Old, deciduous stands support both high biodiversity and carbon storage in German forests

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Abstract:

Ecosystems worldwide face threats related to human-driven degradation, climate change, and biodiversity loss. Addressing these challenges requires management strategies that combine biodiversity conservation with climate change mitigation. Here, we aimed to identify local-scale management actions that promote biodiversity at multiple trophic levels while also promoting carbon storage and sequestration. We combined data on the diversity of nine taxonomic groups (plants, birds, moths, Mollusca, soil fungi, active soil bacteria, Cercozoan and Endomyxan soil protists, Oomycotan soil protists, and nematodes), with above- and belowground carbon storage in 150 temperate forest plots in three regions of Germany. These were dominated by European beech, pine, spruce and oak. We investigated the relationships between multiple forest structure and management variables, biodiversity and carbon storage and sequestration in forest plots with different management types. Carbon storage was 32% higher in uneven-aged than even-aged forests and increased with mean tree diameter, while carbon sequestration in trees was 15% higher in even-aged than uneven-aged stands. Mean tree diameter was positively related to overall biodiversity, especially bird species richness and the richness of forest specialist birds. Oak- or beech-dominated stands also harboured higher biodiversity. One exception to this was the richness of plant and forest specialist plants species, which were highest in spruce plantations. Surprisingly, deadwood input did not significantly affect the diversity of any taxonomic group. By showing that older forests with a high proportion of uneven-aged deciduous trees, or oak-dominated forests, can promote both biodiversity and carbon storage, our results could inform local-scale forest management in Central Europe that promotes both biodiversity conservation and carbon storage. These findings can form the basis of further larger-scale studies investigating such relations at larger spatial scales to inform landscape-level recommendations for sustainable forest management.

Key words:

Forest management, biodiversity loss, carbon storage, climate change mitigation, German forestry

Introduction

Growing concerns on the repercussions of climate change and biodiversity loss on human well-being have led to increasing interest in ecosystem management strategies that tackle both threats (Millennium Ecosystem Assessment, 2005; Pettorelli et al., 2021; Turney et al., 2020; United Nations, 2021). These two challenges are often treated separately, but they share multiple drivers (Seddon et al., 2019) and climate change has also become a key driver of biodiversity loss (Lister & Garcia, 2018; Müller et al., 2023). As a result, the global community is under increasing pressure to address both crises simultaneously (Corlett, 2020; IPBES, 2019; IPCC, 2014).

Forests, as one of the Earth's primary carbon sinks (European Environment Agency, 2016) and home to high biodiversity (de Lima et al., 2020; Leuschner & Homeier, 2022) are often at the core of climate and biodiversity protection policies. Forests are estimated to store about 45 % of organic carbon worldwide (Bonan, 2008) >80% of aboveground carbon, and >70 % of soil organic carbon to a depth of one metre (Birdsey et al., 1993; D. D. Richter et al., 1999; Six et al., 2002; Wellbrock et al., 2017). Many forest ecosystems are recognized as biodiversity hotspots (Soto-Navarro et al., 2020), hosting most of the Earth's terrestrial species (e.g. 80% of amphibian species, 75% of birds and 68% of mammals (FAO and UNEP, 2020)). Despite a high overall importance of forests for both biodiversity and carbon sequestration, high levels of both do not always correspond (Sabatini et al., 2019). In managed forests, stand-level forest management often focuses on narrow objectives like timber production, which shapes the vegetation structure and species composition of the stand (Felipe-Lucia et al., 2018). This impacts biodiversity (Brockerhoff et al., 2008; Brunet et al., 2010; Penone et al., 2019) and the ecosystem's capacity to store carbon in soils and vegetation (Huston & Marland, 2003, Asbeck et al., 2021).

In Germany, forests cover 32% of the land and provide employment for more than 1.1 million people (DFWR, 2022). Almost half (~ 48%) of the forest area is privately owned. The other half is owned by the federal states (~29 %), communities (~ 19%) and the federal government with ~ 4% (BMEL, 2018). German forests have been shaped by a long history of forest management (DFWR, 2022; Gossner, 2013; Grove, 2002). Without human intervention, it is estimated that 92% of German forest area would be dominated by European beech (*Fagus sylvatica*) and oak (*Quercus petraea* and *Quercus robur.*) (Bohn et al., 2007; DFWR, 2022). However, from the 18th up to the late 20th century, conifer monocultures of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) were strongly promoted in Central Europe (Heinrichs et al., 2019; Knoke et al., 2008), resulting in the current national forest composition dominated by four genera: spruce, pine, beech, and oak (BMEL, 2018). Today, the German forestry system is moving away from a production-focused forestry, towards a multi-objective management system. Current guidelines aim to develop 'ecologically and economically valuable forests' through 'close-to-nature' forest management practices. This includes

favouring structurally diverse and mixed stands and long management cycles (DFWR, 2022) and promoting and retaining habitat trees (Dörfler et al., 2020), with expectations that this will promote biodiversity. For instance, greater habitat complexity in uneven-aged and mixed forests promotes biodiversity (Penone et al., 2019), while large trees provide numerous microhabitats (Michel & Winter, 2009; Vuidot et al., 2011; Winter & Möller, 2008). Deadwood left in the stand is also thought to serve as a habitat and nutrition source for a wide range of species (Dittrich et al., 2014; Löfroth et al., 2023; Oettel et al., 2020; Sandström et al., 2019; Scott & Brown, 2008; Siitonen, 2001; Stokland et al., 2012). The impact of the dominant tree species, though, varies across taxa (Edelmann et al., 2022), but in general deciduous forests seem to be preferred by more species overall (e.g. Abele et al., 2014; Charbonnier et al., 2016; Russ & Montgomery, 2002). This knowledge has accumulated in a piecemeal fashion, with studies focusing on either a few taxonomic groups (e.g. Leidinger et al., 2020) or single management variables (Sandström et al., 2019; Schulze, 2018). As a result, trade-offs and synergies between different taxa across multiple forest types have not been quantitatively assessed. A more complete assessment of how these management practices affect the diversity of multiple taxa, as well as forest potential for climate mitigation, could help assess the suitability of current management guidelines and support the sustainable use and conservation of German forests.

In this study, we investigate how forest structure affects synergies and trade-offs between biodiversity and carbon storage and sequestration in Central European forests. We combine data on the biodiversity of above- and below-ground taxa from nine taxonomic groups, carbon storage and sequestration, and forest structure and management variables collected in 150 forest plots with different management types across Germany. We created indices combining either carbon- or biodiversity-related variables (Biodiversity and Carbon indices) to summarise the impacts of forest management variables on each of these two dimensions, as well as their joint response. We then assessed trade-offs and synergies between these aggregate metrics with linear (or generalized linear) models. We hypothesized that (1) carbon storage in trees is higher in older forests, (2) deadwood retention contributes positively to soil carbon storage, (3) biodiversity is higher in uneven-aged forests with older trees with abundant deadwood, and in mixed or deciduous forests rather than coniferous forests, and (4) both Biodiversity and Carbon indices increase with thicker tree diameter and decrease in coniferous stands. If these hypotheses are supported, it would indicate that local-level forest management that lengthens rotation cycles and promotes structural diversity might concurrently promote carbon storage and biodiversity conservation.

Methods:

Study sites and design

This study is part of the Biodiversity Exploratories project (biodiversity-exploratories.de), a large-scale and long-term project located in three regions of Germany: Schwäbische Alb in the south-west, Hainich-Dün in the centre, and Schorfheide-Chorin in the north-east. Each Exploratory comprises 50 forest plots (100 m × 100 m) selected to span the typical range of local tree species composition and management types. The regions were selected to be typical of the major different climate and geology types within Germany (except for the Alps and riparian ecosystems), and are also broadly representative of the most common forest types of Central Europe (Fischer et al., 2010). Further details on methods and data acquisition can be found in Table S1.

Data acquisition

All data preparation and analysis was conducted with R version 4.3.1 (R Core Team, 2023).

Forest management and structure data

Forest features were measured during two comprehensive forest inventories between 2008 and 2010 and 2014-2018, respectively. In each plot, all trees with a diameter at breast height (DBH) > 7 cm were surveyed. We focused on five forest management and structure variables (see Table S1 for details): total deadwood input per year (supply rate of deadwood to consumers), mean tree diameter at breast height (DBH), the degree of forest mixture (1 minus the proportion of the most abundant genus based on crown projection area), the identity of the dominant genera (pine, spruce, oak and pine), and the management type (uneven aged and even aged). Uneven-aged stands included both unmanaged plots and those based on a single-tree selection system. When multiple layers were present, they were combined for the calculation of the forest structure variables.

Carbon storage

We calculated two measures of forests' capability to store carbon: *C storage* was estimated from carbon stocks in soil and in the tree biomass. *C sequestration* was estimated from the annual increment of C in the trees. C stocks in deadwood and C fluxes from soils and vegetation were not considered as these are difficult to estimate accurately over meaningful timescales across many plots. Soil organic carbon storage was measured in 2014 in the topsoil (0-10 cm depth) using the dry combustion analysis. We calculated the tree carbon storage from standing wood volume, measured between 2014 and 2018. To obtain the aboveground *C storage* for each plot, we summed up the C storage for all tree species recorded in the plot. We calculated the *C sequestration* by using the annual wood increment measured between two second inventories conducted in 2008 – 2011 and 2015 – 2016, respectively. The total volume and volume increment was then multiplied by the plot's average wood density, then multiplied by 0.5 to represent the proportion of mass that is carbon, and summed

up per plot to obtain plot-level carbon sequestration. The average wood density used in this approach was calculated from the percentage of basal area occupied by each species in the plot and multiplied by species-specific wood densities from Vries et al. (2003).

Biodiversity

We considered nine taxonomic groups; plants, birds, moths, Mollusca, soil fungi, the active fraction of soil bacteria, soil protists of Cercozoa and Endomyxa, soil protists of Oomycota, and nematodes, to represent a complete picture of the taxonomic diversity of below- and aboveground groups (Wehner et al., 2021). The diversity of individual groups was measured at different time points during the 2015-2018 sampling period (see details in supplementary material Table S1). When multiple sampling years were available, we used the most recent or most complete data. We calculated species richness for each individual group using the R package 'vegan' (Oksanen et al., 2020).

We used two main indicators for biodiversity. First, we calculated the overall ecosystem richness considering all taxonomic groups (i.e., 'multidiversity' *sensu* Allan et al., 2014). Multidiversity is calculated as the average scaled species richness per taxonomic group, where the species richness of each group is scaled to its maximum across all plots (Allan et al. 2014). An advantage of the multidiversity metric over total species richness is the equal weighting of the species, thus preventing the measure from being driven by species-rich groups. As a result, plot-level multidiversity values vary between 0 (all groups simultaneously have their lowest observed richness) and 1 (all groups simultaneously have their highest observed richness) (Allan et al., 2014).

Second, we selected indicators of biodiversity representing high conservation value. We calculated the species richness of red-listed bird species in Germany (including category 1 (Critically Endangered), 2 (Endangered) and 3 (Vulnerable) (Grüneberg et al., 2016)) and the richness of birds and plant forest specialists (Table S2). Plant forest specialists were classified as plants species only found in forests, including open areas in forests (Schmidt et al. 2011). For birds, we used the European forest bird specialists of the list by Gregory et al. (2007). All species considered high conservation value are listed in Table S2.

Correction for environmental covariates

The study regions differ greatly in climatic and geological conditions and the effect of these on biodiversity and carbon storage could mask that of local forest management. To assess the effect of our focus variables independently of environmental covariates, we first corrected for environmental covariates. To do so, we selected five environmental covariates that represent soil, climatic and topographic conditions and with relatively low correlation: soil pH, mean annual temperature, soil depth, proportion of clay in the soil, and the Topographic Wetness Index (Moeslund et al., 2013). We fitted linear models for each response variable with all environmental covariates as well as the region as explanatory variables. We then extracted the residuals from each model. To maintain the relative

ratios of the multiple variables, we added the mean value of each response variable to these residuals; this was especially useful for carbon storage in trees or soil, which are measured on very different scales. These adjusted values were then used in all further analyses. To ensure normal error distributions and a homogeneous variance, a square root transformation was applied to deadwood input.

Statistical analysis

Since the main objective of the study was to identify the conditions that simultaneously maximise biodiversity and carbon storage/sequestration, we created indices combining multiple carbon and/or biodiversity variables (Figure 1). At each aggregation step, variables were scaled between 0 and 1 to ensure equal weighting of all response variables (Manning et al. (2018)), hence all indices ranged from 0 to 1. The '*Carbon index*' was measured as the average of tree and soil carbon storage and tree carbon sequestration, equally weighted. The '*Biodiversity index*' was calculated from the multidiversity measure (Allan et al. 2014) and 'Conservation species index', itself including the species richness with conservation value. Finally, the '*Combined index*' was calculated as the average of carbon and the biodiversity indices (Figure 1). There were a few missing values: 11 for Mollusca, 3 for Cercozoa and Endomyxa Protists and moths, 1 for birds, oomycote and Nematodes, and 14 for deadwood input. Because deadwood input was an explanatory variable in all models, we filled missing values with the average of deadwood input in all plots. Other NAs were not imputed.

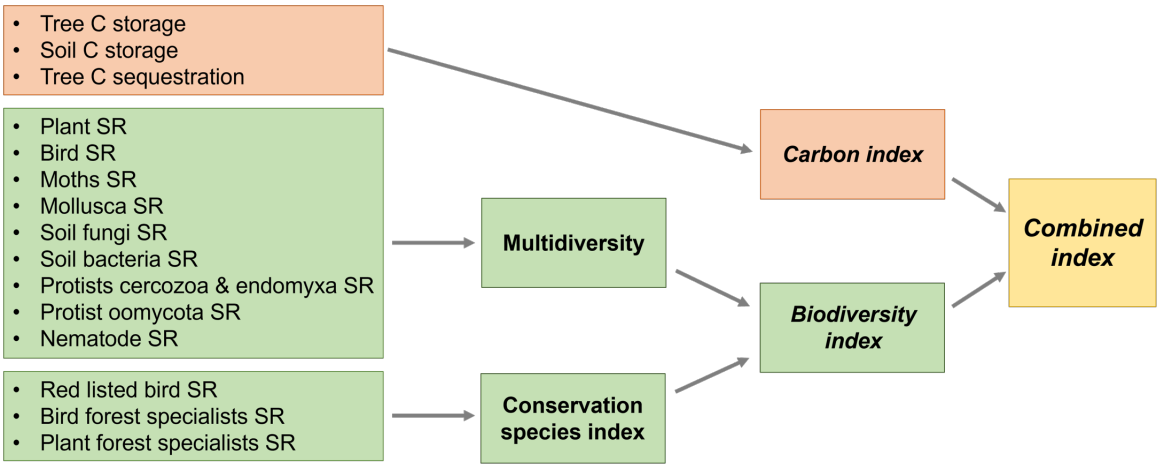

Figure 1: Schematic illustration showing the calculation of the Combined index. All the variables and intermediate indices were adjusted and scaled between 0 and 1. Multidiversity was calculated according to Allan et al. (2014). Grey arrows indicate scaling and averaging of variables into the next level of aggregation. SR = species richness.

Finally, we fitted linear models (function: lm; package: *stats*) between each response variable (richness, carbon variables, or indices) and above-mentioned forest structure variables as explanatory variables. The exception was red-listed bird species, which were fitted using a Poisson

glm. Model tests were conducted using variance analysis (ANOVA). Considering that not all variable combinations were available (e.g. no uneven-aged pine- or spruce-dominated stands) we did not investigate the interactions between the different variables. Model comparisons were done using the *parameters* package and forest plots using the *sjPlot* package.

Results

Management and forest structure variables

European beech was dominant in 70% of the plots (105 plots), followed by Scots pine (~13%; 19 plots), and Norway spruce (~11%; 17 plots). The two oak species were dominant in nine plots (*Quercus robur* and *Quercus petraea,* ~6%). All spruce- and pine-dominated plots were managed as even-aged forests. This was also the dominant management type in plots dominated by beech (~65%: 68 out of 105 plots) and oak (~88 %: 8 out of 9 plots). Pure stands (91 plots) were more common than mixed ones (59 plots), except oak stands which were more mixed (6 stands) than pure (3) (Fig. S1).

Forests dominated by oak and spruce had a higher mean DBH (mean 35.1 cm ± sd 8.5 and 31.8 cm ± 6.4 respectively) than forests dominated by beech and pine (27.5 cm ± 11.9 and 27.4 cm ± 8.4 respectively). Mean DBH was also higher in uneven-aged than even-aged forests (32.3 cm ± 10.4 and 27.1 cm ± 10.9 respectively, p = 0.01) and in pure than mixed forests (31.2 cm ± 10.6 and 24.1 cm ± 10.2, p ≤ 0.001). This shows that mean DBH, dominant genera and management type were not fully independent from each other.

Table 1: Linear model results for the effect of management on the response variables showed as F value (for all groups except red listed birds for which deviance is shown instead). Significance is shown as * 0.05 < p ≤ 0.01; ** 0.01 < p ≤ 0.001; *** p < 0.001, and • reflects marginal effects (0.1 < p ≤ 0.05). The degrees of freedom (df) for each effect are shown for each explanatory variable. Response variables are tree carbon, soil carbon, carbon sequestration, multidiversity, plant specialists, bird specialists, red listed birds and the three indices.

Explanatory variables	***Df***	**Tree C storage**	**Soil C storage (kg.m^{-2})**	**Tree C sequestration**	**Multi-diversity**	**Plant specialists**	**Bird specialists**	**Red listed birds**	**Carbon Index**	**Biodiversity Index**	**Combined Index**
Mean DBH	1	191.3	0.8	**4.3***	**19.6*****	2.2	**17.1*****	6.9	**11.8*****	**19.5*****	**32.6*****
Deadwood input	1	6.8	0.4	0.5	0.9	1.0	1.4	0	0	0.9	0.42
Genus	3	**7.5*****	0.1	0.3	**3.3***	**8.3*****	2.0	**7.8.**	2.0	**3.3****	**4.8 ****
Mixture	1	0	4.6*	0.6	**2.8 .**	**3.5 .**	**8.4****	0.4	0.6	**2.8 .**	**3.1 .**
Management type (even/uneven-aged)	1	**49.7*****	1.3	**22.3*****	0.3	16.6*****	0.4	**8.7***	2.0	0.3	0.6

Forest structure and management for a high *Carbon index*

Overall, the *Carbon index* ranged between 0.29 and 0.84 and tended to be higher in stands with large mean DBH and lower in pine-dominated stands (Fig. 2, Table 1). Soil carbon did not respond to any of the management variables. The component variables of the *Carbon index* differed in their respective responses to the explanatory variables. Tree carbon storage increased with mean DBH (standardised effect size: 0.65 ± 0.06 $p < 0.001$), as expected from its calculation from tree volume. Tree carbon storage was on average 32.13% higher in uneven-aged than even-aged stands (0.26 ± 0.06, $p < 0.001$). High tree carbon storage was also associated with high deadwood input (0.13 ± 0.05 $p = 0.009$), likely due to stands with larger, older trees also having higher tree senescence. Finally, tree carbon storage was 35% lower in pine-dominated stands compared to beech stands (-0.73 ± 0.16, $p < 0.001$). Conversely, carbon sequestration was 15.07% lower in uneven-aged stands (-0.37 ± 0.09 $p < 0.001$) and tended to decrease with mean DBH (-0.13 ± 0.09, $p = 0.1$, Fig. 2). These results support our hypothesis 1, since carbon storage in trees was higher in forests with a higher mean DBH, and rejects hypothesis 2, that deadwood retention contributes to soil carbon storage, since we could not identify a significant relation between any management variable and soil carbon storage.

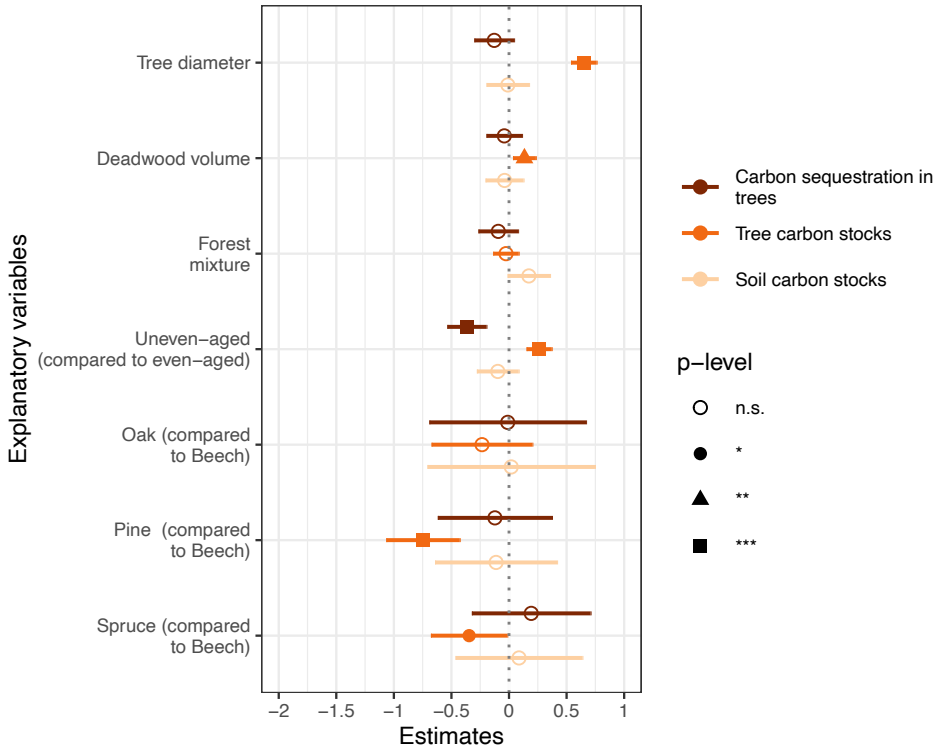

Figure 2: Effect of forest properties on carbon stocks and sequestration. Plots show standardized effect sizes along with 95% confidence interval estimated for the selected management variables affecting carbon stocks in trees and soils and carbon sequestration in trees. For dominant genus, the results are shown in comparison with the reference genus (beech, the most abundant genus). For stand age structure, the results are shown for uneven-aged stands in comparison to even-aged stands. SR = species richness. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = non-significant.

Forest structure and management for a high *Biodiversity index*

The diversity of individual taxa showed contrasting responses to forest structure and management variables, but overall increased with mean DBH and decreased in pine-dominated stands (Fig. 3). Individual responses of the species richness of all considered groups can be found in Fig. 3, Table 1 and Table S3. There was strong evidence that mean DBH positively affected bird (0.28 ± 0.09 p = 0.002) and forest bird specialist species richness (0.38 ± 0.09, p < 0.001). It also positively affected the richness of cercozoan and endomyxan (0.21 ± 0.09 p = 0.016) as well as Oomycotan protists (0.19 ± 0.09 p = 0.041). Forest mixture had a more variable impact, affecting positively the richness of soil fungi (0.29 ± 0.09 p = 0.002), and bird specialists (0.18 ± 0.09 p = 0.038), but negatively the richness of plant forest specialists (-0.16 ± 0.08, p = 0.05). Uneven-aged stands had lower plant (-0.19 ± 0.08 p = 0.015), forest plant specialist (-0.23 ± 0.08 p = 0.005) and nematode (0.18 ± 0.09 p = 0.045) richness, but higher red-listed bird richness (0.29 ± 0.12 p = 0.014) than even-aged stands.

There were also important but contrasting effects of the dominant tree genus on different taxonomic groups. Oak stands promoted higher plant (0.62 ± 0.30 p = 0.043) and red-listed bird richness (0.82 ± 0.39 p = 0.036) than beech stands, but lower moth richness (-0.25 ± 0.12 p = 0.031). Spruce stands had lower bacteria (-1.24 ± 0.25 p < 0.001), nematode (-0.73 ± 0.27 p = 0.008) and mollusc (-0.85 ± 0.28 p = 0.002) richness, but higher plant (1.59 ± 0.23 p < 0.001) and forest plant specialist richness (1.10 ± 0.25 p < 0.001) compared to beech-dominated stands. Pine stands had a strongly negative impact on biodiversity compared to beech stands, with negative impacts on the richness of bacteria (-0.89 ± 0.24 p < 0.001), protists (-1.14 ± 0.25 p < 0.001), nematodes (-0.69 ± 0.26 p = 0.009) molluscs (-0.68 ± 0.30 p = 0.024) and bird forest specialists (-0.59 ± 0.25 p = 0.018).

Overall, multidiversity was highest when mean DBH was high (0.29 ± 0.09 p = 0.001), and lowest in pine-dominated stands (-0.69 ± 0.25 p = 0.007). The diversity of species of high conservation value (forest specialists and red listed birds) increased with mean DBH (0.29 ± 0.09 p = 0.001) and were higher in Oak-dominated stands (0.71 ± 0.34 p = 0.041). These results mostly confirm our hypothesis 3, although contrarily to our expectations deadwood input did not affect biodiversity.

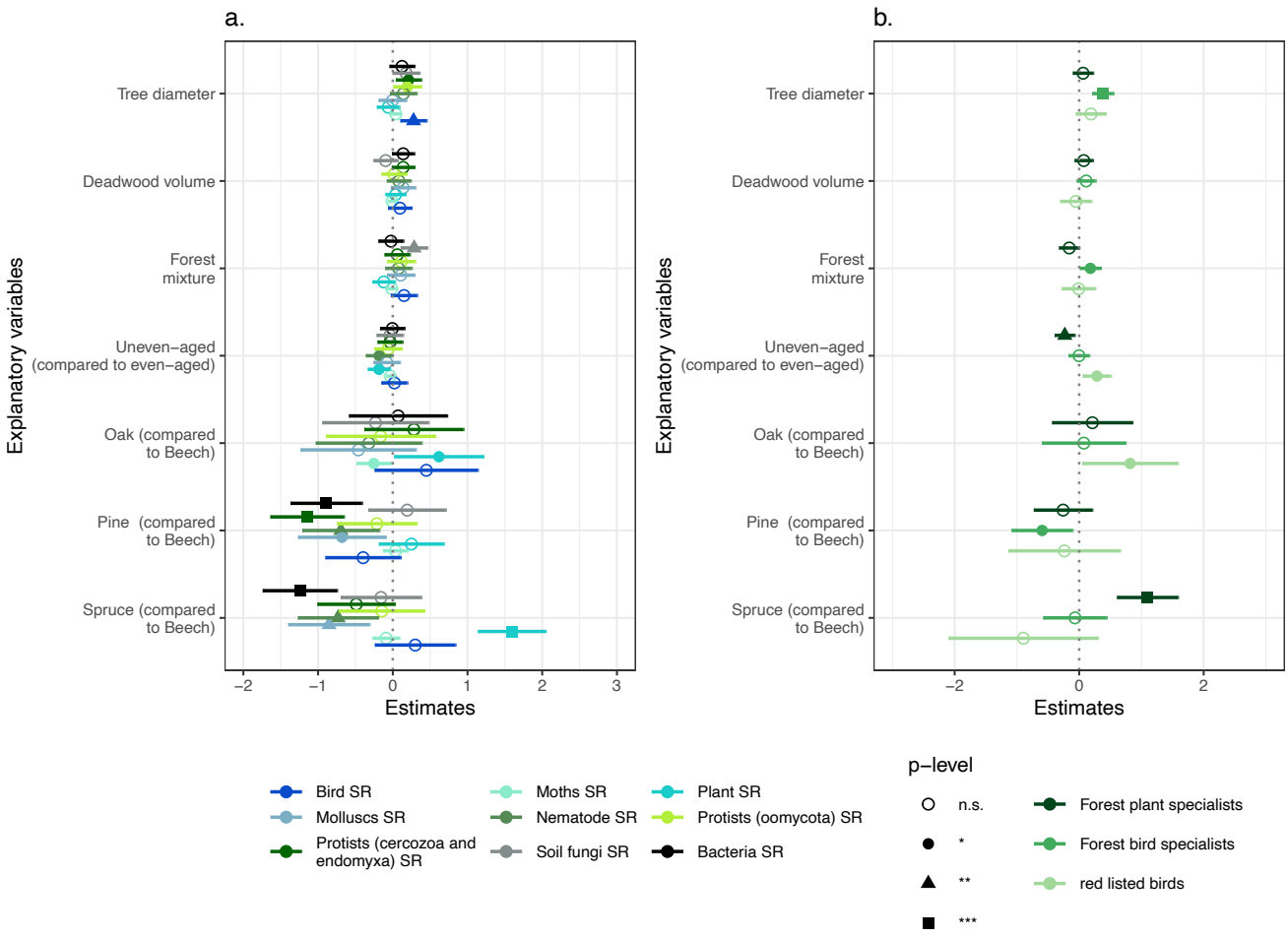

Figure 3: Effect of forest stand properties on biodiversity measures. Plot show standardized effect sizes along with 95% confidence interval estimated for the selected management variables affecting a) species richness of individual groups and b) species richness of groups with specific conservation value. For dominant genus, the the results are shown in comparison with the reference genus (beech, the most abundant genus). For stand age structure, the results are shown for uneven-aged stands in comparison to even-aged stands. SR = species richness. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = non-significant.

Forest structure and management for biodiversity conservation and climate mitigation

Our analysis revealed trade-offs between carbon storage (maximised in uneven-aged stands at high mean DBH) and sequestration (maximised in un-even-aged stands, at low mean DBH), and between some biodiversity groups. For instance, plant richness was the highest in spruce plantations where the diversity of most other groups was the lowest. However, when aggregated into the *Carbon* and *Biodiversity indices*, responses were relatively consistent, and the *Combined index* (ranging from 0.31 to 0.74) followed similar trends to its components: it increased with mean DBH ($p < 0.001$) and was lowest in pine-dominated stands ($p < 0.001$, Fig. 4; Table 1). This overall confirms our Hypothesis

4 by showing that the *Combined index* can be maximised by a higher mean DBH and stands with primarily deciduous trees.

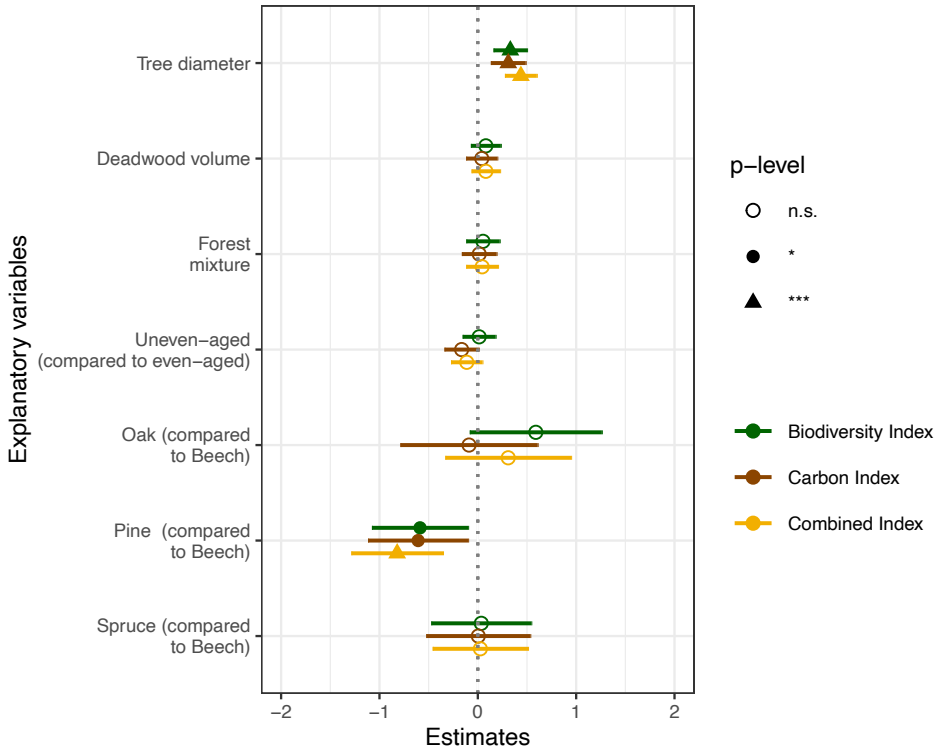

Figure 4: Standardized effect size along with 95% confidence interval estimated for the selected management variables affecting the *Biodiversity, Carbon and Combined indices*. For dominant genus, the results are shown in comparison with the reference genus (beech, the most abundant genus). For stand age structure, the results are shown for uneven-aged stands in comparison to even-aged stands. SR = species richness. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = non-significant.

Discussion

Our results show that carbon storage and biodiversity are typically simultaneously high in older, deciduous stands with large diameter trees. However, beyond this simple conclusion are more nuanced relations between the forest, carbon and biodiversity properties. In the discussion we assess the relation of several forest properties to carbon and biodiversity, and discuss how these can be influenced by management.

Forest structure and composition promoting carbon storage and biodiversity conservation

The dominant tree genus was an important driver that impacted 53% of the biodiversity and carbon variables. Differences were the strongest between pine- and beech-dominated stands, with pine-dominated stands having lower values of nine biodiversity indicators and lower tree carbon stocks. Spruce dominance was negatively related to three out of nine biodiversity indicators and positively related to two (plant species richness and forest plant specialist richness). These biodiversity patterns are consistent with previous studies showing that the plant species richness of German forests is high in coniferous stands (Boch et al., 2013; Budde et al., 2011) and can be explained by the fact that conifer canopies are more open than those of beech stands, allowing higher understorey light availability and more favourable microclimatic conditions (Dormann et al., 2020; Penone et al., 2019; Wagner et al., 2011). Oak-dominated stands had higher plant species richness and red listed bird richness but lower moth species richness than beech stands. Previous studies in Germany also found oak forests to be the most favourable to biodiversity (Carvalho-Santos et al., 2016; Müller et al., 2021). This can be explained by oaks being present in the study regions for centuries, and thus likely having a higher co-evolved diversity (Brändle & Brandl, 2001) than e.g. non-native pines which have been cultivated beyond their natural range, and for a much shorter time. Oaks also have higher microhabitat availability and dead branch accumulation than pines (Paillet et al., 2019). This might promote resource availability for insectivorous birds and provide more microhabitats for molluscs (Abele et al., 2014).

Of the forest structural properties we assessed, mean DBH and management type were strongly related to tree carbon storage, carbon sequestration rates and the biodiversity of multiple groups. Carbon sequestration was lower in forests with low mean DBH and in uneven-aged forests, likely due to slower growth rates in larger trees (Stephenson et al., 2014). This represents a classic trade-off in forest carbon management as stands with higher mean DBH have a higher tree carbon storage. The positive effect of DBH on many groups is likely due to the higher number of microhabitat types in larger trees (Michel & Winter, 2009; Vuidot et al., 2011; Winter & Möller, 2008), and an overall higher resource availability. Additionally, large trees are attractive for bird and arthropod cavity builders, as the high wood thickness of their cavities provides buffered microclimatic conditions for nests (Remm

et al., 2006). Some of our results were more surprising, such as the positive association between mean DBH and protist diversity, which we could not explain, but which may be associated with the presence of a stable and long-lived habitat in which microbial diversity may accumulate. The benefits of habitat heterogeneity for biodiversity are also visible in the positive relationship between forest mixture and most of the biodiversity variables such as forest bird specialists and soil fungi (Leidinger et al., 2021).

Annual deadwood input was positively associated with tree carbon storage, probably because more deadwood is left in older stands with larger trees and because more trees are senescent in older forests. Deadwood is an important structural element in forests at it offers resources for biodiversity (Seibold et al., 2017) by storing large amounts of water, providing energy and nutrients to soil micro- and macro-organisms, and supplying habitats to xylobiontic species (Oettel et al., 2020; Scott & Brown, 2008). It has been estimated that, 20 - 25 % of all forest-dwelling species are dependent on deadwood (Siitonen, 2001). Yet, surprisingly, deadwood input did not significantly affect the diversity of any taxonomic group in our study. This was likely because (i) the taxa analysed did not include saproxylic and xylobiontic species, which are expected to most respond most strongly to deadwood (Sandström et al., 2019) and (ii) only few of the stands had a high rate of deadwood input (mean: 1.2 $m^2.ha^{-1}.yr^{-1}$, max: 28.9 $m^2.ha^{-1}.yr^{-1}$).

Implications for German forest management

German forests are the product of a long history of forest management (DFWR, 2022; Gossner, 2013). In the last centuries, conifer monocultures were promoted in Central Europe (Heinrichs et al., 2019; Knoke et al., 2008; Penone et al., 2019), leading to the current national forest composition, with almost 75 % of the total forest area dominated by four genera: spruce (25 %), pine (23 %), beech (16 %), and oak 10 % (BMEL, 2018). Compared to this national average, in our study beech was overrepresented (70% stands), while spruce is underrepresented, but overall our study plots covered most of the main forest stand types found in Germany.

Current guidelines adopted in Germany aim to develop ‘ecologically and economically valuable forests’ through ‘close-to-nature’ forest management practices. These include the promotion of structurally diverse and mixed stands and long cycles (DFWR, 2022). As part of this, spruce and pine forests are being converted into mixed stands (Ammer, 2019; Ammer et al., 2008; Heinrichs et al., 2019; Knoke et al., 2008; von Lüpke et al., 2004), and deciduous tree cover has increased steadily (+7% between 2002 and 2012, BMEL, 2018). Our results show that these changes are likely to benefit both biodiversity and carbon storage through decreased coniferous (especially pine) cover and a switch from monocultures to mixed forests with larger resource heterogeneity (Heinrichs et al., 2019). Longer forest cycles and thus forest in late development stages, are also becoming more common (BMEL, 2018). This will benefit biodiversity and climate-friendly forestry since large diameter trees

store more carbon than young trees (European Environment Agency, 2016), although the growth and thus carbon sequestration is overall lower in older trees (Johnson & Abrams, 2009, Meinzer et al. 2011). Overall, our results confirm the idea that young stands will allow for new carbon stocks to be sequestered, but that the retention and conservation of old deciduous stands, for both carbon storage and biodiversity should be prioritised.

Future directions

Our results confirm that the current management trends in German forestry should promote more biodiverse and climate-friendly forests at the local stand level. However, other elements need to be assessed for a more comprehensive understanding of the impact of forest management on wider scale biodiversity, other aspects of carbon cycling, and other ecosystem services. More specifically, young stands may become more prevalent in the future due to increasing rates of disturbances due to bark beetles, wind and drought (Seidl et al., 2014; Senf & Seidl, 2021). The above-described trade-off between carbon storage and sequestration means that these young stands will accumulate carbon rapidly but will take time to store significant amounts of carbon. Our results add to this by showing that these new stands may also take time to reach the high biodiversity values of current old forests - although they may support their own distinct biota. This highlights the importance of preserving old forests, which can also act as biodiversity reservoirs from which species can colonise younger stands. The specific tree species (and associated management practices) being promoted will also influence the outcome, considering the role of the dominant tree genus on both biodiversity and carbon storage shown above (Felton et al., 2010).

In this study we considered the impact of stand management on just two aspects of forest carbon: tree and topsoil carbon storage. For a complete picture of climate mitigation, it is also important to account for carbon sequestration and storage in deeper soil layers and the rest of the wood production line (e.g. carbon release from use as firewood vs. long-term storage as timber, effects of thinning). Accounting for these processes would provide more precise estimates of the relative impacts of different forest management practices. The inclusion of other greenhouse gases would also provide a more complete assessment of climate impacts. Finally, we only assessed the impact of forest management on biodiversity and climate change mitigation. Yet, forests provide a wider range of ecosystem services such as the production of timber, the regulation of water and air quality and also have cultural and recreational value (Führer, 2000; Neyret et al., 2023). Different ecosystem services might be favoured by different forest types, and their consideration could highlight additional trade-offs and synergies (Felipe-Lucia et al. 2018) for local management recommendations. Promoting these different services might require maintaining landscape-level diversity in the type and management of forests, likely resulting in a higher overall forest management diversity due to diverse species requirements (Schall, Gossner, et al., 2018; Schall et al., 2020). While our results indicate optimal forest stand properties for maximizing local-scale biodiversity and carbon, we also

recommend maintaining forest diversity and heterogeneity at the landscape level. This can help promote landscape-level multifunctionality, whereby different forest stands simultaneously provide biodiversity protection, climate mitigation options, economic benefits, as well as cultural values (van der Plas et al., 2016).

Conclusion:

Simultaneously promoting biodiversity protection and climate change mitigation is a key challenge of local-scale forest management. Here, we identified the forest management features that support these goals in Central European forests: large average tree diameter and deciduous tree dominance. This study highlights the need to preserve old forests and let them grow in order to reach high levels of biodiversity and carbon storage; further research should however build on these results to assess their resilience to future climates as well as the role of forests with different compositions than those assessed here. As the demand for preserving both climate and biodiversity grows stronger, approaches such as that presented here can help support management decisions and forest management policies, and thus promote more sustainable and multifunctional forests.

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Data availability:

This work is based on data elaborated by several projects of the Biodiversity Exploratories program (DFG Priority Program 1374). Most datasets are publicly available in the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q). However, to give data owners and collectors time to perform their analysis the Biodiversity Exploratories' data and publication policy includes by default an embargo period of three years from the end of data collection/data assembly which applies

to the remaining datasets. These datasets will be made publicly available via the same data repository. All datasets are listed in Tables S1 and corresponding references.

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Appendix:

Table S1. Details to the variables and covariates: Measurement and reference. Each dataset has an ID within the Biodiversity Exploratory project. The dataset can be found using the ID in the Biodiversity Exploratories Information System (BExIS). It is listed under reference. Most biodiversity data were synthesized in BExIS dataset 31206.

Group	Variable/ covariates	Detailed methodology	Data owners	References
Carbon	Soil C stock ($kg.m^{-2}$)	In each of the plot, 14 soil cores (diameter 5cm) were sampled in 2014. A composite sample was then prepared from these cores. Carbon concentration was measured by dry combustion of soil at a temperature of 1100 °C and subsequent determination of evolving CO_2 with a Thermal Conductivity Detector. • Instruments: VarioMax, Elementar, Hanau • Calibration: calibration with Glutamic acid and additionally measurement of a standard soil and blanks • Procedure: soil air-dried, sieved to < 2 mm and ground. Weighing of an aliquot of 250 mg of soil. For inorganic carbon determination removal of organic carbon at a temperature of 450 °C for 16 h Finally, the carbon concentration was multiplied by bulk density to calculate carbon stocks.	Ingo Schöning, Huei Ying Gan, Theresa Klötzing, Jessica Heublein, Steffen Ferber, Susan Trumbore, Marion Schrumpf	BExIS-ID: 20266
	Tree C stock	Species, diameter at breast height and geographical location of all trees (caliper limit dbh > 7 cm) growing on the forest plots were surveyed. Tree height was measured for a subsample of trees across the observed diameter range (per species and plot). Using stand height curves the height of all trees was estimated. Wood volume was estimated using diameter and height. For the calculation of the tree C stock the volume per species per plot was multiplied by species-specific wood densities obtained from Vries et al. (2003).Year of collection: 2014-2018	Peter Schall, Christian Ammer	BExIS-ID: 22907 (Schall, Schulze, et al., 2018; Vries et al., 2003)
	Annual C increment	The data comprises estimates and measurements of timber production. All values are given as volume above bark (> 7 cm in diameter). Measured increment between the 1st (2008 - 2011) and 2nd forest inventory (2015 - 2016). **Calculation (see section 2.3.1):** The annual carbon increment was calculated using the annual wood increment according to Vries et al. (2003).	Peter Schall, Christian Ammer	BExIS-ID: 22868 Vries et al., (2013)
Biodiversity	Protists and	Extracted from fourteen 10 x 5.3 cm soil cores of the A horizon homogenised after removal of root	Anna Maria Fiore-	Protists cercozoa and

	Protists oomycota	material, done in 2017. 1 g of the bulk soil sample was used for DNA extraction and the analyses of the V4 region of the 18S rRNA gene amplified using eukaryotic specific primers. Soil DNA was extracted using the DNeasy PowerSoil Kit (Qiagen GmbH, Hilden, Germany). Sequences were filtered for (1) 100 % forward primer match, (2) length ≥ 200–710 bp, and (3) ambiguities (N). Traces were scanned for chimaeras, trimmed to 530 bp, dereplicated to group 100 % identical amplicons, and singletons removed. Remaining sequences were treated as operational taxonomic units (OTUs) and aligned to the PR2 database using BLASTn (default parameters). One hit per sequence was retained. Only OTUs with 100 % coverage and protist taxa (excluding Metazoa, Fungi and Streptophyta) were retained for analysis.	Donno, Michael Bonkowski	endomyxa: BExIS-ID: 24466 Protists oomycote: BExIS-ID: 25766 (Fiore-Donno et al., 2020)
	Moths	Number of time-based repetitions: 2. Nocturnal moths are attracted to light; a light trap to catch moths during two collection runs in 2018 (June and August which are peak seasons of adult moths) on accessible plots were used; all collected micromoths were identified to species level by an expert taxonomist (H. Hacker). **Procedure:** one automatic light trap was used per plot installed near the plot centre once per collection run (with two collection runs per plot); using light sensors, traps were operated from sunset to sunrise; light traps consisted of a UV bulb with a white plastic funnel underneath opening into a bucket containing chloroform.	Sebastian Seibold, Wolfgang Weisser, Lea Heidrich, Jörg Müller	BExIS-ID: 26026
	Bacteria	Bacterial communities were identified from soil samples in each forest plot based on the following procedure: A molecular marker gene approach to quantify bacterial diversity were used. The RNA was extracted using the modified Lueders method. V3 16S rRNA amplicons were obtained and sequenced on an Illumina NextSeq platform using universal bacterial primers as described previously. The data was then rarefied using the phyloseq package (McMurdie & Holmes, 2013) in R (function rarefy_even_depth)	Johannes Sikorski, Jörg Overmann, Carlo Marzini	BExIS-ID: 25067, 26569
	Birds	Individuals seen or heard were counted during 5-minute point counts on the plot, repeated 5 times (round) a year. The position of observer on the forest plots was as follows: 15 m south of the middle of the northern border of the plot (to avoid entering the vegetation core area which in many cases is in the centre of the plot). Birds were observed in various distance classes: 1 = 0-10 m, 2 = 10-25 m, 3 = 25-50 m, 4 = 50-100 m, 5 = 100-200 m. It was also assessed if the observation was within the plot (1) or outside (0). Two variables indicate which observations are within a 50 and a 100 m radius. Birds flying over and migrating birds were excluded from the dataset.		BExIS-ID: 31521
	Mollusca	In June 2017, surface samples were taken from all 50 forest plots in the Swabian Alb and the Hainich, and from 49 forest plots in the Schorfheide. For each	Katja Wehner,	BExIS-ID: 24986

		plot, surface samples (15 cm × 15 cm in forests, about 2 cm deep) were collected using a sharp knife, along with the herbaceous vegetation, mosses, litter, and the upper soil layer. Samples were taken at the south-east, south-west, and north-west corner of the plot and in the middle of the edges between (five replicates per plot). Snail shells were collected by hand using a stereomicroscope. Slugs were not sampled in this study since the sampling method is inappropriate to give a quantitative and qualitative survey. Shelled snails were subsequently determined to species level using Welter-Schultes (2012), Wiese (2016) and Glöer (2017). No distinction was made between dead and living snails.	Nico Blüthgen	(Wehner et al., 2021)
	Nematodes	Based on soil sampling campaign 2014. The nematodes were extracted according a modified Baermann wet funnel method as described by (Ruess, 1995).The extraction started at room temperature (approx. 20°C) for 24 h, followed by heating from 20 to 45°C in 5°C steps for 6 h. Afterwards, nematodes were fixed in a 4% cold formaldehyde solution. The total number of individuals per sample was assessed via microscope. Of the counted nematodes 10%, but not less than 100 specimens per sample, were determined to trophic group.	Liliane Ruess, Jakob Kühn	BExIS-ID: 31313 (A. Richter et al., 2023)
	Soil fungi	From each plot, a total of 14 soil cores with a diameter of 5 cm were taken along two transects from north to south and from west to east in May 2011/2017. Organic layers were removed before taking the soil cores. The upper 10 cm of the 14 soil cores from each plot were mixed. The composite samples were sieved at a mesh size of 2 mm. From the pooled soil samples, soil aliquots were afterwards stored at -20 °C and DNA was extracted from soil subsamples for each sampled plot using 'MO BIO Power Soil DNA isolation kit' (MO BIO Laboratories, Carlsbad, CA, USA) and with Qiagen (DNeasy PowerSoil Kit (Qiagen GmbH, Hilden, Germany) following the manufacturer's protocol. Afterwards a PCR approach was used to amplify fungal ITS-rDNA by using the primer pair fITS7/ ITS4, containing the Illumina adapter sequences. PCR products were then purified, cleaned, and sequenced using Illumina MiSeq.	Kezia Goldmann, Francois Buscot, Tesfaye Wubet	BExIS-ID: 26468, 26469
	Plants	Each plant species on the whole 20 m x 20 m plot was identified and each species cover in relation to the whole 20 m x 20 m plot was estimated. The cover estimation of each species is done on four different layers. H = Herb layer (all non-woody species, S = Shrub layer (woody species with a height of < 5 m) B1 (woody species with a height between 5 m - 10 m) B2 (woody species with a height of > 10 m). To have a good survey of all species, survey is split in 2 times. In April, the presence and cover of spring grasses (Anemone, Allium, Ranunculus) is estimated and a complete second survey is done in summer (June-August).	Markus Fischer, Ralph Bolliger, Judith Hinderling, Christoph Zwahlen, Svenja Kunze, Daniel Prati	BExIS-ID: 30909

	Red listed bird species	Inventory data was available from multiple sources (e.g. Conservation authorities (Naturschutzbehörden), regional mapping projects). With this data, a threat analysis was carried out for all species. The species were then divided into threat categories. This categorization was based on expert knowledge. **Selection (see section 2.3.1)**: For this study only species in the threat categories 1 to 3 were used.		BExIS-ID: 25067 + Grüneberg et al. (2016)
	Forest plant specialists	German plants were classified into four groups: species only found in forests, in open areas in forests, in both open-lands and forests, and mostly in open-lands. Categorisation was based on expert knowledge. **Selection (see section 2.3.1)**: For this study only species in the groups 'species only found in forests' and 'in open areas in forests' were used.		BExIS-ID: 30909 + Schmidt et al. (2011)
	Forest bird specialists	European birds were categorized into five classes of their habitat specialization: Generalist, farmland, forest, mediterranean and inland wetland. This classification is based on the distribution of populations across Europe and is therefore highly simplified, as the habitats of species may differ in different European regions. The classification of forest specialists was obtained from Tucker & Evans (1997). **Selection (see section 2.3.1)**: For this study only species with the habitat specialization 'forests' were used.		BExIS-ID: 25067 + Gregory et al. (2007) Tucker and Evans (1997)
Management and structure	Mean DBH	**Description of study design:** Within the 'second forest inventory at the plot level' all trees growing on the forest plots were surveyed. Species were classified and diameter at breast height (caliper limit: DBH > = 7 cm) was measured. The second forest inventory was conducted in the off-season from 2014 to 2016 (and 2017 to 2018 for 22 Plots). Sampling area size was generally 10000 m^2, except for: - SEW36: 10080 m2 - SEW49: 7320 m2. Number of time-based repetitions: 2.	Peter Schall, Christian Ammer	BExIS-ID: 22766
	Annual deadwood input	The dead wood increment is based on the 1st (2008 - 2011) and 2nd forest inventory (2015 - 2016). It was measured on diameter and length of all deadwood pieces with a diameter > 10 cm.	Peter Schall, Christian Ammer	BExIS-ID: 22846

		Number of time-based repetitions: 2. The difference was calculated between the two inventories.		
	Mixture	**Classification (see section 2.3.1):** Pure forests are forests consisting out of > 80 % of one main tree species. Mixed forests, on the other hand, are forests that consist of ≤ 80 % of one dominant tree species. Year of collection: 2014-2018		BExIS-ID: 22766
	Management type	Three management systems were distinguished (i.e. age class forestry (even aged system employing shelterwood cuts in the regeneration phase, intervention every 5 – 10 years, trees harvested every ~ 100 years), selection system (uneven aged, intervention every 5 – 10 years, trees harvested every ~ 100 years) and unmanaged (uneven aged)). Year of collection: 2008-2014 **Classification (see section 2.3.1):** Even aged = aged class Uneven aged = selection system + unmanaged	Peter Schall	BExIS-ID: 17706
	Genus	**Classification (see section 2.3.1)**: The species (Beech, spruce, pine, oak) with the highest basal proportion was set as the dominant tree species. Year of collection: 2014-2018		BExIS-ID: 22766
Environment	Core depth	Soil depth was measured as the combined thickness of all topsoil and subsoil horizons, determined by sampling a soil core in the centre of the study plots. A motor driven soil column cylinder with a diameter of 8.3 cm for the soil sampling was used (Eijkelkamp, Giesbeek, The Netherlands).		
	Elevation	Calculated from regional Digital Elevation Models.		BExIS-ID: 20826
	Proportion of clay in the soil	In each of the 150 forest plots of the biodiversity Exploratories 14 soil cores with a split tube sampler (diameter of 5 cm) along two 40 m transects in forests were collected in May 2011. Organic layers were removed before coring. Then a composite sample from the 14 soil cores by mixing the upper 10 cm of the soil was prepared. A subsample of the composite sample was sieved to < 2 mm, dried and subsequently used for soil texture analysis. Texture analysis consists of three main steps: (i) destruction of soil organic matter with hydrogen peroxide, (ii) dispersion of soil aggregates into discrete units, and (iii) separation of soil particles of different size by sieving and sedimentation (DIN-ISO 11277). **Equipment:** • 0.63, 0.2, 0.063 mm sieves for isolation of sand fractions (Retsch, Haan, Germany)	Ingo Schöning, Theresa Klötzing, Marion Schrumpf, Emily Solly, Susan Trumbore	BExIS-ID 14686

		• Atterberg cylinders to separate silt and clay fractions • Reference soil of VDLUFA/LUFA for quality control (LUFA, Speyer, Germany)		
	Soil pH	Composite samples were taken in May 2011 and May 2014 in all plots by mixing 14 mineral topsoil samples (0 – 10 cm, using a manual soil corer with 5.3 cm diameter). Soil samples were air dried and sieved (< 2 mm) and then the soil pH in the supernatant of a 1:2.5 mixture of soil and 0.01 M $CaCl_2$ was measured. **Equipment**: • WTW pH meter 538 (WTW, Weilheim, Germany) • WTW pH glass electrode SenTix 61 (WTW, Weilheim, Germany) **Calculation:** The average of 2011 and 2014 was calculated.	Ingo Schöning, Theresa Klötzing, Huei Ying Gan, Marion Schrumpf, Jessica Heublein, Emily Solly, Susan Trumbore	BExIS-ID: 14447 and BExIS-ID: 19067
	Mean annual temperature	Measured at 2 m above ground level in weather stations in each plot between 2008 and 2018		BExIS-ID: 19007
	Mean annual precipitation	From RADOLAN product (between 2008 and 2018).		BExIS-ID: 19007
	Topographic wetness Index	The topographic Wetness Index combines measures of upslope contributing area (determining the amount of water received from upslope areas) and slope (determining the loss of water from the site to downslope areas) and has been shown in previous analyses to be a better predictor than local humidity measures. It is defined as $ln\left(\frac{a}{tanB}\right)$, where a is the specific catchment area (cumulative upslope area which drains through a Digital Elevation Model (DEM, http://www.bkg.bund.de) cell, divided by per unit contour length) and tanB is the slope gradient in radians calculated over a local region surrounding the cell of interest 88,89. The Topographic wetness Index was calculated from raster DEM data with a cell size of 25 m for all plots, using GIS tools (flow direction and flow accumulation tools of the hydrology toolset and raster calculator). The Topographic wetness Index measure used was the average value for a 4 × 4 window centred on the plot, i.e. 16 DEM cells corresponding to an area of 100 m × 100 m.	Peter Manning, Gaëtane Le Provost	BExIS-ID: 31018 Le Provost et al. (2021)

Table S2. Species of biodiversity with conservation value found in the study area

List of plant forest specialists from Schmidt et al. (2011) present in the study area (n = 113)		**List of bird forest specialists from Gregory et al. (2007) and Tucker and Evans (1997) present in the study area (n = 33)**	**List of bird species from Grüneberg et al. (2016) with conservation status critically endangered, endangered, vulnerable present in the study area (n = 6)**
Abies_alba	*Lathyrus_vernus*	*Coccothraustes*	*Anthus trivialis*
Actaea_spicata	*Lilium_martagon*	*coccothraustes*	*Ficedula hypoleuca*
Adoxa_moschatellina	*Listera_ovata*	*Cyanistes caeruleus*	*Jynx torquilla*
Allium_ursinum	*Lonicera_xylosteum*	*Dendrocopos minor*	*Picus viridis*
Anemone_nemorosa	*Luzula_luzuloides*	*Dryocopus martius*	*Pernis apivorus*
Anemone_ranunculoides	*Luzula_pilosa*	*Ficedula albicollis*	*Sturnus vulgaris*
Anthriscus_sylvestris	*Luzula_sylvatica*	*Ficedula hypoleuca*	
Arctium_nemorosum	*Lysimachia_nemorum*	*Fringilla montifringilla*	
Arum_maculatum	*Maianthemum_bifolium*	*Garrulus glandarius*	
Aruncus_dioicus	*Melampyrum_pratense*	*Hippolais icterina*	
Asarum_europaeum	*Melica_nutans*	*Jynx torquilla*	
Athyrium_filix-femina	*Melica_uniflora*	*Lullula arborea*	
Brachypodium_sylvaticum	*Mercurialis_perennis*	*Luscinia megarhynchos*	
Calamagrostis_arundinacea	*Milium_effusum*	*Muscicapa striata*	
Campanula_trachelium	*Moehringia_trinervia*	*Oriolus oriolus*	
Cardamine_bulbifera	*Myosotis_sylvatica*	*Periparus ater*	
Cardamine_flexuosa	*Neottia_nidus-avis*	*Phoenicurus phoenicurus*	
Cardamine_impatiens	*Oxalis_acetosella*	*Phylloscopus collybita*	
- Carex_alba *Carex_digitata*	*Paris_quadrifolia*	*Phylloscopus sibilatrix*	
Carex_montana	*Phyteuma_spicatum*	*Picus canus*	
Carex_remota	*Poa_chaixii*	*Picus viridis*	
Carex_sylvatica	*Poa_nemoralis*	*Poecile montanus*	
Carpinus_betulus	*Polygonatum_multiflorum*	*Poecile palustris*	
Cephalanthera_damasonium	*Polygonatum_verticillatum*	*Prunella modularis*	
Cephalanthera_rubra	*Polypodium_vulgare*	*Pyrrhula pyrrhula*	
Chaerophyllum_temulum	*Potentilla_sterilis*	*Regulus regulus*	
Chrysosplenium alternifolium	*Prenanthes_purpurea*	*Sitta europaea*	
Convallaria_majalis	*Pseudotsuga_menziesii*	*Sylvia borin*	
Dactylis_polygama	*Pteridium_aquilinum*	*Certhia familiaris*	
Daphne_mezereum	*Pulmonaria_obscura*	*Certhia brachydactyla*	
Digitalis_purpurea	*Quercus_rubra*	*Carduelis spinus*	
Dryopteris_dilatata	*Ranunculus_lanuginosus*	*Carduelis flammea*	
Dryopteris_filix-mas	*Ribes_alpinum*	*Bonasa bonasia*	
Elymus_caninus	*Rubus_idaeus*	*Anthus trivialis*	
Epilobium_angustifolium	*Rumex_sanguineus*		
Epilobium_montanum	*Sambucus_racemosa*		
Euphorbia_amygdaloides	*Sanicula_europaea*		
Euphorbia_dulcis	*Senecio_ovatus*		
Fagus_sylvatica	*Senecio_sylvaticus*		
Festuca_altissima	*Solanum_dulcamara*		
Festuca_gigantea	*Sorbus_aria*		
Fragaria_vesca	*Sorbus_torminalis*		
Gagea_lutea	*Stachys_alpina*		
Galium_odoratum	*Stachys_sylvatica*		
Galium_rotundifolium	*Stellaria_holostea*		
Galium_sylvaticum	*Stellaria_nemorum*		
Gymnocarpium_dryopteris	*Taxus_baccata*		
Hedera_helix	*Tilia_cordata*		
Helleborus_foetidus	*Tilia_platyphyllos*		
Hepatica_nobilis	*Torilis_japonica*		
Hordelymus_europaeus	*Ulmus_glabra*		
Hypericum_hirsutum	*Ulmus_laevis*		
Impatiens_noli-tangere	*Veronica_montana*		
Impatiens_parviflora	*Vicia_sylvatica*		
Larix_decidua	*Vinca_minor*		
Lathraea_squamaria	*Viscum_album*		

Table S 3. Standardised effect size +/- confidence interval and p-values for all response variables.

Explanatory variables	C Increment	Tree stocks	Soil stocks	Plant specialists richness	Bird specialists richness	Red list
(Intercept)	-5.68e-03±0.09 p = 0.952	**0.15±0.06 p = 0.016**	0.0±0.10 p = 0.975	-0.10±0.09 p = 0.244	0.08±0.09 p = 0.401	**-0.74±0.15 p < 0.001**
Mean DBH	-0.13±0.09 p = 0.144	**0.65±0.06 p < 0.001**	-0.01±0.09 p = 0.912	0.06±0.08 p = 0.449	**0.38±0.09 p < 0.001**	0.19±0.12 p = 0.126
Deadwood input (sqrt)	-0.04±0.08 p = 0.600	**0.13±0.05 p = 0.009**	-0.04±0.08 p = 0.646	0.07±0.07 p = 0.319	0.11±0.08 p = 0.144	-0.05±0.13 p = 0.684
Mixture	-0.09±0.09 p = 0.287	-0.03±0.06 p = 0.641	0.17±0.09 p = 0.066	**-0.16±0.08 p = 0.055**	**0.18±0.09 p = 0.038**	0.0±0.14 p = 0.954
Uneven-aged	**-0.37±0.09 p < 0.001**	**0.26±0.06 p < 0.001**	-0.10±0.09 p = 0.291	**-0.23±0.08 p = 0.005**	0.0±0.08 p = 0.978	**0.29±0.12 p = 0.014**
Genus (Oak)	-0.01±0.34 p = 0.974	-0.23±0.22 p = 0.292	0.02±0.37 p = 0.958	0.21±0.33 p = 0.517	0.08±0.34 p = 0.825	**0.82±0.39 p = 0.036**
Genus (Pine)	-0.12±0.25 p = 0.626	**-0.75±0.16 p < 0.001**	-0.11±0.27 p = 0.676	-0.26±0.24 p = 0.279	**-0.59±0.25 p = 0.018**	-0.24±0.46 p = 0.603
Genus (Spruce)	0.19±0.26 p = 0.461	**-0.35±0.17 p = 0.041**	0.09±0.28 p = 0.756	1.**10±0.25 p < 0.001**	-0.07±0.26 p = 0.796	-0.90±0.61 p = 0.144
Observations	150	150	150	150	150	150

Explanatory variables	Bacteria richness	Fungi richness	Protist richness	OOmycota richness	Nematode richness	Mollusca richness	Plant richness	Arthropod richness	Bird richness
(Intercept)	**0.25±0.09 p = 0.007**	0.0±0.10 p = 0.941	0.18±0.09 p = 0.058	0.05±0.10 p = 0.604	0.19±0.10 p = 0.054	0.19±0.10 p = 0.058	**-0.25±0.08 p = 0.003**	**1.33±0.03 p < 0.001**	0.0±0.10 p = 0.928
Mean DBH	0.12±0.08 p = 0.146	**0.18±0.09 p = 0.053**	**0.21±0.09 p = 0.016**	**0.19±0.09 p = 0.041**	0.14±0.09 p = 0.119	0.0±0.09 p = 0.971	-0.06±0.08 p = 0.423	0.04±0.03 p = 0.178	**0.28±0.09 p = 0.002**
Deadwood volume sqrt	0.14±0.08 p = 0.068	-0.10±0.08 p = 0.243	0.14±0.08 p = 0.074	0.02±0.08 p = 0.839	0.08±0.08 p = 0.318	0.14±0.08 p = 0.099	0.04±0.07 p = 0.587	0.0±0.03 p = 0.750	0.10±0.08 p = 0.231
Mixture continuous	-0.02±0.08 p = 0.768	**0.29±0.09 p = 0.002**	0.06±0.09 p = 0.482	0.11±0.09 p = 0.231	0.08±0.09 p = 0.393	0.11±0.09 p = 0.255	-0.12±0.08 p = 0.118	-0.01±0.03 p = 0.653	0.15±0.09 p = 0.094
unevenaged	0.0±0.08 p = 0.940	-0.04±0.09 p = 0.674	-0.04±0.08 p = 0.664	-0.06±0.09 p = 0.508	**-0.18±0.09 p = 0.045**	-0.08±0.09 p = 0.372	**-0.19±0.08 p = 0.015**	-0.03±0.03 p = 0.243	0.02±0.09 p = 0.806
Genus (Oak)	0.07±0.33 p = 0.829	-0.23±0.36 p = 0.522	0.28±0.34 p = 0.401	-0.16±0.37 p = 0.662	-0.32±0.36 p = 0.372	-0.46±0.39 p = 0.240	**0.62±0.30 p = 0.043**	**-0.25±0.12 p = 0.031**	0.45±0.35 p = 0.201
Genus (Pine)	**-0.89±0.24 p < 0.001**	0.19±0.26 p = 0.465	**-1.14±0.25 p < 0.001**	-0.21±0.27 p = 0.432	**-0.69±0.26 p = 0.009**	**-0.68±0.30 p = 0.024**	0.25±0.22 p = 0.260	0.04±0.08 p = 0.674	-0.40±0.25 p = 0.121
Genus (Spruce)	**-1.24±0.25 p < 0.001**	-0.16±0.27 p = 0.565	-0.49±0.26 p = 0.064	-0.15±0.29 p = 0.611	**-0.73±0.27 p = 0.008**	**-0.85±0.28 p = 0.002**	**1.59±0.23 p < 0.001**	-0.09±0.09 p = 0.327	0.30±0.27 p = 0.274
Observations	150	150	147	149	149	139	150	147	149

Figure S1. Distribution of management types, dominant species across mixed and pure forests in the study plots. The management type 'uneven aged' was only present in forests with the main tree species beech or oak.

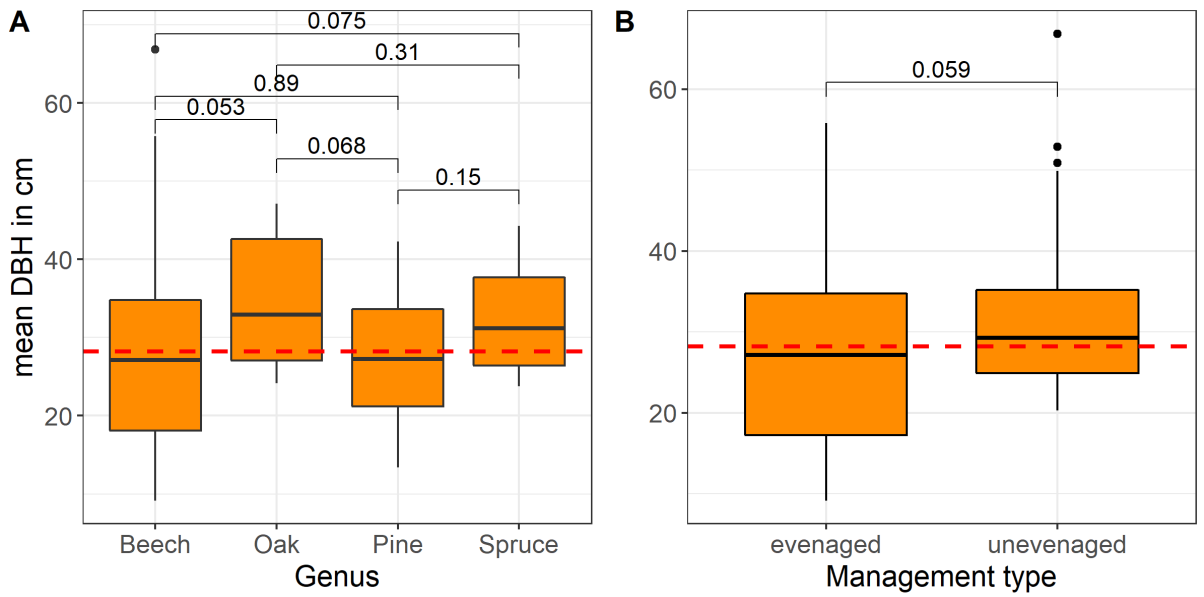

Figure S2. Variation of mean DBH across dominant genera and management type in the study plots; p-values for t-test pairwise comparisons are shown.

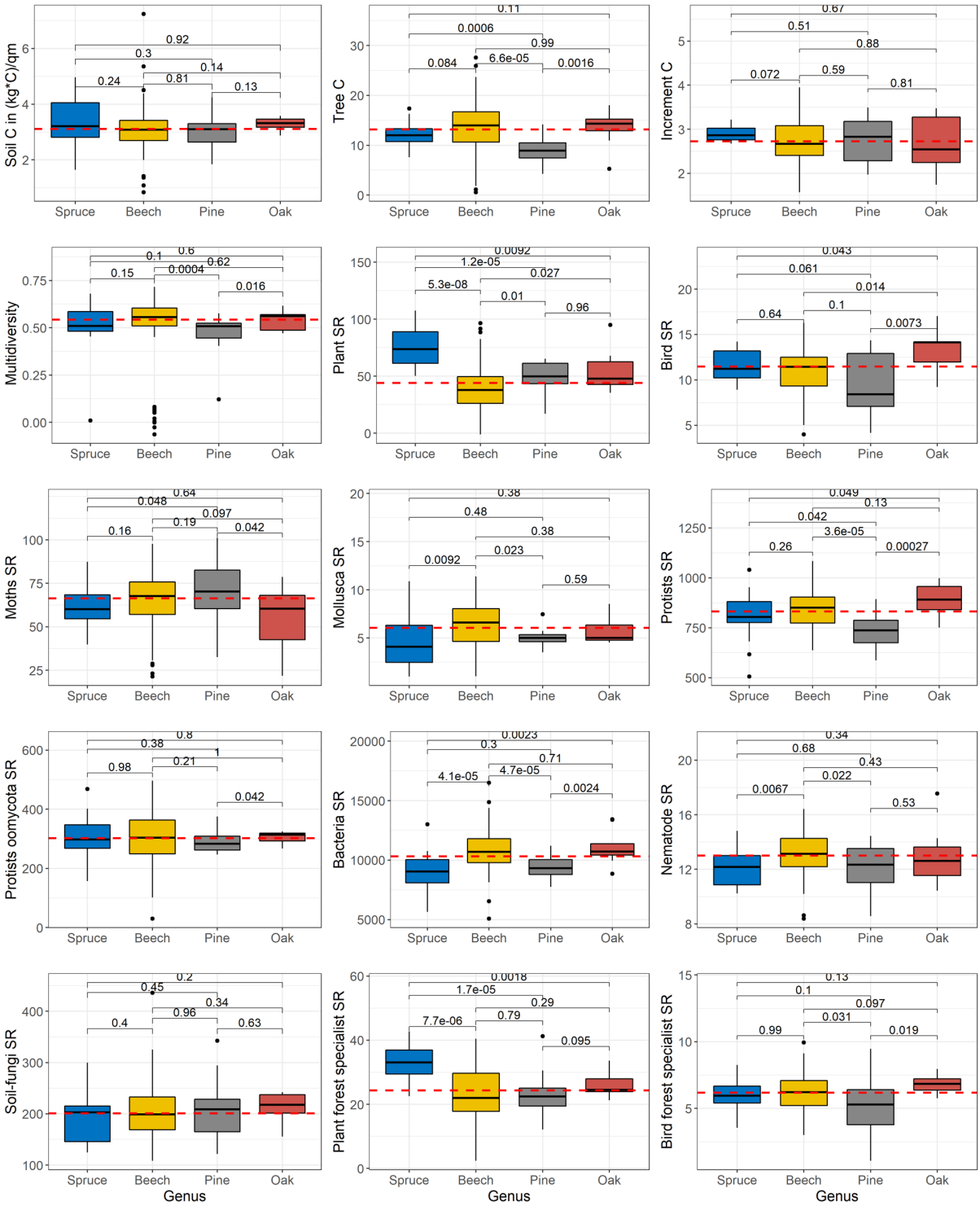

Figure S3. Variation of response variables across dominant species. P values for pairwise t-test comparisons are shown. The red lines mark the individual median of each group. The p-values between each genus are shown.