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Linking structure and species richness to support forest biodiversity monitoring at large scales

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Abstract

Key message Authors have analyzed the possible correlation between measurements/indicators of forest structure and species richness of many taxonomic or functional groups over three regions of Germany. Results show the potential to use structural attributes as a surrogate for species richness of most of the analyzed taxonomic and functional groups. This information can be transferred to large-scale forest inventories to support biodiversity monitoring.

Context We are currently facing a dramatic loss in biodiversity worldwide and this initiated many monitoring programs aiming at documenting further trends. However, monitoring species diversity directly is very resource demanding, in particular in highly diverse forest ecosystems.

Aims We investigated whether variables applied in an index of stand structural diversity, which was developed based on forest attributes assessed in the German National Forest Inventory, can be calibrated against richness of forest-dwelling species within a wide range of taxonomic and functional groups.

Methods We used information on forest structure and species richness that has been comprehensively assessed on 150 forest plots of the German biodiversity exploratories project, comprising a large range of management intensities in three regions. We tested, whether the forest structure index calculated for these forest plots well correlate with the number of species across 29 taxonomic and functional groups, assuming that the structural attributes applied in the index represent their habitat requirements.

Results The strength of correlations between the structural variables applied in the index and number of species within taxonomic or functional groups was highly variable. For some groups such as Aves, Formicidae or vascular plants, structural variables had a high explanatory power for species richness across forest types. Species richness in other taxonomic and functional groups (e.g., soil and root-associated fungi) was not explained by individual structural attributes of the index. Results indicate that some taxonomic and functional groups depend on a high structural diversity, whereas others seem to be insensitive to it or even prefer structurally poor stands.

Conclusion Therefore, combinations of forest stands with different degrees of structural diversity most likely optimize taxonomic diversity at the landscape level. Our results can support biodiversity monitoring through quantification of

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forest structure in large-scale forest inventories. Changes in structural variables over inventory periods can indicate changes in habitat quality for individual taxonomic groups and thus points towards national forest inventories being an effective tool to detect unintended effects of changes in forest management on biodiversity.

Keywords Structural diversity, Taxonomic/functional diversity, Biodiversity monitoring, National Forest Inventory

1 Introduction

Forest biodiversity is of crucial importance to maintain healthy forest ecosystems and provision of multiple ecosystem services (e.g., Felipe-Lucia et al. 2018; Ceballos et al. 2015; Cardinale et al. 2012). Biodiversity loss is one of the major environmental challenges in this century and has shown to also affect forest ecosystems (e.g. Seibold et al. 2019; Lindenmayer and Franklin 2002). Therefore, the protection of forest biodiversity becomes more and more important in political and economic decision-making processes. In many jurisdictions, public-forest authorities are requested to monitor biodiversity and to report on their management efforts to maintain or improve biodiversity, e.g., in the frameworks of the Convention on Biological Diversity (CBD 1992). Here we focus on multitrophic species diversity, an important component of biodiversity, of which monitoring is labour intensive and expensive (Gardner 2010; Lindenmayer and Franklin 2002). The high costs are caused, for example, by taxon-specific characteristics such as high diversity, large home ranges, seasonal appearances, high inter-annual fluctuations or expensive sampling efforts. In addition, there is no established or widely accepted approach to monitor biodiversity comprehensively across large spatial and temporal scales and functional groups (Burrascano et al. 2021; Noss 1990; Pielou 1975). Therefore, the use of information about structural diversity of forests as a surrogate for habitat quality for different taxonomic and functional groups (TGs) has been suggested as a useful approach (Zeller et al. 2022; Gardner 2010; Lindenmayer and Franklin 2002). While we have an extensive spatial coverage of information about forest structure through large-scale forest inventories, quantitative, and comprehensive assessments of species diversity across a wide range of TGs have been carried out at few places only, for example in the Biodiversity Exploratories project (Penone et al. 2019; Fischer et al. 2010).

In ecology, the widely accepted 'habitat heterogeneity hypothesis' (e.g. Müller et al. 2018; MacArthur and Wilson 1967; Simpson 1949) states that structurally diverse forests provide more niches and habitats and thereby harbor a higher species diversity than structurally poor stands (Jung et al. 2012; Taboada et al. 2010; Bazzaz 1975) although this hypothesis does not generally apply (Heidrich et al. 2020). In most forest ecosystems, the woody component of plant communities influences structural diversity and has a considerable impact on species diversity across functional groups (e.g., McCoy and Bell 1991). MacArthur and MacArthur (1961) showed for example that diversity of birds can be influenced more strongly by vertical heterogeneity of forest stands than by composition of tree species. These types of relationships have been well analyzed for some TGs at the local and regional level (Basile et al. 2020; Boch et al. 2013a; Davidowitz and Rosenzweig 1998), but rarely across different types of forest ecosystems or at large scales. The focus of this study is neither on rare or endangered species nor on forest-specific species communities but on many TGs that are important to maintain healthy forest ecosystems. The study did not address the effects of forest management on forest structure, yet it included plots in both long-term unmanaged as well as regularly management forest stands and thus captured structures developing from natural processes as well as those induced by management. We use a set of structural variables, combined in an index of forest structural diversity derived from the large-scale forest inventories of the German National Forest Inventory (Storch et al. 2018), to analyze their importance for different TGs. The results about habitat structures required by individual TGs can then be transferred to large-scale inventories to analyze changes of these important forest structures over inventory periods and to predict changes in biodiversity, similar to the approach of Simons et al. (2021) for ecosystem services. If successful, this approach would allow an indirect species diversity monitoring across forest types at a large scale. Based on the quantification of habitat features for the different TGs and their known relationship with forest structure, their potential diversity can be assessed.

Specifically, we investigated how well stand structural diversity correlates with the number of species across a wide range of TGs. This is based on the assumption that the occurrence of individual TGs is related to specific structural properties in forests. The overall objective of this explorative work was to evaluate whether forest structural variables derived from large-scale forest inventories like the German National Forest Inventory are of relevance for the species richness within different TGs

and thereby support a biodiversity monitoring without additional sampling costs. The purpose of this study was not to develop multivariate models to predict species richness within individual TGs.

2 Material and methods

2.1 The Biodiversity Exploratories project

This study was carried out with data on forest structure and species richness of a wide range of TGs quantified in 150 forest plots of the Biodiversity Exploratories project (Fischer et al. 2010). These plots were located in north-east (Schorfheide-Chorin), central (Hainich-Dün) and south-western Germany (Swabian Alb). In each of these regions, there were 50 plots of 1 ha in size that span a gradient in forest management intensity from intensively managed to unmanaged stands set aside 20–70 years ago. The plots were located in forest stands either dominated by European beech (*Fagus sylvatica* L.) (managed and unmanaged), oaks (*Quercus robur* L. and *Quercus petraea* Liebl.), Norway spruce (*Picea abies* L.) or Scots pine (*Pinus sylvestris* L.) (all managed), or comprised managed mixtures thereof and covered different stand development phases (pole wood (mean DBH 7–14.9 cm), immature (mean DBH 15–30 cm) and mature stands (mean DBH > 30 cm)). A map

of forest locations (Figure 1 in Appendix) and more detailed information about forest stand characteristics (mean and standard deviation of forest structural elements) and number of sampling plots are provided in Table 4 in Appendix.

For the purpose of this study, we selected occurrence data from species of 29 TGs to cover a range of different responses to structural elements of forests (Table 1). Information about the sampling methods are provided in the Additional file 1 and the meta-data of each dataset provided by the German biodiversity exploratories project. We explicitly avoided a focus on rare or endangered species but instead included many TGs that are important for ecosystem functioning (e.g., Formicidae, Coleoptera, deadwood-inhabiting fungi or vascular plants). Classifications of guilds include a certain overlap of species, as e.g. carnivorous Coleoptera can also appear in the guild of ground-dwelling Coleoptera. Forest structure was quantified for the same plots of 1 hectare in size (Schall et al. 2018a). This included different sampling techniques like a complete inventory of living trees (DBH $\geq$ 7 cm) between 2008 and 2014 (Schall and Ammer 2019), sampling of deadwood in 2012 (Kahl and Bauhus 2012) and the regeneration layer (2014–2017; see Schall and Ammer 2020).

Table 1 Overview of analyzed taxonomic/functional groups and sampling dates, based on data of the German biodiversity exploratories project

Taxonomic group	Functional group/guild	Sampling period
Vascular plants		2009 (Boch et al. 2009a)
Herbs (subset of vascular plants)		2009 (Boch et al. 2009a)
Epiphytic bryophytes		2007, 2008 (Müller et al. 2009)
Lignicolous bryophytes		2007, 2008 (Müller et al. 2009)
Terricolous bryophytes		2007, 2008 (Müller et al. 2009)
Epiphytic lichens		2007, 2008 (Boch et al. 2009b)
Lignicolous lichens		2007, 2008 (Boch et al. 2009b)
Fungi (deadwood inhabiting)		2011 (Baber and Bauhus 2013)
Forest fungi (soil and root-associated)		2011 (Buscot et al. 2021)
Araneae (web spiders)	Ground-dwelling and vegetation layer	2008 (Gossner et al. 2017a)
Coleoptera (beetles)	Carnivorous, herbivorous, decomposer, ground-dwelling, herb- and tree-layer	2008 (Gossner et al. 2017b)
Hemiptera (bugs)	Carnivorous, herbivorous, ground-dwelling, herb- and tree-layer	2008 (Gossner et al. 2017c)
Coleoptera and Hemiptera (saproxylic)		2008 (Gossner et al. 2017b, c)
Ambrosia beetles (bark beetles)		2010 (Gossner and Weisser 2016)
Bark beetle antagonists		2010 (Weisser and Gossner 2016)
Formicidae (ants)		2008 (Grevé et al. 2017)
Aves (birds)		2012 (Jung et al. 2019)
Small mammals		2008 (Heinze et al. 2008)
Microchiroptera (bats)		2010 (Jung and Tschapka 2016)
Sum of species of all analyzed TGs[a]		

[a] Species richness within each analyzed taxonomic group was ranged between 0 and 1 (appropriate to formula 1), summed up and divided by the number of TGs

2.2 Structural diversity index

For this study, we calculated an index of stand structural diversity that was originally developed with data from the National Forest Inventory of Germany (Storch et al. 2018). It follows the approach described by McElhinny et al. (2006), combined with criteria suggested by Sabatini et al. (2015). The eleven structural variables included in the index can be calculated for most conventional forest inventories and comprise resource and habitat properties important for many species: standing and downed deadwood in different decay classes (e.g., habitat for many saproxylic species, nesting habitats for birds), the volume of large living trees (diameter at breast height ≥ 40 cm; tree-related microhabitats and important resource for herbivores), species richness of trees in the stand and the regeneration layer (promotes habitat heterogeneity and diversity of herbivores), quadratic mean diameter of trees at breast height (DBH) (old stands provide more niches), diversity of tree dimensions expressed as standard deviation of DBH and tree heights (vertical heterogeneity), as well as the diversity of foraging substrates expressed as diversity of tree bark types and flowering trees (Table 2). Each variable (X, sampled at the inventory plot) is scaled in relation to the minimum (Xmin) and maximum (Xmax) value derived from the dataset to yield variable-indices between 0 and 1 (formula 1).

$$Variable - Index = \frac{(X - Xmin)}{(Xmax - Xmin)} \quad (1)$$

$$FSI = \frac{\sum (variable - indices)}{(number\ of\ applied\ variables)} \quad (2)$$

This index ('FSI'—Forest Structure Index) is then calculated at the plot-level as the sum of the values of structural variable-indices, divided by the number of variables included (formula 2) and subsequently aggregated for forest types. These include the three regions of the Biodiversity Exploratories project separately and combined, broadleaf- and conifer-dominated stands, European beech-, Scots pine-, and Norway spruce-dominated stands, pole wood, immature, and mature stands, as well as managed and unmanaged beech-dominated mature stands. Index-values range between 0 and 1, where 0 implies 'lowest level of structural diversity' and 1 'highest level of structural diversity'. Further information about the selection of structural variables and the development of this index can be found in Storch et al. (2018).

2.3 Correlations between species richness within TGs and structural variables

To correlate the number of species of the different TGs with the forest structure index, the 'cor.test'-function in R v.1.2.5033 (R Core Team 2019) and the package 'tidyverse' (v.1.2.1) were used. For that purpose, sampling plots were aggregated to forest types or stand development phases. To focus on reliable correlations, a p value ≤ 0.1 was used, combined with correlation coefficients (Pearson's r) ≥ 0.3 as one criterion in this analysis. A detailed overview of the correlations is provided in Supplement 1. Additionally, we regarded only those correlations as robust where the direction of the correlation was consistent over several types of forest stands or developmental phases, even if not all correlations were statistically significant. On this basis, robust correlations were finally discussed and assessed by experts who carry out research projects in the German

Table 2 Variables of forest structure, which are used in the forest structure index, and the aspects of forest structure they represent (taken from Storch et al. 2018)

Variable	Acronym	Aspect of forest structure
Quadratic mean diameter at breast height (DBH ≥ 7 cm)	DBHq	Growing stock
DBH, standard deviation (DBH ≥ 7 cm)	DBHsd	Uneven-agedness
Volume / ha of trees (DBH ≥ 40 cm)	Vol40	Volume of large living trees
Tree height, standard deviation (DBH ≥ 7 cm)	HEIGHTsd	Vertical heterogeneity
Downed deadwood, average mean diameter	DW downed	Deadwood downed
Standing deadwood, mean DBH	DW standing	Deadwood standing
Number of decay classes	Decay classes	Deadwood decay classes
Number of tree species in the regeneration layer	SRreg	Tree regeneration diversity
Number of tree species (DBH ≥ 7 cm)	SR	Compositional heterogeneity
Diversity of bark types (based on tree species and DBH)	Bark	Bark-diversity
Diversity of flowering/fruiting trees (based on tree species and tree age)	Flower	Food/ pollen-diversity

DBH Diameter at breast height (1.3 m)

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biodiversity exploratories project; they designed the sampling of TGs and own the data. The correlations were verified by literature for individual TGs to ensure the general validity of the relationships at a national scale. This explorative approach was used to analyze whether the structural variables of the index capture the species richness within different TGs and thereby support a biodiversity monitoring at large scale, as changes of habitat structures over inventory periods can provide hints for changes in species richness of different TGs.

3 Results

All significant correlations between structural variables of forests and the number of species belonging to individual taxonomic groups (TGs) and their interpretations are shown in Table 3. In addition, correlation coefficients of all analyzed TGs are provided in Supplement 1.

The highest species richness over all analyzed TGs was found in old forest stands with a species-rich regeneration layer and downed deadwood (positive correlations with quadratic mean diameter at breast height, species richness within the regeneration layer and downed deadwood in most of the analyzed strata). Most species were found in the region Schorfheide-Chorin located in the north-east of Germany, which is characterized by higher tree species richness than the other regions.

Most vascular plant and herb species were found in young and even-aged forest stands (negative correlations with DBHq, DBHsd, HEIGHTsd, Vol40) with a high species richness within the regeneration layer. In addition, species richness in managed forest stands (mean_vascular plants: 25.8; mean_herbs: 21.4) was higher than in unmanaged forest stands (mean_vascular plants: 17.3; mean_herbs: 12.9).

Species richness of epiphytic lichens was positively correlated with DBHq and tree species richness and negatively by DBHsd and HEIGHTsd. This indicates that best habitat characteristics for this group can be found in old, species-rich and more even-aged forest stands.

Species richness of lignicolous lichens was negatively correlated with DBHq, DBHsd, HEIGHTsd, SRreg and Decay classes. This indicated that even-aged stands with a tree species-rich regeneration provide best habitat characteristics for lignicolous lichens. Species richness was higher in Scots pine-dominated stands (mean 2.4) than in European beech-dominated stands (mean 0.8).

Species richness of epiphytic bryophytes was positively correlated with DBHq and Vol40 and negatively by DBHsd, indicating that even-aged and old forest stands with different species of shrubs like elder provide appropriate habitat characteristics, especially in Norway spruce- and European beech-dominated stands.

Most species of lignicolous bryophytes were found in even-aged stands with a tree species-rich regeneration and downed deadwood. Highest species richness was found in Norway spruce-dominated stands (mean 14.4), whereas species richness in European beech-dominated stands was lower (mean 6.4).

Species richness of terricolous bryophytes was highest in young and even-aged forest stands with a tree species-rich regeneration. Most species were found in Norway spruce-dominated stands (mean 13.3) and Scots pine-dominated stands (mean 6.7). In European beech-dominated stands, the lowest number of terricolous bryophytes were sampled (mean 3.9).

Most species of deadwood-inhabiting fungi were found in species-rich and vertically structured forest stands with high quantities of downed deadwood and a diversity of deadwood decay classes; DBHsd, HEIGHTsd, Decay classes, DW standing, DW downed, and SR were positively correlated. Species richness of root-associated and soil fungi was not related to structural variables of the Forest Structure Index.

Carnivorous Coleoptera seem to prefer old and vertically structured forests stands with a high species richness in the vegetation layer, as highest numbers of species were found in this type of forest stands. Herbivorous and ground-dwelling Coleoptera seem to prefer old forest stands with a species-rich regeneration layer, where most species were found. Most species of Coleoptera living in the herb-layer of forests were found in stands with a species-rich regeneration. Detritivorous Coleoptera (without saproxylic species) prefer tree species rich, old and vertically structured forest stands with species-rich regeneration. Most saproxylic Coleoptera species were found in old forest stands.

Carnivorous Hemiptera favored old forest stands with standing deadwood and a diversity of different deadwood decay classes, whereas ground-dwelling Hemiptera preferred young and even-aged forest stands without standing deadwood. Herbivorous species favor old and even-aged forest stands with species-rich regeneration and species living in the herb- and tree-layer of forest stands prefer species-rich old and uneven-aged forest stands with deadwood and different decay classes.

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Table 3 Taxonomic groups/guilds, important structural variables and a description of forest stands in which the highest species richness of individual TGs can be found

Taxonomic/functional group/guild	Correlations with structural variables	Interpretation
Vascular plants	DBHq (−), DBHsd (−), SRreg (+), Vol40 (−)	Species richness high in even-aged forest stands with higher light availability at the forest floor: therefore, Species richness higher in managed than unmanaged stands, low in beech-dominated stands
Herbs (subset of vascular plants)	DBHq (−), DBHsd (−), HEIGHTsd (−), SRreg (+), Vol40 (−)	Species richness high in even-aged coniferous-dominated stands, more species in managed than in unmanaged stands (owing to light availability at the forest floor and disturbances), high species numbers in spruce stands/ limestone and in pine stands/ sandy soil, low numbers in beech-dominated stands
Epiphytic bryophytes	DBHq (+), DBHsd (−) Vol40 (+)	Species richness high in old forest stands, most species in beech-dominated stands, vertically structured stands are too dark
Lignicolous bryophytes	DBHsd (−), Heightsd (−), SRreg (+), DW downed (+)	Species richness high in even-aged stands with a tree species-rich regeneration and downed deadwood, vertically structured stands are too dark
Terricolous bryophytes	DBHq (−), DBHsd (−), HEIGHTsd (−), SRreg (+), Vol40 (−), Bark (−), Flower (−), DW standing (−), Decay classes (−), SR (−)	Species richness high in young and even-aged stands with a tree species-rich regeneration
Epiphytic lichens	DBHq (+), SR (+), DBHsd (−), HEIGHTsd (−)	Species richness high in old and species-rich, even-aged stands, more species in unmanaged than in managed stands
Lignicolous lichens	DBHq (−), DBHsd (−), HEIGHTsd (−), SRreg (−), Vol40 (−), Decay classes (−)	Species richness high in young and even-aged stands with a tree species-rich regeneration
Fungi (deadwood inhabiting)	DBHsd (+), HEIGHTsd (+), SR (+), DW downed (+), Decay classes (+)	Species richness high in species-rich and vertically structured forest stands with downed deadwood and different deadwood decay classes
Fungi (soil/root-associated)		Not captured by applied forest structure variables
Araneae (ground-dwelling)	DBHsd (−), HEIGHTsd (−), Vol40 (−)	Species richness high in even-aged young forest stands
Araneae (vegetation)	DBHsd (+), HEIGHTsd (+), Vol40 (+), SR (+), Bark (+), Flower (+)	Species richness high in tree species-rich and vertically structured forest stands with regeneration and herbs
Coleoptera (carnivorous)	DBHq (+), DBHsd (+), SRreg (+), Vol40 (+), Bark (−)	Species richness high in uneven-aged, old forest stands with species-rich regeneration
Coleoptera (herbivorous)	DBHq (+), SRreg (+)	Species richness high in old forest stands with species-rich regeneration
Coleoptera (saproxylic)	DBHq (+), Vol40 (+)	Species richness high in old forest stands with large trees
Coleoptera (detritivorous without deadwood)	DBHq (+), DBHsd (+), SR (+), HEIGHTsd (+), SRreg (+)	Species richness high in tree species-rich, old and vertically structured forest stands with species-rich regeneration
Coleoptera (ground dwelling)	DBHq (+), SRreg (+)	Species richness high in old forest stands with species-rich regeneration
Coleoptera (herb-layer)	SRreg (+)	Species richness high in forest stands with species-rich regeneration
Coleoptera (tree-layer)	DBHq (+), Vol40 (+), DBHsd (+), SRreg (+), Bark (−)	Species richness high in old forest stands with large trees and species-rich regeneration
Hemiptera (carnivorous)	DBHq (+), DW standing (+), Decay classes (+)	Species richness high in old forest stands with standing deadwood and different deadwood decay classes
Hemiptera (herbivorous)	DBHq (+), SRreg (+), DBHsd (−), HEIGHTsd (−)	Species richness high in old and even-aged forest stands with species-rich regeneration

Table 3 (continued)

Taxonomic/functional group/guild	Correlations with structural variables	Interpretation
Hemiptera (ground dwelling)	DBHq (−), DBHTsd (−), HEIGHTsd (−), Vol40 (−), Bark (−), Flower (−), DW standing (−)	Species richness high in young and even-aged forest stands without standing deadwood
Hemiptera (herb-layer)	DBHq (+), SRreg (+), Decay classes (+), DW standing (+), DBHsd (−), HEIGHTsd (−), Flower (−)	Species richness high in old and even-aged forest stands with species-rich regeneration, standing deadwood and different deadwood decay classes
Hemiptera (tree-layer)	DBHq (+), DBHsd (+), HEIGHTsd (+), Vol40 (+), Bark (+), Flower (+), DW downed (+), Decay classes (+), SR (+)	Species richness high in species-rich old and uneven-aged forest stands with downed deadwood and different deadwood decay classes
Coleoptera/Hemiptera (saproxylic)	DBHq (+), DBHsd (+), SRreg (+), Vol40 (+)	Species richness high in old and uneven-aged stands with large trees and a species-rich regeneration
Ants (Formicidae)	Vol40 (−), Bark (+), DBHsd (−), HEIGHTsd (−)	Species richness high in young and even-aged forest stands, especially Scots pine-(1), mixed beech (2) and oak-dominated forest stands (3). Norway spruce-dominated stands likely too dark and cold, temperature and light availability on forest floor important (therefore managed better than unmanaged stands)
Bark Beetles (Scolytinae)	Bark (+), Flower (+)	Species richness high in forest stands with high diversity of bark structure
Bark Beetles Antagonists	Vol40(+), Bark (+), Flower (+), DW standing (−), SR (+)	Species richness high in tree species-rich forest stands with different types of bark structures, flowering trees and large trees
Small mammals		Not captured by applied forest structure variables
Aves (birds)[a]	DBHq (+), DBHsd (+), HEIGHTsd (+), SR (+), Bark (+), Flower (+), DW standing (+), DW downed (+), Decay classes (+), Vol40 (+)	Species richness high in old, species-rich and structurally rich forests stands with standing and downed deadwood
Microchiroptera (bats)[a]	DBHq (+), DBHsd (+), SRreg (−), Vol40 (+), Bark (−), Flower (−)	Species richness high in species poor old uneven-aged forest stands
Sum of TGs[b]	DBHq (+), SRreg (+), DW downed (+)	Species richness high in old stands with a species-rich regeneration and downed deadwood

(+) indicates a positive and (−) a negative correlation between structural variables and the species richness within TGs, which is based on correlations provided in the Supplement 1 and discussed and assessed with experts of the German biodiversity exploratories project for its general validity

DBHq quadratic mean diameter at breast height (DBH), *DBHsd* standard deviation of the DBH (for trees with a DBH ≥ 7 cm), *HEIGHTsd* standard deviation of the tree height (for trees with a DBH ≥ 7 cm), *SRreg* species richness of the regeneration layer, *Vol40* volume per hectare of trees with a DBH ≥ 40 cm, *Bark* diversity of bark-types (for more information see Storch et al. 2018), *Flower* diversity of flowering trees (for more information see Storch et al. 2018), *DW standing* mean diameter at breast height of standing dead trees, *DW downed* mean diameter in the middle of downed deadwood, *Decay classes* number of decay classes, *SR* species richness of trees with a DBH ≥ 7 cm

[a] Results verified only by literature

[b] Result not verified

Important habitat characteristics of saproxylic Coleoptera and Hemiptera were DBHq, DBHsd, and Vol40, indicating that old and uneven-aged stands with large trees provide suitable habitats. Most species within these groups were found in immature and mature, species-rich pine-dominated stands with a species-rich regeneration layer.

Highest species numbers of Scolytinae (bark beetles) were found in forest stands showing a high diversity of bark-types. Likewise, most species of bark beetle antagonists occurred in species-rich forest stands with a high diversity of bark-types, flowering trees and large trees.

Negative correlations between ground-dwelling Araneae and DBHsd, Vol40 and HEIGHTsd indicate that even-aged and young forest stands are most suitable for this TG. Araneae in the vegetation-layer (herb- and tree layer) prefer species-rich and vertically structured forest stands with regeneration and herbs.

Species richness of Formicidae was highest in forest stands of low structural diversity. In addition, most ant species were found in pine-dominated stands, followed by beech-mixed and oak-dominated stands. Since most Scots pine stands are even-aged and monospecific stands, this may explain the apparent increase in species richness with decreasing structural diversity. Similar to the results for vascular plants and herbs, the species richness of Formicidae was higher in managed (mean_formicidae 2.0) than in unmanaged forests stands (mean_formicidae 1.1), caused by higher light availability and therefore higher temperatures at the forest floor during the warm season.

Species richness of small mammals could not be explained by structural variables applied in the index.

Species richness of birds was positively correlated with most structural variables, indicating that birds prefer old and tree species rich, vertically structured forest stands including standing and downed deadwood as well as large trees.

Species richness of bats was positively correlated with DBHq, Vol40, and DBHsd indicative of old and uneven-aged forest stands. Diversity of bark types and flowering trees were negatively correlated.

4 Discussion
4.1 Structural variables as surrogates of species richness
The results of our explorative study show the potential of forest structural variables to indicate species richness within certain TGs, whereas species richness in other TGs could not be explained. The numerous correlations show that the set of variables included in the

forest structure index is suitable to capture species richness across many TGs and thereby support a biodiversity monitoring at large scale.

Some of the significant relationships are not based on a direct link but rather indirect reason. For example, correlations between species richness of vascular plants and deadwood-variables were discarded, because there is no evidence for the occurrence of species that require deadwood (personal communication with S. Boch 11/2019). But the presence of deadwood (especially of early decay stage) might indicate open spaces (gaps) in forest canopies, which allow higher temperatures, light availability and a higher heterogeneity in terms of microclimate at the forest floor fostering species richness of vascular plants and insects (e.g., Eckerter et al. 2021).

Our results indicate that forest management strategies can be applied to improve specific habitat structures like the volume of large living trees, tree species richness in the regeneration layer or increase the amounts of standing and downed deadwood, if individual TGs should be fostered. This can be achieved for example by retention forestry (Gustafsson et al. 2020) or management towards old-growth forests (Bauhus et al. 2009). On the other hand, harvesting that creates gaps in stands can foster species that require warm temperatures and a higher light availability at the forest floor like Formicidae (Grevé et al. 2018; Sanders et al. 2007), vascular plants (Boch et al. 2013a), and insects colonizing sun-exposed deadwood (Seibold et al. 2016). Although fungal diversity is affected by forest management (Schröter et al. 2019; Pena et al. 2017) the structural forest indicators of the current study could not retrieve these relationships. In addition, our results show that higher structural diversity at the plot or stand level can result in reductions in species diversity for some of the analyzed TGs (Sullivan and Sullivan 2001; Ralph 1985), e.g., if species like vascular plants or Formicidae depend on structurally poor conditions, pointing towards the conclusion that the 'habitat heterogeneity hypothesis' is not universally applicable.

4.1.1 *Species that were insensitive to analyzed structural variables*
Species richness of soil and root-associated fungi (combined in the analyzed data-set "forest fungi" of the German biodiversity exploratories project) were not associated with the forest structure variables tested here. In the present study regions as well as in other temperate forests (Bahnmann et al. 2018; Glassman et al. 2017), soil and root fungi are driven by soil chemical and

physical properties like soil pH, soil fertility (Nguyen et al. 2020; Schröter et al. 2019; Goldmann et al. 2016; Wubet et al. 2012) and by tree species identity and the ratio of conifers to deciduous trees (Pena et al. 2017; Lang et al. 2011). Species richness of small mammals was also insensitive to stand structural variables in our study, whereas Paniccia et al. (2018) highlighted relationships between occurrence of dormice and forest structures. This may be caused by very general habitat requirements, large home-ranges or the influence of landscape-level factors not captured in forest structure, e.g., vicinity to agricultural land providing food sources (Silva et al. 2005; Bayne and Hobson 1998). In addition, only few species of small mammals were found at individual plots (maximum of 5 species) which made the analysis not robust enough to derive general habitat characteristics for this TG.

4.1.2 Vascular plants and herbs
These TGs clearly prefer even-aged and open forest stands, as light availability on the forest floor is of crucial importance. Most species were found in Norway spruce-dominated stands (16 plots) on limestone, followed by Scots pine-dominated stands on sandy soils (22 plots). Soil characteristics were also important for this TG, as forests on limestone harbor considerably more species than forest stands on sandy soil. In contrast, European beech-dominated stands with low light availability have a lower species richness of herbs, which corresponds with results of Dormann et al. (2020) and Mölder et al. (2008). In managed stands, the species richness of vascular plants and herbs was higher than in unmanaged stands, likely caused by higher light availability near the ground and more frequent disturbances caused by harvesting and management activities, corresponding with results of Boch et al. (2013a) and Paillet et al. (2010). Structural variables of the forest structure index, combined with information on the dominant tree species and soil characteristics can therefore be used to assess the habitat quality for vascular plants and herbs. Likewise, Heinrichs et al. (2019) and Schall et al. (2018b, 2020) showed that a mixture of pure stands dominated by European beech and conifer species as well as among stand heterogeneity of different management systems at the landscape level can increase vascular plant diversity more than a mixture of tree species within forest stands.

4.1.3 Epiphytic lichens and epiphytic bryophytes
Most species were found in old, European beech-dominated forest stands; see also Müller et al. (2019) and Boch

et al. (2013b, c) for all three regions of the Biodiversity Exploratories and Schall et al. (2018b) for the Hainich-Dün region. Species richness of epiphytic lichens was higher in unmanaged stands than in managed forest stands, which might be explained by the occurrence of more old trees, which host most epiphytic lichen species (Boch et al. 2021, 2013c). Tree species richness was also important for the diversity of epiphytic lichens, which corresponds with results of Boch et al. (2021) and Ampoorter et al. (2020).

4.1.4 Lignicolous lichens, lignicolous, and terricolous bryophytes
Most species of lignicolous and terricolous bryophytes, as well as lignicolous lichens, were found in Norway spruce-dominated immature and mature stands, as these species benefited from larger amounts of downed deadwood and stumps (Kahl and Bauhus 2014; Vandekerkhove et al. 2009; Humphrey et al. 2002), probably caused by a more intense forest harvesting (Müller et al. 2015). In addition, wood properties of conifer species like resin content, low nutrient content and low pH, as well as slow decomposition rate (Fengel and Wegener 1984; Kahl et al. 2017) provide suitable habitats for specialist bryophyte species, which results in highly diverse bryophyte communities on coniferous deadwood (Müller et al. 2019). Wood properties of European beech (e.g., moderate pH-value, absence of resin) can lead to a high abundance of bryophytes but only few competitive and opportunistic species (Müller et al. 2019). In contrast, downed deadwood was mainly colonized by common lignicolous lichens and rare species were found on dry and debarked standing deadwood (Boch et al. 2013c).

4.1.5 Deadwood-inhabiting fungi
Deadwood-inhabiting fungi are very important for forest ecosystem functioning, as they make the nutrients locked up in dead phytomass available to higher plants. In addition to the deadwood-variables, vertical structure of forest stands was related to the species richness of deadwood-inhabiting fungi, as the standard deviation of the DBH and tree heights are positively correlated. This might be explained by a higher and more constant humidity (Zellweger et al. 2019; Bader et al. 1995) and darker conditions near the ground. Single tree felling or a more continuous harvesting of trees might also lead to an increase in DBHsd and HEIGHTsd, which produces deadwood in a more frequent way (e.g., stumps, sections of low quality, decayed log sections and branches) and thereby providing different decay classes over longer periods that

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increase the diversity of deadwood-inhabiting fungi, as was also found by Blaser et al. (2013).

4.1.6 Araneae

Ground-dwelling Araneae species seem to prefer even-aged and young forest stands, which provide enough light and higher temperatures at the forest floor. Some species depend on old-growth stands including characteristics like downed deadwood (Pajunen et al. 1995) and a mixture of young and old even-aged forest stands at landscape level can enhance the diversity of ground-dwelling Araneae (Niemelä et al. 1996). In contrast, species richness of Araneae living in the vegetation (herb-, shrub-, and tree regeneration layer) seem to prefer species-rich and vertically structured forest stands that provide the required habitat.

4.1.7 Coleoptera

The numerous guilds within the TG of Coleoptera prefer a variety of structural characteristics. Carnivorous Coleoptera seem to prefer old and uneven-aged forests with a species-rich regeneration layer. Ground-dwelling and herbivorous species favor old forest stands with a species-rich regeneration, as different plant species provide a variety of food sources, which confirms the results of Lange et al. (2014). Species richness of saproxylic Coleoptera tended to be highest in old forest stands including downed deadwood and different decay classes, which corresponds with results of Gossner et al. (2013) and Okland et al. (1996), even though correlations with the tested deadwood variables were not statistically significant. This might be caused by the sampling method of deadwood, but the amount of deadwood in old forest stands is generally higher than in young stands. Species of detritivorous Coleoptera were most numerous in tree species rich, old and vertically structured forest stands with a species-rich regeneration, as different tree species provide a variety of food sources. Positive correlations in some of the analyzed forest types between the number of species and the species richness of the regeneration layer was also found by Hölling (2000).

4.1.8 Hemiptera

Carnivorous Hemiptera and species colonizing the herb- and tree-layer of forests seem to favour old stands including standing deadwood and a variety of decay classes for hibernation and oviposition (Gossner and Damken 2018; Weigelmeier and Gruppe 2008). Hemiptera colonizing the forest floor in contrast prefer young and even-aged forest stands. These different habitat requirements by different guilds within a TG underline the necessity to analyze guilds separately for relationships with habitat attributes.

4.1.9 Scolytinae

Scolytinae (bark beetles) and their antagonists favor forest stands including different tree species and a variety of bark types, as Scolytinae excavate tunnels in dead, stressed, and healthy trees in which they cultivate fungal gardens, their sole source of nutrition (Gebhardt et al. 2005). Not surprisingly, most species of bark beetle antagonists were found in stands showing similar characteristics. The importance of flowering trees and plants can be explained by the fact that some antagonist species supplement their diet with honey agar or honeydew (Führer 1975).

4.1.10 Formicidae

The species richness of Formicidae was correlated with the dominant tree species, combined with the expression of vertical structure within forest stands. Hence the structural variables applied in the index can be used to assess the habitat quality for Formicidae. As Grevé et al. (2018) showed, forest structures like downed deadwood might have little importance for nesting purposes, if forests provide sufficient nesting opportunities for Formicidae. Managed forest stands can provide better habitat conditions than unmanaged stands with lower light availability and temperature near the forest floor in the latter, caused by the expression of vertical forest structure. The importance of temperature and light availability for the diversity of Formicidae was also shown by Sanders et al. (2007), which makes temperature a good indicator for the species richness of this group (Seifert 2017; Del Toro 2013).

4.1.11 Birds

Species richness of birds benefitted from old, tree species- and structurally rich forest stands, including standing and downed deadwood. These stands provide a variety of food sources (insects, invertebrates) as well as tree-related microhabitats that offer breeding opportunities such as cavities. The importance of large living trees for the diversity of birds was previously shown in several studies (e.g., Zarnowitz and Manuwal 1985; Mannan and Meslow 1984) yet specific relationships between the abundance of birds and microhabitats could not be shown (Basile et al. 2020). The significance of the vertical heterogeneity of vegetation or foliage layers for the diversity of birds, as well as the relative lack of importance of tree species composition, was also found by MacArthur and MacArthur (1961). Deadwood-dimensions and decay

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classes are also important structural elements influencing the diversity of forest birds (Mollet et al. 2009; Utschick 1991), which corresponds with results of our study. In addition, the importance of standing deadwood as a source of food was shown for woodpeckers by Drapeau et al. (2009) and Bütler and Schlaepfer (2004). These 'old-growth' characteristics were also described as important bird habitats by Moning and Müller (2009), Laiolo (2002) and Moss (1978).

4.1.12 Bats

The highest species richness of bats was found in old and uneven-aged Scots pine-dominated stands and mixed deciduous forests. Vertically structured stands (positive correlations with DBHsd) provide suitable habitat characteristics for insectivorous bat species, which corresponds with results of Jung et al. (2012). Old trees with cavities or bark pockets can be used for resting purposes, which was described by Larrieu et al. (2018), Yoshikura et al. (2011) and Michel et al. (2011). Tree species richness, as well as different types of bark and flowering trees seem not to influence the diversity of bats. The importance of standing and downed deadwood, which is mentioned, e.g., by Tillon et al. (2016) and Regnery et al. (2013) could not be confirmed in our analysis.

4.2 Transfer of information into National Forest Inventories

The heterogeneous results of our explorative study show that a complete assessment of species diversity in forests is not possible using only the variables of forest structure investigated here and probably even when using additional ones, as e.g., soil chemical and physical properties (important for soil- and root-associated fungi, vascular plants and herbs) or air quality (important for epiphytic lichens) influence species richness or the presence of TGs. Nevertheless, the knowledge about structural characteristics that are important for certain TGs gained in this explorative analysis can be used to support species diversity monitoring based on large-scale inventory data because the analyzed forest structures are standard variables in most inventories. The assessment of changes in important structural variables over inventory periods, for example 10 years in the German National Forest Inventory, could therefore provide hints for trends in species richness of different TGs without additional costs. This information could be used for a more targeted monitoring of TGs that are assumed to be most influenced by changes in forest structure. Further research on the relationship of species richness and composition with the main observed changes is needed to assess the importance of lag periods.

5 Conclusion

Our analysis showed the potential of forest structural variables applied in the tested forest structure index to indicate species richness within many TGs (e.g., vascular plants, bryophytes, lichens, Coleoptera, Hemiptera, Formicidae and birds) in a range of forest types in three study regions of Germany. The results indicate that variation in the species richness of these taxonomic groups cannot be explained by very few structural variables, as one might wish from the monitoring perspective, but on a variety of structural elements and their expressions in forest stands. The number of species in other TGs such as small mammals or soil and root-associated fungi could not be described by these structural variables. This indicates that other structural attributes or further determinants such as environmental factors (climate, topography, light availability or soil properties), management influences and interaction with different land-use systems (e.g., agricultural land) should be considered to explain species richness of these groups. The diverse relationships between structural variables and species richness in different TGs also show that different patch-wise combinations of structural variables will likely provide the highest overall species richness at the landscape scale, indicating that high species richness reflects high diversity of abiotic variation as shown on the landscape level (Schall et al. 2018b). As these variables are sampled in forest inventories, information about habitat characteristics and their changes over inventory periods can be derived easily indicating general trends of habitat changes and support a biodiversity monitoring without additional sampling costs for large areas. Based on the results of our explorative study, important forest structures combined with additional information on soil properties, air quality or landscape characteristics can be applied in multivariate models to predict species richness within individual TGs.

Appendix

Fig. 1 Locations of the German biodiversity exploratories project in three regions of Germany: Schorfheide-Chorin (Brandenburg), Hainich-Dün (Thuringia) and Swabian Alb (Baden-Württemberg)

Table 4 Strata, number of sampling plots, mean values (mean), and standard deviations (SD) of the analyzed forest structural variables of the German biodiversity exploratories project

Stratum	Number of sampling plots	FSI mean (SD)	DBHq mean (SD)	DBH sd mean (SD)	Height sd mean (SD)	SRreg mean (SD)	Vol40 mean (SD)	Bark mean (SD)	Flower mean (SD)	DW Standing mean (SD)	DW Downed mean (SD)	Decay classes mean (SD)	SR mean (SD)
Biodiversity exploratories	150	0.38 (0.12)	32.10 (11.80)	13.11 (6.23)	6.84 (1.70)	2.84 (1.70)	258.74 (201.16)	9.09 (4.70)	4.87 (2.33)	27.35 (25.28)	27.59 (13.11)	1.98 (1.06)	5.95 (2.75)
Schorfheide	50	0.39 (0.15)	37.04 (12.04)	13.45 (6.53)	6.58 (1.75)	2.16 (1.53)	250.95 (217.25)	7.40 (3.93)	4.20 (2.09)	25.28 (27.19)	24.70 (13.44)	1.74 (1.05)	5.14 (2.29)
Hainich	50	0.48 (0.12)	31.05 (10.57)	15.02 (5.61)	7.38 (1.62)	3.28 (1.58)	320.78 (173.59)	9.48 (4.60)	5.12 (2.11)	27.58 (27.89)	30.08 (13.51)	2.14 (1.07)	5.88 (2.19)
Swabian Alb	50	0.39 (0.14)	28.23 (11.19)	10.85 (5.93)	6.56 (1.62)	3.08 (1.78)	204.47 (196.76)	10.38 (5.09)	5.30 (2.65)	29.19 (20.46)	27.99 (12.02)	2.06 (1.04)	6.82 (3.40)
Broadleaf-dominated stands	112	0.41 (0.10)	32.98 (12.72)	14.72 (6.19)	7.24 (1.70)	2.77 (1.61)	276.68 (200.43)	8.81 (4.37)	4.99 (2.18)	31.61 (25.97)	30.11 (11.95)	2.14 (1.01)	5.97 (2.61)
Coniferous-dominated stands	38	0.42 (0.20)	29.54 (8.14)	8.36 (3.23)	5.66 (1.02)	3.05 (1.93)	205.85 (196.42)	9.89 (5.57)	4.53 (2.74)	14.81 (18.29)	20.17 (13.72)	1.50 (1.06)	5.87 (3.16)
Beech-dominated stands	105	0.41 (0.11)	32.71 (13.00)	14.72 (6.36)	7.25 (1.75)	2.84 (1.61)	271.65 (203.94)	8.82 (4.49)	4.96 (2.23)	32.18 (26.19)	30.36 (12.27)	2.15 (1.04)	5.97 (2.68)
Spruce-dominated stands	16	0.44 (0.20)	32.25 (7.22)	8.89 (2.51)	5.90 (0.64)	3.50 (2.22)	286.80 (238.64)	11.63 (6.09)	5.56 (2.73)	16.99 (18.20)	25.12 (11.54)	1.81 (0.91)	6.94 (3.21)
Pine-dominated stands	22	0.42 (0.24)	27.56 (8.36)	7.97 (3.68)	5.49 (1.21)	2.73 (1.67)	146.98 (136.66)	8.64 (4.92)	3.77 (2.54)	13.23 (18.61)	16.57 (14.30)	1.27 (1.12)	5.09 (2.96)
Mature stands	86	0.42 (0.08)	39.12 (8.35)	16.74 (4.76)	7.59 (1.51)	2.87 (1.64)	376.56 (169.02)	8.20 (4.12)	4.80 (2.15)	32.89 (26.95)	31.47 (10.34)	2.17 (0.90)	5.47 (2.11)
Immature stands	36	0.45 (0.17)	29.46 (4.92)	8.82 (2.58)	5.87 (0.72)	3.36 (1.74)	157.63 (113.72)	9.47 (4.85)	4.72 (2.19)	19.46 (18.66)	22.16 (11.96)	1.72 (1.00)	5.69 (2.75)
Pole wood stands	14	0.33 (0.24)	14.33 (2.15)	4.72 (1.14)	4.94 (0.91)	1.93 (1.21)	8.97 (19.86)	10.07 (5.64)	5.14 (3.37)	12.26 (20.89)	12.48 (17.74)	0.93 (1.38)	6.64 (3.95)
Beech-dominated mature stands managed	55	0.41 (0.07)	39.99 (7.58)	17.58 (4.59)	7.99 (1.64)	2.95 (1.26)	303.09 (167.11)	6.56 (3.03)	4.02 (1.68)	31.45 (30.77)	33.15 (10.43)	2.07 (0.96)	4.68 (1.69)
Beech-dominated mature stands unmanaged	25	0.48 (0.09)	39.63 (10.77)	18.78 (4.22)	7.72 (1.39)	2.84 (1.91)	485.96 (125.22)	9.40 (4.73)	5.68 (2.38)	41.31 (23.50)	31.67 (11.72)	2.48 (0.92)	6.04 (2.30)

FSI Forest Structure Index, *DBHq* quadratic mean diameter at breast height (DBH), *DBHsd* standard deviation of the DBH (for trees with a DBH ≥ 7 cm), *HEIGHTsd* standard deviation of the tree height (for trees with a DBH ≥ 7 cm), *SRreg* species richness of the regeneration layer, *Vol40* volume per hectare of trees with a DBH ≥ 40 cm, *Bark* diversity of bark-types (for more information see Storch et al. 2018), *Flower* diversity of flowering trees (for more information see Storch et al. 2018), *DW standing* mean diameter at breast height of standing dead trees, *DW downed* mean diameter in the middle of downed deadwood, *Decay classes* number of decay classes, *SR* species richness of trees with a DBH ≥ 7 cm, *Biodiversity exploratories* all forest sampling plots of the German Biodiversity-Exploratories, *Schorfheide* Region of Brandenburg, *Hainich* region of Thuringia, *Swabian Alb* region of Baden-Wuerttemberg, *Broadleaf-dom. stands* stands dominated by broadleaf tree species, *Coniferous-dom. stands* stands dominated by coniferous tree species, *Beech-dom. stands* stands dominated by European beech (*Fagus sylvatica* L.), *Spruce-dom. stands* stands dominated by Norway spruce (*Picea abies* L.), *Pine-dom. stands* stands dominated by Scotspine (*Pinus sylvestris* L.), *Mature stands* stands of developmental stage mature (mean DBH > 30 cm), *Immature stands* stands of developmental stage immature (mean DBH 15–30 cm); *Pole wood stands* stands of developmental stage pole wood (mean DBH 7–14.9 cm), *Beech-dom. mature stands managed* managed stands dominated by beech (*Fagus sylvatica*) of developmental stage mature (mean DBH > 30 cm), *Beech-dom. mature stands unmanaged* unmanaged stands dominated by beech (*Fagus sylvatica*) of developmental stage mature (mean DBH > 30 cm)

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Authors' contributions

Conceptualization: FS, JB. Methodology: FS, FK. Formal analysis and investigation: FS. Writing—original draft preparation: FS. Writing—review and editing: JB, MMG, SB, PS, CA, JM, FK, AP, HF. Funding acquisition: not applicable. Resources: JB, MMG, SB, PS, CA, JM, AP, HF. Supervision: JB. The author(s) read and approved the final manuscript.

Availability of data and materials

The data that support the findings of this study are available from Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/.

Declarations

Ethics approval and consent to participate

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Competing interests

The authors declare that they have no competing interests.

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