RESEARCH ARTICLE

Tree mixtures mediate negative effects of introduced tree species on bird taxonomic and functional diversity

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Abstract

1. Recent biodiversity loss has emphasized the necessity to critically evaluate the consequences of human alterations of forest ecosystems. Stand diversification via tree species mixtures and the use of non-native trees are two such alterations currently gaining importance as climate change adaptations. However, the effects of local versus regional tree mixing on associated biodiversity and notably the modifying role of tree species growing outside their natural range remain poorly understood.

2. We assessed how monocultures and mixtures of native and introduced tree species influence the taxonomic and functional diversity of bird communities at stand and landscape scales in north-west Germany. We focused on the dominant natural tree species (*Fagus sylvatica*) and economically important conifer species planted outside their natural range (the native *Picea abies* and non-native *Pseudotsuga menziesii*).

3. We found that bird species richness and functional diversity were generally higher in pure and mixed stands of native *F. sylvatica* than in pure conifer stands, especially in comparison to non-native *P. menziesii*. These differences were particularly strong at the landscape scale. Pure conifer stands harboured only a reduced set of functionally similar bird species. Structural diversity based on tree microhabitat availability emerged as a key predictor of bird diversity.

4. *Synthesis and applications.* Our study suggests that tree species mixtures do not necessarily increase bird diversity compared to pure stands of native trees, but can promote bird diversity relative to pure stands of species planted outside their natural range. Moreover, local mixtures, rather than a mosaic of pure stands, may promote bird diversity also at the landscape scale. By contrast, pure stands of tree species planted outside their natural range can increase biotic homogenization of forest birds. Promoting structural diversity of microhabitats via tree retention and ensuring that non-native trees are planted in mixtures

with native trees may alleviate potential limitations of climate change-oriented management for biodiversity.

KEYWORDS
beta-diversity, biotic homogenization, bird functional diversity, Douglas fir, forest management, local and regional scale, non-native tree species, tree species mixtures

1 | INTRODUCTION

Biodiversity loss and biotic homogenization caused by habitat degradation and land use intensification have considerable ecological and socioeconomic consequences (Pereira et al., 2012). Forests, as often less intensively altered ecosystems, play an important role for safeguarding biodiversity (Brockerhoff et al., 2017). However, biodiversity declines are also increasingly reported from forests (e.g. Rosenberg et al., 2019; Seibold et al., 2019), with management alterations strongly influencing biodiversity (Gossner et al., 2014; Hilmers et al., 2018). This necessitates biodiversity-friendly management solutions when it comes to strengthening the role of forests in climate change adaptation and mitigation (Hua et al., 2022).

A promising approach to economic and ecological stability of forests and biodiversity conservation under climate change is stand diversification via tree mixtures (Brockerhoff et al., 2017; Messier et al., 2022). Mixing of tree species—especially of phylogenetically distant species with distinct functional characteristics—can increase structural and resource diversity and benefit various groups of forest biota (Ampoorter et al., 2020; Nell et al., 2018; Scherer-Lorenzen, 2014). However, recent research has suggested that, at least for some taxa, diversity at regional scales (beta and gamma diversity) may be promoted more by a mosaic of local monocultures of different tree species—each providing specific habitat features—than by local tree mixtures (Heinrichs et al., 2019). Moreover, in forests with only few tree species, the effects of stand diversification can strongly depend on tree species identity and its impact on resources (e.g. nutrient availability, microhabitat structures) and environmental conditions (e.g. light availability, microclimate; Scherer-Lorenzen, 2014). Many studies have reported stronger effects of tree species composition in terms of species identities than tree species richness on biodiversity (e.g. Staab & Schuldt, 2020; Vehviläinen et al., 2008).

Tree identity effects become particularly important when considering that forest management often selects for highly productive species and that these species are frequently planted outside their natural range (Pötzelsberger et al., 2020). While these were often native species in the past, non-native species are increasingly favoured because they are expected to be better adapted to climate change (Pötzelsberger et al., 2020). However, tree species planted outside their natural range can compromise positive tree mixture effects on forest biota, as these tree species often show poorer associations with native flora and fauna (Brändle & Brandl, 2001; Castaño-Villa et al., 2019). The ecological consequences of many non-native tree species are still poorly understood, because they have been cultivated for only few generations (Pötzelsberger et al., 2020) and it is often unclear at what mixture proportions potentially negative effects emerge (Leidinger et al., 2021; Oxbrough et al., 2016). For example, North-American Douglas fir *Pseudotsuga menziesii* is promoted in Central Europe to ensure future economic benefits (Thomas et al., 2022), in part replacing native (but planted outside its natural range) Norway spruce *Picea abies* that recently showed large, drought-induced diebacks (Popkin, 2021). Previous studies have shown that planting Norway spruce beyond its natural range does not necessarily reduce species richness but markedly changes species composition of native forest biota (e.g. Heinrichs et al., 2019; Kriegel et al., 2021; Sweeney et al., 2010). By contrast, the impact of non-native Douglas fir on biodiversity is still disputed due to a dearth of research, particularly concerning tree mixtures and consideration of important taxa such as birds (Schmid et al., 2014; Wohlgemuth et al., 2021). Moreover, our general understanding of stand diversification effects on biodiversity is hampered by a lack of data on biodiversity facets beyond species richness. Human alterations do not necessarily result in reduced species richness at local scales, but can nevertheless lead to marked changes in functional composition and to biotic homogenization through the loss of specialized species (Matthews et al., 2014; Rigal et al., 2022). Such effects are also expected to occur when tree species are planted outside their natural range, because especially generalist species might adapt to the novel resources these tree species provide (Gossner & Utschick, 2004; Pedley et al., 2019). A full understanding of tree mixture effects and the impact of (non-native) tree species identity on biodiversity therefore require more research into the abundance distributions and functional characteristics of forest biota.

Here, we studied monocultures and mixtures of economically important tree species in north-west Germany to assess mixture and identity effects on the taxonomic and functional diversity of birds. We focused on European beech *Fagus sylvatica* as the tree species that would be dominant under natural conditions (Leuschner & Ellenberg, 2017), Norway spruce as a Central European conifer largely planted outside its natural range and Douglas fir as a non-native conifer increasingly cultivated in Central Europe (Pötzelsberger et al., 2020; Thomas et al., 2022). Birds are key actors in ecological networks and provide important ecosystem services in forests, such as pest control and seed dispersal (Sekercioglu, 2006). Using multiple forest strata and being highly mobile, birds may show more complex responses to forest management than predominantly studied taxa associated with the

forest floor (e.g. vascular plants, epigeic arthropods), especially when going beyond local stand-scale effects. Therefore, knowledge of bird diversity is essential for sustainable forest management and biodiversity conservation. Birds can show preferences for or avoidance of tree functional groups, due to feeding specialization and in response to structural features such as tree microhabitats (Ampoorter et al., 2020; Paillet et al., 2018). Various studies have shown responses of birds to stand diversification and non-native tree species (e.g. Hanzelka & Reif, 2016; Leidinger et al., 2021; Nell et al., 2018; Pedley et al., 2019; Sweeney et al., 2010), but less is known about how local mixture proportions and the landscape configuration of monocultures versus mixtures influence bird species richness and especially functional diversity (Leidinger et al., 2021; Pedley et al., 2019). While these questions have recently received increased attention in the study of other taxa (e.g. Kriegel et al., 2021; Matevski & Schuldt, 2021), knowledge of Douglas fir effects on birds in Central Europe is limited (Wohlgemuth et al., 2021).

We hypothesized that (i) strong phylogenetic and therefore functional differences between European beech and the two conifer species lead to pronounced differences in bird species composition. This, in turn, (ii) promotes bird species richness and functional diversity in mixtures of beech with conifers compared to monocultures at the local stand scale, whereas mosaics of different monocultures may provide complementary habitats and comprise a larger bird gamma diversity than local mixtures at regional scales. Moreover, we expected that (iii) tree species identity and mixture proportions modify mixture effects via alterations of habitat and environmental conditions, thus determining the extent to which mixtures differ from monocultures in their effects on birds. Although inherently connected to tree species identity in our study, the degree of naturalness for Central Europe might contribute to explaining tree species-specific effects on birds (Pedley et al., 2019), with less negative effects of European Norway spruce than North-American Douglas fir. Finally, we hypothesized that (iv) effects of tree mixtures and tree identity particularly act on bird functional composition and diversity, whereas effects on bird species richness might be obscured by generalist bird species responding less to stand composition.

2 | MATERIALS AND METHODS

2.1 | Study area and design

The study was conducted across six study sites in Lower Saxony, Northwest Germany. The climate in this region is temperate, with a mean annual temperature between 7.6 and 9.2°C and mean annual precipitation between 670 and 1029 mm (Matevski et al., 2021). The six sites were distributed across three regions (Harz mountains, Solling low mountain range, Göhrde lowlands) to include the range of environmental conditions under which the focal tree species are being grown in Central Europe (see Matevski et al., 2021 for details on soil conditions and differences in climate among sites).

Each of the six sites comprised five rectangular study plots with a size of 2500 m^2, representing five different stand types: (1) pure European beech, (2) pure Norway spruce, (3) pure Douglas fir, (4) mixtures of beech and Norway spruce and (5) mixtures of beech and Douglas fir. This amounted to 30 study plots, of which one pure beech plot was excluded, so that analyses are based on 29 plots (see Figure S1 and Table S1 of Appendix S1 for geographic coordinates and further plot details). The excluded plot deviated from all other plots in that it was directly located at the forest edge in a forest otherwise completely composed of pure and mixed conifer stands, and because its stand age (130 years) far exceeded the average age of beech trees in the other plots (89 years). All other plots were located inside larger forest expanses and had an average stand age of 77 years (see Matevski et al., 2021). All plots represent even-aged, uniformly managed, state-owned forests. Mean distance among plots within sites was 1080 (± 708 SD) m.

2.2 | Bird data

Birds were surveyed with standardized 10-min point counts (Bibby et al., 2000) on five sampling dates (late March, late April, early May, late May, early June) for each plot in 2020. Point counts were conducted from the centre of each study plot by always the same observer (P.H.). All bird species seen and heard during the point counts and their abundances were recorded (excluding overflying individuals) within a 50-m radius from the plot centre (since plots were selected within larger stands, the 50-m radius warrants adequate consideration of stand types; see also Pedley et al., 2019; Leidinger et al., 2021). Since most recorded birds were heard, we are confident that surveys were not biased by differences in stand structure that we would expect to particularly affect visual detection probability. High correlation between observed and individual-based rarefied species richness (Pearson's $r = 0.93$; $p < 0.001$) further supports the robustness of our approach. We avoided double counting of individuals as much as possible by keeping track of heard and seen birds over the point count interval. Counts were conducted in the morning hours between sunrise and 11:00 am and in adequate weather conditions (avoiding strong winds and rain). The order of plots visited on consecutive sampling dates was varied to account for potential effects of survey time on detection probability. Permission to access the study plots was granted by the Niedersächsische Landesforsten (NLF). No permission for surveying birds and no ethical approval were required to conduct the study.

We selected key functional traits of the bird species to quantify functional diversity with respect to habitat use and resource requirements. Data were extracted from Renner and Hoesel (2017) and Bauer et al. (2012). Body mass was chosen as a proxy of individual energy demand, clutch size and broods per year as indicators of population-level energy demands. Bill length indicated food choice differences, complemented by a general categorization of diet (granivore, insectivore, carnivore, omnivore) as a measure of resource type utilization. Preferred nest stratum (ground, shrub,

tree) and cavity versus free nests reflect habitat requirements for nesting. Finally, we considered migratory status (non-migrating vs. migrating, which included all species of which most individuals of the local populations migrate each year to southern Europe or Africa) to quantify the temporal dimension of local habitat use and potential differences in resource requirements between migrating and non-migrating species.

For a general characterization of the bird communities, we used the species' threat status from the Red Lists of birds of Germany (Ryslavy et al., 2020) and information on forest affinity (Dorow et al., 2019).

2.3 | Environmental variables

Besides latitude and elevation above sea level, we compiled data on mean annual temperature and precipitation in the period from 1980 to 2019 (Deutscher Wetterdienst, DWD) for all plots.

Because tree mixtures differed in their proportions of conifers and beech, we used tree proportions of the three focal species to quantify their contribution to the overall tree composition in each plot. As an area-based measure of tree proportions, we used the area potentially available (APA) to each target species (Gspaltl et al., 2012) and expressed tree proportions as the percentage of total APA (2500 m^2) per plot. APA is calculated by rasterizing the plot area and assigning each raster point to the mapped tree individual that is closest to this point, while taking into account each tree's crown radius (estimated from tree diameters at breast height using allometric equations; Pretzsch et al., 2015).

To assess the influence of environmental plot characteristics on bird diversity, we measured canopy openness, leaf area index (LAI), mean tree diameter, variability in diameter, number of tree microhabitats, richness of microhabitat types and total deadwood volume in each plot. Canopy openness, leaf area index and tree diameter distributions are indicators of stand structure, which plays an important role for birds (Davies & Asner, 2014; Hanzelka & Reif, 2016). Canopy openness and LAI were measured at 12 sampling points (3×4 sampling grid, 10 m distance between sampling points) per plot with a Solariscope (SOL300, Behling) in July 2019, and averaged values per plot were used for analysis. Tree diameter at breast height (DBH) was measured for all trees ≥7 cm DBH during plot establishment in 2017–2018. Variability in DBH was calculated as coefficient of variation (CV), dividing the standard deviation of DBH values by the mean DBH per plot. Tree microhabitats, such as cavities, bark injuries, crown deadwood, exudates and epiphytes, provide important resources and habitat features to birds (Larrieu et al., 2018). Tree microhabitats and their abundance were recorded for all trees with DBH ≥15 cm on all plots following the general classification of Larrieu et al. (2018), but modified to contain a set of 13 microhabitat types (woodpecker cavities, rot holes, insect galleries and bore holes, other cavities, bark and wood injuries, bark shelter, crown deadwood, burrs and cankers, fungal fruiting bodies, mosses and lichens, ivy, nests, microsoil and fork splits). Richness of tree

microhabitats was calculated as the number of different types per plot; number of microhabitats were the summed occurrences per plot. Total deadwood volume was calculated from length/height and diameter measures of all lying and standing (tree heights estimated based on diameter-based height curves) deadwood with a minimum diameter at the thicker end of 7 cm in the above-mentioned 3×4 sampling grid, covering the central 1200 m^2 of each plot.

2.4 | Statistical analyses

All analyses were conducted with R 4.0.3 (R Core Team, 2020). Bird data per plot were pooled over the five survey dates to analyse the total number of bird species and abundance observed during the survey period. We calculated abundance-weighted functional evenness (FEve) and functional divergence (FDiv) as measures of bird functional diversity using the FD package (Laliberté et al., 2014). Functional evenness quantifies the extent to which species and their abundance distributions reflect a regular spacing (high FEve) of trait distributions in functional trait space (Villéger et al., 2008). Functional divergence specifies how much trait values of the most abundant species deviate from the average community trait values, with larger deviation indicating higher FDiv (Villéger et al., 2008). Body mass, clutch size, broods per year, bill length, diet, nest stratum, cavity breeding and migratory status were included as functional traits. We confirmed that none of the variables were highly correlated with each other (all Pearson's $r ≤ 0.56$) to ensure complementarity of the traits included. We did not consider functional richness (FRic) as it was closely related to bird species richness (Pearson's $r = 0.81$; $p < 0.001$).

Bird community composition was analysed with two-dimensional nonmetric multidimensional scaling (NMDS) ordination (*metaMDS* function in VEGAN package; Oksanen et al., 2020), based on relative abundances (proportional contribution per species to overall abundance) and Morisita–Horn similarity (Jost et al., 2011). The environmental plot characteristics described above were fitted to the ordination via regression analysis with the NMDS axes scores (*envfit* function). Statistical significances were assessed with permutation tests ($N = 999$).

We analysed bird diversity at two spatial scales: the local plot level and the landscape scale. *At the local level of individual plots*, we used linear mixed-effects models (*lme* function in NLME package; Pinheiro et al., 2020) to analyse the influence of stand type, focal tree proportions and environmental plot characteristics as fixed effects on bird species richness, abundance, functional evenness (FEve) and functional divergence (FDiv). All models were fitted with study site as random effect to account for differences in environmental conditions among sites. Variance inflation factors of the initial models were checked (*vif* function in CAR package) to confirm that models were not affected by high multicollinearity (variance inflation factors >5) of predictors.

We conducted the analyses of local bird diversity in three steps because stand types, proportions and plot characteristics were in

part highly correlated and because we were interested in determining the extent to which tree proportions and plot characteristics explain or add to the effects of the general stand type categorization. Therefore, we first fitted models for each of the four response variables with only stand type and region (Harz mountains, Solling low mountain range, Göhrde lowlands), as well as the interaction between the two to see if stand type effects were influenced by region (and therefore also by the spatial proximity of study sites; note that using alternate models fitting region as nested random effect with study site, or using geographic plot coordinates instead of region, did not change the results [data not shown]). In the second step, we replaced stand type by tree proportions (% APA) of Douglas fir and Norway spruce. Since relative proportions sum up to one, beech proportion was implicitly considered as it is complementary to the conifer proportions. In the third step, we tested for the effects of environmental plot characteristics on the four response variables. We excluded environmental variables that were highly correlated with other predictors (Pearson's $r \geq 0.7$), such that the initial models contained elevation, leaf area index, mean tree diameter, variability in tree diameter, number of microhabitats and total deadwood volume as predictors.

In all modelling steps, we used stepwise model simplification based on the Akaike information criterion corrected for small sample sizes (AICc) to drop uninformative predictors and interactions and to obtain a minimum adequate model with the lowest AICc value (Burnham & Anderson, 2004). Model simplification was based on maximum-likelihood estimation, final models were fitted with restricted maximum-likelihood. Differences among stand types were checked with Tukey HSD tests using Holm correction for multiple testing. Model residuals were checked for normality and homogeneity of variances.

At the landscape scale, we quantified beta diversity (species turnover, i.e. the increase in number of species with increasing sample size) and gamma diversity per stand type using the abundance-based rarefaction and extrapolation functions of the ɪNEXT package (Hsieh et al., 2016) based on Hill numbers. This approach enables data-economic and standardized diversity estimates in a unified framework based on effective numbers (taking into account abundance distributions) of species (Hsieh et al., 2016). We calculated species abundance curves from the plot level to the observed species numbers across all study plots and extrapolated to double the sample size of each of the five stand types. We used Hill numbers $q = 0$ to quantify the effective number of all species including rare species, and $q = 1$ (exponential Shannon diversity) as the effective number of common birds (Hsieh et al., 2016). Hill number $q = 2$ (Simpson diversity reflecting the effective number of dominant species) was not considered because of high correlation with values for $q = 1$ (Pearson's $r = 0.98$, $p < 0.001$). To test whether gamma diversity differed when regional diversity was the result of only monocultures or only mixtures, we performed the same analyses but pooled the data of the three monoculture stand types (to obtain monoculture landscapes) and the data of the two mixture stand types (mixture landscapes).

To assess whether environmental plot characteristics are influenced by stand type, we fitted linear mixed-effects models with each plot characteristic as a response variable, stand type as fixed effect and site as random effect. Significant differences among stand types were assessed using Tukey HSD test with Holm correction.

3 | RESULTS

Overall, we recorded 977 birds of 33 species (Table S2 in Appendix S1), with an average of 32 birds of 11 species per plot. Total species numbers per stand type were 19 (pure Douglas fir), 23 (Douglas fir-European beech mixtures), 25 (pure European beech), 28 (Norway spruce-beech mixtures) and 20 (pure Norway spruce). The most abundant species accounting for 52% of all individuals were Common Chaffinch *Fringilla coelebs*, Common Firecrest *Regulus ignicapilla*, Great Tit *Parus major* and Coal Tit *Periparus ater*. Eight species were only recorded as doubletons or singletons (Table S2). All but three species (*Phylloscopus trochilus*, *Turdus merula*, *Sylvia borin*) were species predominantly associated with forest habitats. Only one species, Eurasian Woodcock *Scolopax rusticola*, is red-listed and evaluated as 'near threatened' in Germany.

3.1 | Community composition

Bird species composition markedly differed between pure conifer and pure beech stands (Figure 1). Mixtures showed species compositions intermediate between the pure stands, meaning they harboured a mix of species of the respective pure stands. Pure conifer stands were characterized by species such as Coal Tit, Common Firecrest and Goldcrest *Regulus regulus*, while pure beech stands hosted a larger share of species such as Blue Tit *Cyanistes caeruleus*, European Robin *Erithacus rubecula*, Eurasian Blackcap *Sylvia atricapilla*, Common Chiffchaff *Phylloscopus collybita*, Wood warbler *Phylloscopus sibilatrix* and Eurasian Nuthatch *Sitta europaea* (Figure S2). The gradient from conifers over mixtures to pure beech along the first axis of the NMDS ordination was significantly correlated with canopy openness and mean tree diameter (positively associated with conifers), and with variability in tree diameter, density and diversity of microhabitats (positively associated with pure beech) (Figure 1, Table S3). Moreover, bird community composition varied regionally (effect of latitude), with mixed and pure beech stands showing larger spatial variability than pure conifer stands (larger spread of plots and ellipse area along the second axis; Figure 1).

3.2 | Local stand-scale diversity

At the scale of the individual plots, local bird species richness (alpha diversity) generally tended to be higher in pure beech stands and beech mixtures than in pure conifer stands (Figure 2a). Local bird
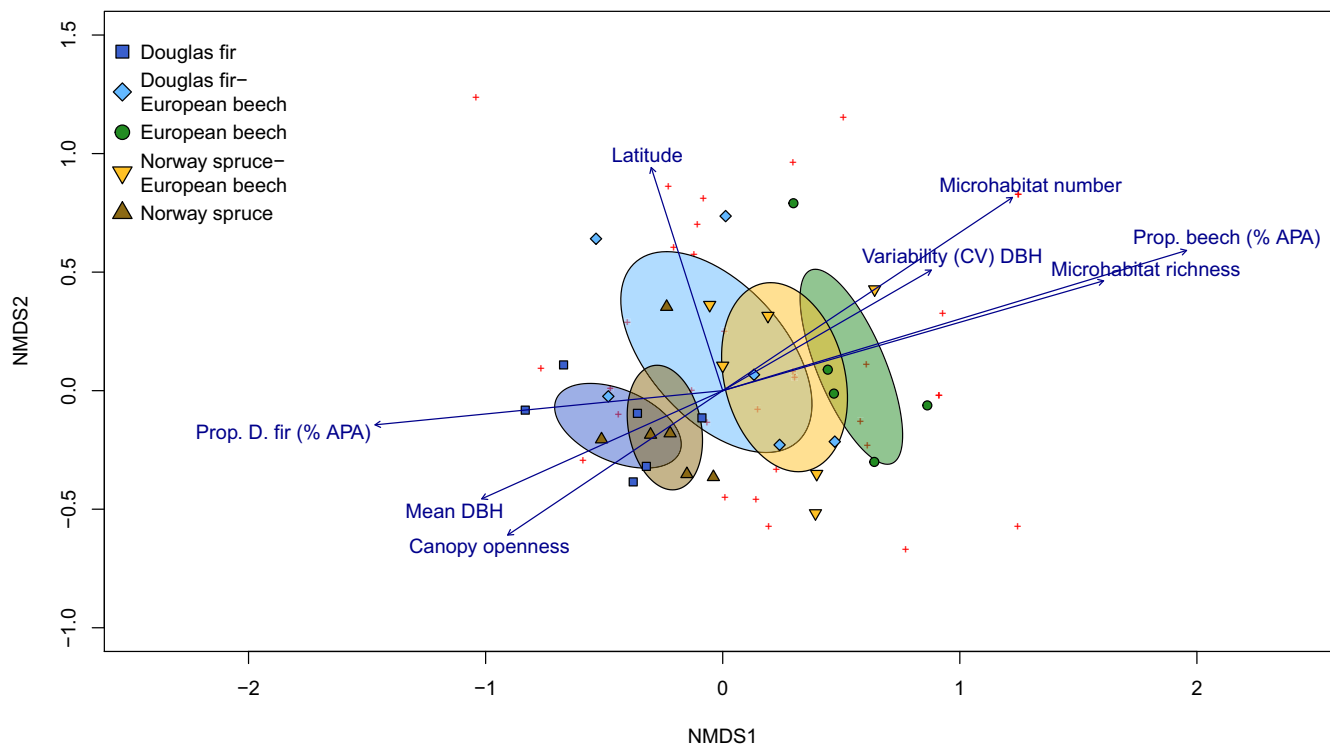
FIGURE 1 Bird community composition across the 29 study plots of the five stand types based on nonmetric multidimensional scaling (NMDS) ordination. Stress = 0.199. Environmental variables were fitted post hoc and show significant correlations with axes scores (see Table S3 for details). Ellipses show standard deviation of stand type point scores. Red crosses represent bird species (see Figure S2 for species names), coloured symbols are the study plots. APA, area potentially available, as a quantification of tree proportions; DBH, diameter at breast height

species richness was significantly lower in pure Douglas fir stands (9.3 ± 2.1 SD) than in pure beech stands (13.2 ± 4.7) and mixtures of Norway spruce and beech (13.7 ± 2.0; $F_{4,19}$ = 3.34; p = 0.031; Figure 2a). The number of recorded bird individuals was highest in pure spruce stands (39.3 ± 5.0) and mixtures of spruce and beech (39.0 ± 7.2), with significantly lower values in pure Douglas fir stands (25.5 ± 5.6; $F_{4,19}$ = 6.54; p = 0.002; Figure 2b). Functional evenness (FEve) of birds did not significantly differ among stand types at the plot level (around 0.75 for all stand types; $F_{4,19}$ = 0.22; p = 0.926; Figure 2c). By contrast, functional divergence (FDiv) was significantly higher in both mixture types (0.89 ± 0.04 for spruce-beech; 0.88 ± 0.05 for Douglas fir-beech) and in pure beech stands (0.90 ± 0.04) compared to pure conifer stand types (0.81 ± 0.05 for Douglas fir; 0.82 ± 0.04 for spruce; $F_{4,19}$ = 6.96; p = 0.001; Figure 2d).

Replacing the stand type categories by continuous tree proportions of Douglas fir and Norway spruce showed that local bird species richness, abundance and functional diversity all significantly declined with increasing proportions of Douglas fir in the study plots (richness by 38% from 13.1 to 8.2 species; abundance by 27% from 36.5 to 26.5 individuals, functional divergence by 9% from 0.88 to 0.8; Figure 3, Table S4). Bird species richness and functional divergence, but not abundance, also declined with increasing Norway spruce proportions (richness by 23%; functional divergence by 12%;

Figure 3, Table S4). Bird functional evenness was not significantly related to tree proportions (Table S4).

Study region did not significantly influence any of the bird diversity metrics and also did not significantly interact with the effects of stand type or tree proportions (Table S4). Environmental plot characteristics explained part of the variability in bird species richness, abundance and functional divergence (FDiv), but not in bird functional evenness (FEve) (Table S5). Bird species richness at the plot level decreased with increasing elevation and increased with leaf area index of the study plots (Table S5, Figure 4a). Bird abundance decreased with elevation as well (Table S5) and increased with the number of tree microhabitats in the plots (Figure 4b). Bird functional divergence increased with increasing variability in tree diameter (Figure 4c), number of tree microhabitats (Figure 4d) and total deadwood volume (Table S5), whereas it decreased with increasing leaf area index (Table S5).

Of the environmental plot variables tested, leaf area index, mean tree diameter and total deadwood volume did not differ significantly among the five stand types (Table S6). Canopy openness was highest in pure spruce stands and lowest in pure beech stands and Douglas fir-beech mixtures. Variability in tree diameter, richness of tree microhabitat types and number of tree microhabitats were all particularly high in pure beech stands as well as in mixtures, with significantly lower values in pure conifer stands (Table S6).

FIGURE 2 Plot-level differences in (a) species richness, (b) abundance, (c) functional evenness (FEve) and (d) functional divergence (FDiv) of bird communities among the five stand types (D = pure Douglas fir; DB = Douglas fir–European beech mixture; B = pure European beech; SB = Norway spruce–European beech mixture; S = pure Norway spruce). Boxplots show median values (vertical lines), open circles are arithmetic means, filled circles are observed values for each of the 29 study plots. Lines above the boxplots connect stand types that were significantly (solid lines) or close to significantly (dashed lines) different from each other, with °$p \leq 0.1$, *$p < 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$.
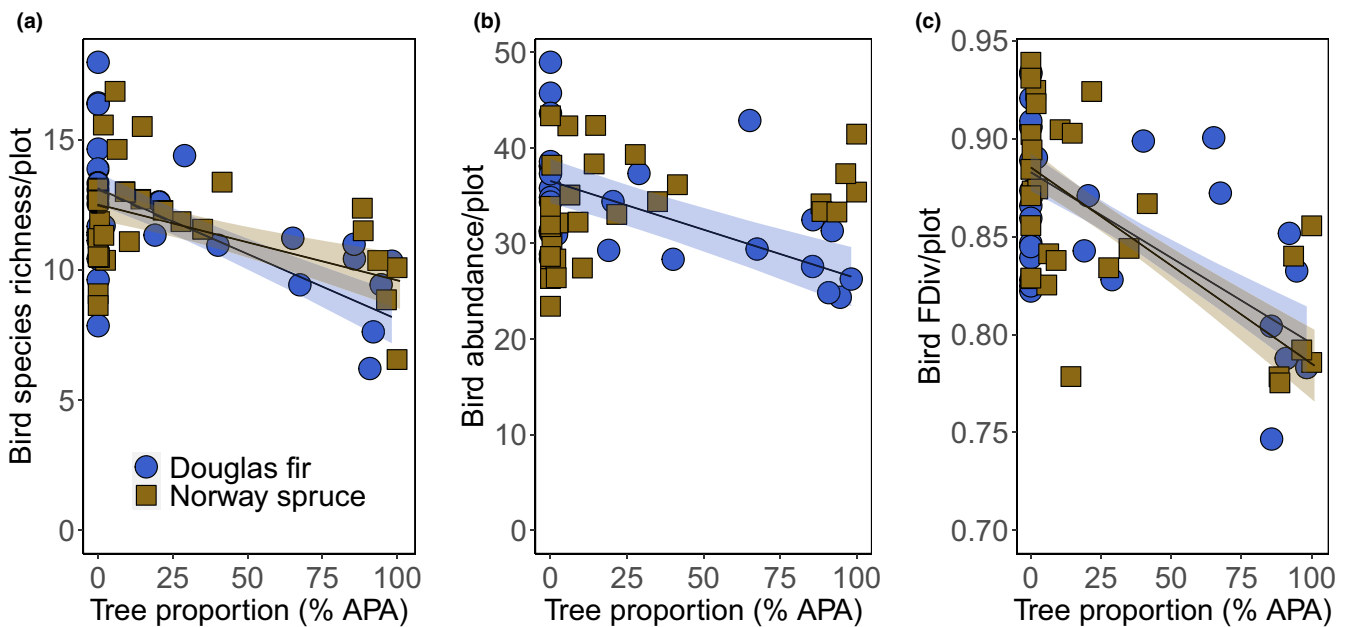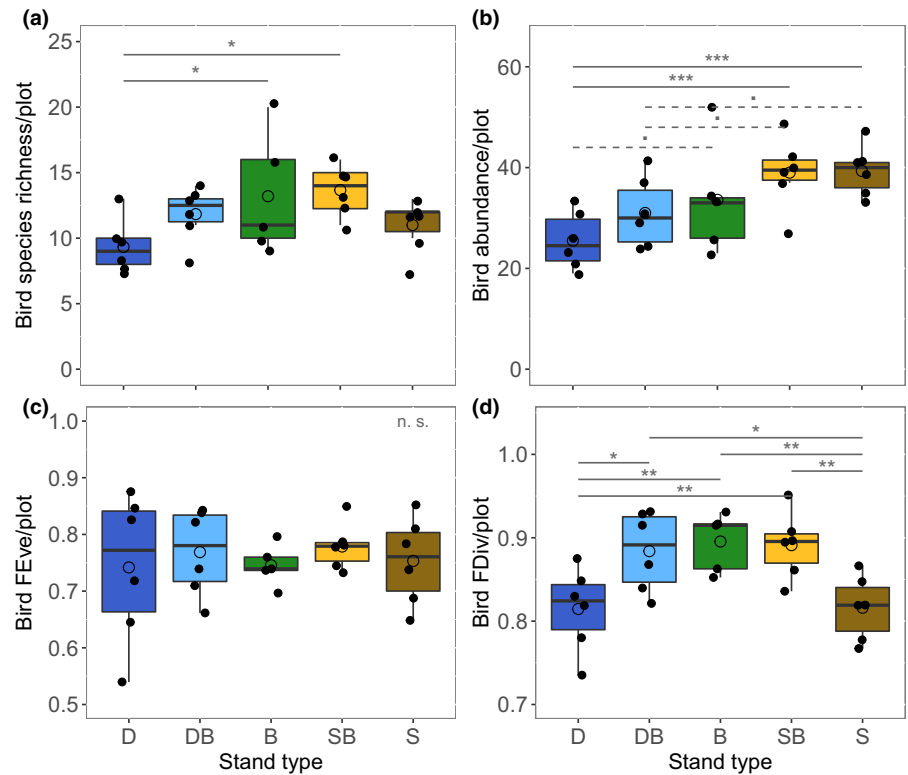

FIGURE 3 Relationships of the proportions of Douglas fir and Norway spruce in each of the 29 study plots (based on APA [area potentially available]) with (a) bird species richness, (b) abundance and (c) functional divergence (FDiv). Regression lines are model predictions adjusted for covariates and indicate significant ($p < 0.05$) relationships.

3.3 | Regional landscape-scale beta- and gamma diversity

At the landscape scale, that is, across all plots per stand type, there were strong differences in both the number of observed and expected species between pure conifer stands (both Douglas fir and Norway spruce) on the one hand and pure beech stands and mixtures of beech with conifers on the other (Figure 5). Especially for common species (Hill number $q = 1$), beta diversity, quantified as increase in species numbers (species turnover), as well as overall species numbers (gamma diversity) were significantly lower (no overlapping confidence bands) in the pure conifer stands, with
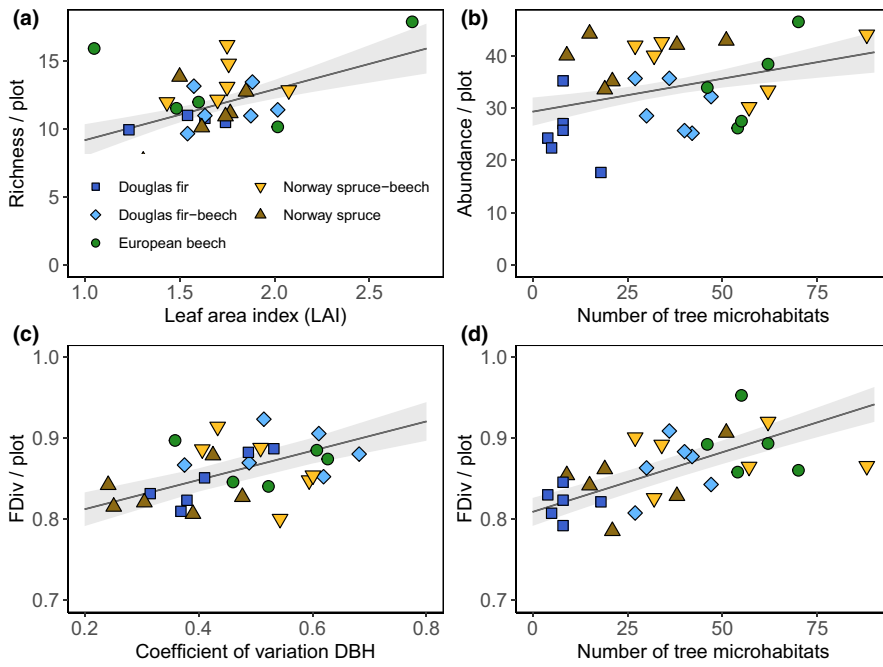
FIGURE 4 Relationships between environmental plot variables and plot-level bird diversity. (a) species richness and leaf area index, (b) abundance and number of tree microhabitats, (c) functional divergence (FDiv) and variability in tree diameter; (d) functional divergence (FDiv) and number of tree microhabitats. Regression lines are model predictions adjusted for covariates and indicate significant ($p < 0.05$) relationships.
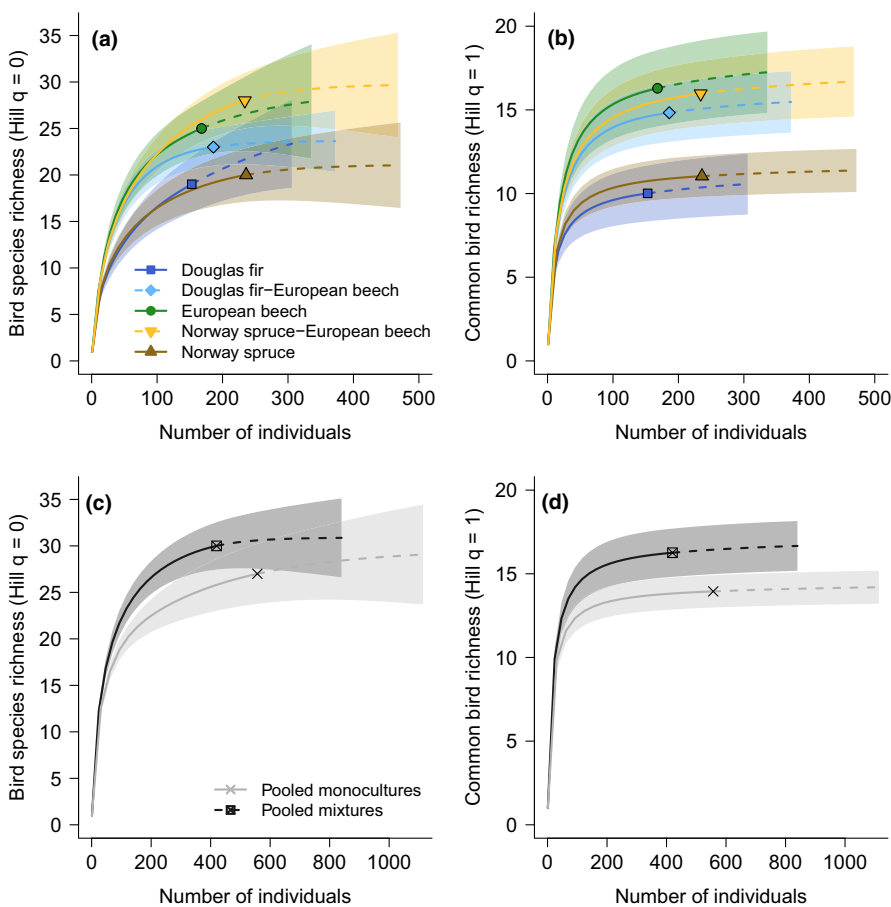

FIGURE 5 Rarefaction (solid lines) and extrapolation (dashed lines) based on the sample size (number of observed individuals) of beta diversity (species turnover with increasing sample size) and gamma diversity for the five stand types (a, b) and for data pooled for the three monoculture types and the two mixture types (c, d). (a, c) Total species richness (Hill number $q = 0$); (b, d) species richness of common birds (Hill number $q = 1$). Coloured symbols show observed species numbers per stand type across five (pure beech) and six (all other stand types) study plots respectively. Data were extrapolated up to double the observed number of individuals. Shaded areas are 95% confidence bands.

around 10 common species expected in these stands versus around 16 in pure beech stands and mixtures with beech (Figure 5b). Results were similar for total species richness (Hill number $q = 0$), but confidence bands overlapped to some extent (Figure 5a). Extrapolated

gamma diversity was similar for monocultures and mixtures when data were pooled for the three monoculture stand types and the two mixture types, although mixtures tended to show slightly higher values especially for common bird species (Figure 5c,d).

4 | DISCUSSION

Our study shows that while tree species mixtures do not necessarily increase bird diversity compared to pure stands of native trees, mixtures may provide improved conditions over pure stands of species planted outside their natural range. Notably, our findings contribute to the current debate on the scale dependence of mixture effects introduced by different management strategies (Heinrichs et al., 2019; Schall et al., 2020) and suggest that local mixtures, rather than a mosaic of different pure stands, can also benefit the diversity of associated forest biota at the landscape scale. By contrast, pure stands of tree species planted outside their natural range increased biotic homogenization by reducing species turnover and supporting only a reduced set of functionally similar bird species. Our results emphasize the direct consequences of forest management on biodiversity, an issue that is not yet fully resolved when it comes to biodiversity declines in forests (see Seibold et al., 2019).

Bird community composition markedly differed between pure beech and pure conifer stands, in line with the expectation that phylogenetically and functionally very different tree species support distinct bird communities. This finding concurs with previous studies of birds and other taxa in deciduous and coniferous forests and can be explained by the very different environmental characteristics (e.g. canopy openness in our study) and resource conditions of these forest types (Felton et al., 2021; Kriegel et al., 2021; Oxbrough et al., 2016; Pedley et al., 2019; but see e.g. Sweeney et al., 2010). Our results point out that the availability and diversity of tree microhabitats might make an important contribution to explaining these differences for birds. Birds can directly depend on tree microhabitats as habitat (e.g. nesting) structures or as feeding sources (Larrieu et al., 2018), responding more strongly to the overall diversity of microhabitats than to individual microhabitat types (Paillet et al., 2018). The fact that tree microhabitats were strongly associated with European beech and much less common on both conifers highlights that within regular rotation periods, these conifers do not develop small-scale structural heterogeneity to the same extent as many deciduous trees (Storch et al., 2018).

Structural characteristics also promoted bird abundance and functional divergence, supporting the notion that higher structural diversity enables tighter species packing and more specialized niche exploitation (Davies & Asner, 2014). Notably, however, local mixtures of beech with either of the two conifer species did not feature higher bird species richness or functional diversity than pure beech stands. This partly contradicts the general expectation that tree mixtures promote the diversity of associated biota (Ampoorter et al., 2020; Leidinger et al., 2021)—although mixtures in fact showed positive effects compared to pure stands of the two conifer species planted outside their natural range. Several reasons may explain the lack of strong and general mixture effects. Many bird species found in conifer stands were also present, although in lower numbers, in pure beech stands, while some species preferring the environmental conditions encountered in pure stands were absent in mixtures (Table S2). In addition, dilution of structural diversity by

the introduction of structure-poor conifers in mixtures, as discussed above, could play a role as well. Interestingly, deviating results have been observed for other taxa at the local plot level—especially forest floor-associated arthropods, for which direct effects of tree identity can differ from those at higher forest strata (Ulyshen, 2011)—with sometimes weak or even positive effects of Douglas fir on overall species richness (Kriegel et al., 2021; Matevski & Schuldt, 2021; Schuldt & Scherer-Lorenzen, 2014). In contrast to forest floor-associated taxa, birds use habitats and resources across strata and up into the canopy. Their diversity patterns thus potentially integrate across forest compartments and provide insights into the notoriously understudied higher forest strata, showing that overall biodiversity responses to management can deviate substantially from frequently studied patterns on the forest floor (see also Gossner & Utschick, 2004; Pedley et al., 2016 for arthropods). The finding that bird diversity and abundance negatively responded to gradual increases of conifer proportions indicates that it can be advisable to add conifers only at low proportions to reduce potentially negative effects on biodiversity. However, defining the most suitable mixture proportions compatible with biodiversity conservation for tree species grown outside their natural range requires further research, as proportion effects can vary nonlinearly with the tree species and associated forest taxa considered (e.g. Felton et al., 2021; Leidinger et al., 2021; Oxbrough et al., 2016).

It is notable that stand type effects varied for different components of bird diversity. While species richness was markedly reduced in pure Douglas fir compared to pure beech stands, abundance was highest in spruce and lowest in pure Douglas fir stands. This suggests an important role of tree identity beyond the general differences between deciduous and coniferous species. Such identity effects could be related to structural differences between the two conifer species that influence habitat and resource availability (Gossner & Utschick, 2004; Halaj et al., 1998). Identity effects might also potentially be related to the degree of naturalness of the species' occurrence in the study region (see also Pedley et al., 2019). Non-native tree species often harbour an impoverished fauna, especially of associated arthropods (Brändle & Brandl, 2001) and a previous study has shown that seasonally reduced prey availability in Douglas fir canopies compared to Norway spruce can negatively affect insectivorous bird densities (Gossner & Utschick, 2004). Similar relationships have been discussed in studies of other non-native tree species (e.g. Hanzelka & Reif, 2016), and Pedley et al. (2019) showed that conifer admixture negatively affects bird diversity particularly when these conifers are not part of the natural species composition of a region. In contrast to bird richness and abundance, bird functional evenness did not differ among stand types in our study, suggesting that forest bird communities show similar degrees of evenness in their niche exploitation irrespective of stand composition (see also Charbonnier et al., 2016). However, bird functional divergence was significantly reduced in pure conifer stands, meaning that the abundant bird species in conifer stands reflected average, general trait values of the overall communities. By contrast, abundant species in mixtures and pure beech stands showed more specialized, functionally divergent

trait patterns. These patterns indicate higher functional homogenization of bird communities in pure conifer stands and support the expectation that tree species growing outside their natural range and therefore lacking many specialized biotic interactions show a stronger dominance of generalist over specialized species (Magura et al., 2008; Pedley et al., 2019). In our study, the effects on bird functional divergence were more pronounced than effects on bird species richness, underscoring that a functionally explicit perspective may be required to detect the effects of forest composition and management on biodiversity. Such effects can go unnoticed with an exclusive focus on overall species richness (Matthews et al., 2014) because vagrant species and chance occurrences in a highly mobile group such as birds might mask patterns for important parts of the overall communities. Our results (abundance-weighted functional divergence, turnover and gamma diversity of common species) show that the abundant species at our study sites and therefore those that play key ecological roles in these forests were particularly affected (see also Burns et al., 2021).

Negative effects of pure conifer stands became even more obvious when moving from the plot level to the landscape scale and considering species turnover and gamma diversity. Lower gamma diversity of common bird species and correspondingly lower species turnover among sites in pure conifer stands mean that biotic homogenization is an important concern for larger scale forest management (see also Magura et al., 2008; Rigal et al., 2022). Our results suggest that local mixtures of beech with conifers might also be beneficial for bird diversity at the landscape scale, possibly because the potential structural and resource deficiencies of pure conifer stands discussed above are amplified at larger spatial scales. Contrary to our results for birds, a recent study showed that landscapes composed of pure beech and pure conifer stands feature a higher gamma diversity of vascular plants and bryophytes than landscapes of local tree species mixtures (Heinrichs et al., 2019). The authors explained this with pure stands offering complementary habitat conditions that resulted in higher species turnover among pure stands of different species than among mixtures (Heinrichs et al., 2019). As discussed above, such effects might be more pronounced for forest floor-associated taxa that are strongly affected by abiotic factors such as light availability and soil conditions. A broader understanding of how tree species identity and mixture effects influence biodiversity therefore requires adequate consideration of different taxa and forest strata (Ampoorter et al., 2020; Irwin et al., 2014; Pedley et al., 2016). Our study adds to the currently limited database by providing insights into the functionally diverse birds to help develop a more differentiated understanding of the consequences that management adaptations in the face of climate change have for biodiversity.

5 | CONCLUSIONS

Our study has implications for both the specific case of Central Europe and for our general understanding of how forest biodiversity responds to stand diversification and the use of tree species outside their natural range. The consistently positive effects of European beech on bird diversity argue for a strong role of this native species in supporting biodiversity in Central European forests, a role that is often debated controversially (Müller et al., 2013; Walentowski et al., 2014). Management adaptations aimed at ensuring economic and ecological stability under climate change should take this into account, especially since mixtures with conifers were not superior to pure beech in terms of bird diversity. Nevertheless, similar performance of mixtures and pure beech stands show that mixtures are a strong option compared to pure conifer stands when aiming at a better balance between economic returns and ecological stability. Tree identity effects of the two conifer species indicate that differences in structural attributes and potentially effects of native origin on resource availability are decisive in determining bird community responses to forest management. Recommendations that can be derived from these findings are that measures to enhance structural heterogeneity—for example, in the form of tree microhabitats—can be beneficial and could be promoted in conifer-dominated stands by tree retention and ensuring that non-native trees are planted in mixtures with native trees.

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SUPPORTING INFORMATION

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