (ANOSIM, $N=999$). We set the number of ordination axes to $k=3$, as it lowered the stress level to <0.2 , and estimated the distances with the Morisita-Horn index, which is robust to under-sampling (Magurran & McGill, 2011). Post hoc pairwise comparisons of community differences between stand types were conducted with 'pairwiseAdonis' (Martinez Arbizu, 2017).

To identify typical species of the investigated stand types, we added an indicator species analysis with the package 'indicspecies' ('multipatt' function; De Cáceres & Legendre, 2009). Note that 'multipatt' does not correct for multiple testing, and therefore significances should be treated cautiously. However, as our aim was not to report overall numbers of indicator species per stand type, p -value corrections for multiple testing were not necessary (De Cáceres et al., 2010).

We ran all analyses a second time, excluding the Harz Mountains site, to test if the high bark beetle calamities observed at this site might have influenced overall beetle responses.

3 | RESULTS

We sampled 5416 beetle individuals, of which 4706 individuals (87%) could be assigned to 326 species in 52 families (Appendix S1: Table S2). The most abundant families were Elateridae (1107 individuals, 18 species, mostly omnivorous), Latridiidae (795 individuals, 11 species, mostly myceto-detritivorous) and Staphylinidae (694 individuals, 78 species, mostly carnivorous). The most abundant species were *Dalopius marginatus* (Elateridae, 467 individuals), *Athous subfuscus* (Elateridae, 352 individuals) and *Corticaria gibbosa* (Latridiidae, 224 individuals). We recorded 17 red-listed species, with one species being listed in the second highest category of concern (*Corticaria fasciatus*, Tenebrionidae).

3.1 | Local abundance and diversity patterns

The presented results are derived from the main models, but see Appendix S1: Table S3 for detailed results of model 1, which was used to preselect landscape covariates. Total beetle abundance, species richness and Shannon diversity at the trap level were significantly higher in monospecific and mixed European beech stands than in monospecific Douglas fir stands (abundance: $F_{(4,28)}=5.51$, $p<0.05$; species richness: $F_{(4,28)}=6.39$, $p<0.005$; Shannon diversity: $F_{(4,28)}=4.75$, $p<0.05$; Figure 2). Beetle abundance was further significantly higher in monospecific spruce stands than in monospecific Douglas fir stands ($p<0.05$), but Shannon diversity was lower in monospecific spruce stands than in beech–Douglas fir mixtures ($p<0.05$). Biomass and rarefied species richness did not differ significantly between stand types (Figure 2, Appendix S1: Table S4). Species evenness was significantly higher in monospecific Douglas fir stands compared to monospecific and mixed Norway spruce stands ($F_{(4,28)}=3.03$, $p<0.05$; Figure 2F).

Beetle functional richness was higher in beech–spruce mixtures compared to beech–Douglas fir mixtures and monospecific Norway spruce stands ($F_{(4,24)}=1.12$, $p<0.05$; Figure 2G). Functional divergence and functional evenness did not differ significantly between stand types (Figure 2), but functional divergence had a negative relationship with increasing Douglas fir share in a 400m radius around the plots ($F_{(1,27)}=4.39$, $p<0.05$; Appendix S1: Table S5). Red-listed beetle species showed non-significant trends of higher abundances and species richness in monospecific European beech stands than in monospecific conifer stands (Figure 3).

Carnivorous beetle abundance and diversity did not differ significantly between stand types (Figure 4A,B), but increasing forest cover around the study plots decreased carnivore abundance ($F_{(1,26)}=4.41$, $p<0.05$; Appendix S1: Table S5). For herbivorous beetles, abundance, species richness, Shannon diversity and evenness were significantly higher in monospecific and mixed European beech stands than in monospecific Norway spruce stands (abundance: $F_{(4,26)}=13.03$, $p<0.001$; species richness: $F_{(4,28)}=6.88$, $p<0.005$; Shannon diversity: $F_{(4,28)}=5.15$, $p<0.05$; evenness:

$F_{(4,28)}=5.01$, $p<0.05$; Figure 4C,D). Further, herbivore abundance in monospecific and mixed European beech stands was higher than in monospecific Douglas fir stands ($p<0.05$), and herbivore species richness was higher in monospecific beech stands compared to monospecific Douglas fir stands ($p<0.05$; Figure 4C). Increasing European beech share around the study plots reduced herbivore abundance ($F_{(1,26)}=4.34$, $p<0.05$; Appendix S1: Table S5).

Myceto-detritivorous beetles had higher abundances in monospecific and mixed Norway spruce stands than in monospecific Douglas fir stands ($F_{(4,28)}=4.63$, $p<0.01$; Figure 4E). Further, myceto-detritivore species richness ($F_{(4,28)}=4.96$, $p<0.001$; Figure 4F), Shannon diversity ($F_{(4,28)}=4.33$, $p<0.001$) and evenness ($F_{(4,28)}=2.54$, $p<0.05$) were higher in beech–spruce mixtures compared to Douglas fir stands.

Omnivorous beetles were more abundant in beech–spruce mixtures than in any other stand type ($F_{(4,28)}=11.46$, $p<0.05$ for all comparisons; Figure 4G). Omnivore abundance in monospecific Norway spruce stands and beech–Douglas fir mixtures was significantly higher than in monospecific Douglas fir stands ($p<0.05$). Moreover, omnivore species richness was higher in beech–spruce mixtures than in monospecific Douglas fir stands ($F_{(4,24)}=3.32$, $p<0.001$; Figure 4H), with particularly high species richness in the northern beech–spruce mixtures ($F_{(4,24)}=2.37$, $p<0.05$; Appendix S1: Tables S4 and S5).

3.2 | From local to regional diversity

Species accumulation and extrapolation curves across traps and sites showed only few differences among stand types for all species ($q=0$), with higher diversity in mixed stands compared to monospecific Douglas fir (Figure 5a). Common species ($q=1$) and dominant species ($q=2$) were more diverse in monospecific European beech stands and beech–Douglas fir mixtures than in all other stands, with particularly pronounced differences compared to monospecific Norway spruce and beech–spruce mixtures (Figure 5b,c). Species accumulation and extrapolation curves for pooled monocultures and mixtures showed no significant differences for $q=0$ and $q=1$ (Figure 5d,e), but indicated higher numbers of dominant species ($q=2$) in monocultures than in mixtures (Figure 5f).

Multiplicative diversity partitioning showed that alpha diversity (within traps and within sites) contributed less to overall gamma diversity than expected by a random distribution (Table 1). The contribution of beta diversity at the trap level (i.e. species turnover between traps) in monospecific coniferous stands was lower than expected by a random distribution, whereas species turnover between traps in monospecific and mixed European beech stands did not deviate significantly from a random distribution. The contribution of beta diversity between sites (i.e. species turnover between sites) to the overall gamma diversity was significantly higher than expected by chance for all stand types. Species turnover between sites was the highest in monospecific European beech stands (2.48) and the lowest in beech–spruce mixtures (1.98; Table 1).

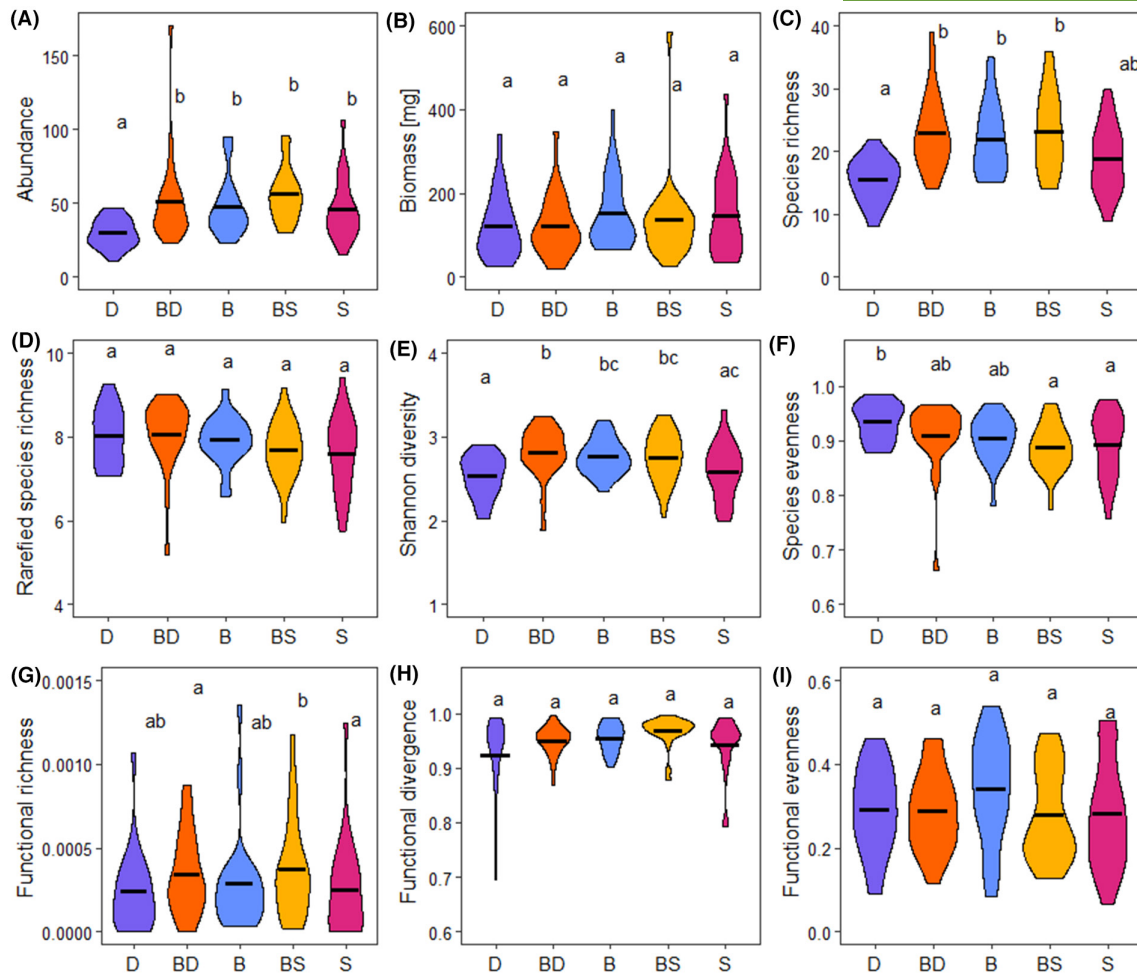


FIGURE 2 Canopy beetle abundance (A), biomass (B), species richness (C), rarefied species richness (D), Shannon diversity (E), species evenness (F), functional richness (G), functional divergence (H) and functional evenness (I) per stand type at trap level ($n = 117$). D, Douglas fir; BD, Beech–Douglas fir; B, European beech; BS, Beech–Spruce; S, Norway spruce. Significant differences are indicated by lower case letters, which were derived from linear mixed-effects models, including study region and landscape composition. Coloured areas reflect the data distribution. Black lines are the mean values per trap.

3.3 | Community composition

Canopy beetle community composition at plot level differed significantly between monospecific Douglas fir plots and all other stand types ($p < 0.05$ for all comparisons), except for beech–Douglas fir mixtures ($p = 0.25$). Similarly, communities in monospecific Norway spruce stands differed significantly from communities in all other stand types ($p < 0.05$ for all comparisons). Pure and mixed European beech stands did not differ significantly from each other ($p > 0.3$ for all comparisons; Figure 6, Appendix S1: Table S6). The patterns were similar for the NMDS axes 2 versus 3, but less pronounced for the NMDS axes 1 versus 3 (Appendix S1: Figure S2).

All five forest stand types had multiple indicator species (Appendix S1: Table S7). Monospecific Douglas fir stands had indicator species from all feeding guilds, including two species of saproxylic Latridiidae. Beech–Douglas fir mixtures were characterized by carnivorous indicator species, such as species of Cantharidae. In monospecific European beech stands, herbivorous weevils (Curculionidae)

dominated the indicator species, including the threatened *Gymnetron rostellum* (J.F.W.HERBST). Monospecific and mixed Norway spruce stands were characterized by saproxylic, myceto-detritivorous indicator species, for example species of Ptinidae.

Results remained largely the same when excluding the Harz Mountain site with its bark beetle calamities (for details, see Appendix S1: Table S8, Figures S3 and S4).

4 | DISCUSSION

Our study shows that beetle communities in the canopy stratum are impacted by plantations of introduced trees in multifaceted ways. The negative consequences of introduced conifer monocultures on beetle abundance and taxonomic and functional diversity were particularly severe for herbivorous beetles, but less pronounced for predatory beetles and often mitigated or even neutralized in admixtures with native European beech. Overall, monospecific and mixed

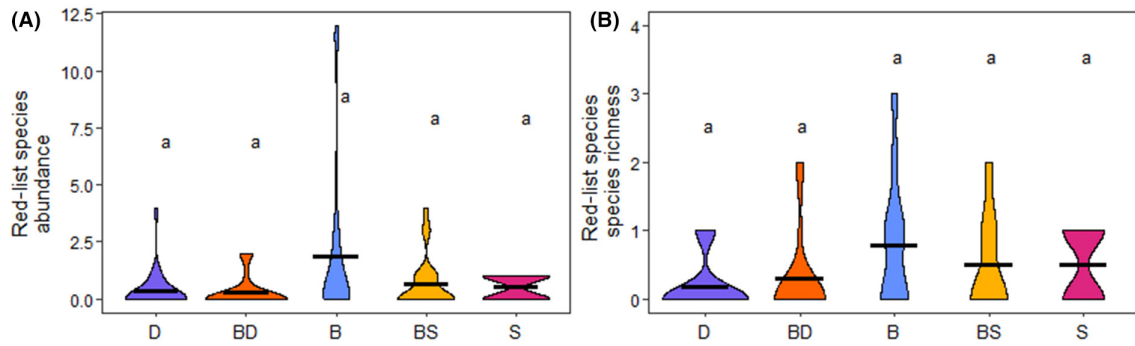


FIGURE 3 Abundance (A) and species richness (B) of red-listed (red list) beetle species per stand type at trap level ($n=117$). D, Douglas fir; BD, Beech-Douglas fir; B, European beech; BS, Beech-Spruce; S, Norway spruce. Significant differences are indicated by lower case letters, which were derived from linear mixed-effects models, including study region and landscape composition. Coloured areas reflect the data distribution. Black lines are the mean values per trap.

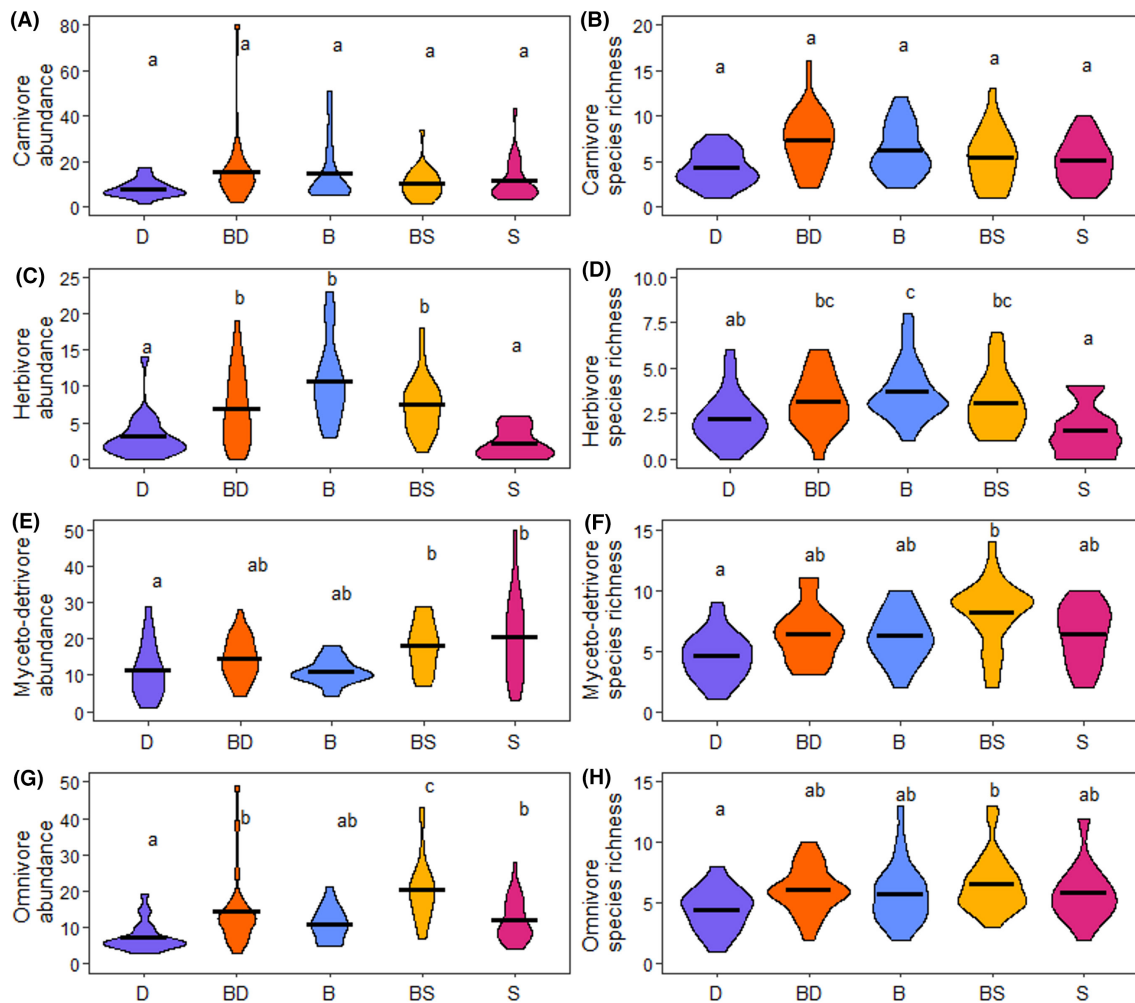


FIGURE 4 Abundance and species richness of carnivorous (A, B), herbivorous (C, D), myceto-detrivorous (E, F) and omnivorous (G, H) canopy beetles per stand type at trap level ($n=117$). D, Douglas fir; BD, Beech-Douglas fir; B, European beech; BS, Beech-Spruce; S, Norway spruce. Significant differences are marked with lower case letters, which were derived from linear mixed-effects models, including study region and landscape composition. Coloured areas reflect the data distribution. Black lines are the mean values per trap.

European beech stands hosted the highest abundance and diversity of canopy beetles from local to regional scales. Mixtures of European beech and non-native Douglas fir had particularly high beetle

diversity at landscape scale with high dissimilarity between local communities (i.e. between traps and between sites; beta diversity), indicating the suitability of such mixtures for biodiversity-friendly

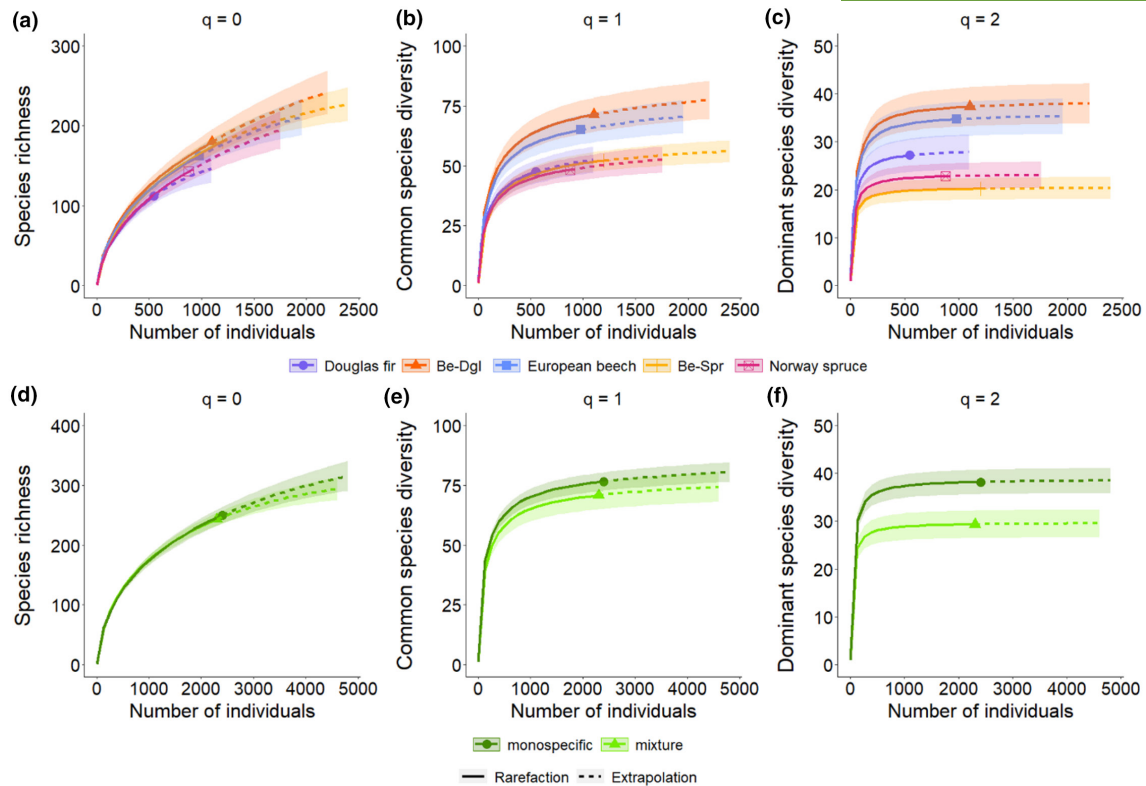


FIGURE 5 Abundance-based rarefaction (solid lines) and short-range extrapolation (dashed lines) of canopy beetle species richness ($q=0$), number of common species ($q=1$) and dominant species ($q=2$) for (a–c) individual forest stand types across plots and (d–f) monoculture stands and mixed culture stands across stand types. Shaded areas represent 95% confidence bands.

TABLE 1 Gamma diversity partitioning across stand types. Alpha.trap: within trap, Alpha.site: within site; Beta.trap: between traps within plot, Beta.site: between sites. (–) lower, (+) higher than expected from a random distribution. Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Stand type	Alpha.trap	Alpha.site	Beta.trap	Beta.site	Gamma
Douglas fir	12.93 (–)***	20.78 (–)***	1.6 (–)***	2.28 (+)***	47.48
Beech–Douglas fir	17.45 (–)***	29.27 (–)***	1.69 n.s.	2.43 (+)***	71.27
European beech	16.18 (–)***	26.23 (–)***	1.64 n.s.	2.48 (+)***	65.02
Beech–spruce	16.41 (–)***	26.41 (–)***	1.61 n.s.	1.98 (+)***	52.17
Norway spruce	14 (–)***	21.53 (–)***	1.55 (–)***	2.25 (+)***	48.38

forest management—with important implications for current discussions about the compatibility of climate change-adapted forest management in the context of close-to-nature forestry and conservation efforts such as the Natura 2000 network. In contrast, mixtures of European beech and Norway spruce, the latter of which is particularly affected by climate change in Germany, showed low landscape-scale diversity of common and dominant beetle species, illustrating that mixture effects also depend on tree species identity. Yet, the observed stark shifts in beetle species community composition between native European beech and introduced conifers were generally mitigated in mixtures (i.e. mixtures hosted many, but not all, species that were present in the respective monospecific stands), corroborating their potential to serve as a compromise between conservational and economic interests.

4.1 | Effects of introduced conifers on local to landscape beetle diversity

In line with our first hypothesis, monospecific stands of non-native Douglas fir locally reduced canopy beetle abundance, species richness and Shannon diversity compared to monospecific and mixed native European beech stands, exceeding the negative effects of Norway spruce planted outside its natural range. Moreover, monospecific Douglas fir stands reduced landscape-scale beetle diversity, yet not more severely than Norway spruce. These results partly corroborate past studies reporting negative effects of non-native conifers on forest biodiversity (Schuldtt et al., 2022; Wildermuth, Seifert, et al., 2023). However, they also highlight that native conifers planted outside their natural range can have

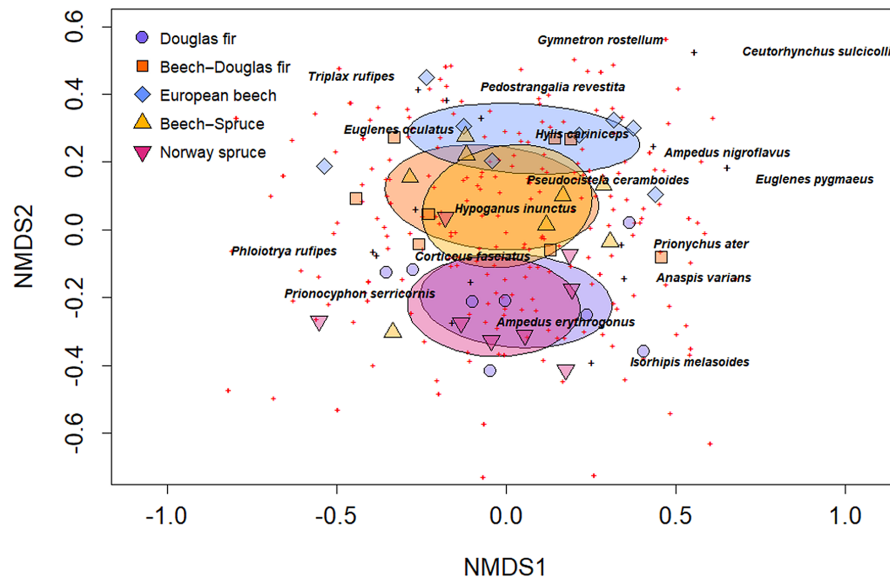


FIGURE 6 Nonmetric multidimensional scaling (NMDS) ordination of canopy beetle community composition per stand type at plot level. Stress <0.2. Ellipses show the standard deviation of stand type point scores. Red crosses represent beetle species (Appendix S1: Table S2). Black crosses and beetle species names represent red-listed species. Filled symbols represent the study plots and stand types. (graphs for the axes 1 vs. 3 and 2 vs. 3 in Appendix S1: Figure S2).

similarly detrimental effects (Staab et al., 2023; Wildermuth, Dönges, et al., 2023). Non-native tree species lack a shared evolutionary history with native arthropod communities and thus cannot harbour native species that are specialized on tree species-specific resources (Ballard et al., 2013; Tallamy et al., 2021). This is particularly relevant for herbivorous taxa (Berthelot et al., 2023; Burghardt & Tallamy, 2015), as reflected by the marked loss of abundance and diversity of herbivorous beetles in Douglas fir. The negative effects of Norway spruce may also stem from a mismatch between local communities and the resources provided by conifers planted outside their natural range, but moreover, Norway spruce plantations in Central Europe have faced unprecedented abiotic stress in recent years, fostering the dominance of pest species, such as bark beetles (Fuchs et al., 2022). In line with this, spruce plots in the Harz Mountain range hosted high bark beetle abundances in our study (see Section 2). Further, the functional richness of canopy beetles was lowered in monospecific Norway spruce stands, underlining that the functioning of beetle communities in these forests is compromised (Cours et al., 2021). Myceto-detritivorous beetles were the most abundant and diverse in monospecific Norway spruce stands. We suppose that the high abundances and diversity in our study are indicating high numbers of struggling and dying spruce trees, while Douglas fir may not have experienced such a decline (Cours et al., 2022). However, myceto-detritivorous saproxylic beetle diversity is important for forest functioning and resilience (Hagge et al., 2021; Neff et al., 2022), and our result could also indicate lower suitability of Douglas fir for breeding of xylophagous conifer specialists compared to Norway spruce (Gossner & Ammer, 2006).

Omnivorous species (e.g. taxa feeding on both plant and animal tissue) had low diversity and abundance in monospecific

non-native Douglas fir stands, contrasting past studies (Gossner & Ammer, 2006; Wildermuth, Seifert, et al., 2023). Whilst tree species selection and geographic coverage of other studies may have occluded this effect previously, we interpret our finding as further support that non-native trees cannot completely sustain native beetle communities, even if they are able to utilize various resources (Tallamy et al., 2021). By contrast, carnivorous beetle species were neither significantly impacted by Douglas fir nor Norway spruce, corroborating that secondary consumers are not necessarily reduced by introduced tree species (Gossner & Ammer, 2006; Oxbrough et al., 2016; Wildermuth, Dönges, et al., 2023). The abundance of carnivorous beetles was rather driven by the forest cover around the plots, with lower forest cover promoting their abundances, possibly due to the recruitment of open-land species (Achury et al., 2023; Seibold et al., 2016).

Notably, regional abiotic differences between our study plots were insignificant drivers of beetle responses compared to forest stand type, emphasizing the strong role of tree species identity in shaping canopy arthropod communities also under varying environmental conditions (Pedley et al., 2016; Wildermuth, Seifert, et al., 2023). Yet, total beetle biomass, rarefied species richness and species evenness did neither differ significantly between regions, nor forest stand type. Although total biomass in trend was lower in monospecific Douglas fir stands, we propose that the net functional impact of canopy arthropod biomass may not be severely lowered by Douglas fir (Wildermuth, Dönges, et al., 2023). Remarkably, evenness was even higher in monospecific Douglas fir stands, and rarefied species richness and beetle functional evenness were not lowered compared to native forest stands. This suggests that none of the few species that can associate with non-native Douglas fir reach dominant abundance levels (Kriegel

et al., 2021). We conclude that while we identified severe negative consequences of monospecific Douglas fir stands on canopy beetle abundance and diversity, the net functioning of canopy beetles may be similar to that in native stands (Yang & Gratton, 2014). This functioning, as assessed by our study, however, only comprises beetle biomass and trophic guild, calling for further research including other traits. Moreover, this result does not consider community composition and species-specific interactions, which are discussed together with Hypothesis 3 below.

4.2 | Mixture effects on local to landscape beetle diversity

Mixed forest stands had distinct effects depending on whether native European beech was mixed with non-native Douglas fir or Norway spruce. Beech–Douglas fir mixtures locally neutralized or, in the case of herbivores, mitigated the negative effects of Douglas fir, partly supporting our second hypothesis and past findings of intermediate diversity in tree mixtures compared to the respective monocultures (Matevski & Schuldt, 2023; Wildermuth, Seifert, et al., 2023). Possible reasons for such averaging effects are that habitat and resource fragmentation prevent that all specialized species associated with native forests can make use of such mixtures (Yguel et al., 2011). Notably, beech–Douglas fir mixtures showed particularly high landscape-scale beetle diversity across Hill numbers, indicating high species turnover between regions and thus promising potential for forest management (Gossner & Ammer, 2006). Although our results cannot identify the threshold of how much Douglas fir should be admixed to exploit such beneficial effects, we suggest that current thresholds of 30% maximum admixture of non-native trees in Natura 2000 areas do not necessarily lead to significant loss of beetle diversity (Kownatzki & Kriebitzsch, 2013). Mixtures of European beech and Norway spruce had high overall beetle species richness, Shannon diversity, functional richness and omnivorous beetle abundance and species richness at local scale, but had low levels of landscape-scale diversity of common and dominant beetle species. We interpret this as local positive effects of tree diversification, adding up the associated communities of the admixed tree species (Ampoorter et al., 2020; Matevski & Schuldt, 2020); but at the landscape scale, negative effects of Norway spruce become evident, caused by low species turnover between sites (beta diversity) and few (myceto-detrivorous and omnivorous) beetle species that dominate this vulnerable, partly dying tree species across large spatial scales (Cours et al., 2022).

Further supporting the value of mixed forests, multiplicative diversity partitioning revealed that beta diversity between traps was equally high in mixed stands as in native European beech forests. This underlines that local communities in mixed stands have high dissimilarity, increasing overall diversity at the stand scale (Matevski & Schuldt, 2020). Notably, also beta diversity between sites was high in beech–Douglas fir mixtures but lowest in

beech–spruce mixtures, corroborating that specifically Douglas fir admixtures have high dissimilarity among stand-scale communities, developing their full potential for biodiversity conservation when planted at large spatial scales (Leidinger et al., 2021; Schuldt et al., 2022). The low species turnover in beech–spruce mixtures and the resulting low total gamma diversity, however, illustrate that while mixed forests may have the potential to reconcile economic and conservational interests, tree species identity effects need to be considered as well (Leidinger et al., 2021). Beta diversity between sites was the highest in monospecific European beech stands, highlighting that the positive effects of beech on arthropod diversity are particularly evident at regional scales (Müller et al., 2013). This strong positive effect of monospecific beech stands explains why we did not detect net positive effects of tree admixture. Coniferous monocultures, meanwhile, homogenized beetle communities with increasing spatial scale, which was observed previously for monospecific plantations (Wildermuth, Dönges, et al., 2023). Even though such effects became evident at the landscape scale, our study suggests that flying beetle assemblages are strongly determined locally (Neff et al., 2022), as their abundance and diversity were foremost determined by the tree species composition of the plots where they were sampled (0.25 ha) and not by the forest composition around the plots. Given the negative effects of monospecific Douglas fir stands, this finding suggests that arthropod communities in patches of conifer monocultures cannot be supported efficiently by surrounding native forests, underscoring that introduced conifers should be admixed at the tree level and not in a mosaic of monocultures if they are to support forest biodiversity (see also Schuldt et al., 2022; Wang et al., 2019 for related findings on other groups of forest organisms).

4.3 | Beetle community composition

Supporting our third hypothesis, canopy beetle communities in introduced coniferous stands were markedly different to those in native European beech stands, which had typical broadleaf specialist indicator species (e.g. *Orcheste fagi* (herbivorous), *Litargus connexus* (myceto-detrivorous)) and harboured high abundances of red-listed species (e.g. *Gymnetron rostellum* (herbivorous)). Douglas fir communities, in contrast, were associated with euryecious, unthreatened indicator species (e.g. *Rhizophagus bipustulatus* (carnivorous)), and beetle indicator species in Norway spruce require forests with substantial amounts of deadwood (e.g. *Anthribus nebulosus*, *Dryophilus pusillus* (myceto-detrivorous)). Such shifts in community composition were expected due to stark differences in provided resources, forest health and, again, a lack of shared evolutionary history between non-native Douglas fir and native consumers (Gossner & Ammer, 2006; Yguel et al., 2011). However, these differences were mitigated in mixed forest stands. The latter underscores the potential of broadleaf–conifer mixtures to provide a compromise between conservational and economic

interests (Löf et al., 2019; Thurm & Pretzsch, 2016; Wildermuth, Seifert, et al., 2023).

5 | CONCLUSIONS

We show that, despite negative impacts when planted in monoculture, admixing non-native Douglas fir to native European beech forests does not reduce canopy beetle diversity. This is particularly true for beta diversity at the landscape scale, where Douglas fir admixtures performed better than admixed vulnerable native Norway spruce planted outside its natural range. This suggests that, from the perspective of biodiversity conservation, admixture of fast-growing non-native Douglas fir to native broadleaved European beech—but not plantation in monocultures—could be an acceptable option for future forest management. Determining optimal mixture proportions, however, requires further research. Yet, mixtures only mitigate shifts in community composition compared to native broadleaves and may not maintain the same numbers of threatened beetle species. This highlights that, whenever possible, native tree species should be prioritized.

AUTHOR CONTRIBUTIONS

Andreas Schuldt, Benjamin Wildermuth, Jonas Hagge and Carlo L. Seifert conceived the ideas and designed the methodology; Benjamin Wildermuth and Roman Tjaden collected the data; Benjamin Wildermuth analysed the data; Benjamin Wildermuth led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from GRO.data at <https://doi.org/10.25625/5AWJBC> (Wildermuth, 2024).

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SUPPORTING INFORMATION

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

Appendix S1: Table S1. Minimum, mean and maximum tree species proportions in the study plots.

Appendix S1: Table S2. List of beetle taxa abundances per stand type with assignment to their feeding guild.

Appendix S1: Table S3. Model summaries of linear mixed-effects models of beetle responses with landscape composition in a 400 m radius around the plots as fixed effect.

Appendix S1: Table S4. Mean abundance, biomass, taxonomic and functional diversity of canopy beetles per stand type \pm standard error.

Appendix S1: Table S5. Model summaries of linear mixed-effects models of beetle responses with stand type, study region (north & south) and landscape composition as fixed effects, including the interaction between stand type and study region.

Appendix S1: Table S6. Pairwise comparison of the species compositions between stand types (pairwiseAdonis).

Appendix S1: Table S7. Beetle indicator species per stand type.

Appendix S1: Table S8. Model summaries of linear mixed-effects models of beetle responses with stand type and study region (north & south) and landscape composition as fixed effects, including the interaction between stand type and study region under exclusion of the Harz mountain site (bark beetle calamities).

Appendix S1: Figure S1. Representative placement of a flight interception trap in a Beech-Douglas fir mixture.

Appendix S1: Figure S2. Axes 2 versus 3 and 2 versus 3 of the nonmetric multidimensional scaling (NMDS) ordination of canopy beetle community composition per stand type at plot level.

Appendix S1: Figure S3. Abundance-based rarefaction (solid lines) and short-range extrapolation (dashed lines) of canopy beetle

species richness ($q=0$), number of common species ($q=1$) and dominant species ($q=2$) for (a–c) individual forest stand types across plots and (d–f) monoculture stands and mixed culture stands across stand types under exclusion of the Harz mountain site (bark beetle calamities).

Appendix S1: Figure S4. Nonmetric multidimensional scaling (NMDS) ordination of canopy beetle community composition per stand type at plot level under exclusion of the Harz mountain site (bark beetle calamities).

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