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REVIEW PAPER

Trade-offs or complementarity between biomass production and biodiversity in European forests: a review

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Abstract
Forestry faces the challenge of balancing the increasing demand for timber, carbon sequestration, and biodiversity protection. Biodiversity plays a crucial role in the stability and adaptability of forest ecosystems, enabling them to withstand disturbances and recover from them. Preserving biodiversity is essential for long-term survival and well-being. Enhancing biodiversity in managed forests is important because they occupy a significant area of forests in Europe. Understanding the relationships between forest production and biodiversity from various perspectives is crucial for developing effective multi-taxa management concepts. Biodiversity loss due to management practices can result in habitat destruction, fragmentation, and species displacement. Biodiversity enhances ecosystem services linked to biomass production, such as pollination, nutrient cycling, and carbon sequestration. This study reviews the relationships between biodiversity and production in Europen forests, emphasising the impacts of biodiversity on ecosystem functioning and production, as well as the effects of production indicators on biodiversity. The effects of biodiversity on productivity are often studied in the same population, most often in the tree layer. However, a lack of knowledge on how biomass production affects the diversity of other ecosystem components limits our understanding of the multifacet relationships. Forest management significantly impacts biodiversity and production, and different management systems have varying effects on forest ecosystems. Diverse ecosystems exhibit niche complementarity, resulting in increased biomass production. Sustainable practices, including land-use planning, habitat protection, agroforestry, and non-invasive species use, can mitigate the adverse effects of biomass production on biodiversity.

Key words: species richness; productivity; climate-smart forest management; multi-taxonomic approaches; biodiversity dynamics

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1. Introduction

Biodiversity varies significantly across biomes, influenced by the distinct climatic conditions that drive soil formation processes, site productivity, and ultimately determine the climax community characteristics (Holdridge 1947). Remarkably, six out of the twelve Earth's biomes are characterized by a rich variety of shrub and forest ecosystems. Forested biomes play a pivotal role in supporting and sustaining a wide array of plant and animal species, making them vital areas of focus for conservation and biodiversity research. In terms of global multitaxonomic diversity, there are only estimations, with insects and myriapods considered the most diverse, followed by fungi, Chelicerata, Protoctista, nematodes, plants, mollusks, crustaceans, and vertebrates (Groombridge & Jenkins 2002; Hassan et al. 2005). The prevailing amount of terrestrial species richness is situated between 10°N and 10°S, where the species are related to the most productive moist tropical rainforest biome. With increasing longitude and altitude gradient, biodiversity as well as productivity, in general, decrease towards the poles and high mountain ranges (Kleidon & Mooney 2000; Plesník 2004). Net primary production, as the most common measure of production, varies from 20–30 t ha^{-1} of carbon per hectare in tropical rainforests to 5–10 t ha^{-1} in boreal forests. European temperate forests lie in the middle of the production as well as biodiversity gradient, with NPP ranging from 10 to 20 t ha^{-1} (Hassan et al. 2005). Estimated multitaxonomic species richness (amphibians, birds, and mammals, reptiles) according to Hassan et al. (2005) varies from more than

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20,000 species in rainforests to less than 1,000 in boreal forests and up to 4,000 in temperate forests. In the case of vascular plants, rainforests consist of 4,000 to 5,000 species in several hotspots (Brazil, Papua, Costa Rica, Panama) (Mutke et al. 2011). European temperate forests contain up to 130 species in a spatial unit of 400 m^2 (Večeřa et al. 2019), with the total number of plant species observed up to 1,800 species (Heinken et al. 2022).

Production of forest ecosystems has been the subject of research for more than a hundred years, while the related biodiversity consequences and its impact on ecosystem functioning are relatively new research interests (Fig. 1).

Forest management has been facing the issues of simultaneously addressing the increasing demand for timber and sequestering carbon, along with a pressure to increase and protect the biodiversity in the forest ecosystems (Aggestam et al. 2020; Bollmann et al. 2020; Krumm et al. 2020). Despite the often-problematic compatibility of approaches that increase production while preserving diversity, the potential of forests for climate change mitigation can be fully utilised only if forest ecosystems are stable and adaptable (D'Amato et al. 2011). Regarding adaptability, biodiversity in all its dimensions is the most important feature of forest ecosystems (Díaz et al. 2009). Biodiversity provides resilience and adaptability to ecosystems, allowing them to withstand and recover from disturbances. The loss of biodiversity due to unsustainable biomass production practices reduces the capacity of ecosystems to adapt to changing environmental conditions (Fischer et al. 2006; Oliver et al. 2015). This, in turn, can make ecosystems more vulnerable to further degradation and limit their ability to recover from disturbances, exacerbating the negative impacts on biodiversity. Therefore, biodiversity protection or enhancement should also be essential in managed forests (Brockerhoff et al. 2017; Bowditch et al. 2020). Only species-rich forests can fulfil functions in terms of connectivity between protected or otherwise valuable areas (Hodgson et al. 2011). Management approaches that include biodiversity aspects should be a priority. However, developing and establishing such multi-taxa management concepts require deep knowledge of the relationships between forest production and biodiversity from various perspectives. Due to anthropogenic processes, we have observed dramatic changes in species composition in forests, including their extinction (Mölder et al. 2008; Staude et al. 2020).

Unsuitable management practices in synergy with climate change, nitrogen deposition, and other pollutants can drive biodiversity loss and homogenisation of species pool (Gilliam & Roberts 1995; Bernhardt-Römermann et al. 2007; Bobbink et al. 2010; Dirnböck et al. 2014; Gilliam et al. 2016). The limited understanding of the impacts of these processes prevents us from predicting the responses of most taxonomic groups. Predicting biodiversity patterns, as an essential characteristic of forest ecosystems, requires a comprehensive knowledge base and systematic collection of data on the broadest possible range of organisms. Intensive research on the relationships between biodiversity and production, both in time and space, will help us understand and predict changes in biodiversity under different management and climate scenarios and identify factors that can have fatal conse-

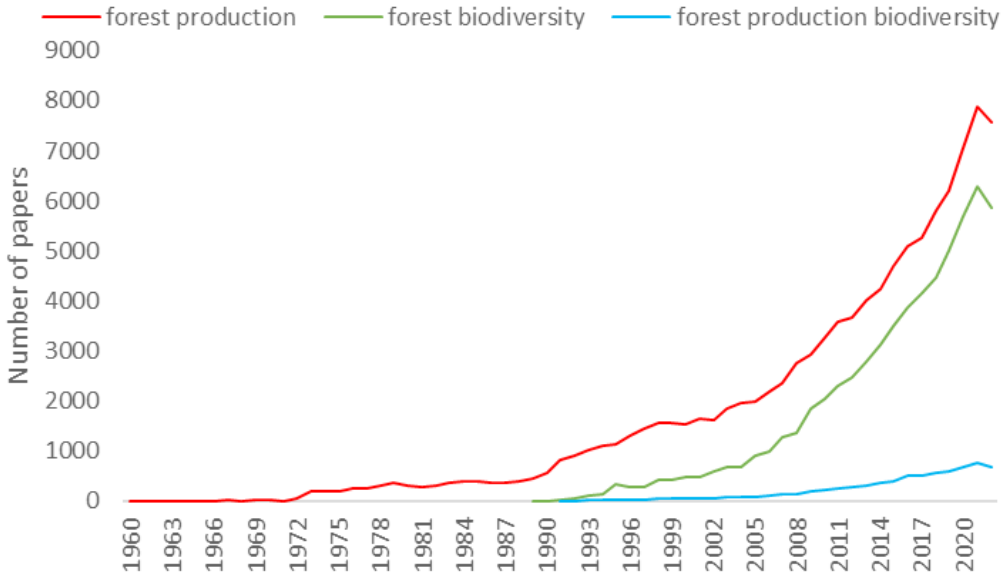


Fig. 1. Number of published papers containing words "forest"; "production" (red), "forest";"biodiversity" (green), and both (blue). Total number of relevant studies in Web of Science database for the first filter was 10,955, for the second 65,509 and for the third 7,540. The first paper containing forest production emerged in 1913, whereas the first paper containing words forest biodiversity was published in 1989.

quences on diversity. The research focused on the multiple taxonomic groups of organisms in relation to production, structural characteristics of forest or management is still rare (Dittrich et al. 2014; Kaufmann et al. 2018; Schall et al., 2018, 2020; Lelli et al. 2019; Sabatini et al. 2019). Conserving and improving biodiversity is critical for maintaining the health and resilience of ecosystems, safeguarding ecosystem services, and promoting sustainable development. It requires efforts to protect and sustainably manage landscapes, ecosystems, species, and their intraspecific variability and promote benefits from biodiversity. Conservation actions include establishing the protected areas, active approaches such as habitat restoration and sustainable resource management, and efforts to address the underlying drivers of biodiversity loss (Angelstam 1998; Fedrowitz et al. 2014; Miklín & Čížek 2014; Doerfler et al. 2017; Kovac et al. 2018). Intensive biomass production practices, such as large-scale forestry, often involve habitat alteration. These activities may lead to the homogenisation of natural habitats, fragmentation of ecosystems, and loss of biodiversity (Jenkins 2003; Laurance et al. 2007; Mortelliti et al. 2010). Deforestation for biomass production, for instance, can destroy critical habitats and displace numerous species, reducing overall biodiversity. Preserving biodiversity is not only a moral imperative but also essential for the long-term survival and well-being of human societies and the global ecosystem. Biodiversity is crucial in providing numerous ecosystem services directly linked to biomass production (Hooper et al. 2005). These services include pollination, nutrient cycling, soil formation, water retention, and purification, among others. The presence of diverse species enhances the efficiency of these services, facilitating increased biomass production. In turn, biomass production contributes to essential processes such as carbon sequestration and climate regulation (Díaz et al. 2009; De Frenne et al. 2021). Here, we provide a comprehensive review of published research papers focusing on the intricate multitaxonomic relationships between biodiversity and production in primary and managed forests, specifically emphasising central European temperate forests. Two perspectives can be considered to study the relationships between production indicators and biodiversity in forest ecosystems:

1. The impact of biodiversity on ecosystem functioning and biomass production.
2. The impact of increasing biomass production on ecosystem biodiversity.

2. What are the effects of biodiversity on biomass production?

Diverse ecosystems often exhibit a phenomenon known as niche complementarity (Tilman et al. 1997), where different species utilise resources in distinct ways, thereby reducing competition. This complementary resource use allows for the efficient utilisation of available resources, leading to increased biomass production (Pretzsch & Schütze 2009; Pretzsch et al. 2015, 2020; Drössler et al. 2018). For instance, plants with varying root structures can access different soil layers, accessing a greater range of nutrients and water (Jose et al. 2006; Meinen et al. 2009). Biodiversity encompasses a wide range of species, each with its unique function within an ecosystem. These species interact with one another in complex ways, forming ecological networks and relationships. These interactions can have profound effects on ecosystem functioning, including biomass production. For example, certain tree species may provide necessary resources, such as nitrogen fixation or nutrient cycling (facilitation), benefiting the growth of other species and ultimately contributing to the overall production.

Biodiversity plays a crucial role in maintaining the overall functioning of ecosystems (Hooper et al. 2005). Each species contributes to specific ecological processes, such as nutrient cycling, pollination, predator-prey, or other trophic interactions. Reduced biodiversity resulting from intensive biomass production can disrupt these processes, leading to imbalances in the ecosystem (dominance). For example, a decline in pollinator species due to habitat loss or pesticide use can negatively impact plant reproduction and reduce overall biodiversity by favouring limtied number of species.

The original scientific papers focused on studying the impact of biodiversity on forest production were driven by the need to improve the efficiency of forest management. The traditional method for these long-term observations involved selection (thinning) experiments (Assmann 1970), which included control plots without intervention as references. These experiments, investigating the influence of biodiversity on production, encompassed both homogeneous and species-rich mixed forests. Recently, there have been studies analysing complex allelopathic, competitive, or facilitative interactions among different tree species and their effects on overyielding or underyielding in mixed stands compared to expected yields from homogeneous stands (Fridley 2001; Hooper et al. 2005; Pretzsch & Schütze 2009; Fabrika & Pretzsch 2011; Zhang et al. 2012; Pretzsch 2022) In these studies, biodiversity is mainly related to the species composition of the tree layer. However, the results of these experiments indicate that despite the expected higher resource utilisation efficiency in a wide variety of conditions (Vilà et al. 2007; Liang et al. 2016; Mensah et al. 2016), significant overyielding is not always observed in species-rich forests compared to homogeneous structures. Expected outcomes associated with niche complementarity theory have proven to be ambiguous. Interspecific interactions and environmental factors can also lead to the opposite effect (Drössler et al. 2018). Nevertheless, it is undeniable that species-rich forest structures are less vulnerable to large-scale disturbances in terms of stability and mortal-

ity, which leads to higher production stability compared to monocultures (Yachi & Loreau 1999). Diverse ecosystems exhibit greater stability and resilience in the face of environmental disturbances. Diverse ecosystems are better equipped to recover and maintain biomass production when a disturbance occurs, such as a natural disaster or climate change (Bengtsson et al. 2000). Redundancy in species function and the presence of adaptable species within a diverse ecosystem ensure that even if some species are negatively affected, others can compensate and maintain ecosystem productivity.

The decrease in production and biodiversity in forest ecosystems along longitudinal and elevational gradients is not straightforward, and there are numerous exceptions, uncertainties, and fluctuations within individual biomes (Adler et al. 2011). The most productive sites often do not exhibit the highest local biodiversity values and are frequently occupied by species that demonstrate exceptional competitiveness under optimal ecological conditions (e.g. monospecific beech stands in temperate deciduous forests). These findings are summarised within the formulation of the Biodiversity-Ecosystem Functioning (BEF) theory, which describes an inverse "U"-shaped relationship (hump-shaped) between biodiversity and production indicators at the regional scale, suggesting the highest biodiversity values at the centre of the production gradient (Hooper et al. 2005; Gonzalez et al. 2020). At the global scale, the relationship tends to be logarithmic (Liang et al. 2016).

It is crucial to adopt sustainable practices to mitigate the adverse effects of biomass production on biodiversity. These measures include implementing land-use planning that considers environment factors (Fig. 2), protecting and restoring natural habitats, promoting agroforestry and mixed species systems, and utilising non-invasive or locally adapted species. Additionally, supporting sustainable certification schemes, biodiversity monitoring and implementing strict environmental regulations can ensure that biomass production minimises its impact on biodiversity (Knoke et al. 2021). However, studies that systematically evaluate and monitor overall biodiversity, encompass various taxonomic groups and examine its influence on ecosystem-wide production are rare. One of the reasons why the relationship between overall biodiversity and ecosystem production is rarely investigated is the low proportion of economically important biomass contributed by other taxonomic groups to the total forest biomass and the difficulty of multitaxon research.

3. What are the effects of biomass production on biodiversity?

When studying biodiversity, it is essential to consider the different production stages of forest ecosystems and their successional development, such as gap dynamics or management schemes in commercial forests aimed at

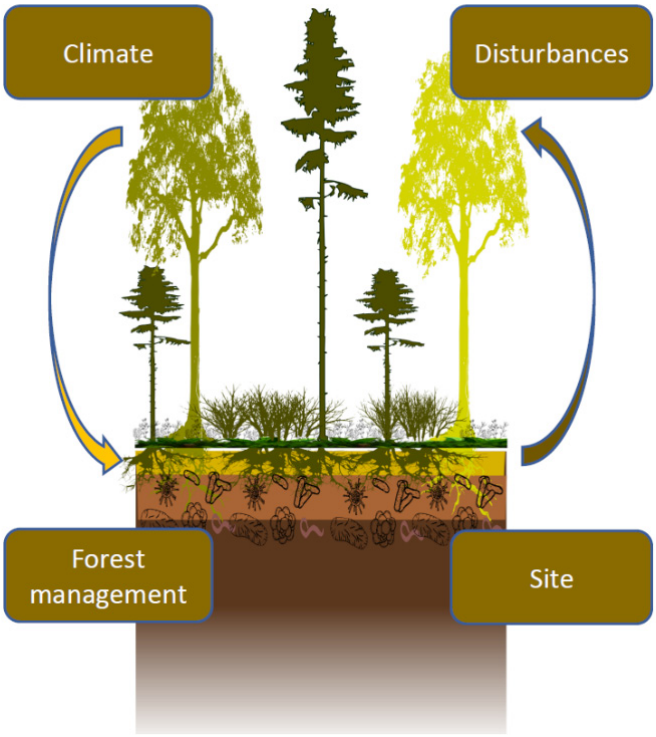


Fig. 2. Biodiversity not only includes tree canopy (as it is often considered in biodiversity-production studies), but multiple components of the forest ecosystem and their mutual relationships driven by various factors.

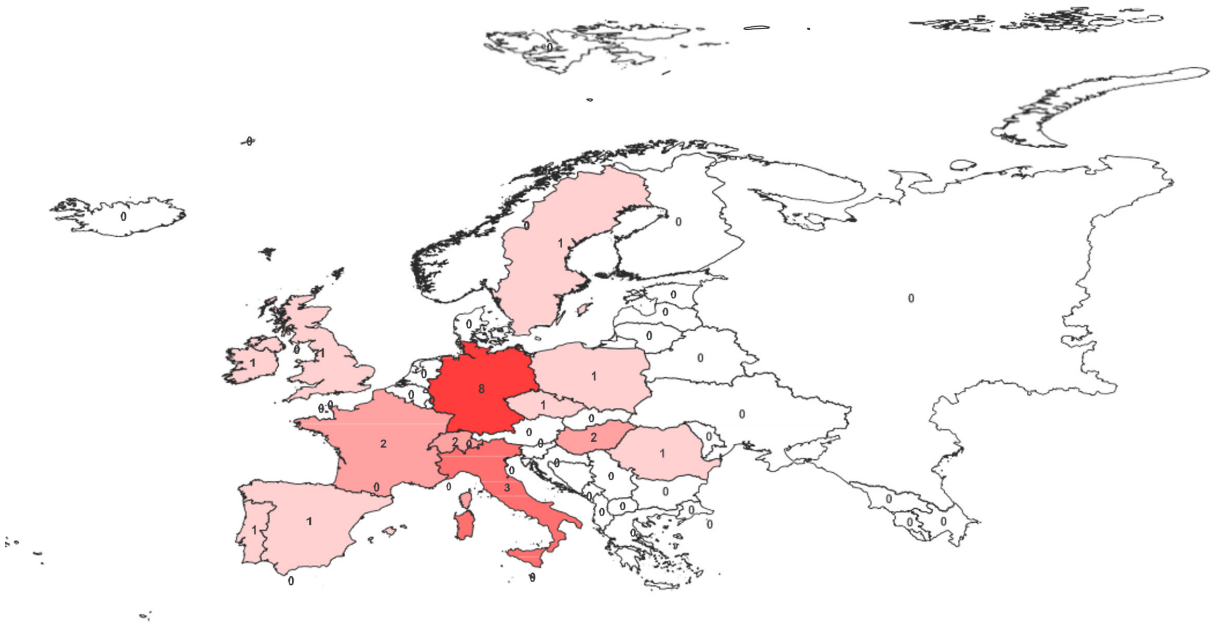


Fig. 3. Map indicating a number of published multitaxonomic studies in European forests. A total number of relevant studies from 148 thoroughly reviewed was 19 published in Web of Science (the following filtering criteria were used: "multiple taxa", "forest", "biodiversity"). The number of taxonomic groups included in the selected studies varied from three to thirteen.

enhancing production. Changing the perspective opens questions regarding biodiversity dynamics within these stages and management approaches. Research results indicate that trees are the most influential producers in forest ecosystems with significant impact on regulating populations of other taxonomic groups in their surroundings. For example, Sabatini et al. (2019) suggested, that along the carbon stock gradient in aboveground biomass, it is possible to identify its influence on the ecosystem's biodiversity and certain species groups with indicative values for different levels of accumulated carbon. According to these authors, the aboveground biomass of trees serves as a significant regulator of multitaxonomic diversity. However, multitaxonomic studies supporting this hypothesis are still rare in European temperate forests (Fig. 3) and worldwide.

In the process of secondary succession, according to the resource ratio hypothesis (Tillman 1985) ruderal species are initially dominant during the migration and colonisation of species on land. With their short existence in a less competitive environment, they facilitate the conditions for the establishment of other species. In the subsequent phase, different strategies emerge, creating a competitive environment that no longer allows the return of ruderals. As pioneer tree species colonise the area, competition increases again, resulting in the decline of some species. The climax species later form long-term structures that limit the reappearance of ruderals and pioneer tree species while facilitating the environment for self-regeneration and forest specialists that rely on a specific microclimate (De Frenne et al. 2021). Biodiversity during the succession process changes along this gradient, ranging from highly diverse and unbalanced communities to moderately diverse and more balanced ones. Productivity and biodiversity typically increase simultaneously only at the beginning of the successional sequence, and as the climax is reached, production reaches its maximum and the diversity of primary producers decreases (Guo 2003; Taylor et al. 2020). Late-successional species achieve higher maximum age and size. Thus, tree species communities can create and maintain forest microclimate more effectively. Long-term stability of these productive late-successional stages is maintained through gap dynamics (Leibundgut 1978, 1993; Korpel 1995; Kenderes et al. 2009; Kucbel et al. 2010).

Forest ecosystems in their mature stages are characterised by high productivity and high carbon stocks in live and dead biomass compared to more species-rich successional stages. Highly productive forest ecosystems are characterised by complex vertical and horizontal structures (Scheuermann et al. 2018), simultaneously allowing efficient solar energy, water, and nutrients to be utilised across various soil horizons. This relationship between forest structure and its productivity has been demonstrated in numerous studies, including the works of Assmann (1970) and Pretzsch and Schütze (2009). Concerning the succession of primary producers, the dynamics of other taxonomic groups along the successional gradient are partially described. We can assume that succession and changes in the basic trophic potential of the ecosystem also result in changes in the spe-

cies ratios of other taxonomic groups (Burrascano et al. 2018). Dynamics of primary producer diversity through succession influence trophic interactions, including predation, herbivory, and mutualism, which are critical for ecosystem energy flow. Niche differentiation helps maintain ecological balance and prevent overconsumption of specific resources and monodominance (Falster et al. 2017). This, in turn, supports sustained biomass production. For example, predator-prey interactions regulate herbivore populations, preventing excessive consumption of primary producers and ensuring a healthier and more productive ecosystem. The inter-specific relationships along a successional gradient and the spatial forest structure become more complex. The complexity of ecological relationships and structural parameters is a fundamental assumption for homeostasis, which is the primary assumption of biodiversity as insurance theory (Mori et al. 2013; Loreau et al. 2021).

The ecosystem functioning of climax ecosystems is typical by efficiently utilising available resources through a stable species composition, which forms a barrier against the invasion of other species. Such conditions are maintained by the autogenic self-regulated microclimate but also through disturbance events that reduce the amount of bound live biomass and local productivity. These changes create niches for new species, their regeneration, and an opportunity for ecosystem adaptive shifts (Buma & Schultz 2020). The dynamics in relationship to disturbances have been addressed in studies such as Levin & Paine (1974); Runkle (1985); Overpeck et al. (1990); Hobbs & Huenneke (1992); Sousa (2003). In the case of primary producers, the highest diversity is observed in intermediate disturbed conditions in terms of range and frequency (Intermediate disturbance hypothesis – IDH) (Watt 1947).

The complex relationship between forest production/productivity and the biodiversity of different taxonomic groups can be described by various functional patterns, with each taxonomic group and trait within the taxa responding to these changes in different ways (Elek et al. 2018). Multitaxon biodiversity assessments (all taxa biodiversity inventory – ATBI) require specialised study designs due to the different sizes and behaviours of inventoried organisms (Tinya et al. 2021). For this purpose, plots with variable sizes or random sampling of a predefined number of microhabitats, as well as acoustic assessment and other special sampling methods such as metabarcoding, are often used. These data are utilised to estimate basic diversity indicators, such as species richness, population size, abundance, and more. In certain taxonomic groups, it may only be possible to determine presence or absence rather than frequency (e.g. fungi and microbiota). These limitations in multitaxon inventories necessitate the use of more straightforward indicators that can be evaluated for each assessed taxon.

4. Consequences of forest management on the production and biodiversity

Forest management significantly impacts primary producers' biodiversity (Kenderes & Standovár 2003; Ujházy et al. 2017). Forests designated for production are usually managed through systems based on principles of even-aged or selection forests. Selection systems typically deviate from the natural dynamics, but the management aims to mimic them to some extent. Measures falling into this category are described as close-to-nature management, continuous cover forestry, single tree selection systems, freestyle silviculture, or retention forestry (Garfitt 1995; Diaci et al. 2011; Schütz 2011; Gustafsson et al. 2012). A common characteristic of these techniques is that they involve small-scale interventions based on logging tree size or maximum area affected at once, which usually does not exceed 0.2–0.5 ha. On the other end of the spectrum are even-aged approach, which exhibits artificial spatial order, leading to a vertical and age structure of the forest divided into a certain number of age classes with limited interaction between tree generations. In addition to these influences through effects on the tree layer's structural parameters, forest management directly impacts processes in the other layers and forest floor through soil compaction and anthropogenic disturbance. Forest management aims to accelerate high-quality timber production and improvement of other societies demanding ecosystem services. As a consequence, forest management inevitably affects the development of plant communities and related taxonomic groups and triggers invasions of new and non-native species (Duguid & Ashton 2013; Nolet et al. 2018; Mercier et al. 2019; Wales et al. 2020; Wei et al. 2020).

Besides forest management, many other factors can cause changes in the species composition of primary producer communities. These influences include pollution deposition, eutrophication, acidification, calcification, and thermophilization. Communities also reflect the history of ecosystem formation and its surroundings, including grazing, fertilisation, leaf litter removal, or charcoal burning and disturbance history (Bernhardt-Römermann et al. 2007; Bobbink et al. 2010; Verheyen et al. 2011; Dirnböck et al. 2014; Máliš et al. 2021a; Koutecký et al. 2022). Although many studies have investigated the impact of management on the taxa under various conditions using parallel plots, the results of these studies are inconsistent. In the case of primary producers, some studies report an increase in diversity and coverage of herbaceous vegetation, while others observe only minor changes in diversity indicators and simultaneously record a decrease in the diversity of bryophytes and lichens (Horvat et al. 2017; Kaufmann et al. 2018; Schall et al. 2018; Sandström et al. 2019). The relationships between the horizontal layers and temporal dynamics are often explained based on ratios between facilitation and competitiveness, as well

as other relationships observed between and inside plant populations (Callaway & Walker 1997).

Tree canopy creates a specific microclimate inside the forest faciltating an occurrence of forest-specific species (Ritter et al. 2005). The spatio-temporal light mosaic, which provides energy sources to the understorey, is primarily influenced by the tree layer structure and is vital for the existence and dynamics of various taxonomic groups such as vascular plants, bryophytes, ferns, as well as soil micro and macrobiota. This overall effect of tree canopy can be generalised as a facilitation mechanism that enhances the occurrence of forest specialists by creating conditions for synergies between mycorrhisal fungi and soil microbial communities and by buffering the effects of climate extremes and amplitutdes (Zellweger et al. 2019). However, relationships between forest overstorey and understorey can be also competitive. The recent evidence suggested that forest structures typical fora higher belowground and aboveground competition can lead to a decrease in the understorey diversity and also biomass production troughout forest succession or gap dynamics (Mölder et al. 2014, 2008; Ujházy et al. 2017; Slezák & Hrivnák 2019; Máliš 2021b).

Lichens are more sensitive to the occurrence or absence of individual mature trees compared to general forest structure parameters (Ranius et al. 2008; Hofmeister et al. 2016). Bacteria, bryophyte and fungi diversity are strongly associated with the diversity, quantity, and quality of deadwood and dead biomass in general (Blaser et al. 2013; Brazee et al. 2014; Purahong et al. 2015; Tomao et al. 2020). In contrast, other taxa, such as arthropods, and vertebrates such as bats, birds, and mammals are dependent on various microhabitats and trophic interactions related to trees and herb species (Fuller 2000; Moning & Müller 2009; Regnery et al. 2013; Ram et al. 2017; Gutzat & Dormann 2018).

The relationship between primary producers and herbivores and its management represents another crucial aspect of biodiversity in forest ecosystem functioning. Existing studies have explored these relationships in various ways, highlighting the essential functions of herbivores in seed dispersal processes (Picard et al. 2016) and their role as "ecosystem engineers" in reducing competition and dominance effects of canopies (Koerner et al. 2018; Villar & Medici 2021) which can ultimately lead to a decrease in overall biodiversity, especially on the more productive sites. However, particularly in temperate zones, where herbivore density is increasing compared to the tropical forest biome, the evidence suggests a significant negative impact of ungulates on forest regeneration and tree species richness. Browsing is considered one of the key factors that lead to a dominance of several tree species such as Norway spruce (Vacek 2017; Konôpka et al. 2021). There is evidence that net carbon uptake can increase three times after herbivore exclusion from the ecosystem (Forbes et al. 2019). These contrasting results suggest that rewilding initiatives, aimed at improving trophic diversity and increasing carnivore pressure, combined with game management to control herbivory populations, hold the potential to enhance the balance of plants-vertebrates' relationships.

The highest species richness in a forest ecosystem is related to the topsoil and hummus layer. The upper soil layers are crucial in terms of nutrient cycling and related decomposition processes (Lukac 2017). These processes, related to the activity of myriads of organisms (fungi, protozoa, bacteria, nematodes, arthropods, molluscs, earthworms, algae, and cyanobacteria), are crucial in stabilizing long-term soil physical and chemical characteristics, which are directly related to the production of primary producers as well as their diversity and overall ecosystem functioning (Delgado-Baquerizo et al. 2020). However, for taxa, such as amphibians, reptiles, land snails, or certain groups within the phylum Arthropoda, only a few sources of information are available regarding the impacts of forest management and production. These sources often cover only a limited range of natural conditions (Prieto-Benítez & Méndez 2011; Romano et al. 2016).

Primary producers can generally be considered as strong indicators of other taxa's diversity (Chamagne et al. 2016; Ampoorter et al. 2020; Storch et al. 2023). Published studies have shown that each taxonomic group responds differently to management-inducted changes in forest structure, production/productivity (Chaudhary et al. 2016; Elek et al. 2018; Schall et al. 2018, 2020), and the conditions maintaining one can decline others (Klein et al. 2020). Even-aged forests exhibit higher γ diversity compared to close-to-nature systems and unmanaged forests. Moreover, forest areas managed with close-to-nature methods or without management show lower values of overall biodiversity for plant and other taxonomic groups. These findings are applicable at a regional scale (Schall et al. 2018, 2020). Based on this study, it can be deduced that regional biodiversity is influenced by the variation (beta diversity) among samples. Even-aged forests exhibit higher variability between the samples (age classes), while close-to-nature approaches demonstrate higher variability within the samples. This difference can be attributed to the larger area and length of ecotones and the size of patches found in even-aged forests, which serve as biodiversity hotspots (Lövei et al. 2006; Laurance et al. 2007; Hofmeister et al. 2013; Aragón et al. 2015; Schall et al. 2018; Gasperini et al. 2021; Schlegel 2022). It is worth noting that the higher species richness observed in the set of even-aged forest stands should be partly due to the presence of invasive and non-native species, and on the other hand, locally there are age classes with critically low diversity indicators. Nevertheless, these findings emphasise the significance of considering not only local alpha diversity but also landscape, habitat and microhabitat diversity, as they play a crucial role in shaping overall multitaxon biodiversity patterns. The consequences of the segregation of spatial habitat and hotspots due to forest

management may be reduced through the integration of biodiversity-improving elements. Integrative approaches may be based on mulitaxon research results in complex silvicultural measures mimicking the key characteristics of species-rich forest and landscape structures (Bauhus et al. 2009).

5. Conclusions and future perspectives

Biodiversity is essential for the proper functioning of ecosystems, as different species contribute to vital processes such as pollination, nutrient cycling, and ecological interactions. Intensive biomass production practices that simplify ecosystems by reducing habitat and species diversity can disrupt these ecological interactions. The expansion of biomass production can lead to shifts in species composition within ecosystems. Despite the evidence of overyielding effects of mixed forest structures, certain species may be favoured for their high biomass production potential, leading to the dominance of a limited number of species at the expense of others. This can reduce biodiversity, as some species may be outcompeted or displaced, leading to a less diverse ecosystem. Except for production alone, the homogenisation of forest structures towards even aged can also lead to biodiversity loss in less productive or mixed forests. Forest development stages in managed forests may show higher overall diversity indicators but as impacts of the presence of non-native and invasive species.

On the intraspecific level, practices prioritising high-yielding varieties or genetically uniform tree plantations can also negatively affect multitaxon diversity. Lower species and intraspecific diversity reduce forest resilience to environmental changes, making them more vulnerable to diseases, pests, and other threats. Concerning the potential adverse effects of biomass production on biodiversity, it is crucial to implement sustainable management practices that prioritise the conservation and restoration of biodiversity. Promoting agroforestry, reforestation, close-to-nature silviculture and management differentiation, together with retaining and protecting natural habitats, can help mitigate the impacts of biomass production on biodiversity. These approaches can foster habitat connectivity, encourage diverse species assemblages, and enhance ecosystem resilience. Recognising the negative effects of biomass production on biodiversity requires comprehensive research encompassing all taxonomic groups. Recent studies have highlighted the importance of establishing reliable multi-diversity indicators to assess the balance or imbalance between different taxa. Implementing reference monitoring in primary forests is crucial, as they provide an unbiased reference environment to study intra- and interspecific relationships.

Achieving the maintenance of all taxa is a challenging task as well as establishing the trade-off solutions. Forest management schemes should consider the dynamic spatio-temporal patterns to preserve diverse taxa populations and allow for species migration. Effective management strategies should incorporate the presence of the diversity hot spots, corridors, and stepping stones in forested landscapes to ensure connectivity among taxonomic groups.

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