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What does literature tell us about the relationship between forest structural attributes and species richness in temperate forests? – A review

Laura Zeller[a,*], Agnes Förster[a], Constanze Keye[b], Peter Meyer[b], Christian Roschak[b], Christian Ammer[a]

[a] Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, D-37077 Göttingen, Germany
[b] Department for Forest Nature Conservation, Northwest German Forest Research Institute, Prof.-Oelkers-Str. 6, D-34346 Hann. Münden, Germany

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ABSTRACT

The effects of forest management on species richness and diversity have become important research interests. The need to maintain biodiversity for forest ecosystem functioning has led to the question of how strongly and in what ways forest management modifies the diversity and abundance of different species groups. It is well known that many forest species rely on specific structures that may be modified by forest management. Assessing the impact of forest management on species richness may therefore require identification of structural properties. For this literature review we identified a large set of structural attributes that can serve as potential drivers of the richness of different species groups. Most studies included here focused on only one or a few structural attributes as explanatory variables and a limited number of species groups as dependent variables; we therefore analyzed the available publications across species and structural properties. We gathered 410 relationships of structure and species richness out of 85 studies from the temperate region in Europe. Positive, negative, and neutral (non-existent) correlations between species richness and the presence of specific structural properties in European temperate forests were then compiled. Canopy gaps and structural attributes related to old-growth successional stage such as stand age and the share of large old trees were mostly positively correlated with species richness of the different taxa. Especially old-growth structures were ranked high in the reviewed literature. The structural attributes that were mainly positively correlated with species richness or the richness of groups of species may be used for further development of biodiversity monitoring concepts and forest management.

1. Introduction

Even though forest management aims to fulfill multiple ecosystem functions and services in many regions of Europe (Felipe-Lucia et al., 2018; Manning et al., 2018), it is increasingly criticised for compromising forest biodiversity (Halme et al., 2010; Jakobsson et al., 2021; Meyer, 2013; Niemelä et al., 2005; Schulze and Ammer, 2015; Winkel and Volz, 2005). Nature conservation and forest management have thus often been in conflict. Nonetheless, both wood production and biodiversity conservation, among other ecosystem functions and services, are necessary. Balancing trade-offs and conflicts are therefore important aspects of forest management (Cosyns et al., 2020) and decision-making requires evidence-based knowledge. The exact effects of forest management on biodiversity or species richness, however, are difficult to capture. Chaudhary et al. (2016), Dieler et al. (2017) and Paillet et al. (2010) summarised many studies on the effects of forest management on biodiversity and found negative, positive, and contradictory results. However, only Chaudhary et al. (2016) explored differences between the applied forest management measures based on the existing literature. Lack of detail about the silvicultural management of the compared studies might have led to their somewhat vague results. Different kinds of silvicultural management regimes including various types, intensities, and frequencies of interventions result in different forest structures (Penone et al., 2019) and make comparisons between studies nearly impossible.

It is also not possible to fully record and monitor species richness; it is therefore necessary to develop comprehensive methods of biodiversity assessment by proxies (Caro and Girling, 2010). Specific species groups or indirect parameters such as forest structures may serve as suitable indicators. Within the last decades multiple approaches have been proposed for assessing biodiversity in forests (Burrascano et al., 2021; Marchetti, 2005; Noss, 1999). However, attempts to agree on a common

* Corresponding author.
E-mail address: laura.zeller@uni-goettingen.de (L. Zeller).

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Table 1
Overview of studies that reported on a correlation between structural attributes in temperate forests and species richness of one or several taxa.

Reference	arthropods	bats	birds	bryophytes	fungi	lichens	molluscs	trees	vascular plants
Ammer and Schubert (1999)	x								
Bae et al. (2018)			x						
Bardat and Aubert (2007)				x					
Begehold (2017)			x						
Blaser et al. (2013)					x				
Boch et al. (2013a)						x			
Boch et al. (2013b)									x
Bouget (2005)	x								
Bouget et al. (2013)	x								
Bouget et al. (2011)	x								
Bouget et al. (2014)	x								
Bouvet et al. (2016)		x	x						
Brin et al. (2011)	x								
Burrascano et al. (2008)									x
Burrascano et al. (2017)									x
Charbonnier et al. (2016a)		x							
Charbonnier et al. (2016b)		x	x						
Chumak et al. (2015)	x								
Czeszczewik et al. (2014)			x						
De Groot et al. (2016)	x								
Díaz (2006)			x						
Di Giovanni et al. (2015)	x								x
Dormann et al. (2020)									x
Erdmann et al. (2006)	x								
Friedel et al. (2006)				x		x			
Friess et al. (2019)	x								
Grevé et al. (2018)	x								
Gunnarsson et al. (2004)	x								
Hanzelka and Reif (2016)			x						
Hauck et al. (2013)						x			
Heidrich et al. (2020)	x	x	x	x	x	x			
Heinrichs and Schmidt (2013)								x	
Hofmeister et al. (2015)				x	x	x			
Hohlfeld (1997)			x						
Horak et al. (2014)	x				x	x			
Humphrey et al. (2002)				x		x			
Ingle et al. (2020)	x								
Jukes et al. (2002)	x								
Kaufmann et al. (2018)				x		x			x
Király et al. (2013)				x		x			
Krah et al. (2018)					x				
Kubartová et al. (2009)					x				
Kubiak et al. (2016)						x			
Kusch and Schotte (2007)		x							
Laiolo (2002)			x						
Laiolo et al. (2004)			x						
Lange et al. (2014)	x								
Leidinger et al. (2020)	x								x
Loch (2002)	x								
Machar et al. (2019)			x						
Mag and Ódor (2015)			x						
Magura et al. (2000)	x								
Márialigeti et al. (2009)				x					
Márialigeti et al. (2016)									x
Mazziotta et al. (2016)				x	x	x			x
Moning et al. (2009)						x			
Moning and Müller (2009)			x			x	x		
Müller (2005)	x		x						
Müller et al. (2007)					x				
Müller et al. (2008)	x								
Müller et al. (2015)				x					
Müller et al. (2018)	x								
Nascimbene et al. (2013)						x			
Nordén et al. (2003)					x				
Ódor et al. (2014)				x		x			
Paltto et al. (2008)				x		x			
Penone et al. (2019)	x			x	x	x			x
Petritan et al. (2012)								x	
Poulsen (2002)			x						
Preikša et al. (2016)				x	x	x			
Przepióra et al. (2020)			x						
Rosenvald et al. (2011)			x						
Sabatini et al. (2014)									x
Schauer et al. (2018)	x								

(continued on next page)

Table 1 (*continued*)

Reference	arthropods	bats	birds	bryophytes	fungi	lichens	molluscs	trees	vascular plants
Scherber et al. (2014)	x								
Schmidt (2005)									x
Seibold et al. (2014)	x								
Seibold et al. (2016)	x								
Seric Jelaska et al. (2010)	x								
Setiawan et al. (2016)	x								
Slezák and Axmanová (2016)				x					x
Sobek et al. (2009)	x								
Svoboda et al. (2010)						x			
Ujházy et al. (2017)									x
Wei et al. (2020)									x

approach have, to date, largely failed.

To bypass the problem of quantifying different management regimes, a forest's potential for biodiversity may be examined by its structural characteristics (Larrieu and Gonin, 2008). Many existing studies have focused on the direct or indirect effects of structural properties on the diversity of different species or species groups (Zeller et al., 2022). Whether those structural properties result from silvicultural management or natural succession is often unclear due to the long history of forest use in Europe and may even be irrelevant for most species. It is therefore of value to quantify present structures and to determine which structural characteristics and species groups correspond with each other. To our knowledge, a systematic compilation of the many studies on the relationships between species or groups of species and forest structural attributes is not yet available. In fact, the relationship between structural attributes at different spatial scales and biodiversity has been identified as a major knowledge gap in forest ecology (Ammer et al., 2018). We chose species richness as proxy for biodiversity, even though it is only one aspect of biodiversity. Many studies used species richness as measure for biodiversity and we aimed at a large number of studies to be included in our analysis. However, our study consequently shows limitations, as the use of other measures than species richness, such as species diversity or composition might have led to different results.

We collected and analysed 85 studies providing 410 correlations between structural attributes and species richness of different taxa in the temperate region of Europe. Additionally, our study revealed knowledge gaps by identifying the least frequently examined structural attributes and species groups, both of which could be promising fields for future investigations. Our results enhance the development of biodiversity monitoring schemes and multi-purpose forest management strategies. Herewith, we contribute to the realignment of silvicultural practices towards an increased awareness of specific important forest structures for biodiversity.

We conducted our review study along the following research questions:

I. *Which structural attributes are correlated with the species richness of different taxa according to existing literature*?

2. Materials and methodology

2.1. Literature search

Relevant literature was identified and collected from the period of June to December 2020 by searching the online databases Scopus, ISI Web of Science, and Google Scholar (Table 1). The following keywords were used for the different databases, each in combination with the different species groups (in brackets):

Forest AND structure AND (diversity OR species richness) AND temperate AND NOT tropical AND (fungi OR fungus OR bird OR lichen OR beetle OR arthropod OR aranea OR spider OR moth OR necrophagous, phytophagous OR plant OR bat OR bryophyte OR moss OR true bug). After the search, a manual selection of the search results was necessary, as unsuitable studies that did not fulfill our requirements had to be excluded. We selected only studies that defined their examined forests as 'temperate'. If information on the biome was lacking, we used the definition of the temperate region by Olson et al. (2001). A further requirement for the selected studies was that they reported on a correlation of certain structural attributes (resulting either from natural forest development, silvicultural management, or unknown origin) with species richness of one or several taxa. The correlations could either be simple linear correlations or effects in more complex models indicating a relationship between forest structure and species richness. We collected only studies including species richness of single species or species groups as output variable. All structural attributes occurring during our search were included without preselection. Studies with species diversity or number of individuals as output variable were not included. Studies on attributes concerning climatic conditions, soil, management, or disturbance were not included. We focused only on structural attributes, independent of their origin.

The following studies were included in our analysis:

Table 2
Number of included studies and number and type of correlations per species group.

species group	n studies*	n correlations	type of correlation		
			positive	negative	no correlation
Arthropods	32	147	82	9	56
Lichens	19	67	50	8	9
Birds	18	50	45	4	1
Bryophytes	15	57	35	8	14
Vascular plants	14	37	19	11	7
Fungi	11	40	26	5	9
Bats	5	8	3	1	4
Trees	2	3	1	2	0
Molluscs	1	1	1	0	0
Sum	117	410	262	48	100

*Total number of studies: 85. Some included studies examined more than 1 species group, leading to a higher than 85 total number of studies in this table.

2.2. Literature analysis

Arthropods were summarised as one group due to the small sample size in the subgroups. Studies providing more detailed analyses on single species were categorised into the species groups. An analysis at the single species level would have led to a very small sample size. Trees were treated as a separate subgroup of vascular plants. Due to the heterogeneity of the examined studies concerning sampling methods, sampling time, plot size and forest type, we conducted a count-based analysis of the examined studies. We analysed the number and type of correlations (positive, negative, or no correlation between structure and species richness) over all studies for each structural attribute and for

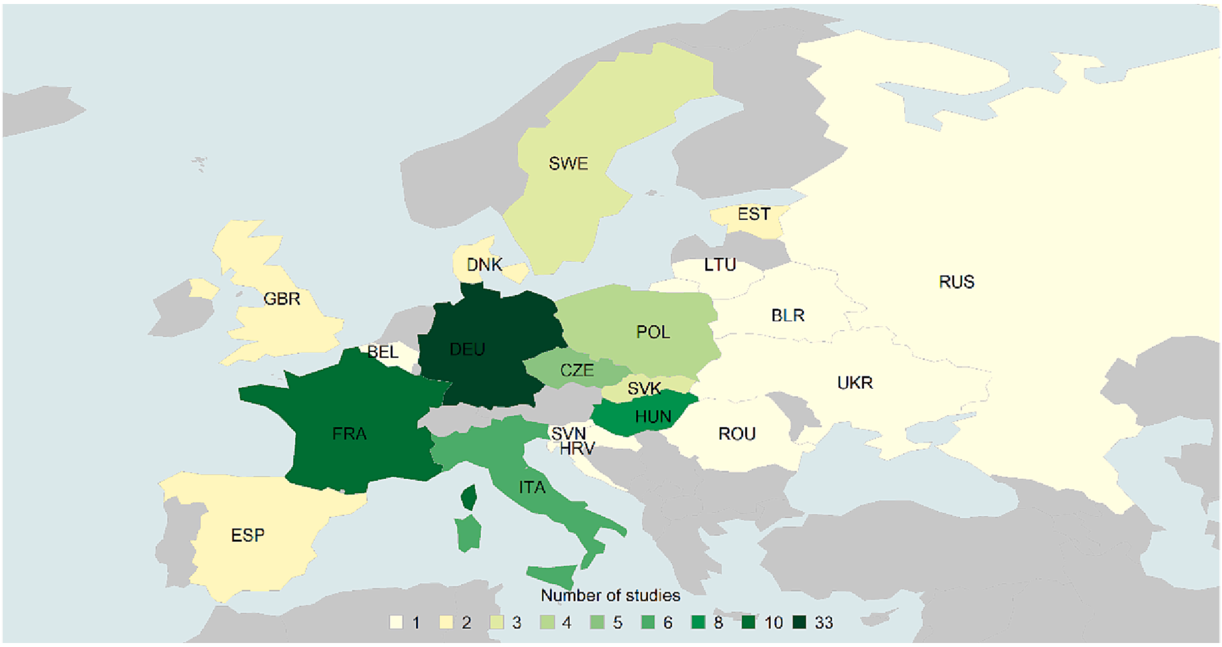

Fig. 1. Map of the number of included studies per country.

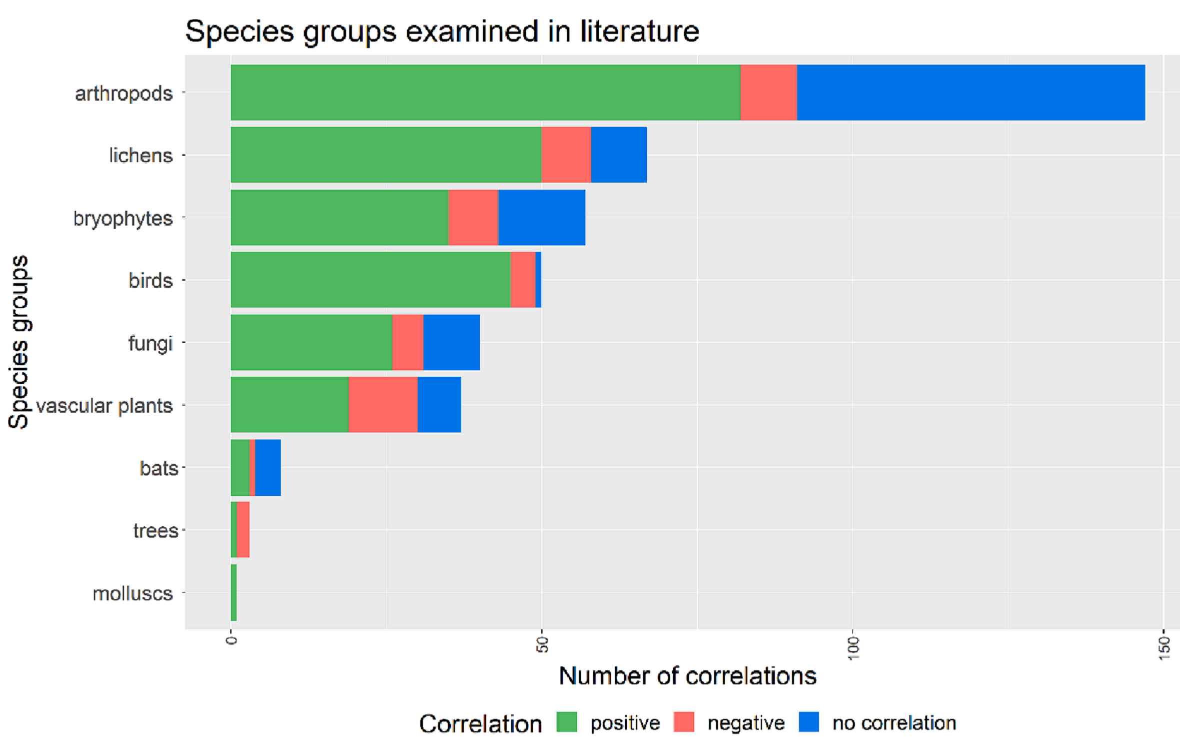

Fig. 2. Ranking of the studied species groups according to number and type of correlations with species richness.

each species group. In this way, we could identify the most frequently studied structural attributes and their correlations with different species groups, as well as knowledge gaps.

3. Results

3.1. *Most and least frequently examined species groups in literature*

The most frequently examined species group was arthropods, with 32 studies providing 147 cases of correlated structure-diversity relationships (Table 2). The species richness of lichens, birds, bryophytes, vascular plants, and fungi were examined by between 10 and 20 studies each, providing between 40 and 67 correlations per species group. The least frequently studied species groups were bats, trees (due to the subdivision and overlap with vascular plants), and molluscs. The studies were distributed throughout Europe; however, most studies had been conducted in Germany and France (Fig. 1). The examined studies were located only in the temperate regions of the indicated countries.

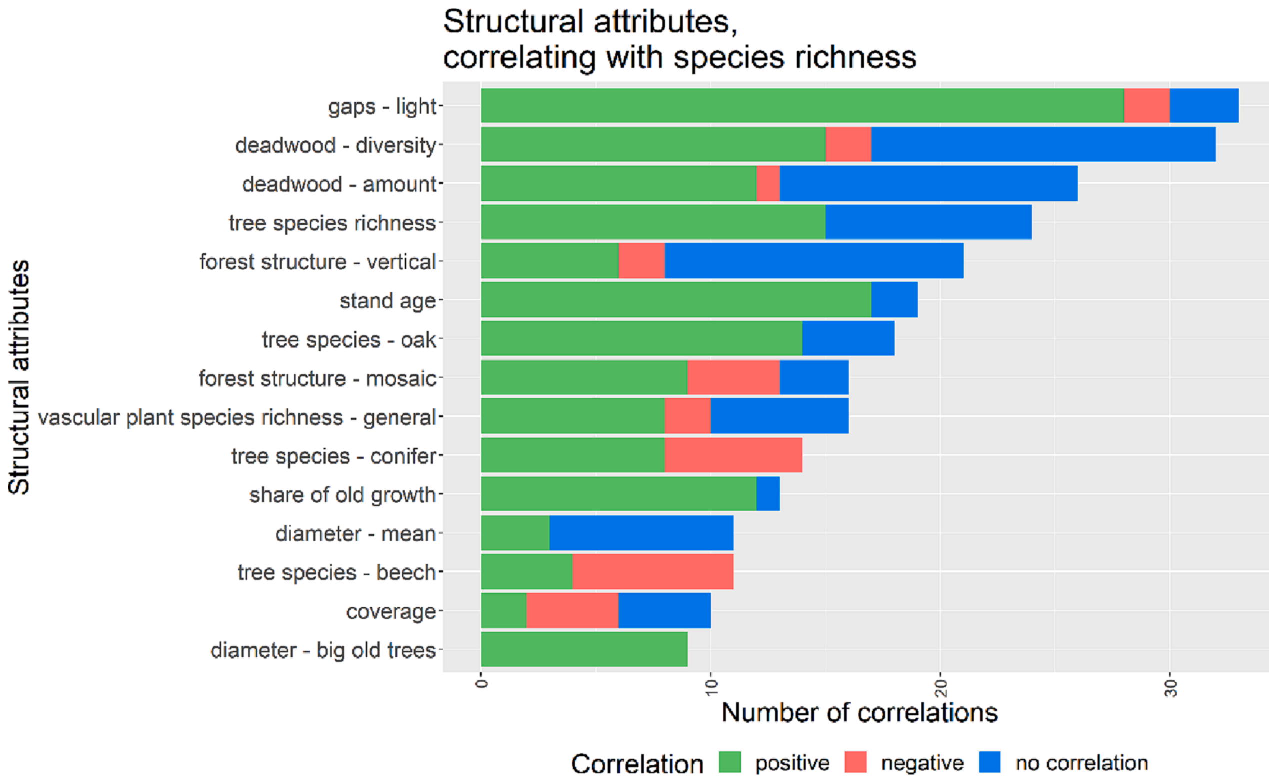

Fig. 3. Ranking of 15 most frequently studied structural attributes according to the number and type of correlations with species richness.

3.2. Ranking of examined species groups in literature

In the literature review, arthropods were the most frequently examined species group, with 82 positive correlations, 9 negative correlations, and 56 cases where no correlation was found (Table 2 and Fig. 2). The second most frequently examined species group was lichens, for which 50 positive correlations, 8 negative correlations, and 9 cases of no correlation and were found. Further species groups according to their occurrence in the literature were bryophytes, birds, fungi, and vascular plants. Here, between 50% (vascular plants) and 90% (birds) of the correlations were positive (Table 2 and Fig. 2). The greatest share of negative correlations between structural attributes and species richness was found for vascular plants (11 out of 37). Very rarely examined species groups were the groups of molluscs, bats, and trees, and thus did not provide enough evidence for this study.

3.3. Ranking of examined structural attributes in literature

The most frequently studied structural attributes in the literature reviewed here are ranked in Fig. 3, and include the type of correlation found (no correlation, negative, or positive correlation). We focussed on the 15 most frequently reported structural attributes; these can be considered as evidence of the correlations between structural attributes and species richness.

Light availability at the forest floor produced by canopy gaps, stand age, the share of oak, the share of old-growth forest, as well as large, old trees, were the structural attributes with the highest positive correlations with species richness. (Fig. 3 and Table A1). Diversity of deadwood and light availability at the forest floor produced by canopy gaps were examined most frequently over all included studies (33 correlations each). The share of conifers and the share of beech were negatively correlated with species richness in nearly half and in more than half the cases, respectively.

3.4. Matrix of correlations found in literature

We further examined the types of correlations observed between structural attributes and species richness of different taxa (Fig. 4).

The species richness of **arthropods** was most clearly positively correlated with canopy gaps, the share of oak, a general forest mosaic, and the share of conifers. Positive correlations with **bat** species richness were found for gaps and the amount of deadwood, but the sample size was low. The species richness of **birds** was mostly positively correlated with nearly all attributes except the share of conifers, where only negative correlations were found. **Bryophyte** species richness was mostly positively correlated with tree species richness, but with a mosaic forest structure only negative correlations were found. Species richness of **fungi** had the most positive correlations with deadwood diversity. The species richness of **lichens** was mostly positively correlated with gaps and stand age, but other structural attributes connected to old-growth characteristics were also positively correlated. The **mollusc** species richness was positively correlated with stand age, but only one study was found. For **tree species** richness as a subgroup of vascular plants, only the share of oak was positively correlated. The low number of studies can be explained by the fact that some studies analysed total species richness of vascular plants and examined tree species richness separately. **Vascular plant** species richness yielded a heterogeneous picture of all types of correlations. Gaps, stand age, the share of oak and conifers, as well as old-growth elements were positively correlated with vascular plant species richness. (Fig. 4).

In summary, the type of correlation between structural attributes and species richness depended strongly on the species group. The clearest correlation was found for gaps providing light, the share of oak, and the structural attributes related to the old-growth successional stage as indicated through stand age, the share of old-growth, and large, old trees.

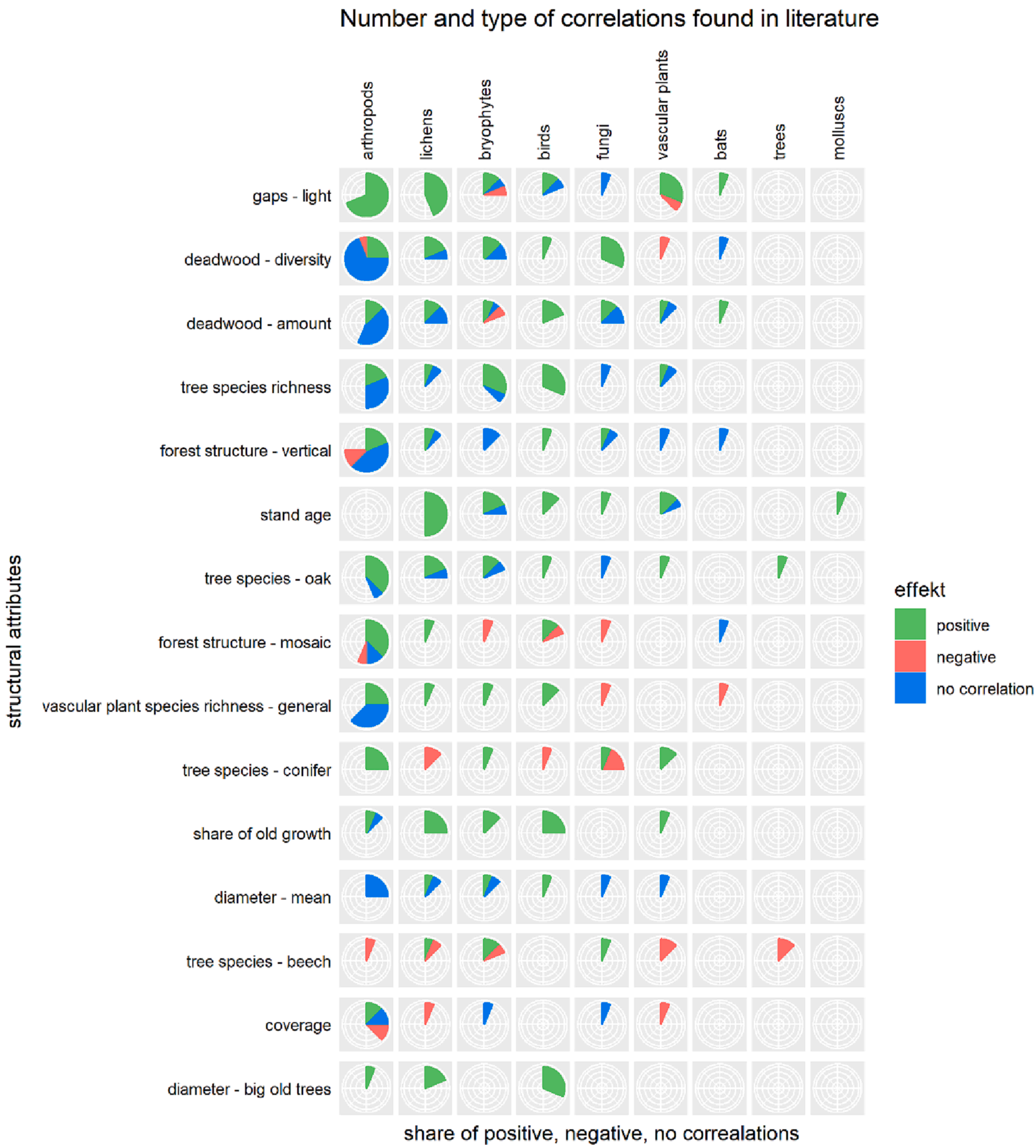

Fig. 4. Matrix of correlations between structural attributes and species richness of different species groups. Full circles represent the highest number of reported tests of correlations; this was the correlation between deadwood diversity and arthropods. Smaller shares of the circle show the relative number of reported correlations compared to the highest possible number of correlations.

3.5. *Identified knowledge gaps*

The least examined species groups regarding correlations with forest structure were bats, molluscs, and tree species as subgroups of vascular plants. The division into the subgroup of trees resulted in a small sample size. The least frequently examined structural attributes were specific microhabitats or deadwood items of a specific size and habitat continuity. Those structures were specific and therefore only occurred in one study each.

4. Discussion

4.1. Results summary

The first question to be answered by our study was:

Which structural attributes are correlated with the species richness of different taxa according to existing studies?

The existence of canopy gaps and structural attributes that are related to old-growth phases such as large diameter trees, stand age, and deadwood were found to be important for many species groups (Fig. 4). This is in agreement with many other studies that have identified old trees (Humphrey et al., 2002; Knuff et al., 2020; Machar et al., 2019; Mag and Ódor, 2015; Moning and Müller, 2009), deadwood (Blaser et al., 2013; Gunnarsson et al., 2004; Przepióra et al., 2020), and increasing stand age (Hofmeister et al., 2015; Kaufmann et al., 2018; Mazziotta et al., 2016; Moning and Müller, 2009) as important structures. The importance of canopy gaps presumably results from the fact that many species groups are favoured by increasing light availability and temperature at the forest floor, e.g., vascular plants and arthropods. It may also be attributed to stages where natural disturbances or silviculture provide abiotic conditions that are related to early successional phases. Those phases are known to be positively related to floristic and faunal diversity (Hilmers et al., 2018). Also, the positive effect of deadwood on saproxylic species has been shown to be much higher in a lighter environment than under shady conditions (Lettenmaier et al., 2022). For the species groups of molluscs, bats, and trees, only a few studies were found that examined correlations with structural attributes. The evidence of our results for these species groups is therefore low.

Contradicting results concerning the share of spruce and beech can result from studies being located in different altitude ranges. The share of spruce can have positive effects on biodiversity in its natural range, meaning in mountain areas (Máliš et al., 2012). In lowlands, however, where it non-native and is or was mostly part of monocultures, it can rather be an indicator for a low biodiversity (Farská et al., 2013). Both positive and negative correlations of beech with species richness can result from occurrence of beech. In managed beech forests the structural homogeneity and the low light availability due to a closed canopy layer can lead to a low species richness. More natural beech forests with low human intervention, however, can provide a high structural heterogeneity and have a high variability in light conditions. Those beech forests therefore belong to the richest habitats for forest biodiversity (Schneider et al., 2021). Also selectively managed beech forests can bear a high potential for species richness (Brunet et al., 2010). Especially the setting-aside of old beech trees can provide important habitats (Hofmeister et al., 2016).

Some of the structural attributes have been long known to foster biodiversity, but our study also showed that there is no single forest structure that could serve as a simple safeguard for biodiversity. Depending on the species group or single species, a range of different structural attributes are needed to ensure and foster high species richness over the long term. This finding was previously stated in the habitat heterogeneity hypothesis (MacArthur and MacArthur, 1961). Our results confirm the benefits of increasing the share of old-growth stages in forests to foster their capacity to support a range of different taxa (Kaufmann et al., 2018; Machar et al., 2019; Moning and Müller, 2009). Spatial scale seems to play a key role in supporting all successional stages, as high habitat heterogeneity at the landscape scale can foster biodiversity (Schall et al., 2018). Larger canopy gaps that are part of the resulting structure, which foster different successional stages, were found to correlate with high species richness of many species groups (Leidinger et al., 2020; Przepióra et al., 2020; Svoboda et al., 2010). Since gaps also result from thinning and final harvests, no trade-offs between wood production and nature conservation are related to these structural elements. This is not the case for microhabitats and deadwood, however, which occur more frequently in unmanaged than in managed forests (Larrieu et al., 2012; Martin et al., 2021) and correlate with high species richness. These structural attributes do therefore need special attention.

4.2. Forest management and species richness

Our findings largely confirm the current knowledge of drivers of species richness in forests. We were able to demonstrate the importance of several structural attributes that can be provided even in production forests. There are strong indications that the retention of old-growth attributes such as habitat trees and deadwood in managed forests significantly contributes to species conservation (Fedrowitz et al., 2014; Storch et al., 2020; Thorn et al., 2020a). Czerepko et al. (2021a) found no differences between a strict forest reserve and managed parts of Bialowiza forest, possibly resulting from a high naturalness of the forest even in the managed parts. A small retention section in a heavily managed forest stand might not, however, be enough to ensure the habitats of specialized species; these would need specific conservation approaches (Fedrowitz et al., 2014). All structural characteristics known to positively influence species richness in forests appeared in our literature search. The most frequently mentioned structural properties are known to be impacted or shaped by silvicultural management. At first glance, from a nature conservationist's perspective, this can be seen as negative. Tree size heterogeneity can, for example, be decreased by thinning from below (Zeller et al., 2021). In commercially managed stands, especially the old-growth and decay phases are often missing due to final tree harvests. This usually leads to lower deadwood volumes than in forests that have been unmanaged for centuries (Winter et al., 2005). Consequently, it has repeatedly been requested that forest patches should be set aside to permit development of features that are known to be typical of old-growth forests (Thorn et al., 2020b) which have been found to correlate with a higher species richness (Czerepko et al., 2021a). Forest management can take these findings into account and can, for example, ensure a minimum of 5–10 habitat trees per hectare that are excluded from any future harvests (Bütler et al., 2013). Such measures may also provide the combination of large living and dead trees that are known to contribute to biodiversity (Spînu et al., 2022). In many parts of Europe forest management aims to increase continuous-cover forests (Larsen et al., 2022; Pommerening and Murphy, 2004). This will increase their resemblance to primeval forests (Hobi et al., 2015; Meyer et al., 2003; Stillhard et al., 2022). It will thus contribute to conserving and restoring the natural biodiversity in managed forests (Meyer and Schmidt, 2008). In particular, young and very old successional phases are often rare in managed forests (Faustmann, 1995) and light-dependent species that occur mostly in those phases cannot find their needed habitats (Hilmers et al., 2018). Light-dependent species may also be outcompeted in later stages by shade-tolerant tree species such as European beech (Meyer, 2005). Most light-demanding tree species are important hosts for phytophagous insects and mites (Brändle and Brandl, 2001). Since tree species richness was found to be positively correlated with stand productivity (Ammer, 2019; Zeller et al., 2018) conservation and production-oriented goals do not necessarily conflict. Silvicultural management can be used to specifically shape stand structure and satisfy different needs. Depending on their management, commercially cultivated forests can provide forest biodiversity and at the same time be stable, resilient, and productive. In managed forests, gaps might be best introduced through single-tree or patch-wise harvesting (Muscolo et al., 2014). Management-induced gaps and other disturbances may, however, attract non-native species (Czerepko et al., 2021a). The aim of forest management – increasing species richness or preserving native species – therefore has to be considered. Other measures that foster small scale structural heterogeneity instead of large scale homogeneous continuous-cover forests or large clear-cuts are also possible. Deadwood items of different sizes and tree species might be left in the stand, while old trees above harvesting age can provide microhabitats. These measures would need to be evaluated under the overall aim of wood production, including conflicts and trade-offs (Pohjanmies et al., 2017; Zeller et al., 2021). How trade-offs can be balanced under the pressure of climate change and increasing demands on forest ecosystem functions and services will remain a big challenge going forward. Encouragingly, recent concepts and reports show that compromises can be found (Mergner, 2021; Sierota and Miścicki, 2022).

4.3. Forest structural attributes in species monitoring

The clear relationships between structural attributes and species richness of many species groups provide the basis for using forest structure in species monitoring programs. Yet, those structures alone do not guarantee the actual presence of species or species groups. Complementing more detailed species monitoring, forest structural attributes can at least provide a first insight into the state of a forest concerning its potential for biodiversity, especially under conditions of modest financial resources (Larrieu and Gonin, 2008; Zeller et al., 2022).

4.4. Critique – Influence of search pattern on included studies

We focussed on the search of correlations between structural attributes and the species richness of different species and species groups. Studies that examined a correlation of forest or stand structure on total species richness were not included. We considered those studies to be too general to answer our research questions and to differentiate between the different species groups. As our search pattern was open to all structural attributes that were named as such, no pre-selection was conducted that could have influenced the search results in advance. Each structural attribute found during the literature search was added to the analysis. Note that our review can only highlight correlations; it cannot identify the quantitative effects of structural properties on the absence or presence of species or groups of species.

4.5. Critique – Focus of studies on positive effects

Non-existent or negative relationships of structural properties and species richness of different species groups are often not considered worth publishing (DeVito and Goldacre, 2019). This may have led to the result that most correlations reported in the literature were positive. But in fact, our results show that there are sometimes contradictory correlations (Fig. 3).

4.6. Critique – Comparability of studies

As in most *meta*-analyses, the examined studies were not comparable with respect to many factors such as plot size, forest type, or sampling method (Burrascano et al., 2021); also they were conducted at different times. The correlations between structural attributes and species richness might therefore be strongly context dependent. Further, the definition of biodiversity always has to be considered. Depending on the focus of the highest possible number of species or ‘naturally occurring’ species composition, different structural attributes would be needed. Our study focussed on literature that examined species richness without evaluating species assemblages and their functions. The concept of species richness is controversially discussed (Hillebrand et al., 2018) since it is not only the number of species that matters. Instead, a certain species richness needs to be evaluated in relation to the typical local species community and the functions that different species fulfil in an ecosystem (if those are known at all).

4.7. Critique – Stand scale vs. Landscape scale

Most of the studies found in the literature were case studies conducted at the stand level. But the habitat heterogeneity theory (MacArthur and MacArthur, 1961) indicates that structural heterogeneity at the landscape level would probably best provide a small-scale mosaic of a variety of structures and habitats (Schall et al., 2018). Especially for vascular plants, lichens, bryophytes, and vertebrates, it has been shown that habitat continuity at the landscape scale is an important driver of biodiversity (Kolb and Diekmann, 2004; Nordén et al., 2014; Wulf, 2004).

4.8. Critique – Soil properties not included

The focus of our study was on the above-ground structures that correlate with biodiversity, as those structures could easily be recorded in biodiversity monitoring programs or inventories. Soil related surveys are often too expensive to be included in species monitoring programs, and they depend on monetary resources and taxonomic expertise. With the aim of identifying structures that can be included in a biodiversity monitoring program, we focused on above-ground structures only. Nonetheless, the greatest share of biodiversity is usually located belowground (insert Wardle, 2002; Bakker et al., 2019). Soil biota play important roles in ecosystem functioning (insert Brussaard et al., 1997; Yang et al., 2018) and it has been repeatedly stated that they should receive greater attention in biodiversity monitoring (insert Burrascano et al 2021, Zeiss et al 2022). Furthermore, soil properties provide important information on the state of biodiversity (Bispo et al., 2009) and soil health. Some measures of soil health as suggested by Zeiss et al. (2022) could easily be included in ongoing monitoring (available phosphorous, total nitrogen, organic carbon, pH-value), whilst others, such as microbial activity and biomass, are more expansive and more complicated to include.

4.9. Critique – Limitations of species richness as measure for biodiversity

Species diversity as measure of biodiversity is often criticized for not showing developments in species composition. A high species richness could hide extinct species as long as other species appeared at that location. For lichen, species richness showed to be a valid indicator for forest naturalness (Czerepko et al., 2021b). For a more complete picture on the state of a forest in terms of biodiversity, additional measures, e.g. species composition should be examined (Fleishman et al., 2006). Species richness was the most common measure in literature and most studies had used a different and thus non-comparable set of variables. We therefore used species richness as simple measure in our analysis but are aware of the shortcomings of that aspect. Its dependency on spatial scale is a further challenge to be considered in biodiversity monitorings (Hillebrand et al., 2018).

5. Conclusions and outlook

Our approach, focussing on structural attributes instead of the category managed vs. unmanaged forests, has the advantage of analysing measurable forest structures across studies. It also provides insights into the diverse relationships between structural attributes and species richness of different species groups. Such insights support the development of efficient monitoring concepts based on forest structure, where a sampling of species is not possible or where classical species monitoring can be extended by assessing relevant structural attributes. In silvicultural management planning, fostering certain structures is similarly more efficient and convincing if reliable data indicates the most important structures.

CRediT authorship contribution statement

Laura Zeller: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Agnes Förster:** Formal analysis, Writing – original draft. **Constanze Keye:** Conceptualization, Methodology, Writing – review & editing. **Peter Meyer:** Conceptualization, Funding acquisition, Methodology,

Table A1
Number of studies and number and type of structural attributes in correlation with species richness.

Structural attribute	n studies*	n correlations	type of correlation		
			positive	negative	no correlation
gaps - light	22	33	28	2	3
deadwood - diversity	11	32	15	2	15
deadwood - amount	14	26	12	1	13
tree species richness	15	24	15	0	9
forest structure - vertical	3	21	6	2	13
stand age	9	19	17	0	2
tree species - oak	8	18	14	0	4
forest structure - mosaic	5	16	9	4	3
vascular plant species richness - general	5	16	8	2	6
tree species - conifer	5	14	8	6	0
share of old growth	11	13	12	0	1
diameter - mean	3	11	3	0	8
tree species - beech	6	11	4	7	0
coverage	3	10	2	4	4
diameter - big old trees	8	9	9	0	0
Sum	128 (88)	273	162	30	81

*Most frequently examined correlations between structural attributes and species richness. Sorted by number of correlations. Total number of studies: 88. Most studies examined more than 1 structural attribute leading to higher sum of studies.

Project administration, Writing – review & editing. **Christian Roschak:** Project administration, Writing – review & editing. **Christian Ammer:** Conceptualization, Funding acquisition, Methodology, Project administration, Writing – review & editing.

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.

Data availability

This is a review article, the examined studies are available online

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Appendix

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