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A systematic meta-review: The relationship between forest structures and biodiversity in deciduous forests

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ABSTRACT

Human activities in deciduous forests over the past centuries have influenced associated species. To reduce extinction risks and mitigate population declines, there is growing interest in forest conservation and restoration, including initiatives by the European Union (EU). For resulting restoration and conservation practices to succeed, it is essential to know which forest characteristics promote biodiversity conservation. This review is the first comprehensive systematic meta-review that examines the consistency of relationships between forest structures and biodiversity in temperate, deciduous forests. Our results suggest that the presence of angiosperm trees and large seed producing trees, deadwood quantity, older and larger trees, as well as tree cavities relate positively to the diversity of multiple taxonomic groups, including lichens, insects, birds, and fungi. These findings support the prioritization of deadwood and presence of old trees as key targets in restoration and conservation practices. In contrast, the connection between many other forest structures and biodiversity were more ambiguous and varied between taxonomic groups, emphasizing the need to be explicit about restoration and conservation goals when formulating targets for forest structures. Even though the relationship between forest structures and biodiversity was thoroughly studied in reviews, molluscs, reptiles, amphibians, and ground-dwelling invertebrates like spiders and ground beetles were underrepresented. Furthermore, significant knowledge gaps were identified for some potential important structures such as deadwood in the canopy, tree height, and tree biomass. The findings of this review show that while some old-growth forest structures can be used as biodiversity indicators, relationships between stand-level structures and biodiversity are difficult to generalize.

1. Introduction

Human activities in natural ecosystems, including direct effects of land use and land-use change and indirect effects such as pollution and climate change, have influenced biodiversity in many terrestrial ecosystems (Harfoot et al., 2021). In the temperate region, human impacts have put a high pressure on forest ecosystems, which has among other effects led to large-scale loss of primary forests by transforming them into young production forests globally (Sabatini et al., 2018; Sommerfeld et al., 2018). Consequently, deciduous forests occurring outside protected areas are often subject to human disturbances related to forestry which can profoundly change their structures and composition (Fischer et al., 2013; Keddy and Drummond, 1996; McGrath et al., 2015; Vilén et al., 2012; but see Neudam et al., 2023). The possible loss and structural changes of deciduous forests caused by forestry have the potential to impact a variety of forest-dependent species (Stupak and Raulund-Rasmussen, 2016; Tinya et al., 2021). Because deciduous forests harbour most of the red-listed forest species in Europe, these forests are a primary concern for nature conservation (Berg et al., 1995; Flensted et al., 2016; Springer et al., 2024).

To avoid the extinction of forest-dependent species in temperate, deciduous forests, the interest to restore and conserve biodiversity within managed and unmanaged forests has increased. For example, the EU Biodiversity Strategy has the goal to protect 30 % of the land area by 2030, including EU's remaining primary and old-growth forest and goals aligning with rewilding practices, to increase the biodiversity and secure ecosystem services (EU, 2024). Forest structures can guide these conservation efforts by acting as indicators of the state of the forest because they provide habitats for organisms and are, thus, at least to some extent linked to biodiversity (Lindenmayer et al., 2000; Zeller et al., 2023). In

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addition, forest structures are generally easier to measure than the biodiversity of associated organisms (Ćosović et al., 2020). For example, the European Nature Restoration Regulation uses standing and lying deadwood, the share of forests with uneven-aged structure, and tree species diversity as biodiversity indicators (EU, 2024). However, there may be other forest structures of importance to biodiversity that have been overlooked, and it is unclear to what extent these biodiversity indicators are consistent across taxonomic groups. Therefore, it is necessary to understand which forest structures sustain high-quality habitats and associated biodiversity, that in turn can be used to measure the effectiveness of restoration and conservation practices. In this study, we define forest structures as bio-physical structures such as deadwood that can be estimated by its volume or tree size that can be measured as tree diameter. We focus not only on estimates of amount, but also on the diversity and distribution of forest structures.

The relationship between habitat structures and biodiversity can follow two widely discussed, non-mutually exclusive hypotheses. Firstly, there is the habitat amount hypothesis, which assumes that an increase in habitat amount – in this case habitat with essential forest structures – will result in an increase in species richness without it being affected by the habitat configuration (Fahrig, 2013). The second hypothesis is the habitat heterogeneity hypothesis which states that an increase in habitat diversity will lead to a higher biodiversity due to the larger variety of available niches (Tews et al., 2004). Following these hypotheses, it can be expected that the presence of forest structures that increase habitat availability and complexity in a forest stand will increase biodiversity. However, these relationships might also be affected by the spatial scale of heterogeneity (Schall et al., 2018). Furthermore, since different species have different habitat requirements, we expect it to be difficult to generalize forest structure - biodiversity relationships across taxonomic groups, such that structural conservation targets need to be tailored to conservation/rewilding goals.

Primary studies that looked at the relationship between structural indicators and biodiversity in forest ecosystems have been summarized in several reviews (Gao et al., 2015; Oettel and Lapin, 2021; Zeller et al., 2023). However, most of these reviews focused on a specific species group, forest structure or management practice, or only included studies conducted in specific regions (Ishii et al., 2004; Lassauce et al., 2011; McElhinny et al., 2006; Oettel and Lapin, 2021; Sandström et al., 2019). Reviews that did take into account several forest structures and species groups have, to our knowledge, focused on European forests in general and not made a clear distinction between coniferous, mixed, and deciduous forests, among other things due to data constraints (Burrascano et al., 2023; Gao et al., 2015; Zeller et al., 2023). As a result, it is still unclear which forest structures are most significant when conserving biodiversity in deciduous forests and to what extent this depends on the taxonomic group in focus. This meta-review combines the results of previous reviews to understand which forest structures are important for biodiversity, if these results are consistent between different taxonomic groups, and identifies research gaps within this field. Additionally, we describe the mechanisms found behind these relationships. The results can be used to locate forest ecosystems with high nature values and to improve and understand the effectivity of forest restoration and conservation practices.

2. Methods

2.1. Article selection

To understand the relationship between forest structures and biodiversity in temperate deciduous forests, we performed a second-order synthesis, i.e. systematically summarized the results of previous reviews. The search was focused on reviews that studied the effects of forest structures on species diversity metrics in temperate (defined by FAO, 2018), deciduous forests. We used a PICO to set the search protocol (Linares-Espinós et al., 2018), in which the Population was defined as temperate, deciduous forests, the Intervention was non-applicable, the Comparison was defined as different forest structures, and the Outcome was multiple measures of aboveground biodiversity, excluding trees. To decrease the search bias, we followed a pre-determined search protocol (Fig. 1) and screened articles found within Scopus and Web of Science (core collection) (Haddaway et al., 2015) after selecting only review articles in the search engine. To find relevant reviews, we used the following keywords on the 12th of September 2023:

forest* AND (structure* OR management*) AND (diversity OR biodiversity OR "species richness") AND (elm OR beech OR oak OR birch OR maple OR aspen OR ash OR alder OR lime OR deciduous OR temperate OR nemoral OR hemiboreal OR broadlea*).

Afterwards, the efficiency of the search was tested by comparing our search results with reviews recommended by two experts. Two out of eight recommended reviews were not found during our search due to the absence of a specified region (temperate, nemoral, or hemiboreal) and forest type (deciduous forest or deciduous tree species) in their abstract, title, or keywords. After removing this limitation in the search, the number of papers increased significantly from 839 to 7239 papers. From the non-included papers, 200 papers were randomly tested for their relevance. Of those 200 papers, only six papers included relevant information, which showed that our search did include most of the important reviews within this field.

After removing the duplicates between Scopus and Web of Science, we read the title and abstract of each review and scanned the article in its entirety to exclude those that did not mention relationships between forest structures and biodiversity, were written in a non-English language, or were inaccessible. Afterwards, each paper was read thoroughly and only papers that described the qualitative or quantitative relationships between forest structures and biodiversity were included, excluding those that described the connection indirectly by only mentioning effects of forest management practices (and not resulting structures) on biodiversity. Furthermore, we excluded relationships between forest structures and biodiversity that were only mentioned in the introduction. Lastly, we excluded reviews about soil organisms, microorganisms, genetic diversity, aquatic diversity, invasive species and pests, and reviews that did not specify forest types or only included information about tropical, coniferous, swamp, riparian, or evergreen forests.

In total, we found 887 review articles (Fig. 1) on the Web of Science and Scopus. After removing duplicates and non-English articles, 687 papers remained. Of these reviews, we read the title and abstract and scanned the main text, which led to an additional exclusion of 504 papers. After thoroughly reading the remaining 183 reviews, 94 papers were excluded because they did not specify a forest type ($n = 14$), only studied coniferous ($n = 8$), evergreen ($n = 4$), or non-temperate forests ($n = 14$), did not describe a direct link between forest structures and biodiversity ($n = 28$), or because they were not review papers ($n = 25$) (Fig. 1). Ultimately, 91 review articles were used for this systematic review. Each review could produce multiple datapoints in our meta-review by describing several relationships between forest structures and biodiversity.

2.2. Data extraction

From every review, we extracted data about forest structures that

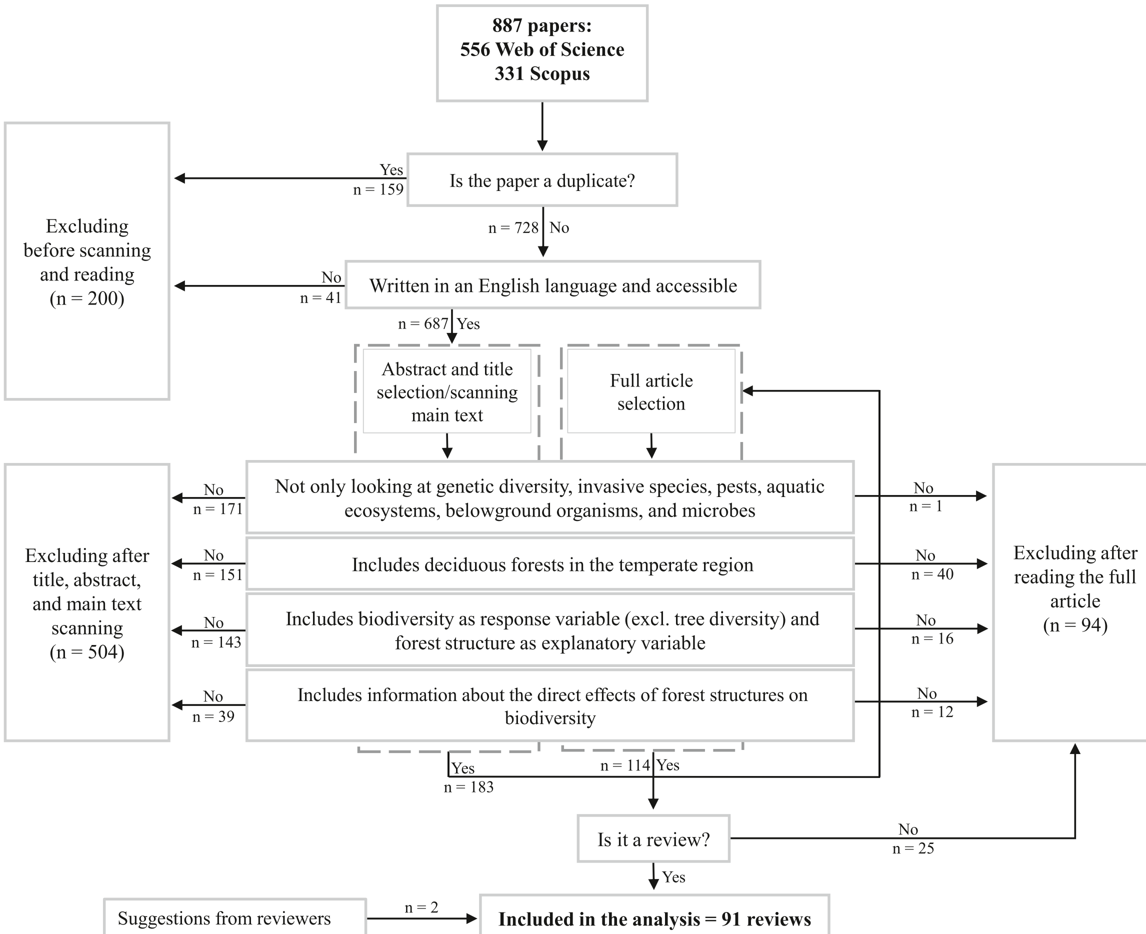

Fig. 1. Review process: A visualization of the review process.

were mentioned in connection to biodiversity (see S.1. for a full description of every forest structure found) and the type of biodiversity metric (diversity, richness, abundances, presence/absence of multiple species, habitat quality, habitat availability or general effects; see S.2. for a full description of biodiversity metrics). Additionally, when possible, we extracted the pattern (positive, negative, mixed or neutral) of the relationship between each forest structure and the studied organism(s). Before the analysis, some groups with the same response patterns found within this study were combined due to limited records and because the groups were often mentioned intertwined within papers. Saproxylic beetles were incorporated in the group "saproxylic insects", ground-dwelling invertebrates were added to "invertebrates", rodents and shrews were incorporated in the group "Small non-flying mammals", and large herbivores were incorporated in the group "Mammals". Furthermore, all insects that were not specified to be saproxylic (e.g. moths, butterflies, bees) were combined into the group "Insects". The group "General" was used when the taxonomic group was unspecified. For each review, we also extracted which continent and forest type (mixed or deciduous) the review focused on and the review type (qualitative or quantitative). If the review included temperate and non-temperate areas, only the locations in the temperate area were recorded. Similarly, if the review included deciduous and coniferous forests, we tried to only include information about deciduous forests.

3. Results & discussion

Most of the reviews included study areas within Europe (63 %) and North America (42 %), and 16 % of the studies included information from Australia, Asia, or South America. Thirteen papers did not specify any region. The earliest review was published in 1997, but most of the reviews were published after 2012 (Fig. 2).

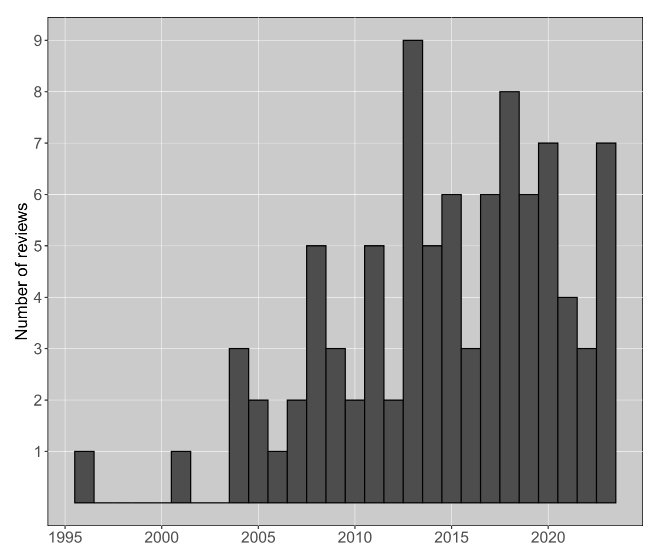

Fig. 2. Publication year: The distribution of the publication year of studies used in this review.

Thirty different forest structures were identified to be connected to biodiversity (Fig. 4a-c; S.1.). Species diversity, richness, and habitat

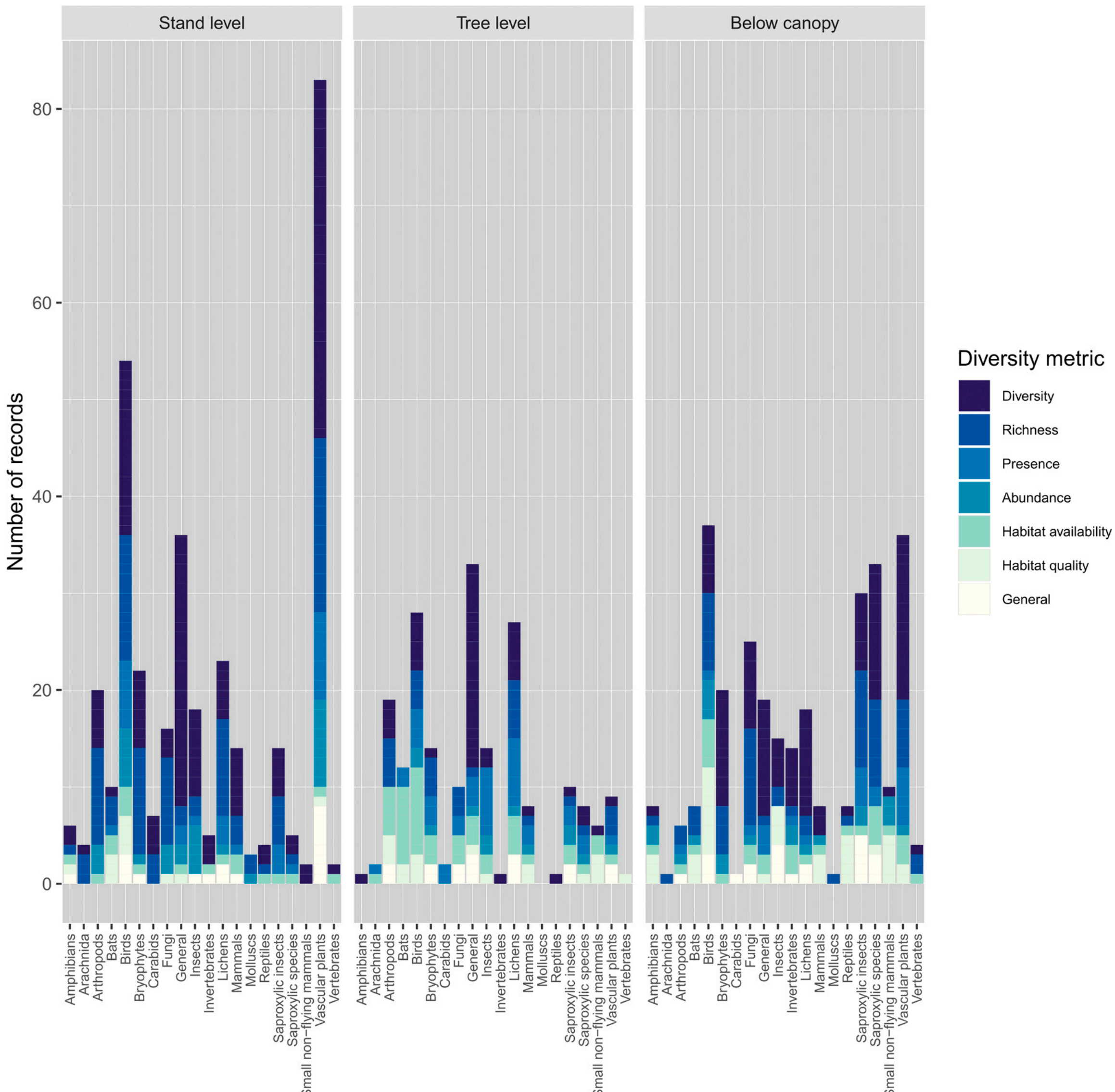

Fig. 3. Biodiversity metrics: The distribution of the biodiversity metrics used by the reviews. A review had multiple records if it described multiple relationships.

availability were the most common biodiversity metrics used, respectively (Fig. 3). The relationship between forest structures and biodiversity was mostly described at the forest stand and tree level scale and, less commonly, at the landscape scale. The two most reported forest structures connected to biodiversity were deadwood volume (49/91 studies) and deadwood type (39/91 studies) (Fig. 4a-c). In addition, tree diversity, structural diversity, and canopy closure were well reported (included in 35 %, 31 %, and 38 % of the studies respectively) in connection to biodiversity. The most common species groups discussed in the reviews were birds and vascular plants, while information on molluscs, reptiles, amphibians, spiders and ground-beetles was often lacking. In the next section, we summarize the effects of forest structures on the biodiversity found during this study.

3.1. *Stand level structures*

3.1.1. *Tree diversity*

The relationship between tree diversity and biodiversity has been commonly reported in previous reviews (Fig. 4a). Here, the effects of tree species are defined as the relationship between tree diversity (n = 39) or tree species composition (n = 18) and biodiversity.

We did not find a clear, consistent positive relationship between the tree diversity and biodiversity (Fig. 4a). For many non-herbivorous organisms, like birds and plants, changes in tree structure may have a

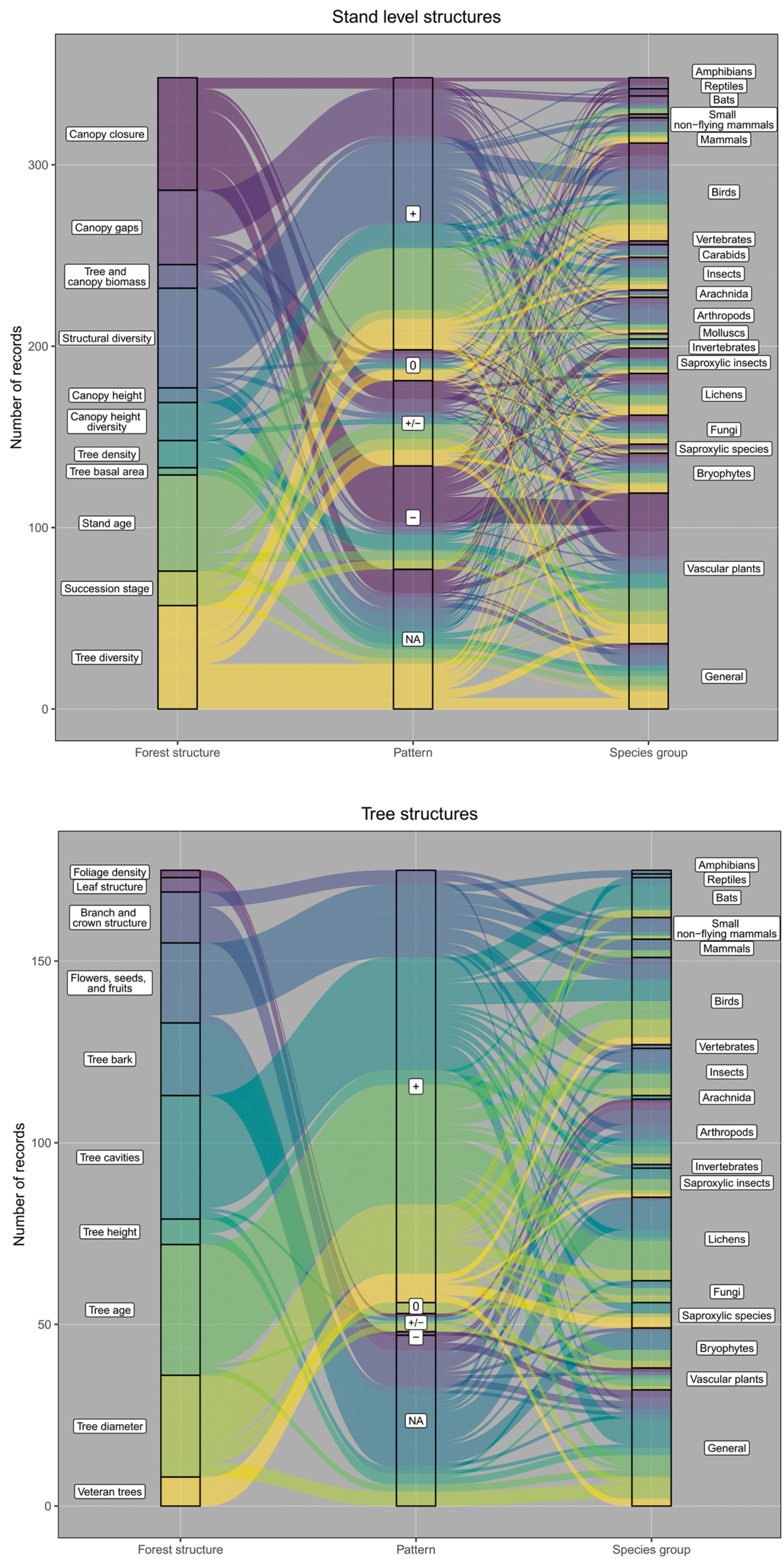

Fig. 4. Relationship between forest structures and biodiversity: The described relationships (+ stands for positive, 0 stands for neutral, +/- stands for mixed, - stands for negative, and NA stands for non-applicable) between a) stand structures, b) tree structures, and c) below-canopy structures and the biodiversity. Alluvial plots were created with the *ggalluvial* package (Brunson, 2020).

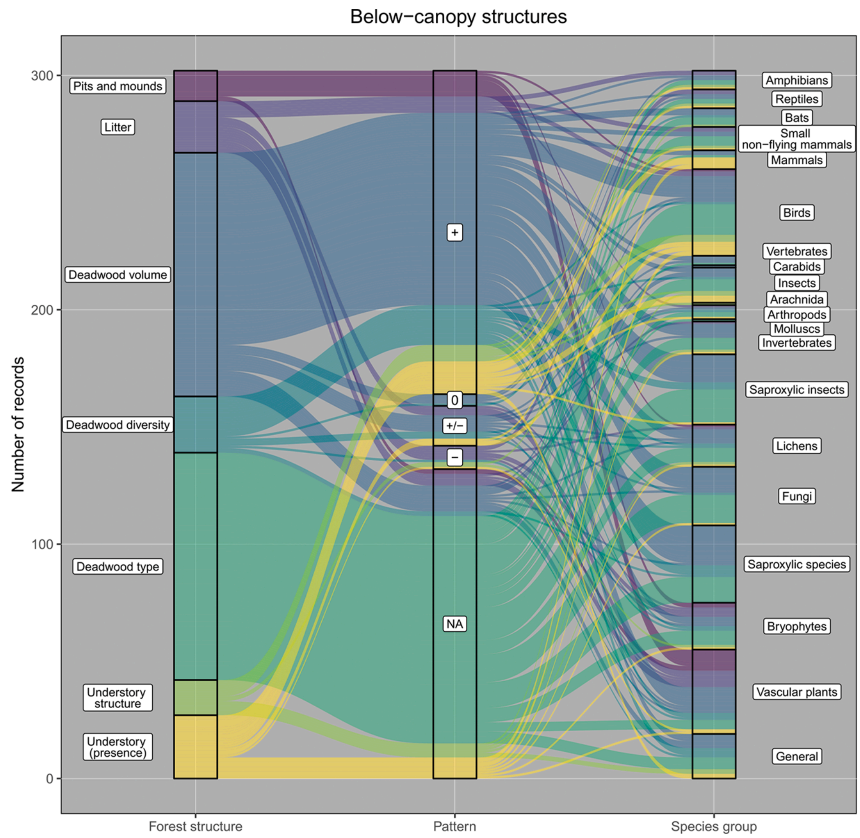

Fig. 4. (*continued*).

higher explanatory power than tree diversity per se because they might not require a specific tree species to create their habitat niches (Ammer et al., 2008; Bergen et al., 2009; Felton et al., 2022; Ishii et al., 2004; Jaroszewicz et al., 2019; Su et al., 2019; Tomiałojć and Wesołowski, 2004). In addition, the effects of tree diversity might also depend on the spatial distribution of different species within stands, in which aggregations of the same tree species in patches might have a stronger effect on the biodiversity than a spatially even mixture of tree species (Felton et al., 2022). However, a positive relationship was occasionally found for the diversity of insects, mammals, birds, and vascular plants. This could be the result of a higher habitat heterogeneity, larger structural complexity, and/or higher productivity as a result of the higher tree diversity, in turn resulting in more available microhabitats and food resources (Dieler et al., 2017; Pommerening and Murphy, 2004; Valencia-Cuevas and Tovar-Sánchez, 2015). For example, combining different tree species that vary in their bark roughness, pH, and light penetration, could provide microhabitats for a variety of organisms (see 3.2.4 and 3.1.2).

To understand how tree species composition on a stand scale can affect the biodiversity, several studies looked at the biodiversity values of forests with different dominant tree species. Here, beech forests were often found to have a low (vascular plant) diversity due to their dense canopies and, therefore, low light conditions in the forest (Leidinger et al., 2021; Schulze, 2018; Zeller et al., 2023). However, this relationship might also be caused by the often extensive management history of such forests in the temperate region (Zeller et al., 2023). In contrast, old aspen and oak forests were found to maintain a high lichen, bryophyte, and vascular plant diversity because of the high availability of light on the forest floor (Dey, 2014; Rogers et al., 2020; Tullus et al., 2012). In addition, both oak and hazel forests often contain many birds and mammals that forage on acorns and hazelnuts (Dey, 2014). Some organisms might be affected only by the presence of their host species instead (Brändle and Brandl, 2001). For example, Nascimbene et al. (2013) stated that tree composition is one of the most determining variables for the lichen diversity because lichens can be specialized on a single tree species.

Table 1
The relationships between forest structures and species groups when patterns could be described. The colour indicates the type of pattern – positive relations (green), neutral relations (blue), mixed results (yellow), and negative relations (red) – that was most recorded for a relationship. A mixed relationship was noted if the highest recorded relationship occurred ≤ 50 % or if most reviews found varying relationships. The darker the colour, the more papers were found describing the relationship shown by the colour. The numbers show how many papers described the pattern according to the colour / all papers that recorded a pattern. The stars and circles (omitted from the "total" column) represent if and how many quantitative reviews were included in these results. A quantitative review that shows the given pattern is represented by a star while a circle means that a quantitative review showed another result.

	Amphi.	Arachn.	Arthrop.	Bats	Birds	Bryoph.	Carabids	Fungi	General	Insects	Inverteb.	Lichens	Mamm.	Mollusc	Reptiles	Sapro. insects	Sapro. species	Small non-flying mamm.	Vascular plants	Vertebr.	Total
Stand level structures																					
Canopy closure	2/3 °	1/1 *	1 *	1/1	4 *	2 °		3 *°		1/1		3 °		1/1 *	2/2 *	5/5 **	1/1	1/1	14/18 ******	2	31/48
Canopy gaps	1/1		2/3 *	3/3 *	6 *	3 *	1/1	1/1 *		1/1	1	2 °			1/1	1/1	1/1		13/14 *		26/39
Canopy biomass			2/2																		2/2
Tree biomass			1/1																1/1		3/5
Structural diversity	1/1	1/1 *	5/6 **	1/1 *	9/10 *°	3 °	2/2 *	2/3 *°	6/6	2/2 *		4/4 *	4/4			1/1		1/1	6/7 **°		44/51
Canopy height			1/1																		1/1
Canopy height diversity			1 *	1/1 *	3/3 ***	1/1 *	1/1 *	2 *°		4/4 *	1/1 *	1 *	1/1			1/1 *			1/1 *		12/18
Tree density					1/1 *	1/1						1/1				1/1			4/4 *		8/9
Tree basal area																			1/1 *		1/1
Stand age			2/3 *°	2/2 *	5/8 **°	3/4 *°		3/3 **	2	2/2	1/1	5/5 **	2/2	2/2 *		2/2	1/1		11 *°°		34/48
Succession stage				1/1	3				2	2		1/1	1/1						6		16
Tree diversity		1/1	2 *		8 *°°	3 °		2 °	4/4	2/3		2 *	1/1				1/1		6 *		17/32
Tree structures																					
Foliage density			1																1/1 *		2
Branch size					2/2 *				1/1 *									1/1			4/4
Flowers, seeds, and fruits	1/1		2/2		4/4				1/1	3/3	1/1		3/3		1/1			3/3		1/1	20/20
Tree cavities		1/1	2/2	6/6 *	6/6			1/1	7/7 **	1/1		2/2				2/3 °	2/2	1/1			31/32
Tree height			2/2	1/1 *								1/1									4/4
Tree age			1/1		4/4 *	3/3		2/2	3/4 *	4/4		8/8 *	2/2			3/3			2/2 *		33/34
Tree diameter			2 °	2/2	5/5 *	2 *°		2 °	2/2 *	2		3/3 *				1/1	1/1	1/1	1/1 *		19/24
Veteran trees					2/2				2/2 *							1/1	3/3				8/8
Below-canopy structures																					
Pits and mounds					1/1	2/2						1/1							7/7		11/11
Litter	2/2 **		1/1 *		2/2	2/3						1/1			2/2 *			2/2 *	4		17
Deadwood volume	2		1 *	3/3 **	9/10 ****°	3/4 °		9/10 *°	3/3 *	2/2 *	5/6 °	5/6 °	2/2		2	12/12 ****	16/16 ****	2/2	8/10 **°°	2/3 *°	84/95
Deadwood diversity			1 *	1/1 *	1/1 *	2 *		2/2 *	3/3	1/1		2 *				3/3 **	4/4 **		2/3 °		18/23
Understory structure	1/1 *	1/1 *			2/3 *	1/1				1/1 *					1/1 *			1/1			7/9
Understory (presence)	1/1		1/1		4				2/2	3/3			3/3		1	1/1		1/1	1		14/18

Strong positive relationship (n > 5 & ≥ 80%)
Positive relationship (n > 2 & ≥ 65%)
Weak positive relationship (n > 0 & > 50%)
Strong negative relationship (n > 5 & ≥ 80%)
Negative relationship (n > 2 & ≥ 65%)
Weak negative relationship (n > 0 & > 50%)
Weak neutral relationship (n > 0 & > 50%)
Mixed relationship (n > 0 & ≤ 50%)

3.1.2. Canopy closure and canopy gaps

The relationship between canopy gaps or canopy closure and biodiversity was described in a large number of reviews (Fig. 4a). Even though these two structures can describe similar forest characteristics, we here distinguished the effects of these structures by defining – when possible – canopy closure as the general openness of the forest stand and canopy gaps as larger contiguous open patches in the forest. Canopy closure depends mostly on the tree density that is shaped by natural conditions or management practices, canopy structure, and tree composition of a forest stand while canopy gaps are created by natural and anthropogenic disturbances like windthrows, management practices, and forest fires (Barbier et al., 2008; Felton et al., 2010). Both canopy gaps and lower canopy densities often increase the light, temperature, and soil moisture (Bauhus and Bartsch, 1995; Hanberry et al., 2020; Moola and Vasseur, 2008; Xi, 2015). We found that, when adding all results together, most reviews reported a positive effect of canopy gaps and a negative effect of canopy closure on biodiversity (Table 1). However, this result depended on the taxonomic group.

Vascular plants were the most studied species group in connection to canopy gaps and canopy closure. Most reviews recorded a positive relationship between light conditions and vascular plant abundance, regeneration, and diversity (Table 1). Additionally, open forests were found to improve plant regeneration by, among other things, attracting more seed dispersers (Kremer and Bauhus, 2020; Wagner et al., 2011). The positive relationship between canopy gaps and plant diversity was primarily observed in larger openings and depended on the gap's shape (Hupperts et al., 2019; Moola and Vasseur, 2008; Muscolo et al., 2014; Su et al., 2019). However, studies also showed that the plant species community in canopy gaps and less dense forests differs from the one in closed forest ecosystems by sustaining more pioneer plant species (Balandier et al., 2006; Barbier et al., 2008; Ellum, 2009; Fischer et al., 2013; Oono et al., 2020; Wagner et al., 2011). Therefore, combining different types of canopy gaps and canopy densities within a forest landscape could enhance plant diversity on larger scales (Ellum, 2009; Mitchell et al., 2014; Muscolo et al., 2014; Su et al., 2019).

The increase in light and temperature conditions caused by more open canopies can also affect vertebrates. Different relationships were described between canopy closure or canopy gaps and birds (Fig. 4a; Table 1). Varying relationships were found between canopy gaps and bird species richness (Zeller et al., 2023). An increase in bird diversity could be caused by a denser understory with many habitat resources or by an improved forage efficiency in open forests (Felton et al., 2022; Hanberry et al., 2020; Harper et al., 2016; Reilly et al., 2022; Sharpe, 1996). The latter was not only found for birds, but also for bats, which can result in the higher bat species richness related to canopy gaps (Fischer et al., 2013; Harper et al., 2016; Zeller et al., 2023). In addition, reptile species richness and diversity were found to mostly have a positive relationship with open forests (Table 1), which is likely caused by higher temperatures (Gandhi et al., 2007; Hanberry et al., 2020; Seibold et al., 2015). For amphibians, the relationship between diversity and canopy closure and canopy gaps was more ambiguous (Table 1).

Lastly, invertebrate diversity was found to relate to the light availability and temperature in the forest (Fig. 4a). Especially in colder climates, increased light conditions – and therefore an increase in temperature and possibly flower availability – could increase the diversity and richness of carabids and spiders (Burton et al., 2018; Gao et al., 2015), (saproxylic) insects (Gandhi et al., 2007; Hanberry et al., 2020; Nilsson et al., 2006; Parisi et al., 2018; Perlík et al., 2023; Seibold et al., 2015; Zeller et al., 2023; Zumr et al., 2021), and lichens (Zeller et al., 2023), while being negatively or unrelated to fungi and molluscs (Seibold et al., 2015; Zeller et al., 2023; Zumr et al., 2021) (Table 1). However, primary studies have found that some insects respond negatively to canopy gaps instead (Staab et al., 2022). Additionally, some lichens were found to be adapted to intermediate or low light conditions (Nascimbene et al., 2013; Ulyshen, 2011). Therefore, variable light conditions may sustain the highest lichen diversity on a larger scale.

3.1.3. Stand age and succession stage

The relationship between stand age and biodiversity was well-described in the reviews and was mostly positive (Fig. 4a; Table 1). In contrast, the relationship between biodiversity and successional stage was less documented and results ambiguous (Fig. 4a; Table 1). Changes in biodiversity were often explained by a change in tree species composition and a decrease in light availability and temperature in older forests (Barbier et al., 2008; Chelli et al., 2023; Su et al., 2019; Zeller et al., 2023).

The relationship between stand age or succession stage and vascular plant diversity was found to be dependent on the forest conditions and the study species (Fig. 4a; Table 1). The mixed results indicate that their relationship could be non-linear, which could be explained by vascular plant diversity increasing over time until light and soil nutrients become scarcer, resulting in a decline in plant diversity (Balandier et al., 2006; Duguid and Ashton, 2013; Ellum, 2009; Su et al., 2019). Furthermore, natural disturbances are more common in very old forests, which can again increase the understory plant diversity if resulting openings are not rapidly recolonized or replanted by trees (see 3.1.2). The species composition of vascular plants was also found to change over time, containing mostly light and nutrient-demanding plant species in young, open forests and canopy gaps while favouring forest specialists in older, closed forests (Chelli et al., 2023; Reilly et al., 2022; Su et al., 2019). When vascular plants disappear, bryophyte diversity was found to increase, as they thrive in forests with lower temperatures and light conditions (Felton et al., 2010; Su et al., 2019). This could explain why most reviews found a positive relationship between stand age and bryophyte species richness and diversity (Table 1).

In addition to plants, other organisms have been connected to stand age and succession stage. Most reviews described a positive relationship between forest age and arthropods, birds, bats, fungi, lichens, mammals, insects, saproxylic species, and molluscs (Table 1). These positive relationships were often explained by the occurrence of old-growth forests structures – e.g., large trees, microhabitats, and a large amount of deadwood – in older forests (Kellett et al., 2023; Milad et al., 2011; Nascimbene et al., 2013; Parisi et al., 2018; Zeller et al., 2023). In addition, the high structural diversity in older forests and their long continuity could be important for many arthropods and (other) saproxylic species (Hilmers et al., 2018; Kellett et al., 2023; Mölder et al., 2019; Oettel and Lapin, 2021; Parisi et al., 2018; Valencia-Cuevas and Tovar-Sánchez, 2015). However, young forests in early successional stages might also be able to sustain a high insect, bat, and bird diversity (Table 1) due to the large number of flowering plants and openness of the forest (Nilsson et al., 2006; Reilly et al., 2022; Roberge et al., 2008; Tomiałojć and Wesołowski, 2004).

3.1.4. Structural diversity

Structural diversity includes the diversity and complexity of forest structures described within this review. Most reviews reported a positive relationship between biodiversity and structural diversity for amphibians, arthropods, birds, fungi, ground-dwelling invertebrates, insects, lichens, mammals, saproxylic species, and vascular plants (Table 1). These results were found at multiple spatial scales depending on the species group. For example, plants and birds were often connected to structural diversity within a forest stand (Felton et al., 2022; Sjölund and Jump, 2013), while arthropod and lichen diversity could also be linked to the structural diversity on trees (Ishii et al., 2004; Sallé et al., 2021; Ulyshen, 2011). The positive relationships were often explained by the high number of available niches, microhabitats, and resources in structurally diverse forests, which is in accordance with the habitat heterogeneity hypothesis (Acebes et al., 2021; Oono et al., 2020; Sallé et al., 2021; Toivonen et al., 2023). For species at lower trophic levels, habitat complexity could also provide shelter against predators (Burton et al., 2018; Maleque et al., 2009; Ranius et al., 2018).

However, if the habitat heterogeneity is very high, the habitat size and continuity in a forest might decrease (Fahrig, 2013). As a consequence, species that require habitat continuity or large interior forest areas – e.g., bryophytes, lichens, saproxylic beetles, and forest specialist birds – could decline in very diverse landscapes (Felton et al., 2010; Greenwald et al., 2005; Zeller et al., 2023). This could explain why some studies found mixed or even negative relationships between structural diversity and arthropods (n = 1/6), vascular plants (n = 1/7), birds (n = 1/9), bryophytes (n = 2/3), and fungi diversity (n = 1/3) (Fig. 4a). However, to evaluate this hypothesis, a more thorough analysis on data from primary studies, including the life-history traits of species and the scale of the heterogeneity, would be necessary.

3.1.5. Canopy height and vertical heterogeneity

The connection between canopy height or vertical heterogeneity, i.e. the variation in canopy height within a stand, and biodiversity was described less frequently than that of other forest stand structures (Fig. 4a). Only one review described a relationship between canopy height and biodiversity, reporting that a reason that an increase in height relates to a higher arthropod diversity could be larger vertical gradients and, consequently, habitat niches (Table 1) (Ulyshen, 2011; Wildermuth et al., 2024). The few reviews that studied vertical heterogeneity found a positive relationship between the vertical heterogeneity and the bird, invertebrate, (saproxylic) insect, and mammal diversity and richness (Table 1). This could be due to a higher complexity and, therefore, microhabitat availability in forests with a higher vertical diversity (Ishii et al., 2004; Maleque et al., 2009; Oettel and Lapin, 2021; Ulyshen, 2011; Valencia-Cuevas and Tovar-Sánchez, 2015). Microhabitats created by vertical heterogeneity could be habitats with various temperatures, wind velocities, leaf areas, and floristic compositions (Valencia-Cuevas and Tovar-Sánchez, 2015). In contrast, Zeller et al. (2023) found no or varying relationships between the vertical heterogeneity and the species richness of arthropods, bats, fungi, vascular plants, and bryophytes, which suggests that the importance of this forest structure depends on the species group. However, conclusions per taxonomic group are tentative because of the low number of reviews on this.

3.1.6. Tree density and tree basal area

Few reviews described the relationship between tree density or tree basal area and biodiversity (Fig. 4a). Studies found that tree basal area can have a negative relationship with the vascular plant abundance, but this was only reported once (Table 1). Furthermore, a couple of reviews found that the tree density was mostly negatively related to the diversity of vascular plants and saproxylic species caused by low light penetration and temperatures in dense forests (Table 1) (Ammer et al., 2008; Dey, 2014; Dey and Schweitzer, 2018; Felton et al., 2022; Kremer and Bauhus, 2020; Mölder et al., 2019; Xi, 2015). The low number of reviews connecting biodiversity to tree density and tree basal area might be because the relationship between light conditions and biodiversity is more commonly described by studying the canopy closure.

3.1.7. Stand, canopy, and tree biomass

The canopy and tree biomass were mentioned thirteen times in connection to biodiversity (Fig. 4a) and the pattern of the relationship was only described for arthropods, fungi, vascular plants, and bryophytes (Table 1). Here, reviews found that, because many arthropods occur in the tree canopy, a higher canopy biomass could lead to an increase in species abundance and richness of this species group, according to the species-energy hypothesis (Sallé et al., 2021; Ulyshen, 2011; Wright, 1983). Additionally, a higher tree and stand biomass could lead to a more complex and heterogeneous forest stand and an increase in available resources (Parisi et al., 2018; Valencia-Cuevas and Tovar-Sánchez, 2015). However, for plants, an opposite effect might occur due to an increase in competition for resources (Su et al., 2019). Tree and canopy biomass might also be important, overlooked characteristics for other species, since it is related to the age, density, and productivity of the forest stand, but we did not find enough reviews studying these patterns to draw any conclusions and this relationship might vary between different taxonomic groups (Sabatini et al., 2019).

3.2. Tree structures

3.2.1. Tree diameter, age, and height

Tree diameter, age, and height are strongly correlated because an older tree is likely to be both thicker and taller (Nascimbene et al., 2013). The relationship between tree diameter or tree age and biodiversity has been studied thoroughly in reviews (Fig. 4b). In contrast, only few reviews have mentioned the relationship between tree height and biodiversity, which might be because measuring tree height requires more effort.

Almost all reviews found a positive relationship between tree diameter, height, or age and (cavity nesting) birds, bats, bryophytes, fungi, insects, invertebrates, lichens, mammals, and saproxylic species (Table 1) and such relationships could even be stronger when older trees occur close to each other in the landscape (Horák, 2017; Nilsson et al., 2006). The positive effects of large, old trees were mostly explained by an associated high habitat continuity that these trees provide (Mölder et al., 2019; Ulyshen, 2011). In addition, older and larger trees can increase habitat complexity, improve feeding substrates, and provide many tree related microhabitats such as cavities of different sizes, which all can contribute to increasing diversity and abundance of birds, squirrels, arthropods, lichens, and bats (Asbeck et al., 2021; Berger et al., 2013; Brändle and Brandl, 2001; Dieler et al., 2017; Drake et al., 2020; Hiers et al., 2014; Mölder et al., 2019; Nascimbene et al., 2013; Nilsson et al., 2006; Roberge et al., 2008; Rogers et al., 2020; Sharpe, 1996; Stupak and Raulund-Rasmussen, 2016; Ulyshen, 2011). For example, oak trees in Sweden were found to develop hollows mainly when they are older than 150 years (Nilsson et al., 2006). Other microhabitats that were found to be more common on older trees were rougher barks, which can provide high-quality habitats for epiphytes, bats, and bark-dwelling arthropods (see 3.2.4), and flowers (often most abundant at a medium or old age), that provide food resources for many (in)vertebrates (see 3.2.5) (Berger et al., 2013; Kellett et al., 2023; Nilsson et al., 2006; Rogers et al., 2020; Ulyshen, 2011). However, some reviews noted that a variation in tree height, age, and diameter in a forest landscape is necessary to provide habitats for many different species (Bergen et al., 2009; Gandhi et al., 2007; Oettel and Lapin, 2021).

3.2.2. Tree cavities

There are two different types of cavities: decay cavities that have been produced by a combination of wood-decay processes and the activity of invertebrates and excavated cavities that have been created by primary cavity-nesters, e.g. woodpeckers (Remm and Lõhmus, 2011). Many reviews described a positive relationship between tree cavities and the habitat availability of many species, and eight studies found a positive relationship between tree cavities and the arthropod, saproxylic species, and bird diversity and richness (Fig. 4b; Table 1). These relationships were often explained by that tree cavities are suitable nesting places for birds and can be high-quality substrates for, among others, insects and lichens (Berger et al., 2013; Christensen et al., 2005; Drake et al., 2020; Harper et al., 2016; Martin et al., 2022; McIver et al., 2012; Nascimbene et al., 2013; Nilsson et al., 2006; Remm and Lõhmus, 2011; Rogers et al., 2020; Sallé et al., 2021; Vítková et al., 2018; Zumr et al., 2021).

Cavities are more common in older and dying trees and the cavity size depends on the tree age and height (see 3.2.1) (Dieler et al., 2017; Ulyshen, 2011). Different types of tree cavities were found to be used by different organisms, increasing the total biodiversity (Tomiałojć and Wesołowski, 2004; Ulyshen, 2011).

3.2.3. Foliage density, branch structure, and crown structure

Foliage density, branch structure, and crown structure have been reported infrequently in connection to biodiversity (Fig. 4b). The low number of reviews studying these structures might be due to the practical difficulty of measuring such structures in the field.

Ishii et al. (2004) and Roberge et al. (2008) found a positive relationship between branch size and bird and small mammal populations, because larger branches can provide nesting sites and dens (Table 1). Furthermore, a complex crown structure and evenly distributed foliage was found to increase the habitat heterogeneity and, therefore, population sizes and biodiversity in a forest (Dieler et al., 2017; Sallé et al., 2021; Ulyshen, 2011). For example, a complex crown was described to have a positive effect on arthropod diversity and the presence of various lichens because it can create different niches that vary in their light, air, and temperature conditions (Ishii et al., 2004; Mölder et al., 2019; Sallé et al., 2021; Ulyshen, 2011). In addition, complex crowns can provide a better protection against predators, improving their habitat quality (Sallé et al., 2021).

3.2.4. Tree surfaces

We found two different types of tree surfaces that were connected to biodiversity. The most reported one was the tree bark, while the leaf surface was less studied (Fig. 4b). Several reviews stated that rougher, thicker barks with bark pockets – often present on older, larger trees – can increase the diversity of arthropods, insects, bryophytes, and lichens (Burrascano et al., 2013; Felton et al., 2010; Gandhi et al., 2007; Kellett et al., 2023; Nilsson et al., 2006; Rogers et al., 2020; Ulyshen, 2011). This was mostly explained by the high ability of rough bark to hold moisture and provide hiding spaces for arthropods, which improves the habitat quality for many species (Gandhi et al., 2007; Kellett et al., 2023; Schowalter, 2017). Furthermore, the pH of the bark and exfoliating bark was found to be able to change the species composition of bark-dwelling organisms and can create important microhabitats for bats and invertebrates (Berger et al., 2013; Drake et al., 2020; Felton et al., 2022; Nascimbene et al., 2013).

The leaf structure – leaf shape, area, and structures such as hairs and domatia – was only described in connection to arthropods and the general biodiversity (Fig. 4b). The few reviews on this reported that structures that increase leaf complexity, such as domatia, can improve the habitat quality for some arthropods because they can utilize these structures to hide from predators (Ulyshen, 2011).

3.2.5. Flowers, fruits, and seeds from trees

Twenty reviews reported the importance of flowers, fruits, and seeds for the biodiversity (Fig. 4b; Table 1). Flowering trees, including wind-pollinated trees, contain important, although temporary, food sources – such as nectar, seeds, and fruits – for many insects (Felton et al., 2013; Hanberry et al., 2020; Sallé et al., 2021; Ulyshen, 2011; Valencia-Cuevas and Tovar-Sánchez, 2015). Additionally, many vertebrates, such as (small) mammals, reptiles, amphibians, and birds, consume nectar, seeds, and fruits (Balandier et al., 2006; Hanberry et al., 2020; Hiers et al., 2014; Sjölund and Jump, 2013). For example, beechnuts, acorns and hazelnuts were found to be important food sources in temperate, deciduous forests for many species and could be more important than conifer seeds (Dey, 2014; Hanberry et al., 2020; Hiers et al., 2014; Mittelman et al., 2024). No information was found on the relationship between the diversity or abundance of flowers, seeds, and fruits and biodiversity specifically, which is necessary to get more in-depth knowledge on the importance of this structure.

3.2.6. Veteran trees

Veteran trees are trees that provide multiple microhabitats that are elsewhere described in this review, such as rough barks, hollows, and dead branches (Horák, 2017; Oettel and Lapin, 2021). The difference between old trees and veteran trees is that old trees are defined by their age while veteran trees are defined by the microhabitats that they provide. Consequently, not every old tree is a veteran tree, however, old trees are more likely to possess important microhabitats and, thus, be veteran trees. Veteran trees can increase the habitat heterogeneity and, therefore, increase the biodiversity in the forest stand (Schulze et al., 2016). However, only few reviews described the relationship between veteran trees and biodiversity (Fig. 4b). A positive relationship was mostly found between veteran trees and saproxylic species diversity, especially when the trees occur in a sunny environment (Table 1) (Horák, 2017; Schulze et al., 2016; Zumr et al., 2021). In addition, Christensen et al. (2005) found that birds sometimes prefer veteran trees as nesting habitats and foraging substrates.

3.3. Below-canopy structures

3.3.1. Deadwood volume

The most reported forest structure connected to biodiversity was deadwood volume (Fig. 4c). Saproxylic species and fungal diversity were mostly suggested to have a positive relationship with deadwood volume, but even the non-saproxylic species diversity was found to be positively related to deadwood (Fig. 4c).

The clear positive relationship between deadwood volume and biodiversity that was found by the reviews (Table 1) could be explained by deadwood creating many habitats and serving as a food substrate for many saproxylic species such as fungi, insects, and lichens (Asbeck et al., 2021; Berger et al., 2013; Bouget et al., 2012; Burrascano et al., 2013; Christensen et al., 2005; Dieler et al., 2017; Gandhi et al., 2007; Gao et al., 2015; Götmark, 2013; Hupperts et al., 2019; Jaroszewicz et al., 2019; Lassauce et al., 2011; Maleque et al., 2009; Mölder et al., 2019, 2017; Nascimbene et al., 2013; Nilsson et al., 2006; Parisi et al., 2018; Sandström et al., 2019; Schulze et al., 2016; Schulze, 2018; Seibold et al., 2015; Sjölund and Jump, 2013; Stupak and Raulund-Rasmussen, 2016; Su et al., 2019; Vítková et al., 2018; Zehetmair et al., 2015; Zumr et al., 2021). In addition, reviews found that vascular plants and bryophytes can use deadwood as a substrate to grow on (Dieler et al., 2017; Gandhi et al., 2007; Götmark, 2013; Jaroszewicz et al., 2019; Landuyt et al., 2018; Moola and Vasseur, 2008; Parisi et al., 2018; Schulze et al., 2016; Su et al., 2019).

We also found a positive relationship between deadwood volume and the species richness and diversity of birds and bats (Table 1). These organisms can use deadwood as a feeding and nesting/roosting substrate and, additionally, forage on insects that live in the deadwood (Basile et al., 2023; Drake et al., 2020; Harper et al., 2016; Roberge et al., 2008; Seibold et al., 2015; Stupak and Raulund-Rasmussen, 2016; Tomiałojć and Wesołowski, 2004; Zeller et al., 2023). Furthermore, some mammals and (litter-dwelling) invertebrates had a positive relationship with deadwood because they can use it as a shelter and can benefit from the moist environment that it creates (Table 1) (Oono et al., 2020; Parisi et al., 2018; Perry and Herms, 2017; Stupak and Raulund-Rasmussen, 2016).

However, not all studies found a positive relationship between deadwood volume and biodiversity (Table 1). The results might also depend on the type of deadwood available and the local environmental conditions in the forest (see 3.3.2) (Lassauce et al., 2011; Vítková et al., 2018).

3.3.2. Deadwood type and quality

Deadwood can vary in diameter, tree species, decay stage, position, and environmental conditions which was found to impact the habitat quality for organisms (Bouget et al., 2012; Bujoczek et al., 2018; Parisi et al., 2018). We found many reviews describing how deadwood type relates to biodiversity (Fig. 4c).

Many of the reviews reported that deadwood with a larger diameter can host more (red-listed) fungi, lichen, bryophyte, insect, bird, bat, mammal, amphibian, and vascular plant species because it contains more microhabitats, resources, moisture, and a stable microclimate with a slow decay rate (Bouget et al., 2012; Frelich, 2017; Gandhi et al., 2007; Harper et al., 2016; Liu et al., 2014; Maleque et al., 2009; McIver et al., 2012; Mölder et al., 2019; Parisi et al., 2018; Perry and Herms, 2017; Stupak and Raulund-Rasmussen, 2016; Su et al., 2019; Toivonen et al., 2023; Ulyshen, 2011; Vítková et al., 2018; Zumr et al., 2021). The latter results in habitat continuity which is especially important for immobile organisms that face more difficulties when colonizing a substrate (but see Komonen and Müller, 2018). However, Bouget et al. (2012) and Berger et al. (2013) found that there are also species that specialize on fine woody debris (FWD) which shows that not all species prefer deadwood with large diameters.

Decay stage was also reported to affect the species diversity (Bouget et al., 2012; Bujoczek et al., 2018; Maynard et al., 2015; Oettel and Lapin, 2021; Parisi et al., 2018; Sandström et al., 2019; Seibold et al., 2015; Ulyshen, 2011; Vítková et al., 2018). Early stages of coarse woody debris (CWD) were found to be more preferred by lichens and small vertebrates, while vascular plants, saproxylic beetles, bryophytes, and fungi preferred intermediate or later decay stages (Basile et al., 2023; Berger et al., 2013; Bouget et al., 2012; Christensen et al., 2005; Seibold et al., 2015; Stupak and Raulund-Rasmussen, 2016; Su et al., 2019; Vítková et al., 2018). Furthermore, tree species with slow decay rates, such as oak trees, were reported to host many saproxylic species because of the habitat continuity (Mölder et al., 2019; Vítková et al., 2018; Zumr et al., 2021). Other types of deadwood that were found to host many species were substrates of European hornbeams and sycamores while beech and ash trees were found to attract fewer species (Schulze, 2018; Vítková et al., 2018; Zumr et al., 2021).

Deadwood can be found in different positions such as hanging in the canopy, standing in the forest (i.e. snags and stumps), and lying on the ground (i.e. CWD, FWD). Studies that compare the species diversity of lying and standing deadwood have found varying results, which could be explained by effects depending on the species group studied. Lying deadwood seemed to be mostly important for ground-dwelling organisms such as ground-living invertebrates, reptiles, amphibians, and small rodents that can use deadwood as shelter, nesting and/or feeding sites (Berger et al., 2013; Bouget et al., 2012; Gandhi et al., 2007; Harper et al., 2016; Liu et al., 2014; Ranius et al., 2018; Roberge et al., 2008). Furthermore, a higher diversity of fungi and bryophytes was found on laying logs because of a more stable microhabitat (Christensen et al., 2005; Parisi et al., 2018; Vítková et al., 2018). In contrast, birds, bats, and small mammals such as squirrels were found to use mostly standing deadwood as feeding, nesting, and roosting sites and stumps were found to contain a higher saproxylic insect diversity than lying deadwood (Basile et al., 2023; Berger et al., 2013; Harper et al., 2016; Roberge et al., 2008; Sharpe, 1996; Stupak and Raulund-Rasmussen, 2016; Ulyshen, 2011; Zumr et al., 2021). Less mentioned – likely due to the measurement difficulties – was the deadwood in the canopy. This deadwood might create important microhabitats for canopy-dwelling organisms such as arthropods (Seibold et al., 2015; Ulyshen, 2011).

Lastly, the environment surrounding the deadwood can affect the quality of the deadwood and thereby species composition and diversity in the substrate (Seibold et al., 2016, 2015; Su et al., 2019). Deadwood in sunny, warm conditions – especially in colder climates – differs in species composition from deadwood under a dense canopy and was found to maintain a higher saproxylic insect, lichen, reptile, and amphibian diversity (Bouget et al., 2012; Christensen et al., 2005; Felton et al., 2022; Milad et al., 2011; Mölder et al., 2019; Nilsson et al., 2006; Schulze et al., 2016; Seibold et al., 2015; Vítková et al., 2018; Zeller et al., 2023; Zumr et al., 2021). In contrast, molluscs, fungi, and mosses were reported to prefer more shaded conditions (Parisi et al., 2018; Seibold et al., 2015; Vítková et al., 2018; Zumr et al., 2021).

3.3.3. Deadwood diversity

The positive relationship found between deadwood volume and biodiversity might not only be caused by an increase in the volume, but also be the result of an associated increase in its diversity (Müller and Bütler, 2010; Vítková et al., 2018). We found that most reviews described a positive relationship between deadwood diversity and the biodiversity, even though distinguishing the effects of deadwood diversity and deadwood volume is often difficult (Fig. 4c). This positive relationship has mostly been described for biodiversity in general, saproxylic species, fungi, and vascular plants (Table 1) and could be explained by the higher diversity of niches that different types of deadwood can provide (Felton et al., 2010; Jaroszewicz et al., 2019; Maleque et al., 2009; Müller and Bütler, 2010; Nilsson et al., 2006; Parisi et al., 2018; Sing et al., 2018; Su et al., 2019; Vítková et al., 2018). However, the relationship between deadwood diversity and biodiversity was more ambiguous for arthropods, bats, bryophytes, and lichens (Table 1). This could be the result of a possible decrease in habitat amount when habitat heterogeneity increases (see 3.1.4) (Komonen and Müller, 2018).

3.3.4. Understory vegetation

The understory effects were divided into understory structure (its density and vertical heterogeneity) and understory presence. The definition of the understory often depends on the niche of the species. In this review, we defined the understory vegetation as a vascular plant layer that occurs below the canopy layer but, in case of bryophytes, lichens and vascular plants, occurs above the focal species of the review. The presence or absence of a midstory and understory depends on the density of the forest layers above. Consequently, not only a dense canopy layer, but also a dense midstory can decrease the herbaceous plant cover and an herbaceous plant layer can decrease the bryophyte diversity (Table 1) (Barbier et al., 2008; Felton et al., 2010; Hanberry et al., 2020).

The presence of a (diverse) understory was stated to mostly increase the biodiversity (Table 1; Fig. 4c), which could be explained by the understory containing important habitats and food resources – e.g. leaves, seeds, fruits, and insects – for birds, mammals (e.g. rodents, large herbivores), and amphibians (Table 1) (Balandier et al., 2006; Bergen et al., 2009; Dey, 2014; Felton et al., 2022; Hanberry et al., 2020; Lugo, 2008; Maleque et al., 2009; McIver et al., 2012; Reilly et al., 2022; Toivonen et al., 2023; Ulyshen, 2011). Furthermore, a dense understory vegetation can increase moisture levels in the forest which can improve the habitat quality of amphibians and small mammals (McIver et al., 2012) and increase the species richness of *Arachnida* (Gao et al., 2015). In contrast, reptiles might prefer bare mineral soil for basking (McIver et al., 2012). The relationship between the understory and bird diversity and species richness varied between reviews and was positive for shrub-nesting birds, while negative for other species like the red-cockaded woodpecker (Harper et al., 2016; Hiers et al., 2014; Toivonen et al., 2023).

3.3.5. Pits and mounds

Pits and mounds, often created by treefalls, have mostly been connected to the vascular plant and bryophyte diversity in a forest (Fig. 4c). The abiotic conditions – such as soil moisture and nutrient availability – of pits and mounds are typically different from those of intact soils, thus providing new microhabitats and therefore different plant compositions locally (Fischer et al., 2013; Gandhi et al., 2007; Lugo, 2008; Moola and Vasseur, 2008; Xi, 2015). Consequently, the plant diversity can increase because of the increase in habitat complexity and heterogeneity in forest stands (Table 1) (Gandhi et al., 2007; Gilliam, 2007; Lugo, 2008; Moola and Vasseur, 2008; Su et al., 2019). Pits were found to have a higher plant diversity than mounds and mostly included plants that prefer soil moisture, while mounds were preferred by plants that specialize on drier soils (Gandhi et al., 2007; Xi, 2015). Furthermore, pits and mounds were reported to have a positive relationship with bird richness and lichen diversity, but these relationships were only described by one review each (Table 1).

3.3.6. Litter

Various relationships were described between the leaf litter and biodiversity (note that soil biodiversity was not part of the review) (Fig. 4c). First of all, most reviews reported that the relationship between leaf litter and vascular plant richness could be both negative and positive, depending on the type, amount, and decomposition rate of the litter (Table 1) (Barbier et al., 2008; Landuyt et al., 2018). Positive relationships can be explained by leaf litter creating microhabitats with many nutrients – especially if the decomposition rate is high – and soil moisture (Barbier et al., 2008; Landuyt et al., 2018; Xi, 2015). However, negative effects on vascular plant diversity could emerge when leaves contain high levels of phytotoxic substances, acidify the soil, or when the leaf layer is very thick (Barbier et al., 2008; Hernandez et al., 2020; Landuyt et al., 2018). The latter results in a decrease in light conditions on the forest floor, the inability for seeds to make physical contact with the forest floor, or the inability for seedlings to penetrate the litter layer (Barbier et al., 2008; Hernandez et al., 2020; Landuyt et al., 2018; Xi, 2015). Only three reviews included the effects of leaf litter on bryophytes, and found that, by acidifying the soil, the litter layer could promote bryophyte diversity as long as the layer was penetrable (Barbier et al., 2008; Su et al., 2019).

Some animal abundances can increase with the presence of a leaf litter even though this has only been mentioned in few papers (Fig. 4c; Table 1). For example, salamanders and some small mammals require leaf litter for shelter against predators and prefer the higher soil moisture on the forest ground (Harper et al., 2016; McIver et al., 2012). Furthermore, leaf litter can lead to more forest-dwelling insects which can attract bird species that forage on these organisms (Felton et al., 2013). In contrast, lizards might prefer less litter because it can decrease the ground temperatures in the forest stand (Harper et al., 2016; McIver et al., 2012).

3.4. Limitations and research gaps

This systematic meta-review highlights important relationships between forest structures and biodiversity. However, the results are based on vote counting without considering data overlaps between reviews and thus may bias the representation of primary research (Haddaway et al., 2015). For a quantitative secondary order meta-analysis, there are formal methods to handle overlap between reviews (Beillouin et al., 2021; Lajeunesse, 2011), but this method cannot be used when the analysis includes qualitative reviews. Consequently, there is, to our knowledge, no method available to correct for this bias. In addition, both quantitative and qualitative reviews were included in this study to obtain an overall overview on all potentially significant forest structures. To account for the difference in review quality, we have added the availability of quantitative reviews in Table 1 and have been careful with making conclusions when quantitative studies were showing contrasting results. Our results also show that there often is a need for more quantitative reviews on the effects of forest structures on biodiversity. These studies are also necessary to be able to separate the effects of forest structures that are often collinear. Collinearity is a reoccurring problem within ecological studies and could lead to possible misinterpretations about the mechanism behind observed relationships (Müller and Bütler, 2010). Consequently, our review was only able to study relationships between forest structures and biodiversity. More quantitative studies could help understand correlative effects in future studies.

During our meta-review, we found that some forest structures are still poorly summarized in connection to biodiversity (Fig. 4a-c). For crown structure, canopy deadwood, tree and canopy biomass, and canopy and tree height, this could be the result of measurement challenges and, therefore, exclusion in primary research. Laser technology may increase our ability to describe such structures in the near future. Other structures that were underrepresented in the reviews are structures that are not always described as forest structures, such as the leaf structure. Not only forest structures, but also some species groups were underrepresented in reviews. For example, we found that molluscs, reptiles, amphibians, and ground beetles and spiders were rarely included in reviews. In addition, most studies focused on the alpha-diversity of species within a forest stand and did not include the beta- or gamma-diversity in the landscape. This could lead to a misunderstanding of the relationship between forest structures and biodiversity patterns on a landscape scale (Müller et al., 2023; Schall et al., 2018; Socolar et al., 2016).

Lastly, reviews were not always consistent with specifying the forest ecosystems studied within their research. Additionally, studies that did specify that they studied deciduous forests, often also included results of other forest types such as coniferous forests and it was not always clear if, how, and why they combined their results. To deal with this uncertainty, we tried to only collect the information about deciduous forests when results of different forest types were combined. However, there is still a likelihood that we included some information about coniferous forests when reviews were unclear about the separation of the forest types.

4. Conclusions

This is the first comprehensive systematic meta-review that shows the (in)consistency of relationships between forest structures and various taxonomic groups. The results show that a multitude of forest structures relate to the biodiversity in deciduous forests, but that the relationships of many (especially stand-level) forest structures are inconsistent and depend on the taxonomic group and their habitat requirements. While the habitat amount hypothesis could not be addressed within this review, this finding does support the habitat heterogeneity hypothesis and suggests that – when trying to restore and conserve forests with diverse species communities – it is important to create diverse forest landscapes that include different habitats and niches. However, some forest structures were found to have a positive relationship with many taxonomic groups, suggesting their general importance during forest restoration, rewilding, and conservation.

Many of the forest structures that were consistently reported to have positive relationships with various species groups were connected to forest age. For example, stand age, tree cavities, and tree age were found to be positive related to almost all species except understory plants, which were sometimes more likely to thrive in younger forests due to light availability. Other important forest structures that had positive relationships with almost all study species were the presence of angiosperm trees that produce large seeds and deadwood volume. However, we also found that the quality of deadwood depended on the position, environmental conditions, diameter, decay stage, and tree species of the substrate and that different species prefer different types of deadwood. In addition, the importance of some forest structures, such as canopy deadwood and biomass and tree height, might be underestimated due to an under-representation in reviews.

In contrast to deadwood volume, the presence of angiosperm trees, and tree age, many forest stand level structures, like tree diversity, canopy gaps, and canopy closure, were found to have relative weak or inconsistent relationships to biodiversity in temperate deciduous forests. This indicates that the use of these structures as biodiversity indicator, as is partly done in the European Nature Restoration regulation, can lead to poor estimations of biodiversity values. Instead, general conservation efforts should first focus on protecting old forests, adding and leaving deadwood, and allowing for the presence of flowering and seed producing trees and older trees, even in production forests. When the objective is to promote a certain species group, conservation efforts could include changing canopy densities and adding specific tree species or a specific type of deadwood that increases the habitat quality of the focal taxonomic group. Considering different forest structures for different organisms is a key component of successful restoration practices and should even be considered on different spatial scales. Such forest heterogeneity could either be linked to management of production forests or part of conservation strategies that allow "rewilding" in the form of natural disturbances.

Disclaimer

Views and opinions expressed are those of the author(s) only and do not necessarily reflect those of the European Union or European Climate, Infrastructure and Environment Executive Agency. Neither the European Union nor the granting authority can be held responsible for them.

CRediT authorship contribution statement

Lydwin Freija Wagenaar: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ola Olsson:** Writing – review & editing, Supervision, Conceptualization. **Martin Stjernman:** Writing – review & editing, Conceptualization. **Henrik G. Smith:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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.

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Data availability

The data is publicly available and can be obtained by using this DOI: 10.17632/7v88vggz6n.1.

Data: A systematic meta-review: the effects of forest structures on the biodiversity in deciduous forests. (Mendeley Data)

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