

Review

Bridging the gap between forest planning and ecology in biodiversity forecasts: A review

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ABSTRACT

Including biodiversity indicators into forest planning is increasing in importance as it is a supporting service for other ecosystem services. To forecast biodiversity potential, forest planners use models that simulate forest growth and other biological and ecological processes. As models are simplifications of reality, they may ignore components of biodiversity's multi-scales and multi-facets. To address this issue, we explored if current models used in forest planning can characterize biodiversity in a similar way as it is defined in ecology. We performed a narrative review of ecological papers to identify the main aspects of biodiversity defined in ecology. We then reviewed 64 forest planning articles to identify the indicators they use and what aspects of biodiversity they represent. We compared the aspects identified in ecology and forest planning to evaluate the discrepancies between the two fields and suggest improvements for future biodiversity studies in forest planning.

We identified spatial and temporal connectivity, structure, and abiotic factors as the main biodiversity drivers defined in ecology and genetic, species, and functional diversity as the main responses. Based on this classification, we found that biodiversity models used in forest planning mainly focus on structure and species elements, with minor focus on connectivity and functions and none on genetic diversity. We found that most studies base their choice of biodiversity indicators on the outputs available from traditional forest simulators. Additionally, many studies do not frame biodiversity rigorously or acknowledge its complexity. This trend is explained by the traditional focus of forest planning on the economic value of the forest and maximization of timber volumes rather than its ecological value and the presence of diverse habitats. Our results describe and quantify the importance given to the different biodiversity aspects in forest planning studies and highlight the current limitations. We anticipate that improvements can be achieved through the inclusion of connectivity and we suggest paths to improve future biodiversity models.

1. Introduction

With growing populations and the resulting high demand for natural resources, the pressure on production landscapes to be multifunctional is increasing (FAO, 2022). Forest landscapes are not an exception as they are expected to produce multiple environmental, social, and economic services to human societies (Mori et al., 2017).

A central service provided by forests is biodiversity that in turn supports and is key to many other ecosystem services that we are dependent upon. According to the FAO (2022), 80% of the developing world's population depends on non-wood forest products for health and nutrition. Biodiversity and forests are also critical for water quality as 75% of the world's freshwaters come from forests (FAO, 2022). Plants

from forests have been and are still used both for modern and traditional medicine (Cunningham et al., 2012; Ssenku et al., 2022) and studies have shown that biodiversity and nature in general have a positive effect on mental health (Kotera et al., 2022; Joschko et al., 2023). Using a wider perspective, biodiversity may play a role to improve gender equality and education. Women in rural Asia and Africa are the main collectors of wild plants for food and health and have a lot of knowledge that can be valorized and contribute to their social status (Convention on Biological Diversity, 2018). Biodiversity also plays a key role in the resilience and stability of ecosystems against climate-change induced disturbances. Bird communities facilitate seed dispersion through the fragmented landscape or predate on insects during outbreaks (Garcia et al., 2010; Niemi et al., 1998), decomposers decrease the amount of

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flammable deadwood on the floor (Gibb et al., 2022) and genetic diversity of trees improve their chances to adapt to future environmental changes (Jump et al., 2009).

According to the IPBES, land use change is the first driver of biodiversity loss, threatening multifunctionality and provision of other services (IPBES, 2019). The intensive use of forests for wood production has led to uniformization, a loss of habitats and a decrease in species richness (Burton et al., 2010; Triviño et al., 2017). Silvicultural practices that are based on economic incentives have resulted in a decrease of old and mature forests and their associated habitats (Burton et al., 2010). Large scale logging is associated with a decrease in dead wood volumes as the stands are thinned and harvested before natural mortality can intervene (Tikkanen et al., 2012). When focusing on economic incentives, trees are cut too early for them to develop cracks and cavities that would host invertebrates (Asbeck et al., 2021). Forests' biodiversity is also threatened by fragmentation caused by the increase in agricultural or urban land (Haddad et al., 2015). This is exacerbated through the ownership structure of the forest. In Europe approximately 60% of the forests are privately owned (European Parliament, 2023) and belong to multiple small-scale owners which results in fragmentation and lack of coordination.

Climate change and global warming are dramatically impacting the forest's biodiversity, as it changes the distribution of species with an even greater impact on rather immobile species such as trees and plants (Abbass et al., 2022; Lowe et al., 2011). Species that cannot migrate as fast as the progress of climate change will be subject to pests and diseases as they are weakened and under stress (Abbass et al., 2022). Climate change also leads to thriving invasive species that will directly compete with indigenous species (IPCC, 2022). Lastly, the increased frequency of extreme events also impacts negatively the perennity of forest ecosystems (Abbass et al., 2022; Machado Nunes Romeiro et al., 2022).

The biodiversity and climate crises are unprecedented in human history (IPBES, 2019) and call for a redefinition of traditional forest management and silviculture to include biodiversity concerns. A wide variety of international agreements, such as the Aichi targets in 2010, the Sustainable Development Goals in 2015 or the more recent Kuning-Montreal Global Biodiversity Framework adopted in December 2022, have been developed to define biodiversity objectives for the 21st century and motivate conservation actions. Regarding forestry, these agreements require that forests be managed sustainably so that the use of forest resources will not lead to long term biodiversity decline (Aichi targets) (Convention on Biological Diversity, 2011), and to set up global indicators such as protecting red list species or increase forested land (SDGs) (UN, 2015). To be implemented in practice, it requires forest managers to be able to accurately forecast biodiversity indicators to form relevant conservation strategies, adapt silvicultural practices, and reconcile timber management and biodiversity.

Since the development of the first growth and yield tables, forest practitioners have relied on models to forecast the future impacts of management decisions and solve complex decision problems with a long-term horizon (Lexer et al., 2000). Later, computers enabled the development of increasingly advanced models taking into consideration several facets of forestry to support decision making (Segura et al., 2014). Relying on improved processing power, simulation studies have become common in forestry to predict the change and possible outcomes of management interventions on forests (Burton et al., 2003). Those studies also had to adapt to the rise of biodiversity policies and society's demand for more sustainable forestry. This has resulted in the integration of sustainable forest management criteria along with the usual economic and productivity criteria (Diaz-Balteiro & Romero, 2008; Kangas et al., 2015). The first studies to integrate biodiversity management into forest planning were recorded in the 1990s with use cases related to national parks, reserves, and protected land whereas biodiversity indicators used in typical forestry problems started in the late 90s (Diaz-Balteiro & Romero, 2008). The inclusion of biodiversity goals in

forest planning called for the definition and inclusion of reliable indicators for biodiversity in simulation studies. This trend has resulted in biodiversity conservation objectives to be assessed using a wide and diverse range of indicators satisfying different constraints such as practicality, cost-effectiveness, and possibility to model their future value (Botequin et al., 2021).

However, a challenge for the inclusion of biodiversity models in forest planning is the complexity and the multitude of scales that can potentially be included when making forecasts. It is therefore necessary to define biodiversity clearly, identify its main aspects and find indicators for those aspects. In this study, biodiversity aspects are defined as the core elements constituting biodiversity (i.e., species, function, temporal connectivity etc.) and are presented in section 3 while indicators are defined as proxies used in biodiversity models to forecast the impact of forest activities on the different aspects. Studies have used indicators for biodiversity assessment and monitoring in forest ecosystems and highlighted that European forest research does not rely on a consistent definition of biodiversity and sometimes lack a definition at all (Cosovic, 2022; Gao et al., 2015). However, in the literature there seems to be a lack of assessing the appropriate application of biodiversity indicators in forest simulation studies. This is important as decisions made in the forest are informed by simulation studies and this can impact the future provision of biodiversity.

As ecology studies interactions between living organisms and their environment, we presuppose that the way biodiversity is defined in ecology could be a reference for other fields such as forestry. In this paper we compare the way ecologists define biodiversity with the way biodiversity is forecasted in forest planning. The objectives of the paper are to:

- (i) Define the main aspects of biodiversity in ecology.
- (ii) Highlight the indicators used in forest planning to model biodiversity and what aspects of biodiversity they correspond to.
- (iii) Find the discrepancies between biodiversity aspects covered in forest planning and the ecological definition of biodiversity.
- (iv) Identify improvement paths for integrating biodiversity in forest planning.

2. Literature review

A narrative literature review was performed to synthesise an overall definition of biodiversity in ecology. The literature in the review focused on peer-reviewed articles dealing with biodiversity concepts, ecology textbooks and papers recommended by experts. When a core aspect of biodiversity was identified, a snowball approach was used to further examine its sub-components.

A systematic literature review was performed to investigate how biodiversity is defined in forest planning articles. This review was conducted between July 2022 and December 2022 in Web of Science and Scopus databases. The following keywords were used: "forest" AND "biodiversity" AND "indicators" AND "models" OR "forecast" OR "planning". The first 3 keywords were necessary to select articles dealing with indicators of forest biodiversity while the last 3 keywords targeted specifically studies dealing with forecasting or modelling the future state of the forest as opposed to empirical studies or studies on monitoring and assessment of the current state of biodiversity. These keywords were searched for in Topic (title, abstract, author keywords) in Web of Science and results were filtered to return articles only. The articles obtained were assessed in two stages: title and abstract first and full text when the first stage was not sufficient to take a decision. The assessment was based on the following set of criteria and their justification:

- dealing with forest ecosystems – to narrow the results to our field of study,
- situated in the temperate zone (between the tropics and polar circles and excluding the sub-tropical zone) – to narrow the results to boreal

and temperate forests for standardisation and applicability of the results,

- looking at biodiversity as a whole – to eliminate studies concerned with a specific species as those do not provide much information on the implicit definition of biodiversity in forest planning,
- aiming at making future predictions of biodiversity – to eliminate studies looking at the past evolution or current state of biodiversity and focus on studies dealing with the future provision of biodiversity.

The same keywords were used in Scopus in title, abstract and keywords and duplicate articles that were already found in Web of Science were eliminated. The remaining articles were assessed in the same way as for Web of Science’s results. An overview of the process with the number of articles included after each phase is presented in Fig. 1. To assess the consistency of the evaluation a second reviewer assessed 10% of the articles found in Web of Science to ensure that the decision to include or exclude articles was consistent.

For each reviewed forest planning article, we gathered the biodiversity indicators and grouped them under the aspects and sub-components identified in the narrative review of the ecological definition of biodiversity.

3. Biodiversity in ecology

The word “biodiversity” encompasses the idea that natural systems are heterogenous at different ecological levels (Haila & Kouki, 1994). The concept is ambiguous and fuzzy, as it can be defined in different contexts and cover different meanings (Haila & Kouki, 1994). To provide clarity in the context and meaning, it is necessary to identify the conceptual discourse one refers to when defining biodiversity. In this study, we chose the discourse in ecology as a reference point to define biodiversity. A central ecological definition was developed by Noss (1990) who described biodiversity as a nested hierarchy of organizational, spatial, and temporal scales within three main aspects: composition, structure, and function. Ever since, ecology has kept on moving towards a multi-scale and multi-faceted view of biodiversity (Pollock et al., 2020) and multiple studies highlight the importance of biodiversity’s complexity to ensure ecosystems resilience, productivity and support the provision of other ecosystem services (Mori et al., 2017; Paquette & Messier, 2011; Pollock et al., 2020).

Starting from the complexity and multi-scaled nature of biodiversity, we divided the different aspects identified in the literature into drivers and responses. We define biodiversity drivers as elements that mostly

contribute to the physical and biological characteristics of ecosystems. We define responses as elements that are mostly impacted by the characteristics of ecosystems. However, it is important to bear in mind that these categories are not rigid as some elements can both be impacted and impact the ecosystem and its biological diversity. Additionally, there are constant feedback loops between drivers and responses which means that responses such as species richness can influence drivers such as structure. The drivers and responses identified and used to categorize the indicators of biodiversity in forest planning are presented in Fig. 2.

3.1. Drivers

Ecological connectivity is a crucial driver of biodiversity that can be understood across the spatial and temporal continuums (Nordén et al., 2014). Spatial connectivity has been defined as the degree to which the landscape facilitates movement among resource patches to allow recolonization and dispersion (Kindlmann & Burel, 2008; Mony et al., 2022). One of the most important theories for spatial connectivity is the Island Biogeography (MacArthur & Wilson, 1967). This theory, generalised for any habitat patch, indicates that larger and connected patches are better to host a larger number of plant and animal species as they are easier to find and can contain more diversity. Connection via corridors (strips of habitat) and steppingstones (discontinued patches) facilitates movement between different habitat patches and are key structural characteristics for the dispersion of organisms (Kindlmann & Burel, 2008; Mony et al., 2022). Studies typically assess spatial connectivity in two ways: structural connectivity which is based on physical attributes of the landscape, its structure, and patterns, and functional connectivity which is relative to specific organisms and their dispersion ability and mobility (Kindlmann & Burel, 2008; Mony et al., 2022).

Temporal continuity is defined as the continuous existence of habitats over time (Fritz et al., 2008). Forests with temporal continuity (long lasting presence) host higher diversity and specialist species than new ones (Nordén et al., 2014). Indeed, time allows for colonisation and development of communities in an ecosystem, the evolution towards complex structures and the development of ecosystem functions (Nordén et al., 2014). Temporal connectivity is important to improve dispersal processes over generations and habitats overlapping in time enhance the steppingstone effect (Huang et al., 2020). Colonisation also depends on the different successional stages that result in a change in the species community. Early successional species for instance thrive on newly established stands after disturbances whereas late successional species might have habitat requirements that can only appear after many years (Nordén et al., 2014).

Another predominant biodiversity driver is “structure”, defined by Noss (1990) as “the physical organization or pattern of a system”. The stand structural diversity hypothesis states that a heterogeneous stand structure results in an increase in species diversity and has been tested and approved in several studies (Gao et al., 2014; Patthey et al., 2012). Structural diversity is generally divided into vertical and horizontal diversity (Fischer et al., 2019; Gao et al., 2014), though some studies consider deadwood to be a distinct category due to its predominant importance for biodiversity (Gao et al., 2014; Parisi et al., 2021). Vertical diversity consists in the stratification of the forest in different vertical layers such as overstorey, understorey, bushes, ground vegetation (Gao et al., 2014; Hui et al., 2019). Having a stratified forest is important, as different species rely on different part of the vegetation layers to feed, nest, or get cover (Gao et al., 2014). Horizontal diversity pertains to the spatial arrangement of structural elements in the stand such as spacing of the trees or crown width. This gives an indication on the quantity of solar radiation or water hitting the forest floor and has a direct impact on the species present under the canopy (Barnes et al., 1997; Zellweger et al., 2020). Lastly, deadwood serves as a habitat for invertebrate species or small mammals or amphibians, as a food source for various species from invertebrates to birds and as a substrate for bryophytes and lichen (Parisi et al., 2021). Structure can change the

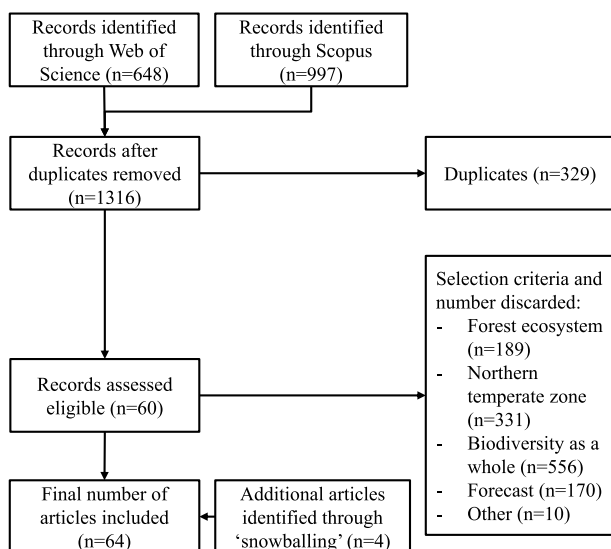


Fig. 1. Flow diagram of the systematic literature review process.

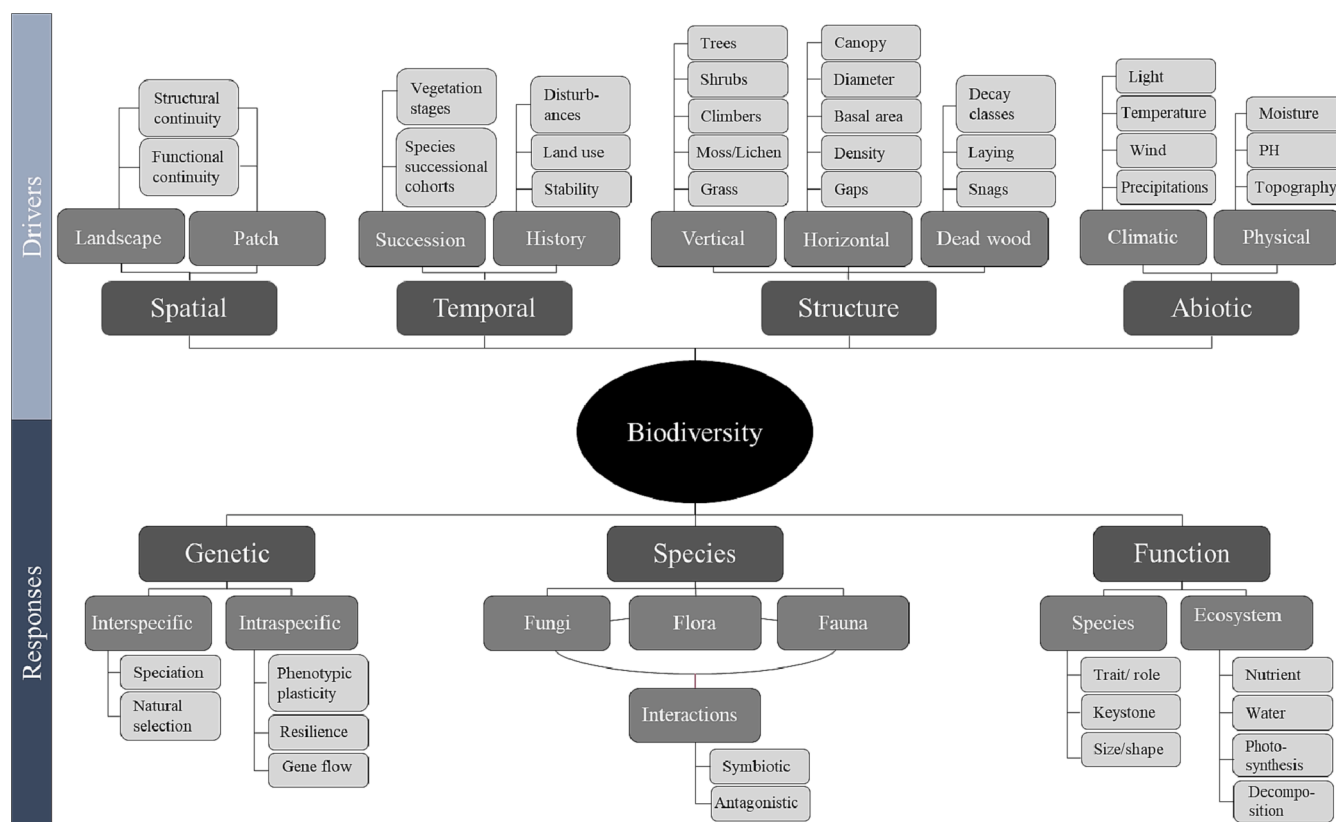


Fig. 2. The main aspects of biodiversity based on the narrative review of biodiversity definition in ecology. The aspects are organised between drivers and responses (dark grey squares) with their relevant sub-components (in lighter shades of grey). Feedback loops and interactions between the aspects are not represented for simplification.

local abiotic conditions such as moisture or solar radiation and is in turn influenced by abiotic factors such as climatic events.

Abiotic factors consist in all non-living factors in an ecosystem that can originate from the climate or the physical situation of the ecosystem. Climate partly explains large scale differences in biodiversity as it is responsible for the world's biomes and their associated diversity (Kimmins, 2004). A warm and wet climate harnesses more biodiversity than extreme climates with dry or cold conditions (Byamungu et al., 2021; Currie et al., 2004) since a wider range of functional strategies can be supported in environments with high solar energy and abundant water (Spasojevic et al., 2014). Physical conditions and structural elements such as topography and vegetation also contribute to the creation of a microclimate through light and precipitations interception or air mixing for instance (Zellweger et al., 2020). Lastly, climatic and physical factors can be responsible for large- and small-scale variations affecting the phenotypes of species or the ecosystem dynamics (Kimmins, 2004).

All four biodiversity drivers described are impacted by anthropogenic activities. Indeed, land use change strongly affects spatio-temporal connectivity at the landscape and patch levels. Management treatments such as thinnings or drainage for instance modify the stand structure, the light and moisture of the ecosystem (Chen et al., 1999; Zellweger et al., 2020) and in turn possibly have an impact on the organisms living in it.

3.2. Responses

Genetic diversity is considered one of the pillars of biodiversity as it determines the biotic responses to the physical and biological environment (Giraud, 2022). Genetic diversity consists in a combination between interspecific diversity (genetic diversity between two species) and intraspecific diversity (diversity within one species) (Barnes et al., 1997; Kimmins, 2004). Populations with higher allelic, genotypic, or

phenotypic richness have a positive impact on biodiversity-ecosystem functions (Raffard et al., 2019). Intraspecific diversity indeed can affect ecological processes to the same extent as the removal or addition of species due to ecological complementarity among genotypes and phenotypes (Raffard et al., 2019). It allows species to adapt to environmental changes and thereby provides resilience against pest and diseases for instance or change in environmental conditions (Kimmins, 2004; Raffard et al., 2019).

Species diversity is a response to adaptation to various physical and biological environments and is also responsible for ecosystem stability and resilience. This is due to the complementarity between species to use the available resources or their different resistance ability to pests and diseases (Paquette & Messier, 2011; Tilman et al., 2014), and to the diversity of reactions to environmental change among species that influence the same ecosystem functions (Elmqvist et al., 2003). Diverse and complex communities are therefore important to ensure ecosystem resilience and productivity (Paquette & Messier, 2011; Silva Pedro et al., 2017) and the interactions between species are also central for biodiversity distribution. Interactions can be symbiotic (when one or both species benefits from the other) or antagonistic (when one or both species is harmed because of the other) (Giraud, 2022; Kimmins, 2004). Symbiotic interactions partly explain why certain species co-occur (e.g., trees and their associated mycorrhiza) whereas antagonistic interactions can result in a spatial differentiation of species. However, species apparently competing for the same resource can also co-exist in an ecosystem due to different sets of requirements for resource acquisition (Kimmins, 2004). The diversity of species, their interactions, and their role in the ecosystem and towards each other can also be defined in terms of functional diversity.

Functional diversity represents the diversity of species traits and links species richness and diversity to ecosystem functions. A trait is a

physical, biochemical, behavioural or phenological characteristic that influences an individual's performance or fitness and defines its ecological role in its ecosystem (Cadotte et al., 2011; Díaz & Cabido, 2001). The trait-based approach explains spatial and seasonal distribution and ecosystem structure and functioning through interactions between the different traits of individuals in the ecosystem, transcending species or taxa characteristics (Díaz & Cabido, 2001; Elmqvist et al., 2003; McGill et al., 2006). The stability and productivity of an ecosystem submitted to environmental variability will be enhanced if it has many functionally redundant species (i.e. species that have similar functions or traits in the ecosystem) (Yachi & Loreau, 1999; Shanafelt et al., 2015). This is based on the fact that species have asynchronous responses to environmental fluctuations and will therefore show temporal complementarity where ecosystem's functions will remain stable over time with a high biodiversity (Elmqvist et al., 2003; Yachi & Loreau, 1999). The presence of diverse species functional groups has a positive effect on ecosystems' functions (van der Plas, 2019) which are the natural processes taking place in an ecosystem such as nutrient and water cycles, photosynthesis, weathering, or decomposition for instance (Barnes et al., 1997). Ecosystems' functions are regulated by abiotic conditions, species composition, resource availability and disturbances (van der Plas, 2019) and are necessary to maintain terrestrial life. If researchers agree that biodiversity contributes to ecosystem functioning, the precise feedbacks between them are still poorly understood (Gonzalez et al., 2020; van der Plas, 2019).

4. Biodiversity in forest planning

Studies of biodiversity in forestry may be divided into two categories. The first one aims to assess the current state of biodiversity, relying on direct sampling methods in the field or remote sensing (Ćosović et al., 2020). The second category aims to forecast the biodiversity potential under different scenarios or futures and relies on the outputs of simulations and assumptions about the future state of the forest. In this study, we focused on the second category by reviewing forest planning studies based on simulations and forecasting models.

The literature review resulted in the selection of 64 studies to include in the review (a list of the reviewed studies can be found in the [supplementary material](#)). The studies selected were distributed mostly in the temperate and boreal biomes with a few exceptions in the Mediterranean zone (Fig. 3). Sweden, Finland, and the Alps region (in Austria, Switzerland, and France) were the regions in which most of the studies were located.

More than 80% of the studies were performed in the last decade with an increase in the end of the 2010 s which seems to indicate a growing interest for including biodiversity in multifunctionality planning.

A minority of studies were dedicated solely to biodiversity, since

80% of the reviewed articles deal with forests' multifunctionality and include other ecosystem services such as economic value, carbon sequestration, or protection for instance. Most of these studies were interested in exploring the tradeoffs between biodiversity and other ecosystem services which highlights the importance of having equally good definitions to make a fair assessment.

A majority of the studies provided a definition of biodiversity, however only a few defined specific aspects (structure, species etc.). Out of the articles acknowledging the various aspects of biodiversity, there was a gradient in the precision used to define the aspects and the number of elements included. Furthermore, the choice of indicators used to evaluate biodiversity was not always justified by the literature on biodiversity which might indicate a confirmation bias in choosing indicators that have historically been used in forest planning studies.

4.1. Forecasting methods

All the reviewed articles use a Decision Support System (DSS) to model the forest's future development. DSSs are computerised tools used by decision makers to help them solve complex decision-making problems (Segura et al., 2014). Since forest decisions involve various spatial and temporal scales, multiple objectives, and stakeholders, forest practitioners and researchers often rely on DSSs. The majority of the DSSs used in the studies focus on economic return and carbon sequestration and have no specific biodiversity module (a list of the systems can be found in the [supplementary material](#)). Some models, such as Heureka (Wikström et al., 2011) and SIMO (Rasinmäki et al., 2009) for northern Europe or 4C (Lasch-Born et al., 2020) and iLand (Seidl et al., 2012) for central Europe and the US, include a mortality or deadwood compartment, which outputs can also be included in a biodiversity forecast.

Most of the articles directly used the outputs of the DSS to forecast biodiversity. Seventeen percent of studies openly based the choice of biodiversity indicators solely on the outputs of the forest simulator used to forecast other ecosystem services. The use of direct outputs from the simulators is practical as it does not require additional models or tools. However, it limits the variety of indicators to structural or tree species indicators and other biodiversity aspects are ignored. Another 33% of the studies used the direct outputs of DSSs though they guided the selection of indicators following existing literature or policies on forest biodiversity. This method requires authors to discuss the advantages of using certain indicators based on biodiversity aspects described in research. Even though all the indicators also come from the output of the DSS(s) used, they are described and justified regarding their importance for biodiversity. The framing is therefore more precise and reflected as it acknowledges the need to rely on ecological knowledge.

The habitat suitability method, which also relies on the DSSs' direct outcomes was used in 16% of the articles. The method selects species

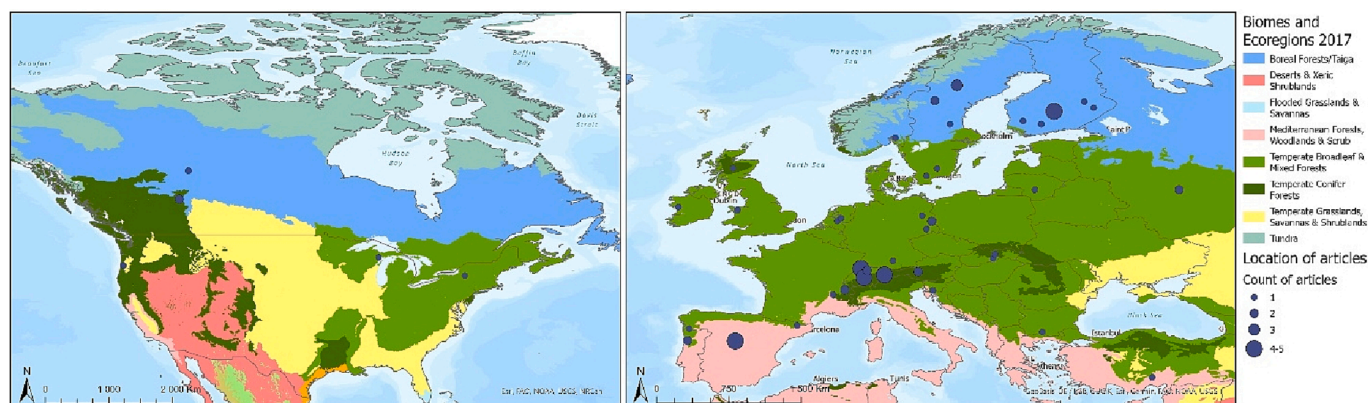


Fig. 3. Map of the reviewed studies' locations, the size of the circles indicates how many studies were located in one area. In addition to Europe and North America, 1 study was located in Japan and 1 in south Chile.

deemed important for the ecosystem based on various criteria (endemic, endangered, functionally important, keystone etc.), defining their habitat requirements and deciding on proxies. Most habitat proxies rely on the outputs of the forest simulator and are therefore linked with tree species or structural elements. The habitat approach requires a wider reflection around the species to include and the reason to include in the analysis. It involves consideration of species functions and their needs in terms of spatial and temporal connectivity or abiotic factors. Habitat suitability methods included a larger number of biodiversity aspects on average than the previous methods described.

A minority of studies included indicators that were not directly taken out of the DSSs used to perform other parts of the analysis. A few articles (8%) used a scoring method whereby experts scored the conditions forecasted by the DSS based on a reference state or on knowledge of biodiversity status in similar present conditions. Though this method relies on the forest's state forecasted by the DSS used, it allows the inclusion of elements that would be difficult to forecast with the DSS such as nutrient or water cycling. However, this method might be limited as it is qualitative and subjective and could vary with different experts. Another 9% of the studies added specific models to forecast biodiversity aspects that they could not derive from the outputs of the DSS. Specific models predict the presence and quantity of certain elements based on parameters such as abiotic conditions and structural elements. Models for microhabitats, shrubs, wood decay, herbaceous cover, lichen, and fauna were recorded. Studies using specific models were able to include biodiversity aspects not covered by outputs of a DSS. However, this requires that such models and functions already exist in the literature or to create them for the study. It therefore adds an element of complexity which could explain why so few studies have used this method.

The remaining 17% of the articles used a combination of two or more methods to forecast biodiversity. Those articles were able to cover on average a high number of biodiversity aspects as they combined the

advantages of each method.

4.2. Biodiversity indicators

As expected, the great majority of articles used indicators of species and structure since these are easy to measure and forecast and are integrated in Decision Support Systems. This was followed by indicators of abiotic conditions, spatial continuity, functional diversity, and lastly temporal continuity (Fig. 4). The underrepresentation of temporal continuity was also expected as it is a concept that is not accounted for in many ecology studies and therefore ill-defined (Huang et al., 2020). The only biodiversity aspect not included in any of the studies was genetic diversity, as it is hard to forecast. However, genetic diversity and gene flow is improved with spatial connectivity that allows different pools of the same species to reproduce and exchange genes (Klinga et al., 2019), so studies considering spatial connectivity might indirectly take genetic diversity into account.

With 94% of the studies using structural elements as biodiversity indicators, structure was the most represented biodiversity aspect according to the classification established in this study. The most used indicator related to structure was tree age, followed by diameter and basal area. Overall, more indicator types were used to describe horizontal structure (n = 8) than vertical structure (n = 5) or deadwood (n = 4). Canopy complexity and the presence of other layers such as shrubs were used in less than 3% of the studies which differs greatly from the importance given to layers heterogeneity in ecology (Hui et al., 2019). Furthermore, indicators for microhabitat structures such as bark on dead wood, flower buds, dead flowers are also missing though tree age and size can act as proxies. Only 8% of the studies included deadwood diversity, meaning tree type, decay class, size of the deadwood, though these elements are very important to define for example which insect cohorts will be present in the wood (Parisi et al., 2021; Sandström et al.,

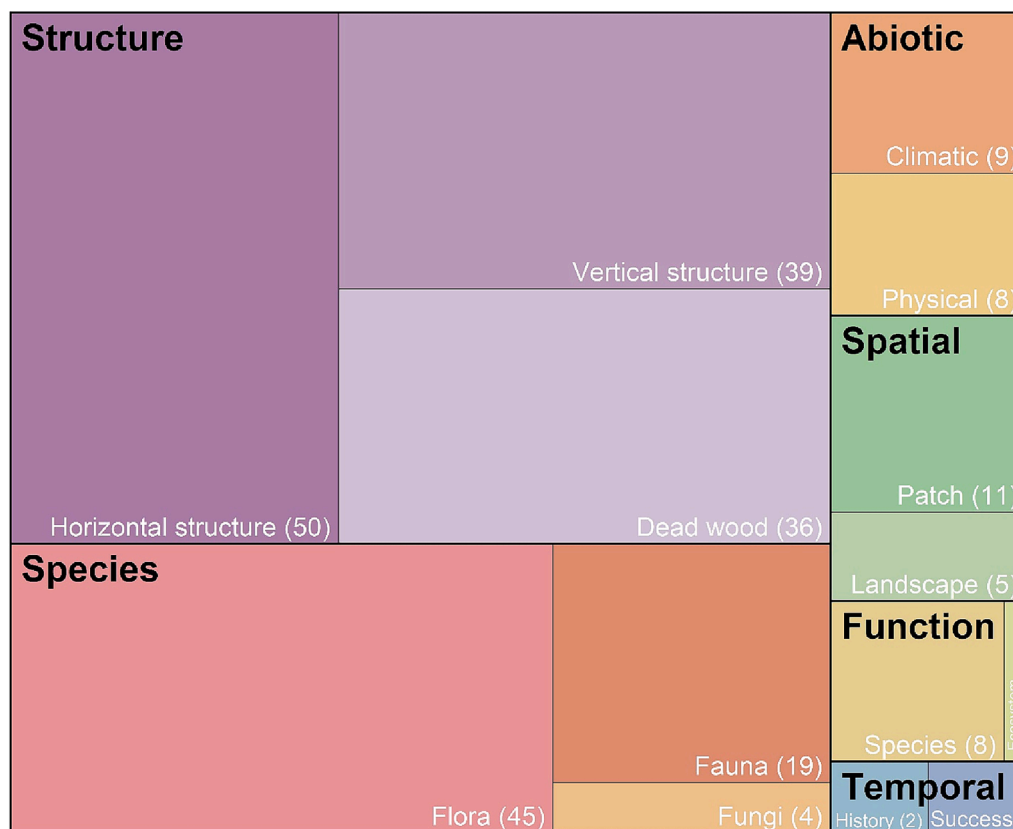


Fig. 4. Tree map of the biodiversity aspects covered in forest simulation studies. The classification relies on the ecological definition of biodiversity defined in section 3 of the study. The size of the boxes is determined by the number of studies covering the aspect.

2019). Compared to the other aspects, structure was well covered by the studies due to the inclusion of structural indicators in many DSSs.

Species diversity was covered in 81% of the studies. However, the representation of the different taxa was fairly unbalanced with a bias towards flora (Fig. 5). Indeed, 52% of the studies integrated flora-only indicators and only 2% of all studies integrated species from different kingdoms (Fig. 5a). When looking closely at the split of indicators, tree species diversity was overrepresented compared to other plants or even compared to fauna diversity (Fig. 5b). This can once more be explained by the use of DSSs designed for timber management, using tree diversity as a variable. On the contrary, fauna diversity is not included in most DSSs, so this was either forecasted via habitat proxies or, in fewer cases, via specific models and regressions on structural, abiotic, tree species, or spatial parameters. The fungi kingdom was also under-represented with only four studies dealing with fungi or lichens, which is striking when we know their importance for other biodiversity aspects such as ecosystem functioning (Pérez-Moreno et al., 2021; Policelli et al., 2020) or as food source for other species and humans (Pérez-Moreno et al., 2021). Forecasting species that will become established in a forest beside the main planted tree species is a challenging task since it relies mostly on habitat suitability indicators and therefore on potential for establishment. It is indeed impossible to know with certainty if an organism will colonize a forest stand, even with all of the habitat requirements being fulfilled. This uncertainty becomes even greater knowing that habitat suitability models are simplified and miss some subtle habitat characteristics or might ignore the differences between feeding, mating, or nesting sites for instance.

Less than 22% of the articles included abiotic indicators even though they could have been included based on present conditions of the sites or via proxies such as canopy opening or gaps. The indicators for physical factors used were altitude, slope, ground structure, water, and pH, while the indicators for climatic factors were light, temperature, climate, and precipitation. One reason for the non-inclusion of abiotic factors is that forest planning studies focus on the direct effects of management on biodiversity indicators, whereas climatic and physical abiotic factors tend to be defined by large scale elements such as latitude or landform.

The issue of connectivity was tackled in a minority of articles. Spatial connectivity was addressed in 20% of the studies with more indicators at the patch than at the landscape level. This was expected since the stand or forest patch is the most common management unit in forest planning. Spatial indicators were mostly used in habitat suitability indexes, relying on known spatial requirements of certain species. This forecasting of connectivity based on species behaviour corresponds to functional connectivity described in section 3.2. In contrast, few studies integrated structural connectivity and landscape patterns. Most of the studies including spatial indicators relied on the use of a geographic

information system and relatively simple indicators such as patches size, position, or proximity to other patches. Temporal continuity was only covered in four studies through the selection of species representative of different succession stages, an evaluation of time since latest disturbance or via habitat persistence. This choice is understandable since it is hard to find clear indicator suggestions or definitions for temporal continuity, even in ecology. Furthermore, adding time considerations to the models increases their complexity as it requires linking the periods together or defining a reference period. Overall, the fact that a minority of studies integrate connectivity in their biodiversity forecasts is problematic when comparing with the central importance of the concept in ecology.

Lastly, functional diversity was only tackled in 14% of the studies with very little focus on ecosystem functions. Species functional indicators were qualitative and related to the potential presence of species that play a role as umbrella or key stone species or have specific habitat needs or life strategies. None of the articles reviewed considered specific functions such as dispersion, predation, or pollination as those are difficult to model. Similarly, ecosystem functions were rarely included even though they can be used to indicate the resilience and state of the system (Gonzalez et al., 2020; van der Plas, 2019). This could be linked with the fact that ecosystem functions such as decomposition, photosynthesis or productivity for instance are accounted for through other ecosystem services than biodiversity. Additionally, the lack of species and ecosystem functions' indicators could be explained by the relative recency of functional ecology and the lack of existing models or references.

5. Discussion

The results of this review demonstrate that the characterization of biodiversity in forest planning and simulation studies is limited in comparison with its definition in ecology. Indicators used in forest planning studies continue to ignore important biodiversity aspects and the weight given to basic overall structural elements compared to area-specific and functionally important aspects is unbalanced. This could result in a misinterpretation of the simulated biodiversity potential, leading to few opportunities to improve biodiversity protection. Additionally, management scenarios providing a satisfactory biodiversity potential based on very few biased indicators are likely to be insufficient to guarantee ecosystem functions in the future. This is concerning given that simulations are the basis for decision making in forestry.

We will discuss several challenges for biodiversity forecasting in forest planning and avenues to overcome them.

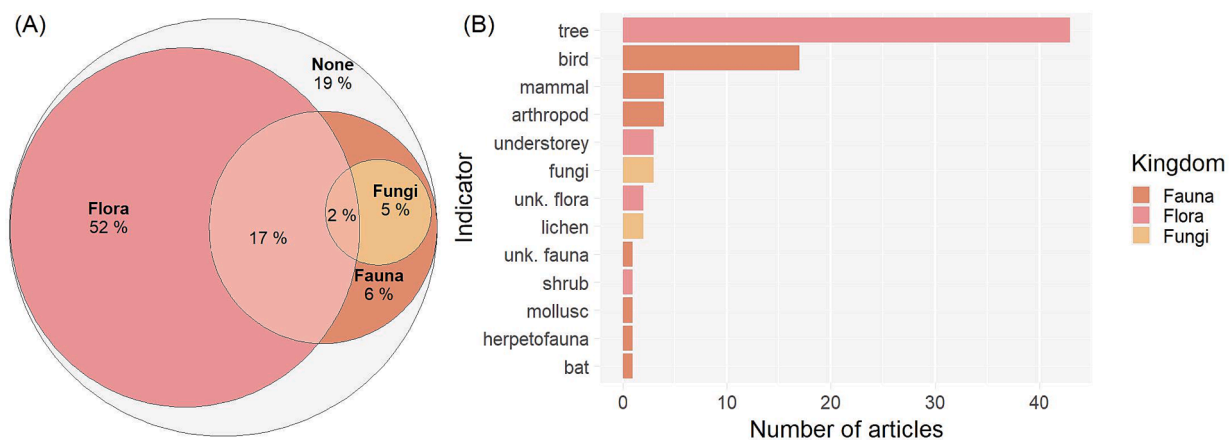


Fig. 5. Indicators used under the species diversity aspect. The figure shows a. the bias towards the selection of flora indicators compared to other kingdoms and b. the count for each specific indicator with a predominance of tree diversity.

5.1. Multi-criteria decisions

All the studies in this review explored biodiversity in conjunction with other ecosystem service. This reflects the reality of the field where biodiversity considerations are embedded in a wider decision context with conflicted goals and objectives. The need to understand tradeoffs between objectives is at the center of the multi-criteria decision approach adopted in several studies included in the review (Blattert et al., 2018, 2020; Carpentier et al., 2017; den Herder et al., 2017; Eggers et al., 2019; Ezquerro et al., 2019; Langner et al., 2017; Merganić et al., 2020; Pohjanmies et al., 2019, 2021; Seidl et al., 2011; Thripleton et al., 2021). The approach consists of eliciting relevant criteria and indicators for each objective of the decision maker(s) before evaluating them across different alternative scenarios (Kangas et al., 2015). To efficiently measure the achievement of the objective, these criteria should hold the nine properties of being essential, controllable, complete, measurable, operational, decomposable, nonredundant, concise, and understandable (Keeney, 1992).

Including biodiversity as a goal in a multi-criteria analysis entails several challenges. Firstly, the complexity of biodiversity and its multiple definitions make it likely to be understood differently from one decision maker to the next. Secondly, biodiversity can neither be measured with a natural scale (e.g., cubic meters, tons of carbon) nor with a constructed scale (e.g., 1 to 10, low to high) but must be measured via proxy criteria (Kangas et al., 2015; Keeney, 1992). Lastly, several of the properties defined by Keeney (1992) as desirable to guide criteria selection seem to conflict with the ecological discourse on biodiversity. This is the case with the “complete” and “concise” properties which require a finite number of criteria to cover all relevant aspects of the decision. This can be difficult to achieve when there may be a very large number of criteria that could be considered relevant. Another tricky property is the measurability whereby a criterion should specify the degree to which the objective is achieved, since identifying how much biodiversity is enough is subjective. Lastly the nonredundancy property states that the effects of the decision should not be counted several times, which might not be possible when some criteria overlap. For instance, a criterion “increase habitat diversity” and another “increase area of old growth forest” are interrelated in that an increase in old growth forests might result in more diverse habitats.

Due to these challenges, it is difficult to properly include biodiversity in a multi-criteria decision analysis. However, since this method is central in forest decision making, one must find a common ground between the ecological definition and operations research. This could be achieved through the breaking down of biodiversity into different objectives, based on the history and priority of the area and corresponding ecological knowledge. Multi-criteria analysis studies should therefore strive to be more specific with the biodiversity objectives targeted and refrain from stating they include biodiversity as an objective when only a few aspects are included.

5.2. Decision support systems

Embedding biodiversity indicators into DSSs has been previously explored. For example, Lexer et al. (2000) had defined a list of biodiversity indicators representing composition, structure, and function that they argued could be embedded in various DSS types. In a report about biodiversity conservation and decision models, Johnson et al. (2007) discussed how DSSs can be used to support biodiversity assessment. This shows progress towards integrating biodiversity indicators into DSSs facilitating studies with ready-to-use biodiversity indicator outputs. However, our analysis shows that the inclusion of biodiversity indicators in DSSs is not yet a priority as most studies used the traditional structural or tree species outputs from DSSs in the absence indicators for other aspects.

To overcome this problem, some studies combined the use of forest simulators with geographic information systems or habitat model

systems. Forsius et al. (2021) for instance used the species distribution modelling software Maxent (Elith et al., 2011) to model nesting suitability for bird species and performed the spatial analysis in ArcGIS. Gustafson et al. (2007) used a habitat modelling software developed specifically for Michigan state. Other studies developed their own specific models to include more indicators than those found in the simulators. Moor et al. (2022) for instance used the forest simulator Heureka coupled with 11 species models. They purposely chose species across different groups (fauna and fungi) and used the simulator’s outputs for tree species, thereby covering fauna, flora, and fungi kingdoms. These examples show that despite the lack of biodiversity modules in most DSSs, there are ways to integrate more biodiversity indicators that represent additional biodiversity aspects in a model.

5.3. Connectivity

Biodiversity is often modelled with indicators for habitat quantity and quality but not for persistence (Pollock, 2020). Persistence is critically important for habitat continuity and legacy in time for biodiversity (Nordén et al., 2014). In our review only one study (Moor et al. 2022) covered both spatial and temporal continuity. In this study, the authors used spatially explicit habitat models for 11 species and included the persistence of habitat trees in one of the models. Indeed, the lichen model had a colonization-extinction component that modelled the potential dispersion of lichen based on the distance from what was considered host trees in precedent periods (Moor et al., 2022).

Recent studies have developed spatio-temporal frameworks to forecast and simulate connectivity dynamically that shifts from the traditional comparison of connectivity between two static snapshots (Huang et al., 2020; Martensen et al., 2017). Spatio-temporal connectivity accounts for sequential interactions between habitat patches that appear and disappear over time, creating temporal stepping-stones for species (Martensen et al., 2017). The framework models habitat patches as nodes that can be in a stable, gain or loss state (whether the habitat remains, gets created or disappears between periods). Each node is linked in space with other reachable habitat patches and in time with itself and other patches at a later stage (Martensen et al., 2017). This allows to model whether a habitat is reachable in space and time for a species or a set of species and captures the effect of ecological processes on habitat patches (Filotas et al., 2023). This spatio-temporal framework is based on graph theory, which is used to model forest ecosystems, improve biodiversity conservation planning, and is gaining attention in forest management (Filotas et al., 2023; Tarabon et al., 2021).

Another way to include the connectivity component and specifically spatial connectivity is to integrate spatial aggregation in the models. Mazziotta et al. (2023) examined the effect of spatial aggregation on biodiversity and specifically used the clique method (Weintraub & Murray, 2006) to define groups of adjacent stands assigned to a biodiversity priority (here, deadwood). This method allows to implement connectivity between stands by aggregating them and implementing specific measures on cliques or groups of stands.

5.4. Species choice

The main challenge when modelling species relates to the initial choice and framing of the studies. Relevant use of habitat suitability models relies on the selection of species that are affected by forest management activities (Edenius & Mikusiński, 2006). Next, priorities should be elicited to drive the choice: is the goal to restore the area, conserve threatened species or promote a certain ecosystem function? The answers will inform the choice, and the consideration of underlying objectives allows to be case specific and potentially avoid confirmation bias towards certain species selected in previous studies. Additionally, species identity and their functional role in the ecosystem must be taken into consideration. Indeed, studies have shown that disappearance of rare species for instance has more impact on community functional

structure than more common ones (Burner et al., 2022). Another element to consider from an ecological point of view is the status of the species in term of generalist or specialist species. There is indeed a uniformization of the world's species in favour of generalist species which can adapt to anthropogenic changes better than specialists though the latter are responsible for specific, irreplaceable ecosystem functions (Nordén et al., 2013; Prach et al., 2018).

Another starting point for choosing the species to be included in the planning framework, would be to assess whether certain rare or specialist species are present at the beginning of the planning period and model their habitat evolution. However, using species records requires reliable data on their presence and persistence in the area. This approach is therefore better suited for immobile species such as plants, fungi, and lichen. Forecasting the consistency of habitat for the aforementioned taxa requires having habitat models for them based on proxies that can be simulated. Data to build biodiversity forecasts is incomplete, even for well-studied species which limits the number of available models (Urban et al., 2016).

5.5. Framing of simulation studies

Biodiversity forecasts would ideally cover all the drivers and responses of biodiversity as defined in ecology but this complexity conflicts with the need for practicality and communicability. Studies exploring biodiversity and ecosystem services trade-offs in general indeed need to be understandable for various stakeholders and transposable to policy making which causes some indicators to be preferred by authors. Studies show that the structure and species aspects for instance are relatively easy to assess, forecast and communicate which explains why species indicators are prioritised in forestry (Angelstam et al., 2001; Gao et al., 2015). The challenge for simulation studies is to strike a balance between the tractability and precision of biodiversity depiction.

The results of this study also reflect a gap between the objectives and focus of forest planners and ecologists. Simulation studies used to plan forest use often focus on easy-to-model biodiversity indicators to meet certification or public requirements while promoting other ecosystem services. Ecologists, on the other hand, prioritise the quality of the natural environment. The former approach considers biodiversity as an ecosystem service among others whereas the latter considers biodiversity as a supporting service for all others. There is an inherent opposition between these two approaches, that can result in a failed attempt to characterise biodiversity properly in simulation studies. Additionally, many forest management studies using biodiversity indicators do not make a clear link between indicator and indicandum, meaning that they fail to link the proxies to the "endpoint" of the fundamental biodiversity aspect that is affected (Gao et al., 2015). These issues call for a better framing of simulation studies that should acknowledge the complexity of biodiversity, elicit their priorities, and carefully choose corresponding indicators.

Another way to improve simulation studies would be to compare the biodiversity scenarios with a reference level. Natural ecosystems tend to be more biodiverse and resilient than managed ones (Barlow et al., 2007; Brockerhoff et al., 2008; van der Plas, 2019). Although managed forests may never match the biodiversity levels of old growth forests, comparing them can provide a transparent perspective and enable the selection of the best or least detrimental scenario. Overall, it is the authors' choice to include indicators covering various biodiversity aspects or comparing the managed scenarios with a natural state and increase the severity of their models. This conscious decision to provide an honest representation of biodiversity, despite technical and economic constraints, should be the starting point of future simulation studies that aim to assess trade-offs between biodiversity and other objectives.

5.6. Limitation of current study

Earlier reviews have explored the use of biodiversity indicators in forestry, focusing broadly on biodiversity assessment in forest ecosystems and categorizing indicators based on the definition of Noss (1990) (Ćosović et al., 2020; Gao et al., 2015). In this study, we have focused specifically on simulation studies and biodiversity forecasts and have gone one step further in building a biodiversity framework based on research in ecology to define a base for analyzing the indicators. This cross-field approach has to our knowledge not been used to highlight the gaps in the approach to biodiversity in forest planning.

This review aimed to be as comprehensive as possible, however there are some unavoidable biases linked to the choice of keywords, the definition of inclusion criterion, the geographic distribution of the studies, or human error in assessing the search results. A different choice of keywords will produce different search results; however, the chosen keywords are rather open and resulted in a large number of articles in the two databases we used so we believe they were general enough to identify most of the relevant literature. The geographical clustering of some studies on certain regions might result in a greater similarity among them, and we indeed observed that some reviewed studies referred to others for their choice of biodiversity indicators. However, this situation depicts a reality of the research field and was integrated into our results as it supports our argument about confirmation biases when choosing a biodiversity indicator. Lastly, it is possible that mis-categorisation of biodiversity indicators might have occurred due to some indicators possibly falling in different categories, but we do not believe that this affects the overall trends presented in our analysis.

6. Conclusion

The current coverage of biodiversity by forest planning studies is incomplete. A few aspects that are central in ecology are overlooked in planning studies. This is done intentionally for simplification purposes or because the choice of indicators available in simulators or planning softwares does not connect with ecological knowledge of biodiversity. A more precise framing of forest planning studies is necessary to ensure that they do not overpromise biodiversity improvements if trade-offs are based on indicators representing a single component of biodiversity. The results of this review along with the framework to define biodiversity aspects in forestry can hopefully be used to improve future biodiversity simulation studies.

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

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110620>.

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