# Shifting tree species composition affects biodiversity of multiple taxa in Central European forests 

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#### Abstract

Central Europe's temperate forests are heavily shaped by centuries of human activity. Their natural vegetation, mainly consisting of beech-dominated (Fagus sylvatica) deciduous forests, has been widely replaced by more profitable species grown outside of their natural ranges. This has strongly influenced forest-dwelling communities. Necessary adaptations to changing climatic conditions and the increasing demand for forest ecosystem multifunctionality are reversing these shifts in tree species composition. Integrative approaches that seek to balance production and conservation goals promote mixed forests of beech with spruce (Picea abies), pine (Pinus sylvestris), or oak (Quercus spp.). These mixed forests more closely resemble the natural vegetation and have reduced vulnerability to disturbances compared to coniferous monocultures, but higher commercial value compared to pure beech forests. However, our understanding of how different levels of admixture of commercially relevant tree species to beech forests affect multi-trophic diversity and community composition remains limited.

We investigated herbaceous plants, fungi, oribatid mites, springtails, true bugs, beetles, birds and bats in 41 mature forest stands differing in tree species composition. We assessed the effects of admixtures on abundances and alpha and gamma diversity, i.e. the total number of species per forest type, and a measure of multidiversity by comparing reference beech stands with stands containing varying proportions of admixed species. At the plot level, the proportion of admixtures was especially important regarding oak and pine. Increasing shares of oak positively affected birds, true bugs and herbivorous beetles. Increasing shares of pine benefitted herbivorous true bugs and understory plants but negatively affected other true bugs, bats, and litter-decomposing fungi. Spruce admixture resulted in higher saproxylic beetle and bird diversity. At the landscape level, admixture significantly increased gamma diversity in plants, mycorrhizal and litter decomposing fungi and herbivorous and saproxylic beetles. Only springtail gamma diversity decreased in the presence of admixture. Admixture also


significantly altered community composition for six out of 13 taxa. Indicator species were found for all forest types, and seven species groups included species significantly associated with pure beech stands.

Our results indicate that forestry decisions determine forest biodiversity across trophic levels via tree species composition, combining habitat heterogeneity effects and tree species-specific associations. Even low shares of admixed species affect local abundances and diversity. By displacing some species while benefitting others, admixing also alters species composition. This study provides a basis for estimating how altering tree species composition in Central European forests changes the diversity and composition of forest communities.

Keywords: Integrative forest management; Mixed forest; Beech forest; Forest structure; Fagus sylvatica; Multidiversity

## 1. Introduction

Central Europe's temperate forests are heavily shaped by centuries of human activity, with barely any vestiges of pristine forest (Sabatini et al., 2018). In the absence of anthropogenic land use, these forests would cover most of the terrestrial landmass (Leuschner and Ellenberg, 2017), with beech (Fagus sylvatica) dominating the natural vegetation (Bohn and Gollub, 2007). Modern forestry's focus on timber production has re-shaped the composition of Europe's forests (Röhrig et al., 2019), and today fast-growing and profitable tree species like spruce (Picea abies) and Scots pine (Pinus sylvestris), often grown outside of their natural range, make up the largest shares of the forested area (BMEL, 2014).

The tree species composition of the forest canopy is a defining feature of forest ecosystems (Barbier et al., 2008), and coniferous production forests differ drastically from European beech forests (Pretzsch et al., 2010). Inherent differences in tree species traits lead to vastly different stand structures and with them, microclimate and light conditions (Chamagne et al., 2016; Zellweger et al., 2016), which in turn affect species assemblages across trophic levels (Barbier et al., 2008; Cavard et al., 2011). Coniferous plantation forests are often age-class forests with regular production cycles (Bauhus et al., 2009) that place focus on economically relevant ecosystem functions like biomass gains, at the expense of other functions (Augusto et al., 2002). Conifer-dominated forests outside of their natural ranges are vulnerable to abiotic and biotic disturbances such as wind throws or pest outbreaks (Schelhaas et al., 2003; Jactel et al., 2009), phenomenona that are expected to intensify in the future (Seidl et al., 2011). These characteristics of coniferous production forests led to changes in the forestry policies of many European countries (Rametsteiner and Mayer, 2004), which have initiated a transition towards mixed forests that more closely resemble the natural vegetation but allow the admixture of economically more profitable tree species (Knoke et al., 2008). In practice, this is mostly
achieved through the conversion of former coniferous plantations to mixed forests by the promotion of broadleaved species (Mosandl and Küssner, 1999).

Mixed stands have been thoroughly assessed from an economic perspective (Knoke et al., 2008). Mixing tree species at the stand level has been linked to higher rates of ecosystem functioning (Gamfeldt et al., 2013), including benefits for overall stability in the face of novel disturbances (Bauhus et al., 2017), productivity (Pretzsch et al., 2010; Pretzsch et al., 2013; Fichtner et al., 2018) and increased resistance to pest and diseases (Jactel et al., 2017). Evidence shows that shifts in tree species composition will also affect the communities they host: Close evolutionary associations between tree species and other species groups, e.g. herbivorous or saproxylic insects, lead to distinct biotic communities between tree species and genera, particularly between gymnosperms and angiosperms (Brändle and Brandl, 2001). Mixing tree species may thus increase species richness as communities of different tree species are combined. Moreover, tree species differ in functional traits (Benavides et al., 2019; Pretzsch, 2014; Williams et al., 2017) and thus mixed forests are structurally more complex compared to monocultures (Juchheim et al., 2019). Tree species composition also affects the availability and diversity of tree-related microhabitats (Vuidot et al., 2011). Higher habitat heterogeneity in turn can lead to an increase in supported biodiversity (Heidrich et al., 2020; Stein et al., 2014). There is strong evidence that mixed forests indeed increase biodiversity for birds and fungi (Cavard et al., 2011). Furthermore, studies have also shown benefits of tree diversity for true bugs (Sobek et al., 2009) and for defoliating insects (Ampoorter et al., 2019). But recent findings suggest that spatial scale has to be taken into account when assessing the consequences of conversion of coniferous monocultures to mixed stands (Heinrichs et al., 2019) and comprehensive assessments of the biodiversity effects of admixture of economically relevant tree species in Central European forests remain scarce.

As in ecosystem function research, the effects of tree species composition on biodiversity are likely highly dependent on tree species identity (Brändle and Brandl, 2001). Additionally, the proportion of the admixed species might be of importance. While single trees of a particular tree species can already affect the distribution and movement of some species (Wehnert and Wagner, 2019), local biodiversity might depend on the share in basal area occupied by or the number of individuals of a certain tree species or functional group (Müller and Gossner, 2007; Penone et al., 2019). Little is known about tree species-specific effects on overall biodiversity in real-world ecosystems, and even less about whether thresholds for admixture at the plot level might exist below or above which the diversity of certain species groups is significantly increased or reduced compared to naturally occurring beech forests.

Here, we studied how the presence of different proportions of spruce, pine and oak (Quercus spp.) in mature beech stands affect the diversity and composition across multiple species groups compared to pure beech stands. These tree species have the longest management tradition in Europe (Spiecker, 2003), and in the case of oak also a natural co-occurrence with beech. We hypothesize that:

1) tree species-related changes in stand structure and availability of tree-related microhabitats lead to increased niche diversity and higher abundances and higher alpha and gamma diversity (multidiversity as well as taxon-level diversity) in tree species mixtures compared to pure beech forests;
2) because of minimum required habitat and resource amounts, admixture thresholds at the plot level exist beyond which effects of admixture on abundance and diversity become significantly more pronounced;
3) because of increased habitat and resource heterogeneity and tree-species specific associations, the admixture of tree species leads to changes in species composition and the presence of indicator species for certain tree species combinations.

## 2. Methods

### 2.1 Study region and study design

The study was conducted in the predominantly forested northern Steigerwald region in southern Germany. Elevations range from 300 to 450 m a.s.1., the mean annual temperature is $7-8{ }^{\circ} \mathrm{C}$ with $600-800 \mathrm{~mm}$ of precipitation. All research plots were located in the forestry district Ebrach, within an area of roughly $300 \mathrm{~km}^{2}$ between $49^{\circ} 47^{\prime} 10^{\prime \prime}$ to $49^{\circ} 58^{\prime} 2^{\prime \prime} \mathrm{N}$ and $10^{\circ} 27^{\prime} 18^{\prime \prime}$ to $10^{\circ} 39^{\prime} 59^{\prime \prime} \mathrm{E}$. The entire region is managed by the Bavarian State Forest Company and the harvesting is conducted as single tree harvesting in a shelterwood system, with a uniform management regime across all research plots and typical extraction volumes of $25-60 \mathrm{~m}^{3} \mathrm{ha}^{-1}$ every 5-8 years (U. Mergner, personal communication).

We focused on pure beech and mixed beech-oak, beech-pine and beech-spruce stands (henceforth 'forest types'), thus including the four predominant and most economically relevant tree species in Germany (BMEL, 2014). For the selection of research plots, we used 2010 data from pre-existing forest inventory sites. These inventory sites are permanently marked and cover the entire state-owned forest in a rectangular $200 \mathrm{~m} \times 200 \mathrm{~m}$ grid. Each forest inventory site consists of a circular area of 0.05 ha . These data allowed to us select candidate sites where the tree species composition on the inventory site matched one of the various target tree species compositions. We used additional available inventory information on the three dominant tree species at the stand level to further filter the suitable 0.05 ha-inventory areas for those with a matching tree species composition in the immediate surroundings. From this pool, we selected inventory sites with a slope $<10 \%$ and distances to forest roads and edges of $>30 \mathrm{~m}$ and $>100$ m , respectively. Remaining candidate inventory sites were examined on-site to estimate tree species composition and stand structure on a larger, rectangular $60 \mathrm{~m} \times 60 \mathrm{~m}$ area (plot) with the forest inventory site at the center. To reduce environmental heterogeneity further, we dismissed plots if the estimated canopy cover was below $50 \%$, if stand age was less than
approximately 80 years ( 35 years for admixed conifers), or if regeneration covered more than $80 \%$ of the plot area. Plots were also dismissed if the estimated aggregated basal area share of non-target tree species was $>10 \%$ (for 12 out of 41 the aggregated basal area share of nontarget tree species exceeded $10 \%$ after a detailed stand inventory, see Table S1).The final set of research plots included 9 plots of pure beech, 11 mixed beech-oak plots, 11 beech-pine plots and 10 beech-spruce plots (Fig. S1). There was a minimum distance of 200 m between plot centers. Share of basal area for the admixed target species ranged from 11 to $77 \%$ in mixed beech-oak stands, from 11 to $42 \%$ in beech-pine stands and from 14 to $69 \%$ in beech-spruce stands.

### 2.2 Inventory of forest structures

A detailed forest inventory was carried out on all 60 mx 60 m plots between December 2017 and April 2018 (Fig. S2A). All trees with a diameter at breast height (DBH) $\geq 7 \mathrm{~cm}$ were recorded. Following the guidelines of the Bavarian State Forestry Company, the diameter and length of any standing and lying deadwood object with a diameter $\geq 20 \mathrm{~cm}$ and a minimum height or length of 1.3 m were recorded to estimate deadwood volume. Tree stumps from harvesting operations fell below the height threshold and were not considered for deadwood estimates. Microhabitat structures on trees were recorded along a spiral-shaped transect starting at the plot center, with time-standardized surveys lasting 60 min per plot. Binoculars were used and spotted microhabitat structures were classified according to Kraus et al. (2016). The observations were subsequently aggregated by plot over all individual trees and assigned to broader categories 'tree cavities' and 'crown deadwood objects'. Crown deadwood objects included all dead branches and limbs in the tree crown. Light availability was measured at each research plot using a $5 \times 5$ rectangular grid spaced by 15 m that covered the entire 60 mx 60 m plot. At each grid point, an automated fisheye lens camera (Solariscope SOL300, Behling) was used to measure the indirect site factor (ISF), i.e. the amount of indirect sunlight as a percentage
of the amount of light at a completely unshaded location (Annighöfer et al., 2019), and measurements were then compiled to a mean value for each research plot.

### 2.3 Biodiversity surveys

## Plants

Plants were surveyed on an area of $20 \mathrm{~m} \times 20 \mathrm{~m}$ around the center of each plot between May and June of 2017 (Fig. S2D). All plant species of the herb layer were identified and their cover was estimated as a percentage of the subplot area.

## Fungi

Three surveys of fungal fruitbodies were conducted on all plots by expert taxonomists in April, September and November 2017 (Fig. S2C) on circular areas of $1,000 \mathrm{~m}^{2}$ around the plot center. Subplots were searched for fungal fruitbodies of macromycetes with diameters $>2 \mathrm{~mm}$. Fungi were identified to species level in the field or sampled for later microscopic analysis. Surveys were time-standardized for deadwood-inhabiting fungi on standing and lying deadwood (30 minutes) and for soil saprotrophs and mycorrhiza on the ground ( 15 minutes). After identification, fungi were classified into mycorrhiza, wood-decomposing species (this group included some fungal parasites) and others, the latter consisting of predominantly litterdecomposing species.

## Soil and litter arthropods

Litter samples were taken at five $15 \mathrm{~cm} \times 15 \mathrm{~cm}$ subplots at the plot center and the corners of a 5 mx 5 m square around the plot center (Fig. S2F). Loose leaf litter and 1 cm of the upper organic layer ( $\mathrm{O}_{1}$ horizon) were collected and placed in air-tight plastic bags. Samples were then weighed and placed in a modified Kempson heat extractor (Kempson et al., 1963) for 48 hours to extract soil and litter-dwelling arthropods. Sample temperature in the extractor was successively increased from room temperature to $50^{\circ} \mathrm{C}$ in steps of $5{ }^{\circ} \mathrm{C}$ every hour. After
extraction, the dry weight of the litter sample was determined and catches were transferred to $70 \%$ ethanol for sorting and subsequent identification. Adult oribatid mites were determined to species, genus, or family level following Weigmann (2006). Springtails were all determined to species level.

## Beetles and true bugs

Beetles (Coleoptera) and true bugs (Hemiptera: Heteroptera) were sampled using two flight interception traps per plot installed 1.5 m above the ground 5 m north and south of the plot center (Fig. S2E). Traps consisted of a crossed pair of transparent plastic boards measuring 40 $\mathrm{cm} \times 60 \mathrm{~cm}$ and funnels at the bottom and at the top with attached sampling jars that contained $3 \% \mathrm{CuSO}_{4}$ solution with a drop of detergent to reduce surface tension. Traps were installed in late March and emptied monthly until sampling ended in late September 2017. Catches were transferred to $70 \%$ ethanol and identified to species level. Both groups were split into herbivorous and other species. Beetles were additionally classified into saproxylic, i.e. deadwood-dependent species, following Schmidl and Bussler (2004). Samples were pooled per plot over months and traps for the calculation of abundances and diversity metrics.

Birds

Birds were surveyed five times on all plots between late March and early June 2017 using pointstop transect sampling (Moning and Müller, 2009). Individuals were identified based on sightings and calls along a 60 m north-to-south transect through the plot center ranging from the northern to the southern plot boundary (Fig. S2B). Birds were sampled for one minute at the start and end points of the transect, and for 5 minutes at the plot center through which the transect ran. Birds were also sampled for the duration of the walks between the three points. Only individuals within a 1 ha ( 100 mx 100 m ) area surrounding the plot center were recorded, disregarding flyovers. Mapping took place between sunrise and midday and was not carried out
in case of rain or strong winds. Data from all five surveys per research plot were pooled for the computation of abundances and diversity metrics.

## Bats

Bats were surveyed with standardized acoustic recordings, sampling one night per plot and month from early June to late September 2017 using Batcorder 3.1 (ecoObs GmbH; quality: 20; threshold: -36 dB ; post-trigger: 800 ms ; critical call frequency: 14 kHz ). Recorders were set up at the top of 2.5 m poles at the plot center or as close to the plot center as possible while maintaining a distance of at least 3 m to the nearest vertical structure (Fig. S2G). Recordings started one hour before sunset and ended one hour after sunrise. No sampling was conducted in case of rain or strong winds. Recorded sequences were identified in a two-step process using batIdent (Marckmann and Runkel, 2010) and manual quality control (Supplemental material), resulting in 15 OTUs (operational taxonomic units). Bat activity, measured as the number of 1-minute-intervals per night with at least one recorded bat call (minute calls), and species numbers per plot were computed after aggregating all surveys. Above species-level OTUs were considered in computing plot-level species numbers only if this procedure did not pose any danger of erroneously inflating species numbers.

### 2.4 Statistical analyses

## Effects of admixture on abundance and alpha diversity

All analyses were performed in R 3.3.1 ( R Core Team, 2018). In a first step, we tested the effects of admixture on abundance and alpha diversity using generalized linear models with forest type (beech, beech-oak, beech-pine, beech-spruce) as a categorical predictor variable. As response variables, we used abundance (cover for plants, abundance for arthropods and birds, activity for bats), species richness (all groups) and the exponential Shannon diversity index (Jost, 2007; henceforth 'Shannon diversity'; all groups but fungi). The latter weighs species by
their abundance, thus reducing the influence of rare species on the metric. Given the high environmental heterogeneity of his real-world study design, a higher-order diversity index such as the Shannon diversity may help detect effects of forest type on diversity caused by differences in the evenness of samples (Hill, 1973) that the simple species number might miss. Cover (plants) and activity (bats) are only proxies of abundance, and the diversity index should be interpreted accordingly. Separate models were specified for each measure of abundance and alpha diversity and species group. An additional model was specified with an index of multidiversity as the dependent variable. This index is the mean proportional species richness across all species groups, calculated with standardized species richness values for each group by scaling them to the highest observed species richness across all forest types (Allan et al., 2014). This index is sensitive to the identity of the included taxonomic groups and does not correct for phylogenetic distance between them. We used Poisson error distributions with quasipoisson models for under- and overdispersed dependent count data variables. If appropriate regarding the distribution, dependent variables were modeled with Gamma distributions with $\log$ or identity links.

In a second step, we tested whether the share of an admixed tree species based on the total basal area affected abundance and alpha diversity using recursive partitioning analyses from the ctree function in the 'party' package (Hothorn et al., 2006). For each admixture gradient of either oak, pine, or spruce, this function creates binary splits of the admixture proportion variable and identifies the split that maximizes association with the species richness variable. This analysis was conducted separately for each admixed tree species by using subsets of the dataset each consisting of the 9 pure beech stands and the 10 to 11 plots of admixtures with oak, pine, or spruce, resulting in sample sizes of 19 to 20 plots.

## Effects of stand structure and tree-related microhabitats on species richness

In a third step, we tested for the effect of stand structure on species richness to assess whether structural differences might be driving differences in species richness between forest types. For this, we first used generalized linear models to estimate differences between forest types regarding variables of stand structure and tree-related microhabitats at the plot level. The complete list of dependent variables was: the total number of tree species present, the total basal area, light availability, deadwood volume, the number of tree cavities and the number of crown deadwood objects. We then conducted a generalized linear regression for each of the surveyed taxa with species richness as the dependent variable and the above-mentioned measures of stand structure and tree-associated microhabitats as predictors.

Gamma diversity, species composition and indicator species analysis

In a fourth step, we assessed differences in gamma diversity between forest types, i.e. whether the cumulated species richness and diversity of all plots differed between forest types. We calculated frequency-based species accumulation curves for each forest type and two different diversity measures representing species richness and Shannon diversity within the framework of Chao et al. (2014) based on rarefaction and extrapolation using the 'iNext' package (Hsieh et al., 2016). This was done separately for each species group and an index of multidiversity as the mean of the standardized diversity measures across all species groups. We derived significant differences in diversity from non-overlapping confidence intervals for $\mathrm{n}=10$ plots, using extrapolated values for the pure beech forest type with only 9 replicates (Schenker and Gentleman, 2001).

In a fifth step, we analyzed differences in community composition by conducting non-metric multidimensional scaling (NMDS) on presence-absence data for each species group using the metaMDS function in the 'vegan' package (Oksanen et al., 2018). We used permutational multivariate analyses of variance (PERMANOVA) to test for significant effects of forest type
on the species composition using the adonis function. Finally, we conducted indicator species analyses to test whether any species were significantly associated with a certain forest type or combination of forest types, using the function multipatt in the 'indicspecies' package (Cáceres and Legendre, 2009). We predefined a set of possible forest type combinations (Cáceres et al., 2010) consisting of each forest type individually and in addition combinations of both broadleaved forest types (beech, beech-oak) and both forest types with conifer admixture (beech-spruce, beech-pine).

## 3. Results

### 3.1 Effects of admixture on abundance and alpha diversity

There were no significant differences in abundance and alpha diversity between pure beech and mixed beech-oak, beech-pine and beech-spruce stands regarding multidiversity (Fig. 1N, Table S3), plants, all fungal guilds, oribatid mites, and bats (Figs. 1 and S3, Table S3). All other taxa showed significant differences between at least two forest types in one abundance or alpha diversity metric: There were significantly fewer springtail species in beech-oak stands compared to stands with pine or spruce admixture (Fig. 1F, Table S3). The species richness and diversity of herbivorous true bugs, the species richness of herbivorous beetles and the diversity of other beetles were highest in beech-oak mixtures, differing significantly from beech-spruce mixtures (Figs. 1G+I and S3, Table S3). Beech-oak also had the highest numbers for the abundance and species richness of non-herbivorous true bugs, differing significantly from beech-pine mixtures. Values for pure beech and beech-spruce stands were intermediate (Figs. 1 H and $\mathrm{S} 3 \mathrm{P}+\mathrm{Q}$, Table S 3 ). The diversity of saproxylic beetles was significantly higher in beechspruce stands compared to all other stands (Fig. S3X, Table S3). The diversity of birds was also highest in beech-spruce stands, differing significantly from pure beech stands (Fig. S3AD, Table S3).


Figure 1: Plot-level multidiversity and individual taxa species richness for the different forest types based on generalized linear models specified in Table C1. Points show actual data points while bars show estimated means and $95 \%$ confidence intervals based on back-transformed standard errors. Letters indicate significant differences between groups with $\mathrm{p} \leq 0.05$ after Tukey post-hoc tests.


Figure 2: Recursive partitioning of abundance, species number and Shannon diversity by admixture with ctree. Plots show mean $+/-$ SE species numbers for subsets below and above the threshold admixture value calculated by binary recursive partitioning. Points represent measured data. Only significant ( $p \leq 0.05$ ) results are displayed.

### 3.2 Effects of admixture proportion on abundance and diversity

For eight of 13 species groups, the proportion of at least one admixed tree species significantly impacted the abundance or alpha diversity (species richness or Shannon diversity) of the surveyed taxa in a way that allowed for a meaningful binary split by recursive partitioning. The diversity of plants was significantly higher in cases where pine admixture exceeded $17 \%$ share of basal area (Fig. 2E). The number of mycorrhizal fungi species was slightly lower in mixtures above $23 \%$ oak admixture (Fig. 2A), and the number of litter-decomposing fungi was lower in mixtures exceeding $17 \%$ pine admixture (Fig. 2F). Herbivorous true bugs, on the other hand, were significantly more abundant (Fig. 2G) and diverse (Fig. 2H+I) from 17 and $11 \%$ pine admixture, respectively. Other true bugs showed significantly lower abundance, species richness and diversity beyond a threshold of pine admixture of 0,8 and $17 \%$, respectively (Fig. 2J-L), but were significantly more abundant in mixtures with at least $28 \%$ oak (Fig. 2B). The species number of herbivorous beetles (19 \%) and bird diversity (7\%) were also significantly higher in the presence of a minimum share of oak (Fig. 2C+D). Bat species richness was significantly higher if pine admixture did not exceed $8 \%$ (Fig. 2M).

### 3.3 Effects of stand structure on species richness

Forest types differed significantly in the number of tree species per plot, the total basal area, light availability and the number of crown deadwood objects (Fig. 3, Table S2). No significant differences were found for the amount of deadwood and the number of tree cavities (Fig. 3, Table S2). As a result of the presence of non-target species on the research plots, beech-spruce and beech-pine stands had a significantly higher number of tree species, including target tree species, compared to pure beech stands. Beech-spruce mixtures additionally had a significantly higher number of tree species compared to beech-oak stands (Fig. 3A, Table S2). The total basal area was highest in beech-pine plots, significantly differing from beech-oak plots (Fig. 3B, Table S2). Deadwood volumes were highest in pure beech stands but highly variable and


Figure 3: Differences in forest structure between forest types of differing tree species composition (Beech; +Oak: Beech-oak; + Pine: Beech-pine; +Spruce: Beech-spruce). Letters indicate significant differences between groups with $\mathrm{p} \leq 0.05$ after posthoc tests. Points show actual data points while bars show estimated means and $95 \%$ confidence intervals based on backtransformed standard errors.

Testing for the association of these structural features with the species richness of various species groups revealed that basal area was positively correlated with the species number of springtails (Fig. S4, Table 1). Light availability was positively associated with plants and saproxylic beetles, but negatively with the number of wood-decomposing and other fungi species as well as springtails (Fig. S4, Table 1). Wood-decomposing fungi species richness increased with the deadwood volume (Fig. S4, Table 1). The species richness of springtails increased while the species richness of herbivorous true bugs declined with the number of tree species. The number of crown deadwood objects, in turn, was positively correlated with the species richness of herbivorous true bugs (Fig. S4, Table 1).

Table 1: Standardized coefficients ( $\pm$ standard errors) for generalized linear regression models on the species number of the surveyed taxa with all 41 research plots. Colours mark effect directions (positive $=$ green; negative $=$ red) for significant $(\mathrm{p} \leq$ 0.05 ) coefficients. See Fig. S4 for a graphical representation.

|  | Basal area ( $\mathrm{m}^{2} \mathrm{ha}^{-1}$ ) | Light availab. (ISF) | Deadwood ( $\mathrm{m}^{3} \mathrm{ha}^{-1}$ ) | Nr. of tree species | Tree cavities | Crown deadwood |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Plants | $0.20 \pm 0.12$ | 0.27 $\pm 0.13$ * | $-0.00 \pm 0.13$ | $-0.30 \pm 0.16$ | $0.04 \pm 0.13$ | $0.11 \pm 0.14$ |
| Fungi (mycorrhiza) | $-0.09 \pm 0.09$ | $0.00 \pm 0.10$ | $-0.01 \pm 0.09$ | $0.09 \pm 0.10$ | $-0.07 \pm 0.09$ | $-0.02 \pm 0.09$ |
| Fungi (saproxylic) | $-0.02 \pm 0.04$ | -0.07 $\pm 0.03$ * | 0.06 $\pm 0.03$ * | $0.02 \pm 0.03$ | $-0.01 \pm 0.03$ | $-0.05 \pm 0.03^{+}$ |
| Fungi (others) | $0.21 \pm 0.61$ | $-1.40 \pm 0.41^{* *}$ | $0.67 \pm 0.60$ | $0.53 \pm 0.60$ | $0.09 \pm 0.56$ | $-0.93 \pm 0.49^{+}$ |
| Mites | $0.42 \pm 0.63$ | $-0.38 \pm 0.70$ | $0.24 \pm 0.60$ | $0.73 \pm 0.71$ | $-0.85 \pm 0.61$ | $0.03 \pm 0.63$ |
| Springtails ${ }^{\text {N }}$ | 0.65 $\pm 0.30$ * | $-0.57 \pm 0.26$ * | $0.23 \pm 0.24$ | 0.78 $\pm 0.28 * *$ | $0.37 \pm 0.23$ | $0.06 \pm 0.24$ |
| True bugs (herbivores) | 0.07 $\pm 0.09$ | $0.18 \pm 0.09$ | $-0.15 \pm 0.10$ | -0.23 $\pm 0.11$ * | $0.01 \pm 0.09$ | 0.18 $\pm 0.09$ * |
| True bugs (others) | $-0.03 \pm 0.09$ | $-0.11 \pm 0.11$ | $0.05 \pm 0.09$ | $0.03 \pm 0.10$ | $-0.11 \pm 0.09$ | $-0.06 \pm 0.09$ |
| Beetles (herbivores) | $-0.05 \pm 0.04$ | $0.02 \pm 0.05$ | $-0.07 \pm 0.04$ | $-0.08 \pm 0.05$ | $-0.06 \pm 0.04$ | $-0.03 \pm 0.04$ |
| Beetles (saprox.) | $0.05 \pm 0.04$ | 0.14 $\pm 0.05^{* *}$ | $0.07 \pm 0.04$ | $-0.02 \pm 0.05$ | $0.04 \pm 0.04$ | $0.05 \pm 0.04$ |
| Beetles (others) | $0.01 \pm 0.04$ | $0.06 \pm 0.05$ | $0.02 \pm 0.04$ | $-0.07 \pm 0.05$ | $-0.06 \pm 0.04$ | $0.01 \pm 0.04$ |
| Birds | $0.51 \pm 0.46$ | $0.69 \pm 0.51$ | $0.72 \pm 0.43$ | $0.79 \pm 0.51$ | $-0.38 \pm 0.41$ | -0.18 ${ }^{\text {a }}$. 44 |
| Bats | $0.05 \pm 0.05$ | $-0.06 \pm 0.06$ | $0.05 \pm 0.05$ | $-0.09 \pm 0.06$ | $0.05 \pm 0.05$ | $0.01 \pm 0.06$ |

### 3.4 Effects of admixture on gamma diversity

Plant gamma diversity (species richness, Shannon diversity) was significantly higher for all mixed forest types (beech-spruce only regarding Shannon diversity) compared to pure beech forests (Fig. 4A). While there were no significant differences regarding wood-decomposing fungi (Fig. 4C), beech-spruce mixtures showed a significantly higher gamma diversity of mycorrhizal fungi compared to beech-pine mixtures (species richness, Shannon diversity) and pure beech forests (species richness; Fig. 4B). Other fungi had a significantly higher Shannon diversity in beech-oak mixtures compared to pure beech forests (Fig. 4D). Oribatid mite gamma diversity (species richness, Shannon diversity) was highest for mixtures involving conifers, differing significantly from beech-oak mixtures, and showed intermediate levels for pure beech stands (Fig. 4E). Similarly, springtail gamma diversity was lowest in beech-oak mixtures compared to beech-pine and beech-spruce (species richness, Shannon diversity) and pure beech
stands (Shannon diversity; Fig. 4F). Gamma diversity of herbivorous true bugs (species richness) was highest in beech-oak mixtures, significantly differing from the lowest levels observed in beech-spruce mixtures (Fig. 4G). Other true bugs did not differ significantly between forest types regarding gamma diversity, but there was a clear trend towards higher diversity in beech-oak mixtures (Fig. 4H). Similar to herbivorous true bugs, herbivorous beetles showed the highest gamma diversity (species richness, Shannon diversity) in beech-oak stands, significantly differing from diversities in beech-spruce and pure beech stands (Fig. 4I). Gamma diversity of saproxylic beetles (species richness, Shannon diversity) was highest in mixtures involving conifers but differed significantly only between pure beech and beech-pine stands (Fig. 4J). Gamma diversity of other beetles (Shannon diversity) was highest in beech-oak and beech-pine mixtures, which both differed significantly from beech-spruce stands but not from pure beech stands (Fig. 4K). There were no significant differences between forest types regarding gamma diversities of birds and bats, with exception of beech-pine stands exhibiting a significantly lower bat species richness compared to beech-spruce (Fig. 4L+M). Gamma multidiversity (species richness, Shannon diversity) was significantly higher in beech-oak (species richness, Shannon diversity) and beech-spruce (Shannon diversity) compared to pure beech stands (Fig. 4N).


Figure 4: Gamma diversity species richness (SR) and the exponential Shannon index $(\exp (\mathrm{H})$ ) based on rarefaction/extrapolation for $\mathrm{n}=10$ plots by forest type (green: beech; orange: beech-oak; blue: beech-pine; red: beechspruce). Significant differences are assumed for non-overlapping $95 \%$-confidence intervals.

### 3.5 Community composition and indicator species analysis

Community composition differed significantly between pure beech forests and at least one forest type with admixed tree species for saproxylic fungi, non-herbivorous true bugs, all beetle guilds, and birds (Fig. S5, Table S4). For all mentioned taxa, as well as for springtails and herbivorous true bugs, stands with oak admixture differed significantly from one or both forest types with conifer admixture. Stands with admixed pine and stands with admixed spruce were
more similar regarding their communities, and only differed significantly from each other regarding true bugs (both guilds) and herbivorous beetles. Forest type did not significantly affect the community composition of plants, other fungi, oribatid mites and bats, and pairwise comparisons were not significant regarding mycorrhizal fungi (Fig. S5, Table S4).

Indicator species analyses revealed in total 112 species that were significantly associated with a certain forest type or combination of forest types (Table S5). 21 species were significantly associated with pure beech stands, 20 with beech-oak stands, 9 with beech-pine stands, and 17 with beech-spruce stands. Furthermore, 24 species were characteristic of deciduous stands in general while 21 species were characteristic of mixed deciduous and coniferous stands.

## 4. Discussion

Our study showed that the admixture of economically profitable tree species in beech forests affects the plot-based local abundance, species richness, or diversity as well as the landscapescale gamma diversity of several species groups. Because of taxa-specific and contrasting responses to these admixtures, overall multidiversity did not differ among forest types at the plot level. Admixtures of pine and oak had significant effects on many species groups even at low shares of total basal area. Observed patterns only partly coincided with differences in stand structure between forest types and their effect on individual taxa. The importance of tree species identity was further emphasized by a significant change in community composition between tree species admixture for six species groups and significant associations of several specialist species with particular forest types.

We hypothesized that forest types with admixed tree species would sustain higher abundances and diversities of the surveyed taxa compared to pure beech stands. At the plot level, this was true only for saproxylic beetles and birds, where beech-spruce stands showed significantly higher diversity than pure beech stands. The species richness of saproxylic beetles has been
reported to increase with deadwood diversity (Seibold et al., 2016), thus benefitting from the presence of different tree species. Combinations of deadwood from spruce or hornbeam with beech support a particularly high diversity of saproxylic beetles (Gossner et al., 2016) because of distinct communities associated with these species (Müller et al., 2015). As saproxylic beetles, birds also react positively to tree functional diversity (Ampoorter et al., 2019). This is supported by the indicator species analysis, that found known specialists of coniferous trees, e.g. Periparus ater, Lophophanes cristatus, Regulus ignicapilla (Müller, 2005), or the bark beetles Hylastes cunicularius and Pityophthorus pityographus, to be indicators of coniferous admixture. Accordingly, the Cyanistes caeruleus and beetle species Xyloterus domesticus and Platycerus caraboides were indicators of broadleaved forest in our dataset.

Differences between mixtures were more frequent. Springtails, all true bugs and both other beetle guilds exhibited significant differences between at least two mixed forest types for one or more of the investigated metrics, with intermediate values for pure beech stands. True bugs and both non-saproxylic beetle guilds in the understory benefitted from the admixture of oak, a tree species known to host a large number of specialist species (Brändle and Brandl, 2001), especially true bugs (Gossner, 2008; Sobek et al., 2009) and leaf-chewing herbivores (Leidinger et al., 2019).

Differences in species richness and Shannon diversity between forest types were more pronounced when observing gamma diversity, as variation of admixture proportions within forest types increase heterogeneity in environmental conditions and thus species turnover and gamma diversity (Heinrichs et al., 2019). In addition to the heterogeneity within forest types, the choice of spatial scale regarding the reference area of 60 mx 60 m might have masked effects of tree species composition on certain groups, as the level of mobility varies drastically between taxonomic groups and effects might only be detectable at smaller or even larger scales.

Compared to pure beech stands, admixture increased gamma diversity of at least one mixed forest type significantly for five species groups, but only decreased diversity in one instance. Admixture of any tree species led to higher gamma diversity of vascular plants without significant shifts in community composition. Ordination spaces of all forest types largely overlapped, as effects on understory plants are largely due to changes in soil conditions and stand structure such as light availability and less specific to tree species identity (Barbier et al., 2008; Chamagne et al., 2016). This is in line with previous studies that found no evidence for a significant number of vascular plant mixedwood specialists in the understory that would profit from admixed tree species (Cavard et al., 2011).

Other gamma diversity effects varied among taxa and depended on the identity of the admixed tree species. The large influence of tree species identity on many forest taxa has been described before, for example regarding herbivorous insects (Vehviläinen et al., 2007). Contrary to previous findings that mixed beech-spruce forests are less species-rich compared to pure beech forests (Heine et al., 2019), gamma diversity of mycorrhizal and litter-decomposing fungi was higher in mixed stands. This was mainly due to larger ordination spaces and thus increased turnover in beech-spruce stands for mycorrhiza and beech-oak and beech-spruce for litter decomposers. Furthermore, the larger amount of non-target tree species in beech-spruce stands (Fig. 3A) and consequently sporadic occurrence of correspondent mycorrhizal fungi in these plots might have contributed to a higher gamma diversity. Both groups of soil arthropods showed significantly lower gamma diversity in beech-oak stands compared to all other mixed forest types, and in the case of springtails also compared to pure beech stands. This is possibly due to differences in litter quality, as soil arthropod communities are strongly shaped by bottomup forces (Korboulewsky et al., 2016; Lange et al., 2011; Scheu et al., 2003). Humus form is especially relevant to oribatid mite communities (Maraun and Scheu, 2000), which benefit from recalcitrant persistent litter over rapidly decomposing litter of high nutrient quality (Eissfeller
et al., 2013) such as oak litter. Similarly, springtail diversity has been shown to vary little between beech, spruce, and mixed stands, and the communities are often driven more strongly by abiotic factors like soil pH and water content (Salamon et al., 2008). Gamma diversity patterns confirmed the importance of oak admixture for true bugs and non-saproxylic beetles and the positive effects of spruce admixture on saproxylic beetles found at the plot scale. Additionally, pine was shown to be almost as beneficial to the gamma diversity of herbivorous true bugs and non-saproxylic beetles as oak and, like spruce admixture, beneficial for the gamma diversity of saproxylic beetles. As for oak, this might be owed to a large amount of Pinus-associated biodiversity, especially regarding beetles (Brändle and Brandl, 2001). As a coniferous species, it is also effective in increasing functional diversity - a key driver of forest biodiversity - of otherwise beech-dominated forests (Ampoorter et al., 2019).

Because of high beta diversity in the pure beech forest type, local-scale effects of spruce admixture on bird diversity did not translate to gamma diversity. This may be a consequence of their high mobility and the sporadic occurrence of mixed-stand or conifer specialists even in pure beech stands either due to adjacent habitats or the presence of admixed tree species on pure beech plots below the exclusion threshold for this study.

We tested the effects of parameters of stand structure and microhabitat availability on the species richness of the surveyed species groups, to compare whether differences in species richness between forest types might correspond to forest types' inherent differences in stand structure. This was rarely the case, as differences in stand structure between forest types were mostly small and species groups are most likely driven by a combination of factors and often to a great extent by tree species identity. Nevertheless, observed effects of stand structure on species communities were noteworthy. Light availability was significantly higher in beechspruce stands compared to pure beech stands, but did not differ significantly between forest types with admixture. It had significant effects on five species groups, consistent with other
studies (Penone et al., 2019) and showing that it is a primary driver of forest communities. As expected, it had a positive impact on plants and saproxylic beetles, with the latter possibly benefitting from microclimate-related habitat heterogeneity in deadwood (Vogel et al., 2020). Fungi and many litter-dwelling arthropods are sensitive to dry conditions (Peguero et al., 2019; Salamon et al. 2008), which may explain negative effects of light availability on these groups. We hypothesized that minimum required habitat amounts would lead to admixture thresholds at the plot level below or above which effects of admixture on abundance and diversity become significantly more pronounced. The results of the recursive partitioning analyses emphasized the importance of oak and pine admixture at varying but mostly low thresholds for many species groups. While beneficial effects of pine on herbivorous true bugs and plants became apparent at 11 to $17 \%$ admixture, between $19 \%$ and $28 \%$ oak admixture were the respective thresholds for significant increases in the species richness of herbivorous beetles and the abundance of non-herbivorous true bugs. This shows that single trees might not always suffice to achieve significant beneficial effects of admixture on biodiversity (Müller and Gossner, 2007). Similar to our study, Müller and Gossner (2007) showed that $30 \%$ oak admixture is necessary to significantly increase the proportions of oak specialists among herbivorous beetles and true bugs. Larger quantities of oak individuals increase the availability of oak-associated habitats and resources, resulting in a higher number of sustained individuals which in turn increases oak-associated biodiversity (Brändle and Brandl, 2001). That even a few individuals of admixed tree species can have a relevant impact is highlighted by the fact that bird diversity benefitted starting from $7 \%$ oak admixture. Admixture can also shape a given stand in a way that has negative consequences for certain taxa. Even low pine admixtures were sufficient to lead to fewer soil-saprotrophic fungi and bat species and non-herbivorous true bug abundance and diversity. The relatively low and unevenly distributed number of replicates within our gradients of admixture renders these thresholds rather coarse estimates, and larger sample sizes
will be needed to generate more reliable numbers. This is further exacerbated by the environmental heterogeneity within gradients. The high frequency of the $17 \%$-threshold regarding pine admixture in the results for example might be in part attributable to the fact that the research plots with low pine admixture bear relatively high levels of non-target spruce admixture.

We further hypothesized that shifts in tree species composition, and thus, stand structure and habitat availability, would lead to shifts in species composition and the presence of indicator species that are closely associated with certain tree species or mixtures. For six species groups, community composition in forest types with admixed tree species differed significantly from that in pure beech stands. Differences were even more prevalent when comparing mixed forest types among each other (Table S4). Five species groups showed no significant shifts in community composition. Vascular plant communities did not differ significantly between forest types and the only two indicator species (Carex pallescens for beech-spruce and Impatiens parviflora for beech-oak) are typical forest species (Honnay et al., 1998), but light-demanding (Tinya and Ódor, 2016) and aided by anthropogenic disturbances (Hejda, 2012). This confirms that plants in the herbaceous layer are driven mostly by abiotic environmental conditions rather than tree species composition. Even though community composition of mycorrhizal and soil saprotrophic fungi did not shift significantly for mixed forest types, several species were characteristical of certain forest types. Typical beech-related species like Mycena rosea and Macrotyphula fistulosa were significantly associated with broadleaved stands, i.e. the absence of coniferous admixture, while spruce specialists like saprotrophs Phragmotrichum chilletii and Mycena metata and also ectomycorrhizal Lactarius tabidus were significantly associated with beech-spruce stands. Fungal communities in beech forest reserves are most sensitive to the introduction of coniferous species (Blaschke et al., 2004).

While community composition of Oribatid mites did not shift significantly either, slightly higher species turnover and higher gamma diversity in stands with pine and spruce admixtures indicate that the changes in litter properties caused by conifer admixture provide additional habitat for specialist species like indicator of coniferous admixture Adoristes ovatus (Maraun et al., 2020). This possibly displaces other species, like indicator of pure beech stands Oppiella M. translamellata, a species typical for broadleaved temperate forests (Magilton et al., 2019). Bat species were mostly ubiquitous regarding forest types and thus did not show any significant differences in community composition, but one species was associated with broadleaved stands in our dataset (Myotis myotis). Although effects of tree functional diversity on bats have been described before (Charbonnier et al., 2016a; Charbonnier et al., 2016b; Barbaro et al., 2019), they are mostly driven by understory structure and prey abundance (Müller et al., 2012) with large within-group variability regarding habitat preferences (Renner et al., 2018). Most are highly mobile with sizable home ranges, and larger spatial scales might be more suited to assess environmental effects on bats than stand-level presence records (Russo et al., 2010). The communities of the remaining taxa are often strongly stratified between broadleaved stands and those with coniferous admixture, and most communities that displayed significant shifts in composition did not differ regarding pine and spruce admixtures. This highlights the distance in functional traits between angiosperms and gymnosperms that leads to marked splits in communities with high host specialization (Brändle and Brandl, 2001; Müller et al., 2020) and underscores the importance of functional diversity regarding forest biodiversity. True bugs and herbivorous beetles constitute a noteworthy exception, differing significantly in species composition also between pine and spruce admixtures, likely due to their often immediate dependence on host species identity.

Consequently, indicator species were most numerous for the broader categories of broadleaved and mixed broadleaved and coniferous stands, including species from ten out of 13 species
groups and further confirming that functional tree diversity is as much a driving force behind the effects of tree species admixture on forest diversity as effects of individual tree species. Both mechanisms increase the diversity of ecological niches compared to stands of single tree species. There were also species significantly associated with pure beech stands for seven species groups, showing that while admixture of tree species might lead to higher overall gamma diversity, beech forests host specialist species and characteristic communities. This emphasizes that it is heterogeneity at the landscape scale that often yields the highest overall biodiversity (Heinrichs et al., 2019), including heterogeneity in environmental conditions among beech forests of different developmental phases (Schall et al., 2020). Species of the same taxonomic group can vary widely in their responses to environmental factors and the use of even more fine-grained functional groups or individual species could further improve our understanding of the relationship between biodiversity and tree species composition (Bouvet et al., 2016; Renner et al., 2018).

In a real-world study of forest ecosystems, some undesired environmental heterogeneity within forest types is unavoidable. Together with the intentional gradient of admixture proportions, this was likely responsible for overall large amounts of variation in the data. This adds to effects of tree species composition being potentially masked due to the dimension of the reference area ( $60 \mathrm{~m} \times 60 \mathrm{~m}$ ) with regard to certain taxonomic groups. Especially the presence of non-target tree species, sometimes in the form of tree species that constitute target tree species of other forest types, has a high potential to introduce noise capable of influencing the outcome of comparisons between forest types. Finally, our findings are based on a set of mature forest stands selected to conform to certain criteria that have to be kept in mind when drawing conclusions from our results.

## 5. Conclusions

Our study shows that the effects of tree species admixture on forest biodiversity are highly dependent on the identity of the tree species and vary among species groups. The proportion of admixture matters, as even modest shares of admixed tree species significantly impacted the abundance and diversity of several taxa both positively and negatively, but more highresolution admixture gradients are needed to refine the identified thresholds. The effects of tree species admixture are detectable at the plot scale but become more pronounced at gamma diversity level. They confirm that by increasing structural heterogeneity, functional diversity in tree species composition is a key driver of forest biodiversity. This is complemented by tree species-specific associations, that are especially relevant for communities of herbivorous insects. Oak, but also pine, play a prominent role for the biodiversity of groups like true bugs and non-saproxylic beetle guilds.

The low generality of species' responses to forest management, varying depending on the taxonomic group, the observed metric and the spatial scale, among others, presents a challenge for effective forest biodiversity conservation. Our results provide forestry practitioners with a basis to estimate the ecological effects that decisions regarding tree species composition have for forest biodiversity across trophic levels. The diversity of many taxa benefits from promoting mixtures of the naturally dominating beech with economically relevant tree species oak, pine, and spruce, sometimes at or above certain admixture thresholds. But depending on the target species group, the preferred tree species composition and admixture levels can vary widely. Differences in species composition between pure-beech and mixed stands, as well as the existence of indicator species of pure beech stands, show that the presence of beech stands within the forest landscape is likely needed for the preservation of typical beech communities. Future research could contribute to the conservation of forest biodiversity by identifying
combinations of forest types on large spatial scales that support objectives of forest biodiversity conservation.

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