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The Presence of Alternative Tree Species in European Beech Forests Drives Change in Functional Diversity and Composition of Forest Floor Plant Communities

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ABSTRACT

Questions: The diversity and composition of functional traits within plant communities have repeatedly been shown to be important predictors of overall ecosystem stability and the provision of basic ecosystem services. Admixing alternative tree species to monodominant European beech forests, a common measure of silvicultural climate change adaptation, is known to affect species diversity and composition of forest floor vegetation. Here we studied whether this adaptation measure also affects the functional diversity and composition of understorey plant communities.

Location: The study was carried out in temperate beech forests of southwest Germany in Central Europe.

Methods: We used the four key plant traits seed mass (SDM), plant height (PHV), leaf dry-matter content (LDMC) and specific leaf area (SLA) to calculate the distance-based functional richness (*FRic*), functional evenness (*FEve*), functional divergence (*FDiv*) and the community-weighted mean (CWM) plant traits of herb layer plant communities. Generalised mixed models were built to test the effects of gradually admixed Douglas fir (*Pseudotsuga menziesii*), silver fir (*Abies alba*), sessile oak (*Quercus petraea*), red oak (*Quercus rubra*) and various mixtures of native broadleaves on functional diversity and composition.

Results: The presence of Douglas fir and silver fir was associated with increased *FRic* of the understorey, silver fir and sessile oak (on base-rich soils only) with increased *FDiv*, whereas mixed broadleaves were associated with slightly decreased *FEve*. Regarding CWM trait values, the presence of silver fir (only acidic soils) and sessile oak (only base-rich soils) was linked with increased SDM, Douglas fir, red oak and mixed broadleaves with decreased LDMC. PHV was increased at higher proportions of Douglas fir but lowered in the presence of mixed broadleaves, and SLA was negatively affected by sessile oak presence on acidic soils.

Conclusion: Our results show that herb layer functional diversity and composition are distinctively affected by the diversification of beech forest canopies, which is indicative of environmental changes and might ultimately affect ecosystem functions such as nutrient cycling and litter decomposition. Regarding the conservation of plant communities typical of European beech forests, changes were most unfavourable in non-native red oak and Douglas fir and most favourable in native silver fir and sessile oak.

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1 | Introduction

The diversity and composition of functional traits within plant communities have repeatedly been shown to be important predictors of overall ecosystem stability and to play a key role in the provision of basic ecosystem functions such as nutrient cycling, water balancing and resource acquisition (Díaz and Cabido 2001; Hanisch et al. 2020). Functional traits are measurable features of a given organism, which are related to its ecological performance by either being responsive to environmental conditions (i.e., response traits) or by actively affecting ecosystem processes (effect traits; de Bello et al. 2021). Analysing the distribution of functional traits within an ecosystem is therefore an essential addition to measurements of only phylogenetic units such as species diversity, which are often insufficient to explain underlying ecosystem processes (McGill et al. 2006; Cadotte et al. 2011). Looking only at the role of understory plants in forest ecosystems, a large literature review by Pan et al. (2022), for example, identified more than 50 different plant traits that were found to significantly affect at least one, but mostly several forest ecosystem services. In that study, plant leaf traits such as specific leaf area (SLA) and leaf dry-matter content (LDMC) or traits not related to leaves, such as vegetative plant height (PHV) or seed mass (SDM) were shown to drive a variety of ecosystem services, such as soil fertility, biomass accumulation, herbivory control, soil water content or even fire protection and erosion control.

Whilst functional composition can be analysed by simply averaging the values of individual plant traits within communities, the assessment of functional diversity is more complex, as, analogously to species diversity, there is a vast amount of partly redundant measures of functional diversity (Mouchet et al. 2010). However, there is consensus that there are three main components of functional diversity, which are described as functional richness (*FRic*), functional evenness (*FEve*) and functional divergence (*FDiv*; Mason and Mouillot 2013).

Global climate change directly affects the distribution of both plant species and accordingly also of plant functional traits along ecological gradients (Skov and Svenning 2004; Walther 2010; Hauck et al. 2019). Considering the temperate forest biome, plant functional traits are additionally affected indirectly, as the result of the climate change adaptations of forest management, such as proactive changes of forest canopy composition (Brang et al. 2014; Spathelf et al. 2015), a major determinant of understorey plant diversity (Barbier et al. 2008). Worldwide, temperate forests witness an unprecedented trend of increasing air temperatures and higher vapour pressure deficits, resulting in generally decreased forest health (Millar and Stephenson 2015; IPCC 2023). So do Central European forests (Brasseur et al. 2023), where more frequent and more intense drought spells and heat waves are considered as main drivers of rising forest mortalities (Allen et al. 2010; Lindner et al. 2014). The relatively high climate susceptibility of Central Europe's most cultivated tree species, especially Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), makes these changes an even more pressing issue, which is expected to have both severe ecological (Hlásny et al. 2011; Lindner et al. 2014) and economic consequences (Hanewinkel et al. 2013; Baumbach et al. 2019) across Europe.

To counter these prospects, two widespread strategies of silvicultural climate change adaptation are the diversification of cultivated tree species and the active conversion of monocultures into mixed forests (Brang et al. 2014; Larsen et al. 2022; Bolte et al. 2023). These measures are thought to spread mortality risks (Felton et al. 2010; Ammer 2019) and to maintain a critical level of vital ecosystem services such as biomass production, water and nutrient cycling or habitat provision (Bauhus 2022). Admixing alternative tree species is also discussed for forests of European beech (*Fagus sylvatica*) that would naturally dominate Central Europe's vegetation and is still Central Europe's third most abundant tree species (Leuschner and Ellenberg 2017). However, beech is already facing reductions in productivity and increased mortality rates mainly attributed to reduced water supply during the early growing season and summer drought spells (Dulamsuren et al. 2017, 2022; del Martinez Castillo et al. 2022; Leuschner et al. 2023).

Concerning potential alternative tree species that could be used to enrich beech forests, there is a wide range of recommendations dependent on prioritised ecosystem services and the intended naturalness of forest stands. Native broadleaves such as sessile oak (*Quercus petraea*), which is considered to be quite tolerant to a drier and hotter climate in Central Europe (Hanewinkel et al. 2013; Hauck 2023) or different presently less abundant tree species, like maple (*Acer*), lime (*Tilia*), service tree (*Sorbus*), elm (*Ulmus*) and hornbeam (*Carpinus betulus*), are considered best compatible with biodiversity, but mostly exhibit slow growth rates (Hemery et al. 2010; Bauhus 2022). On the other hand, more productive tree species such as native silver fir (*Abies alba*) or non-natives such as Douglas fir (*Pseudotsuga menziesii*) or red oak (*Quercus rubra*) are considered plausible options when timber production is prioritised (Thurm et al. 2018; Bauhus 2022; Wrzesiński et al. 2024).

European beech forests harbour a distinct flora of highly specialised herbs, bryophytes and lichens, which were able to adapt to the shady, cool and humid interior of beech forests since the evolution of *Fagus sylvatica* in the Pleistocene (Schulze et al. 2016; Leuschner and Ellenberg 2017). Due to its high competitive strength especially in the regeneration phase, European beech is able to establish monodominant forest stands on most of its natural sites. As virtually any European tree species is less shade-casting and more light-demanding than European beech (Leuschner and Meier 2018), adding alternative tree species to beech canopies inevitably alters the microclimate below the canopy and will consequently affect the forest floor vegetation dependent on this microclimate. Besides the forest microclimate, the ground flora might also be affected by changes in leaf litter quality and accordingly decomposition rates, which were, for example, evidenced in mixtures with maple, hornbeam, linden and ash (*Fraxinus excelsior*; Jacob et al. 2010). Shifts in beech forest understorey vegetation with changing canopy compositions were evidenced by several Central European monitoring studies, for example, for admixtures of Douglas fir (Budde 2006; Podrázský et al. 2014; Bärmann et al. 2023), sessile oak (Rodríguez-Calcerrada et al. 2011; Dölle et al. 2017; Leidinger et al. 2021) or red oak (Stanek et al. 2020). These changes in the ground vegetation consisted of shifts in plant community composition but were also characterised by increases in species richness

(mostly due to the spread of light and nutrient-demanding species). Similar findings were reported by Mölder et al. (2008, 2014), who showed that increased plant diversity is not just attributable to beneficial effects of additional tree species but also to mitigation of the strong negative effects of pure beech canopies on herb layer diversity.

Given the correlation between species diversity and functional diversity (Mayfield et al. 2010; Schleuter et al. 2010; Tilman et al. 1997) as well as the close linkage between resource availability and functional composition of temperate forest understoreys (Maes et al. 2020), it is highly plausible that changes in the canopy composition of European beech forests do not only affect species diversity and composition but also the functional diversity and composition of the herb layer. However, there are to date no published studies that systematically tested this assumption. We therefore used a trait-based approach to study the effect of five different tree species (from hereon called target tree species) on the major components of herb layer functional diversity and functional composition, when they were gradually mixed into temperate beech forests. Based on recently published silvicultural recommendations for alternative tree species in Central Europe (Bauhus et al. 2021), these target species included

- Douglas fir (*Pseudotsuga menziesii*);
- Silver fir (*Abies alba*);
- Sessile oak (*Quercus petraea*);
- Red oak (*Quercus rubra*);
- Mixed broadleaves, that is, varying mixtures of multiple native deciduous tree species including maple (*Acer campestre*, *A. platanoides*, *A. pseudoplatanus*), hornbeam (*Carpinus betulus*), ash (*Fraxinus excelsior*), wild cherry (*Prunus avium*), sessile oak (*Quercus petraea*), wild service tree (*Sorbus torminalis*; *Syn.: Torminalis glaberrima*), lime (*Tilia cordata*, *T. platyphyllos*) and elm (*Ulmus glabra*, *U. minor*).

The analysed tree species thus covered a wide spectrum of broadleaves and conifers, natives and non-natives, and both highly productive and slow-growing species. In accordance with the wide range of potential sites for the cultivation of silver fir and sessile oak regarding different soil acidities (JRC 2016), we tested these species separately on acidic and base-rich soils, whereas all other species were only tested on acidic soil. Forest stands were sampled along a gradient of increasing target species canopy fractions, from pure beech forests to pure stands of all target species, to analyse the dependency of given effects on both the identity of the admixed tree species as well as their relative abundance within forests.

Given recent findings of increased species diversity after admixing alternative tree species to beech forests and the generally strong correlation between species diversity and functional diversity, we hypothesised that (1) the presence of different target species in beech forests also comes with increased functional diversity of the herb layer, in dependence on the target species identity and canopy fraction. Corresponding to earlier reports of lower degrees of functional specialisation due to increased availability of important resources such as light and nutrients (Depauw et al. 2020; Lelli et al. 2019) or increased management intensities (Chelli et al. 2021, 2022), we tested the hypothesis that (2) herb layer plant communities become more generalist with higher proportions of admixed target species, by means of greater plant heights, leaves rather adapted to resource turnover than conservation (i.e., higher SLA and lower dry-matter content) and a shift towards smaller seeds allowing efficient dispersal (Westoby et al. 2002).

2 | Methods

2.1 | Study Area

The study was conducted in the southwestern German scarplands, predominantly spanning the Black Forest, the Swabian Jura, Kraichgau, the Hohenlohe Plain and Steigerwald (Figure 1). Elevations of the studied forests were between 113 and 901 m a.s.l.; mean annual temperatures were 8°C to 11°C, and mean annual precipitations ranged from 700 to 1400 mm (Climate Data Center, Deutscher Wetterdienst, Offenbach, Germany). The forests grew predominantly on Cambisols over acidic rock (granite, sandstone and paragneiss) or on Cambisols (or partly Leptosols) over base-rich rock (Jurassic and Triassic limestone, marl and mudstone formations). Consequently, the potential natural vegetation of the study area would typically be either acidic (*Luzulo-Fagetum*) or mesic to calcareous beech forests (*Galio odorati-Fagetum* to *Hordelymo-Fagetum*) with co-occurrences of silver fir in the montane belt (Leuschner and Ellenberg 2017; Reidl 2013).

2.2 | Study Design and Sample Plot Selection

The study design follows a space-for-time approach (Kharouba and Williams 2024), as we assessed the effects of potential future target species admixtures by studying present forest stands of beech and target tree species. To this end, we scanned recent forest inventory data to identify pure and mixed stands of European beech and of the individual target species within the GIS application QGIS (version 3.16.9 Hannover). Pure stands needed to consist of ≥90% beech coverage or the target species, respectively, and mixed stands were categorised as either beech-dominated (65%–85% beech and 15%–35% of the target species), co-dominant mixed stands (40%–60% of beech and 40%–60% target species) or mixed stands dominated by the target species (65%–85% target species and 15%–35% beech). By allowing the mixing proportions to vary by ±10%, we ensured to sample forest stands along a mixing gradient whilst keeping comparable numbers of replicates within each category (Appendix S1). For the mixed broadleaves variant, we identified stands where the total combined proportion of relevant tree species fitted our classification. We further filtered for stands of representative age based on typical silvicultural rotation periods for each species to ensure sampling fully-developed herb layer vegetation.

After assessing all candidate sites in the field and selecting 5 to 7 replicates per combination of target species and mixture category, we selected three circular plots of 300 m^2 from a grid of randomised points in each forest site for vegetation sampling. All sample plots had a minimum distance of 40 m to the nearest

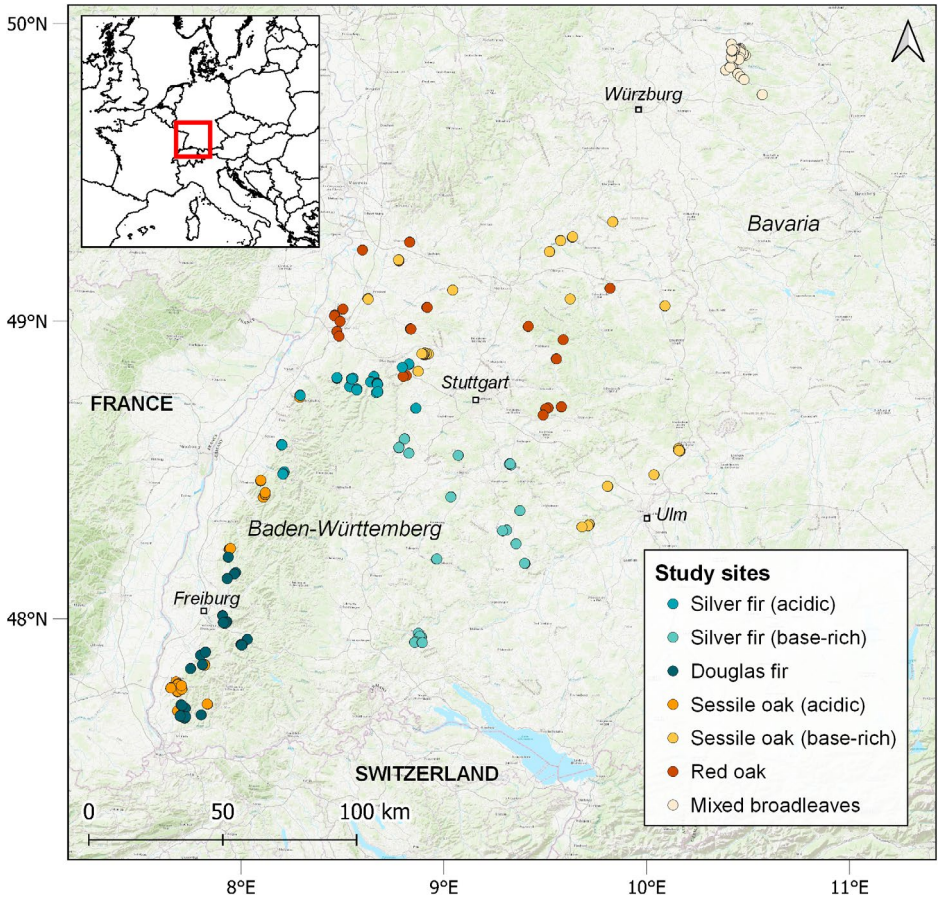


FIGURE 1 | Map of the study area with locations of 189 studied forests.

neighbouring plot within the stand and at least 25 m to neighbouring stands, open land or forest roads. Randomised points that were near larger clearings or on steep slopes (> 30°) were excluded prior to this selection process. In this way, we selected 567 study plots of 300 m^2 each distributed over 189 forests for vegetation sampling.

2.3 | Vegetation Sampling, Environmental Data and Plant Traits

Vegetation was sampled during the peak growing seasons of 2021–2023. We recorded all vascular plant species within the herb layer (< 0.5 m height) of each plot according to the taxonomic nomenclature of Jäger and Rothmaler (2017) and estimated their cover in 5% steps for species covering ≥ 10% of the plot, in 1% steps for species covering < 10%, and as 0.5% (if more than one individual was present) or 0.1% (if only one individual was present) for species covering < 1%.

Observer estimates of total canopy cover and stand basal area were recorded as proxies for light availability (Depauw et al. 2020; Dormann et al. 2020) and stand density, respectively. We further measured topsoil pH and C/N ratios by taking three 25 cm soil cores randomly distributed within a plot. For pH analyses, 10 g of the 2 mm fraction were measured with a Schott CG 842 pH meter (Mainz, Germany) in both water and 0.01 M $CaCl_2$ solution. Total C and N content was measured by dry combustion of 0.8 g milled material with a C/N analyser (TruSpec, Leco, St. Joseph, USA).

We compiled plant trait data on propagation (seed mass, SDM) and plant growth and performance (vegetative plant height, PHV; leaf dry-matter content, LDMC; specific leaf area, SLA) for all vascular plant species of the understory from the TRY plant trait database (Kattge et al. 2020; Kleyer et al. 2008). Plant traits (Appendix S2) were selected based on the leaf-height-seed scheme proposed by Westoby (1998), as these traits are assumed to largely characterise the ecological performance and strategy of vascular plant species (Cornelissen et al. 2003; Laughlin 2014; Pérez-Harguindeguy et al. 2013). Further, these traits were shown to be associated with a wide range of distinct forest ecosystem services in a recent literature review (Pan et al. 2022). Prior to analyses, tree regeneration, shrubs and climbing species were removed from the dataset, as these plants do not remain part of the herb layer throughout their life cycle (Perring et al. 2018). In the case of tree regeneration, acquired plant traits also mostly referred to adult individuals, which are not representative for the forest understory and would bias subsequent analyses. Tree regeneration further underlies factors on temporal and spatial scales distinctively different from the ones driving typical herb layer species. Woody dwarf-shrub species such as *Calluna vulgaris* or *Vaccinium myrtillus* were included, as they remain structurally and functionally part of the herb layer throughout their life cycle. A list of all plant species included and their corresponding trait values is compiled in Appendix S3.

Plots where the herb layer only consisted of species that were removed from the data for the above-mentioned reasons ($n = 19$) and plots where the total number of species was < 3

($n = 44$) were excluded from any further analysis, leaving a total of 504 plots (Appendix S4).

2.4 | Calculation of Functional Diversity Parameters

We calculated the functional richness (*FRic*), functional evenness (*FEve*) and functional divergence (*FDiv*) for each community according to the distance-based methods introduced by Villéger et al. (2008). In this mathematical framework, plant communities are depicted as point clouds in an n-dimensional space, in which each plant trait is represented as a separate axis on which each individual species is located according to its individual trait value. *FRic* is calculated as the convex hull volume occupied by the species community within the functional space. *FEve* is calculated as abundance-weighted distances between all species, and *FDiv* accounts for the abundance-weighted distances between species and the abundance-weighted centre of the community cloud. *FRic* and *FEve* can be interpreted analogously to species richness and species evenness. *FRic* quantifies the richness of different combinations of functional traits in an ecosystem. A high *FEve* means that a wide range of potential combinations of functional traits is rather evenly occupied by species. *FDiv* is interpreted in a way that low values indicate abundant species to fill rather similar functional niches, whereas higher values of *FDiv* imply a community where the functional niches of the most abundant species are more differentiated. These three indices are considered to cover the major components of functional diversity (Mason et al. 2005; Mason and Mouillot 2013), as they comprehensively characterise the distribution of communities within a multidimensional trait space (Villéger et al. 2008; Mouchet et al. 2010; Schleuter et al. 2010). Given the strong correlation between *FRic* and taxonomic richness (Mayfield et al. 2010), we created null models for each plot as recommended by Swenson (2014) to assess possible effects on *FRic* beyond effects on species richness. For each plot, we created 999 randomised communities by keeping the species number and identity constant, but shuffling species names across trait combinations each in replicate (unconstrained row name shuffling). Standardised effect sizes (SES) were calculated for each plot as the deviation of observed *FRic* (obs) from the expected *FRic* under a null model hypothesis (null):

$$\mathrm{SES} = \frac{FRic_{\mathrm{obs}} - \mathrm{mean}\left(FRic_{\mathrm{null}}\right)}{\mathrm{SD}\left(FRic_{\mathrm{null}}\right)}$$

We further computed the community-weighted mean (CWM) and the community-weighted variance (CWV) for all traits and communities:

$$\mathrm{CMM} = \frac{\sum_{i=1}^{S} \mathrm{trait}_i \times \mathrm{cover}_{ij}}{\sum_{i=1}^{S} \mathrm{cover}_{ij}}$$

$$\mathrm{CMV} = \sum_{i=1}^{S} \mathrm{cover}_{ij} \times \left(\mathrm{trait}_i - \mathrm{CWM}\right)^2$$

CWM is therefore the mean value of a trait across all species S weighted by the abundance (in our case cover) of each individual species i at each plot j. CWV is the corresponding mean deviance within a trait across all species of a plot and therefore a measure of functional diversity within single traits (Sonnier et al. 2010). As all traits were scaled to a mean of 0 and a standard deviation of 1, reported CWV values are unitless. Calculations were done in R 4.1.2 (R Core Team 2021; Vienna, Austria) and within the 'FD' package version 1.0-12 (Laliberté and Legendre 2010).

2.5 | Statistical Analyses

All statistical analyses were done in R 4.1.2. Given the generally strong effects of topsoil pH on forest floor vegetation, all analyses were done separately for samples from acidic ($n = 339$) and base-rich sites ($n = 165$), respectively.

We used linear mixed effect models to determine the effects of target tree species admixtures to beech forest on several components of functional diversity of the forest herb layer. Models were fitted using the R package 'lme4' 1.1-32 (Bates et al. 2015). Full model equations were as follows:

$$\begin{aligned} y \sim\ & \%\text{Douglas fir} + \%\text{Silver fir} + \%\text{Sessile oak} + \%\text{Red oak} \\ & + \%\text{Mixed broadleaves} + \text{Total canopy cover} \\ & + \text{Basal area} + \text{Soil pH} + \text{Soil C/N} + (1 \mid \text{Stand}) \end{aligned}$$

Using this formula we modelled *FRic*, *FEve*, *FDiv* and the CWM plant traits. Among the explanatory variables, % tree species (e.g., % Douglas fir) refers to the measured canopy fraction of a given target tree species as continuous predictor. 'Stand' was included as a random factor, as we assumed most uncontrolled variability at the stand level. We transformed response variables to normal distribution using the transformation procedure recommended for each variable in the R package 'bestNormalize' 1.9.1 (Peterson 2021). Recommendations by Zuur et al. (2010) were followed prior to formal analyses to avoid violations of the underlying model assumptions, and possible multicollinearities among predictor variables were excluded using the R package 'performance' 0.10.2 (Lüdecke et al. 2021). All variables were scaled to a mean of 0 with a standard deviation of 1 by subtracting the sample mean from the single values and dividing the results by the sample standard deviation. This allows direct comparison of effect sizes between different dependent and independent variables. Model fits were tested with the R package 'DHARMa' 0.4.6. As reducing model terms did not lead to decreases > 2 in the Akaike information criterion (AIC), we kept the original model as suggested by Burnham and Anderson (2004). Tables reporting model results contain both the conditional R^2 (i.e., the variance explained by both fixed and random factors) and the marginal R^2 (variance explained only by fixed factors). R^2 values given in the main body of the results section refer to the overall explanatory power of a given model and therefore conditional R^2.

3 | Results

3.1 | Effects of Target Tree Species Admixtures on Functional Diversity

Linear mixed models identified admixtures of Douglas fir, silver fir and mixed broadleaves as well as topsoil pH and C/N ratios

as drivers of plant functional diversity on acidic soils (Table 1; Appendix S5). Douglas fir and silver fir canopy fractions and site factors soil pH and soil C/N ratio drove *FRic*, in terms of high proportions of the admixed target species, more base-rich soils and narrower C/N ratios leading to increased *FRic*. On base-rich soils, *FRic* was only positively affected by silver fir canopy cover (Table 2; Appendix S6). The only significant effect on *FEve* was found in the canopy fraction of mixed broadleaves, which slightly decreased *FEve*. *FDiv* was positively affected by silver fir canopy fraction on acidic soils and by silver fir and sessile oak canopy fraction on base-rich soils. Model predictions for acidic sites were best for *FRic* ($R^2 = 0.52$) and covered less variance in *FEve* and *FDiv* (R^2 0.15–0.27). On base-rich soils, predictions were also best for *FRic* ($R^2 = 0.46$), but had less explanatory power for *FEve* and *FDiv* (R^2: 0.24–0.33). In the case of Douglas fir, results from the null models indicated that observed values of *FRic* at plot level were slightly lower than the ones expected from a random trait distribution. Nonetheless, the expected *FRic* under a null hypothesis showed the same trend of higher *FRic* towards higher Douglas fir canopy fractions (Appendix S5). However, models predicting SES (i.e., effects on functional richness independent of effects on species richness) only found

TABLE 1 | Results of linear mixed-effects models predicting functional diversity of the ground vegetation in forest stands on acidic soil.

	FRic			*FEve*			*FDiv*		
Predictor[a]	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***
Intercept	0.01	−0.12 to 0.13	0.88	0.00	−0.14 to 0.13	0.95	0.00	−0.11 to 0.11	0.99
% Douglas fir	0.32	0.18 to 0.46	**< 0.001*** **	−0.1	−0.26 to 0.05	0.20	0.09	−0.05 to 0.23	0.19
% Silver fir	0.23	0.09 to 0.37	**0.001** **	−0.05	−0.20 to 0.10	0.53	0.28	0.15 to 0.40	**< 0.001*** **
% Sessile oak	−0.04	−0.17 to 0.08	0.50	−0.03	−0.17 to 0.11	0.65	0.04	−0.07 to 0.16	0.46
% Red oak	0.00	−0.13 to 0.14	0.96	−0.13	−0.27 to 0.02	0.08	−0.01	−0.13 to 0.11	0.84
% Mixed broadleaves	0.09	−0.06 to 0.25	0.25	−0.20	−0.37 to −0.03	**0.02***	−0.04	−0.19 to 0.12	0.63
Stand basal area	0.06	−0.04 to 0.17	0.26	0.08	−0.05 to 0.20	0.23	−0.09	−0.21 to 0.03	0.15
Canopy cover	0.03	−0.07 to 0.13	0.57	0.01	−0.11 to 0.13	0.86	−0.05	−0.17 to 0.07	0.38
Soil pH	0.18	0.06 to 0.31	**0.004** **	0.08	−0.07 to 0.23	0.28	−0.07	−0.20 to 0.07	0.33
Soil C/N	−0.19	−0.31 to −0.06	**0.004** **	−0.07	−0.22 to 0.07	0.33	0.01	−0.12 to 0.15	0.88
Marginal R^2/ Conditional R^2		0.22/0.52			0.04/0.27			0.10/0.15	

Note: Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
Abbreviation: CI, 95% confidence intervals.
[a]% Douglas fir (silver fir, sessile oak, red oak and mixed broadleaves), canopy fractions of admixed target tree species.

TABLE 2 | Results of linear mixed-effects models predicting functional diversity the ground vegetation in forest stands on base-rich soil.

	FRic			*FEve*			*FDiv*		
Predictor[a]	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***
Intercept	0.00	−0.20 to 0.20	0.99	0.00	−0.18 to 0.19	0.98	0	−0.18 to 0.18	1.00
% Silver fir	0.37	0.16 to 0.59	**0.001** **	0.16	−0.06 to 0.37	0.15	0.22	0.00 to 0.43	**0.05***
% Sessile oak	0.09	−0.13 to 0.32	0.40	0.06	−0.16 to 0.27	0.59	0.25	0.04 to 0.47	**0.02***
Stand basal area	0.00	−0.16 to 0.16	0.98	−0.07	−0.24 to 0.10	0.43	0.04	−0.12 to 0.21	0.60
Canopy cover	−0.03	−0.18 to 0.12	0.72	0.05	−0.12 to 0.22	0.55	−0.09	−0.25 to 0.07	0.25
Soil pH	−0.05	−0.22 to 0.11	0.52	−0.10	−0.27 to 0.07	0.27	0.03	−0.13 to 0.20	0.71
Soil C/N	0.09	−0.08 to 0.25	0.30	0.09	−0.09 to 0.26	0.34	0.08	−0.09 to 0.25	0.34
Marginal R^2/ Conditional R^2		0.13/0.47			0.04/0.24			0.08/0.33	

Note: Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
Abbreviation: CI, 95% confidence intervals.
[a]% Douglas fir (silver fir, sessile oak, red oak and mixed broadleaves), canopy fractions of admixed target tree species.

the presence of silver fir to be a significant positive factor for *FRic*, but not Douglas fir (Appendix S7). Mixed broadleaves had a negative effect on *FRic* in this model. On acidic soil, also low C/N ratios increased *FRic* and so did higher pH values on base/rich soils.

3.2 | Effects of Target Tree Species Admixtures on Functional Composition

Linear mixed models of CWM plant traits found silver fir at acidic sites and sessile oak at base-rich sites to be drivers of SDM. SDM was further affected by soil C/N ratio in base-rich forests, with higher C/N ratio leading to larger seeds (Tables 3 and 4; Appendices S8 and S9). LDMC was decreased by admixtures of Douglas fir, red oak and mixed broadleaves and by topsoil pH at acidic sites. The effect of silver fir on LDMC at base-rich sites was not significant. PHV increased with admixtures of Douglas fir but was lowered by the addition of mixed broadleaves and by topsoil C/N ratio. There were no significant predictors of PHV in base-rich forests. The same applied to SLA at base-rich sites, whereas, on acidic soils, SLA was negatively affected by sessile oak admixtures, stand basal area. and positively affected by soil pH. However, effects on SLA were generally weak with low model estimates. Models predicting CWM traits performed generally better than those predicting functional diversity. At acidic sites, explained variance ranged from $R^2 = 0.50$ to 0.65, including random effects and from $R^2 = 0.16$ to 0.29 if only fixed factors were considered. Random site effects turned out to be much more important at base-rich sites, where the overall explained variance (R^2: 0.47–0.56) was much higher than variance explained exclusively by fixed factors (R^2: 0.04–0.16). On acidic soil, silver fir canopy fractions significantly increased the variance of LDMC and SLA, whereas sessile oak was a negative factor for the variance of SLA and mixed broadleaves for the variance of PHV and SLA (Appendix S10). On base-rich soil, the presence of silver fir increased the variance of LDMC and SLA whilst sessile oak canopy presence positively affected the variance of SDM and PHV (Appendix S11).

4 | Discussion

We hypothesised that admixtures of alternative tree species to beech forests would increase functional diversity of understory plant communities because European beech generates very uniform site conditions on the forest floor when forming monospecific stands (Willner et al. 2017). This can be confirmed for at least Douglas fir, silver fir (on acidic and base-rich soils) as well as sessile oak at base-rich sites, as the occurrence of these tree species increased *FRic*, *FDiv* or both. We found no significant effect of red oak and sessile oak at acidic sites on functional diversity and therefore need to reject our first hypothesis with respect to these species. Mixed broadleaves even had a slightly negative effect on *FEve*, which also contradicted our expectations.

Within the conceptual framework of functional diversity, high *FRic* is thought to indicate generally good use of resources by plant communities, resulting in high productivity and high ecosystem stability (Mason et al. 2005; Schleuter et al. 2010). However, this relationship implies communities in ecosystems with sufficient availability of resources. Starting this study from monodominant *Fagus sylvatica* forests on acidic soils, we looked at ecosystems where some of the most important resources for vascular plants (i.e., light and nutrients) are strongly limited. Nutrients in acidic beech forests of Central Europe are not only limited by poor nutrient supply from the soil and the slow decomposition rates of beech leaves, but also by long-lasting anthropogenic nutrient depletion through logging for fuel and construction wood and litter-raking for centuries and acidic air pollution since the onset of industrialisation (Schulze et al. 2016). Values of *FRic* were uniformly low at acidic sites, which we interpret as a sign of resource limitation in these forests (Harpole and Tilman 2007). This interpretation is supported by our findings of overall higher *FRic* in pure beech forests on base-rich soils, which are known to entail higher resource availability for vascular plants (Willner et al. 2017).

There is evidence that diversifying the canopy of temperate forests by admixtures of alternative tree species can increase the overall availability or the heterogeneity of plant resources, for example by allowing more light to transmit through less shade-casting canopies or by increased soil nutrient cycling due to complementary resource use and improved litter quality (Forrester and Bauhus 2016; Pretzsch et al. 2017; Richards et al. 2010). We thus conclude that the positive effects of admixtures of Douglas fir and silver fir on functional richness are caused by increased resource availability for vascular plants on the forest floor, allowing more species to colonise these habitats, leading to an increase in occupied functional niche spaces (Mayfield et al. 2010). Given that canopy cover was the only predictor that did not significantly affect any of the response variables, whereas soil pH and soil C/N ratio did, we think that changes in soil parameters were more important than changes in light availability. This is in line with earlier reports of signals of increased nutrient availability after Douglas fir admixtures to acidic beech forests (Budde 2006; Pastorelli et al. 2021; Podrázský et al. 2014), but somewhat contradicts findings of Depauw et al. (2020), who found light availability to be a main driver of functional change in temperate forest herb layer communities. However, such shifts in resource availability can be expected to negatively affect the occurrence of beech forest specialists, which were already shown to decline at the expense of increasing proportions of more competitive generalists when Douglas fir was introduced into beech forests (Bärmann et al. 2023). Further, it needs to be noted that increasing species richness after admixtures of Douglas fir and silver fir might have at least in part produced a sampling bias in these stands, that is, a higher probability to capture extreme trait values (and therefore higher *FRic*) with higher numbers of sampled species (Mayfield et al. 2010). Results from the models of SES back this interpretation in the case of Douglas fir, whereas the increased *FRic* after silver fir admixtures appeared to be independent of increased species richness.

In contrast to *FRic*, both *FEve* and *FDiv* are known to be independent of species numbers (Schleuter et al. 2010). *FEve* and *FDiv* were generally high in all pure beech stands, indicating efficient utilisation of available resources by herb layer plant communities in these forests, which have the highest

TABLE 3 | Results of linear mixed-effects models predicting cover-weighted means of plant functional traits of the ground vegetation in stands on acidic soil, including seed mass (SDM), leaf dry-matter content (LDMC), vegetative plant height (PHV) and specific leaf area (SLA).

	SDM			LDMC			PHV			SLA		
Predictor[a]	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***
Intercept	0.03	−0.11 to 0.16	0.70	0.00	−0.13 to 0.12	0.97	0.02	−0.11 to 0.14	0.79	−0.02	−0.15 to 0.12	0.82
% Douglas fir	0.01	−0.14 to 0.16	0.90	−0.16	−0.29 to −0.03	**0.02***	0.19	0.05 to 0.34	**0.007**	0.07	−0.08 to 0.22	0.39
% Silver fir	0.37	0.22 to 0.51	**<0.001*****	0.11	−0.03 to 0.24	0.11	−0.10	−0.24 to 0.04	0.16	0.12	−0.03 to 0.27	0.11
% Sessile oak	−0.03	−0.17 to 0.10	0.62	0.07	−0.06 to 0.19	0.29	−0.07	−0.19 to 0.06	0.32	−0.16	−0.30 to −0.03	**0.02**
% Red oak	−0.01	−0.15 to 0.13	0.92	−0.29	−0.42 to −0.16	**<0.001*****	0.07	−0.07 to 0.20	0.31	0.10	−0.05 to 0.24	0.19
% Mixed broadleaves	0.16	−0.01 to 0.32	0.06	−0.23	−0.38 to −0.08	**0.002****	−0.33	−0.48 to −0.17	**<0.001*****	0.13	−0.04 to 0.30	0.13
Stand basal area	0.02	−0.09 to 0.12	0.76	0.03	−0.06 to 0.13	0.47	0.10	−0.01 to 0.20	0.07	−0.12	−0.23 to −0.01	**0.04**
Canopy cover	−0.09	−0.19 to 0.02	0.10	−0.05	−0.15 to 0.04	0.25	0.02	−0.09 to 0.12	0.74	0.03	−0.08 to 0.14	0.58
Soil pH	0.00	−0.13 to 0.13	1.00	−0.12	−0.24 to −0.01	**0.03***	0.07	−0.05 to 0.20	0.25	0.17	0.04 to 0.30	**0.01**
Soil C/N	−0.04	−0.17 to 0.09	0.58	0.11	−0.01 to 0.22	0.07	−0.23	−0.36 to −0.11	**<0.001*****	−0.07	−0.20 to 0.06	0.306
Marginal R^2/ Conditional R^2		0.17/0.53			0.29/0.65			0.19/0.51			0.16/0.50	

Note: Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
Abbreviation: CI, 95% confidence intervals.
[a]% Douglas fir (silver fir, sessile oak, red oak and mixed broadleaves), canopy fractions of admixed target tree species.

TABLE 4 | Results of linear mixed-effects models predicting cover-weighted means of plant functional traits of the ground vegetation in stands on base-rich soil, including seed mass (SDM), leaf dry-matter content (LDMC), vegetative plant height (PHV) and specific leaf area (SLA).

	SDM			LDMC			PHV			SLA		
Predictor[a]	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***	**Estimate**	**CI**	***p***
Intercept	0.00	−0.20 to 0.20	1.00	0.00	−0.22 to 0.21	0.98	−0.01	−0.22 to 0.21	0.97	0.00	−0.20 to 0.20	1.00
% Silver fir	0.15	−0.07 to 0.37	0.17	0.07	−0.15 to 0.29	0.52	0.18	−0.04 to 0.40	0.10	0.17	−0.04 to 0.38	0.11
% Sessile oak	0.40	0.17 to 0.62	**0.001****	0.06	−0.17 to 0.29	0.63	0.15	−0.08 to 0.37	0.21	−0.09	−0.31 to 0.13	0.41
Stand basal area	−0.07	−0.23 to 0.09	0.37	−0.05	−0.21 to 0.11	0.52	0.06	−0.10 to 0.21	0.47	0.15	−0.01 to 0.31	0.06
Canopy cover	0.09	−0.05 to 0.24	0.21	−0.13	−0.27 to 0.01	0.08	−0.04	−0.18 to 0.10	0.56	−0.05	−0.19 to 0.10	0.53
Soil pH	−0.04	−0.20 to 0.12	0.60	−0.08	−0.24 to 0.08	0.35	0.02	−0.14 to 0.18	0.79	0.00	−0.16 to 0.15	0.95
Soil C/N	0.21	0.04 to 0.37	**0.01***	0.07	−0.09 to 0.23	0.37	0.12	−0.04 to 0.28	0.13	−0.01	−0.17 to 0.15	0.88
Marginal R^2/Conditional R^2		0.12/0.50			0.04/0.54			0.05/0.56			0.09/0.47	

Note: Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
Abbreviation: CI, 95% confidence intervals.
[a]% Douglas fir (silver fir, sessile oak, red oak and mixed broadleaves), canopy fractions of admixed target tree species.

similarity to the primaeval forest vegetation of Central Europe before forests were widely reshaped as the result of human colonisation (Leuschner and Ellenberg 2017). Reduced *FEve* after admixture of mixed broadleaves could be interpreted as a sign of underutilisation of certain resources (Mason et al. 2005), although these effects were generally small and values of *FEve* remained high even at high canopy fractions of mixed broadleaves.

Similar to effects on functional diversity, effects on functional composition (i.e., CWM trait values) were more complex than expected and highly dependent on the admixed target tree species. In our second hypothesis, we assumed that increasing target species admixtures would lead to less specialised understories, by means of plant species becoming taller with smaller seeds and smaller leaves rather suited for competition and dispersal than for enduring in a resource-limited environment (Liancourt et al. 2009). These assumptions were confirmed for Douglas fir and red oak, whereas results from sites with silver fir, sessile oak and mixed broadleaved partly contradicted our hypothesis.

Higher SDM due to admixture of silver fir at acidic sites and of sessile oak at base-rich sites could have different causes. SDM represents an important trade-off for vascular plants. Whilst heavy plant seeds provide more energy reserves and therefore often come with better chances of successful establishment and higher growth rates in early life stages, smaller seeds are quicker to disperse and further allow plants to produce higher numbers of diaspores with the same investment (Westoby 1998). Therefore, SDM is regarded as a good indicator of overall plant strategies, with ruderal species typically producing smaller seeds and stress-tolerating species producing heavier seeds (Grime 2001). However, heavier seeds could also point towards plant species with more specialised dispersal strategies, such as epi- or endo-zoochory, in contrast to species relying on less directed dispersal vectors such as wind dispersal (Albert et al. 2015). High herb layer CWM SDM was also shown to be indicative of stronger litter accumulation on the forest floor (Maes et al. 2020), which is in line with the general assumption of higher SDM in plant species that are adapted to environments with highly pronounced stress factors. Somewhat contrasting, Kermavnar and Kutnar (2020) found CWM SDM to increase with increasing topsoil pH and nutrient availability, which would partly contradict the concept of heavier seeds as a response to stressful environments, but is consistent with our finding of soil C/N driving SDM in calcareous forests.

Considering plant traits related to the productivity and biotic interaction of different herb layer communities, we found LDMC to be the most affected trait. Lowered average LDMC after admixture of Douglas fir, red oak and mixed broadleaves implies a shift towards plant communities that are more directed to resource uptake and turnover than resource conservation (Liu et al. 2017; Power et al. 2019). Just as SDM, LDMC is likewise regarded to display a basic trade-off in plants (Wright et al. 2004). Leaves with high LDMC are generally regarded as more resistant, long-lasting, water-conserving and less vulnerable to herbivory, but at the price of reduced photosynthetic capacity. Low LDMC, on the other hand, comes with more efficient

photosynthetic capacity resulting in higher growth rates, but also with reduced leaf lifespans, higher nutrient and water consumption and susceptibility to herbivory (Wright et al. 2004). Similar to the more widely used SLA (Reich et al. 1997), LDMC is a reliable predictor of plant primary production and consequently often linked to several ecosystem services related to productivity and biomass accumulation (Miedema Brown and Anand 2022; Smart et al. 2017). In temperate forests, low understory LDMC can therefore indicate habitats with good resource availability, especially light (Burton et al. 2017) and soil nutrients (Hodgson et al. 2011) and plant communities rather driven by competition than by resource limitation (Grime 2001). As LDMC and SLA are inversely related, reduced CWM SLA after admixtures of sessile oak to acidic beech forests is not only influenced by shifts in resource availability (Maes et al. 2020), but even more caused by the specific character of European beech to produce high leaf areas of thin hygro-mesomorphic leaves with a leaf area index (LAI) as high as 4.5–9.5 not only to increase carbon assimilation but also to exclude competitors by shade-casting (Leuschner 2020).

PHV was higher in the presence of Douglas fir, whereas it was lowered at higher canopy fractions of mixed broadleaves. As taller forest plant communities are thought to be more resource-consuming and competitive (Pan et al. 2022), we see increased PHV after Douglas fir admixture as yet another signal of increased resource availability and resource use in these forests. This interpretation is also in line with our model results of narrower C/N ratios leading to, on average, taller plant communities. This interpretation also corresponds to findings by Kermavnar and Kutnar (2020), who report CWM plant heights to be largely driven by soil nutrients and light availability. In the case of mixed broadleaves, the interpretation of reduced PHV is less straightforward. Explaining the negative effect of mixed broadleaves on PHV by assuming reduced plant resource availability does not seem adequate here. On the one hand, such an interpretation would contradict the findings of decreased LDMC in these sites. On the other hand, we can assume good supply of nutrients in these forests due to good litter decomposability and the complementary resource use of diverse forest stands (Thoms et al. 2010; Morin et al. 2011). With this said, we would most likely attribute the somewhat ambiguous results found exclusively in admixtures of mixed broadleaves to the fact that these forests were naturally more complex than others, by means of alternating, but always manifold canopy compositions of up to seven different tree species. We assume that the higher degree of complexity in canopy and stand structure ultimately also results in much higher complexity in the relationship between canopy and understory vegetation (Pretzsch et al. 2017). Additionally, our study only looked at above-ground plant traits and did not include any below-ground traits or traits related to clonal growth. These might, however, help explain some of the contradicting findings, as they were shown to be partly independent and to be indicative of biotic and abiotic interactions; only looking at above-ground trait responses might miss (Chelli et al. 2024).

5 | Conclusion

Our results show that admixing alternative tree species to temperate beech forests came with distinct shifts in both functional diversity and functional composition of the herb layer. However, these changes were highly dependent on the tree species, as the individual tested target tree species led to a different outcome (Figure 2).

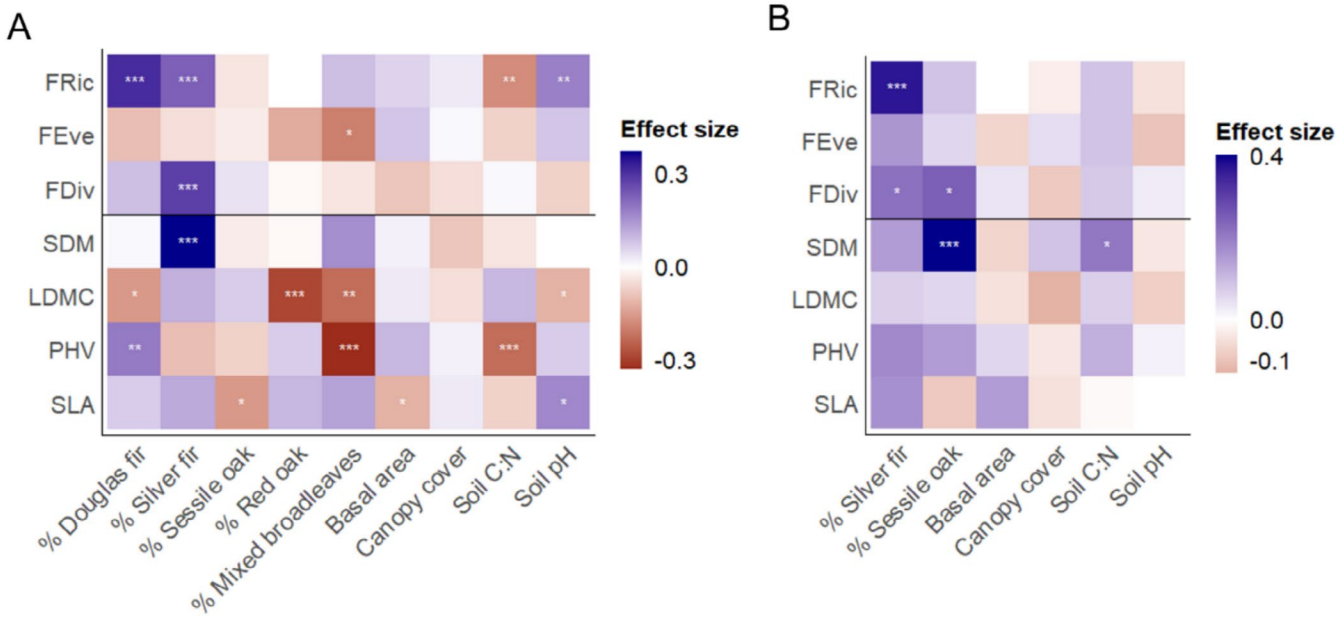


FIGURE 2 | Drivers of functional diversity of the ground vegetation on acidic (A) and base-rich (B) soils. Relative effects of explanatory variables (*X*-axis) on response variables (*Y*-axis) resulting from linear mixed-effects modelling. Response variables included the functional diversity components functional richness (*FRic*), functional evenness (*FEve*) and functional divergence (*FDiv*) and the community-weighted means of four plant traits: Seed mass (SDM), leaf dry-matter content (LDMC), vegetative plant height (PHV) and specific leaf area (SLA). Explanatory variables included the canopy fraction of five different admixed target species (%), stand basal area, total canopy cover, topsoil C/N ratios and topsoil pH. Blue colours represent positive effects and red colours represent negative effects. Asterisks indicate significant effects (***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$).

Although admixtures of non-native Douglas fir resulted in overall higher functional diversity, the observed shifts in functional composition also indicated changes in underlying ecosystem processes, such as shifts away from a strongly resource-limited environment towards a richer and more competition-driven ecosystem, a trend that also applied to red oak. Silver fir resulted in significant increases in functional diversity of understory plant communities on both acidic and calcareous soils, but with less severe implications for functional composition. The same applies to sessile oak, whose presence in the canopy partly also led to increased functional diversity without concerning adverse effects on functional composition. In our view, this makes sessile oak and silver fir the better alternatives to Douglas fir and red oak with regard to nature conservation.

Canopy presence of mixed broadleaves caused mixed responses in functional diversity and functional composition, which led to contradicting interpretations and also prevents us from making a consistent conclusion in this case. However, our results highlight the complexity of the underlying ecosystem processes in such mixed forests consisting of multiple tree species and underline the need for further research on this possible scenario for European beech forests.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.15856353.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** jvs70058-sup-0001-supinfo.docx.