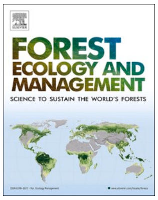
Forest Ecology and Management 572 (2024) 122328

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Identifying the stand properties that support both high biodiversity and carbon storage in German forests

K. Springer[a,b], P. Manning[b,c], A.L. Boesing[b], C. Ammer[d], A.M. Fiore-Donno[e], M. Fischer[f], K. Goldmann[g], G. Le Provost[h], J. Overmann[i], L. Ruess[j], I. Schöning[k], S. Seibold[l,m], J. Sikorski[i], M. Neyret[b,n,*]

[a] *Department of Life Sciences and Engineering, TH Bingen University of Applied Science, Bingen am Rhein, Germany*
[b] *Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany*
[c] *Department of Biological Sciences, University of Bergen, Bergen, Norway*
[d] *University of Göttingen, Göttingen, Germany*
[e] *University of Cologne, Cologne, Germany*
[f] *University of Bern, Bern, Switzerland*
[g] *UFZ Helmholtz Centre for Environmental Research, Dept. Soil Ecology, Halle (Saale), Germany*
[h] *INRAE, Bordeaux Sciences Agro, ISVV, SAVE, Villenave d'Ornon, France*
[i] *Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures GmbH, Germany*
[j] *Humboldt-Universität zu Berlin, Berlin, Germany*
[k] *Max Planck Institute for Biogeochemistry, Jena, Germany*
[l] *Technical University of Munich, TUM School of Life Sciences, Freising, Germany*
[m] *TUD Dresden University of Technology, Forest Zoology, Tharandt, Germany*
[n] *Alpine Ecology Laboratory, CNRS, Grenoble Alpes University, Grenoble, France*

ARTICLE INFO

Keywords:
Forest management
Biodiversity loss
Carbon storage
Climate change mitigation
German forestry

ABSTRACT

Forest ecosystems 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 manageable local-scale forest properties 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, molluscs, 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, Scots pine, Norway spruce, and sessile and pedunculate oak. We then investigated the relationships between multiple forest structure and management variables, and multiple biodiversity and carbon storage and sequestration measures. Soil carbon did not respond to deadwood input or any other variable, except in spruce-dominated forests where a higher proportion of other tree species had positive effects on soil carbon storage. Carbon storage in trees was lower in pine- and spruce-dominated stands than in beech stands where it increased with mean tree diameter. Carbon sequestration (i.e. stand uptake) in trees decreased with mean tree diameter. Mean tree diameter was positively related to the biodiversity of multiple taxa, especially taxonomic richness of forest specialist birds; as well as red-listed birds in pine stands. Beech-dominated stands harboured a higher taxonomic richness of many investigated taxa compared to stands dominated by conifers (especially pine). One exception to this was the richness of plant species and forest specialist plants, which were highest in spruce plantations. Deadwood input had limited effects on biodiversity with few exceptions such as bacteria diversity, probably because many deadwood dwelling organisms were not measured in this study. By showing that forests of larger trees with a high proportion of broadleaved trees can promote both biodiversity and carbon storage, our results could help inform sustainable local-scale forest management in Central Europe. 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 multifunctional forest management.

---

* Corresponding author at: Alpine Ecology Laboratory, CNRS, Grenoble Alpes University, Grenoble, France.
E-mail address: margot.neyret@univ-grenoble-alpes.fr (M. Neyret).

https://doi.org/10.1016/j.foreco.2024.122328
Received 23 July 2024; Received in revised form 4 October 2024; Accepted 5 October 2024

1. 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 are fundamentally connected and interact with each other (Pettorelli et al., 2021; Pörtner et al., 2021). Climate change has also become a key driver of biodiversity loss, e.g. in arthropods (Lister and 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; Pörtner et al., 2021).

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 and 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). 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 aboveground carbon storage, 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 (Simons et al., 2021), which can shape, depending on management choices, species composition and potentially stand structure (Dieler et al., 2017; Schall and Ammer, 2013). 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 (Asbeck et al., 2021a; Huston and Marland, 2003; Mayer et al., 2020). These trade-offs have led to the development of multiple approaches that aim to combine multiple goals at the scale of landscapes (Edwards et al., 2014, Himes et al., 2022), by exploring how segregating management styles in space can support multiple land use objectives. However, local-scale management that combines multiple goals could complement landscape-strategies and support the development of multi-scale management approaches.

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; Spathelf and Ammer, 2015). Without human intervention, it is estimated that 92 % of German forest area would be dominated by European beech (*Fagus sylvatica*) and, to a much lesser extent, 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). In the last few decades, the German forestry system has been 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 the expectation that this will promote biodiversity. For instance, retaining deadwood and habitat trees in uneven-aged and mixed forests promotes biodiversity at the stand scale (Penone et al., 2019), while large trees provide numerous microhabitats (Asbeck et al., 2021b; Paillet et al., 2019; Vuidot et al., 2011). 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 and Brown, 2008; Siitonen, 2001; Stokland et al., 2012). The impact of the dominant tree species, though, varies across taxa (Edelmann et al., 2022; Leidinger et al., 2021), but broad-leaved dominated forests seem to be preferred by more species overall (e.g. Abele et al., 2014; Penone et al., 2019; Russ and 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 a few stand characteristics or management regimes (Sandström et al., 2019; Schulze, 2018). Further, the relationship between biodiversity and carbon, and their joint response to stand features and management, has also not been fully assessed. This means that a comprehensive assessment of trade-offs and synergies between the diversity of multiple taxa and carbon storage across multiple forest types has not been performed in Germany. 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, e.g. by providing information on which tree-planting or stand management strategies to increase carbon storage in forests would also benefit biodiversity.

In this study, we investigate how forest structure affects synergies and trade-offs between biodiversity and carbon storage and sequestration in German forests. We combine data on the taxonomic diversity 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 differing in their management and stand variables, located in three regions of Germany. We created indices combining either biodiversity- or carbon-related variables (*Multidiversity* and *Carbon* indices) and assessed the impacts of forest structure and management variables on each of these two dimensions, as well as their joint response, using linear models. We hypothesised that (1) aboveground carbon storage is higher in forests composed of larger trees (2) deadwood input rate contributes positively to soil carbon storage, (3) biodiversity is higher in stands with larger trees and abundant deadwood, and in mixed or broad-leaved forests than in coniferous forests, and (4) both *Multidiversity* and *Carbon* indices are higher in broadleaved than coniferous stands and both increase in stands of larger trees. 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 at the stand level.

2. Methods

2.1. 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 region comprises 50 forest plots (100 m × 100 m) selected to span the typical range of local tree species composition and management types. One plot in the Hainich region was changed in 2016 and is not used in this study, resulting in 149 plots in total. The regions were selected to be typical of the major climate and geology types within Germany and are also broadly representative of the most common forest types of Central Europe (Fischer et al., 2010). While we outline the main methods here, further details on methods and data acquisition can be found in Table S1.

2.2. Data acquisition

All data manipulation and analysis were conducted with R version 4.3.1 (R Core Team, 2023). All data used were existing data from the Biodiversity Exploratories project.

2.3. Forest structure and management data

Forest structure and management variables were measured during two comprehensive forest inventories between 2008–2014 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 structure and management variables (see Table S1 for details): total deadwood input per year (which represents supply rate of deadwood to consumers), mean tree diameter at breast height (DBH), the identity of the dominant genera (beech, spruce, oak and pine), and a forest mixture index. The mixture index was calculated as 1 minus the proportion of the most abundant genus based on crown projection area; thus it decreased with increasing dominance of the main genus. When multiple layers were present, they were combined for the calculation of forest structure variables.

There were 14 missing values for deadwood input. Because deadwood input was used as an explanatory variable in all models described below, we imputed missing values with the average of deadwood input for stands with the same dominant genus.

2.4. Carbon storage

We calculated two indicators of the capability of a forest to store carbon: C storage was estimated from carbon storage in soil and in the above-ground tree biomass. C sequestration was estimated from the annual increment of C in the trees (above-ground only). We use the terms storage and sequestration for consistency with widely accepted climate policy terminology, but these terms can be considered broadly equivalent to C stocks and accumulation rates, respectively, in ecosystem ecology. C storage 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; total soil depth ranged from 10 to 161 cm) using the dry combustion analysis, as the product of soil C concentration and bulk density. We focused on topsoil storage for comparability across plots and because it is the most responsive to the part most likely to have responded to recent forest management and current stand properties. 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 C sequestration by using the annual wood increment measured between first and second inventories. 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 de Vries et al. (2003).

2.5. Biodiversity

We considered nine taxonomic groups; vascular plants (hereafter: plants), birds, moths, molluscs, soil fungi, soil bacteria (active fraction only), soil protists of Cercozoa and Endomyxa, soil protists of Oomycota, and nematodes, to represent a comprehensive picture of the taxonomic diversity of below- and aboveground groups. The taxonomic richness of individual groups was measured at different time points during the 2015–2018 sampling period (see details in supplementary material Table S1). Taxonomic resolution was at species level for moths, birds, plants, molluscs, OTU for protists (both groups) and bacteria, ASV for fungi and family for nematodes. When multiple sampling years were available, taxonomic richness (hereafter richness) was calculated as the total number of taxa found in a given plot across years. There were missing values for molluscs (11 plots), cercozoan and endomyxan protists (3), moths (3), birds (1), oomycotan protists (1) and nematodes (1). These were not imputed.

In addition, we selected indicators of biodiversity representing high conservation value. We calculated the taxonomic 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 plant 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 of high conservation value are listed in Table S2.

2.6. 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 forest structure and management variables independently of environmental covariates, we first corrected for environmental covariates. To do so, we selected environmental covariates that represent soil, climatic and topographic conditions: elevation, soil pH, mean annual temperature, mean annual precipitation, soil depth, proportion of clay in the soil, the Topographic Wetness Index (Moeslund et al., 2013) and the region as a factor variable. To avoid collinearity, we then excluded variables that were too collinear, removing most collinear variables first (based on the variance inflation factor, with a threshold of $\mathrm{GVIF}^{1/2^*\mathrm{Df}} < 3$). The region, soil pH, mean annual temperature, soil depth and proportion of clay were retained. We fitted individual regressions for each response variable (carbon storage and sequestration; taxonomic richness for each group) with these five environmental covariates as well as the region as explanatory variables. When appropriate, generalised linear models with Poisson family were used: this was the case for all richness variables except for groups with very high species numbers (fungi, bacteria, both protist groups). Otherwise, we used linear regressions with Gaussian error as the data was not bounded. To ensure normal error distributions and a homogeneous variance, we applied a transformation $y = \log(x+1)$ to deadwood input before fitting the model. We then extracted the residuals from each model, which represent the variation of the response variables after "removing" variation associated with environmental covariates. These residual values were then used in all further analyses.

2.7. Calculation of aggregated indices

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 (Fig. 1).

We first calculated a *Multidiversity index* from the taxonomic richness of all considered groups. Multidiversity is calculated as the average scaled richness per taxonomic group, where the richness of each group is scaled between 0 and 1 across all plots (Allan et al., 2014). An advantage of the multidiversity metric over total taxonomic richness is the equal weighting of the taxa, thus preventing the index 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). Because all groups, including groups with high conservation priority, were included, this index captures both the overall diversity and the uniqueness of the community to forest ecosystems.

We took a similar approach for carbon-related variables. Carbon storage in trees, soil and carbon sequestration in trees were scaled between 0 and 1 to ensure equal weighting in the final index, as we lacked information of which properties were prioritized by conservation managers (Manning et al., 2018). They were then averaged to calculate a

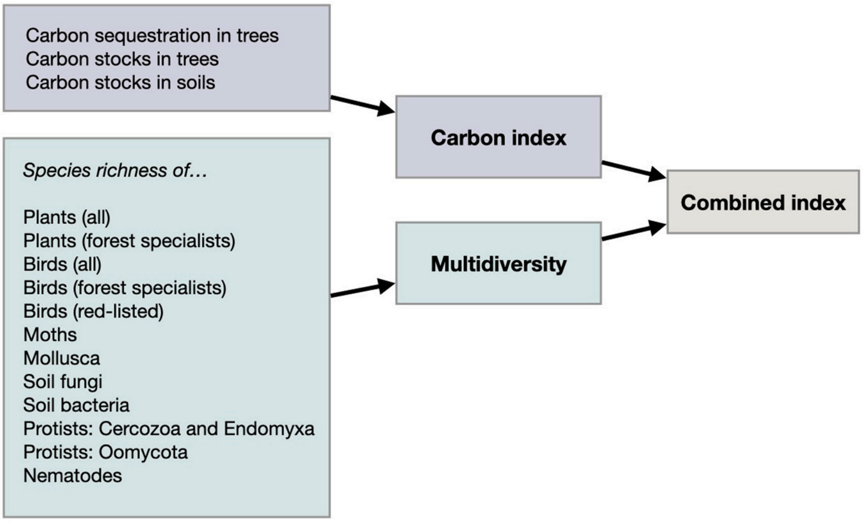


Fig. 1. **:** Schematic illustration showing the calculation of the *Combined index*. All the variables and intermediate indices were adjusted for environmental covariates and scaled between 0 and 1. Multidiversity was calculated according to Allan et al. (2014). Black arrows indicate scaling and averaging of variables into the next level of aggregation.

Carbon index.

Finally, the *Combined index* was calculated as the average of *Carbon* and the *Multidiversity* indices (Fig. 1).

2.8. Statistical analysis

We fitted multiple linear regressions between each response variable (all shown in Fig. 1: richness of each individual group and carbon-related variables after correction for environmental covariates (see above), or aggregated indices) and forest structure and management variables (dominant genus, mean DBH, mixture index, deadwood input) as explanatory variables. We included interactions between the dominant genus and the other explanatory variables (mixture index, mean tree diameter, deadwood input), as we expected that these variables could have contrasting effects in different stand types. We did not include other interactions to avoid overfitting the models. We checked for multicollinearity in the main explanatory variables (excluding interactions): all variance inflation factors were below 2. We then performed model selection using the step function (based on model AIC) to select the most parsimonious models. Linear models were chosen because we did not have clear expectations for non-linear relationships; we checked model residuals visually and did not find a clear departure from the assumptions of normality. Finally, we calculated standardised effect sizes (i.e., the beta parameter divided by standard deviation) and their confidence intervals for all explanatory variables in each model, and represented them as forest plots using the *sjPlot* package. Results are shown with no correction for multiple testing. In the results, model results are presented as standardised effect size with beech-dominated stands as the reference. This reference was chosen because beech stands were the most common among our study sites.

To assess the effect of using the correction for environmental covariates described above, we also ran models including all response variables as well as these environmental covariates, with the uncorrected values as response variables. The results were mostly similar to those presented here (see Figs. S1–3). In these models, the relative importance (package relaimpo) of environmental covariates was on average 24 % of the total variance (ranging from 5 % (tree carbon stocks) to 51 % (bacteria richness)) while the relative importance of forest structure and management variables and their interactions was on average 29 % of the total variance (see Figure S4).

3. Results

3.1. Forest structure and management variables

European beech was dominant in 70 % of the plots (105 plots), followed by Scots pine (~13 %; 19 plots), and Norway spruce (~11 %; 16 plots). Oak species were dominant in nine plots (*Quercus robur* and *Quercus petraea,* ~6 %). Table S3 shows the variation of forest structure and management variables across dominant genera. The mixture index was on average 0.17 ± 0.16. Forests dominated by oak and spruce tended to have a higher mean DBH (mean 35.1 cm ± sd 8.5 and 32.2 cm ± 6.3, respectively) than forests dominated by beech and pine (27.5 cm ± 11.9 and 27.4 cm ± 8.4, respectively), but this was not significant (Tukey test: $p > 0.15$). Mean DBH was also lower in mixed forests (correlation between mean DBH and mixture index: $r = -0.33$, $p < 0.001$). Plots with the highest average DBH also had the largest individual trees (correlation between mean DBH and maximum DBH: Pearson $r = 0.34$, $p < 0.001$) and lower deadwood input (Pearson $r = -0.19$, $p = 0.02$).

3.2. Forest structure and management for a high Carbon index

Overall, the *Carbon index* ranged between 0.27 and 0.82 and tended to be higher in stands with large mean DBH (Fig. 3, Table S6). The component variables of the *Carbon index* differed in their respective responses to the explanatory variables (model results shown in Table S4). Soil carbon did not respond statistically significantly to any of the forest structure and management variables, except in spruce-dominated stands where the mixture index had a positive effect ($p = 0.005$) (in beech-dominated-stands: 0.16 ± 0.10, $p = 0.09$; this estimate and all following estimates are provided as standardised effect sizes, p-values are extracted from corresponding multivariate regressions. Slope in pine and oak stands not significantly different from beech). Tree carbon storage increased with mean DBH (0.82 ± 0.06, $p < 0.001$), as expected from its calculation from tree volume, which itself depends on tree size and density. When controlling for all other management and structure variables, high tree carbon storage was also associated with high deadwood input (0.12 ± 0.05, $p = 0.03$). Finally, tree carbon storage was lower in pine-dominated (-1.0 ± 0.15, $p < 0.001$) and spruce-dominated (-0.43 ± 0.19, $p = 0.02$) stands compared to beech stands, likely due to lower wood densities and typically lower DBH in coniferous stands. Carbon sequestration in trees decreased with mean

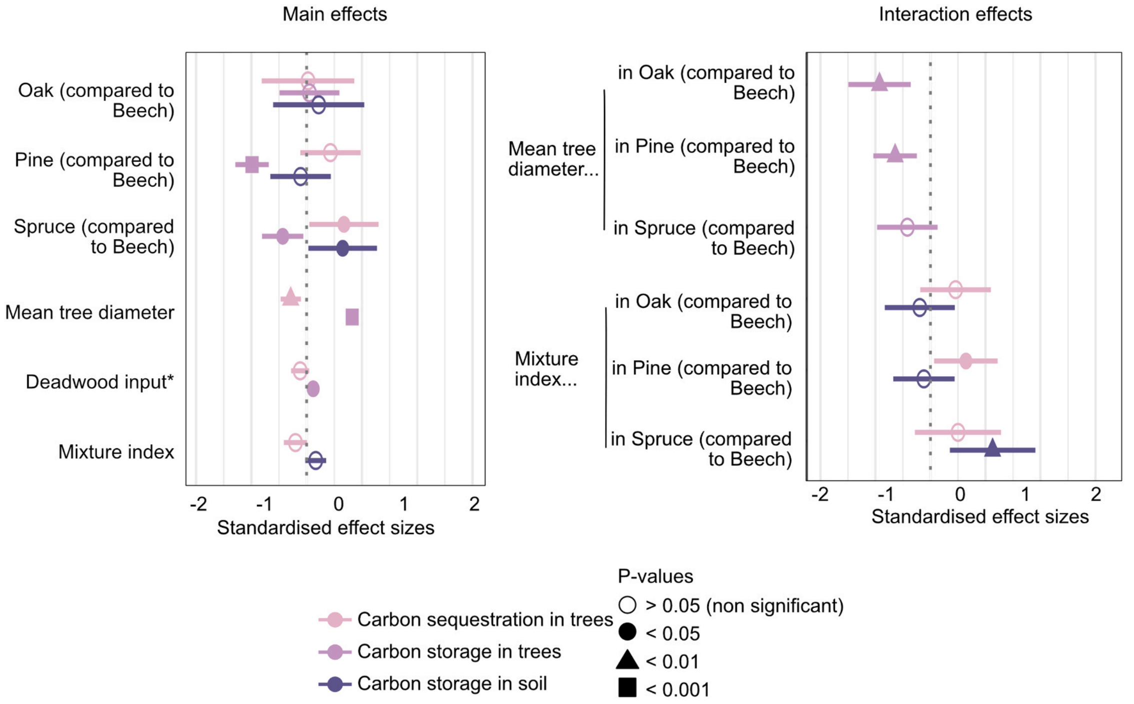


Fig. 2. **:** Effect of forest structure and management variables on carbon-related variables. Plots show standardised effect sizes along with 95 % confidence intervals estimated for the selected structure and management variables affecting taxonomic richness of individual groups. Left: main effects. Right: interaction effects. The results are shown with beech as the reference genus. * Deadwood input was transformed (log(x) +1) before analysis.

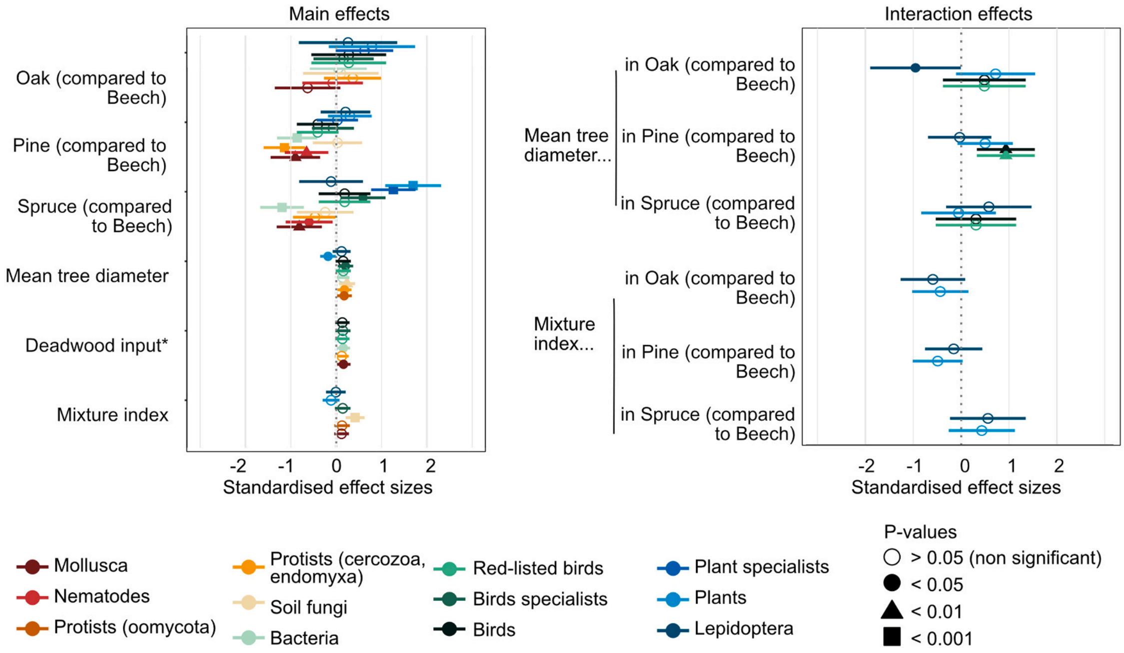


Fig. 3. **:** Effect of forest structure and management variables on biodiversity. Plots show standardised effect sizes along with 95 % confidence intervals estimated for the selected structure and management variables affecting taxonomic richness of individual groups. Left: main effects. Right: interaction effects. The results are shown with beech as the reference genus. * Deadwood input was transformed (log(x+1)) before analysis.

DBH (-0.29 ± 0.09, $p = 0.002$) but was higher in spruce- than beech-dominated stands (0.67 ± 0.31, $p = 0.035$). The mixture index had a positive effect on carbon sequestration, but only in pine stands (0.64 ± 0.29, $p = 0.029$). 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 input contributes to soil carbon storage, since we could not identify a significant relation between deadwood input and soil carbon storage.

3.3. *Forest structure and management for a high Multidiversity index*

The taxonomic richness of individual taxa showed contrasting responses to forest structure and management variables, but increased with mean DBH and decreased in pine-dominated stands compared to beech-dominated stands for many taxa (Fig. 3). Individual responses of the taxonomic richness of all considered groups can be found in Fig. 3, and Table S5. Mean DBH positively affected red-listed birds in pine more so than in beech stands (0.93 ± 0.31, p = 0.003). It also positively affected the richness of cercozoan and endomyxan protists (0.18 ± 0.08, p = 0.022) as well as oomycotan protists (0.18 ± 0.09, p = 0.044). The forest mixture index positively affected the richness of soil fungi (0.42 ± 0.11, p < 0.001). Deadwood input positively affected bacteria richness (0.15 ± 0.07, p = 0.04) and molluscs richness (0.16 ± 0.08, p = 0.044).

There were also important but contrasting effects of the dominant tree genus on different taxonomic groups. Spruce stands had lower bacteria (-1.19 ± 0.24, p < 0.001), nematode (-0.60 ± 0.26, p = 0.024) and mollusc (-0.81 ± 0.5, p = 0.002) richness, but higher plant (1.70 ± 0.31, p < 0.001) and forest plant specialist richness (1.26 ± 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 (-0.87 ± 0.22, p < 0.001), endomyxan and cercozoan protists (-1.14 ± 0.25, p < 0.001), nematodes (-0.65 ± 0.24, p = 0.008) and molluscs (-0.90 ± 0.28, p = 0.001). We did not find significant differences in taxonomic richness between oak and beech stands.

Overall, the *Multidiversity index* varied between 0.34 and 0.81. It was highest when mean DBH was high (0.20 ± 0.09 p = 0.039), and lowest in pine-dominated stands (-0.61 ± 0.25, p = 0.002). The positive effect of DBH was higher in pine and spruce than beech-dominated stands (p < 0.05). These results mostly confirm our hypothesis 3, although contrary to our expectations deadwood input did not significantly affect *Multidiversity*.

3.4. *Forest structure and management for biodiversity conservation and climate mitigation*

Our analysis revealed trade-offs between carbon storage (maximised at high mean DBH) and sequestration (maximised at low mean DBH), and between some biodiversity groups. For instance, plant richness was the highest in spruce stands, where the diversity of many other groups was low. When aggregated into the *Carbon* and *Multidiversity indices*, responses were relatively consistent, and the *Combined index* (ranging from 0.39 to 0.74) followed similar trends to its components (see Table S6): it increased with mean DBH (0.26 ± 0.09, p = 0.003), and even more so in spruce than beech stands (0.99 ± 0.39, p = 0.01). The *Combined index* was lower in pine- than beech-dominated stands (-0.58 ± 0.24, p = 0.017, Fig. 4; Table S6). It increased with the mixture index in spruce stands only (1.17 ± 0.35, p < 0.001). This partially confirms our hypothesis 4 that the *Combined index* is maximised by a higher mean DBH and is lower in pine-dominated stands, if not those of spruce.

4. Discussion

Our results show that carbon storage and multidiversity are typically simultaneously higher in beech- rather than pine- dominated stands and in stands with larger trees. However, beyond this simple conclusion more nuanced relations between individual forest, carbon and biodiversity variables were observed. In the discussion, we assess the relation of several forest structure and management variables to carbon and biodiversity, and discuss how these can be influenced by management.

4.1. *Forest structure and composition promoting carbon storage and biodiversity*

In this study, we relate stand properties to biodiversity and carbon. While it is clear how some of these properties relate to management, e.g. stand composition, which can be planted or modified via selective logging, other features, e.g. tree size, have a more complex relationship with management. Many stand structural properties vary naturally, and across stand development stages, as well as with management factors such as thinning and extraction rates. Further, management is often applied at scales larger than that studied here, e.g. via the fraction of forest stands in different developmental stages. We therefore suggest that managers think carefully about how their actions may affect the stand properties of interest when assessing the results discussed below.

The dominant tree genus was an important driver that significantly influenced most of the variables included in the *Multidiversity* and *Carbon* indices. Differences were the strongest between pine- and beech-dominated stands, with pine-dominated stands having lower values of four of the taxonomic richness measures, and lower tree carbon storage. Spruce dominance was negatively related to three out of nine taxonomic richness measures and positively related to three, in particular plant

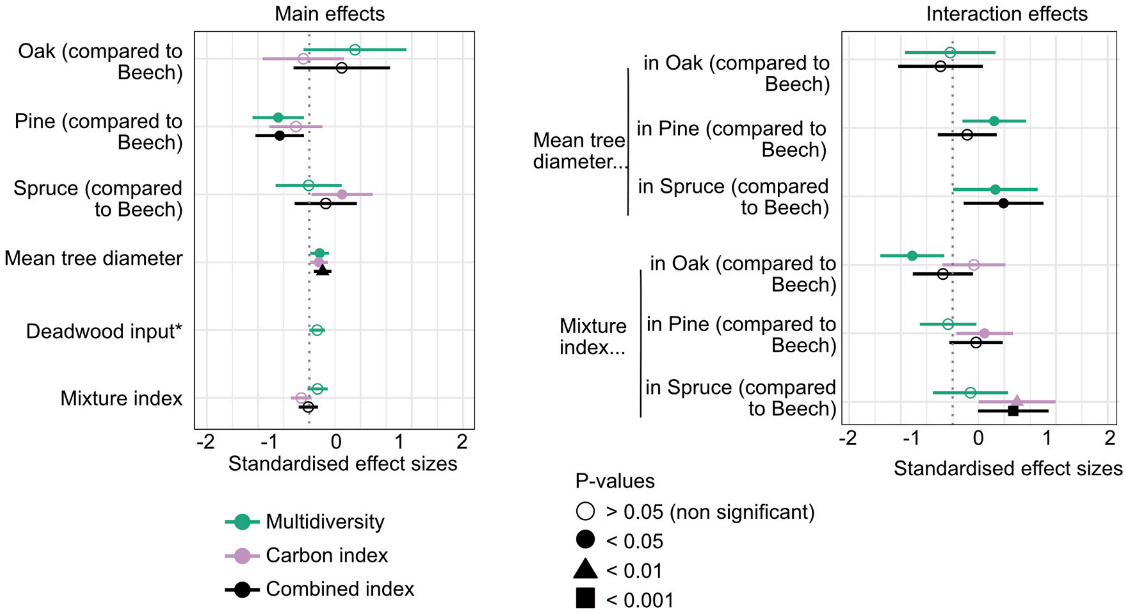


Fig. 4. **:** Effect of forest structure and management variables on the *Multidiversity, Carbon and Combined indices*. Plots show standardised effect sizes along with 95 % confidence intervals estimated for the selected structure and management variables affecting taxonomic richness of individual groups. Left: main effects. Right: interaction effects. The results are shown with beech as the reference genus. *Deadwood input was transformed (log(x+1)) before analysis.

taxonomic richness and forest plant specialist richness. Higher plant taxonomic richness in spruce stands is consistent with previous studies showing that the plant taxonomic richness of German forests can be relatively high in coniferous stands (Boch et al., 2013; Budde et al., 2011) and may be due to a higher openness in the spruce canopies of our study compared to those of the beech stands (Boch et al., 2013), thus 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 did not significantly differ from beech stands in terms of taxonomic diversity, thus differing from previous studies in Germany that found oak forests to be the most favourable to biodiversity (Carvalho-Santos et al., 2016; Müller et al., 2021). Indeed, oaks have likely been in the study regions for centuries, and thus likely have a higher co-evolved and co-accumulated diversity (Brändle and Brandl, 2001) than e.g. pine which has been cultivated beyond its natural range, and more recently, since about 1850. Oaks can 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). The lack of any detectable oak effect in our study was probably due to a relatively low sample size for oak stands (nine plots) and the inclusion of other variables (DBH, deadwood input) which might underlie responses observed in previous studies. Besides, the mixture index tended to have positive impacts (especially on the *Carbon index*) only in pine- and spruce-dominated stands, suggesting that increased proportions of other genera, such as broadleaved trees, has a favourable impact on carbon storage in coniferous stands.

Of the forest structure and management variables we assessed, mean DBH was strongly related to tree carbon storage, carbon sequestration rates and the biodiversity of multiple groups. Carbon sequestration was lower in forests with high mean DBH, likely due to slower growth rates in larger trees (Meyer et al., 2021). This represents a classic trade-off in forest carbon management as stands with higher mean DBH have a higher tree carbon storage, although stand and wood density also play a role. Soil carbon storage did not respond to most management variables. In the case of deadwood input this might be consistent with previous studies which show that deadwood promotes the relatively small fraction of soil dissolved organic carbon (Shannon et al., 2022) but has little effect on overall soil organic carbon stocks (Kahl et al., 2012). This lack of response might have been due to the predominance of other factors not included in the analysis, such the stand history. We suggest that the positive effect of DBH on the richness of many taxonomic groups may be due to three related factors. First, there is likely to be a higher abundance and diversity of microhabitats in larger trees (Martin et al., 2022; Michel and Winter, 2009; Vuidot et al., 2011; 2022), including a higher provision of suitable structures for bird and arthropod cavity dwelling species (Remm et al., 2006). Second, there is an overall higher resource availability where trees are larger and tree biomass is high, that may cascade across the food web allowing larger and healthier populations to thrive. Finally, forests with larger trees are also likely to be older, and so provide a continuous and stable habitat for the accumulation of many populations of many tree-dwelling species. 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 either high resource inputs over time, and/or the presence of a stable and long-lived habitat in which microbial diversity may accumulate. Other research from grasslands in the same three regions indicates that the nearby presence of permanent forest areas increases diversity of some soil protist groups, supporting these ideas (Le Provost et al., 2021). The benefits of habitat heterogeneity for biodiversity are also likely to drive the positive relationship between forest mixture and some of the biodiversity variables such as the richness of soil fungi (Leidinger et al., 2021, Heidrich et al., 2020).

Deadwood is an important structural element in forests as 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 saproxylic species (Oettel et al., 2020; Scott and Brown, 2008). It has been estimated that 20 - 25 % of all forest-dwelling species are dependent on deadwood (Siitonen, 2001). Although our analysis did not include saproxylic species, which are expected to respond most strongly to deadwood (Sandström et al., 2019), and we found no significant effect on *multidiversity*, we found a limited but positive effect of deadwood input on the richness of bacteria and molluscs, confirming its importance for multiple groups.

4.2. *Implications for German forest management*

German forests are the product of a long history of forest management (DFWR, 2022). 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 was 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 broad-leaved tree cover has increased steadily (+7 % between 2002 and 2012, BMEL, 2018). Our results show that these changes are likely to provide moderate gains to both biodiversity and carbon storage through both 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), meaning that larger trees could become more prevalent. Overall, our results confirm the idea that young stands with small trees will allow for new carbon storage to be sequestered, but that a considerable number of old stands with larger trees should be kept as long as possible, to promote both carbon storage and diversity of taxa that require late forest developmental stages.

4.3. *Future directions*

Our results provide evidence 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, on other aspects of carbon cycling, and on other ecosystem services. More specifically, young stands may become more prevalent in the future due to increasing rates of disturbance due to bark beetles, wind and drought (Seidl et al., 2014; Senf and Seidl, 2021). The above-described trade-off between carbon storage and sequestration means that these stands of small trees will accumulate carbon rapidly but will take time to store significant amounts of carbon. Our results add to this by showing that stands of small trees, which are likely to be young, may also take time to reach the high biodiversity values of forests with larger trees, which are likely to be old - although they may support their own distinct biota. This highlights the importance of 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 tree and topsoil carbon storage. For a more complete picture, it is also important to account for carbon in deeper soil layers. Indeed, carbon storage in deeper soil layers can be driven by other, longer-term, factors such as soil development stage and past land uses. Thus, the impact of dominant tree genera might differ, and be weaker, when considering total rather than topsoil carbon storage (Hüblová and Frouz, 2021). Assessing overall forest carbon storage would also require accounting for carbon stored in deadwood, which represents a significant carbon pool globally (FAO and UNEP, 2020), though in these managed forests, where deadwood inputs are low and removal is common, it may be of lesser importance. Considering the fate of harvested wood carbon (e.g. whether firewood or timber) could also affect the conclusions, as if these fractions are large then the main drivers may differ from those identified here. The inclusion of other greenhouse gases would also provide a more complete assessment of climate impacts. Similarly, while our biodiversity data is comprehensive, the inclusion of other taxa, e.g. saproxylic beetles or other arthropods associated with deadwood, could alter our conclusions, as such groups might respond differently to stand structural properties and composition. Finally, we only assessed the impact of forest structure and 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 they also have cultural and recreational value (Führer, 2000; Neyret et al., 2023). Different ecosystem services might be favoured by different forest types to those that favour carbon and biodiversity (Felipe-Lucia et al., 2018), and their consideration could alter local management recommendations. While our results suggest a single set of forest stand properties for promoting a wide range of local-scale biodiversity and carbon features, we also showed that individual taxa require diverse conditions (Savilaakso et al., 2021; Schall et al., 2018, 2020) which are not always aligned with maximising carbon storage. This is consistent with previous results by Sabatini et al. (2019), who highlighted that stand-level management prioritising either biodiversity or carbon storage could be balanced by maintaining forest diversity and heterogeneity at the landscape level, thus promoting different objectives at different locations. This may also 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).

5. Conclusion

Simultaneously promoting biodiversity protection and climate change mitigation is a key challenge of local-scale forest management. Here, we identified several forest structure and management variables that may support these goals in German forests: large average tree diameter and avoiding dominance of certain species, particularly pine. Of course, these guidelines should be adapted to local contexts by choosing species adapted to local soil types or climatic conditions. The importance of large trees highlights the need to pay special attention to old forests, where such trees are more likely to be found, due to their importance for biodiversity and carbon storage. Further research should build on our results to assess the resilience of old forests 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.

Authors contributions

KS, PM, MN designed the study. KS and MN performed the analyses with contributions from PM, GLP and ALB. CA, AMFD, MF, KG, GLP, JO, LR, IS, SS, JS provided data. KS, PM and MN wrote the manuscript with significant input from all authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Exploratories managers: Konstans Wells, Swen Renner, Kirsten Reichel-Jung, Sonja Gockel, Kerstin Wiesner, Katrin Lorenzen, Andreas Hemp, Martin Gorke and all former managers for maintaining the plot and project infrastructure; the Biodiversity Exploratories Office for central office support, Jens Nieschulze and Michael Owonibi for database management, and Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for establishing the Biodiversity Exploratories project. We also thank all data contributors.

The work has been funded by the DFG 1374. Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122328.

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 Table S1 and corresponding references.

References

Abele, S.E., Macdonald, S.E., Spence, J.R., 2014. Cover type, environmental characteristics, and conservation of terrestrial gastropod diversity in boreal mixedwood forests. Canadian Journal of Forest Research *44* (1), 36–44. https://doi.org/10.1139/cjfr-2013-0210.

Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T., Blüthgen, N., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ, S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., Fischer, M., 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Sciences *111* (1), 308–313. https://doi.org/10.1073/pnas.1312213111.

Ammer, C., 2019. Beech regeneration under spruce canopy growth and carbon storage performance of regeneration stands in long-term regeneration cycles. Allgemeine Forst- und Jagdzeitung *190* (3–14), 73–89. https://doi.org/10.23765/afjz0002039.

Ammer, C., Bickel, E., Kölling, C., 2008. Converting Norway spruce stands with beech—A review of arguments and techniques. Austrian Journal of Forest Science *125*, 3–26.

Asbeck, T., Großmann, J., Paillet, Y., Winiger, N., Bauhus, J., 2021b. The Use of Tree-Related Microhabitats as Forest Biodiversity Indicators and to Guide Integrated Forest Management. Current Forestry Reports *7*. https://doi.org/10.1007/s40725-020-00132-5.

Asbeck, T., Sabatini, F., Augustynczik, A.L.D., Basile, M., Helbach, J., Jonker, M., Knuff, A., Bauhus, J., 2021a. Biodiversity response to forest management intensity, carbon stocks and net primary production in temperate montane forests. Article 1. Scientific Reports *11* (1). https://doi.org/10.1038/s41598-020-80499-4.

BMEL. (2018). *Bundeswaldinventur: The Forest in Germany: Selected Results of the Third National Forest Inventory* (3; p. 56). Bundesministerium für Ernährung und Landwirtschaft. ⟨https://www.bundeswaldinventur.de/dritte-bundeswaldinventur-2012/waldland-deutschland-waldflaeche-konstant/⟩ [last access: 23rd June 2024].

Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.-D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic and Applied Ecology *14* (6), 496–505. https://doi.org/10.1016/j.baae.2013.06.001.

Bohn, U., Zazanashvili, N., & Nakhutsrishvili, G. (2007). The Map of the Natural Vegetation of Europe and its application in the Caucasus Ecoregion. 175, 11..

Bonan, G.B., 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science *320* (5882), 1444–1449. https://doi.org/10.1126/science.1155121.

Brändle, M., Brandl, R., 2001. Species richness of insects and mites on trees: Expanding Southwood. Journal of Animal Ecology *70* (3), 491–504. https://doi.org/10.1046/j.1365-2656.2001.00506.x.

Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation *17*, 925–951. https://doi.org/10.1007/s10531-008-9380-x.

Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. Ecological bulletins 19.

Budde, S., Schmidt, W., Weckesser, M., 2011. Impact of the admixture of European beech (Fagus sylvatica L.) on plant species diver-sity and naturalness of conifer stands in Lower Saxony. *Waldökologie*. Landschaftsforschung und Naturschutz 11, 49–61.

Carvalho-Santos, C., Sousa-Silva, R., Gonçalves, J., Honrado, J.P., 2016. Ecosystem services and biodiversity conservation under forestation scenarios: Options to improve management in the Vez watershed, NW Portugal. Regional Environmental Change *16* (6), 1557–1570. https://doi.org/10.1007/s10113-015-0892-0.

Corlett, R.T., 2020. Safeguarding our future by protecting biodiversity. Plant Diversity *42* (4), 221–228. https://doi.org/10.1016/j.pld.2020.04.002.

Courbaud, B., Larrieu, L., Kozak, D., Kraus, D., Lachat, T., Ladet, S., Müller, J., Paillet, Y., Sagheb-Talebi, K., Schuck, A., Stillhard, J., Svoboda, M., Zudin, S., 2022. Factors influencing the rate of formation of tree-related microhabitats and implications for biodiversity conservation and forest management. Journal of Applied Ecology 59, 492–503. https://doi.org/10.1111/1365-2664.14068.

de Lima, R.A.F., Oliveira, A.A., Pitta, G.R., de Gasper, A.L., Vibrans, A.C., Chave, J., ter Steege, H., Prado, P.I., 2020. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. Nature Communications *11* (1), 6347. https://doi.org/10.1038/s41467-020-20217-w.

de Vries, W., Reinds, G.J., Posch, M., Sanz-Sanchez, M.-J., Krause, G.H.M., Calatayud, V., Renaud, J.-P., Dupouey, J.-L., Sterba, H., Vel, E.M., Dobbertin, M., Gundersen, P., & Voogd, J.C.H. (2003). *Intensive Monitoring of Forest Ecosystems in Europe: Technical Report 2003*.EC, UN/ECE Brussels, Geneva, 163 pp.

DFWR. (2022). *Forest facts—German forestry—300 yrs of sustainability campaign*. Forest Facts - German Forestry - 300 Yrs of Sustainability Campaign. ⟨https://www.forstwirtschaft-in-deutschland.de/german-forestry/forest-facts/?L=1⟩ [last access: 27th September 2024].

Dieler, J., Uhl, E., Biber, P., Müller, J., Rötzer, T., Pretzsch, H., 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. European Journal of Forest Research *136* (4), 739–766. https://doi.org/10.1007/s10342-017-1056-1.

Dittrich, S., Jacob, M., Bade, C., Leuschner, C., Hauck, M., 2014. The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. Plant Ecology *215* (10), 1123–1137. https://doi.org/10.1007/s11258-014-0371-6.

Dörfler, I., Cadotte, M.W., Weisser, W.W., Müller, J., Gossner, M.M., Heibl, C., Bässler, C., Thorn, S., Seibold, S., 2020. Restoration-oriented forest management affects community assembly patterns of deadwood-dependent organisms. Journal of Applied Ecology *57* (12), 2429–2440. https://doi.org/10.1111/1365-2664.13741.

Dormann, C.F., Bagnara, M., Boch, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., Hartig, F., 2020. Plant species richness increases with light availability, but not variability, in temperate forests understorey. BMC Ecology *20* (1), 43. https://doi.org/10.1186/s12898-020-00311-9.

Edelmann, P., Ambarlı, D., Gossner, M.M., Schall, P., Ammer, C., Wende, B., Schulze, E.-D., Weisser, W.W., Seibold, S., 2022. Forest management affects saproxylic beetles through tree species composition and canopy cover. Forest Ecology and Management *524*, 120532. https://doi.org/10.1016/j.foreco.2022.120532.

Edwards, D.P., Gilroy, J.J., Woodcock, P., Edwards, F.A., Larsen, T.H., Andrews, D.J.R., Derhé, M.A., Docherty, T.D.S., Hsu, W.W., Mitchell, S.L., Ota, T., Williams, L.J., Laurance, W.F., Hamer, K.C., Wilcove, D.S., 2014. Land-sharing versus land-sparing logging: Reconciling timber extraction with biodiversity conservation. Global Change Biology 20 (1), 183–191. https://doi.org/10.1111/gcb.12353.

European Environment Agency. (2016). *European forest ecosystems: State and trends*. Publications Office. ⟨https://data.europa.eu/doi/10.2800/964893⟩.

FAO and UNEP. (2020). *The State of the World's Forests 2020. In brief: Forests, biodiversity and people*. FAO and UNEP. https://doi.org/10.4060/ca8985en.

Felipe-Lucia, M.R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M.M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., Allan, E., 2018. Multiple forest attributes underpin the supply of multiple ecosystem services. Nature Communications *9* (1), 4839. https://doi.org/10.1038/s41467-018-07082-4.

Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management *260* (6), 939–947. https://doi.org/10.1016/j.foreco.2010.06.011.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., Weisser, W.W., 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology *11* (6), 473–485. https://doi.org/10.1016/j.baae.2010.07.009.

Führer, E., 2000. Forest functions, ecosystem stability and management. Forest Ecology and Management 10.

Gregory, R.D., Vorisek, P., Van Strien, A., Gmelig Meyling, A.W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P., Burfield, I.J., 2007. Population trends of widespread woodland birds in Europe: population trends among widespread woodland birds. Ibis *149*, 78–97. https://doi.org/10.1111/j.1474-919X.2007.00698.x3.

Grüneberg, C., Bauer, H.-G., Haupt, H., Hüppop, O., Ryslavy, T., Südbeck, P., 2016. Red List of Breeding Birds of Germany. (52; Berichte zum Vogelschutz 19–67.

Heidrich, L., Bae, S., Levick, S., Seibold, S., Weisser, W., Krzystek, P., Magdon, P., Nauss, T., Schall, P., Serebryanyk, A., Wöllauer, S., Ammer, C., Bässler, C., Doerfler, I., Fischer, M., Gossner, M.M., Heurich, M., Hothorn, T., Jung, K., Kreft, H., Schulze, E.-D., Simons, N., Thorn, S., Müller, J., 2020. Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. Nat Ecol Evol 4, 1204–1212. https://doi.org/10.1038/s41559-020-1245-z.

Heinrichs, S., Ammer, C., Mund, M., Boch, S., Budde, S., Fischer, M., Müller, J., Schöning, I., Schulze, E.-D., Schmidt, W., Weckesser, M., Schall, P., 2019. Landscape-scale mixtures of tree species are more effective than stand-scale mixtures for biodiversity of vascular plants, bryophytes and lichens. Forests *10* (1), 73. https://doi.org/10.3390/f10010073.

Himes, A., Betts, M., Messier, C., Seymour, R., 2022. Perspectives: Thirty years of triad forestry, a critical clarification of theory and recommendations for implementation and testing. Forest Ecology and Management 510, 120103. https://doi.org/10.1016/j.foreco.2022.120103.

Hüblová, L., Frouz, J., 2021. Contrasting effect of coniferous and broadleaf trees on soil carbon storage during reforestation of forest soils and afforestation of agricultural and post-mining soils. Journal of Environmental Management 290, 112567. https://doi.org/10.1016/j.jenvman.2021.112567.

Huston, M.A., Marland, G., 2003. Carbon management and biodiversity. Journal of Environmental Management *67* (1), 77–86. https://doi.org/10.1016/S0301-4797(02)00190-1.

IPBES. (2019). *The global assessment report on Biodiversity and Ecosystem services: Summary for policy-makers*. 60.

Kahl, T., Mund, M., Bauhus, J., Schulze, E.-D., 2012. Dissolved Organic Carbon from European Beech Logs: Patterns of Input to and Retention by Surface Soil. Ecoscience 19 (4), 364–373. https://doi.org/10.2980/19-4-3501.

Knoke, T., Ammer, C., Stimm, B., Mosandl, R., 2008. Admixing broadleaved to coniferous tree species: a review on yield, ecological stability and economics. European Journal of Forest Research *127* (2), 89–101. https://doi.org/10.1007/s10342-007-0186-2.

Le Provost, G., Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M., van der Plas, F., Ayasse, M., Bardgett, R.D., Birkhofer, K., Boch, S., Bonkowski, M., Buscot, F., Feldhaar, H., Gaulton, R., Goldmann, K., Gossner, M.M., Klaus, V.H., Kleinebecker, T., Manning, P., 2021. Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. Nature Communications *12* (1), 3918. https://doi.org/10.1038/s41467-021-23931-1.

Leidinger, J., Weisser, W.W., Kienlein, S., Blaschke, M., Jung, K., Kozak, J., Fischer, A., Mosandl, R., Michler, B., Ehrhardt, M., Zech, A., Saler, D., Graner, M., & Seibold, S. (2020). Formerly managed forest reserves complement integrative management for biodiversity conservation in temperate European forests. *Biological Conservation*, 242, 108437. https://doi.org/10.1016/j.biocon.2020.108437.

Leidinger, J., Blaschke, M., Ehrhardt, M., Fischer, A., Gossner, M.M., Jung, K., Kienlein, S., Kózak, J., Michler, B., Mosandl, R., Seibold, S., Wehner, K., Weisser, W. W., 2021. Shifting tree species composition affects biodiversity of multiple taxa in Central European forests. Forest Ecology and Management *498*, 119552. https://doi.org/10.1016/j.foreco.2021.119552.

Leuschner, C., & Homeier, J. (2022). Global Forest Biodiversity: Current State, Trends, and Threats. In U. Lüttge, F. M. Cánovas, M.-C. Risueño, C. Leuschner, & H. Pretzsch (Eds.), *Progress in Botany* (Vol. 83, pp. 125–159). Springer. https://doi.org/10.1007/124_2022_58.

Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proceedings of the National Academy of Sciences *115* (44). https://doi.org/10.1073/pnas.1722477115.

Löfroth, T., Birkemoe, T., Shorohova, E., Dynesius, M., Fenton, N.J., Drapeau, P., Tremblay, J.A., 2023. Deadwood Biodiversity. In: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), Boreal Forests in the Face of Climate Change, Vol. 74. Springer International Publishing, pp. 167–189. https://doi.org/10.1007/978-3-031-15988-6_6.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham, M.J., Fischer, M., 2018. Redefining ecosystem multifunctionality. Nature Ecology & Evolution *2* (3), 427–436. https://doi.org/10.1038/s41559-017-0461-7.

Martin, M., Paillet, Y., Larrieu, L., Kern, C.C., Raymond, P., Drapeau, P., Fenton, N.J., 2022. Tree-related microhabitats are promising yet underused tools for biodiversity and nature conservation: a systematic review for international perspectives. Frontiers in Forests and Global Change *5*, 818474. https://doi.org/10.3389/ffgc.2022.818474.

Mayer, M., Prescott, C.E., Abaker, W.E.A., Augusto, L., Cécillon, L., Ferreira, G.W.D., James, J., Jandl, R., Katzensteiner, K., Laclau, J.-P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J.A., Vanguelova, E.I., Vesterdal, L., 2020. Tamm review: influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. Forest Ecology and Management *466*, 118127. https://doi.org/10.1016/j.foreco.2020.118127.

Meyer, P., Nagel, R., Feldmann, E., 2021. Limited sink but large storage: Biomass dynamics in naturally developing beech (*Fagus sylvatica*) and oak (*Quercus robur*, *Quercus petraea*) forests of north-western Germany. Journal of Ecology *109* (10), 3602–3616. https://doi.org/10.1111/1365-2745.13740.

Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. Forest Ecology and Management *257* (6), 1453–1464. https://doi.org/10.1016/j.foreco.2008.11.027.

Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Synthesis; a report of the Millennium Ecosystem Assessment*. Island Press.

Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., Ejrnæs, R., Odgaard, M.V., Svenning, J.-C., 2013. Topographically controlled soil moisture drives plant diversity patterns within grasslands. Biodiversity and Conservation *22* (10), 2151–2166. https://doi.org/10.1007/s10531-013-0442-3.

Müller, J., Scherer-Lorenzen, M., Ammer, C., Eisenhauer, N., Seidel, D., Schuldt, B., Biedermann, P., Schmitt, T., Künzer, C., Wegmann, M., Cesarz, S., Peters, M., Feldhaar, H., Steffan-Dewenter, I., Claßen, A., Bässler, C., von Oheimb, G., Fichtner, A., Thorn, S., & Weisser, W. (2021). *Enhancing the structural diversity between patches for improving multidiversity and multifunctionality in production forests.*. Universität Würzburg. https://doi.org/10.25972/OPUS-29084.

Müller, J., Hothorn, T., Yuan, Y., Seibold, S., Mitesser, O., Rothacher, J., Freund, J., Wild, C., Wolz, M., Menzel, A., 2023. Weather explains the decline and rise of insect biomass over 34 years. Nature. https://doi.org/10.1038/s41586-023-06402-z.

Neyret, M., Peter, S., Le Provost, G., Boch, S., Boesing, A.L., Bullock, J.M., Hölzel, N., Klaus, V.H., Kleinebecker, T., Krauss, J., Müller, J., Müller, S., Ammer, C., Buscot, F., Ehbrecht, M., Fischer, M., Goldmann, K., Jung, K., Mehring, M., Manning, P., 2023. Landscape management strategies for multifunctionality and social equity. Nature Sustainability *6* (4), 391–403. https://doi.org/10.1038/s41893-022-01045-w.

Oettel, J., Lapin, K., Kindermann, G., Steiner, H., Schweinzer, K.-M., Frank, G., Essl, F., 2020. Patterns and drivers of deadwood volume and composition in different forest types of the Austrian natural forest reserves. Forest Ecology and Management *463*, 118016. https://doi.org/10.1016/j.foreco.2020.118016.

Paillet, Y., Debaive, N., Archaux, F., Cateau, E., Gilg, O., Guilbert, E., 2019. Nothing else matters? Tree diameter and living status have more effects than biogeoclimatic context on microhabitat number and occurrence: an analysis in French forest reserves. PLOS ONE *14* (5), e0216500. https://doi.org/10.1371/journal.pone.0216500.

Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M.R., Gossner, M.M., Seibold, S., Simons, N.K., Schall, P., Plas, F., Manning, P., Manzanedo, R.D., Boch, S., Prati, D., Ammer, C., Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., Fischer, M., 2019. Specialisation and diversity of multiple trophic groups are promoted by different forest features. Ecology Letters *22* (1), 170–180. https://doi.org/10.1111/ele.13182.

Pettorelli, N., Graham, N.A.J., Seddon, N., Maria da Cunha Bustamante, M., Lowton, M. J., Sutherland, W.J., Koldewey, H.J., Prentice, H.C., Barlow, J., 2021. Time to integrate global climate change and biodiversity science-policy agendas. Journal of Applied Ecology *58* (11), 2384–2393. https://doi.org/10.1111/1365-2664.13985.

R Core Team. (2023). *R: A Language and Environment for Statistical Computing* [Computer software]. R Foundation for Statistical Computing.

Remm, J., Lõhmus, A., Remm, K., 2006. Tree cavities in riverine forests: What determines their occurrence and use by hole-nesting passerines? Forest Ecology and Management *221* (1–3), 267–277. https://doi.org/10.1016/j.foreco.2005.10.015.

Russ, J.M., Montgomery, W.I., 2002. Habitat associations of bats in Northern Ireland: Implications for conservation. Biological Conservation *108* (1), 49–58. https://doi.org/10.1016/S0006-3207(02)00089-7.

Sabatini, F.M., de Andrade, R.B., Paillet, Y., Ódor, P., Bouget, C., Campagnaro, T., Gosselin, F., Janssen, P., Mattioli, W., Nascimbene, J., Sitzia, T., Kuemmerle, T., Burrascano, S., 2019. Trade-offs between carbon stocks and biodiversity in European temperate forests. Global Change Biology *25* (2), 536–548. https://doi.org/10.1111/gcb.14503.

Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J., Jonsson, B.G., 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. Journal of Applied Ecology *56* (7), 1770–1781. https://doi.org/10.1111/1365-2664.13395.

Savilaakso, S., Johansson, A., Häkkilä, M., Uusitalo, A., Sandgren, T., Mönkkönen, M., Puttonen, P., 2021. What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. Environmental Evidence *10* (1), 1. https://doi.org/10.1186/s13750-020-00215-7.

Schall, P., Ammer, C., 2013. How to quantify forest management intensity in Central European forests. European Journal of Forest Research *132* (2), 379–396. https://doi.org/10.1007/s10342-013-0681-6.

Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology *55* (1), 267–278. https://doi.org/10.1111/1365-2664.12950.

Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., Fischer, M., Goldmann, K., Overmann, J., Schulze, E., Sikorski, J., Weisser, W.W., Wubet, T., Gossner, M.M., 2020. Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems? Journal of Applied Ecology *57* (7), 1363–1375. https://doi.org/10.1111/1365-2664.13635.

Schmidt, M., Kriebitzsch, W.-U., & Ewald, J.. (Eds.). (2011). *Forest species lists of ferns, flowering plants, mosses and lichens of Germany*. Bundesamt für Naturschutz (BfN).

Schulze, E.D., 2018. Effects of forest management on biodiversity in temperate deciduous forests: An overview based on Central European beech forests. Journal for Nature Conservation *43*, 213–226. https://doi.org/10.1016/j.jnc.2017.08.001.

Scott, N.A., Brown, S., 2008. Measuring the Decomposition of Down Dead-Wood. In: Hoover, In.C.M. (Ed.), Field Measurements for Forest Carbon Monitoring. Springer Netherlands, pp. 113–126. https://doi.org/10.1007/978-1-4020-8506-2_9.

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S., Müller, J., 2017. An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology *98* (6), 1613–1622.

Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nature Climate Change *4* (9), 806–810. https://doi.org/10.1038/nclimate2318.

Senf, C., Seidl, R., 2021. Persistent impacts of the 2018 drought on forest disturbance regimes in Europe. Biogeosciences *18* (18), 5223–5230. https://doi.org/10.5194/bg-18-5223-2021.

Shannon, V.L., Vanguelova, E.I., Morison, J.I.L., Shaw, L.J., Clark, J.M., 2022. The contribution of deadwood to soil carbon dynamics in contrasting temperate forest ecosystems. European Journal of Forest Research 141 (2), 241–252. https://doi.org/10.1007/s10342-021-01435-3.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecological Bulletins *49*, 11–41.

Simons, N.K., Felipe-Lucia, M.R., Schall, P., Ammer, C., Bauhus, J., Blüthgen, N., Boch, S., Buscot, F., Fischer, M., Goldmann, K., Gossner, M.M., Hänsel, F., Jung, K., Manning, P., Nauss, T., Oelmann, Y., Pena, R., Polle, A., Renner, S.C., Weisser, W.W., 2021. National Forest Inventories capture the multifunctionality of managed forests in Germany. Forest Ecosystems *8* (1), 5. https://doi.org/10.1186/s40663-021-00280-5.

Soto-Navarro, C., Ravilious, C., Arnell, A., de Lamo, X., Harfoot, M., Hill, S.L.L., Wearn, O.R., Santoro, M., Bouvet, A., Mermoz, S., Le Toan, T., Xia, J., Liu, S., Yuan, W., Spawn, S.A., Gibbs, H.K., Ferrier, S., Harwood, T., Alkemade, R., Kapos, V., 2020. Mapping co-benefits for carbon storage and biodiversity to inform conservation policy and action. Philosophical Transactions of the Royal Society B: Biological Sciences *375* (1794). https://doi.org/10.1098/rstb.2019.0128.

Spathelf, P., Ammer, C., 2015. Forest management of Scots pine (Pinus sylvestris L.) in northern Germany – a brief review of the history and current trends. Forstarchiv *86*, 59–66. https://doi.org/10.4432/03004112-86-59.

Pörtner H.-O., Scholes, R.J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W.L. (William), Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M.A., Handa, C., Hickler, T., Hoegh-Guldberg, O., … Ngo, H. (2021). Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change. https://doi.org/10.5281/zenodo.5101125.

Stokland, J.N., Siitonen, J., & Jonsson, B.G. (2012). *Biodiversity in Dead Wood*. Cambridge University Press.

Turney, C., Ausseil, A.-G., Broadhurst, L., 2020. Urgent need for an integrated policy framework for biodiversity loss and climate change, 996–996 Nature Ecology & Evolution *4* (8). https://doi.org/10.1038/s41559-020-1242-2.

van der Plas, F., Manning, P., Soliveres, S., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Fischer, M., 2016. Biotic homogenization can decrease landscape-scale forest multifunctionality. Proceedings of the National Academy of Sciences *113* (13), 3557–3562. https://doi.org/10.1073/pnas.1517903113.

von Lüpke, B., Ammer, C., Bruciamacchie, M., Brunner, A., Ceitel, J., Collet, C., Deuleuze, C., Di Placido, J., Huss, J., Janković, J., Kantor, P., Larsen, J.B., Lexer, M., Löf, M., Longauer, R., Madsen, P., Modrzyński, J., Mosandl, R., Pampe, A., Zientarski, J., 2004. Silvicultural Strategies for Conversion. In: Spiecker, H., Hansen, J., Klimo, E., Skovsgaard, J.P., Sterba, H., von Teuffel, K. (Eds.), Norway Spruce Conversion. BRILL, pp. 121–164. https://doi.org/10.1163/9789047412908_009.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation *144* (1), 441–450. https://doi.org/10.1016/j.biocon.2010.09.030.

Wagner, S., Fischer, H., Huth, F., 2011. Canopy effects on vegetation caused by harvesting and regeneration treatments. European Journal of Forest Research *130* (1), 17–40. https://doi.org/10.1007/s10342-010-0378-z.

United Nations. (2021). Tackling Biodiversity & Climate Crises Together and Their Combined Social Impacts. *United Nations Sustainable Development*. ⟨https://www.un.org/sustainabledevelopment/blog/2021/06/tackling-biodiversity-climate-crises-together-and-their-combined-social-impacts/⟩ [last access: 27th September 2024].

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management *255* (3–4), 1251–1261. https://doi.org/10.1016/j.foreco.2007.10.029.