SAPIENZA
UNIVERSITÀ DI ROMA

Exploring monitoring and management strategies towards European forests multifunctionality

Facoltà di Scienze Matematiche, Fisiche e Naturali
Dipartimento di Biologia Ambientale
Dottorato in Biologia Ambientale ed Evoluzionistica

PhD Candidate: Lorenzo Balducci

Tutor: Prof. Sabina Burrascano

Co-tutor: Doc. Francesco Chianucci
Prof. Robert Muscarella

A.A. 2024-2025

Summary

Abstract

In light of current European EU policies, such as the Biodiversity and Forest strategies for 2030, this work highlights the inherent complexity in achieving multifunctionality in European forests. Biodiversity conservation, timber production, and climate change mitigation are among the most crucial functions currently required from forest ecosystems. In this thesis I contributed to a harmonized, Europe-wide database of forest multi-taxon biodiversity and stand structure in the framework of COST Action CA18207 “Bottoms-Up”, enabling a comprehensive analysis of the trade-offs and feasibility of integrating these three major functions. Using this dataset, I explored four main objectives: (1) assess whether carbon and biodiversity policies have the potential for a win-win outcome at the stand scale, finding that aboveground carbon storage alone does not consistently support multi-taxon biodiversity, while positive biodiversity-carbon relationships depend largely on deadwood carbon pools for taxa like wood-inhabiting fungi and saproxylic beetles; (2) evaluating how individual species within three taxonomic groups—vascular plants, bryophytes, and lichens—respond to different silvicultural regimes, which showed that species responses to management are highly variable and often challenge conventional management approaches; (3) identifying structural attributes that support species richness in Mediterranean forests, specifically deadwood quality, canopy openness, and basal area, thus underscoring the unique ecological conditions in these underrepresented ecosystems; and (4) analyzing the completeness of *in-situ* biodiversity data across taxonomic groups, revealing substantial variation in sampling effort requirements by group and region. This research underscores the challenge of achieving biodiversity conservation, timber production, and climate mitigation within the existing policy framework in European forests. We stress the flaws of a one-size-fits-all approach given the diverse ecological needs and species-specific responses observed across forest types and silvicultural systems. These findings emphasize the importance of adaptive, comprehensive strategies tailored to different forest ecosystems. To ensure sustainable forest landscapes that balance these essential functions, it is crucial to integrate policy objectives with detailed ecological knowledge. Looking forward, enhanced monitoring strategies across Europe are essential to address data gaps, enabling management approaches that support long-term forest resilience and multifunctionality.

Introduction

According to the Food and Agriculture Organization of the United Nations, a forest is an area of land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10%, or trees able to reach these thresholds in situ (FAO, 2020). Following this definition, forests cover approximately 31% of the world's land area and encompass a wide variety of distinct ecosystems, from open woodland areas to dense, closed-canopy forests, from tropical forests to taiga at the edge of the arctic tundra.

Given this diversity, the concept of what constitutes a forest can vary significantly across different regions of the world. To grasp what a forest is, it’s necessary to understand that this concept is strictly context dependent, each forest being a unique environment with its own natural development and disturbance regime, either human-made or natural.

1. Recent history of European forests

The forested area in Europe has undergone significant changes over the last millennia. Current forests are remnants of the maximum forest extent reached during the early Holocene, approximately 9,000 to 6,000 years ago. During this period, known as the Holocene Climatic Optimum, Europe experienced warmer and wetter conditions that supported extensive forest cover (Fyfe et al., 2015). Before significant human intervention, it is estimated that forests covered a substantial portion of Europe, potentially up to 80-90% of the continent, including areas temporarily cleared by natural disturbances ranging from windthrows to ungulates grazing (Svenning et al., 2024).

Studies using pollen analysis, historical records, and landscape reconstructions indicate that deforestation and land use changes, driven by agricultural expansion, urbanization, and industrial activities, dramatically reduced the forest cover over millennia (Gaillard et al., 2010; Kaplan et al., 2009; Williams, 2000). Ancient practices such as slash-and-burn agriculture, medieval land clearing, and modern industrial forestry have significantly altered the original forest ecosystems, transforming the structure, composition, and distribution of forests. What we are calling European forests today is a deeply altered and fragmented landscape following human activity (Peterken, 1996). These processes reached their asymptote in the past century, with the minimum forest cover in Europe occurring around the mid-20th century, particularly during the 1950s and 1960s. During this period, extensive deforestation led to forest cover being reduced to approximately 28-30% of the land area. This represented a significant decline from the pre-industrial levels, highlighting the severe impact of human activities on European forests (Kaplan et al., 2009). Post-war reconstruction, mining activities and industrial and agricultural

expansion were among the key drivers that contributed to the deforestation of European forests in the last century, with different impacts of these drivers across European regions (Mather, 2001). Countries like France, Germany, and the UK experienced deforestation due to industrialization and urbanization. However, they also began to implement reforestation and afforestation programs in the mid-20th century, aiming to restore forest cover (Mather, 1992). The deforestation trend was more pronounced in Central and Eastern Europe due to a combination of industrial expansion, agricultural policies, and coal mining. Countries such as Poland, the Czech Republic, and Slovakia saw extensive forest clearing, which only began to reverse with the socio-economic changes after the fall of communism (Turnock, 1998). Mediterranean countries like Spain, Italy, and Greece experienced deforestation due to agricultural expansion, urbanization, and tourism development. However, reforestation efforts in the latter part of the 20th century helped to stabilize forest cover in some areas (Forest Europe, 2020).

Following this period of decline, several areas of the continent experienced a steep increase in forest cover. This process was largely driven by the abandonment of pasture lands, mountainous areas, and rural countryside, as populations moved towards urban areas and agricultural practices concentrated in lowlands. This trend has been particularly evident over the past 50-70 years, with differences among European regions (Keenleyside & Tucker, 2010; Navarro & Pereira, 2012), several of which experienced active reforestation and afforestation efforts, while others underwent natural succession processes. In Western Europe, countries such as France, Germany, and the United Kingdom saw significant reforestation and afforestation efforts beginning in the mid-20th century. These efforts were partly driven by national policies aimed at forest conservation and land restoration (Forest Europe, 2020). In Southern Europe, the abandonment of marginal agricultural lands, particularly in mountainous and rural areas, led to natural succession dynamics leading to the increase of forested areas. Countries like Spain, Italy, and Greece experienced significant forest regrowth as traditional farming practices declined and rural populations migrated to urban areas (Lasanta et al., 2017). In Central and Eastern Europe, political and economic changes following the collapse of communism in the late 20th century also contributed to an increase in forest cover, with the abandonment of farming areas and a reduction in intensive agricultural practices, leading to natural regeneration in countries like Poland, Slovakia, and the Czech Republic. Additionally, EU policies and funding for rural development and environmental conservation further supported active reforestation efforts in these regions (Munteanu et al., 2014).

2. Current state of European forests

Currently, European forests (excluding those in the Russian Federation) represent approximately 5% of the world's forests (FAO, 2020). In Europe, forests cover

approximately 33% of the land area, totaling about 215 million hectares. Despite their relatively small extent compared to the global forest cover, European forests are characterized by a variety of types, ranging from the boreal forests in the north to the temperate and Mediterranean forests in the central and southern regions.
The long-term impacts of past activities have driven forest patterns and biodiversity in ways that will persist for decades. The high rates of deforestation followed by forest expansion, driven by either natural regrowth or afforestation and reforestation efforts, shaped the forests that Europe hosts today. Such diverse pathways occurring across a continent with a broad environmental heterogeneity, created a diverse and dynamic landscape, with considerable regional and local variations in tree species composition, related biodiversity and structural attributes. Only a small proportion of European forests, approximately 2%, remains undisturbed by human activity and can be classified as primary forests (Forest Europe, 2020; Barredo et al., 2021; Sabatini et al., 2021). Most of Europe's forests today are young secondary or managed forests. These deeply altered forests often have reduced genetic and species diversity even after millennia (Dambrine et al., 2007) as compared to forests that were never cleared for agriculture (Vellend, 2004). Slow-colonizing species with low fecundity, unassisted dispersal, or large seeds are particularly affected (Verheyen et al., 2003).

European forests are required to fulfill several functions. Forest multifunctionality refers to the concept and practice of managing forests to accomplish multiple ecological, economic, and social functions simultaneously. This approach recognizes that forest ecosystems may provide a wide range of services that go beyond traditional timber production, including biodiversity conservation, carbon sequestration, water regulation, soil protection, recreation, and cultural values. Pursuing multifunctionality means adopting forest management strategies that balance and integrate these different functions, i.e., preserving biodiversity while allowing for sustainable timber harvesting, or enhancing carbon storage while providing recreational opportunities. Forest multifunctionality constitutes the foundation of sustainable forest management (SFM), which aims to provide these functions both at present and in the future by maintaining the potential to fulfill them at local, national, and global scales (Forest Europe, 2020).

Biodiversity conservation, climate change mitigation, timber production, non timber forest products, water regulation, soil protection and recreational and cultural values are constituting the long list of services required from European forest ecosystems. Among these functions, biodiversity conservation, timber production and climate change mitigation are particularly emphasized in European national and international policies due to their immediate relevance to both environmental and economic sustainability (European Commission, 2021; European Commission, 2023; Forest Europe, 2020).

2.1 Biodiversity conservation

Forests host about three-quarters of the global terrestrial plant, fungi and animal species diversity, and are globally considered biodiversity hotspots (FAO, 2020). European forests are considered key habitats for biodiversity as about 30% of forest area is referred to as a habitat of conservation value in the EU (Forest Europe, 2020). However, the current state of biodiversity in European forests is deeply tied with management history and its consequences on forest ecosystems.
Forest management in Europe has drastically altered forest structure and composition (Aude & Poulsen, 2000; Baessler et al., 2010), with profound effects on several taxonomic groups (Müller et al., 2007; Paillet et al., 2010). Historically, as the focus was on maximizing timber production, management practices have favored , over the past centuries, the increase of certain tree species, and the structural and compositional homogenization of forest stands. As a result, local and regional communities have been deeply altered over time (Peterken, 1996) and the natural variety of species, structures, and successional stages has been significantly reduced (Brunet et al., 2010; Paillet et al., 2010). Forest management changed the availability of habitat for forest species, either on the landscape scale with the distribution of forested area (Crowther et al., 2015; Kouki et al., 2001) or on a stand scale with the distribution of forest structures, e.g. tree related microhabitats (Asbeck et al., 2021; Paillet et al., 2010). This loss of habitat diversity has had significant consequences for species richness, particularly for those species that rely on specific forest structures for survival (Brunet et al., 2010; Lachat et al., 2012; Paillet et al., 2010). While forest area is increasing in Europe, about 80% of forest habitat assessments report a decrease in habitat conservation status, with about 20% of the species related to forest ecosystems having a declining conservation status, or threatened with extinction (European Environment Agency, 2020; Forest Europe, 2020).

Among the taxonomic groups with known influences from forest management, birds are particularly impacted by the reduction of old-growth features like deadwood and large trees. These changes affect cavity-nesting birds, such as woodpeckers and owls, which depend on these features for nesting. Habitat fragmentation, changes in forest structure, and the increase in monocultures further limit the availability of suitable nesting and feeding sites (Paillet et al., 2010), with approximately 13% of forest bird species currently considered threatened (BirdLife International, 2022), especially old-growth-dependent species. Also bryophytes are known to be highly sensitive to management. They rely on specific microclimatic conditions, such as consistent humidity and low light levels. Changes in forest structure due to thinning and clear-cutting can drastically alter these conditions, leading to declines in bryophyte diversity. About 20% of European bryophyte species are threatened (Hodgetts, 2019; Hodgetts et al., 2020), especially those reliant on the shaded, moist environments provided by older forests. Fungi, particularly wood-decaying species, are dependent on deadwood, a resource that is often extremely scarce in managed

forests. Forest management practices involving timber harvesting disrupt the availability of decaying wood, which is essential for species like polypores and mycorrhizal fungi (Gossner et al., 2013). Although fungi are often underrepresented in conservation assessments, it was demonstrated that many species that rely on old-growth structures are experiencing population declines, with some even facing local extinction (Christensen et al., 2005). Lichens are similarly vulnerable to changes in forest microhabitat and air quality. Forests managed for timber production typically lack the structural complexity and a sufficient number of old trees necessary for epiphytic lichens to thrive. As a result, many species have declined, particularly in regions where old-growth features are lacking (Ellis, 2009). This decline is most pronounced in areas where habitat loss is severe, often due to the simplification of forest structures (Forest Europe, 2020). Saproxylic beetles, which depend on decaying wood, are also particularly sensitive to changes in forest structure and to the scarcity of deadwood and senescing trees, which often leads to population decline (Gossner et al., 2013). As a result, 18% of saproxylic beetle species are now considered threatened in Europe (Cálix et al., 2018), especially those that require specific tree species or large quantities of deadwood. Last but not least, vascular plants are impacted by the homogenization of forest stands that often occurs in managed forests. The reduction in the diversity of light and microclimate conditions negatively affects plant species richness, particularly in the understorey. The shift toward more uniform forest structures with fewer canopy gaps may lead to a decline in species diversity, with many species facing local declines as a result of forest management practices (Brunet et al., 2010; Paillet et al., 2010).

In response to the ongoing biodiversity crisis, European national and international policies have increasingly emphasized the need for effective biodiversity conservation within forest ecosystems. The EU Biodiversity Strategy for 2030 and the EU Forest Strategy for 2030 are among the latest comprehensive legislations affecting biodiversity conservation related to forests. The European Union's Biodiversity Strategy for 2030, as a core component of the European Green Deal, outlines a framework addressing ambitious targets for halting biodiversity loss and restoring degraded ecosystems, including forests. The strategy emphasizes protecting 30% of the EU’s land and sea areas by 2030, restoring degraded ecosystems, and promoting sustainable practices in agriculture, forestry, and fisheries. It underlines the need for the protection of old-growth forests, enhancing the Natura 2000 network, and improving the health of ecosystems critical for climate regulation and human well-being. A plan to plant at least 3 billion additional trees by 2030 is among the landmark goals (European Commission, 2020). The EU Forest Strategy for 2030 aims at ensuring forest multifunctionality at different spatial scales by integrating essential forest functions, such as timber production, carbon sequestration, and climate change mitigation, with biodiversity conservation by promoting, among other actions, sustainable forest management (SFM). A significant component of the Forest Strategy is the promotion of close-to-nature forestry practices, aiming to foster silvicultural practices involving selective logging

techniques with the target of enhancing structural diversity, deadwood amount and tree species diversity. Close-to-nature forestry is supposed to enhance habitat quality for species that depend on old-growth features and deadwood, such as saproxylic beetles and cavity-nesting birds . In combination with these policies, the European Union is also advancing the use of financial mechanisms and incentives to support biodiversity-friendly forest management. For instance, the Common Agricultural Policy (CAP) provides financial support to landowners and forest managers who adopt practices that enhance biodiversity, such as maintaining mixed-species forests, reducing the intensity of forest management, and increasing the amount of deadwood left in forests (European Commission, 2021). These financial incentives are crucial for encouraging widespread adoption of biodiversity-enhancing practices, particularly in areas where timber production is a significant economic activity. A key component of this framework is the proposed EU Biodiversity Monitoring Law, which aims to establish a comprehensive and harmonized biodiversity monitoring system across the EU. The law is designed to standardize data collection methodologies and ensure regular reporting on species and habitat status. This law is expected to play a crucial role in improving the effectiveness of conservation efforts and ensuring that biodiversity conservation is integrated into forest management practices (European Commission, 2023).

While these EU policies reflect a growing recognition that biodiversity is essential for the long-term conservation of European forests' functions and services, there is still a significant gap in the pathways towards addressing the conservation of biodiversity across different taxonomic groups and forest habitats. One of the fundamental challenges is the lack of explicit information on how biodiversity conservation should be implemented at various spatial scales. Policies such as the EU Biodiversity and Forest Strategies for 2030 emphasize biodiversity goals, yet they often fail to provide detailed instructions for integrating these goals into forest management at local, regional, and national scales (European Commission, 2020; European Commission, 2021). This is particularly relevant given the heterogeneity of the forest landscape across Europe, in terms of ownership, historical and current management, species composition, human and natural pressures; especially in the perspective of global and regional climate change scenarios. This issue is particularly evident in areas where economic pressures from timber production are relevant, creating conflicts between biodiversity objectives and economic interests (Forest Europe, 2020). Moreover, the means of application of these strategies result especially insufficient when several forest-dwelling taxonomic groups are accounted for. Forest ecosystems are home to a diverse range of species, from vascular plants and fungi to saproxylic beetles, birds, lichens and bryophytes. Each one of these taxonomic groups are both directly and indirectly affected by management practices (Paillet et al., 2010). Therefore, the improvement of their conservation status is intrinsically associated with specific forest management practices (European Environment Agency, 2020). However, most of the indicators used to assess the sustainability of

forest management, are either indirect indicators of biodiversity,i.e., based on forest or landscape structure, or focus on a narrow set of metrics, i.e., common bird species, which may not adequately capture the ecological needs of many taxonomic groups.

A general feature of the current SFM indicators is their reliance on structural metrics that may not fully capture all the aspects of biodiversity. Deadwood volume (Indicator 4.5), for instance, may not be sufficient to assess the conservation status of several ecologically critical groups since it does not ensure the occurrence of certain sizes or decay stages that may be crucial for wood-inhabiting species (Larrieu et al., 2018). Saproxylic beetles, bryophytes, lichens, and fungi, are highly sensitive to microhabitat conditions like humidity and the quality of decaying wood, yet there is no comprehensive framework to monitor their status. Accordingly, indicators related to forest protection status, like the percentage of forested areas under protection (Indicator 4.9), do not necessarily translate into effective biodiversity outcomes, especially when these protected areas are managed primarily for timber production rather than for biodiversity conservation (Forest Europe, 2020).

Direct biodiversity indicators, on the other hand, are strongly limited and do not cover the diversity of taxonomic groups found in European forests. For instance, the indicator "tree species diversity" (Indicator 4.6), while being useful in addressing habitat diversity, does not capture the whole diversity of vascular plants within a forest ecosystem. Common forest bird species (Indicator 4.10) offer a closer link to forest biodiversity, however, even this indicator is not without limitations since rare bird species may be those particularly sensitive to changes in forest habitats (Bełcik et al., 2020). Importantly, there is no direct indicator for bryophytes, invertebrates, fungi, or lichens within the current framework. Overall, the existing indicators are far from providing a comprehensive understanding of forest biodiversity conservation status, and direct and soundly tested indicators are urgently needed to assess the state of biodiversity in managed forests (Forest Europe, 2020).

In conclusion, the current status of European forest biodiversity is still far from being completely assessed. The difficulty in defining clear indicators for assessing species and taxonomic groups conservation statuses and implementing practices for integrating biodiversity goals into forest management at several scales is magnified by a significant lack of data for several taxonomic groups, especially those that are less studied or more difficult to monitor. This knowledge gap makes it difficult to draw accurate conclusions about the overall trends in biodiversity and to implement evidence-based sustainable forest management. While the EU's Biodiversity and Forest strategies for 2030 are important steps toward integrating biodiversity conservation into forest management, the current frameworks are still lacking in precision and comprehensiveness that call for more targeted policies to meet biodiversity conservation goals in forests (European Environment Agency, 2020; Forest Europe, 2020).

2.2 Timber production

Among the major functions of European forests, timber production has always been a critical economic asset across Europe. Timber production plays a significant role in the European economy, especially in rural areas where forestry is often a major source of income and employment. Approximately 60-65% of European forests are managed primarily for timber production, making it one of the dominant uses of forested land across the continent (Forest Europe, 2020). Countries with extensive forest resources rely heavily on timber exports. In Finland, for example, the forestry sector contributes around 4% to the national GDP, and in Sweden, it accounts for approximately 2.5% of GDP (Eurostat, 2020).

Timber harvesting methods across Europe vary according to forest type, management history and regional or national policies. Several approaches have tried to harmonize silvicultural systems across Europe based on the existing data (Trentanovi et al., 2023). Here we report about the pressures on biodiversity of some of the most widespread silvicultural regimes in Europe. Clear-cutting, one of the most widespread methods, involves harvesting all trees within a designated area, leading to completely open conditions at first, and even-aged forest stands and homogeneous structural attributes after forest regeneration. This method is commonly used in northern European countries like Sweden and Finland, where fast-growing species such as *Picea abies* and *Pinus sylvestris* are harvested in cycles ranging from 60 to 100 years (Kuuluvainen & Gauthier, 2018). In Portugal and Spain, fast-growing plantations of *Eucalyptus globulus* and *Pinus pinaster* are managed with significantly shorter rotation times (Dias & Arroja, 2012; Rodríguez-Soalleiro et al., 2018). Clear-cutting is efficient for maximizing timber yield, but it has significant impacts on forest biodiversity and ecosystem functioning. Clear-cutting is often associated with the establishment of plantations and monocultures, which magnify the effects of this management strategy on biodiversity. These simplified forest systems typically have reduced structural complexity and species diversity as compared to forests undergoing natural dynamics (Brockerhoff et al., 2008; Carnus et al., 2006). The practice of clear-cutting followed by tree plantation, although it may temporarily increase the number of species adapted to open habitats, mostly leads to a significant loss of habitat for many forest-dwelling species, particularly those dependent on old-growth forest conditions (Lindenmayer & Franklin, 2002). To increase productivity, these forests are often subjected to fertilization, which can alter soil chemistry and affect the composition of understory vegetation (Hedwall et al., 2010). Furthermore, the trees used in these plantations have frequently been selected based on their rapid growth regardless of the reduced genetic diversity deriving from these selection processes (Lefèvre et al., 2013). This genetic homogeneity can make forests more vulnerable to environmental and anthropogenic disturbances (Aitken & Bemmels, 2016). The consequences of these practices on biodiversity include reduced species richness and abundance of forest-dependent organisms, including birds, mammals, and invertebrates

(Bohada-Murillo et al., 2020; Calviño-Cancela et al., 2012; Goded et al., 2019a), also in relation to a decreased structural diversity, which is crucial for many species' habitat requirements (Lindenmayer et al., 2006). Selective logging is another widespread silvicultural strategy, involving the removal of individual or small groups of trees, promoting heterogeneous and uneven-aged forest structures. Selective logging is deeply linked with Continuous Cover Forestry (CCF), which aims to maintain forest cover and ecological continuity while allowing for periodic timber extraction (Larsen et al., 2022; Schütz, 2011). CCF and selective logging practices generally have a lower impact on biodiversity compared to clear-cutting. These methods can maintain a more diverse forest structure, which supports a wider range of forest-dwelling species (Fedrowitz et al., 2014). By preserving a continuous canopy cover, these approaches help to sustain microclimatic conditions that are crucial for many organisms, in particular shade-tolerant species and moisture-dependent invertebrates (Pommerening & Murphy, 2004). However, the ecological benefits of selective logging can vary depending on its intensity and frequency. Over-intensive selective logging can lead to a simplification of forest structure and composition over time, potentially reducing habitat quality for some species (Angers et al., 2005). Selective logging and CCF can contribute to the preservation of old-growth forest characteristics, such as large old trees and deadwood, which are critical for many specialized forest species (Bauhus et al., 2009). These management approaches can also enhance the resilience of forest ecosystems to climate change by promoting structural and species diversity (O'Hara, 2016). As compared to selective logging, shelterwood systems also maintain a certain degree of continuous forest cover by shifting treatments across time to favour shade-tolerant over shade-intolerant species. However, the final outcome is an even-aged forest, and a much more homogeneous structure than the one developing in forests under selective logging (Chaudhary et al., 2016). This can lead to reduced habitat heterogeneity, which can limit the range of ecological niches available to forest species, particularly those dependent on varied microhabitats and deadwood (Bauhus et al., 2009). This structural uniformity may favor generalist species over specialists, reducing the richness and abundance of taxa such as bryophytes, lichens, and saproxylic invertebrates, which rely on old-growth structural attributes (Lindenmayer & Franklin, 2002). Coppicing, a traditional method of cutting trees near ground level to encourage the regeneration through suckers, is still practiced in part of Southern and Eastern Europe, particularly in Mediterranean regions. This method promotes early successional stages and provides materials for fuelwood, but it has decreased in prevalence due to changing socioeconomic conditions (Forest Europe, 2020). Coppicing creates a unique forest structure that can support high levels of biodiversity, particularly for light-demanding species and those adapted to frequent disturbance (Vild et al., 2013). The cyclical nature of coppicing creates a mosaic of different growth stages within the forest, which can increase overall landscape diversity (Kirby et al., 2017). Many rare and threatened species, including certain butterflies and birds, depend on the open, sunny conditions created by recently coppiced areas (Fuller & Warren, 1993); as a consequence, the decline in traditional

coppicing practices has led to concerns about the loss of these specific habitats and associated biodiversity (Müllerová et al., 2015). It's worth noting that the effectiveness of these management methods in promoting biodiversity can depend on the specific context, including forest type, local species pools, and landscape-level factors. Integrating a variety of management approaches across a landscape can often provide the best outcomes for both timber production and biodiversity conservation (Lindenmayer et al., 2012).

European timber production trends in recent decades followed shifts in both market demands and sustainability priorities. Timber production in Europe has been growing steadily in the last decades, leading to increasing harvest rates in countries like Sweden, Finland, and Germany (Forest Europe, 2020; Pelli et al., 2017). Despite the push for sustainable practices, plantation forestry remains a major contributor to timber production, particularly in southern and western Europe. Countries like Spain, Portugal, and France have seen significant expansion of fast-growing plantations, primarily of *Eucalyptus* and *Pinus* species (Cardellini et al., 2018). While these plantations are efficient for timber production, they often lack the biodiversity and ecosystem complexity of naturally regenerating forests (Brockerhoff et al., 2008; Carnus et al., 2006). In response to growing concerns about biodiversity loss and climate change, many European countries are adopting more sustainable forest management practices. Certification schemes such as the Forest Stewardship Council (FSC) and Programme for the Endorsement of Forest Certification (PEFC) have gained significant traction, ensuring that timber production meets environmental and social sustainability criteria (Maesano et al., 2018). As of 2020, over 50% of Europe's forests were certified under one or both of these schemes, representing a substantial increase from previous decades in response to the market demand for sustainable products (Forest Europe, 2020).
The timber production landscape in Europe is evolving in response to complex and sometimes conflicting demands. While timber remains a crucial economic resource, particularly in rural areas, there is growing recognition of the need to balance production with biodiversity conservation and ecosystem resilience. The shift towards more sustainable forest management practices, as highlighted by the widespread adoption of certification schemes, represents a positive step. The EU Forest Strategy for 2030 has introduced initiatives to further support this balance, including the development of a voluntary "closer-to-nature" certification scheme. This certification aims to provide biodiversity-friendly management practices with an EU quality label, incentivizing forest managers to adopt approaches that enhance ecosystem diversity and resilience (European Commission, 2021). Despite these advances,challenges remain, particularly in reconciling the efficiency of plantation forestry with the need for more diverse and resilient forest ecosystems.

Looking ahead, European forest management for timber production will likely continue to adapt to address climate change concerns (Nabuurs et al., 2018), evolving market demands, and increasing emphasis on ecosystem services. The EU

Biodiversity Strategy for 2030, together with other policies and the markets demand for sustainable products are expected to further influence forest management practices, potentially leading to more integrated approaches that consider timber production alongside biodiversity conservation, carbon sequestration, and other ecosystem services (European Commission, 2020; Konczal et al., 2023).

2.3 Climate change mitigation

One of the most important functions currently expected from forests is climate change mitigation. Forests act as significant carbon reservoirs, with carbon stored in both above-ground and below-ground biomass, as well as in other pools such as deadwood, litter, and soil. Carbon in aboveground biomass is often the most easily assessed pool. The European average above-ground biomass carbon stock for managed forests is about 50 tonnes per hectare (t/ha) in temperate regions, though this value can vary significantly depending on forest type and management intensity (Nabuurs et al., 2013). On average, deadwood contributes around 5-10% of the total above-ground carbon pool (Köster et al., 2015; Mund & Ernst Detlef, 2006; Pan et al., 2013). While deadwood is increasingly recognized as an important carbon pool and biodiversity resource, it is often underrepresented in national carbon stock inventories (Russell et al., 2015). Comprehensive surveys of deadwood, including its decomposition rates and carbon storage potential, are needed across Europe. Below-ground carbon stocks include root biomass and soil organic carbon (SOC). Root systems contribute significantly to forest carbon stocks, but their accurate measure is challenging. Estimates suggest that root biomass accounts for about 20-30% of total tree biomass in temperate and boreal forests (Cairns et al., 1997). This ratio can vary depending on tree species, age, and environmental conditions. Soil is a major carbon reservoir in forest ecosystems. European forest soils store more carbon than all living and dead biomass combined (Scharlemann et al., 2014), with estimates suggesting that SOC in the upper 30 cm of mineral soil ranges from 30 to 120 Mg C ha^{-1} (De Vos et al., 2015), corresponding to up to 60% of the total carbon in forests is found in the soil (FAO, 2020). SOC, especially in the upper layers of the soil, plays a vital role in carbon sequestration when compared to tropical ecosystems, where a greater proportion of carbon is stored in the living biomass. Below-ground carbon stock is extremely difficult to measure directly, and most assessments rely on models that estimate root biomass based on above-ground characteristics. Improved monitoring, including deeper soil sampling and better representation of forest soils in carbon models, is necessary for accurate carbon accounting. Soil carbon is relatively stable compared to biomass carbon, but it is vulnerable to disturbances such as clear-cutting, soil degradation, and climate change. Other carbon pools include the forest floor litter layer, consisting of fallen leaves, twigs, and other organic matter, estimated to range from 1.3 to 38.1 Mg C ha^{-1} (De Vos et al., 2015). While often small compared to tree biomass, understory vegetation can also contribute to carbon stocks, especially in open forest systems. However, data on this pool is limited at the European scale.

Between 2001 and 2019, global forests' ability to store carbon resulted in a net sink of about 7.6 Gt of CO_2 per year, with a decreasing trend. The majority of the global net sink (68%) was in temperate (47%) and boreal (21%) forests (Harris et al., 2021), as European forests absorb approximately 10% of the continent's greenhouse gas emissions annually. According to Forest Europe (2020), the total forest area in

Europe has increased by 9%, while the growing stock has increased by 50% between 1990 and 2020, contributing to the rising carbon stocks in both living and dead biomass. Despite overall increases in carbon stocks across European forests, recent research suggests that the rate of carbon sequestration may be slowing (Forest Europe, 2020; Nabuurs et al., 2013). This phenomenon, referred to as "carbon sink saturation", occurs when forests reach a point where their capacity to store additional carbon remains positive but may be limited as compared to earlier developmental stages (Luyssaert et al., 2008; Nabuurs et al., 2013). It should also be taken into account that climate change may amplify the severity and extent of some natural disturbances such as wind throws and pest outbreaks. There are multiple factors contributing to this trend, as human (e.g., land-use change, timber extraction) and natural (e.g., fires, storms, pest outbreaks) disturbances can rapidly alter forest carbon stocks (Pilli et al., 2021; Seidl et al., 2014). Combined, these pressures have significant implications for the ability of forests to sequester carbon.

One of the primary pressures on European forests' carbon pools is timber production. Balancing carbon sequestration with timber production is a significant policy challenge. Timber extraction has a double function: it removes carbon stored in forest ecosystems, but it also initiates processes that can store carbon in other pools outside of the ecosystem, i.e., the technosphere (Giuntoli et al., 2022). As timber production can contribute to carbon storage outside forest ecosystems, it has become increasingly addressed by environmental policies aimed at mitigating carbon loss. Key European policies promote carbon storage outside of forest ecosystems in two primary pools, harvested wood products (HWP), which can serve as long-term carbon sinks, and renewable energy, which temporarily store carbon before it is released during energy generation. The use of wood for renewable energy has been steadily increasing in the last decades, driven largely by European policies like the new Renewable Energy Directive (RED III), which promotes the use of wood biomass to replace fossil fuels and reduce overall carbon emissions. RED III strengthens the goals of RED II, setting an ambitious target for the EU to achieve at least 42.5% of its energy consumption from renewable sources by 2030 (European Commission, 2023). Wood biomass plays a key role in this strategy, particularly for countries with significant forest resources, where it is used to replace carbon-intensive energy sources. While wood biomass is seen as a key renewable resource, important trade-offs remain. The combustion of biomass inevitably releases carbon back into the atmosphere, meaning that the sequestration benefits of wood used for bioenergy are temporary and relatively short-term. In particular, the carbon neutrality of wood biomass as a fuel depends on forest regrowth rates, as the carbon emitted during their combustion is ideally offset by the carbon absorbed by forest regrowth. However, the efficiency of this cycle is tightly linked to sustainable forest management practices and to a careful balance between harvest rates and regrowth, especially when compared to more stable carbon sequestration methods. Harvested wood products (HWP), on the other hand, can store carbon in materials for a longer time frame. The volume of carbon stored in HWP is growing, with these

products contributing an active net carbon sink of approximately -40 MtCO2e/year in the European Union (Grassi et al., 2021). However, it is essential to highlight that only long-lasting wood products are effective in this regard. These long-lived products ensure that sequestered carbon remains outside the atmospheric cycle for extended periods, making them a key component in achieving climate neutrality (Profft et al., 2009). In contrast, short-lived HWPs, such as paper or packaging, release their carbon back into the atmosphere in the garbage disposal process, hampering their effectiveness as a long-term carbon storage solution.

Regardless of the fate of woody biomass, moving carbon stocks from forest ecosystems to the technosphere (Giuntoli et al., 2022), may hamper the ability of forests to store carbon within their ecosystem carbon pools, while promoting excessive carbon emissions from forest degradation and deforestation. The increasing need of carbon stored in HWP and the growing demand for bioenergy may increase pressure on European forests, reducing their ability to act as effective long-term carbon sinks (Forest Europe, 2020; Pukkala, 2014). The amount of carbon stored inside the ecosystem carbon pools depends mainly on the management strategies. Plantation forestry, in particular, including monocultures of fast growing species and short rotation periods, may be promoted to meet bioenergy and HWP demands, but may be less effective at long-term carbon sequestration within the environment (Brockerhoff et al., 2008). Young forests with short rotation periods, although rapidly capturing carbon, tend to store a lower amount of carbon in the long term in comparison to old-growth forests (Luyssaert et al., 2008). Intensive management strategies release substantial amounts of stored carbon in biomass and soil during harvest (Pukkala, 2014) and keeps none to small amounts of deadwood, which contributes to long-term carbon storage (Köster et al., 2015; Mund & Ernst Detlef, 2006; Pan et al., 2013). These management techniques may also hamper the resilience of forest ecosystems, which is a key element in forest management to ensure forests' role as carbon sinks under changing climate conditions (Reyer et al., 2014). Intensive management may promote less diverse and structurally complex forests, which tend to be less resilient to climate stressors like drought, pests, and disease outbreaks, altering their ability to store carbon (Lindner et al., 2010). The homogeneous structure and composition of these forests may lead to less stable productivity and higher disturbance rates, jeopardizing their carbon storage role (Mohr et al., 2024; Rio et al., 2017; Scherrer et al., 2023).

Management strategies focused on maximizing carbon storage rate, may affect not only ecosystem carbon pools, but also the support to another crucial forest function, i.e., support to forest biodiversity. Simplifying natural or semi-natural ecosystems and reducing the variety of habitats available may lead to biodiversity loss for several taxonomic groups, by promoting homogeneous and fast growing stands of both exotic and native trees, which have high carbon sequestration rates (Bernal et al., 2018). This is already happening across several European countries, and the limited potential of these stands for supporting biological diversity was widely assessed (da

Silva et al., 2019; Felton et al., 2010). In non-native tree species (e.g., *Eucalyptus*) plantations, the species richness of herbs, birds and lichens can be lower than in native forests, with a composition shift towards non-forest communities (Goded et al., 2019b; González-Montelongo & Pérez-Vargas, 2019). Even in native species (e.g., *Picea abies)* plantations understorey vegetation is scarce and species poor, and the habitat conditions for epiphytic lichens and bird species are unfavorable (Felton et al., 2010). Not to mention the differences of these stands in terms of species composition, with generalistic and wide distribution species being far more frequent than specialized and narrowly distributed species (Ódor et al., 2013).

One of the most important objectives of the 2030 EU Forest Strategy is to plant at least 3 billion additional trees by 2030 (European Commission, 2021) as part of the European Union's effort to address climate change mitigation, restore ecosystems, and promote biodiversity. While this ambitious goal presents a valuable opportunity for increasing carbon sequestration and supporting biodiversity, it is crucial to carefully consider what kind of forest ecosystems we are creating, as these choices will have long-term implications for both carbon storage and the biological diversity of European forests.

2.4 Connecting the dots: is forest multifunctionality achievable?

In the previous chapters we have discussed the main functions required from European forests: biodiversity conservation, timber production, and climate change mitigation, within the framework of forest multifunctionality.

Several policies have been designed to support forest multifunctionality at the national, regional, and continental level. The EU Biodiversity Strategy for 2030 emphasizes integrating biodiversity conservation into forest management while recognizing the economic importance of timber production and the role forests play in climate change mitigation (European Commission, 2020). The EU Forest Strategy for 2030 highlights sustainable forest management (SFM) as a means to achieve multifunctionality, seeking to balance timber production with biodiversity and carbon storage objectives (European Commission, 2021). The Renewable Energy Directive (RED III) promotes the use of wood biomass for renewable energy, aiming to meet sustainable criteria for biodiversity conservation and climate change mitigation goals (European Commission, 2023). The LULUCF Regulation (Land Use, Land-Use Change, and Forestry) requires EU countries to account for greenhouse gas emissions and removals from land use, including forests, while ensuring forests contribute to biodiversity and sustainable timber production.

While these policies underline the importance of forest multifunctionality and promote general win-win options, it is still not clear how, and through which practices, this challenge would be achievable.
Sustainable Forest Management (SFM) is often cited as the cornerstone of multifunctionality. In terms of environmental sustainability, SFM includes practices which aim to balance timber extraction with biodiversity conservation and carbon storage. However, SFM criteria and indicators do not fully integrate information on these environmental functions. For instance, biodiversity lacks direct and sound indicators for its assessment at different scales (Forest Europe, 2020). Without these indicators, it would be impossible to assess if a forest is managed sustainably and whether it meets the targets of multifunctionality.

Significant challenges lie underneath the broad reliance on forest multifunctionality. The core issue lies in the trade-offs among different functions (Fig. 1). As discussed in the previous chapters, due to the tight relationships that exist among them, targeting these challenges individually may hamper not only the achievement of the others, but also of multifunctionality itself. Biodiversity is directly related to forest structure, which is substantially affected by timber production. Timber production strategies can change in relation to climate change mitigation goals, by shaping carbon stocks within or outside the forest ecosystem. These three functions are therefore deeply tied with one another.

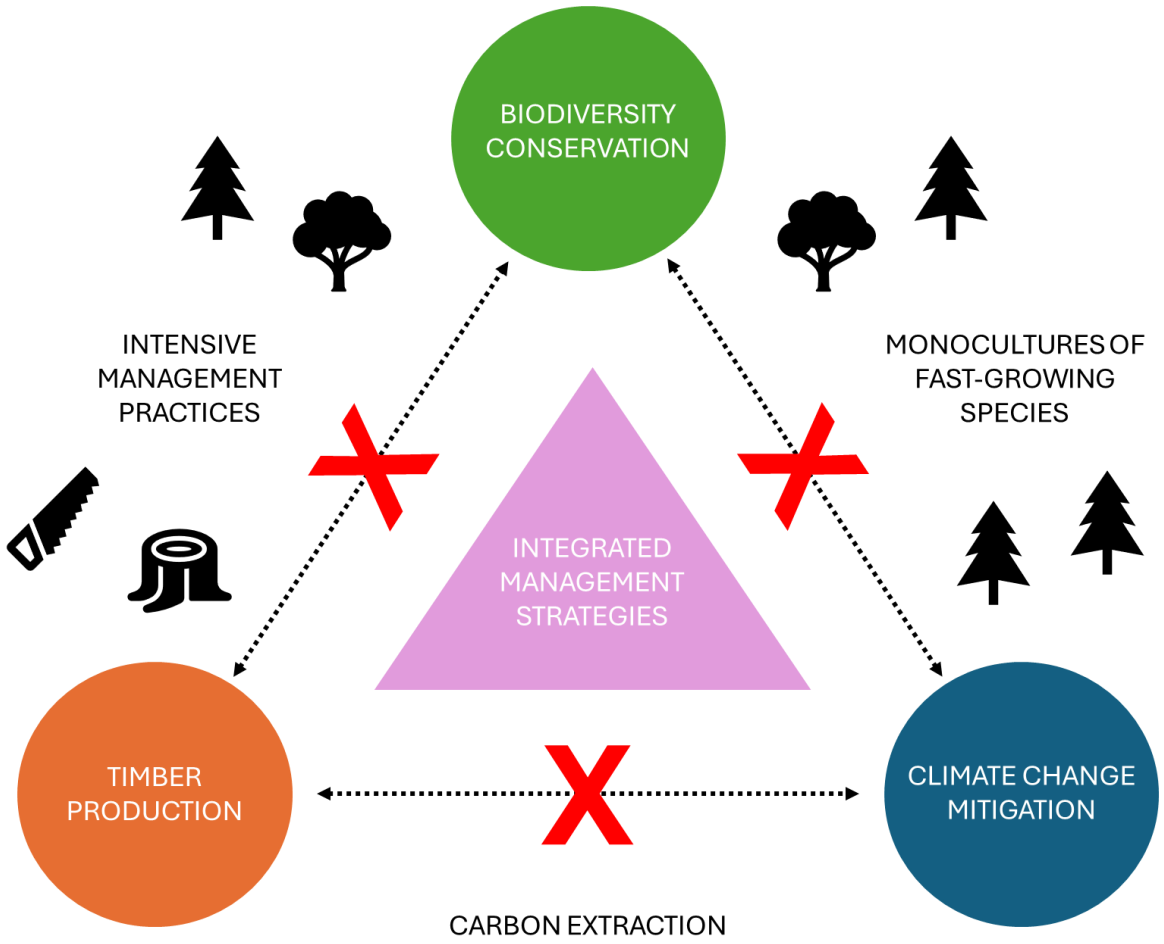


Figure 1 - Conceptual framework for the trade-offs affecting multifunctionality in European forests. Each vertex represents a key forest function. These trade-offs hinder efforts to simultaneously achieve all three functions, as prioritizing one function often reduces the capacity to fully support the others. Integrated management strategies, positioned at the center, offer a potential pathway to balance these competing demands and promote a multifunctional forest landscape, but require overcoming these inherent trade-offs.

Current European policies are primarily focused on promoting win-win solutions that aim to satisfy both climate change mitigation goals and timber production, often through strategies aligned with Climate-Smart Forestry (Nabuurs et al., 2018). These practices are designed to optimize forest management for carbon sequestration, resilience to climate impacts, and sustainable wood production. However, despite these advancements, significantly less progress has been made towards achieving biodiversity conservation targets, which are crucial for maintaining ecosystem resilience and functionality. Monospecific and fast-growing plantations may address the production of timber and the storage of carbon through HWC but with negative impacts on the biological diversity of several taxonomic groups. This perspective probably derives from the fact that, in several European regions, timber production is

a key economic driver, and economic pressures often favor short-term gains from timber extraction over long-term biodiversity sustainability goals.

2.5 Filling the gaps: moving forward to achieve forest multifunctionality

Effective implementation of multifunctionality requires a comprehensive approach, which should start from filling existing data gaps. This would require an extensive monitoring of biodiversity, carbon stocks, and management strategies for timber production in European forests. A significant step forward lies in enhancing data collection for biodiversity, particularly for taxonomic groups that are underrepresented in current monitoring efforts (Burrascano et al., 2021). The heterogeneity of monitoring strategies and the various scales used across research (e.g., stand, regional, national) have made it difficult to create a harmonized dataset for European forests' biodiversity, structure and management (Forest Europe, 2020), hampering the possibility of upscaling the results. In this framework, the Cost Action CA18207 "Bottoms-Up" emerged as a starting point to create a Europe-wide dataset of multi-taxon diversity to start investigating the relationship between these functions.

Additionally, to further evaluate the feasibility of achieving these multiple functions simultaneously, it is essential to expand our approach beyond traditional metrics. This involves assessing the effects of forest management not only on overall species richness but also on species identity, accounting for the different ecological requirements of single species and for the mechanisms through which changes in forest structure could affect their occurrence (Messier et al., 2019).

The difficulty of this achievement is exacerbated by an uneven representation of forest categories in forest biodiversity research, particularly the underrepresentation of Mediterranean forests (Burrascano et al., 2023; Tinya et al., 2023). Central Europe has long been a focal point for forest research due to its managed forest landscapes and the availability of extensive long-term data, especially regarding temperate and boreal forests (Lindner et al., 2010). In contrast, Mediterranean forests, which face unique ecological pressures such as droughts, changes in fire regimes, and soil degradation, which are likely to intensify under climate change, remain understudied (Lionello & Scarascia, 2018; Palahi et al., 2008). These ecosystems have unique ecological and management conditions, and integrating insights from them will be instrumental in developing robust, adaptable strategies for forest multifunctionality across Europe (Nocentini et al., 2022).

The future of European forests will depend on finding innovative solutions to maintain or increase forest carbon stocks and timber yields while enhancing forest biodiversity and resilience. This involves soundly based forest planning encompassing multiple scales so that the diverse needs of society can be met while ensuring the long-term health and sustainability of these vital ecosystems.

3. Aims

In collaboration with a wide network of researchers within the framework of the Cost Action CA18207 “Bottoms-Up”, I contributed to the harmonization of a Europe-wide database of forest multi-taxon biodiversity and stand structure. This novel database currently includes 34 datasets and 3,591 sampling units across 12 European countries, containing field-sampled multi-taxon biodiversity data (i.e., at least three groups of organisms, including animals, plants, or fungi), stand structure and management information.

I used this database to:

- Assess whether carbon and biodiversity policies have the potential for a win-win outcome at the stand scale that may support silvicultural strategies focused on forest multifunctionality.

- Define the impact of different silvicultural regimes on the occurrence of individual species across three taxonomic/functional groups (vascular plants, epiphytic and epixylic bryophytes, and lichens) in European forests.

- Identify the structural attributes that shape the species richness of three taxonomic/functional groups (vascular plants, epiphytic lichens, and saproxylic invertebrates) in Mediterranean forests.

- Define the completeness of *in-situ* multi-taxon biodiversity data in European forests using the “Bottoms-up” platform as a pilot database.

4. Thesis structure and collaborations:

This thesis is organized according to the following key publications:

- **Chapter 1. Where are we now with European forest multi-taxon biodiversity and where can we head to?**

  Burrascano, S., Chianucci, F., Trentanovi, G., Kepfer-Rojas, S., Sitzia, T., Tinya, F., Doerfler, I., Paillet, Y., Nagel, T. A., Mitic, B., Morillas, L., Munzi, S., Van der Sluis, T., Alterio, E., Balducci, L., de Andrade, R. B., Bouget, C., Giordani, P., Lachat, T., … Ódor, P. (2023). Where are we now with European forest multi-taxon biodiversity and where can we head to? Biological Conservation, 284, 110176. https://doi.org/10.1016/j.biocon.2023.110176

- **Chapter 2. Do European forest carbon and biodiversity policies have a win-win potential?**

  Balducci, L.,Alterio, E., Ammer, C., Archaux, F., Boch, S., Bouget, C., Brazaitis, G., Chianucci, F., Cutini, A., De Smedt, P., Doerfler, I., Dvořák, D., Fischer, M., Giordani, P., Gosselin, M., ... , Burrascano, S. Do European forest carbon and biodiversity policies have a win-win potential? Submitted to Nature Communications, currently under major revisions.

- **Chapter 3. Biodiversity at stake: winners and losers of forest management in Europe.**

  Balducci, L., Rota, F., Chojnacki, L., The “Bottoms-Up Consortium”, Muscarella, R., Burrascano, S. Biodiversity at stake: winners and losers of forest management in Europe. Manuscript pending submission.

- **Chapter 4. Guiding management practices to enhance multi-taxon diversity in Mediterranean forests.**

  Balducci, L., Caprasecca, E., Di Pietro, F., Legnaro Diamanti, M.,, Bertagni, G., The “GoProFor MED” Consortium, Burrascano, S. “Guiding management practices to enhance multi-taxon diversity in Mediterranean forests”. Manuscript pending submission.

- **Chapter 5: Towards an effective multi-taxon biodiversity assessment in European forests.**

  Burrascano, S., Chojnacki, L., Balducci (*), L., Chianucci, F., Haeler, E., Kepfer-Rojas, S., Paillet, Y., Barreto de Andrade, R., Boch, S., De Smedt, P., Fischer, M., García-Mijangos, I., Heilmann-Clausen, J., Hofmeister, J., Hošek, J., …, Ódor, P. Towards an effective multi-taxon biodiversity assessment in

European forests. Submitted to Basic and Applied Ecology, currently under major revisions. (*): corresponding author

As part of my PhD research, I contributed to the following collaborative projects:

- Chianucci, F., Napoleone, F., Ricotta, C., Ferrara, C., Fusaro, L., Balducci, L., Trentanovi, G., Bradley, O., Kovacs, B., Mina, M., Cerabolini, B. E. L., Vandekerkhove, K., De Smedt, P., Lens, L., Hertzog, L., Verheyen, K., Hofmeister, J., Hošek, J., Matula, R., … Burrascano, S. (2024). Silvicultural regime shapes understory functional structure in European forests. Journal of Applied Ecology, 61(10), 2350–2364. https://doi.org/10.1111/1365-2664.14740

- Paillet, Y., Zapponi, L., Schall, P., Monnet, J.-M., Ammer, C., Balducci, L., Boch, S., Brazaitis, G., Campanaro, A., Chianucci, F., Doerfler, I., Fischer, M., Gosselin, M., Gossner, M. M., Heilmann-Clausen, J., Hofmeister, J., Hošek, J., Jung, K., Kepfer-Rojas, S., Ódor, P., Tinya, F., Trentanovi, G., Vacchiano, G., Vandekerkhove, K., Weisser, W. W., Wohlwend, M., Burrascano, S. One to rule them all? Assessing the performance of sustainable forest management indicators against multitaxonomic data for biodiversity conservation. Submitted to Biological Conservation, currently in press.

- Basile, M., Lachat, T., Balducci, L., Chianucci, F., Chojnacki, L., Archaux, F., Avtzis, D., Bouget, C., De Smedt, P., Doerfler, I., Dumas, Y., Elek, Z., Gosselin, M., Gossner, M. M., Heilmann-Clausen, J., Hofmeister, J., Hošek, J., Janssen, P., Just Justesen, M., Hansen, A., Schmidt, I. K., Rojas, S., Mårell, A., Matula, R., Müller, J., Nordén, B., Ódor, P., Paillet, Y., Ravera, S., Sitzia, T., Tinya, F., Burrascano, S., Brockerhoff, E. Managed forests are a stronghold of non-native species in Europe. Submitted to Journal of Applied Ecology, currently under major revisions.

- Duflot, R., Heinrichs, S., Balducci, L., Chianucci, F., Hofmeister, J., Paillet, Y., Trentanovi, G., Archaux, F., Bouget, C., Boch, S., Dvořák, D., Gosselin, F., Gosselin, M., Gossner, M. M., Fischer, M., Holá, E., Hošek, J., Jung, K., Palice, Z., Renner, S. C., Weisser, W. W., Nagel, T. A., Burrascano, S., Schall, P. Biodiversity and landscape-scale forest management: an empirical assessment of Triad functional zoning. Submitted to Communications Earth & Environment, currently under major revisions.

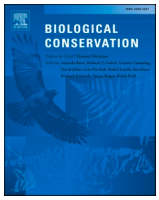
Chapter 1. Where are we now with European forest multi-taxon biodiversity and where can we head to?

Biological Conservation 284 (2023) 110176

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Review

Where are we now with European forest multi-taxon biodiversity and where can we head to?

Sabina Burrascano [a,b,*], Francesco Chianucci [b,c], Giovanni Trentanovi [d], Sebastian Kepfer-Rojas [e], Tommaso Sitzia [b,f], Flóra Tinya [g], Inken Doerfler [h,i], Yoan Paillet [j], Thomas Andrew Nagel [k], Bozena Mitic [l], Lourdes Morillas [m,n], Silvana Munzi [n,p], Theo Van der Sluis [q], Edoardo Alterio [f], Lorenzo Balducci [a], Rafael Barreto de Andrade [s], Christophe Bouget [t], Paolo Giordani [u], Thibault Lachat [v,w], Dinka Matosevic [x], Francesca Napoleone [a], Juri Nascimbene [y], Chiara Paniccia [z], Nicolas Roth [v,w], Réka Aszalós [g], Gediminas Brazaitis [ab], Andrea Cutini [c], Ettore D'Andrea [b,ac], Pallieter De Smedt [ad], Jacob Heilmann-Clausen [ae], Philippe Janssen [j], Daniel Kozák [af], Anders Mårell [ag], Martin Mikoláš [af], Björn Nordén [ah], Radim Matula [af], Peter Schall [ai], Miroslav Svoboda [af], Mariana Ujhazyova [aj], Kris Vandekerkhove [ak], Michael Wohlwend [al], Fotios Xystrakis [am], Michele Aleffi [an], Christian Ammer [ai], Frederic Archaux [ag], Thomas Asbeck [ao], Dimitrios Avtzis [ap], Manfred Ayasse [aq], Simonetta Bagella [ar], Rosario Balestrieri [as], Anna Barbati [at], Marco Basile [au], Ariel Bergamini [au], Giada Bertini [c], Alessandro Bruno Biscaccianti [ax], Steffen Boch [ay], János Bölöni [g], Pierluigi Bombi [az], Yves Boscardin [ag], Giorgio Brunialti [ba], Hans Henrik Bruun [bb], François Buscot [bc,bd], David Bille Byriel [be], Thomas Campagnaro [b,f], Alessandro Campanaro [b,bf], Matthieu Chauvat [bg], Michał Ciach [bh], Marek Čiliak [aj], Luca Cistrone [bi], Joao Manuel Cordeiro Pereira [bj], Rolf Daniel [bk], Bruno De Cinti [az], Gabriele De Filippo [bl], Wouter Dekoninck [bm], Umberto Di Salvatore [bn], Yann Dumas [ag], Zoltán Elek [bo,cz], Fabrizio Ferretti [c], Dimitrios Fotakis [ap], Tamás Frank [g], Julian Frey [bp], Carmen Giancola [bq], Erika Gomoryová [br], Marion Gosselin [ag], Frederic Gosselin [ag], Martin M. Gossner [au], Frank Götmark [bs], Elena Haeler [bt], Aslak Kappel Hansen [bu], Lionel Hertzog [bv], Jeňýk Hofmeister [bw], Jan Hošek [bx], Vivian Kvist Johannsen [be], Mathias Just Justensen [be], Nathalie Korboulewsky [ag], Bence Kovács [g], Ferenc Lakatos [ca], Carlos Miguel Landivar [cb], Luc Lens [cc], Emanuele Lingua [f], Fabio Lombardi [cd], František Máliš [br], Luca Marchino [c], Vitas Marozas [cf], Giorgio Matteucci [cg], Walter Mattioli [ch], Peter Friis Møller [ci], Jörg Müller [cj,ck], Csaba Németh [g], Gábor Ónodi [cl], Francesco Parisi [b,bq], Thomas Perot [ag], Sandrine Perret [ag], Anna Maria Persiani [a], Alessia Portaccio [f], Mario Posillico [cn], Žydrūnas Preikša [cf], Carsten Rahbek [ae], Nolan James Rappa [bj], Sonia Ravera [cp], Antonio Romano [cq], Ferenc Samu [cr], Christoph Scheidegger [au], Inger Kappel Schmidt [be], Sebastian Schwegmann [bj], Flavia Sicuriello [az], Andreea Petronela Spinu [ct], Gavriil Spyroglou [ap], Jonas Stillhard [au], Eleni Topalidou [ap], Anders P. Tøttrup [cu], Karol Ujházy [cv], Katalin Veres [g], Kris Verheyen [ad], Wolfgang W. Weisser [cw], Livia Zapponi [cx], Péter Ódor [g,cy]

[a] *Sapienza University of Rome, 00185, Rome, Italy*
[b] *National Biodiversity Future Center, Palermo, Italy*

* Corresponding author at: Sapienza University of Rome, 00185 Rome, Italy.
E-mail address: sabina.burrascano@uniroma1.it (S. Burrascano).

https://doi.org/10.1016/j.biocon.2023.110176
Received 25 February 2023; Received in revised form 9 May 2023; Accepted 20 June 2023
Available online 30 June 2023

[c] Council for Agricultural Research and Economics (CREA), Research Centre for Forestry and Wood, V.le Santa Margherita 80, I-52100 Arezzo (AR), Italy
[d] Research Institute on Terrestrial Ecosystems, National Research Council, 50019 Sesto Fiorentino, FI, Italy
[e] University of Copenhagen, Department of Geosciences and Natural Resource Management, 1958 Frederiksberg, Denmark
[f] Department Land, Environment, Agriculture and Forestry, Università degli Studi di Padova, 35020 Legnaro, PD, Italy
[g] Centre for Ecological Research, Institute of Ecology and Botany, 2163 Vácrátót, Hungary
[h] University of Oldenburg, 26129 Oldenburg, Germany
[i] Technical University of Munich, Freising, Germany
[j] Univ. Grenoble Alpes, INRAE, Lessem, 38402 Saint Martin d'Heres, France
[k] University of Ljubljana, Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, 1000 Ljubljana, Slovenia
[l] University of Zagreb, Faculty of Science, Department of Biology, 10000 Zagreb, Croatia
[m] University of Seville, Department of Vegetal biology and Ecology, 1749-016 Seville, Spain
[n] Universidade de Lisboa, Center for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Lisbon, Portugal
[p] Centro Interuniversitário de História das Ciências e da Tecnologia, Lisbon, Portugal
[q] Wageningen Environmental Research, 6800 AA Wageningen, Netherlands
[s] University of Maryland, 20742 College Park, United States
[t] INRAE, UR EFNO, 45290 Nogent-sur-Vernisson, France
[u] DIFAR, University of Genova, 16148 Genova, Italy
[v] Bern University of Applied Sciences, School of Agricultural, Forest and Food Sciences HAFL, 3052 Zollikofen, Switzerland
[w] Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
[x] Croatian Forest Research Institute, 10450 Jastrebarsko, Croatia
[y] BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum, University of Bologna, 40126 Bologna, Italy
[z] Institute for Alpine Environment, Eurac Research, 39100 Bolzano, Italy
[ab] Department of Forest Science, Ariculture Academy, Vytautas Magnus University, 53361 Kaunas dist., Lithuania
[ac] Research Institute on Terrestrial Ecosystems, National Research Council, 05010 Porano, Italy
[ad] Ghent University, 9090 Melle-Gontrode, Belgium
[ae] Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, DK-2100 Copenhagen, Denmark
[af] Czech University of life Sciences in Prague, 16500 Prague, Czechia
[ag] INRAE, UR EFNO, 45290 Nogent-sur-Vernisson, France
[ah] Norwegian Institute for Nature Research, 0855 Oslo, Norway
[ai] Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, 37077 Göttingen, Germany
[aj] Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, 96001 Zvolen, Slovakia
[ak] INBO-Research Institute for Nature and Forests, 9500 Geraardsbergen, Belgium
[al] Albert-Ludwigs-University Freiburg, 79085 Freiburg, Germany
[am] Forest Research Institute, Hellenic Agricultural Organization Demeter, 5700 Vassilika, Greece
[an] School of Biosciences, University of Camerino, 62032 Camerino, MC, Italy
[ao] Unique landuse GmbH, 79098 Freiburg, Germany
[ap] Forest Research Institute, Hellenic Agricultural Organization Demeter, 57006 Vassilika, Greece
[aq] Ulm University, Institute of Evolutionary Ecology and Conservation Genomics, Ulm, Germany
[ar] University of Sassari, Department of Chemical, Physical, Mathematical and Natural Sciences, Sassari, Italy
[as] Department of Marine Animal Conservation and Public Engagement, Anton Dohrn Zoological Station, 00015 Napoli, Italy
[at] University of Tuscia, Department for Innovation in Biological, Agro-food and Forest systems (DIBAF), 01100 Viterbo, Italy
[au] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland
[ax] Dept. PAU, Mediterranea University of Reggio Calabria, 89124 Reggio Calabria, Italy
[ay] WSL Swiss Federal Research Institute, 8903 Birmensdorf, Switzerland
[az] Institute of Research on Terrestrial Ecosystems, National Research Council, Montelibretti, Italy
[ba] TerraData Environmetrics, Spin-Off Company of the University of Siena, 58025 Monterotondo Marittimo, Italy
[bb] University of Copenhagen, Dept Biology, 2100 Copenhagen, Denmark
[bc] Helmholtz Centre for Environmental Research (UFZ), 06120 Halle (Saale), Germany
[bd] German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[be] University of Copenhagen, Department of Geosciences and Natural Resource Management, Rolighedsvej 23, 1958 Frederiksberg C, Denmark
[bf] Council for Agricultural Research and Economics (CREA), Research Centre for Plant Protection and Certification, Via Lanciola 12A, I-50125 Florence, Italy
[bg] Normandie UNIV, UNIROUEN, INRAE, ECODIV, 76821 Mont Saint Aignan, France
[bh] University of Agriculture in Krakow, Department of Forest Biodiversity, Krakow, Poland
[bi] Forestry and Conservation, 03043 Cassino, Italy
[bj] Albert-Ludwigs-University of Freiburg, Chair of Nature Conservation and Landscape Ecology, 79106 Freiburg, Germany
[bk] Genomic and Applied Microbiology & Göttingen Genomics Laboratory, Institute of Microbiology and Genetics, Georg-August University of Göttingen, Grisebachstr. 8, 37077 Göttingen, Germany
[bl] Istitute of Wildlife Management, 80126 Napoli, Italy
[bm] Royal Belgian Institute for Natural Sciences, Brussels, Belgium
[bn] Council for Agricultural Research and Economics (CREA), Research Centre for Agricultural Policies and Bioeconomy, Via Lombardia, c.da Bucceri, I-65012 Cepagatti (PE), Italy
[bo] Department of Biostatistics, University of Veterinary Medicine, István utca 2, 1078, Budapest, Hungary
[bp] Albert-Ludwigs-University of Freiburg, Chair of Forest Growth and Dendroecology, 79106 Freiburg, Germany
[bq] Department of Biosciences and Territory, Università degli Studi del Molise, Campobasso, Italy
[br] Technical University in Zvolen, 96001 Zvolen, Slovakia
[bs] University of Gothenburg, 40530 Göteborg, Sweden
[bt] Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW), 1131 Vienna, Austria
[bu] Natural History Museum of Denmark, Univeristy of Copenhagen, 2100 Copenhagen, Denmark
[bv] Thünen Institute of Biodiversity, 38116 Braunschweig, Germany
[bw] Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Department of Forest Ecology, 16500 Praha, Czech Republic
[bx] Ecological Services, 26801 Hořovice, Czech Republic
[ca] University of Sopron, H-9400 Sopron, Hungary
[cb] Albert-Ludwigs-University of Freiburg, Dept of Biometry and Environmental System Analysis, 79106 Freiburg, Germany
[cc] Ghent University, Ghent, Belgium
[cd] Agraria Department, Mediterranean University of Reggio Calabria, 89122 Reggio Calabria, Italy
[cf] Agriculture Academy, Vytautas Magnus University, 53361 Kaunas distr., Lithuania
[cg] National Research Council of Italy, Institute of BioEconomy (CNR-IBE), 50019 Sesto Fiorentino, FI, Italy
[ch] Council for Agricultural Research and Economics (CREA), Research Centre for Forestry and Wood, Via Valle della Quistione 27, I-00166 Rome, Italy
[ci] Geological Survey of Denmark and Greenland, 1350 Copenhagen K, Denmark
[cj] University Würzburg, 96181 Rauhenebrach, Germany

[ck] Nationalpark Bavarian Forest, Grafenau, Germany
[cl] National Laboratory for Water Science and Water Security, Balaton Limnological Research Institute, H-8237 Tihany, Hungary
[cn] Reparto Carabinieri Biodiversità Castel di Sangro, 67031 Castel di Sangro, Italy
[cp] Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STEBICEF), University of Palermo, 90123 Palermo, Italy
[cq] Institute for Bioeconomy, National Research Council of Italy, 00100 Roma, Italy
[cr] Plant Protection Institute, Centre for Agricultural Research, ELKH, H-1029 Budapest, Hungary
[ct] Albert-Ludwigs-University of Freiburg, Chair of Silviculture, 79106 Freiburg, Germany
[cu] Natural History Museum of Denmark, Univeristy of Copenhagen, DK-1350 Copenhagen, Denmark
[cv] Faculty of Forestry, Technical University in Zvolen, 96001 Zvolen, Slovakia
[cw] Technical University of Munich, Terrestrial Ecology Research Group, Department of Life Science Systems, School of Life Sciences, 85354 Freising, Germany
[cx] Institute of BioEconomy, National Research Council, 38098 San Michele All'adige, TN, Italy
[cy] University of Sopron, Institute of Environmental Protection and Nature Conservation, Sopron, Hungary
[cz] ELKH-DE Anthropocene Ecology Research Group, University of Debrecen, Egyetem tér 1, 4032, Debrecen, Hungary

ARTICLE INFO

Keywords:
Forest biodiversity
Multi-taxon
Sustainable management
Biodiversity conservation
Forest stand structure

ABSTRACT

The European biodiversity and forest strategies rely on forest sustainable management (SFM) to conserve forest biodiversity. However, current sustainability assessments hardly account for direct biodiversity indicators. We focused on forest multi-taxon biodiversity to: i) gather and map the existing information; ii) identify knowledge and research gaps; iii) discuss its research potential. We established a research network to fit data on species, standing trees, lying deadwood and sampling unit description from 34 local datasets across 3591 sampling units. A total of 8724 species were represented, with the share of common and rare species varying across taxonomic classes: some included many species with several rare ones (e.g., *Insecta*); others (e.g., *Bryopsida*) were represented by few common species. Tree-related structural attributes were sampled in a subset of sampling units (2889; 2356; 2309 and 1388 respectively for diameter, height, deadwood and microhabitats). Overall, multi-taxon studies are biased towards mature forests and may underrepresent the species related to other developmental phases. European forest compositional categories were all represented, but beech forests were over-represented as compared to thermophilous and boreal forests. Most sampling units (94%) were referred to a habitat type of conservation concern. Existing information may support European conservation and SFM strategies in: (i) methodological harmonization and coordinated monitoring; (ii) definition and testing of SFM indicators and thresholds; (iii) data-driven assessment of the effects of environmental and management drivers on multi-taxon forest biological and functional diversity, (iv) multi-scale forest monitoring integrating *in-situ* and remotely sensed information.

1. Introduction

Forests support about three-quarters of terrestrial plants, fungi and animal species (FAO, 2020), and are at the base of other ecosystem services including the provisioning of raw materials and the regulation of geochemical cycles. These services are threatened by climate change, forest loss and degradation, invasions by non-native species, and over-harvesting (Felipe-Lucia et al., 2020). The increasing concern related to these threats has imposed a paradigm shift from single-objective forest management (i.e., timber production-oriented) to the embracement of forest multifunctionality (Mori et al., 2017).

Sustainable Forest Management (SFM) is defined as the management that concomitantly maintains forest biodiversity, productivity, regeneration capacity, and vitality, as well as forests' potential to fulfill a wide range of functions and services (MCPFE, 1993). As such, SFM is globally recognized as a crucial tool to counteract biodiversity loss, and to promote sustainable development (UN, 2015). Managing forests sustainably is particularly relevant in Europe, where, although about 24 % of forests are formally protected, only a small fraction (2 % of total forest area) is not subject to harvesting interventions (Forest Europe, 2020). Accordingly, the SFM definition reported in the European Union regulation (2020/852) includes a criterion of biodiversity maintenance, reported as the contribution to "enhancing biodiversity, halting or preventing the degradation of ecosystems, deforestation and habitat loss".

Nevertheless, the effects of forest management on the diversity of multiple taxonomic groups, hereafter multi-taxon biodiversity, are not sufficiently known, and the links between indicators of biodiversity and of management sustainability are not always evident and strong (Oettel and Lapin, 2021). As a matter of fact, multi-taxon biodiversity sampling and analysis is highly demanding in terms of funding, time, and a broad range of expertise and competences (Tomppo et al., 2010). For these reasons, it remains uncertain to which extent, and for which taxonomic groups could forest management for wood supply deteriorate biodiversity compared to unharvested forests, and how SFM can mitigate these effects.

The challenges of multi-taxonomic field sampling are being increasingly addressed at the local or regional scales. In Europe, these efforts often consist of exhaustive species censuses across single- or multiple sites to assess the effects of forest structure and management on the diversity of multiple taxonomic groups (see references in Table 1).

Table 1
Definitions of the silvicultural systems used in the platform.

Silvicultural systems	Treatment description
Unmanaged	No silvicultural interventions applied in the recent past, stands currently under natural development
Selection cutting	Single-tree and group selection cutting are uniformly distributed across the stand.
Shelterwood	Overstorey trees in a forest stand are completely removed through multiple progressive cuts designed to promote regeneration making use of the shelter and seed source of remaining trees
Clearcutting with retention	The forest stand is clear-felled in a single harvesting operation except for solitary trees or tree groups that are deliberately spared
Clearcutting	The forest stand is entirely harvested in a single operation, resulting in a treeless open area mostly artificially regenerated
Coppice with standards	The two vertical strata of the forest stand (even-aged coppice as the understorey, and an overstorey of standards which are trees of seed- rather than sprouting origin) are harvested respectively by a clearcutting and a selection cutting. Standards can be uneven-aged and the two components have quite different rotation periods. This category also includes the combination of coppice and high forest (i.e. compound coppices)

Relatively few examples of such studies can be found in other continents within the temperate and boreal zones (Murray et al., 2017; Bowd et al., 2021; Stokely et al., 2022). The efforts of European researchers to test the effectiveness of SFM reflect the long-lasting and widespread land-sharing approach to forest zoning that characterizes Europe, at least since Möller (1922), as compared to regions where a sparing approach is more common (e.g., Australia, North America). However, compared to continent-wide health forest monitoring networks (e.g., International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests - ICP Forests), research activities related to European forest biodiversity remain uncoordinated at the continental scale and suffer from a lack of harmonization and integration across local studies.

Here we aim to i) review the existing information on forest multi-taxon biodiversity associated with stand structure and management and ii) identify knowledge gaps in multi-taxon forest biodiversity studies. Starting from this basis, we aim to iii) discuss future research challenges associated with multi-taxon biodiversity in European forests. Ultimately, we intend to encourage new institutional forms of broad-scale forest biodiversity data collection and usage to inform forest conservation and management policies in Europe and elsewhere.

2. Methods

2.1. Data collection

We aimed at gathering forest biodiversity and stand structural data from many independent research projects and studies on multi-taxon forest biodiversity performed across Europe in the last 20 years. We created a network connecting research groups that collected forest multi-taxon biodiversity data in Europe from local to national scales. The initial network was progressively enlarged by contacting researchers involved in past and ongoing forest multi-taxon biodiversity projects identified through project databases (i.e., LIFE projects' database: https://webgate.ec.europa.eu/life/publicWebsite/search), publications and personal information.

We defined a *forest* as an ecosystem in which tree cover was equal or greater than 40 % (Sasaki and Putz, 2009). We intended *multi-taxon* to include simultaneous information on a minimum of three taxonomic groups, representing at least Plantae or Fungi, and Animalia. *Stand structure* data was defined as tree species composition, volume and size distribution of standing trees (both living or dead), and of lying deadwood when available.

To test the comprehensiveness of the platform, we surveyed the research network on relevant literature and gathered 117 published articles (Trentanovi et al., n.d.). We added further articles found through a literature search on ISI Web of Science (accessed on November, 17, 2022 and limited to articles published before 2022) with the formula (TS = (forest AND multi-tax* AND biodiversity)). This search resulted in 130 additional articles, of which 61 describe studies performed in Europe. Among these, 17 focused on non-forest habitats (e.g., wood pastures, urban or agricultural areas), 17 did not fit the multi-taxon or stand structure requirements, five had a different focus (sampling methods, biotic disturbance). Only 22 articles fitted the platform requirements, among which 11 were already listed in the literature gathered through the research network, and five were relative to datasets already included in the platform. Based on this literature assessment we deemed the platform as significantly representative.

For each dataset in the platform, we firstly gathered and harmonized the information on sampling designs and protocols (see the 'protocols' of Fig. 1) into three ancillary tables that include standardized sampling protocol descriptions of: standing trees, lying deadwood, and biodiversity data. (i.e., 'protocol data' in the output section of Fig. 1).

The spatial hierarchy of the platform encompasses plots (i.e., delimited forest areas of known geographical coordinates) that are nested into stands (i.e., management spatial units), and stands that are nested into sites (i.e., environmentally homogeneous geographical

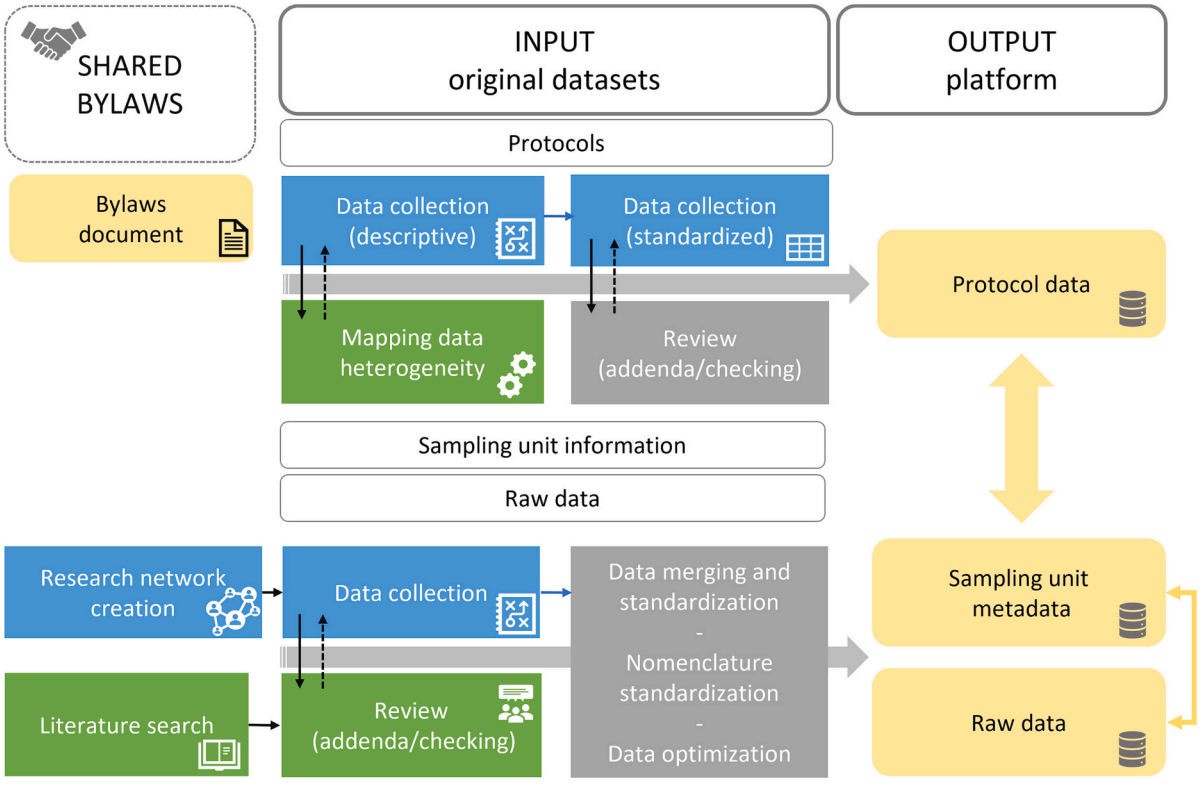


Fig. 1. Workflow of the platform building process. Blue boxes identify in-progress products; green boxes identify phases of common decisions, brainstorming and comparison with scientific literature; gray boxes indicate data processing; yellow boxes are the outcomes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

areas). We generally refer to sampling units to include both plots and stands, since in a minority of cases (about 15 % of the stands do not have plot IDs but stand IDs), data were sampled at the stand scale, without specific sampling plots. It is also relevant to point out that for most of the collected datasets, several ecosystem components, i.e., taxonomic groups and stand structure, were sampled in the same *plots*, but in a minority of cases different components were sampled using various designs across a forest stand, allowing for cross-taxon analysis only at the stand scale (see Burrascano et al., 2021 for a thorough discussion of the pros and cons of the two approaches).

The studies included in the platform were mainly observational but some experimental studies were also included. In both cases, we collected information on stand age and/or development stage, a categorical definition of the silvicultural system adopted, and many other associated quantitative management data (e.g., time since last harvesting).

2.2. Data management

Each original dataset was associated with one data custodian, responsible for data preparation and handling within the platform, and for communication with the dataset contributors. The heterogeneity in sampling designs, measurement methods, spatial scales, target variables and taxonomic groups required the definition of standardized procedures to harmonize raw information and produce a common data structure.

We built a relational structure encompassing several tables whose organization and templates derived from an iterative process of proposals and refinements carried out through a wide and open discussion (see connections between boxes in the 'Input' section in Fig. 1).

The core of the platform (i.e., 'Sampling unit metadata' and 'Raw data' in Fig. 1) consists of four tables: one containing sampling unit metadata and the others containing the raw data separately for standing trees, lying deadwood, and multi-taxon species composition.

The sampling unit metadata includes location, ownership, structure, regeneration and management type. Two key variables within this table are the forest compositional category and the silvicultural system. The former refers to the classification into 14 categories of ecologically distinct forest communities in Europe dominated by specific assemblages of tree species (SI-1). These categories were designed to facilitate the interpretation and communication of indicators on the status and trends of forests in Europe (EEA, 2006; updated by Barbati et al., 2014). The classification into broad silvicultural systems was based on the type of regeneration cut according to Matthews (1989) and refined through an extensive discussion within the network (Table 1).

Data were processed in the R programming environment (R Core Team, 2021, R version 4.1.1) using version control to ensure the widest possible hands-on collaboration and data cross-checking. Data inconsistencies that may have originated from data entry errors (e.g., typographical errors), data type storage, species nomenclature, and adherence of datasets to the table structure (e.g., column names, list of possible and plausible values) were qualitatively checked through several validation rules. These (semi)automatic rules were based on data range, length, column reference name, list values, null values, blank values, and data types. After this validation process, data have been corrected or integrated mostly through back-checking to data providers.

Species names and higher taxonomic information were extracted from databases and corroborated by experts. All species names were firstly checked using the gnr_resolve() function in the 'taxize' package (Chamberlain and Szöcs, 2013). The species names obtaining scores greater than 0.90 were accepted, while those with lower scores were sent to experts for corroboration. For vascular plants, a further screening was performed through the 'WorldFlora' package (Kindt, 2020). Finally, species names that could not be corroborated by experts were checked against the GBIF database (https://www.gbif.org/). Complete taxonomic classification was extracted with the taxonomy() function in the 'myTAI' package (Drost et al., 2018).

Relationships across tables operate at different spatial scales through univocal IDs for sites, stands, and plots. The templates of the tables for contributing data to the platform are available at: https://www.bottoms-up.eu/en/participants/contribute/contribute-data.html to promote further implementation of the data.

Data management is coordinated by a governing board elected by the consortium involving all data contributors according to common bylaws that were discussed and accepted by all the consortium participants (downloadable here: https://www.bottoms-up.eu/en/participants/contribute/propose-a-project.html). The bylaws are composed of eight regulation articles partly based on previous experiences of shared datasets (e.g., Biurrun et al., 2019). As it is always the case in the beginning of these sharing processes, a give-and-take approach has been chosen (Kattge et al., 2020; Bruelheide et al., 2019); therefore, joining the consortium is possible for researchers that provide a dataset complying with the bylaws requirements. Data usage is open to anyone proposing a research project involving at least one consortium member by following the instructions at: https://www.bottoms-up.eu/en/participants/contribute/propose-a-project.html. A Shiny Web-App (https://www.bottoms-up.eu/en/results/data-explorer.html) was created to smooth the proposal of projects by allowing for data exploration and filtering based on the sampling unit metadata (SI-2).

2.3. Data analysis and visualization

The proportion of sampling units for each compositional category was compared with the share of such categories in the European Union forest area as reported in Barbati et al. (2014). Similarly, sampling unit distribution across broad regeneration strategies (high forest and coppice), and unmanaged areas were compared with the share of forest area under these conditions as reported in McGrath et al. (2015). Sampling unit metadata were visualized through alluvial plots using the 'ggalluvial' R-package (Brunson, 2020).

The distribution of species and species records across higher taxonomic ranks (phyla and classes) was represented through a phylogenetic tree, encompassing 7335 out of the 8724 species of the platform. The tree was obtained through PhyloT (https://phylot.biobyte.de/) in Newick format and imported in R through the 'ape' package (Paradis and Schliep, 2019). To each species in the tree, we associated its higher taxonomic ranks derived through the 'myTAI' package (Drost et al., 2018) and the number of occurrences across sampling units (SI-3). The combined information was visualized by using the 'ggtree' package (Yu et al., 2017).

In addition to the mentioned check for plausible ranges of values, structural data were subjected to specific integration processes. Heights of standing trees were integrated by means of height-diameter relationships (hypsometric models); whereas deadwood fragments measurements were integrated through data imputation performed using the 'mice' package (van Buuren and Groothuis-Oudshoorn, 2011). Data integration was performed individually for each dataset by applying the predictive mean matching (PMM), i.e., assessing imputation uncertainty through the examination of the variation in imputed values when treated as real, and including forest compositional categories and types, and spatial variables (plot and site). Few datasets lacked any measures of height/length and were integrated by using the whole data platform. A total of 42,643 tree heights out of 178,098 were calculated by means of hypsometric models; and 5011 diameters and 9317 lengths were imputed out of 58,824 lying deadwood fragments. Based on these data, the distributions of sampling unit mean of Diameter at Breast Height (DBH) for standing trees and of diameter for lying deadwood were calculated (SI-4, SI-5).

Biodiversity and stand structure indices may be related to environmental conditions by using parameters published in the framework of other research projects. For instance, each sampling unit was spatially associated with data on soil characteristics that were obtained from the

European topsoil physical properties map (Ballabio et al., 2016). Among the multiple soil properties available in this dataset, those currently linked to each forest multi-taxon sampling unit over a 1000 m buffer from the center of the sampling unit are: Available Water Capacity, Bulk density (derived from soil texture datasets), Soil textural classes derived from clay, silt, and sand maps. Similarly, climatic data were obtained from CHELSA v.2.1 (Karger et al., 2017), at 1000 m resolution. Bioclimatic variables were derived as long-term means or sums over the 1981–2010 period, and included mean annual temperature, annual range of air temperature, annual precipitation amount, and precipitation seasonality. Each sampling unit is also associated to a heat load index (HLI) expressing the topographic influence on incident solar radiation (McCune and Keon, 2002).

3. Results

3.1. Overview of the existing data

3.1.1. Sampling units

A total of 3591 sampling units across 220 sites in 12 European countries were gathered (SI-2, https://zenodo.org/record/7886698#.ZFEs7HZBxD8), ranging from Sweden to southern Italy in latitude, and from France to Lithuania in longitude (Fig. 2). The harmonization involved 34 local datasets (Table 2) and 185 researchers.

In general, no clear pattern of association appears between silvicultural systems and forest compositional categories. For instance, shelterwood is applied to almost all compositional categories (Fig. 3); even though coppice with standards were associated mostly with mesophytic and thermophilous deciduous forests.

Importantly, most sampling units (94 %) were referred to a habitat type of conservation concern according to the European cornerstone of biodiversity conservation, the Habitats Directive (92/43/EEC). The highest representation (82 %) was found for the forests of temperate Europe (group 91). About a quarter (27 %) of the total number of sampling units referred to as priority habitat types, with, in order of decreasing frequency, 91H0*- Pannonian woods with Quercus pubescens, 91G0*- Pannonic woods with *Quercus petraea* and *Carpinus betulus*, 91E0*- Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, Salicion albae).

3.1.2. Taxonomic information

The dataset comprises a wide range of taxonomic groups across the kingdoms of fungi, plants, and animals (SI-3, https://zenodo.org/record/7886698#.ZFEs7HZBxD8), with 8724 species, 2979 genera, 729 families, 193 orders, 44 classes, and nine different phyla (Fig. 4). The taxonomic groups originally considered in each study include heterogeneous taxonomic ranks, from kingdom to order, and, in some cases, include only specific morphological or ecological groups commonly used in sampling and identification (e.g., macrofungi, epiphytic lichens, saproxylic beetles). Most plots have information on four or more different taxonomic groups, with an average of 4.6 groups per plot. Some plots have information on only one or two taxonomic groups, but on at least three taxonomic groups at the stand level, as required by the platform bylaws.

The classes that are represented by the highest number of species are also those represented by the highest number of records (Fig. 5), i.e.,

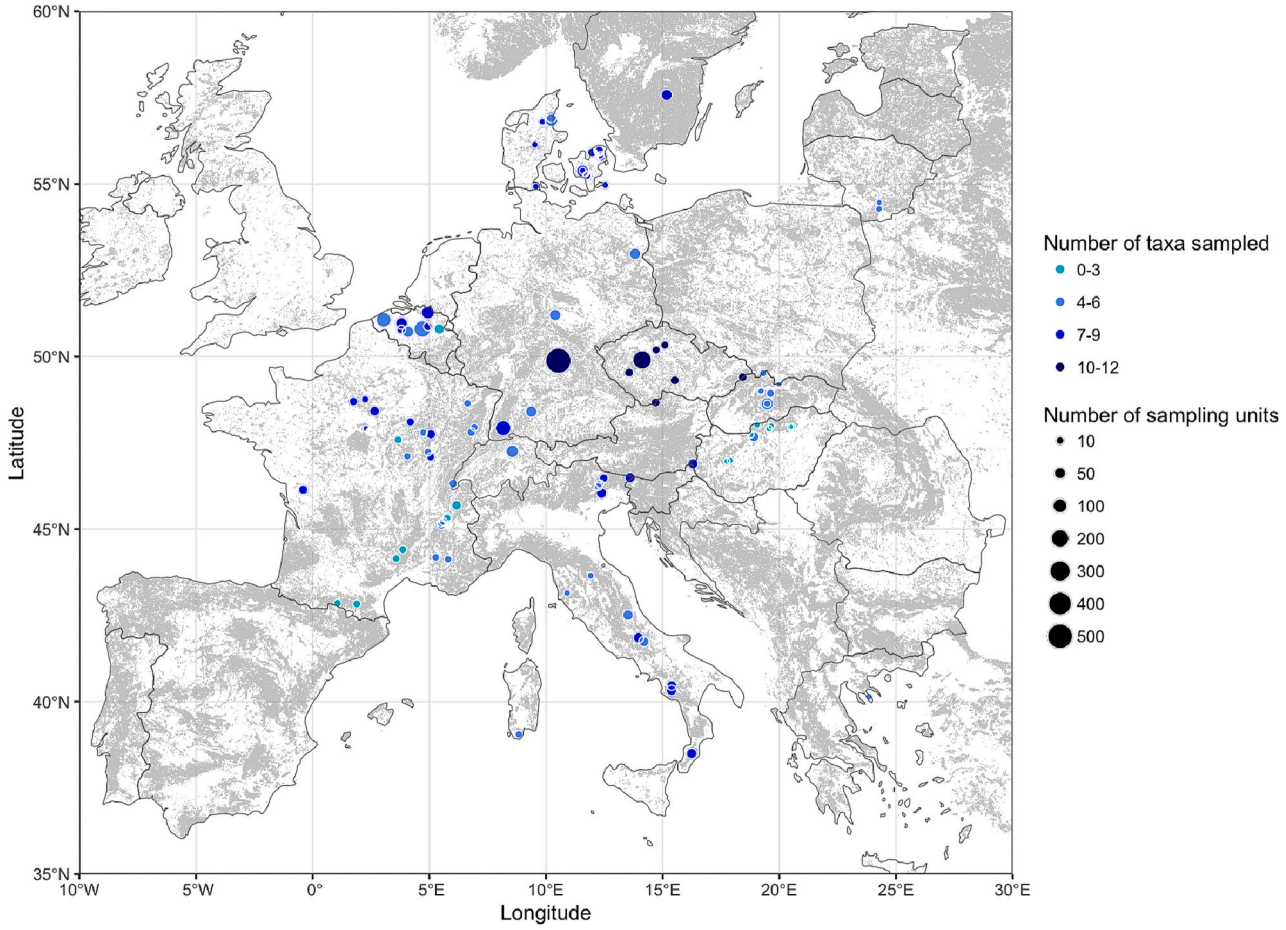


Fig. 2. Distribution of the platform sampling sites in Europe. Gray areas are covered by forests with a tree cover greater than 40 % according to the European Forest Institute Forest Map of Europe (Kempeneers et al., 2011). Number of taxa are represented by color, while number of sampling units by dot size.

Table 2
General descriptors of the local datasets. Dataset ID: ID of dataset, Country: country where the study has been made, N sites: number of sampled sites, N units: number of sampling units, Reference: main literature references of the 34 datasets collected for this work.

Dataset ID	Country	N sites	N units	Reference
BE_PS1	BE	2	32	De Smedt et al., 2019
BE_PS2	BE	1	53	de Groote et al., 2017
BE_KV1	BE	5	462	Vandekerkhove et al., 2016
CH_TL	CH	1	69	Haeler et al., 2021
CZ_JH1	CZ	6	106	Hofmeister et al., 2019
CZ_JH2	CZ	1	230	Hofmeister et al., 2013
CZ_MR	CZ	1	45	Chamagne et al., 2016
DE_ID	DE	1	526	Doerfler et al., 2017
DE_JP	DE	1	135	Storch et al., 2020
DE_PS	DE	3	150	Schall et al., 2018
DK_JC1	DK	6	40	Lelli et al., 2019
DK_JC2	DK	2	107	Mazziotta et al., 2016
DK_JC3	DK	1	30	–
DK_SK	DK	16	386	Byriel et al., 2020
FR_AM	FR	12	33	Cocquelet et al., 2019
FR_JP	FR	3	70	Janssen et al., 2018
FR_NK	FR	35	43	Korboulewsky et al., 2021
FR_YP	FR	24	300	Paillet et al., 2015
GR_FX	GR	1	4	–
HU_FT	HU	1	36	Horváth et al., 2023
HU_PO1	HU	1	35	Tinya et al., 2021
HU_PO2	HU	1	30	Elek et al., 2018
HU_RA	HU	8	22	–
IT_AC	IT	3	18	Cutini et al., 2021
IT_EA	IT	6	199	D'Andrea et al., 2016
IT_SB1	IT	1	36	Blasi et al., 2010
IT_SB2	IT	2	66	Sabatini et al., 2016
IT_TS	IT	2	20	Sitzia et al., 2017
LT_GB	LT	20	143	–
SK_DK	SK	3	18	Kameniar et al., 2021
SK_MM	SK	3	22	Kozák et al., 2021
SK_MS	SK	3	18	Langbehn et al., 2021
SK_MU	SK	1	65	Ujházy et al., 2018
SW_BN	SW	25	50	Götmark, 2013

Insecta (3244 species across 88,338 records), *Agaricomycetes* (2077 species across 44,418 records), *Magnoliopsida* (1182 species across 71,458). However, this pattern differs for *Bryopsida*, which are represented by only 280 species in a very high number of records (27,551). This means that some *Bryopsida* species occur in a very high number of sampling units; for instance, *Hypnum cupressiforme* is the species occurring in the highest number of sampling units (5082) among all species in the platform (see also Blasi et al., 2010). On the other hand, *Insecta*, *Magnolipsida* and *Agaricomycetes* are the most represented classes among species singletons (i.e., species occurring only once in the platform) with respectively 35 %, 29 % and 13 % of sinlgetons vs. less than 3 % for *Bryopsida*.

3.1.3. Structural attributes

Being required by the bylaws, diameters of standing trees are available for all sampling units, either at the plot or stand scale, with a total 2889 sampling units, with additional data on tree height, deadwood and tree-related microhabitats in respectively 2356, 2309, and 1388 plots.

The mean diameters of standing trees (both living and dead) and lying deadwood within each sampling unit across the platform vary across silvicultural regimes. The former shows a left-skewed distribution for clearcutting and clearcutting with retention and a bimodal distribution for coppice with standards. The lying deadwood mean diameters have a peak at lower values if compared with standing tree DBH distributions, and often show a wider range, in some cases with a bimodal distribution (Fig. 6).

3.2. Gaps in knowledge

3.2.1. Sampling units

Sampling units with multi-taxon biodiversity data associated with stand structure and management information (SI-2) are available for all the 14 European forest compositional categories (Barbati et al., 2014) although unevenly distributed among them. European beech forests are over-represented with respect to the area they occupy (Fig. 5A), with lowland and mountainous beech forests representing more than 55 % of the sampling units (Barbati et al., 2014) (Fig. 5A). The distribution of sampling units across management systems, i.e., timber harvesting relying on resprouting (coppice) or seed regeneration (high forest) or no harvesting (unmanaged), differed from their area extent (McGrath et al., 2015) only for coppices (Fig. 5B).

Relevant gaps remain for some crucial management information, for instance type and year of last intervention were not available for about 40 % of sampling units. This indicates that detailed management information is often not available to forest biodiversity researchers. However, the sampling unit metadata allow a close look into the management and composition of the forests included in the platform. Most of the available sampling units are within public forests, naturally regenerated, with shelterwood and selection cutting systems being by far the most represented, and single- and multi-storied forests being similarly frequent (Fig. 3).

3.2.2. Taxonomic information

Some taxonomic classes are underrepresented both in terms of species and records, and this is especially true for fungi other than Agaricomycetes. For instance, Eumycetozoa, Mucoromycetes and Pucciniomycetes are represented by only one species that occurs in less than 5 sampling units. The rarity of these classes is even more striking if we account for the fact that fungi were among the most commonly sampled groups of organisms.

3.2.3. Structural attributes

Notwithstanding differences in the forest definition adopted and in DBH threshold, the diameter distributions of the data within the platform reflect the distribution of growing stock across diameter classes at the European level (Forest Europe, 2020), with most sampling units having a mean DBH between 20 and 40 cm (Fig. 6). On the other hand, in European multi-taxon studies, the share of trees over 40 cm is higher than the share below 20 cm. This means that multi-taxon studies are partly biased towards mature developmental phases. On the one hand, this may result in an underrepresentation of species related to different phases of the forest succession (Hilmers et al., 2018), especially of the earliest; on the other hand, it may contribute to demonstrate the links between large trees and forest biodiversity (Kozák et al., 2023).

4. Discussion

4.1. Solids and voids of the existing data

This study is the first attempt, both in Europe and globally, to encompass extensive and comprehensive information on forest management, structural attributes, and multi-taxon biodiversity in a single, harmonized and publicly explorable platform.

Although we collected most data deriving from forest multi-taxon studies performed in Europe, the resulting data is unevenly distributed across compositional categories. Further efforts should thus focus on attaining a good representation for boreal, hemiboreal, thermophilous and Mediterranean compositional categories, as well as for mire, swamp, and floodplain forests. Among these, boreal and hemiboreal forests are widespread in Europe, thus their underrepresentation in the platform is a clear knowledge gap. Other categories, instead, have a limited extent across Europe, with floodplain forests displaying the lowest cover (Barbati et al., 2014). Although floodplain forests are

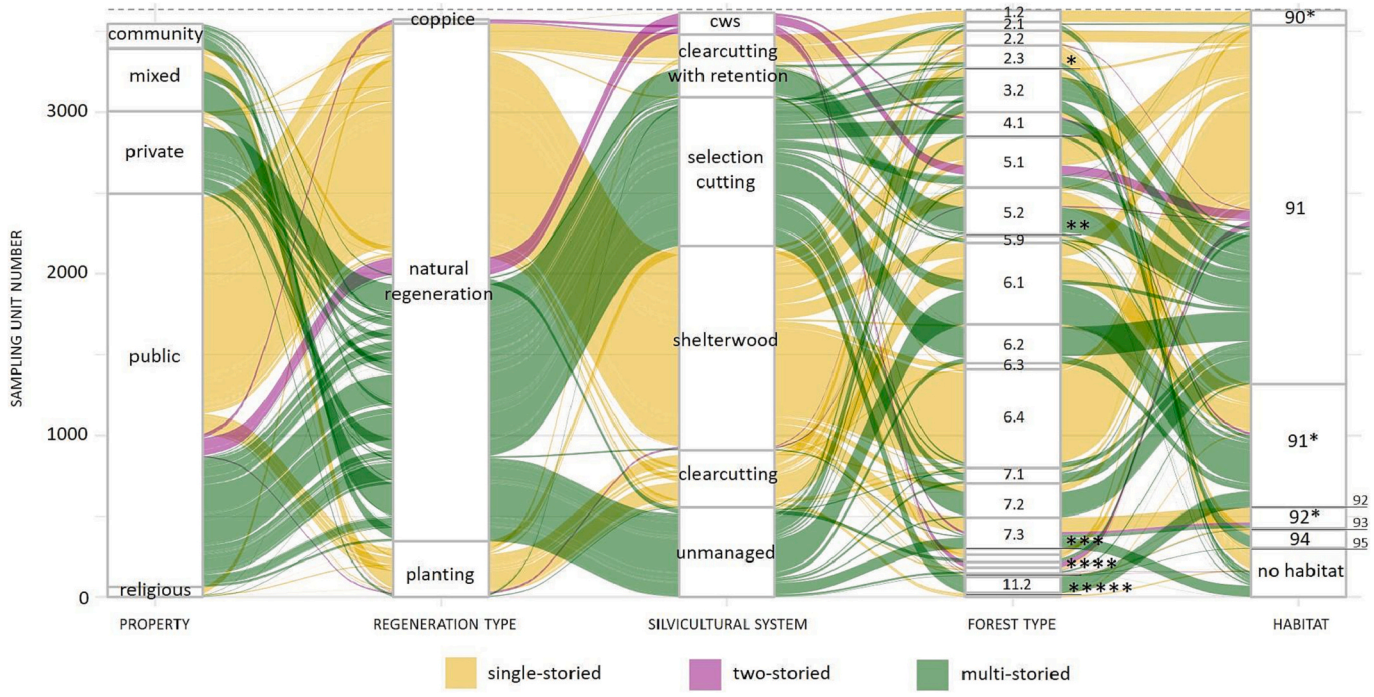


Fig. 3. One-, two-, and multi-storied forest sampling unit distribution across type of ownership, regeneration, silvicultural system (cws: coppice with standards), forest type, and habitat type. Vertical blocks represent clusters of sampling units for which the same condition (e.g., natural regeneration) occurs, with block height depending on the number of sampling units for which that condition occurred across structural types (single-, two- and multi-storied). Flows between the blocks show the combination of values for different structural types (e.g., number of one-storied plots within a public property originated from planting). In the forest type column, left numbers refer to the forest categories as reported in SI 1 and in EEA (2006), while the number after the dot refers to a specific type within that category (please refer to EEA, 2006). Forest types represented by less than 50 sampling units are identified by stars (* 3.1; ** 4.2; *** 7.4, 7.5; **** 8.1, 8.2, 8.7, 8.8, 9.1, 10.1, 11.1; ***** 11.3, 11.4, 12.1, 13.2, 14). In the Habitat column, sampling units are gathered in groups of habitat types divided among those having priority (followed by "*") or not, and referred to the codes: 90: Forests of Boreal Europe, 91: Forests of Temperate Europe, 92: Mediterranean deciduous forests, 93: Mediterranean sclerophyllous forests, 94: temperate mountainous coniferous forests, 95: Mediterranean and Macaronesian mountainous coniferous forests.

considered as biodiversity hotspots (Przepióra and Ciach, 2022), these habitats are nowadays not only rare in European landscapes, but occur in settings that have been profoundly altered by humans, thus characterized by high habitat fragmentation and low ecosystem integrity. For these reasons, floodplain forests should be primarily addressed by biodiversity studies, especially in view of restoration actions (Dufour et al., 2019). On the other hand, the share of sampling units referred to as priority habitat types (27 %) is higher than what is reported in terms of area, i.e., 23 % according to European Commission (2019), showing a great potential of the existing data in the assessment of the conservation status and relation with management of forests of primary conservation concern in Europe.

The distribution of the existing data across silvicultural systems shows a tendency among researchers to perform multi-taxon biodiversity studies in forests that are perceived as less intensively managed, such as those under selection or shelterwood management regimes. Clearcutting is represented mainly in plots related to experimental studies testing novel harvesting practices as this silvicultural system is deemed as strongly threatening forest depending species (Savilaakso et al., 2021). Unmanaged forests have often been sampled as a relevant reference in comparison to managed forests, especially if strategies that are generally perceived as sustainable are applied (Paillet et al., 2010). However, it should be noted that the unmanaged sampling units in the platform may not be associated with old-growth condition since they vary widely in terms of time passed since the last management intervention, i.e., from 20 to more than 100 years, and these differences have to be accounted for when contrasting managed and unmanaged forests within the platform.

The distribution across unmanaged, coppiced and high forests confirms that coppicing systems are relatively understudied, particularly for multi-taxonomic biodiversity. This may be partly related to the perception of these forests as less relevant for biodiversity and related ecosystem services. Nevertheless, some studies suggest the opposite (Hédl et al., 2010) and demonstrated a certain degree of association of species of conservation concern with actively coppiced stands (Kosulic et al., 2016). This uneven distribution may also be related to the progressive reduction of coppiced forests in Europe, which are gradually being actively or passively converted into high forests, or simply abandoned (Burrascano et al., 2017). In general, the lack of multi-taxon biodiversity information from coppices represents a knowledge gap for supporting policy decisions on coppice forest management, which is especially relevant in view of their renewed prominence in climate adaptation policies and forest multifunctionality (Cutini et al., 2021).

4.2. *Research potential and working hypotheses*

Conversely to other data sharing platforms focusing on individual aspects of ecosystems, e.g., vegetation (Bruelheide et al., 2019), forest multi-taxon studies put in place different expertise and data on the three main components of ecosystems: species composition, structure and function. As such, these data collectively have the potential to promote interdisciplinary studies and to unveil the outcomes of different conservation and management policies on the biodiversity of multiple taxonomic groups as mediated by structural stand features, e.g., the diameter distributions of standing trees and lying deadwood.

4.2.1. *Harmonizing methods and schemes*

The joint assessment of existing forest multi-taxon biodiversity data already stimulated a harmonization effort for sampling protocols (Burrascano et al., 2021). Similarly, a harmonized platform may serve as a

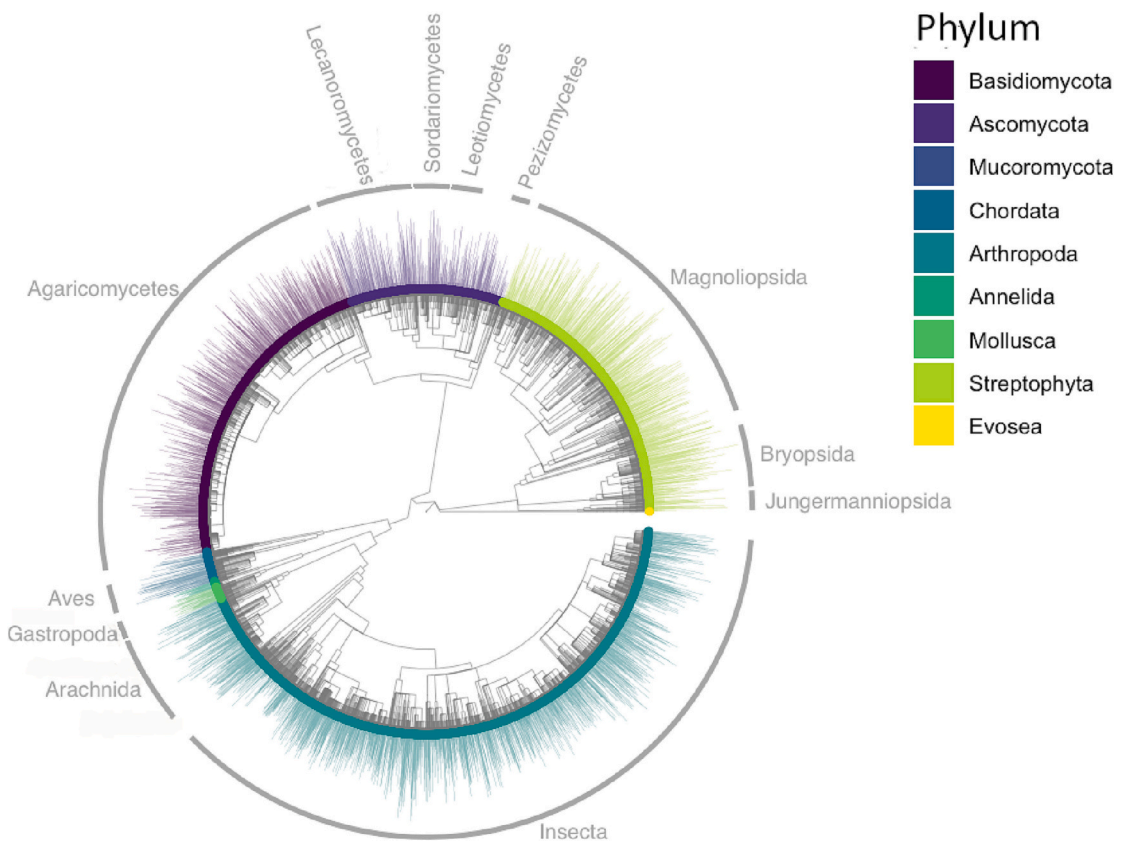


Fig. 4. Phylogenetic tree of the species enclosed in the data platform (7335 out of the 8724 could be included). The colored sectors refer to phyla; external bars show the log-transformed number of records for each species; gray circular sectors show the representation of the classes for which more than 50 species occur.

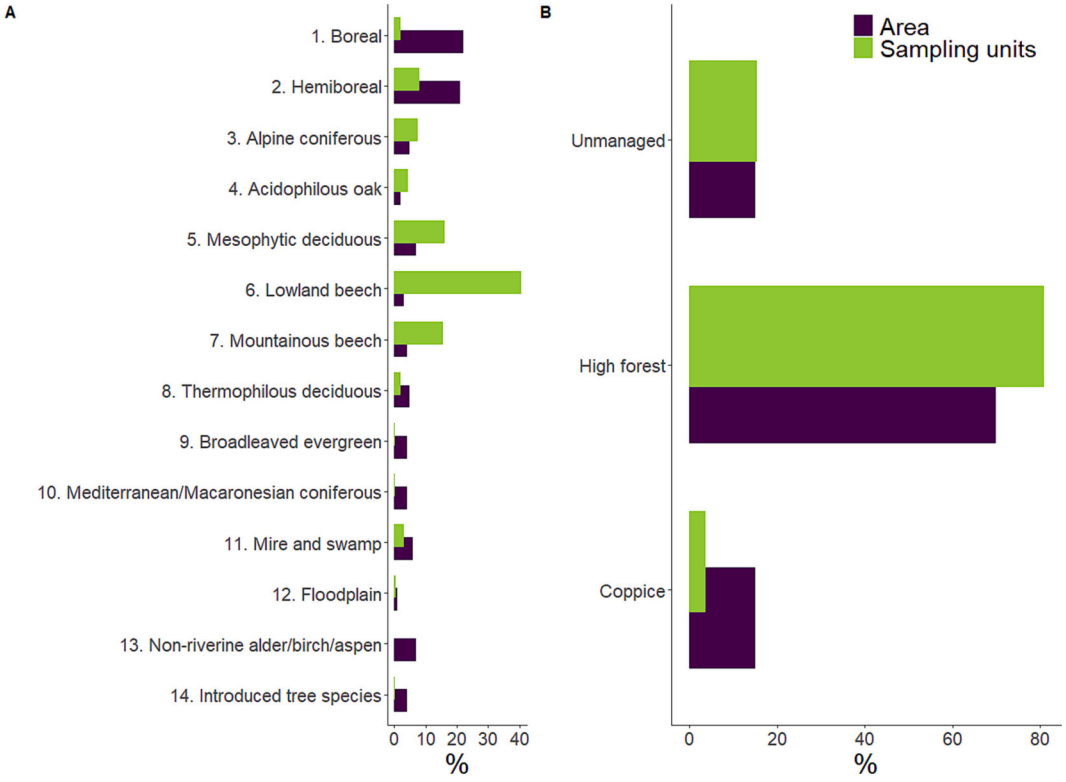


Fig. 5. A: Share of the number of sampling units and of forest area across different forest compositional categories (A) in EU-28 based on Barbati et al. (2014); and across two broad methods of regeneration (coppice and high forest) and the absence of silvicultural intervention (B) based on McGrath et al. (2015) .

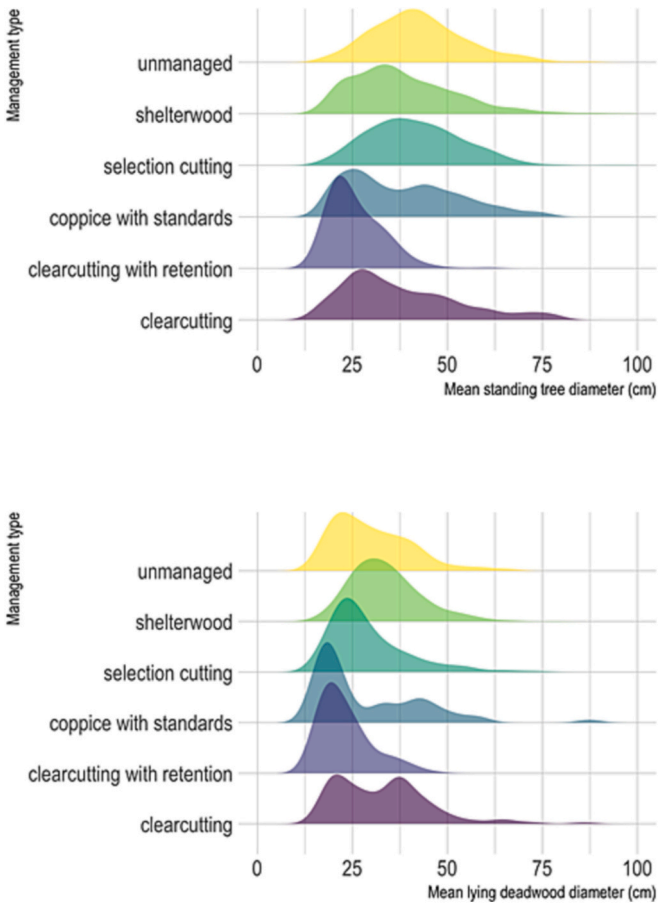


Fig. 6. Distribution of sampling unit's mean diameters for living (Diameter at Breast Height – DBH) and dead standing trees (upper portion) and lying deadwood (lower portion) across different silvicultural systems. Mean diameters were calculated after applying a lower threshold of 15 cm to limit the effect of different sampling protocols within the platform.

pilot dataset to assess the effort needed in terms of number of sampling units and sites (Guerra-Castro et al., 2021) to investigate how European forest species richness and composition changes along management and environmental conditions, respectively included in the platform and associated from external datasets. This will inform integrated European projects that could be able to provide useful information for the newborn FISE platform (Forest Information System of Europe - https://forest.eea.europa.eu/).

Harmonized sampling protocols and designs are relevant in view of the monitoring and conservation status assessment of forest habitat types for the implementation of the EU Habitats Directive. Important assessment criteria include the actual status and the prospects of structures and functions and typical species (Campagnaro et al., 2019). Up to date, the interpretation manual of European habitats as only a limited descriptions of typical species that mainly include vascular plants, also due to the lack of datasets and methodological frameworks for the consideration of additional taxonomic groups. Nevertheless, the need for a multi-taxon approach to habitat types' typical species has already been indicated (Tsiripidis et al., 2018) and this platform steps towards this direction.

4.2.2. Implementing indicators and thresholds of forest management sustainability for biodiversity conservation

The existing knowledge paves the way to directly test biodiversity indicators of SFM and their thresholds, and to overcome the current approach of assessing forest management sustainability through proxies that mostly showed weak correlation with the *indicandum* (Gao et al., 2015). For biodiversity sustainability, these proxies include tree composition, size and age distribution, gap structure, deadwood amount and tree-related microhabitats (Müller and Bütler, 2010; Larrieu et al., 2018). Their indirect indication is intrinsically limited (Barton et al., 2020; Zeller et al., 2022) and would need to be complemented with a direct analysis of several taxonomic groups (Burrascano et al., 2018). Recently, in addition to the usual set of indicators of forest management impact on biodiversity (MCPFE, 1993), 34 bird species were accounted for (Forest Europe, 2020), but still, most taxonomic groups contributing to forest biodiversity remain neglected. This is the case for extremely species rich groups including species of high conservation concern, such as fungi (Halme et al., 2017), and saproxylic beetles (Calix et al., 2018). The broad-scale tree level dendrometric information included in the platform may be linked to environmental factors, i.e., climate and soil, and thus contribute to the calibration of habitat-based indicators of forest ecosystem condition (Jucker et al., 2022).

4.2.3. Forest functioning and resilience

Forest functions depend not only on tree species characteristics, but also on the ecological roles of several species across multiple taxonomic groups. For instance, understorey vegetation and saproxylic organisms play a key role in nutrient cycling (Landuyt et al., 2019; Seibold et al., 2021). To maintain forest functions in the face of major environmental changes, these specific functions have to be accounted for in management plans and forest policies. The recent advances in functional traits measurement and harmonization, and their increasing availability for multiple taxonomic groups (e.g., Bernhardt-Römermann et al., 2018; Moretti et al., 2017) allow to trace back the effects of different management approaches and environmental scenarios on different guilds and taxonomic groups and on their role for ecosystem functioning. Accounting for species interactions, also when studying the effect of environmental or management drivers on ecosystem biodiversity and functioning, is emphasized in recent approaches on joint species distribution modelling that could be applied to the platform data (Ovaskainen and Abrego, 2020).

4.2.4. Integration with remote sensing approaches

The continent-wide information on important components of forest biodiversity that are not directly visible by means of remote sensing devices is highly valuable to test and integrate information acquired through remote sensing techniques, such as Airborne Laser Scanning. For instance, the 3591 points of the platform may serve to discriminate the probability of occurrence of different forest types that currently represents the most detailed information in Europe (Mücher and Hennekens, 2019). The platform information may be used to integrate and improve multi-scale ecosystem assessment by fine-tuning the links between structural diversity measured by means of Airborne Laser Scanning and multi-taxon biodiversity (Moeslund et al., 2019). Furthermore, specific habitat variables that could be derived from Airborne Laser Scanning were recently identified to improve species distribution models (Moudrý et al., 2023), and to model dark diversity (Moeslund et al., 2022), and such advancements would highly benefit from broad-scale harmonized multi-taxon information.

4.3. Conservation implications

The European Union Biodiversity Strategy for 2030 is focused on protected areas and its main objectives are to legally protect a minimum of 30 % of land area, which should be effectively managed and appropriately monitored, and to strictly protect at least a third of such protected areas. In this view, gathering and harmonizing the available information on forest multi-taxon biodiversity can promote the widespread collection of forest biodiversity data through shared approaches and methodologies, with a special emphasis on understudied forest types, which are often also particularly relevant for biodiversity conservation, e.g., floodplain or thermophilous forests.

The availability of widespread forest multi-taxon biodiversity and stand structure information at the continental scale will allow to prioritize forest areas to be protected, or strictly protected, and will set the basis for their appropriate monitoring, in line with the current Biodiversity Strategy.

On the other hand, the European Union Forest Strategy for 2030 is focused on the sustainability of forest management, within and outside protected forests. This would start from the identification of additional indicators, as compared to those assessed by Forest Europe, with thresholds or ranges for SFM concerning forest ecosystem conditions, including biodiversity.

The availability of extensive multi-taxon biodiversity data would allow to define such indicators of management sustainability, as well as their thresholds and ranges, based on their direct links with the diversity of multiple taxonomic groups with different functions in forest ecosystems. This would represent a crucial step forward from the current criteria and indicators whose effectiveness for biodiversity is questionable.

The EU Forest Strategy also stresses how management sustainability indicators, and their thresholds and ranges, should be built on existing work and take into account forest variability, biogeographic regions and forest typology. Our work is perfectly in line with this statement, since we reviewed and valued existing data on forest biodiversity by accounting for different forest habitats, compositional and management categories. Refining indicators of SFM will feed guidelines on closer-to-nature forestry that will be translated into voluntary certification scheme, so that the most biodiversity friendly management practices could benefit from an EU quality label.

Europe has a leading role in the improvement of forest protection and management standards globally. By supporting the objectives of the EU biodiversity and forest strategy, we think that, in the long-term, our work may lead to the improvement of indicator schemes across multiple regions and support an increased sustainability of forest management globally.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110176.

Author contribution

SB, PO, FC, GT, SKR, JHC, TS, FT, YP and ID developed the idea for this manuscript. SB, FC, GT, TC, SKR, TS, LB, EA, RBA and FN collected and harmonized the data. FC, SKR, SB, GT, LB, EA ran the analyses. DM, CP, JN, PG, NR, TL, CB, PO, JHC and FN revised the taxonomic nomenclature and substrate association. All the authors but EA, RBA, DM, CP, NR and FN contributed data. All the authors contributed to the text.

Declaration of competing interest

Neither I nor any co-authors have any conflict of interest related to this manuscript, i.e., we exclude any financial and personal relationships with other people or organizations that could inappropriately influence (bias) their work.

Data availability statement

All the data used in this manuscript are provided in the supplementary material available at this link https://zenodo.org/record/7886698.

An interactive tool for their exploration and filtering, as well as instructions for proposing a project with the data here presented are available at: https://www.bottoms-up.eu/en/participants/contribute/propose-a-project.html. Data may be requested for specific projects as described at this link: https://www.bottoms-up.eu/en/participants/contribute/propose-a-project.html.

Acknowledgements

This review was funded by the EU Framework Programme Horizon 2020 through the COST Association (www.cost.eu): COST Action CA18207: BOTTOMS-UP – Biodiversity Of Temperate forest Taxa Orienting Management Sustainability by Unifying Perspectives. The authors are thankful to all those experts contributing to the data here harmonized and resumed that were not listed as data contributors.

References

Ballabio, C., Panagos, P., Monatanarella, L., 2016. Mapping topsoil physical properties at European scale using the LUCAS database. Geoderma 261, 110–123.

Barbati, A., Marchetti, M., Chirici, G., Corona, P., 2014. European forest types and Forest Europe SFM indicators: tools for monitoring progress on forest biodiversity conservation. For. Ecol. Manag. 321, 145–157.

Barton, P.S., Westgate, M.J., Foster, C.N., Cuddington, K., Hastings, A., O'Loughlin, L.S., Lindenmayer, D.B., 2020. Using ecological niche theory to avoid uninformative biodiversity surrogates. Ecol. Indic. 108, 105692.

Bernhardt-Römermann, M., Poschlod, P., Hentschel, J., 2018. BryForTrait – a life-history trait database of forest bryophytes. J. Veg. Sci. 29, 798–800.

Biurrun, I., Burrascano, S., Dembicz, I., Guarino, R., Kapfer, J., Pielech, R., Dengler, J., 2019. GrassPlot v. 2.00 – first update on the database of multi-scale plant diversity in Palaearctic grasslands. Palaearctic Grasslands 44, 26–47.

Blasi, C., Marchetti, M., Chiavetta, U., Aleffi, M., Audisio, P., Azzella, M.M., Burrascano, S., 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. Plant Biosyst. 144 (1), 160–170. https://doi.org/10.1080/11263500903560538.

Bowd, E., Blanchard, W., McBurney, L., Lindenmayer, D., 2021. Direct and indirect disturbance impacts on forest biodiversity. Ecosphere 12, e03823.

Bruelheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S.M., Chytrý, M., Zverev, A., 2019. sPlot – a new tool for global vegetation analyses. J. Veg. Sci. 30, 161–186.

Brunson, J.C., 2020. Ggalluvial: layered grammar for alluvial plots. J. Open Source Softw. 5, 2017.

Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Blasi, C., 2017. It's a long way to the top: plant species diversity in the transition from managed to old-growth forests. J. Veg. Sci. 29 (1), 98–109.

Burrascano, S., de Andrade, R.B., Paillet, Y., Ódor, P., Antonini, G., Bouget, C., Persiani, A.M., 2018. Congruence across taxa and spatial scales: are we asking too much of species data? Glob. Ecol. Biogeogr. 27 (8), 980–990.

Burrascano, S., Trentanovi, G., Paillet, Y., Heilmann-Clausen, J., Giordani, P., Bagella, S., Ódor, P., 2021. Handbook of field sampling for multi-taxon biodiversity studies in European forests. Ecol. Indic. 132, 108266.

Byriel, D.B., Schmidt, I.K., Justesen, M.J., Pape, T., Hansen, A.K., Riis-Nielsen, T., Kepfer-Rojas, S., 2020. Forest management affects crane fly (Tipuloidea) community structure through changes in edaphic conditions. For. Ecol. Manag. 457, 117756 https://doi.org/10.1016/j.foreco.2019.117756.

Calix, M., Alexander, K.N., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Istrate, P., 2018. European Red List of Saproxylic Beetles. IUCN, Brussels, Belgium. Available at. https://portals.iucn.org/library/node/47296.

Campagnaro, T., Sitzia, T., Bridgewater, P., Evans, D., Ellis, E.C., 2019. Half Earth or whole Earth: what can Natura 2000 teach us? BioScience 69 (2), 117–124.

Chamagne, J., Paine, C.E.T., Schoolmaster, D.R., Stejskal, R., Volařík, D., Šebesta, J., Matula, R., 2016. Do the rich get richer? Varying effects of tree species identity and diversity on the richness of understory taxa. Ecology 97, 2364–2373. https://doi.org/10.1002/ecy.1479.

Chamberlain, S.A., Szöcs, E., 2013. Taxize: taxonomic search and retrieval in R. F1000Research 2, 191.

Cocquelet, A., Mårell, A., Bonthoux, S., Baltzinger, C., Archaux, F., 2019. Direct and indirect effects of ungulates on forest birds' nesting failure? An experimental test with artificial nests. For. Ecol. Manag. 437, 148–155. https://doi.org/10.1016/j.foreco.2019.01.025.

Cutini, A., Ferretti, M., Bertini, G., Brunialti, G., Bagella, S., Chianucci, F., Calderisi, M., 2021. Testing an expanded set of sustainable forest management indicators in Mediterranean coppice area. Ecol. Indic. 130, 108040.

D'Andrea, E., Ferretti, F., Zapponi, L., 2016. Indicators of sustainable forest management: application and assessment. Ann. Silvicultural Res. 40, 31–103. https://doi.org/10.12899/asr-1214.

de Groote, S.R.E., van Schrojenstein Lantman, I.M., Sercu, B.K., Dekeukeleire, D., Boonyarittichaikij, R., Smith, H.K., Lens, L., 2017. Tree species identity outweighs the effects of tree species diversity and forest fragmentation on understorey diversity and composition. Plant Ecol. Evol. 150 (3), 229–239. https://doi.org/10.5091/plecevo.2017.1331.

De Smedt, P., Baeten, L., Proesmans, W., Van de Poel, S., Van Keer, J., Giffard, B., Verheyen, K., 2019. Strength of forest edge effects on litter-dwelling macroarthropods across Europe is influenced by forest age and edge properties. Divers. Distrib. 25, 963–974.

Doerfler, I., Müller, J., Gossner, M.M., Hofner, B., Weisser, W.W., 2017. Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. For. Ecol. Manag. 400, 607–620. https://doi.org/10.1016/j.foreco.2017.06.013.

Drost, H.G., Gabel, A., Jiu, J., Quint, M., Grosse, I., 2018. myTAI: evolutionary transcriptomics with R. Bioinformatics 9, 1589–1590.
Dufour, S., Rodríguez-González, P.M., Laslier, M., 2019. Tracing the scientific trajectory of riparian vegetation studies: main topics, approaches and needs in a globally changing world. Sci. Total Environ. 653, 1168–1185.
EEA, 2006. European Forest Types. Categories and Types for Sustainable Forest Management, Reporting and Policy. Technical Report 09/2006. Copenhagen.
Elek, Z., Kovács, B., Aszalós, R., Boros, G., Samu, F., Tinya, F., Ódor, P., 2018. Taxon-specific responses to different forestry treatments in a temperate forest. Sci. Rep. 8, 16990. https://doi.org/10.1038/s41598-018-35159-z.
European Commission, 2019. Natura 2000 and forests. Part I-II, European Commission Technical Report 2015-088. https://op.europa.eu/en/publication-detail/-/publication/855ca711-8450-11e5-b8b7-01aa75ed71a1/language-en.
FAO, 2020. Global Forest Resources Assessment 2020: Main Report. Rome.
Felipe-Lucia, M.R., Soliveres, S., Penone, C., Fischer, M., Ammer, C., Boch, S., Allan, E., 2020. Land-use intensity alters networks between biodiversity, ecosystem functions, and services. Proc. Natl. Acad. Sci. 117, 28140–28149.
Forest Europe, 2020. State of Europe's Forests 2020. Ministerial conference on the protection of forests in Europe. Liaison Unit Bratislava. https://foresteurope.org/wp-content/uploads/2016/08/SoEF_2020.pdf.
Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol. Indic. 57, 420–434. https://doi.org/10.1016/j.ecolind.2015.05.028.
Götmark, F., 2013. Habitat management alternatives for conservation forests in the temperate zone: review, synthesis, and implications. For. Ecol. Manag. 306, 292–307.
Guerra-Castro, E.J., Cajas, J.C., Simões, N., Cruz-Motta, J.J., Mascaró, M., 2021. SSP: an R package to estimate sampling effort in studies of ecological communities. Ecography 44, 561–573.
Haeler, E., Bergamini, A., Blaser, S., Ginzler, C., Hindenlang, K., Keller, C., Lachat, T., 2021. Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. Landsc. Ecol. 36 (1), 89–104. https://doi.org/10.1007/s10980-020-01115-4.
Halme, P., Holec, J., Heilmann-Clausen, J., 2017. The history and future of fungi as biodiversity surrogates in forests. Fungal Ecol. 27, 193–201.
Hédl, R., Kopecky, M., Komarek, J., 2010. Half a century of succession in a temperate Oakwood: from species-rich community to Mesic forest. Divers. Distrib. 16, 267–276.
Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. J. Appl. Ecol. 55, 2756–2766.
Hofmeister, J., Hošek, J., Brabec, M., Hédl, R., Modrý, M., 2013. Strong influence of long-distance edge effect on herb-layer vegetation in forest fragments in an agricultural landscape. Perspect. Plant Ecol. Evol. Syst. 15 (6), 293–303. https://doi.org/10.1016/j.ppees.2013.08.004.
Hofmeister, J., Hošek, J., Brabec, M., Hermy, M., Dvořák, D., Fellner, R., Kadlec, T., 2019. Shared affinity of various forest-dwelling taxa point to the continuity of temperate forests. Ecol. Indic. 101, 904–912. https://doi.org/10.1016/j.ecolind.2019.01.018.
Horváth, C.S.V., Kovács, B., Tinya, F., Locatelli, J.S., Németh, C.S., Crecco, L., Illés, G., Csépányi, P., Ódor, P., 2023. A matter of size and shape: microclimatic changes induced by experimental gap openings in a sessile oak–hornbeam forest. Sci. Total Environ. 873, 162302.
Janssen, P., Fuhr, M., Bouget, C., 2018. Small variations in climate and soil conditions may have greater influence on multitaxon species occurrences than past and present human activities in temperate mountain forests. Divers. Distrib. 24 (5), 579–592. https://doi.org/10.1111/ddi.12705.
Jucker, T., Fischer, F.J., Chave, J., Coomes, D.A., Caspersen, J., Ali, A., Zavala, M.A., 2022. Tallo: a global tree allometry and crown architecture database. Glob. Chang. Biol. 28, 5254–5268.
Kameniar, O., Baláž, M., Svitok, M., Reif, J., Mikoláš, M., Pettit, J.L., Svoboda, M., 2021. Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition. For. Ecol. Manag. 481, 118647 https://doi.org/10.1016/j.foreco.2020.118647.
Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4 (1), 1–20.
Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Chang. Biol. 26, 119–188. https://doi.org/10.1111/gcb.14904.
Kempeneers, P., Sedano, F., Seebach, L., Strobl, P., San-Miguel-Ayanz, J., 2011. Data fusion of different spatial resolution remote sensing images applied to forest-type mapping. IEEE Trans. Geosci. Remote Sens. 49, 4977–4986. https://doi.org/10.1109/TGRS.2011.2158548.
Kindt, R., 2020. WorldFlora: an R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. Appl. Plant Sci. 8, e11388.
Korboulewsky, N., Heiniger, C., De Danieli, S., Brun, J.J., 2021. Effect of tree mixture on Collembola diversity and community structure in temperate broadleaf and coniferous forests. For. Ecol. Manag. 482, 118876 https://doi.org/10.1016/j.foreco.2020.118876.
Kosulic, O., Michalko, R., Hula, V., 2016. Impact of canopy openness on spider communities: implications for conservation management of formerly coppiced oak forests. PLoS One 11, e0148585.
Kozák, D., Svitok, M., Wiezik, M., Mikoláš, M., Thorn, S., Buechling, A., Svoboda, M., 2021. Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests. Ecosystems 24 (1), 37–55.
Kozák, D., Svitok, M., Zemlerová, V., Mikoláš, M., Lachat, T., Larrieu, L., Paillet, Y., Buechling, A., Bače, R., Keeton, W.S., Vítková, L., Begovič, K., Čada, V., Dušátko, M., Ferenčík, M., Frankovič, M., Gloor, R., Hofmeister, J., Janda, P., Kameniar, O., Knír, T., Majdanová, L., Mejstřík, M., Pavlin, J., Ralhan, D., Rodrigo, R., Roibu, C.-C., Synek, M., Vostarek, O., Svoboda, M., 2023. Importance of conserving large and old trees to continuity of tree-related microhabitats. Conserv. Biol. 37, e14066 https://doi.org/10.1111/cobi.14066.
Landuyt, D., De Lombaerde, E., Perring, M.P., Hertzog, L.R., Ampoorter, E., Maes, S.L., Verheyen, K., 2019. The functional role of temperate forest understorey vegetation in a changing world. Glob. Chang. Biol. 25 (11), 3625–3641.
Langbehn, T., Hofmeister, J., Svitok, M., Mikoláš, M., Matula, R., Halda, J., Svoboda, M., 2021. The impact of natural disturbance dynamics on lichen diversity and composition in primary mountain spruce forests. J. Veg. Sci. 32 (5), e13087.
Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Vandekerkhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. Ecol. Indic. 84, 194–207.
Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Heilmann-Clausen, J., 2019. Biodiversity response to forest structure and management: comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. For. Ecol. Manag. 432, 707–717. https://doi.org/10.1016/j.foreco.2018.09.057.
Matthews, J. (Ed.), 1989. Silvicultural Systems. Oxford Science Publications, Oxford.
Mazziotta, A., Heilmann-Clausen, J., Bruun, H.H., Fritz, Ö., Aude, E., Tøttrup, A.P., 2016. Dataset on species incidence, species richness and forest characteristics in a Danish protected area. Data Brief 9, 895–897.
McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13 (4), 603–606.
McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., Valade, A., 2015. Reconstructing European forest management from 1600 to 2010. Biogeosciences 12, 4291–4316.
MCPFE, 1993. Proceedings of the Ministerial Conference on the Protection of Forests in Europe, Helsinki, Finland, 16–17 June 1993; Documents. Helsinki, Finland, MCPFE Liaison Unit Helsinki, p. 1993.
Moeslund, J.E., Zlinszky, A., Ejrnæs, R., Brunbjerg, A.K., Bøcher, P.K., Svenning, J.C., Normand, S., 2019. Light detection and ranging explains diversity of plants, fungi, lichens, and bryophytes across multiple habitats and large geographic extent. Ecol. Appl. 29, e01907.
Moeslund, J.E., Clausen, K.K., Dalby, L., Fløjgaard, C., Pärtel, M., Pfeifer, N., Hollaus, M., Brunbjerg, A.K., 2022. Using airborne lidar to characterize North European terrestrial high-dark-diversity habitats. Remote Sens. Ecol. Conserv. 9, 354–369. https://doi.org/10.1002/rse2.314.
Möller, A., 1922. Der Dauerwaldgedanke. Sein Sinn und seine Bedeutung. J. Springer, Berlin.
Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J., Berg, M.P., 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Funct. Ecol. 31, 558–567.
Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. J. Appl. Ecol. 54, 12–27.
Moudrý, V., Cord, A.F., Gábor, L., Laurin, G.V., Barták, V., Gdulová, K., Malavasi, M., Rocchini, D., Stereńczak, K., Prošek, J., Klápště, P., Wild, J., 2023. Vegetation structure derived from airborne laser scanning to assess species distribution and habitat suitability: the way forward. Divers. Distrib. 29, 39–50.
Mücher, C.A., Hennekens, S.M., 2019. Processing European Habitat Probability Maps for EUNIS Forest (T), Heathland, Scrub and Tundra (S) and Grassland (R) Habitat Types Based on vegetation relevés, Environmental Data and Copernicus Land Cover: ETC/BD Technical Paper 2/2019.
Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur. J. For. Res. 29, 981–992.
Murray, B.D., Holland, J.D., Summerville, K.S., Dunning Jr., J.B., Saunders, M.R., Jenkins, M.A., 2017. Functional diversity response to hardwood forest management varies across taxa and spatial scales. Ecol. Appl. 27, 1064–1081.
Oettel, J., Lapin, K., 2021. Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. Ecol. Indic. 122, 107275 https://doi.org/10.1016/j.ecolind.2020.107275.
Ovaskainen, O., Abrego, N., 2020. Joint species distribution modelling: with applications in R. In: Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge.
Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24, 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x.
Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. For. Ecol. Manag. 346, 51–64. https://doi.org/10.1016/j.foreco.2015.02.037.
Paradis, E., Schliep, K., 2019. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528.

Przepióra, F., Ciach, M., 2022. Tree microhabitats in natural temperate riparian forests: an ultra-rich biological complex in a globally vanishing habitat. Sci. Total Environ. 803, 149881.

R Core Team, 2021. R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria (URL). https://www.R-project.org/.

Sabatini, F.M., Burrascano, S., Azzella, M.M., Barbati, A., de Paulis, S., di Santo, D., Blasi, C., 2016. One taxon does not fit all: herb-layer diversity and stand structural complexity are weak predictors of biodiversity in *Fagus sylvatica* forests. Ecol. Indic. 69, 128–137. https://doi.org/10.1016/j.ecolind.2016.04.012.

Sasaki, N., Putz, F.E., 2009. Critical need for new definitions of "forest" and "forest degradation" in global climate change agreements. Conserv. Lett. 2, 226–232.

Savilaakso, S., Johansson, A., Häkkilä, M., Uusitalo, A., Sandgren, T., Mönkkönen, M., Puttonen, P., 2021. What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. Environ. Evid. 10, 1.

Schall, P., Schulze, E.D., Fischer, M., Ayasse, M., Ammer, C., 2018. Relations between forest management, stand structure and productivity across different types of Central European forests. Basic Appl. Ecol. 32, 39–52. https://doi.org/10.1016/j.baae.2018.02.007.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R.S., Birkemoe, T., Boros, G., Brandl, R., Brustel, H., Burton, P.J., Cakpo-Tossou, Y.T., Castro, J., Cateau, E., Cobb, T.P., Farwig, N., Fernández, R.D., Firn, J., Gan, K.S., González, G., Gossner, M.M., Habel, J.C., Hébert, C., Heibl, C., Heikkala, O., Hemp, A., Hemp, C., Hjältén, J., Hotes, S., Kouki, J., Lachat, T., Liu, J., Liu, Y., Luo, Y.-H., Macandog, D.M., Martina, P.E., Mukul, S.A., Nachin, B., Nisbet, K., O'Halloran, J., Oxbrough, A., Pandey, J.N., Pavlíček, T., Pawson, S.M., Rakotondranary, J.S., Ramanamanjato, J.-B., Rossi, L., Schmidl, J., Schulze, M., Seaton, S., Stone, M.J., Stork, N.E., Suran, B., Sverdrup-Thygeson, A., Thorn, S., Thyagarajan, G., Wardlaw, T.J., Weisser, W.W., Yoon, S., Zhang, N., Müller, J., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81.

Sitzia, T., Campagnaro, T., Dainese, M., Cassol, M., Dal Cortivo, M., Gatti, E., Nascimbene, J., 2017. Contrasting multi-taxa diversity patterns between abandoned and non-intensively managed forests in the southern dolomites. IFor.-Biogeosci. For. 10 (5), 845–850. https://doi.org/10.3832/ifor2181-010.

Stokely, T.D., Kormann, U.G., Verschuyl, J., Kroll, A.J., Frey, D.W., Harris, S.H., Mainwaring, D., Maguire, D., Hatten, J.A., Rivers, J.W., Fitzgerald, S., Betts, M.G., 2022. Experimental evaluation of herbicide use on biodiversity, ecosystem services and timber production trade-offs in forest plantations. J. Appl. Ecol. 59, 52–66.

Storch, I., Penner, J., Asbeck, T., Basile, M., Bauhus, J., Braunisch, V., Yousefpour, R., 2020. Evaluating the effectiveness of retention forestry to enhance biodiversity in production forests of Central Europe using an interdisciplinary, multi-scale approach. Ecol. Evol. 10 (3), 1489–1509. https://doi.org/10.1002/ece3.6003.

Tinya, F., Kovács, B., Bidló, A., Dima, B., Király, I., Kutszegi, G., Ódor, P., 2021. Environmental drivers of forest biodiversity in temperate mixed forests – a multi-taxon approach. Sci. Total Environ. 795, 148720 https://doi.org/10.1016/j.scitotenv.2021.148720.

Tomppo, E., Gschwantner, T., Lawrence, M., McRoberts, R.E., 2010. National Forest Inventories: Pathways for Common Reporting. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-90-481-3233-1_1.

Trentanovi, G., Campagnaro T., Sitzia T., Chianucci F., *et al.* Submitted. Words apart: standardizing forestry terms and definitions across European biodiversity studies. Curr. For. Rep.

Tsiripidis, I., Xystrakis, F., Kallimanis, A., Panitsa, M., Dimopoulos, P., 2018. A bottom–up approach for the conservation status assessment of structure and functions of habitat types. Rend. Lincei. Sci. Fisiche Nat. 29, 267–282.

Ujházy, K., Ujházyová, M., Bučinová, K., Čiliak, M., Glejdura, S., Mihál, I., 2018. Response of fungal and plant communities to management-induced overstorey changes in montane forests of the Western Carpathians. Eur. J. For. Res. 391, 96–105.

UN General Assembly, 2015. Transforming our world: the 2030 agenda for sustainable development, 21 October 2015, A/RES/70/1. available at: https://www.refworld.org/docid/57b6e3e44.html [accessed 14 July 2022].

van Buuren, S., Groothuis-Oudshoorn, K., 2011. Mice: multivariate imputation by chained equations in R. J. Stat. Softw. 45 (3), 1–67. https://doi.org/10.18637/jss.v045.i03.

Vandekerkhove, K., Thomaes, A., Crèvecoeur, L., de Keersmaeker, L., Leyman, A., Köhler, F., 2016. Saproxylic beetles in non-intervention and coppice-with-standards restoration management in Meerdaal forest (Belgium): an exploratory analysis. IForest 9 (4), 536–545. https://doi.org/10.3832/ifor1841-009.

Yu, G., Smith, D., Zhu, H., Guan, Y., Lam, T.T., 2017. ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. Methods Ecol. Evol. 8, 28–36.

Zeller, L., Baumann, C., Gonin, P., Heidrich, L., Keye, C., Konrad, F., Ammer, C., 2022. Index of biodiversity potential (IBP) versus direct species monitoring in temperate forests. Ecol. Indic. 136, 108692.

Chapter 2. Do European forest carbon and biodiversity policies have a win-win potential?

Do European forest carbon and biodiversity policies have a win-win potential?

Lorenzo Balducci*[1], Edoardo Alterio [2], Christian Ammer [3], Frédéric Archaux [4], Steffen Boch [5], Christophe Bouget [4], Gediminas Brazaitis [6], Francesco Chianucci [7], Andrea Cutini [7], Pallieter De Smedt [8], Inken Doerfler [9], Daniel Dvořák [10], Markus Fischer [11], Paolo Giordani [12], Marion Gosselin [4], Elena Haeler [13], Jacob Heilmann-Clausen [14], Eva Holá [15], Jeňýk Hofmeister [16], Jan Hošek [17], Philippe Janssen [18], Kirsten Jung [19], Sebastian Kepfer-Rojas [20], Nathalie Korboulewsky [4], Daniel Kozák [16], Tomáš Kuras [21], Thibault Lachat [22], Jiří Malíček [23], Anders Mårell [4], Martin Mikoláš [24], Jörg Müller [25], Francesca Napoleone [1] , Björn Nordén [26], Péter Ódor [27], Yoan Paillet [18], Zdeněk Palice [23], Peter Schall [3], Tommaso Sitzia [2], Kastytis Šimkevičius [6] , Miroslav Svoboda [24], Aleš Tenčík [17] , Flóra Tinya [27], Giovanni Trentanovi [28], Mariana Ujhazyova [29], Kris Vandekerkhove [30], Michael Wohlwend [31], Wolfgang W. Weisser [32], Sabina Burrascano [1]

[1] Sapienza University of Rome, 00185, Rome, Italy

[2] Department of Land, Environment, Agriculture and Forestry, Università degli Studi di Padova, 35020 Legnaro, PD, Italy

[3] University of Göttingen, Silviculture and Forest Ecology of the Temperate Zones, Büsgenweg 1, 37077 Göttingen, Germany

[4] INRAE, UR EFNO, Nogent sur Vernisson, France

[5] WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland

[6] Department of Forest Science, Ariculture Academy, Vytautas Magnus University, 53361 Kaunas dist., Lithuania

[7] Council for Agricultural Research and Economics (CREA), Research Centre for Forestry and Wood, V.le Santa Margherita 80, I-52100 Arezzo (AR), Italy

[8] Forest & Nature Lab, Department of Environment, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode (Melle), Belgium

[9] Institute of Biology and Environmental Science, Vegetation Science & Nature Conservation, University of Oldenburg, Ammerlaender Heerstraße 114–118, 26129 Oldenburg, Germany

[10] Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 267/2, 611 37 Brno, Czechia

[11] University of Bern, Institute of Plant Sciences, Altenbergrain 21, 3013 Bern, Switzerland

[12] DIFAR, University of Genova, 16148 Genova, Italy

[13] Austrian Research Centre for Forests (BFW), Seckendorff-Gudent-Weg 8, 1130 Vienna, Austria

[14] University of Copenhagen, Globe institute, Center for Macroecology, Evolution and Climate, Universitetsparken 15, DK-2100 Copenhagen, Denmark

[15] Department of Botany, Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czechia

[16] Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Czechia

[17] Ecological Services, Tichá 784/4, 268 01 Hořovice, Czechia

[18] Univ. Grenoble Alpes, INRAE, Lessem, 38402 Saint Martin d'Heres, France

[19] University of Ulm, Evolutionary Ecology and Conservation Genomics, Albert-Einstein Allee 11, 89069 Ulm, Germany

[20] Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark

[21] Department of Ecology and Environmental Sciences, Faculty of Sciences, Palacký University Olomouc, Šlechtitelů 241/27, 783 71 Olomouc - Holice, Czechia

[22] Bern University of Applied Sciences, School of Agricultural, Forest and Food Sciences HAFL, 3052 Zollikofen, Switzerland

[23] Institute of Botany of the Czech Academy of Sciences, Zámek 1, 252 43 Průhonice, Czech Republic

[24] Czech University of Life Sciences in Prague, 16500 Prague, Czechia

[25] Bavarian Forest Nationalpark, Freyunger Str. 2, 94481 Grafenau, Germany; University of Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany

[26] Norwegian Institute for Nature Research NINA, Sognsveien 68, 0855 Oslo, Norway

[27] Institute of Ecology and Botany, HUN-REN Centre for Ecological Research

[28] Institute of Research on Terrestrial Ecosystems (IRET) of the National Research Council (CNR)

[29] Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, 96001 Zvolen, Slovakia

[30] INBO-Research Institute for Nature and Forests, 9500 Geraardsbergen, Belgium

[31] Albert-Ludwigs-University Freiburg, 79085 Freiburg, Germany

[32] Technical University of Munich, Terrestrial Ecology Research Group, Department of Life Science Systems, School of Life Sciences, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

* Corresponding author

E-mail: lorenzo.balducci@uniroma1.it

Abstract:

It is still unclear whether it is possible to jointly pursue climate change mitigation and biodiversity conservation in timber-managed forests. This study focuses on European forests to i) define the importance of aboveground carbon stocks in determining species richness of six taxonomic groups; ii) assess the relationship between species richness of these groups and stocks; iii) discuss the potential to jointly enhance carbon and biodiversity and implications for forest policies. We used a Europe-wide dataset of forest multi-taxon diversity and stand structure. We found a positive carbon/diversity relationship for several groups, which, however, mainly depends on deadwood pools.

Forest policies should consider the complex relationship between different carbon pools and taxonomic groups. Prioritizing the increase of living aboveground carbon alone does not necessarily lead to the conservation of biodiversity for multiple groups. Sustainable forest management should acknowledge that deadwood carbon instead may translate into positive outcomes for biodiversity conservation.

Keywords: biodiversity, carbon stocks, forests, Europe, climate change, forest management

1. Introduction

For several centuries, European forests have been subject to human-driven disturbances, which shaped forest spatial distribution, structure, and composition. Across history, one of the primary objectives of forest management has been timber production, which has exerted a profound influence on forest ecosystems. While 24% of European forests are currently protected for biodiversity conservation, only a small proportion (about 2%) is undisturbed by humans [1] and/or considered as primary [2,3].

Several policies in force recognize the urge to simultaneously satisfy several goals, among which biodiversity conservation (i.e., European Biodiversity Strategy for 2030 [4]) and climate change mitigation are often prioritized (i.e., European Forest Strategy for 2030 [5]). Still, the extent to which these goals may be pursued at the same time is largely unknown; and trade-offs are likely.

One of the most important functions currently expected from forests is climate change mitigation. Between 2001 and 2019, global forests' ability to store carbon resulted in a net sink of about 7.6 Gt of CO_2 per year, with a decreasing trend. The majority of the global net sink (68%) was in temperate (47%) and boreal (21%) forests [6].

In European forests, the carbon stock associated with living biomass keeps increasing, i.e., from 8 to almost 12 Mt from 1990 to 2020 [1]. Yet, evidence suggests a carbon sink saturation [1,7], and further data and analyses are needed to account for other carbon pools.

The general goal of reducing at least 55% of greenhouse gas emissions by 2030 requires a wide range of measures, some of which are directly affecting forest ecosystems by increasing or reducing mainly their aboveground carbon pools. One of the main pressures on European forests' carbon pools is timber production which, in particular, may initiate processes that store carbon outside the forest ecosystem. When timber is harvested and directed towards

wood-based products, it provides a means of capturing and storing carbon. However, it is important to highlight how only long-lasting wood products are effective in this regard. These products ensure that the sequestered carbon remains out of the atmospheric cycle for extended periods, thereby contributing to achieving climate neutrality by substituting fossil-based materials [8]. Overall, harvested wood products represent an active net carbon sink of around -40 MtCO2e/year in the European Union [9].

Regardless of the fate of woody biomass, moving carbon stocks from forest ecosystems to the technosphere [10], may hamper its support to another crucial forest function, i.e., the support to forest biodiversity. Forests host about three-quarters of the global terrestrial plant, fungi and animal species diversity, and are globally considered biodiversity hotspots [11].

European forests are considered key habitats for biodiversity and about 30% of forest area is referred to as a habitat of conservation value in the EU. Accordingly, biodiversity conservation is among the priorities of the European Forest Strategy [5]. While forest area is increasing in Europe, about 80% of forest habitat assessments report a decrease in habitat conservation status, with about 20% of the species related to forest ecosystems having a declining conservation status, or threatened with extinction [1,12]. The taxonomic groups with the highest proportions of threatened species are bryophytes with 22% [13], saproxylic beetles with 18% [14] and birds with 13% [15].

The need to improve the condition of forest habitats and species is intrinsically associated with sustainable forest management practices that are expected to support biodiversity conservation, while sustaining the ecological functions and services that forests provide, such as carbon sequestration and climate regulation [12].

Notwithstanding the relevance of both climate mitigation and biodiversity conservation in European forests, only few studies have explicitly tested the relationship between forest biodiversity and carbon stock [16–18] or related functions [17].

Indeed, the ecological relationship between carbon stocks and biodiversity may include different direct and indirect mechanisms which are hard to disentangle. Forest carbon pools represent a substrate [19], a habitat [20] and an essential resource for a multitude of taxonomic groups, and determine forest microclimate conditions that may have differential effects on different species and taxonomic groups [21–24].

The expected relationship between carbon stock and species diversity is strictly related to the carbon pool of interest. On the one hand, the amount of carbon stored in living trees may be associated with species and taxonomic groups related to long local ecological continuity and old-growth conditions [25,26] dependent on woody substrates, i.e., epiphytic lichens and bryophytes. Not all species groups, however, profit from high carbon stocks: trade-offs could emerge for those taxonomic groups primarily composed of species linked to light resources, e.g., vascular plants [27,28].

On the other hand, the amount of lying and standing deadwood, along with the carbon it sequesters, plays a crucial role in sustaining species that are intimately associated with decaying wood, including saproxylic beetles and wood-decaying fungi [1,29,30], by providing microhabitats and resources while contributing to soil development and nutrient cycling [31]. Deadwood effects on biodiversity, however, depend on its origin and decay stage, along with other parameters. Standing deadwood, e.g, snags, and lying deadwood provide different kinds of habitats for birds, bats, insects and in general multiple taxonomic groups involved in the detritus food web [32] that use it for nesting, shelter, and foraging [20]. Overall, the impact of carbon stock on biodiversity varies greatly depending on the carbon pool and the taxonomic group in question.

In-depth knowledge of the trade-offs between biodiversity conservation and climate change mitigation in European forests is urgently needed. Targeting only one of these challenges may not only hamper the achievement of the other one, but also limit the achievement of the

primary target due to the tight relationships that exist between the two [10]. Management strategies focused on carbon sequestration could interfere with biodiversity conservation targets by promoting homogeneous and fast growing stands of both exotic and native trees, which have high carbon sequestration rates [33]. This is already happening across several European countries, and the limited potential of these stands for supporting biological diversity was widely assessed [34,35]. In non-native tree species (e.g., *Eucalyptus*) plantations, the species richness of herbs, birds and lichens can be lower than in native forests, with a composition shift towards non-forest communities [36,37]. Even in native species (e.g., *Picea abies)* plantations understorey vegetation is scarce and species poor, and the habitat conditions for epiphytic lichens and bird species are unfavourable [35]. This is particularly relevant since one the most important objectives of the 2030 EU Forest Strategy is to plant at least 3 billion additional trees by 2030 [5]. The homogeneous structure and composition of these forests may also jeopardize their carbon storage role since they may display a less stable productivity and higher disturbance rates [38]. Therefore, especially if poorly executed, these afforestation efforts will have negative effects on both biodiversity conservation and carbon emission mitigation targets, given few exceptions [10].

Despite the recent awareness on the importance of forests for jointly addressing biodiversity conservation and climate change mitigation, current forest policies only partially incorporate this link. The 2015 Paris Agreement recognizes how action addressed to climate change should ensure ecosystem integrity. The REDD+ initiative includes only mild measures for biodiversity into the plans for reducing emissions from deforestation and forest degradation. Overall, policies with a synergistic approach to both these environmental crises are yet to come, even if the EU Forest Strategy for 2030 ambitiously aims at contributing to both biodiversity and climate goals.

Here we test the possibility of forests across Europe to simultaneously host high amounts of

carbon and high levels of biodiversity for multiple taxonomic groups which could be directly or indirectly related to carbon stocks (birds, epiphytic and epixylic bryophytes and lichens, wood decaying fungi, saproxylic beetles and vascular plants) with the ultimate goal of supporting forest policies and management strategies that contribute to the mitigation of these environmental crises.

Our specific aims are to i) define the relative importance of different aboveground carbon stocks in determining species richness of six taxonomic groups in European forests; ii) assess the relationship between the species richness of these groups and carbon stocks; iii) discuss the potential to enhance carbon stocks and biodiversity together and the related implications for forest policy objectives.

We used the novel European multi-taxonomic database from the "Bottoms-Up" platform [39] and performed Boosted Regression Trees using the standardized species richness of six taxonomic groups, i.e., vascular plants, epiphytic and epixylic bryophytes and lichens, wood-inhabiting fungi, saproxylic beetles, and birds, and the carbon stocks in living aboveground biomass, standing and lying deadwood, also accounting for potential confounding effects related to the dataset or the forest category.

Given the different role that each carbon pool has in relation to different components of forest biodiversity [1,40], we expect differential responses depending on the taxonomic group and the carbon pool considered. Conversely, we hypothesize that different taxonomic groups may respond differently to the level of carbon stored in a forest, and that different carbon pools may be linked to different outcomes for biodiversity.

2. Results

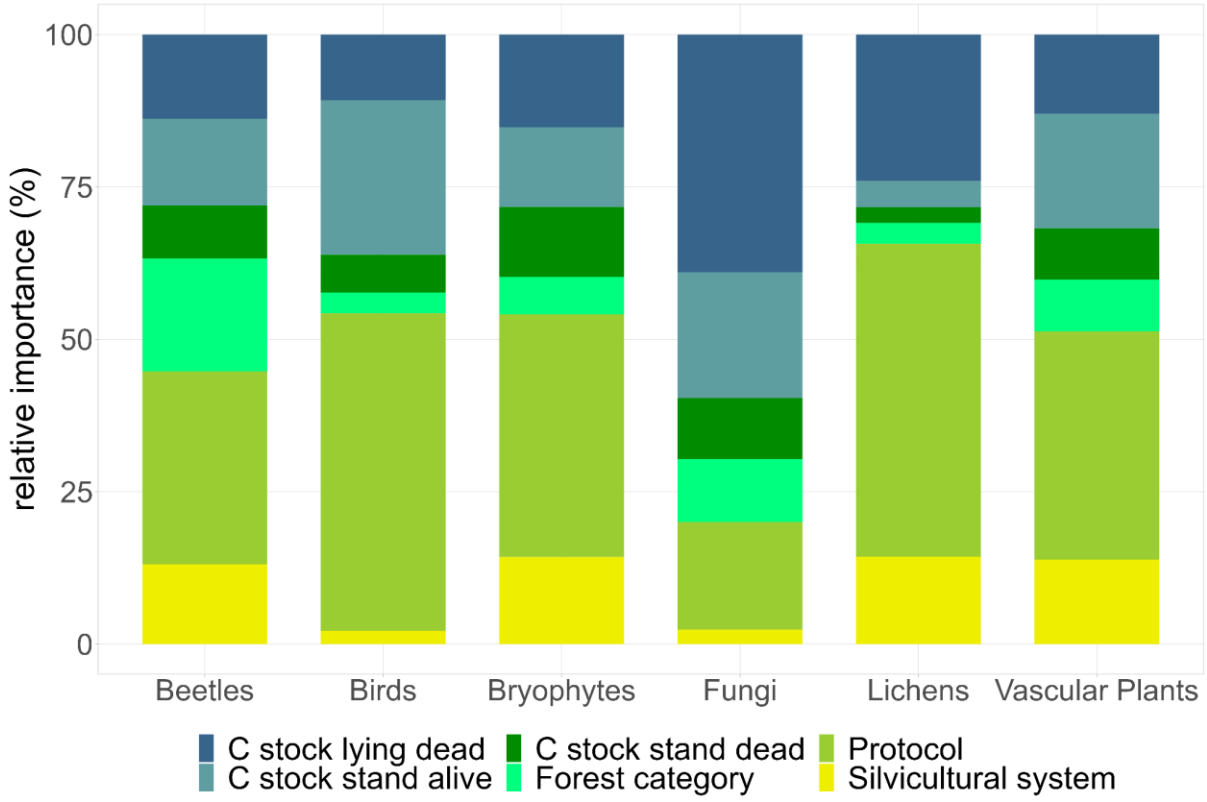
2.1 Relative importance of carbon stocks in determining the variation in species richness

Protocol, i.e., site conditions and sampling protocol, was the most important variable explaining variations in species richness, ranging from a share of explained deviance of 52% for birds to 18% for fungi (Fig. 1).

Carbon pools had a prominent role in explaining the variation in species richness, with differences across taxonomic groups (Fig. 1). The carbon stocks of lying deadwood showed the highest shares of explained deviances, ranging from 32%, for fungi, to 8%, for birds. The carbon stocks of standing living trees were related to the species richness of birds and vascular plants (highest share of deviance, 25%, for birds, lowest, 4%, for lichens). Standing deadwood showed the lowest shares of explained deviances, ranging from 11% for bryophytes to 5% for lichens).

Forest category had the greatest effect (18%) on the species richness of beetles and the lowest (4%) on lichens.

The silvicultural system showed the highest value of explained deviance (14%) for lichens and the lowest one (2%) for birds.



227

228 Figure 1. Relative importance of the predictor variables in determining the scaled species

229 richness of different taxonomic groups according to BRTs.

230

231 A high share of deviance was explained by the models for lichens (80%), fungi (76%), birds

232 (74%), beetles (72%), while the predictive value was lower for bryophytes (58%) and

233 vascular plants (47%) (Table 1).

	Nº trees	LR	TC	BF	D^2	CV corr	SS corr
Beetles	3250	0.005	5	0.5	0.72	0.72	0.86
Birds	2100	0.005	5	0.75	0.74	0.78	0.86
Bryophytes	1250	0.005	5	0.75	0.58	0.64	0.78
Fungi	3450	0.005	5	0.75	0.76	0.73	0.85
Lichens	1550	0.005	5	0.5	0.80	0.86	0.90
Vascular plants	3050	0.005	5	0.50	0.47	0.57	0.70

Table 1. Statistics of the selected Boosted Regression Trees (BRTs). LR refers to Learning rate; TC to Tree complexity, BF to Bag Fraction, D^2 to Explained Deviance, CV corr to cross-validated mean correlation coefficient, SS corr to self statistics.

2.2 Effect of aboveground living carbon stocks on forest multi-taxon species richness

Standing alive trees showed a positive effect mainly on wood inhabiting fungi (Fig. 2), with an increase of the marginal effect on the logit of the scaled species richness of 0.2, starting at 1.5 (31.6 t C/ha); and a negative effect on vascular plants, with a decrease of 0.2, starting at 0

(1 t C/ha). The scaled species richness of saproxylic beetles, in particular, showed a weak increase, starting at 0.5 (3.16 t C/ha).

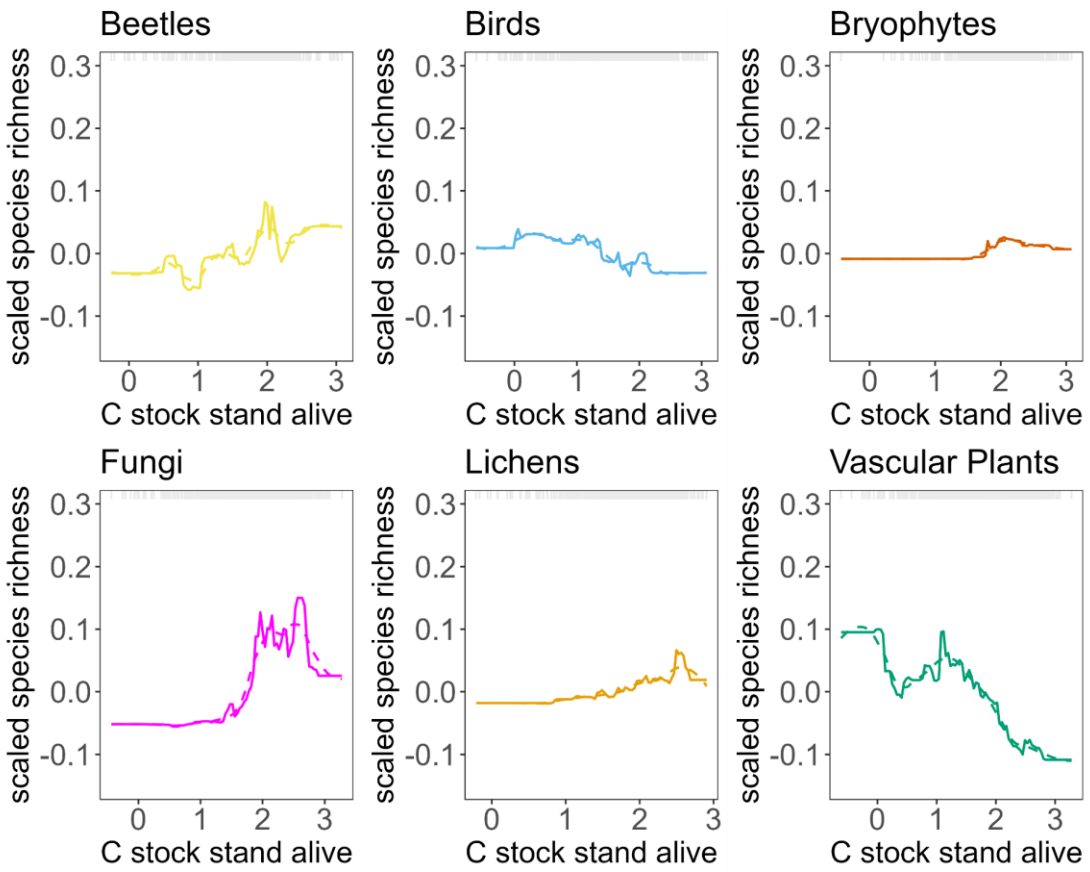


Figure 2. Partial dependence plots showing the marginal effect of standing alive C stock on scaled species richness of selected taxonomic groups. Grey stripes on the top of each graph represent the distribution of the data.

2.3 Effect of deadwood carbon stocks on forest multi-taxon species richness

Lying deadwood showed the strongest relationships with wood inhabiting fungi and epiphytic and epixylic lichens (Fig. 3), with an increase of the marginal effect on the logit of the scaled

species richness of respectively 0.4 and 0.2. Interestingly, the scaled species richness of these two taxonomic groups showed a steep increase at different points in the gradient of carbon stocked in lying deadwood , i.e., while a value of -1.5 (0.03 t C/ha) was sufficient to determine an increase in fungi species richness, only a value of -1 (0.1 t C/ha) was relevant for lichens.

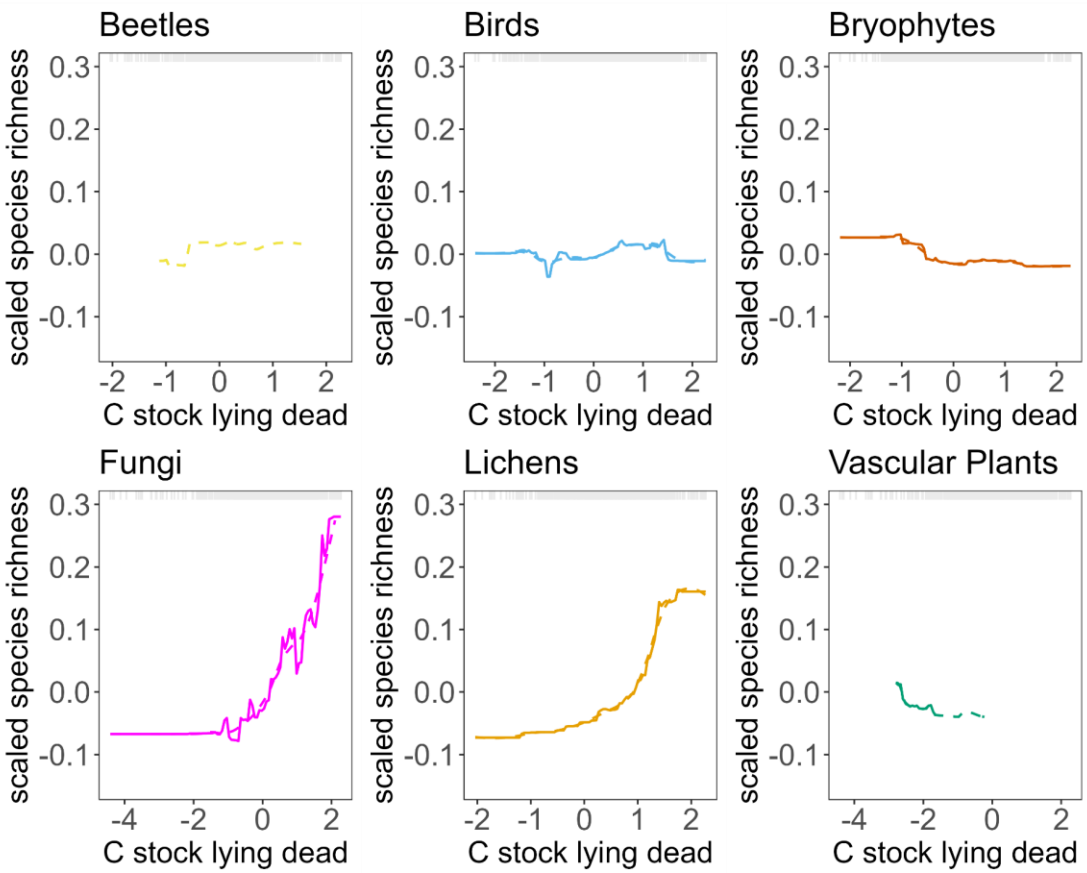


Figure 3. Partial dependence plots showing the marginal effect of lying deadwood C stock on scaled species richness of different taxonomic groups. Gray stripes on the top of each graph represent the distribution of the data.

Standing deadwood had an effect on both saproxylic beetles and wood inhabiting fungi (Fig. 4), with an increase of the marginal effect on the logit of the scaled species richness of respectively 0.3 and 0.1, starting at -1 (0.1 t C/ha).

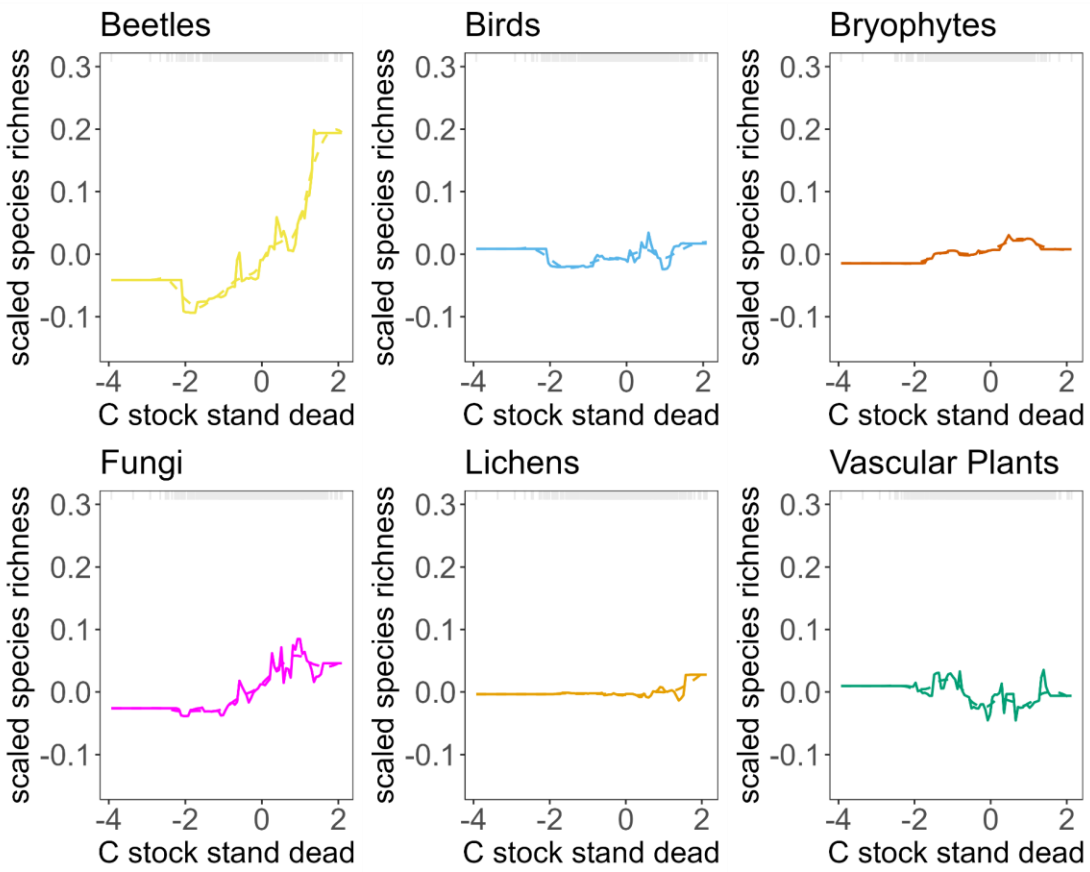


Figure 4. Partial dependence plots showing the marginal effect of standing deadwood C stock on scaled species richness of selected taxonomic groups. Gray stripes on the top of each graph represent the distribution of the data.

3. Discussion

3.1 Carbon stocks have an important role in determining the variation in species richness of multiple taxonomic groups

Carbon stocks played a prominent role in explaining the variation in species richness. Deadwood is a fundamental component of the forest carbon pool (7% of growing stock in Europe) and has a key role in nutrient cycles [1], affecting several taxonomic groups that are crucial in the detritus food web [32] and providing habitat for many saproxylic insects [41], lichens, fungi [42], and bryophytes [43]. On the other hand, living biomass, and the carbon stock associated to it, has both direct and indirect effects on biodiversity: it directly determines forest structure and the related habitats for several species [40], and indirectly influences forest species composition by driving microclimate and resources availability (light, water, soil nutrients) [44]. Our results show how climate change mitigation actions focused on moving carbon stocks outside of the environment [10] are actively subtracting one of the main factors that shape European forest ecosystems biodiversity. Policies should investigate how allowing trees to remain in their natural forest environment can greatly enhance carbon sequestration. Unharvested trees continue to grow, thereby sequestering additional carbon and contributing to long-term carbon storage [45] and supporting biodiversity in forest ecosystems. Our findings also underscore the influence of site conditions and sampling protocols on the variations in species richness for several taxonomic groups. The discrepancies among sampling methods, particularly in the context of multi-taxon sampling in European forests, significantly affect the biodiversity data collected. To ensure the comparability of data between studies and achieve consistent results in biodiversity research across European forests, it is imperative to

harmonize these sampling methods [46]. This need for standardization is particularly urgent in light of the new European Union Forest Monitoring Law [47].

3.2 Aboveground living carbon stock cannot be a proxy of forest multi-taxon diversity

Our findings highlight that the relationship between aboveground living carbon stock and species richness of most taxonomic groups is often weak, in accordance with previous studies [18], or negative, e.g., vascular plants. The absence of a positive response may be attributed to the different drivers of carbon stock accumulation in aboveground living biomass and their direct and indirect effects on the diversity of the taxonomic groups we have studied. For many forest categories, the increase of the carbon stock associated with standing biomass is paired with a general long-term increase in forest stand age [48]. When a forest stand ages, the accumulation of carbon in living biomass largely influences the diversity of several taxonomic groups, with the increase of species associated with local ecological continuity and specific habitat structures [25]. Many species, however, require neither long ecological continuity (i.e., species related to disturbance with high dispersal ability [25]), nor habitat structures associated with late-successional conditions [25]. These species can represent a prominent part of a forest species diversity, thus weakening the links between live aboveground carbon stock and species richness. Moreover, in the European context, high amounts of aboveground living carbon stock are not necessarily linked with long ecological continuity, as anthropogenic disturbances strongly drives changes in forest carbon stocks [49], with direct and indirect effects on biodiversity [50]. Forests managed for timber production purposes can reach high carbon storage rates due to the silvicultural promotion of biomass accumulation processes (e.g., fast growing species in even-aged forests). This may result in relatively high carbon stocks accompanied neither by long local ecological continuity, nor

abundant habitat structures that would be beneficial to biodiversity [34,35].

In this context, the decrease observed for vascular plants species richness starting at 1 t C/ha may be attributed to the decreasing light intensity at the forest floor [28]. In this case, the presumed increase of shade tolerant species may not counterbalance the decrease of species related to open areas, with the exception of old-growth conditions in which both groups may co-occur in a fine mosaic of developmental forest phases [51]. Based on our results, we should not expect high species richness for several taxonomic groups in a forest rich in living carbon.

3.3 Deadwood carbon stocks have a key role in driving forest multi-taxon diversity

We found positive relationships between deadwood carbon stocks and species richness of several taxonomic groups, following previous research [29,30]. Our results showed that carbon in lying deadwood had strong positive links with fungi and lichens species richness in European forests. This can be explained by lying deadwood's role as both the substrate and a resource for these two taxonomic groups. Interestingly, their scaled species richness showed a steep increase at different values of lying deadwood carbon, with fungi responding slightly earlier than epiphytic lichens, thus suggesting differential preferences of these taxonomic groups for the amount of lying deadwood. Fungal diversity is substantially driven by lying deadwood carbon stock [52,53], and in some cases a low amount of lying deadwood was found to support a large group of species [54]. Lichen diversity, on the other hand, may have a latter response due to the gap light conditions that may be associated with the occurrence of large amounts of deadwood. Bryophytes did not show a positive response to increasing carbon stock in lying deadwood, even if previous works have highlighted the significance of deteriorating wood as a crucial substrate for the diversity of bryophytes in general within

342 forest ecosystems [19,43], along with forest microclimate [24]. It is possible that the relatively low
343 number of bryophyte species at the continental level [55] may have hampered the detection of a
344 consistent increasing trend in species richness across our database. Deadwood diversity, stand
345 openness and large lying deadwood volume are largely recognized as the main drivers of
346 saproxylic beetles species richness in temperate forests [56]. However, we were not able to
347 detect a substantial positive response of this group to an increasing carbon stock in lying
348 deadwood. This unexpected outcome may be associated with the fact that the vast majority of
349 sampling units in the dataset showed a relatively low amount of lying deadwood volume
350 mostly composed of relatively fine deadwood fragments (see Supplementary Fig. 2), which
351 may not be able to support a high level of saproxylic beetle diversity. Additionally, our study
352 encompasses different climatic conditions that are known to have a strong influence on
353 saproxylic beetle species richness [57]. Interestingly, we found different results for standing
354 deadwood, with a strong positive response of saproxylic beetles and a weak positive response
355 for fungi. This may be linked to the fact that the main structural drivers of saproxylic beetle
356 species richness are large deadwood elements and the canopy openings that may support
357 beetle species in their adult phase [56]. Theoretically, an increasing amount of standing
358 deadwood carbon should have been associated with an increasing amount of surface available
359 for epixylic groups, i.e., bryophytes and lichens. For these groups, however, an increase of
360 available surface does not necessarily mean an increase in species richness, which are rather
361 influenced by tree species composition [58] for both groups and stand-scale ecological
362 continuity [59], local species dispersal capacity [60], microclimatic conditions [61] for lichens; or
363 seasonal rainfall distribution [62] for bryophytes. Our results indicate that numerous taxonomic
364 groups can benefit from a forest ecosystem abundant in carbon associated with deadwood.

3.4 Policies should account for the complex links between carbon stocks and biodiversity in European forests

Increasing aboveground carbon stock in forests does not necessarily lead to a significant increase in species richness across different taxonomic groups. Species richness responses vary considerably depending on the carbon pool and taxonomic group. While aboveground living carbon stock showed weak or negative responses for most taxonomic groups, deadwood carbon stocks, including both lying and standing deadwood, demonstrated positive relationships with saproxylic, epiphytic, and epixylic groups.

Our findings suggest that European and global policies focused on climate change mitigation may not jointly achieve the biodiversity conservation targets they emphasize [5] if they continue to prioritize the carbon stocks in aboveground living biomass. Pursuing the target of carbon and biodiversity rich forests should account for the complex pathways that may link these two forest functions (e.g., by promoting biodiversity-friendly measures in highly productive forest stands through integrated closer-to-nature forest management [63]). Similarly, the measure of living biomass without accounting for a comprehensive set of information on successional pathways, human and natural disturbance regimes, landscape context and original species composition, may not be used as a proxy of multi-taxon forest biodiversity, whereas it is commonly used as such [18,64]. This is particularly relevant in view of the current proposal for a European Union Forest Monitoring Law, whose investments seem to target forest living biomass above all [47].

On the other hand, our work highlights the importance of deadwood carbon pools for both climate change mitigation and biodiversity conservation targets. Over the past decades, the extraction of deadwood from European forests has been increasing and it increasingly included fine woody debris, as required by the need to achieve climate neutrality by

substituting fossil-based materials [65]. Additionally, the limited assessment of deadwood forest carbon stock [66], constrained by the scarcity of broad-scale data [67] have led to an underestimation of both the losses in deadwood carbon pools in European forests, and of the impacts of deadwood dependent biodiversity [68].

It is crucial for policymakers to consider the multifaceted nature of these ecological interactions. Innovative approaches and case studies that address these dual objectives are required to inform and refine policy frameworks towards comprehensive and effective forest management strategies.

4. Conclusions

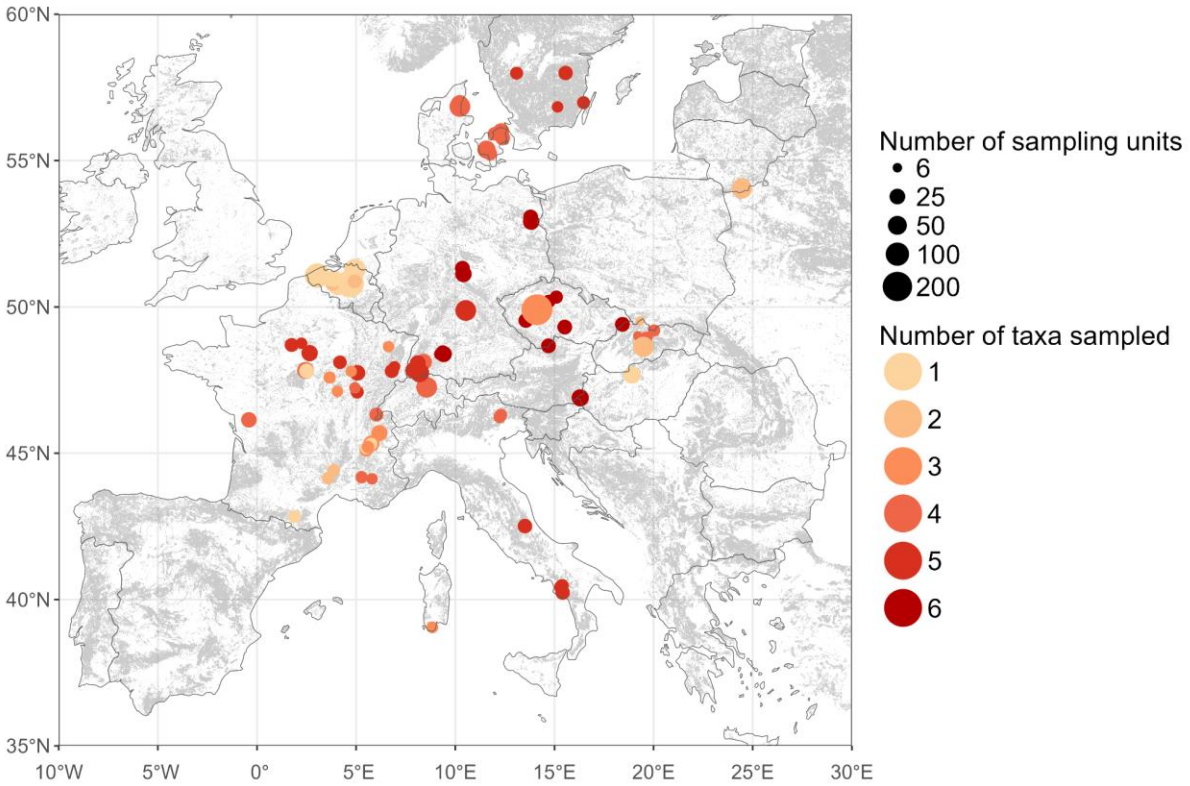
The urge to simultaneously satisfy several goals set both for biodiversity conservation (i.e., European Biodiversity Strategy for 2030 [4]) and for climate change mitigation (i.e., European Forest Strategy for 2030 [5]) is putting European forests under multiple pressures. As the carbon stock associated with biomass in European forests keeps increasing [1], it is important to understand the biodiversity outcomes of this trend. We focused on the spatial overlap between these two fundamental forest functions, putting the basis for further investigations of these relationships across time, by taking into account carbon flux dynamics and biodiversity temporal patterns. The dataset we used may be further implemented by filling the gaps for boreal and southern Europe of the dataset that we used. Similarly, further information on stand age, forest size and connectivity and local environmental and climatic conditions could have improved our ability to understand the links between forest carbon stocks and biodiversity. Despite these limitations, our work represents a step towards understanding the biodiversity-carbon stock relationships and dynamics in European forests, for which we did not find a univocal relation. Among the carbon pools, lying and standing deadwood were proven as much more relevant than living biomass carbon pools in explaining the variation in

European forest species richness. Aboveground living biomass carbon stock can be a strong resource in global forest assessments thanks to the wide amount of available data; however, it cannot be a proper proxy when assessing forest biodiversity. Regional and national forest inventories, as well as carbon accounting initiatives (e.g., REDD) should account for the deadwood carbon pool since it emerges as the prominent support for several taxonomic groups. The achievement of biodiversity conservation targets will be hampered if climate change mitigation policies will not account for the conservation of deadwood storages inside forest ecosystems and not only as a resource for fuel or secondary woody products, but also as a support to species diversity.

5. Methods

5.1 Data

We used a novel database encompassing 12 European countries and resulting from the harmonization of 34 datasets containing both field-sampled multi-taxon biodiversity information (i.e., at least three groups of organisms among animals and either plants or fungi), and stand structure data. Each sampling unit (i.e., a concretely delimited forest area of known geographical coordinates) was clustered in a forest site (i.e., an environmentally homogeneous geographical area) [39]. We used data on six functional and taxonomic groups (saproxylic beetles, birds, epiphytic and epixylic bryophytes and lichens, wood-inhabiting fungi, vascular plants). We analyzed a total of 134,136 observations of 3,532 species in 7,457 plots (see Supplementary Fig. 1). Most sampling units comprise two or more functional and taxonomic groups resulting in a total of 2,500 spatially distinct multi-taxon plots across 94 sites (Fig. 5).



435

436 Figure 5. Distribution of the sampling sites in Europe. Gray areas are covered by forests with
437 a tree cover greater than 40 % according to the European Forest Institute Forest Map of
438 Europe [69]. The number of taxonomic groups sampled at each site is represented by different
439 shades of red, while the number of sampling units is indicated by the dot size.

440

441 The sampling protocols used for each taxonomic group are based on comparable approaches
442 [46]: vascular plants and wood-inhabiting fungi were sampled in plots or blocks of plots rising
443 to an overall sampling area in the order of hundreds of square meters; epiphytic and epixylic
444 lichens and bryophytes were sampled respectively on 2 to 12 and 5 to 18 standing living trees
445 and deadwood items per plot; birds were sampled by point counts mostly during time frames
446 from 5 to 20 minutes [70]; saproxylic beetles were sampled through window-flight interception
447 traps (1 to 6 in each plot), in some cases also with emerging traps and Winkler extractors [71].
448 Species names and higher taxonomic information were checked automatically using the
449 packages 'taxize' [72] and, for vascular plants, 'WorldFlora' [73] and either corroborated by

experts or checked against the GBIF database (https://www.gbif.org/).

5.2 Data preparation

5.2.1 Species richness standardization

An exact assessment of plot-level species richness is almost impracticable due to the multiple constraints of sampling activities as opposed to the vastness and complexity of biological diversity [74]. A general rule is that, as the number of encountered individuals increases, species richness exhibits a non-linear increase [75]. It is thus necessary to standardize richness data when comparing datasets obtained through different sampling efforts. Rarefaction operates by down-sampling data to achieve an equal sampling effort, i.e., the one of the smallest samples. A complementary approach is to extrapolate species richness to a larger sample size through an estimated asymptotic species richness [75,76]. The latter approach, also estimates the sample completeness, i.e., the proportion of the total number of individuals/observations that belong to each species in the sample, and in turn the magnitude of the differences in species richness among communities.

We estimated the expected species richness for each site for each taxonomic group using the "estimateD" function within the R package "iNEXT," set for sample-based incidence data [77]. Finally, a comparable measure of species richness (= scaled species richness) was computed as the ratio between observed species richness for each taxonomic group (i.e., the quantity of sampled species) in each specific sampling unit (alpha diversity) and the expected species richness within each specific site (gamma diversity).

5.2.2 Carbon stock calculation

Stand structure data were thoroughly checked and corrected for possible errors (e.g., related to measurement units). Missing data for standing tree heights, diameters and lengths of lying deadwood were estimated based on other available measurements for the specific tree or fragment (e.g., unit length/height, unit diameter and unit ID). This process also took into account additional measurements of living and dead elements available for the sampling unit, site, and forest category. The predictive mean matching method of the mice function (R-package 'mice' [78])was used for these estimations. Overall, we modeled 25% of standing trees' heights. Since some protocols included only one diameter measure for lying deadwood, 70 and 78% of the second (smaller) diameter of respectively stumps and logs were imputed. Stump heights were derived for 11% and log lengths for 25% of the records.

We used various equations to calculate tree/deadwood fragment's volume and thus biomass and carbon stocks for each sampling unit for three aboveground carbon pools (standing living trees, standing deadwood and lying deadwood) (Fig. 6 and see Supplementary Methods 1 and Supplementary Methods 2).

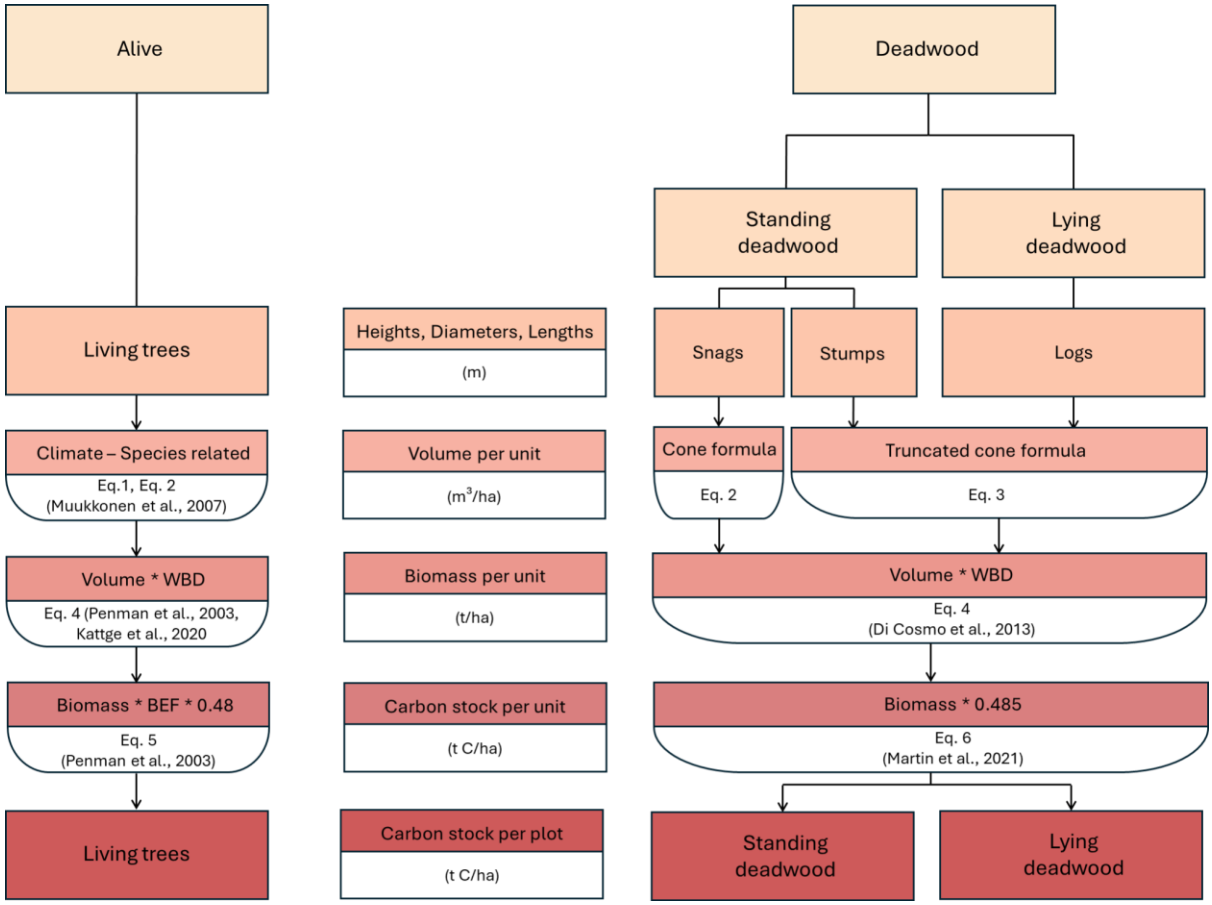


Figure 6. Workflow of the carbon stocks assessment for each sampling unit. Equation 1 is obtained from literature [79]; Equation 2 and 3 refer to the formula of the volume of the cone and truncated cone respectively; Equation 4 [80] uses Wood Basic Density (WBD) derived from existing literature [81] or, when not available in the former paper, from TRY database [82]; Equation 5 [80] uses different Biomass Expansion Factors (BEF) based on the climatic conditions of the sampling unit (boreal or temperate) and the dominant species group (coniferous or broadleaf); Equation 6 [83] uses an improved Carbon fraction of 0.485 for deadwood.

5.3 Statistical analyses

The carbon stock for the standing living trees, standing deadwood and lying deadwood carbon pools in each plot were logarithm base 10 transformed to achieve a normal

distribution.

We ran six boosted regression trees (BRTs) to assess the relationship between the scaled species richness of each taxonomic group as response variable and carbon stocks, along with other selected predictors at the plot level (Tab. 2).

Variable	*Type*	*Selection*	*References*
Scaled species richness	continuous	response	[77]
C stock standing alive	continuous	predictor	from raw data
C stock standing dead	continuous	predictor	from raw data
C stock lying dead	continuous	predictor	from raw data
Forest category	categorical	predictor	[84]
Silvicultural system	categorical	predictor	[85]
Protocol	categorical	predictor	[46]

Table 2. Variables used in the Boosted Regression Trees: name, type, role in the model and source (BRTs).

BRTs effectively model complex non-linear relationships, and enable reliable identification of relevant variables and interactions, with a strong predictive performance and robustness against overfitting, missing data, and collinearity [86].

The model setting involves finding the optimal combination of four main parameters ("number of trees", "learning rate", "tree complexity" and "bag fraction") to minimize predictive error: the number of trees refers to the total count of individual decision trees, influencing both predictive performance and model stability; the learning rate controls the contribution of each tree to the final model, providing a balance between accuracy and the risk of overfitting; tree complexity determines the maximum depth of each tree, affecting the model's ability to capture complex patterns in the data; and the bag fraction specifies the proportion of the training set randomly selected for each iteration [86].

We used the "gbm.step" function from the 'dismo' package [87] to test various BRT settings by combining different learning rates (0.001, 0.0025, 0.005), tree complexity values (2, 3, 5), and bag fraction values (0.5, 0.75), and assess the relative importance (sum up to 100%) of each explanatory variable [86]. We used the Gaussian error distribution.

We selected parameter combinations that resulted in models with over 1000 trees and evaluated their performance using three metrics, following the approach of Napoleone and colleagues [88] : (i) explained deviance (D^2), calculated as $D^2 = 1 - (\text{residual deviance/total deviance})$. This metric ranges from zero to one, where a value of one indicates a perfect fit, and is considered a generalization of the traditional R^2 used in regression analysis [88]; (ii) the cross-validated mean correlation coefficient (CV), which measures the average correlation

between the training and test datasets; and (iii) self-statistics (SS), which assesses the correlation between predicted and observed values. These correlation metrics are commonly used to evaluate the efficiency of Boosted Regression Trees (BRTs) [18,88].

Data availability

The data used for this study are available upon request using the Data Explorer within the Cost Action website (https://www.bottoms-up.eu/en/results/data-explorer.html).

References

1. FOREST EUROPE. FOREST EUROPE, 2020: State of Europe's Forests 2020. *FOREST EUROPE, 2020: State of Europe's Forests 2020* (2020).
2. Barredo, J. *et al. Mapping and Assessment of Primary and Old-Growth Forests in Europe*. (2021) doi:10.2760/797591 (online),10.2760/13239 (print).
3. Sabatini, F. M. *et al.* European primary forest database v2.0. *Sci Data* **8**, 220 (2021).
4. *COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS EU Biodiversity Strategy for 2030 Bringing Nature Back into Our Lives*. (2020).
5. *COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS New EU Forest Strategy for 2030*. (2021).
6. Harris, N. L. *et al.* Global maps of twenty-first century forest carbon fluxes. *Nat. Clim. Chang.* **11**, 234–240 (2021).
7. Nabuurs, G.-J. *et al.* First signs of carbon sink saturation in European forest biomass. *Nature Climate Change* **3**, 792–796 (2013).
8. Profft, I., Mund, M., Weber, G.-E., Weller, E. & Ernst Detlef, S. Forest management and carbon sequestration in wood products. *European Journal of Forest Research* **128**, 399–413 (2009).
9. Grassi, G. *et al. Brief on the Role of the Forest-Based Bioeconomy in Mitigating Climate Change through Carbon Storage and Material Substitution*. (2021).
10. Giuntoli, J. *et al.* The quest for sustainable forest bioenergy: win-win solutions for climate and biodiversity. *Renewable and Sustainable Energy Reviews* **159**, 112180 (2022).
11. FAO. *Global Forest Resources Assessment 2020: Main Report*. (FAO, Rome, Italy, 2020). doi:10.4060/ca9825en.
12. European Environment Agency (EU body or agency). *State of Nature in the EU: Results*

from Reporting under the Nature Directives 2013 2018. (Publications Office of the European Union, LU, 2020).

13. Hodgetts, N. *A Miniature World in Decline*. (IUCN, 2019). doi:10.2305/IUCN.CH.2019.ERL.2.en.
14. Cálix, M. *et al. European Red List of Saproxylic Beetles*. (IUCN, 2018).
15. BirdLife International, Directorate-General for Environment (European Commission), & IUCN. *European Red List of Birds 2021*. (Publications Office of the European Union, 2022).
16. Anthony, M. A. *et al.* Fungal community composition predicts forest carbon storage at a continental scale. *Nat Commun* **15**, 2385 (2024).
17. Asbeck, T. *et al.* Biodiversity response to forest management intensity, carbon stocks and net primary production in temperate montane forests. *Sci Rep* **11**, 1625 (2021).
18. Sabatini, F. M. *et al.* Trade-offs between carbon stocks and biodiversity in European temperate forests. *Global Change Biology* **25**, 536–548 (2019).
19. Hofmeister, J., Hošek, J., Holá, E. & Novozámská, E. Decline in bryophyte diversity in predominant types of central European managed forests. *Biodivers Conserv* **24**, 1391–1402 (2015).
20. Dittrich, S., Jacob, M., Bade, C., Leuschner, C. & Hauck, M. The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecol* **215**, 1123–1137 (2014).
21. Di Nuzzo, L. *et al.* Little time left. Microrefuges may fail in mitigating the effects of climate change on epiphytic lichens. *Sci. Total Environ.* **825**, 153943 (2022).
22. Frey, S. J. K., Hadley, A. S. & Betts, M. G. Microclimate predicts within-season distribution dynamics of montane forest birds. *Divers. Distrib.* **22**, 944–959 (2016).
23. Seibold, S. *et al.* Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *J. Appl. Ecol.* **53**, 934–943 (2016).
24. Táborská, M., Kovács, B., Németh, C. & Ódor, P. The relationship between epixylic bryophyte communities and microclimate. *Journal of Vegetation Science* **31**, 1168–1180

(2020).
25. Nordén, B. *et al.* Effects of Ecological Continuity on Species Richness and Composition in Forests and Woodlands: A Review. *Ecoscience* **21**, 34–45 (2014).
26. Nordén, B. & Appelqvist, T. Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation* **10**, 779–791 (2001).
27. Burton, J. I., Ares, A., Olson, D. H. & Puettmann, K. J. Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests. *Ecological Applications* **23**, 1297–1310 (2013).
28. Dormann, C. F. *et al.* Plant species richness increases with light availability, but not variability, in temperate forests understorey. *BMC Ecology* **20**, 43 (2020).
29. Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* **11**, 1027–1039 (2011).
30. Parajuli, R. & Markwith, S. H. Quantity is foremost but quality matters: A global meta-analysis of correlations of dead wood volume and biodiversity in forest ecosystems. *Biological Conservation* **283**, 110100 (2023).
31. Parisi, F. *et al.* Linking deadwood traits with saproxylic invertebrates and fungi in European forests - a review. *iForest - Biogeosciences and Forestry* **11**, 423 (2018).
32. Stokland, J. N. The saproxylic food web. in *Biodiversity in Dead Wood* (eds. Jonsson, B. G., Stokland, J. N. & Siitonen, J.) 29–57 (Cambridge University Press, Cambridge, 2012). doi:10.1017/CBO9781139025843.004.
33. Bernal, B., Murray, L. & Pearson, T. Global carbon dioxide removal rates from forest landscape restoration activities. *Carbon Balance and Management* **13**, (2018).
34. da Silva, L. P. *et al.* Natural woodlands hold more diverse, abundant, and unique biota than novel anthropogenic forests: a multi-group assessment. *European Journal of Forest Research* **138**, 461–472 (2019).
35. Felton, A., Lindbladh, M., Brunet, J. & Fritz, Ö. Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest

biodiversity in northern Europe. *Forest Ecology and Management* **260**, 939–947 (2010).
36. Goded, S. *et al.* Effects of eucalyptus plantations on avian and herb species richness and composition in North-West Spain. *Global Ecology and Conservation* **19**, e00690 (2019).
37. González-Montelongo, C. & Pérez-Vargas, I. Looking for a home: Exploring the potential of epiphytic lichens to colonize tree plantations in a Macaronesian laurel forest. *Forest Ecology and Management* **453**, 117541 (2019).
38. Mohr, J., Thom, D., Hasenauer, H. & Seidl, R. Are uneven-aged forests in Central Europe less affected by natural disturbances than even-aged forests? *Forest Ecology and Management* **559**, 121816 (2024).
39. Burrascano, S. *et al.* Where are we now with European forest multi-taxon biodiversity and where can we head to? *Biological Conservation* **284**, 110176 (2023).
40. Pan, Y., Birdsey, R. A., Phillips, O. L. & Jackson, R. B. The Structure, Distribution, and Biomass of the World's Forests. *Annual Review of Ecology, Evolution, and Systematics* **44**, 593–622 (2013).
41. Jacobs, J. M., Spence, J. R. & Langor, D. W. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. *Agricultural and Forest Entomology* **9**, 3–16 (2007).
42. Ranius, T., Eliasson, P. & Johansson, P. Large-scale occurrence patterns of red-listed lichens and fungi on old oaks are influenced both by current and historical habitat density. *Biodiversity and Conservation* **17**, 2371–2381 (2008).
43. Müller, J. *et al.* Effects of forest management on bryophyte species richness in Central European forests. *Forest Ecology and Management* **432**, 850–859 (2019).
44. Prescott, C. E. The influence of the forest canopy on nutrient cycling. *Tree Physiology* **22**, 1193–1200 (2002).
45. Luyssaert, S. *et al.* Old-growth forests as global carbon sinks. *Nature* **455**, 213–215 (2008).
46. Burrascano, S. *et al.* Handbook of field sampling for multi-taxon biodiversity studies in

652 European forests. *Ecological Indicators* **132**, 108266 (2021).
653 47. *Proposal for a REGULATION OF THE EUROPEAN PARLIAMENT AND OF THE*
654 *COUNCIL on a Monitoring Framework for Resilient European Forests*. (2023).
655 48. Keeton, W. S., Whitman, A. A., McGee, G. C. & Goodale, C. L. Late-Successional
656 Biomass Development in Northern Hardwood-Conifer Forests of the Northeastern United
657 States. *Forest Science* **57**, 489–505 (2011).
658 49. Naudts, K. *et al.* Europe's forest management did not mitigate climate warming. *Science*
659 **351**, 597–600 (2016).
660 50. Paillet, Y. *et al.* Biodiversity Differences between Managed and Unmanaged Forests:
661 Meta-Analysis of Species Richness in Europe. *Conservation Biology* **24**, 101–112
662 (2010).
663 51. Burrascano, S. *et al.* It's a long way to the top: Plant species diversity in the transition
664 from managed to old-growth forests. *J. Veg. Sci.* **29**, 98–109 (2018).
665 52. Atrena, A. *et al.* Quality of substrate and forest structure determine macrofungal richness
666 along a gradient of management intensity in beech forests. *For. Ecol. Manage.* **478**,
667 118512 (2020).
668 53. Persiani, A. M. *et al.* Stand structure and deadwood amount influences saproxylic fungal
669 biodiversity in Mediterranean mountain unmanaged forests. *iForest* **9**, 115–124 (2016).
670 54. Doerfler, I., Gossner, M. M., Müller, J., Seibold, S. & Weisser, W. W. Deadwood
671 enrichment combining integrative and segregative conservation elements enhances
672 biodiversity of multiple taxa in managed forests. *Biological Conservation* **228**, 70–78
673 (2018).
674 55. Hodgetts, N. *et al.* An annotated checklist of bryophytes of Europe, Macaronesia and
675 Cyprus. *Journal of Bryology* **42**, 1–116 (2020).
676 56. Bouget, C., Larrieu, L., Nusillard, B. & Parmain, G. In search of the best local habitat
677 drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.*
678 **22**, 2111–2130 (2013).
679 57. Müller, J. *et al.* Increasing temperature may compensate for lower amounts of dead

680 wood in driving richness of saproxylic beetles. *Ecography* **38**, 499–509 (2015).
681 58. Kiraly, I., Nascimbene, J., Tinya, F. & Odor, P. Factors influencing epiphytic bryophyte
682 and lichen species richness at different spatial scales in managed temperate forests.
683 *Biodivers. Conserv.* **22**, 209–223 (2013).
684 59. Boch, S., Prati, D., Hessenmoeller, D., Schulze, E.-D. & Fischer, M. Richness of Lichen
685 Species, Especially of Threatened Ones, Is Promoted by Management Methods
686 Furthering Stand Continuity. *PLoS One* **8**, e55461 (2013).
687 60. Dettki, H., Klintberg, P. & Esseen, P. A. Are epiphytic lichens in young forests limited by
688 local dispersal? *Ecoscience* **7**, 317–325 (2000).
689 61. Nascimbene, J., Marini, L. & Odor, P. Drivers of lichen species richness at multiple
690 spatial scales in temperate forests. *Plant Ecol. Divers.* **5**, 355–363 (2012).
691 62. Medina, N. G. *et al.* Species richness of epiphytic bryophytes: drivers across scales on
692 the edge of the Mediterranean. *Ecography* **37**, 80–93 (2014).
693 63. Larsen, J. *et al.* Closer-to-Nature Forest Management. From Science to Policy 12.
694 (2022) doi:10.36333/fs12.
695 64. Rybár, J. & Bošeľa, M. Trade-offs or complementarity between biomass production and
696 biodiversity in European forests: a review. *Central European Forestry Journal* **69**, 201–
697 213 (2023).
698 65. Verkerk, P. J. *et al. Forest-Based Climate Change Mitigation and Adaptation in Europe*.
699 https://efi.int/publications-bank/forest-based-climate-change-mitigation-and-adaptation-
700 europe (2022) doi:10.36333/fs14.
701 66. Puletti, N., Giannetti, F., Chirici, G. & Canullo, R. Deadwood distribution in European
702 forests. *Journal of Maps* **13**, 733–736 (2017).
703 67. Rondeux, J. & Sanchez, C. Review of indicators and field methods for monitoring
704 biodiversity within national forest inventories. Core variable: Deadwood. *Environmental*
705 *Monitoring and Assessment* **164**, 617–630 (2010).
706 68. Ranius, T. *et al.* The effects of logging residue extraction for energy on ecosystem
707 services and biodiversity: A synthesis. *Journal of Environmental Management* **209**, 409–

425 (2018).

69. Kempeneers, P., Sedano, F., Seebach, L., Strobl, P. & San-Miguel-Ayanz, J. Data Fusion of Different Spatial Resolution Remote Sensing Images Applied to Forest-Type Mapping. *IEEE Transactions on Geoscience and Remote Sensing* **49**, 4977–4986 (2011).
70. Bouvet, A. *et al.* Effects of forest structure, management and landscape on bird and bat communities. *Environmental Conservation* **43**, 148–160 (2016).
71. Janssen, P. *et al.* Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodivers Conserv* **25**, 1167–1185 (2016).
72. Chamberlain, S. A. & Szöcs, E. taxize: taxonomic search and retrieval in R. *F1000Res* **2**, 191 (2013).
73. Kindt, R. WorldFlora: An R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. *Applications in Plant Sciences* **8**, e11388 (2020).
74. Pärtel, M., Szava-Kovats, R. & Zobel, M. Dark diversity: shedding light on absent species. *Trends in Ecology & Evolution* **26**, 124–128 (2011).
75. Colwell, R. K. *et al.* Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* **5**, 3–21 (2012).
76. Chao, A. & Jost, L. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* **93**, 2533–2547 (2012).
77. Hsieh, T. C., Ma, K. H. & Chao, A. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7**, 1451–1456 (2016).
78. Buuren, S. van & Groothuis-Oudshoorn, K. mice: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software* **45**, 1–67 (2011).
79. Muukkonen, P. Generalized allometric volume and biomass equations for some tree

736 species in Europe. *Eur J Forest Res* **126**, 157–166 (2007).
737 80. Penman, J. *et al.* Good Practice Guidance for Land Use, Land-Use Change and
738 Forestry. in (2003).
739 81. Di Cosmo, L., Gasparini, P., Paletto, A. & Nocetti, M. Deadwood basic density values for
740 national-level carbon stock estimates in Italy. *Forest Ecology and Management* **295**, 51–
741 58 (2013).
742 82. Kattge, J. *et al.* TRY plant trait database – enhanced coverage and open access. *Global*
743 *Change Biology* **26**, 119–188 (2020).
744 83. Martin, A. R., Domke, G. M., Doraisami, M. & Thomas, S. C. Carbon fractions in the
745 world's dead wood. *Nat Commun* **12**, 889 (2021).
746 84. EEA. European forest types — European Environment Agency.
747 https://www.eea.europa.eu/publications/technical_report_2006_9 (2006).
748 85. Trentanovi, G. *et al.* Words apart: Standardizing forestry terms and definitions across
749 European biodiversity studies. *Forest Ecosystems* **10**, 100128 (2023).
750 86. Elith, J. & Leathwick, J. Boosted Regression Trees for Ecological Modeling. (2013).
751 87. Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J. & Hijmans, M. R. J. Package 'dismo'
752 Version 1.3-8. (2022) doi:https://CRAN.R-project.org/package=dismo.
753 88. Napoleone, F., Giarrizzo, E. & Burrascano, S. Habitat conservation state and plant
754 diversity respond to different drivers in semi-natural grasslands. *Journal of Vegetation*
755 *Science* **32**, e13055 (2021).

756 Acknowledgements

757 This article was funded by the EU Framework Programme Horizon 2020 through the COST
758 Association (www.cost.eu): COST Action CA18207: BOTTOMS-UP – Biodiversity Of
759 Temperate forest Taxa Orienting Management Sustainability by Unifying Perspectives. The
760 experimental site OPTMix in Centre-Val de Loire, France, was installed and equipped by

INRAE EFNO thanks to the support of the region, the French National Forest Office, and belongs to the network ANAEE-F (http://www.anaee-france.fr/).

Author contributions

Lorenzo Balducci and Sabina Burrascano contributed to the data preparation, analysis and writing of the introduction, methods, results and the discussion of the manuscript. Elena Haeler, Yoan Paillet and Nathalie Korboulewsky contributed greatly to the structuring of the paper. Francesca Napoleone and Edoardo Alterio contributed to the methodological section. Steffen Boch and Thibault Lachat contributed to the discussion. Francesco Chianucci worked on the harmonization of the database we have used for this research. Christian Ammer, Frédéric Archaux, Steffen Boch, Christophe Bouget, Gediminas Brazaitis, Andrea Cutini, Pallieter De Smedt, Inken Doerfler, Daniel Dvořák, Markus Fischer, Paolo Giordani, Marion Gosselin, Jacob Heilmann-Clausen, Eva Holá, Jeňýk Hofmeister, Jan Hošek, Philippe Janssen, Kirsten Jung, Sebastian Kepfer-Rojas, Daniel Kozák, Tomáš Kuras, Jiří Malíček, Anders Mårell, Martin Mikoláš, Jörg Müller, Björn Nordén, Péter Ódor, Yoan Paillet, Zdeněk Palice, Peter Schall, Tommaso Sitzia, Kastytis Šimkevičius, Miroslav Svoboda, Aleš Tenčík, Flóra Tinya, Giovanni Trentanovi, Mariana Ujhazyova, Kris Vandekerkhove, Michael Wohlwend and Wolfgang W. Weisser contributed to the manuscript through fundamental feedback to the proposed draft. All authors have been involved in collection of the data and building of the dataset.

Competing interests statement

All authors declare that there are no conflicts of interest.

Chapter 3. Biodiversity at stake: winners and losers of forest management in Europe

Biodiversity at stake: winners and losers of forest management in Europe

Lorenzo Balducci, Francesco Rota, Lucas Chojnacki, The “Bottoms-Up Consortium”, Robert Muscarella, Sabina Burrascano.

Abstract: Silvicultural regimes impact forest biodiversity, with many species experiencing declines in conservation status. However, most studies investigate biodiversity response in terms of species richness rather than focusing on the effects on individual species that could face declining trends.
Here we identified species-level responses to specific silvicultural regimes focusing on three key taxonomic/functional groups: vascular plants, epiphytic bryophytes and lichens.
We ran Species Distribution Models to explore the habitat suitability of the species included in a Europe-wide dataset of multi-taxon biodiversity and forest stand management. Then, we applied generalized linear models to evaluate how silvicultural regimes shape the occurrence of each of these species while controlling for habitat suitability. We found both positive and negative impacts on individual species and discussed them in terms of management insights relevant to each taxonomic group. Ultimately, we stress the importance of considering species-specific requirements towards an effective framework for biodiversity conservation in European forests managed for timber production.

keywords: multi-taxon, management, forests, europe, SDM, SFM

1. Introduction

Forests host about three-quarters of the global terrestrial plant, fungi and animal species diversity, and are globally considered biodiversity hotspots. Forests in Europe cover approximately 43% of the land area, representing one of the most important ecosystems for biodiversity conservation (FAO, 2020) and one of the priorities of European policies (European Commission 2021). European forests are key habitats for biodiversity and about 30% of forest area is referred to as a habitat of conservation value in the EU (EEA, 2020).

Despite the increasing awareness of their ecological value, European forests face numerous threats, including habitat fragmentation, climate change, and unsustainable management practices (EEA, 2020). While forest area is increasing in Europe, approximately 20% of forest habitats in the EU show a decline in their conservation status, with many species facing range contractions, population declines, or local extinctions (EEA, 2020; Hodgetts, 2019). The conservation status of species associated with forest habitats is increasingly alarming, with 25% of vascular plant species and 22.5% of bryophytes species assessed as threatened (European Commission, 2011; Hodgetts et al., 2020). Other taxonomic groups, such as lichens, are yet to be comprehensively assessed, but their vulnerability is also likely high given their sensitivity to habitat changes (Di Nuzzo et al., 2022; Nascimbene et al., 2012).

The biological components of forest ecosystems are particularly sensitive to changes in forest structure, microclimatic conditions, and habitat quality, all of which are strongly influenced by forest management practices. The majority of forests in Europe have been shaped by silvicultural interventions aimed at maximizing timber production, a long-lasting priority across Europe (Gaillard et al., 2010; Kaplan et al., 2009; Williams, 2000). Currently, only about 2% of European forests are classified as primary or old-growth, remaining largely undisturbed by human activity (Sabatini et al., 2021). Consequently, forest management has played a crucial role in driving the conservation status and species diversity patterns of various taxonomic groups.

Different taxonomic groups have distinct responses to forest management. As regards to vascular plants, forest structural changes due to silvicultural practices such as thinning, selective logging, and gap creation significantly affect species richness and composition. These interventions primarily influence the canopy structure, altering light penetration and resource availability in the understory. Increased light availability under relatively open canopies often leads to greater understory plant diversity (Valladares & Niinemets, 2008). However, the extent of these effects varies depending on management approach and forest type.

Bryophytes and lichens, on the other hand, are sensitive to changes in microclimatic conditions, such as humidity, temperature, and air quality, all of which are affected by

forest management practices (Nascimbene et al., 2012). Bryophytes, in particular, require moist microhabitats and stable environmental conditions, often found in old-growth forests or areas with dense canopies (Hodgetts, 2019). Epiphytic lichens are also dependent on bark substrate quality and microclimatic conditions, making them vulnerable to changes in forest structure. For these taxa, retaining older, larger trees and maintaining canopy continuity is crucial for sustaining populations (Boch et al., 2013; Kiraly et al., 2013).

Importantly, even within the same taxonomic group, individual species respond differently to forest management based on their specific ecological preferences (Nordén et al., 2014). Among vascular plants, some species are forest specialists, adapted to low-light conditions and long ecological continuity, while others are light-demanding and thrive in open habitats (Nordén et al., 2014; Nordén & Appelqvist, 2001). Excessive thinning or gap creation may promote generalist species at the expense of forest specialists, leading to shifts in community composition and a decline in shade-tolerant species (Burrascano et al., 2018). Similarly, bryophyte and lichen species differ in their sensitivity to changes in humidity, light availability, and substrate quality (Alatalo et al., 2020; Ladrón de Guevara et al., 2018). For instance, some bryophytes species are supported by humid, shaded environments, while others are more adaptable to varying light conditions (Frego, 2007). Lichens also exhibit species-specific substrate and light availability preferences, with some lichen species suffering from intense light conditions under the canopy (Gauslaa & Solhaug, 1999), and other epiphytic species taking advantage of direct light (Ódor et al., 2013).

Throughout Europe, forest management encompasses a wide range of strategies and treatments, each of which affects differently forest structure and, consequently, biodiversity. Clear-cutting practices lead to even-aged stands by removing all trees in a stand. While efficient for timber production, this method significantly reduces habitat heterogeneity (Dias & Arroja, 2012). Clear-cutting is often associated with fast-growing, even-aged plantations with limited habitat value, particularly for species that rely on old-growth characteristics like deadwood and long ecological continuity (Carnus et al., 2006; Lindenmayer et al., 2012). This approach also contributes to habitat fragmentation, threatening species that require large, contiguous forest areas (Hanski, 2011). Selective logging strategies, on the other hand, involve the removal of individual or small groups of trees and, promote uneven-aged stands and, in turn, structural complexity. Overall, the strategies known as Continuous Cover Forestry (CCF), which include selective logging, can sustain microclimatic conditions essential for several species of bryophytes and lichens (Fedrowitz et al., 2014; Nascimbene et al., 2012). The retention of old trees and deadwood can further support saproxylic invertebrates and epiphytic lichens species (Bauhus et al., 2009; Lindenmayer et al., 2012). Coppicing, a traditional practice in southern Europe, enhances regrowth by cutting trees near the ground. By harvesting all or almost all trees in a stand, coppicing supports species related to early successional stages.

The decline of this management approach due to the abandonment of rural areas has raised concerns about the loss of these specific habitats and their associated species (Müllerová et al., 2015).

Recognizing species-specific responses to individual forest management strategies is crucial for developing plans and practices that support specific target species or that may support both generalist and forest specialist species.

The need to improve the condition of forest habitats and of the threatened species they host is intrinsically associated with sustainable forest management (SFM) practices that can support biodiversity conservation while sustaining the ecological functions and services that forests provide (EEA, 2020). The development of SFM is one of the main objectives of the European Forest and Biodiversity strategies for 2030 (European Commission, 2020; European Commission, 2021) and other related policies focused on forestry and biodiversity conservation. Sustainable Forest Management (SFM) indicators typically rely on structural attributes as proxies for biodiversity, offering only indirect assessments of habitat and species conservation status. While useful, these structural metrics are not direct measures of biodiversity and may overlook taxon- and species- specific responses. Therefore, current indicators often fail to capture the impacts that different management strategies have on the conservation status of forest dwelling species depending on their ecological requirements and sensitivities. Our study emphasizes the need to provide direct biodiversity indicators that go beyond structural metrics and account for species-specific responses to forest management. By integrating species-specific data, forest managers could accurately assess the ecological outcomes of their interventions, ensuring the effectiveness of conservation efforts either at the stand or at the landscape scale. Such indicators could inform Sustainable Forest Management practices, aligning them with biodiversity conservation goals.

Starting from the “Bottoms-Up" database, encompassing more than 3,500 sampling units across 12 European countries, we focused on species belonging to three major forest-dwelling taxonomic groups (epiphytic and epixylic bryophytes, epiphytic and epixylic lichens and vascular plants).

Through the use of this extensive database, we aim to:

1. Assess the extent of the effect of different silvicultural regimes on the occurrence of individual species;

2. Discuss management implications to effectively account for species diversity.

2. Methods

2.1 Biodiversity data

We used a novel database encompassing 12 European countries and resulting from the harmonization of 34 datasets containing both field-sampled multi-taxon biodiversity information (i.e., at least three groups of organisms among animals and either plants or fungi), and stand management data. Each sampling unit (i.e., a concretely delimited forest area of known geographical coordinates) was clustered in a forest site (i.e., an environmentally homogeneous geographical area) (Burrascano et al., 2023). We used data on three taxonomic groups (epiphytic and epixylic bryophytes and lichens, vascular plants), for which we have harmonized presence-absence data.

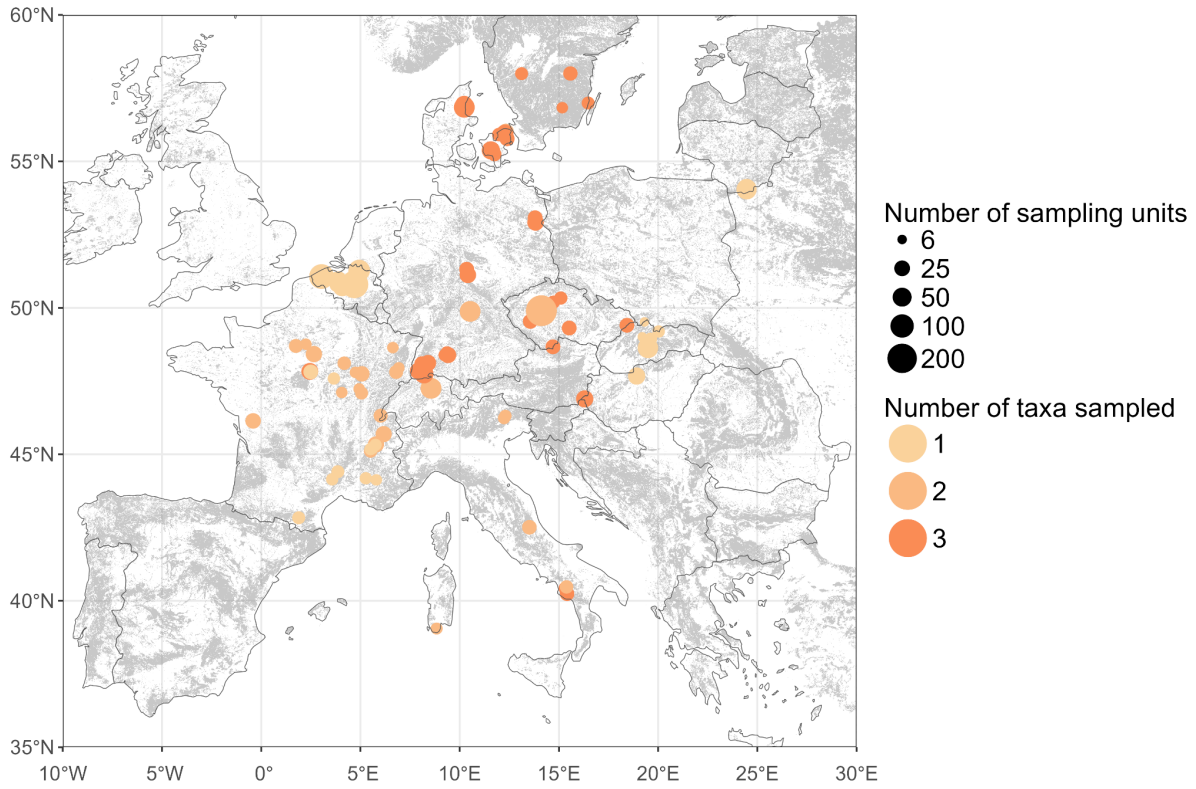


Figure 1 - Distribution of the sampling sites in Europe. Gray areas are covered by forests with a tree cover greater than 40 % according to the European Forest Institute Forest Map of Europe (Kempeneers et al., 2011). The number of taxonomic groups sampled at each site is represented by different shades of red, while the number of sampling units is indicated by the dot size.

We analysed a total of 65,844 observations of 965 species in 4,367 plots, collected from 2004 to 2019. Most sampling units comprise two or more functional and

taxonomic groups resulting in a total of 2,364 spatially distinct multi-taxon plots across 111 sites (Fig. 1, Fig. 2).

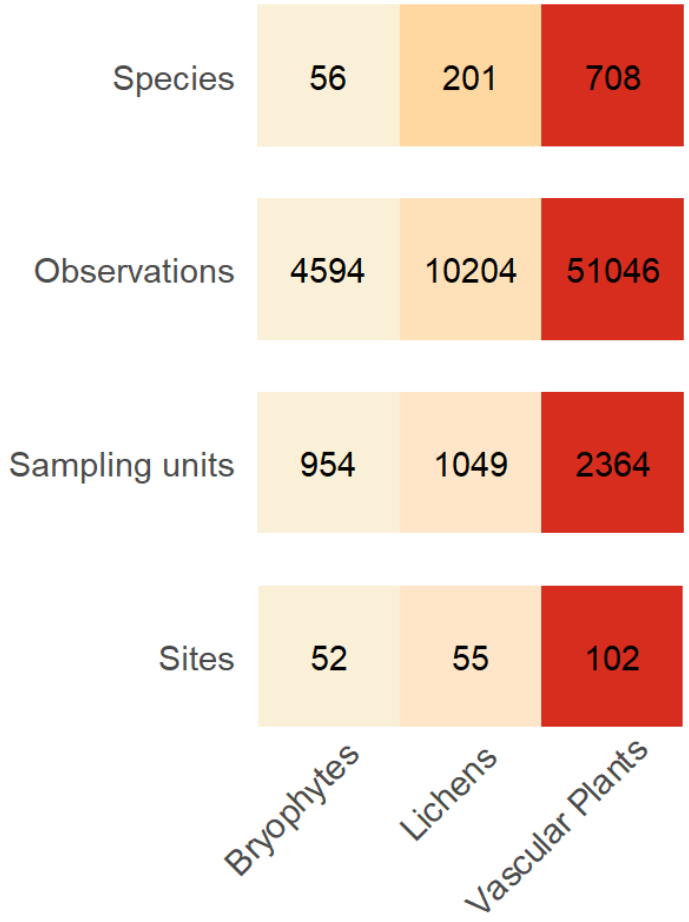


Figure 2 - Distribution of species, observations, sampling units and sites across taxonomic groups.

The sampling protocols used for each taxonomic group are based on comparable approaches (for details, see Burrascano et al., 2021): vascular plants were sampled in plots or blocks of plots rising to an overall sampling area in the order of hundreds of square meters; epiphytic lichens and bryophytes were sampled on respectively 2 to 12 and 5 to 18 standing living trees per plot, or across the whole plot. Species names and higher taxonomic information were checked automatically using the packages ‘taxize’ (Chamberlain & Szöcs, 2013) and, for vascular plants, ‘WorldFlora’ (Kindt, 2020) and either corroborated by experts or checked against the GBIF database (https://www.gbif.org/).

The sampling effort for each taxonomic group was determined by the number of trees surveyed per sampling unit for bryophytes and lichens, which ranged from 1 to 46 trees for bryophytes and from 1 to 82 trees for lichens. For vascular plants,

sampling effort was based on the area of the sampling unit, which ranged from 16 m² to 1,256 m².

2.2 Habitat suitability assessment

For all the species of vascular plants, epiphytic bryophytes and lichens with more than 30 occurrences in the Bottoms-Up database, we assessed habitat suitability values at the sampling unit level. Habitat suitability is typically evaluated by correlating species occurrence data with key climatic predictors, allowing us to estimate the environmental conditions that best support each species (Fig.3).

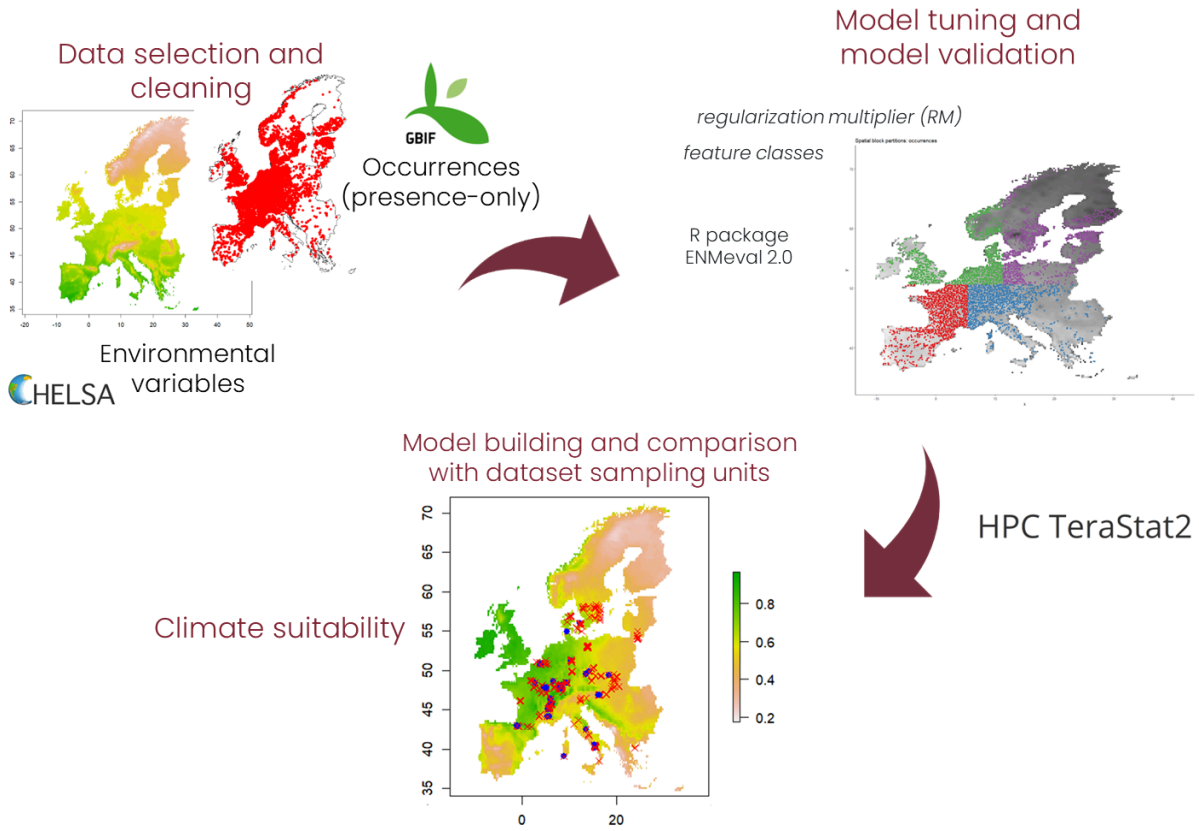


Figure 3 - Summary of the methodology to run SDMs and obtain the habitat suitability values.

2.2.1 Download and select occurrences

For each species, we retrieved up to 20,000 occurrence records from the Global Biodiversity Information Facility (GBIF), limiting the search to countries within the European Economic Area (EEA). Additionally, we covered Switzerland, as it includes part of the “Bottoms-Up” database, and extended the search to Albania, Bosnia, Kosovo, Montenegro, Serbia, Ireland and the UK, which share common forest categories included in the database (EEA, 2006). This extent ensured data continuity and prevented gaps in the ecological representation of shared forest ecosystems; thus avoiding truncation or sampling bias at the extremes of the species' climatic

distribution. Such issues can arise when species occurrence data are limited or clustered within the central part of their environmental range, causing the extreme values of their ecological niche (the limits of their tolerance to climate) to be underrepresented (Dormann et al., 2013; Elith & Franklin, 2013).

To ensure data quality and avoid pseudoreplication, we applied a series of quality control tests using the 'CoordinateCleaner' package (Zizka et al., 2019). These tests filtered out occurrences erroneously assigned to country capitals, institutional centroids, or missing coordinates. We also removed duplicate records with identical coordinates. To allow comparison with CHELSA bioclimatic predictors (Karger et al., 2017) and ensure spatial accuracy; we also excluded records with coordinate uncertainties greater than the spatial grain of the climatic data, e.g., 1km. Finally, we filtered the dataset to include only direct observations, excluding unsuitable data sources such as fossil records.

2.2.2 Climate predictors

We retrieved all 19 bioclimatic predictors for the 1981-2010 time-frame from the CHELSA database (Karger et al., 2017). To further analyze the climatic variables, we randomly sampled 1,000 points.

We run a Principal Component Analysis (PCA) to explore the relative importance of the bioclimatic predictors. PCA is a statistical technique used to reduce the dimensionality of a dataset while retaining as much variance as possible. By transforming the original variables into principal components, it simplifies complex datasets to identify underlying patterns (Jolliffe, 2011).

In our analysis, the first principal component (PC1) captures a significant portion of the overall variability in the dataset, explaining 71.2% of the variation in the bioclimatic data, while the second principal component (PC2) accounted for an additional 24.5%. We used the absolute scores of each predictor on PC1 to rank their importance, identifying bio18 as the most influential predictor (Jolliffe, 2011).

To avoid multicollinearity issues, we built a correlation matrix for all 19 bioclimatic predictors (Fig. 4) and removed predictors to avoid absolute correlation coefficient greater than $|r| > 0.7$ before selecting the next predictor.

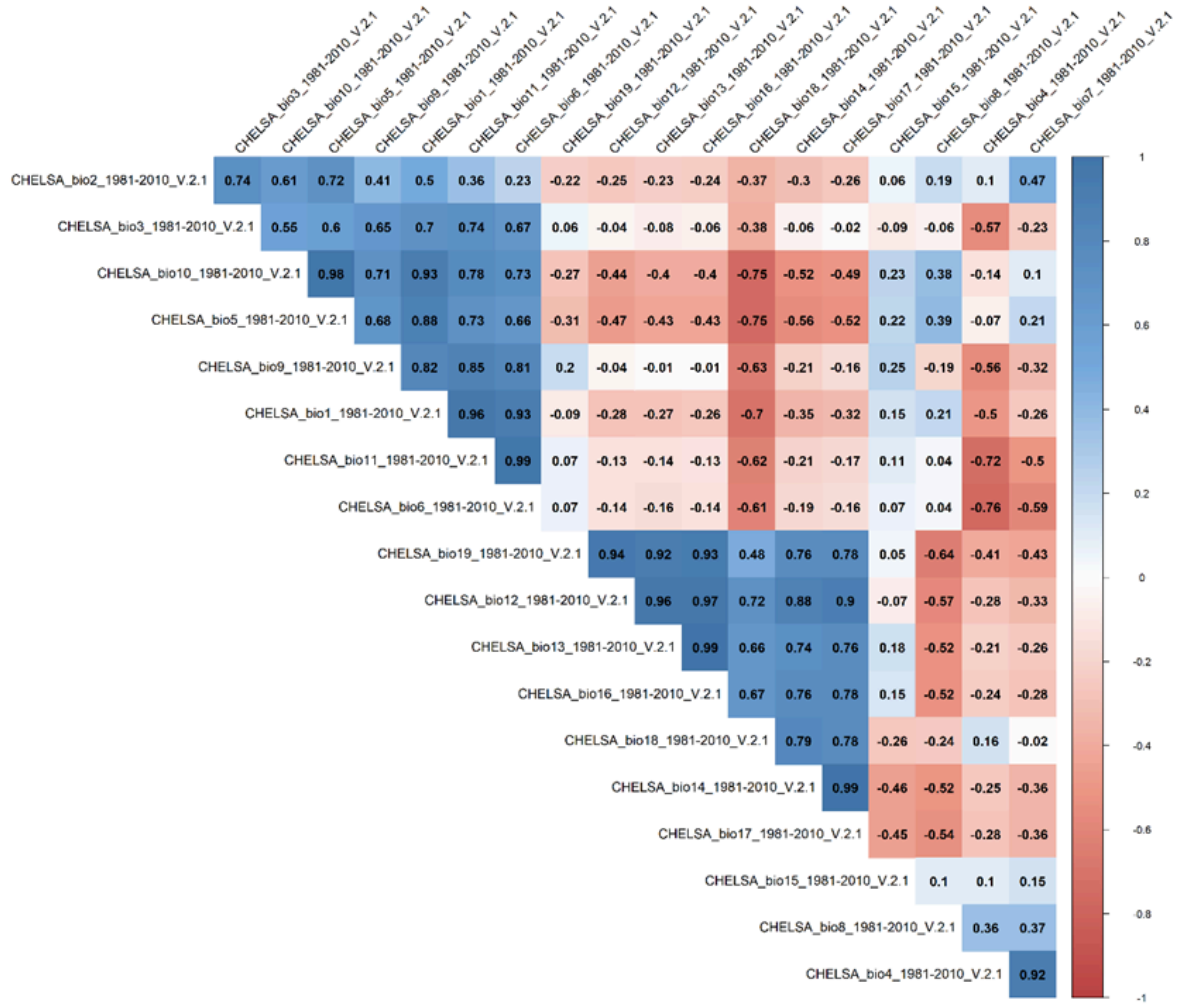


Figure 4 - Correlation matrix derived from 1000 random points extracted from the 19 bioclimatic predictors from CHELSA database (Karger et al., 2017).

Ultimately, we kept four predictors with high scores on the first axis and one from the second axis, resulting in a total of five bioclimatic predictors with correlations below the 0.7 threshold that cover the degree of climate continentality (bio2, bio7, bio16), the influence of Mediterranean climate (bio18) and the limitations imposed to photosynthetic organisms by cold winters (bio11) (Tab. 1).

Variable	*Description*	*Unit*	*Scale*
bio2	mean diurnal air temperature range	°C	0.1
bio7	annual range of air temperature	°C	0.1

bio11	mean daily mean air temperatures of the coldest quarter	°C	0.1
bio16	mean monthly precipitation amount of the wettest quarter	kg m^{-2}	0.1
bio18	mean monthly precipitation amount of the warmest quarter	kg m^{-2}	0.1

Table 1 - Summary of the five selected bioclimatic predictors.

2.2.3 Species Distribution Models

By integrating occurrence data with bioclimatic predictors, we produced accurate habitat suitability (HS) maps that reflect the ecological niches of the selected species. HS refers to the suitability of a certain spatial area to support a particular species, taking into account the most relevant environmental factors influencing its survival and reproduction. HS is often expressed on a scale from 0 to 1, where 0 indicates unsuitable habitat and 1 represents optimal conditions for the species (Phillips et al., 2006). These values provide crucial insights into where species are likely to thrive, informing conservation efforts and habitat management.

To assess HS for each selected species of vascular plants, epiphytic lichens and bryophytes, we used species Species Distribution Models (SDMs). SDMs are statistical or machine-learning tools used to predict the distribution of species across geographical areas by combining information on the environmental conditions that allow the presence of each species and the species occurrence data (Elith & Franklin, 2013). They integrate ecological and biogeographical data to estimate the potential HS for a species in a given area, which is crucial for understanding species-environment relationships and assessing biodiversity trends under changing environmental conditions (Elith & Leathwick, 2009).

SDMs are widely implemented in ecological research and biodiversity conservation to assess species distributions in relation to climate change, habitat loss, and other pressures. A wide range of different modeling techniques are used (Elith et al., 2006; Phillips et al., 2006). However, these modeling approaches often rely on default parameters or lack proper validation, which can significantly diminish their predictive performance and ecological relevance (Porfirio et al., 2014; Radosavljevic & Anderson, 2014). In this study, we applied the MaxEnt algorithm, particularly effective for presence-only data (Phillips et al., 2006), and we used R studio version

4.2.1 (RStudio Team, 2020) and the package “ENMeval 2.0” to tune and validate SDMs (Kass et al., 2021). For each selected species of vascular plants, bryophytes and lichens, we extracted a set of 1,000 background points to provide a comprehensive representation of the environmental conditions across the study area. Background points are used as a reference against which the presence of species is evaluated, allowing for a more accurate modeling of habitat suitability. We tested 16 combinations of feature classes (L, LQ, LQH, H) and beta multipliers (1, 2, 3, 4) for each species, allowing for fine model tuning. Feature classes in MaxEnt represent the types of relationships between species presence and environmental variables. For example, the linear (L) feature models simple linear relationships, while the quadratic (Q) feature allows the model to detect curvilinear patterns. The hinge (H) feature enables more flexible relationships, often useful for capturing complex interactions (Kass et al., 2021; Phillips et al., 2006). The beta multiplier controls model regularization, essentially tuning the complexity of the model. Higher beta values produce more generalized models, while lower values create more complex ones. Testing different beta values ensures that the model is neither too simple nor too overfit to the occurrence data (Phillips et al., 2006). We used checkerboard cross-validation, a spatially independent validation method that splits the data into partitions. This technique helps ensure that training and test data are spatially distinct, thus avoiding overfitting to specific spatial patterns in the occurrence data and improving model robustness (Kass et al., 2021).

The best model hyperparameters were determined by ranking the models first based on the minimum omission rate (Peterson et al., 2007; Warren et al., 2014). In cases where multiple models had the same omission rates, we prioritized those with the highest validation Area Under the Curve (AUC) values (Phillips et al., 2006), followed by the maximum weighted Akaike Information Criterion (AIC) (Burnham & Anderson, 2004). For species with identical scores across models, the model with the less complex feature class was retained.

Through this modeling process, we obtained habitat suitability maps for our study area for 56 bryophyte species, 201 lichen species, and 708 vascular plant species, with a spatial grid of 1 km^2.

2.3 Generalized Linear Models

To test the hypothesis that the occurrence of each species in the “Bottoms-Up” database is influenced by different silvicultural regimes, while accounting for the species' climatic niche (Fig. 5), we built generalized linear models (GLMs). GLMs are a flexible extension of linear models that allow non-normal error distributions for response variables. They are widely used in ecological modeling to analyze binary data (e.g., species presence or absence) under various environmental and management conditions (Guisan et al., 2002).

In our case, the dependent variable was species occurrence (presence = 1, absence = 0) in each sampling unit, and the predictors included the silvicultural regime, the habitat suitability (HS), and the variables describing the sampling protocol to account for potential biases in sampling effort at the stand level. The silvicultural regime was treated as a categorical predictor, with the "unmanaged" category set as the reference (intercept), i.e., we assessed the effects of different silvicultural regimes in comparison to unmanaged forests.

For each species, the model was built as follows:

```
md <- glm(occ ~ HS + silsl2 + sampling_protocol, data = ..., family = "binomial")
```

Here, `occ` represents the binary occurrence of the species, `HS` represents habitat suitability values (ranging from 0 to 1), and `silsl2` denotes the silvicultural systems, as described in Trentanovi et al. (2023), (e.g., selection cutting, shelterwood, coppice with standards, retention clearcutting, simple clearcutting). The binomial family was used to model the presence-absence data.

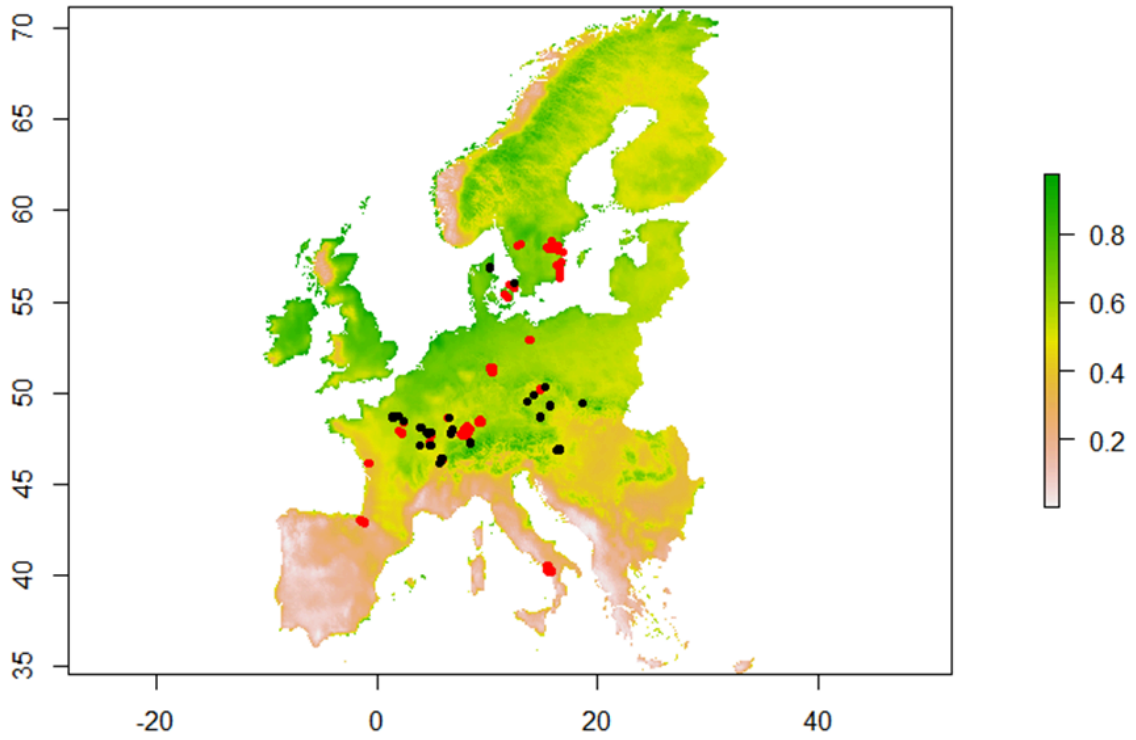


Figure 5 - Habitat suitability map of the best model for an example species (*Orthodicranum montanum*). In background, the habitat suitability for the best model, built with the species occurrences from GBIF database (www.gbif.org). Dots represent the sampling units of the BottomsUp database (black: presence; red: absence).

3. Results

3.1 Bryophytes

Out of 56 bryophyte species studied, 26 species (46.4%) showed significant responses to habitat suitability, and 20 species (35.7%) were influenced by the sampling effort. Among silvicultural regimes, shelterwood management had the greatest impact, affecting 21 species (37.5%), followed by retention clearcutting and simple clearcutting, which influenced 15 species (26.8%) and 13 species (23.2%), respectively. Coppice with standards had the least effect, impacting only 9 species (16.1%).

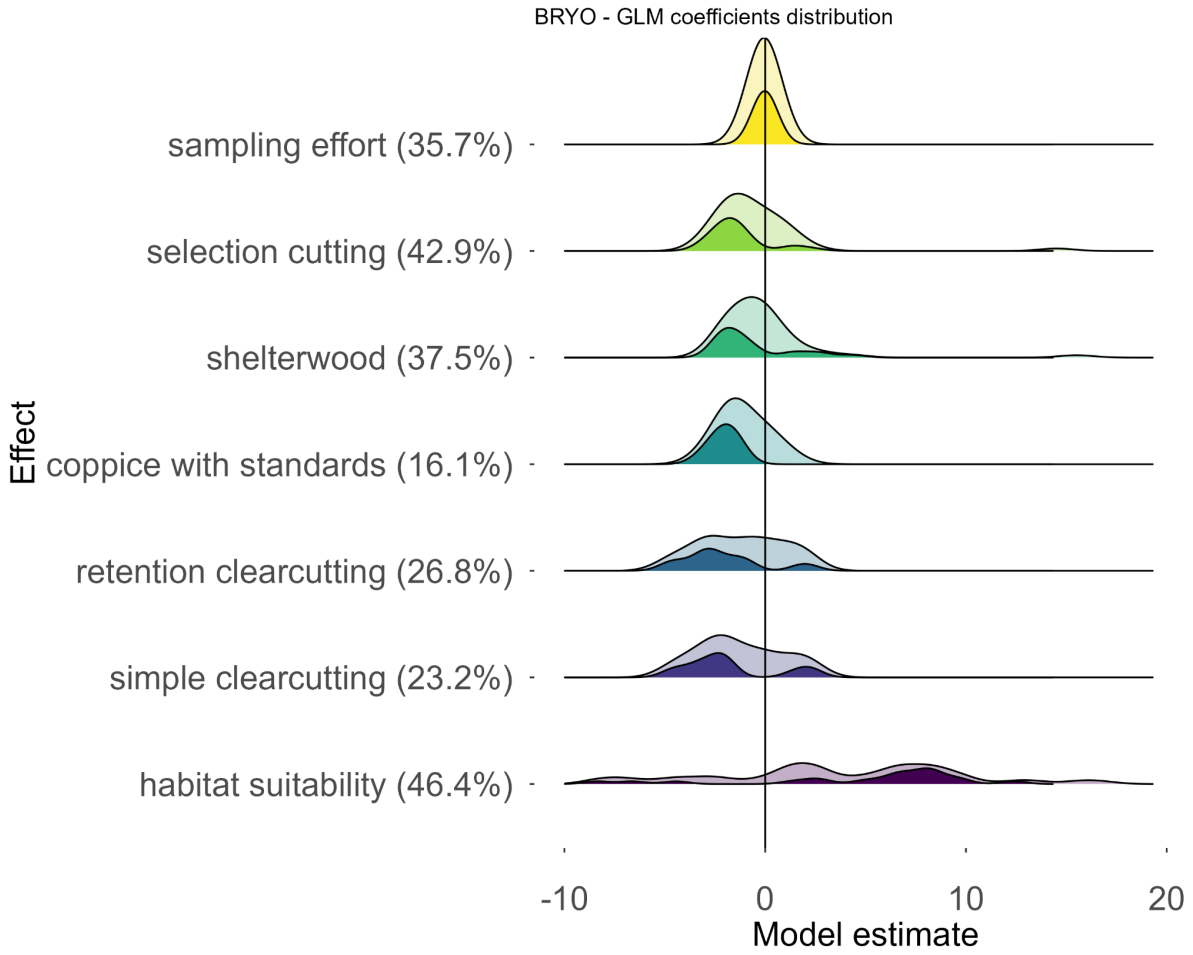


Figure 6 - Distribution of GLM coefficient estimates for bryophyte species occurrences in response to different predictors. Pale colors represent the distribution of all species, while the darker shade highlights species with significant effects. The percentage next to each predictor refers to the proportion of species significantly affected by it.

Unsurprisingly, HS had the strongest positive influence on bryophyte species occurrence, with 21 species (37.5%) showing positive responses compared to only 5

species (8.9%) showing negative responses. The unit level sampling effort significantly influenced bryophyte occurrences, with 11 species (19.6%) showing positive responses and 9 species (16.1%) showing negative responses, indicating that higher sampling effort does not always enhance species detection. Among silvicultural regimes, selection cutting and shelterwood had predominantly negative impacts on bryophytes (Supplementary Information 1.1). Selection cutting resulted in 21 species (37.5%) with negative responses and only 3 species (5.4%) with positive responses. Similarly, shelterwood management yielded 16 species (28.6%) with negative responses and only 5 species (8.9%) with positive responses. Retention clearcutting and simple clearcutting also had predominantly negative effects on bryophytes, with 13 species (23.2%) and 10 species (17.9%) showing negative responses, respectively. Coppice with standards exhibited 9 species (16.1%) with negative responses and no positive responses

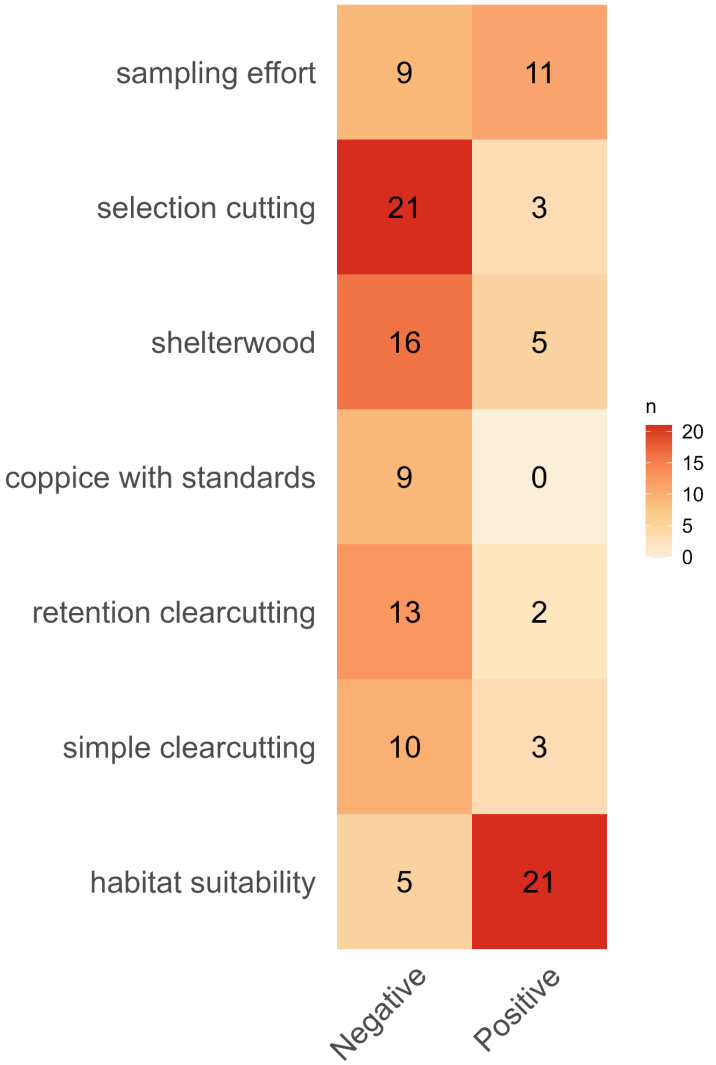


Figure 7 - Heatmap representing the number of species with significant positive and negative coefficients for the predictors for bryophytes. Each tile's color intensity represents the count of species (n) responding positively or negatively to the

respective predictor, where warmer (more intense) colors indicate higher counts. The numerical values in each tile display the exact number of species in each category.

3.2 Lichens

Among the 201 lichen species analyzed, 111 species (55.2%) were significantly influenced by habitat suitability, and 49 species (24.4%) were affected by sampling effort. Of the silvicultural regimes, selection cutting impacted the most species, influencing 55 species (27.4%), followed by shelterwood, which affected 43 species (21.4%). Coppice with standards influenced 24 species (11.9%), while simple clearcutting and retention clearcutting impacted 18 species (9%) and 8 species (4%), respectively.

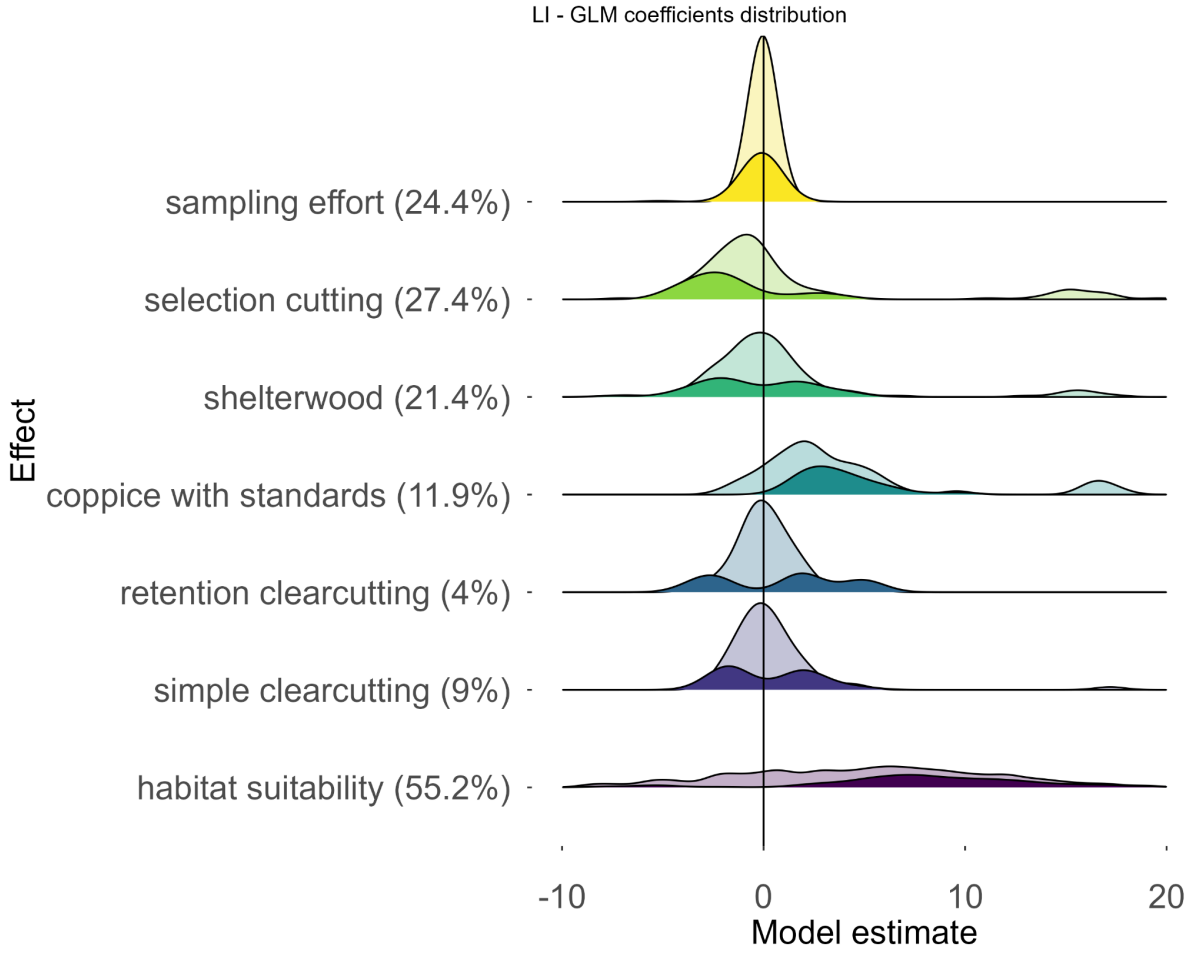


Figure 8 - Distribution of GLM coefficient estimates for bryophyte species occurrences in response to different predictors. Pale colors represent the distribution of all species, while the darker shade highlights species with significant effects. The percentage next to each predictor refers to the proportion of species significantly affected by it.

Among the species with significant responses (Fig. 9), habitat suitability had the

strongest impact, with 93 species (46.3%) showing positive responses and 18 species (9%) exhibiting negative responses. The sampling effort influenced 28 species (13.9%) positively and 21 species (10.4%) negatively. Coppice with standards had a positive impact on 24 species (11.9%), with no negative responses recorded (Supplementary Information 1.2). Retention clearcutting had a smaller influence, with 5 species (2.5%) responding positively and 3 species (1.5%) negatively. Selection cutting led to a substantial number of negative responses, with 45 species (22.4%) being negatively affected and only 10 species (5%) showing positive responses. Shelterwood impacted 19 species (9.5%) positively and 24 species (11.9%) negatively. Simple clearcutting affected 9 species (4.5%) both positively and negatively.

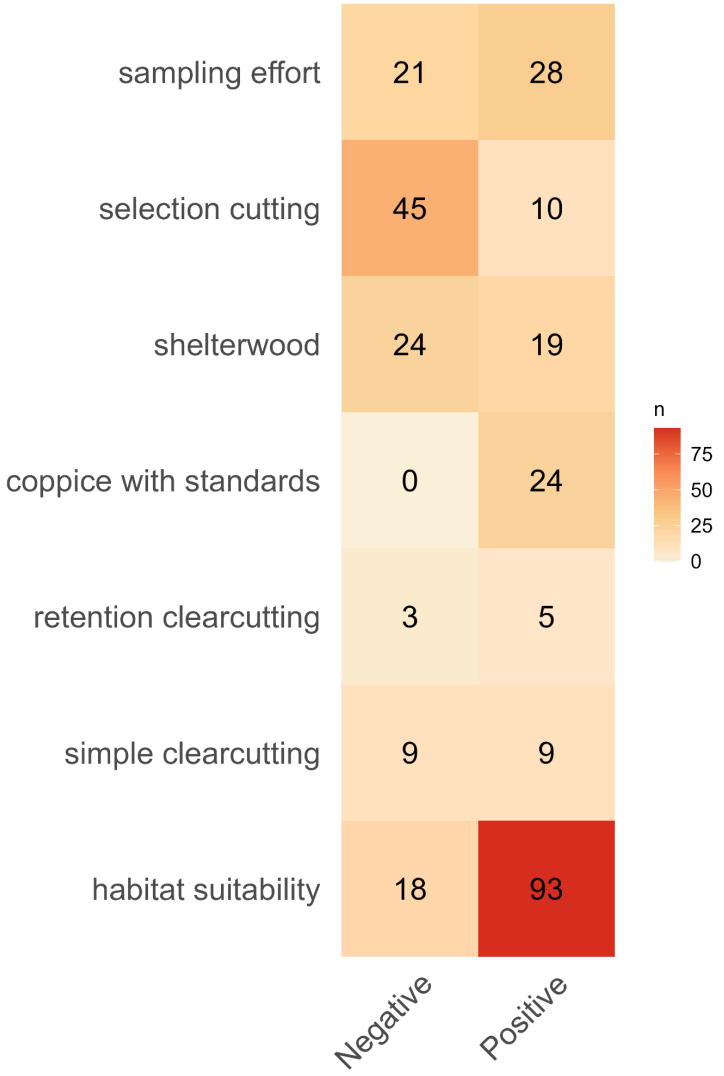


Figure 9 - Heatmap representing the number of species with significant positive and negative coefficients for the predictors for lichens. Each tile's color intensity represents the count of species (n) responding positively or negatively to the

respective predictor, where warmer (more intense) colors indicate higher counts. The numerical values in each tile display the exact number of species in each category.

3.3 Vascular plants

Our analysis showed that among 708 vascular plant species, 354 species (50%) were significantly influenced by habitat suitability, while sampling effort had a notable effect on 270 species (38.1%). Regarding silvicultural regimes, retention clearcutting impacted the highest number of species, affecting 159 species (22.5%), followed by selection cutting, which influenced 152 species (21.5%). Simple clearcutting impacted 135 species (19.1%), shelterwood affected 126 species (17.8%), and coppice with standards influenced 61 species (8.6%).

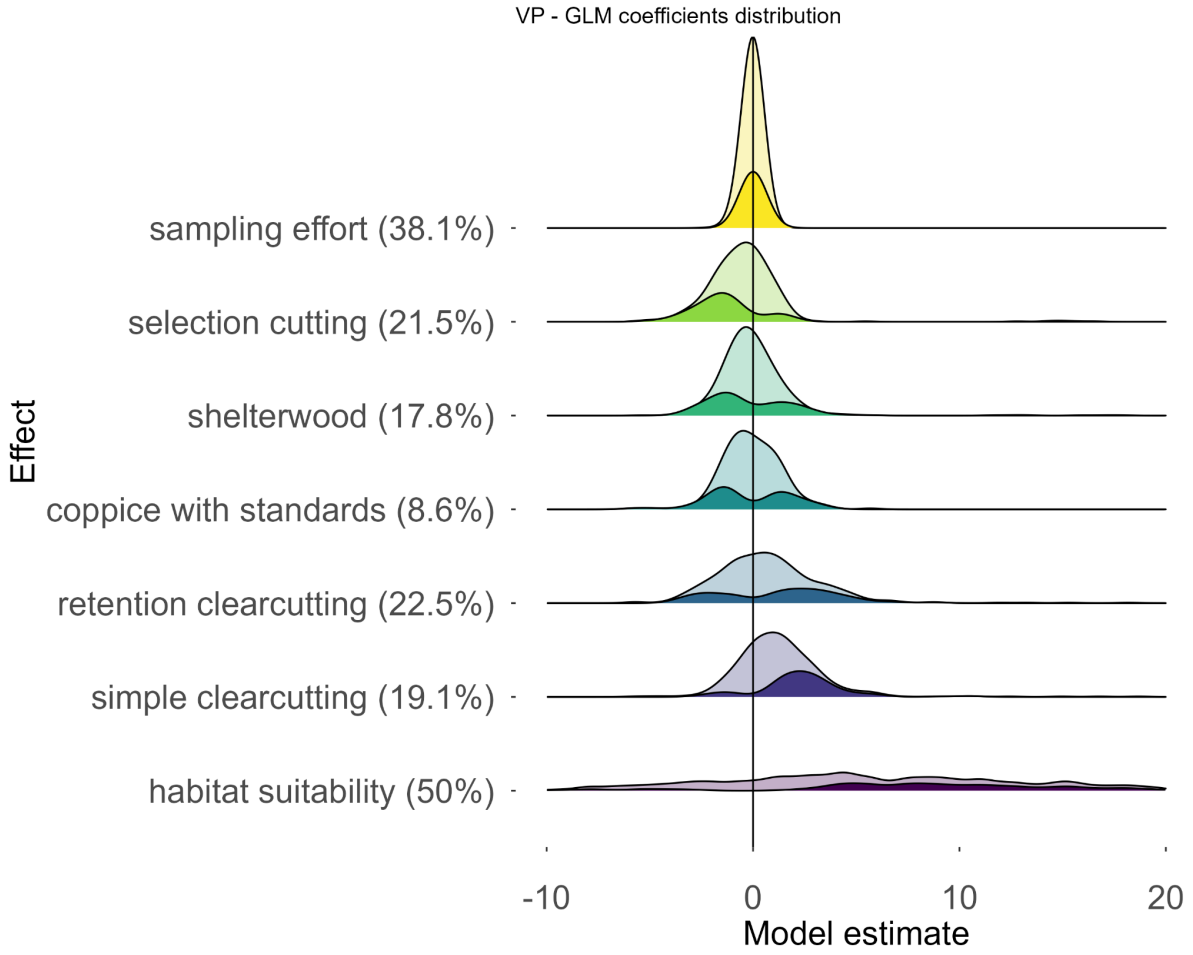


Figure 10 - Distribution of GLM coefficient estimates for vascular plants species occurrences in response to different predictors. Pale colors represent the distribution of all species, while the darker shade highlights species with significant effects. The percentage next to each predictor refers to the proportion of species significantly affected by it.

Among the species with significant responses (Fig. 11), HS had the most substantial impact, with 305 species (43.1%) showing positive responses and 49 species (6.9%) showing negative responses (Supplementary Information 1.3). The sampling effort influenced 24 species (3.4%) positively and 20 species (2.8%) negatively. Retention clearcutting showed a strong influence as well, with 103 species (14.6%) responding positively and 56 species (7.9%) negatively. Selection cutting primarily had a negative impact, with 128 species (18.1%) negatively affected, compared to only 24 species (3.4%) positively affected. Simple clearcutting yielded mixed results, positively affecting 120 species (16.9%) while negatively affecting only 15 species (2.1%). Shelterwood management also impacted a considerable number, with 50 species (7.1%) positively affected and 76 species (10.8%) negatively affected. Coppice with standards influenced 28 species (4%) positively and 33 species (4.7%) negatively.

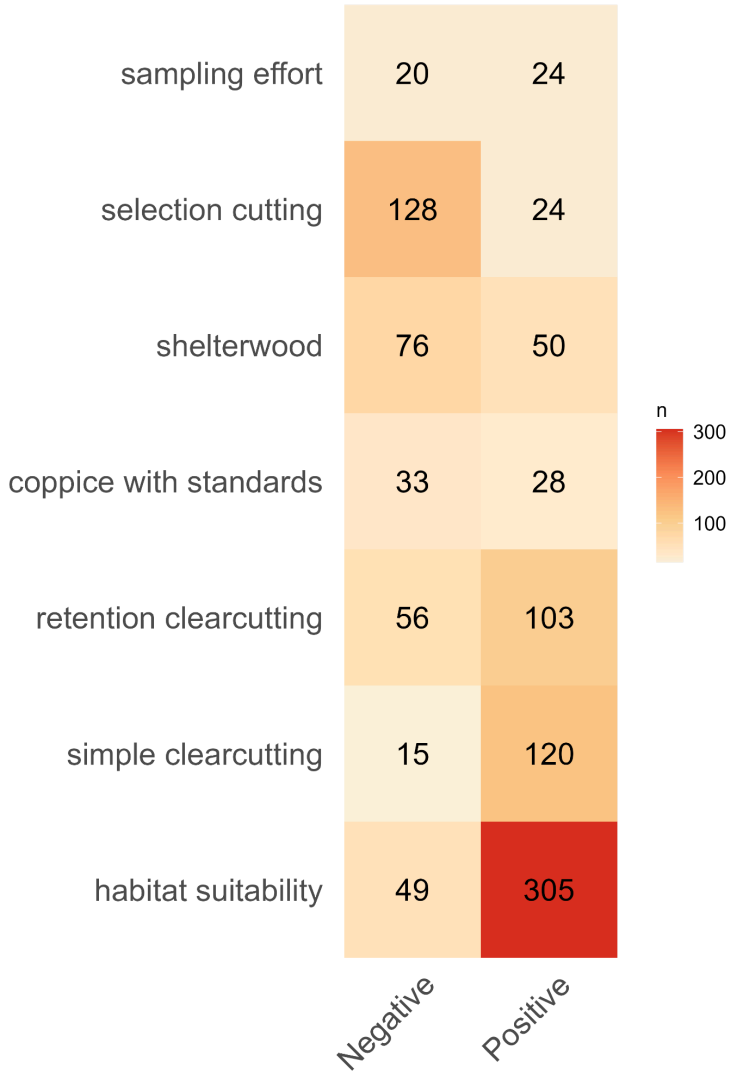


Figure 11 - Heatmap representing the number of species with significant positive and negative coefficients for the predictors for vascular plants. Each tile's color intensity represents the count of species (n) responding positively or negatively to the

respective predictor, where warmer (more intense) colors indicate higher counts. The numerical values in each tile display the exact number of species in each category.

4. Discussion

This study is the first attempt to assess the impact of different silvicultural regimes on the individual species of three taxonomic groups. Our results definitely hush up ideological contrasts on forest management sustainability for biodiversity by providing a highly complex and nuanced picture deriving from the interplay of species-specific ecological requirements and the range of modifications deriving from different silvicultural regimes.

As a matter of fact, accounting for fine-grain multi-taxon biodiversity data across a continental extent, we were not able to identify a good or a bad management for biodiversity, but we demonstrated that all the silvicultural regimes commonly applied in Europe do have an impact on species diversity. This species-specific impact should be acknowledged and accounted for in forest management planning and implementation. Further analyses on species conservation and ecological value will allow to define broad-scale pathways towards a fine-scale management that is actually sustainable for biodiversity.

Our work also paves the road to the identification of direct biodiversity indicators that could be used to evaluate the impact of different silvicultural practices in different contexts.

Notwithstanding limitations related to data heterogeneity and the coarseness of the silvicultural categories here used, this study is an unprecedented effort to identify mechanistic links between silvicultural regimes and the presence of individual species.

4.1 Bryophytes species are negatively affected by management practices

Our results underline how the vast majority of bryophyte species are negatively affected by forest management practices, when compared to unmanaged forests. Ecologically speaking, epiphytic bryophytes are highly sensitive to changes in their environment, particularly when related to microclimatic conditions, such as light availability, moisture levels, and substrate quality and availability (Hodgetts, 2019). In terms of microclimate, epiphytic bryophytes typically need stable, moist, and shaded conditions provided by dense, undisturbed canopies, which can be altered by silvicultural interventions (Berg et al., 2002). Even a minor increase in light intensity can cause substantial shifts in moisture levels and result in habitat conditions that are unsuitable for many bryophyte species (Frego, 2007). The availability of substrates is another key factor determining the diversity and distribution of epiphytic organisms, including bryophytes, which develop on living trees and deadwood (Dittrich et al., 2014). The larger a tree, the greater and more diverse the surface and microhabitats it provides. Importantly, varying levels of moisture, bark texture, and

decay stages, which can support a diverse bryophyte community (Ódor & Van Hees, 2004). Deadwood, especially in later stages of decay, is a crucial substrate for epiphytic bryophytes. As wood decays, its structural complexity increases, providing a variety of microhabitats and microclimatic conditions to this group of species (Harmon et al., 1986).

In unmanaged forests, the canopy cover continuity over time and the high amounts of deadwood determine environmental conditions that are extremely favorable for bryophyte communities, such as stable humidity, and low variability in temperature, are critical for bryophyte survival and growth (Angers et al., 2005). In contrast, all forms of active management, including the least intensive ones, tend to disrupt these environmental conditions by periodically removing part of the canopy and releasing low to none deadwood within forest ecosystems (Bauhus et al., 2009). When comparing different silvicultural regimes, selection cutting and shelterwood, which are considered less intensive than clear cutting regimes for instance, still negatively impacted respectively 37.5% and 28.6% of the bryophyte species we analysed. These methods involve the partial removal of canopy cover and the decrease of deadwood amount and quality, which still result in changes in environmental conditions (Angers et al., 2005), leading to the subsequent decline of sensitive epiphytic bryophytes.

Individual species responses reveal that these responses are linked to specific ecological needs (Supplementary Information 1.1). Among the species responding positively to harvesting practices, however, only *Orthotrichum pumilum* may be associated with high light intensity, i.e., has a low "forest" affinity in the Bryophytes of Europe Traits (BETs) dataset (Zuijlen et al., 2023).

Therefore, it is likely that most bryophyte species are limited by the lack of structural attributes that may support them (Alatalo et al., 2020; Dittrich et al., 2014; Ódor & Van Hees, 2004). The retention of trees and deadwood, especially in later stages of decay, maintains the microclimatic conditions more stable and provides key substrates to bryophyte communities (Gustafsson et al., 2012). Close-to-nature forestry techniques, which aim to mimic the natural processes and disturbances of old-growth forests, could provide a solution. These practices include continuous cover forestry and variable retention harvesting, both of which focus on maintaining forest structure and preserving key microhabitats such as deadwood and mature trees (Pommerening & Murphy, 2004). In some cases, passive restoration or the intentional creation of microhabitats that mimic unmanaged conditions may be necessary to support bryophyte populations in managed forests (Fedrowitz et al., 2014), as even the most conservative silvicultural strategies still need to be adjusted to minimize their impacts on bryophytes.

Since, the lack of specific forest structures is tightly intermingled with the low ecological continuity of forests, creating set-aside areas which ensure the

occurrence of ecologically continuous patches where even slow-colonizing species may thrive may be a successful option (Nordén et al., 2014).

4.2 Lichens show a variety of responses depending on the type of management

Lichen species displayed heterogeneous responses to forest management. Selection cutting, shelterwood, and coppice with standards emerged as important drivers of the occurrence of epiphytic lichen species. Surprisingly, selection cutting, which could be considered one of the least intensive in our categorization, influenced the largest share of species, affecting 55 species (27.4%), with a predominance of negative responses, when compared to unmanaged conditions. Shelterwood affected 43 species (21.4%), resulting in both positive and negative responses. Coppice with standards, while affecting fewer species overall, still had a noticeable positive impact on all of them (24 species, 11.9%). Other management strategies, including simple clearcutting and retention clearcutting, showed influence on a low number of lichen species and a relatively balanced array of positive and negative responses.

Similarly to bryophytes, epiphytic lichens are highly sensitive to changes in light, moisture, and substrate availability, all of which are affected by forest management practices (Boch et al., 2013; Nascimbene et al., 2012). Higher-intensity management practices are generally associated with a decrease in epiphytic lichen species richness and a shift in community composition, as a more substantial habitat disturbance alters the stable conditions many lichens depend on (Aragón et al., 2001). Selection cutting is supposed to retain substantial canopy cover, preserving the structure of the forest and environmental conditions crucial for lichen communities (Nascimbene et al., 2007, 2012). Our results show, however, opposite trends, with low-intensity practices, such as selection cutting, negatively impacting the occurrence of several lichen species.These results stress the wide range of ecological requirements across lichen species and the need to account for these differences. We found species adapted to open, light-rich environments, species needing stable, shaded microclimates, and species with mixed needs (Supplementary Information 1.2) . Species showing only positive responses to management (32 species) include several fruticose lichens, which thrive in higher light conditions (Ódor & Van Hees, 2004). Species with only negative responses (46 species) should be considered as adapted to stable, low-disturbance conditions, and confirm the strong dependence of many lichen species to undisturbed forest structures. For example, several crustose lichens, which rely on stable, undisturbed, and humid environments, showed negative responses to more disruptive practices. For mixed-effect species (11 species), the variation in response likely stems from their flexible ecological requirements, allowing them to adapt to a wider range of management impacts (Kiraly et al., 2013).

The different responses of lichen species to forest management highlight the need for integrated practices that can account for their varied ecological requirements (Nascimbene et al., 2007). Lichen communities are complex, encompassing species that range widely in their tolerance to light, moisture, and habitat continuity. A one-size-fits-all approach is unlikely to be effective for this taxonomic group. A landscape-level strategy, incorporating a mix of management practices as proposed in the triad framework (Betts et al., 2021), could provide a solution by fostering a patchwork of conditions that meets the ecological demands of a broader array of lichen species. By further investigating the conservation value of lichen species, it will be possible to align management practices with the habitat preferences and sensitivities of endangered and protected species.

4.3 Vascular plants show positive responses to intensive management strategies

Intensive silvicultural regimes, such as simple clearcutting and retention clearcutting, showed a positive influence on the occurrence of several vascular plant species, with 120 species (16.9%) and 103 species (14.6%) responding positively, respectively. On the other hand, selection cutting, a less intense practice aimed at maintaining partial canopy cover, had a negative impact on a large share of vascular plant species (128 species, 18.1%). Other practices had a more balanced and less significant effect on species occurrence.

The impacts of forest management on vascular plant species are largely tied to the effect of these practices on understory light availability, moisture levels and soil disturbance (Chianucci et al., 2024). Intensive practices, like simple clearcutting and retention clearcutting, often expose the forest floor to high levels of sunlight, which can promote the presence of light-demanding plant species (Dormann et al., 2020), often early-successional and generalist species. Additionally, these practices can increase soil disturbance, which further enhances the presence of species adapted to disturbed habitats with positive effect on species richness (Vellend, 2004). In contrast, less intensive methods such as selection cutting, preserve canopy cover by avoiding sudden shifts in light availability and soil conditions (Gustafsson et al., 2012; Pommerening & Murphy, 2004). While these practices often support less abundant, shade-tolerant species, they restrict the presence of light-demanding plants. Shelterwood cutting tend to create a mosaic of light conditions, promoting both light-tolerant and shade-adapted species (Kirby et al., 2017), leading to a more balanced but less significant effect on vascular plant species occurrence. On these basis we identified three groups of vascular plant species' response to management (Supplementary Information 1.3). The first group, comprising 152 species, showed only positive effects from management practices. Many of these species are generalist or disturbance-tolerant species that thrive in high-light environments and increased nutrient availability following canopy removal, taking advantage of the reduced competition in these disturbed areas. The second group, encompassing 114

species, showed exclusively negative responses to management practices. These species are shade-tolerant understory plants that require stable, closed-canopy environments, explaining their sensitivity to management-related disturbances. The third group, consisting of 62 species, exhibited mixed responses to management strategies. These species may be considered habitat generalists, with the capacity to adapt to a range of conditions generated by different management intensities.

While intensive forest management can indeed promote the presence of a large amount of vascular plant species, many of these are likely adapted to open environments that are not strictly forest-dependent (Dormann et al., 2020; Pykälä, 2004). Shade-tolerant species, which often rely on stable microclimates, consistent canopy cover, and regulated moisture levels may be particularly vulnerable to the disruptions caused by intensive practices (Burrascano et al., 2018). These plants generally have more specialized habitat requirements and lower colonization ability, making them less resilient to the rapid shifts in light and soil conditions that management can induce. Sustainable forest management should prioritize strategies that maintain the ecological integrity necessary to support also forest-specialist species, ensuring that conservation efforts foster the diversity of forest-dependent communities.

5. Conclusions

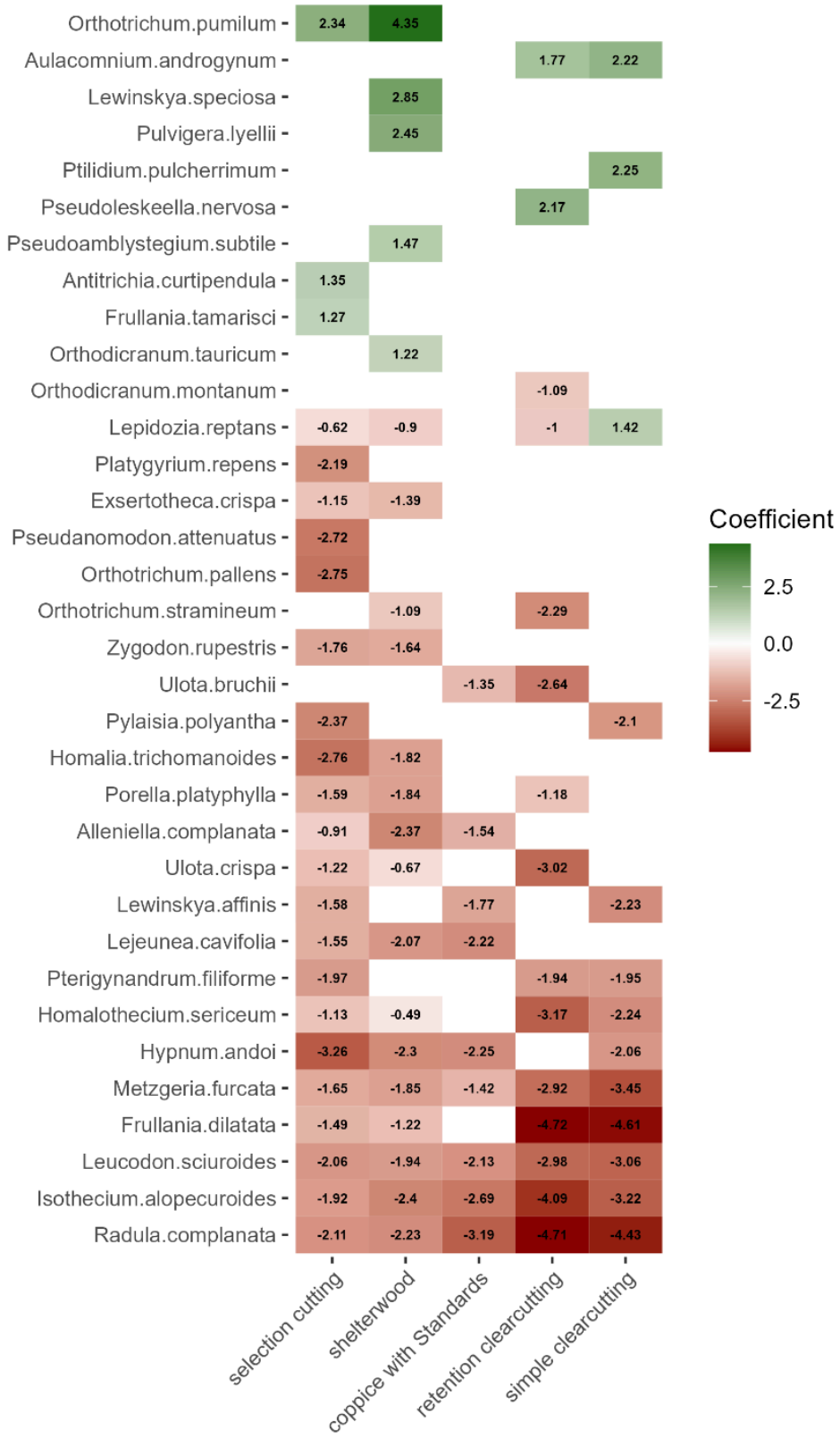
Based on our findings, focusing exclusively on species richness as a measure for biodiversity conservation in managed forests has substantial flaws. Overlooking the unique ecological roles and habitat requirements of individual species may lead to biased recommendations for biodiversity Sustainable Forest Management (SFM). Some taxonomic groups, like bryophytes, respond relatively consistently to forest management, however, we found a considerable degree of variability within each taxonomic group, highlighting the limitations of a one-size-fits-all approach. This underscores the need for management approaches to meet species-specific habitat needs, rather than only aiming to maximize total species counts. An integrated landscape-level management approach, incorporating heterogeneous forest management practices, could help sustain a wide range of species and ecological niches by generating a mosaic of habitats (Betts et al., 2021; Blattert et al., 2023) while also maintaining forest connectivity and continuity, which are especially crucial for the long-term maintenance of forest-specialist species relying on stable conditions and habitat structures (Nordén et al., 2014).

Through this study, we provide a comprehensive dataset detailing broad scale species-specific responses to forest management practices across three taxonomic groups. This offers a foundation for assessing management impacts on biodiversity and supports the development of targeted, sustainable forest conservation strategies. This dataset, thus, has the potential to inform policies and management plans that prioritize biodiversity conservation in European forests.

While our study provides comprehensive insights into the responses of bryophytes, lichens, and vascular plants to forest management practices, there are limitations associated with data coverage and typological gaps in the database that we used. Expanding biodiversity monitoring efforts and filling these typological gaps will be essential to have a more accurate and complete picture of forest biodiversity dynamics, especially in light of the EU Biodiversity Monitoring law (European Commission, 2023).

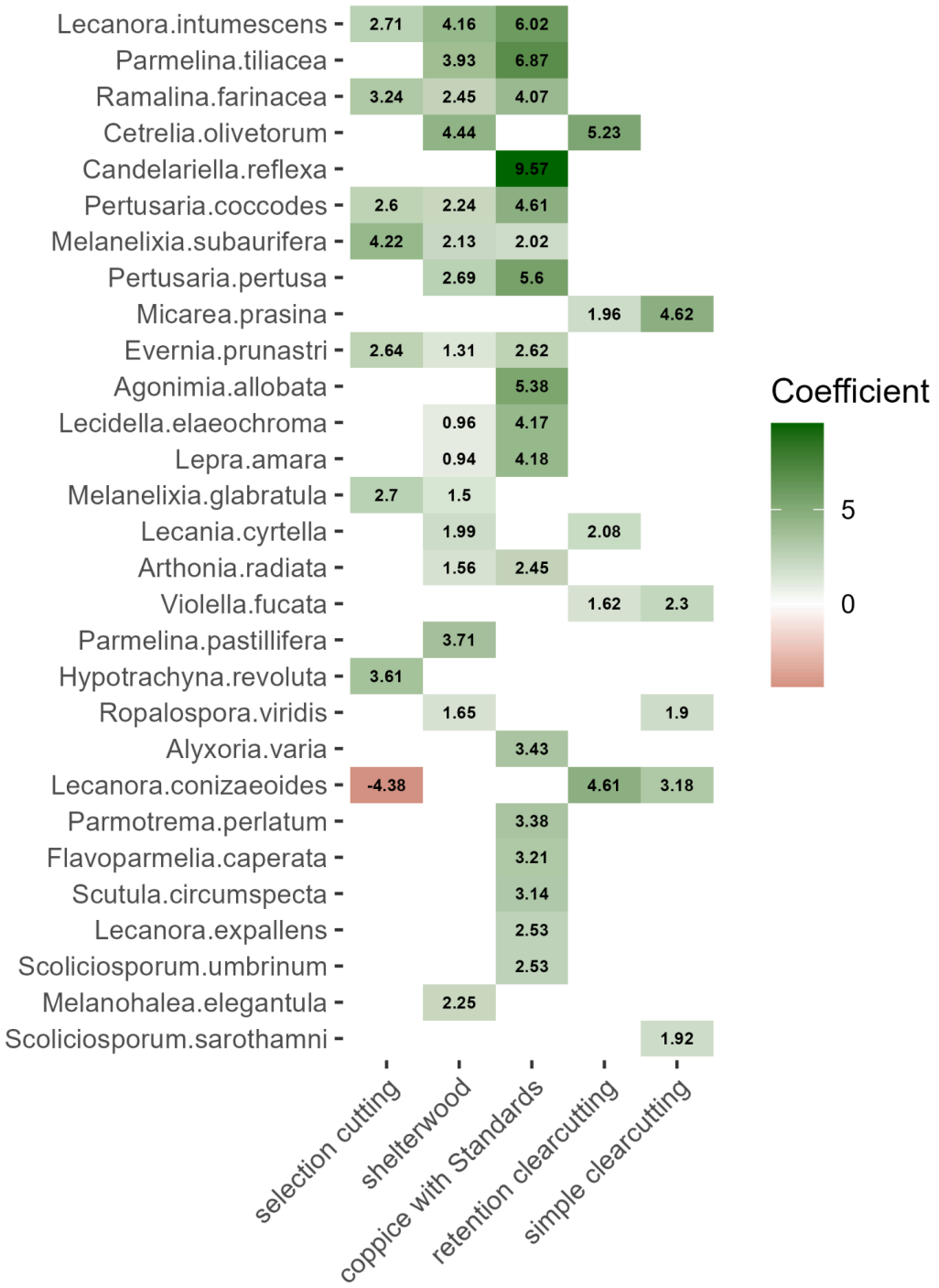
Supplementary Information

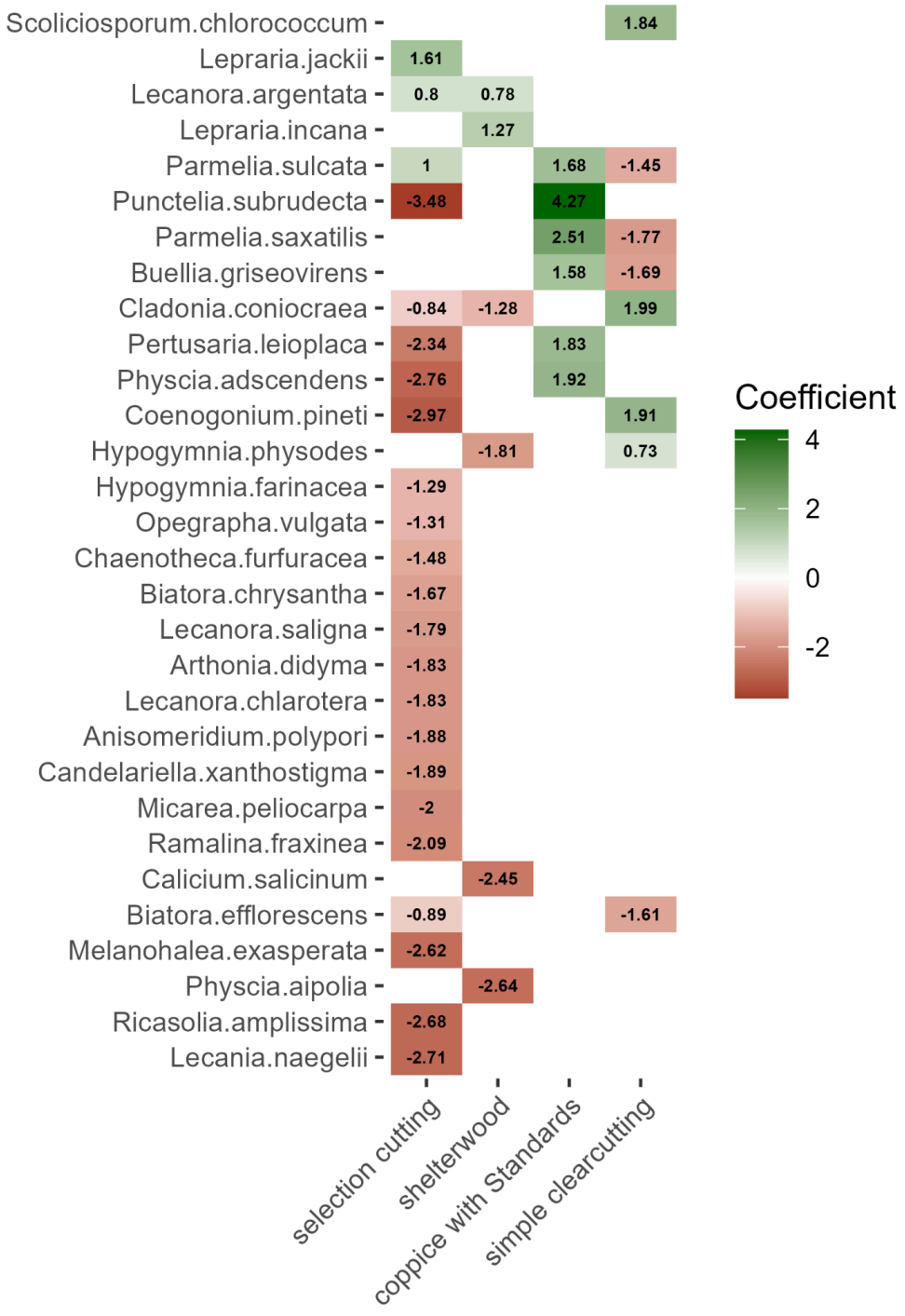
Supplementary Information 1.1

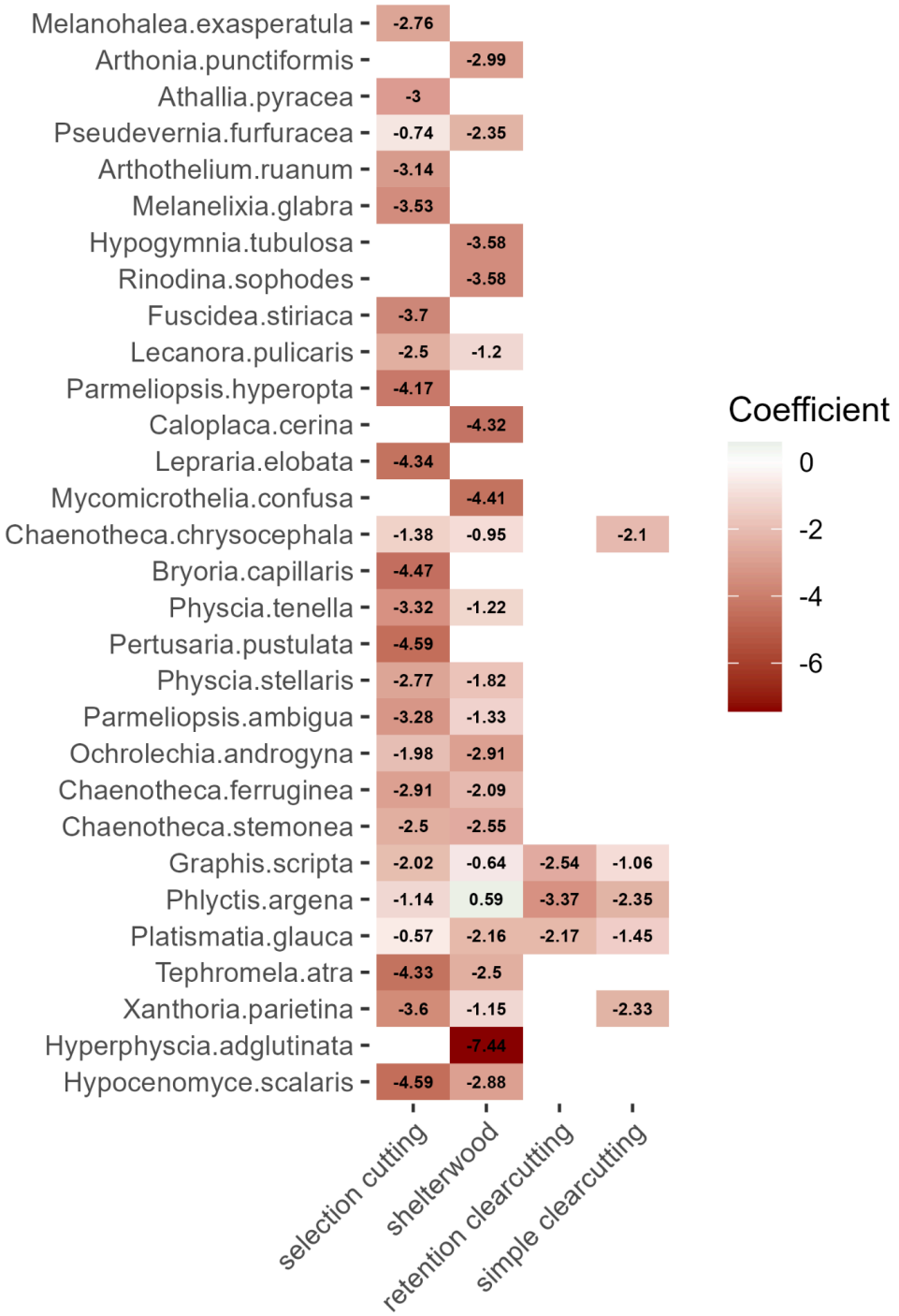


Supplementary Information 1.1 - Heatmap displaying significant bryophyte species coefficients across various management strategies, adapted from Trentanovi et al. (2023). Species are arranged in descending order from top to bottom, with those at the top exhibiting the highest cumulative positive coefficient values. Only significant coefficients are shown, providing insights into each species' response to management practices.

Supplementary Information 1.2

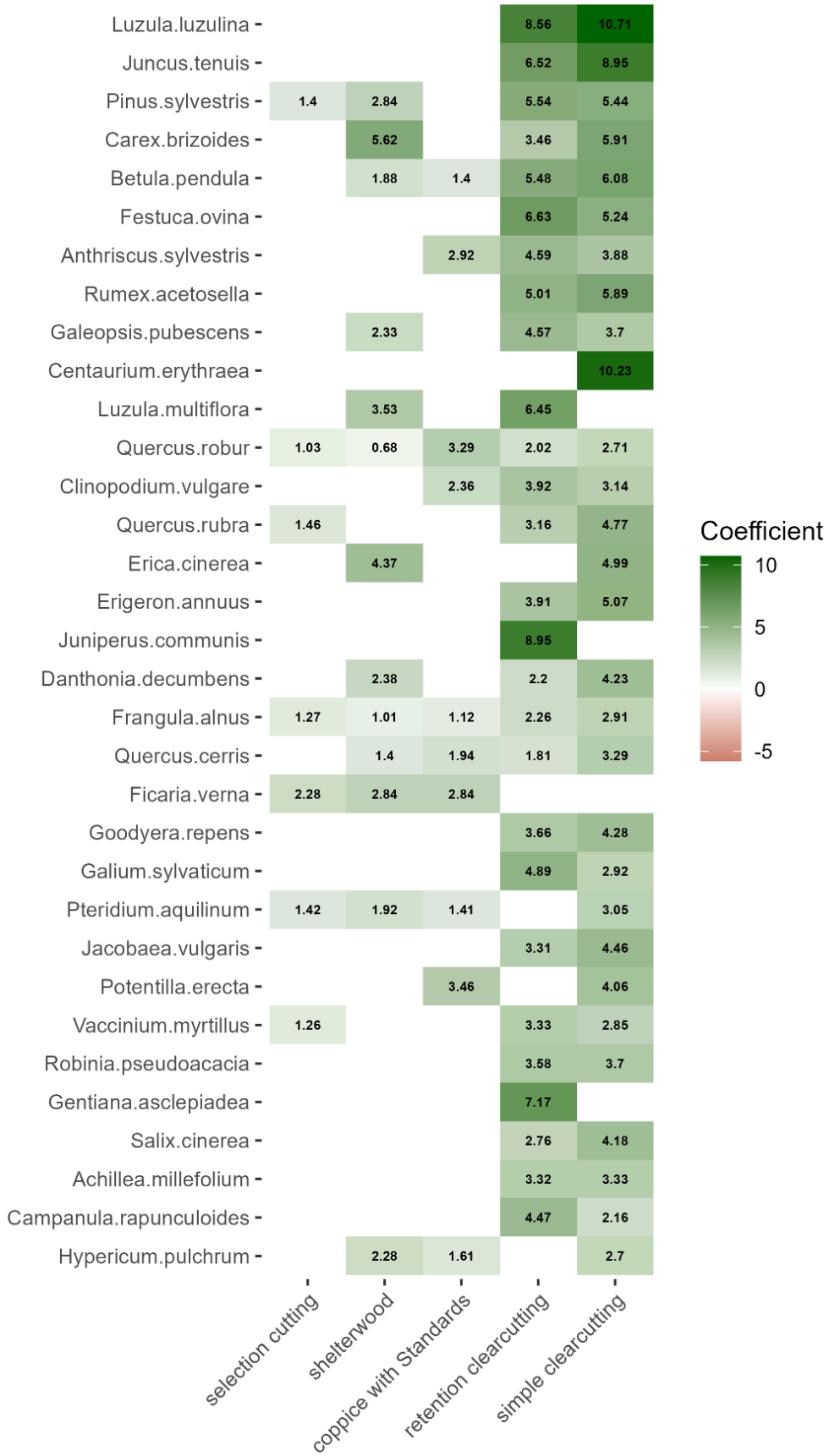


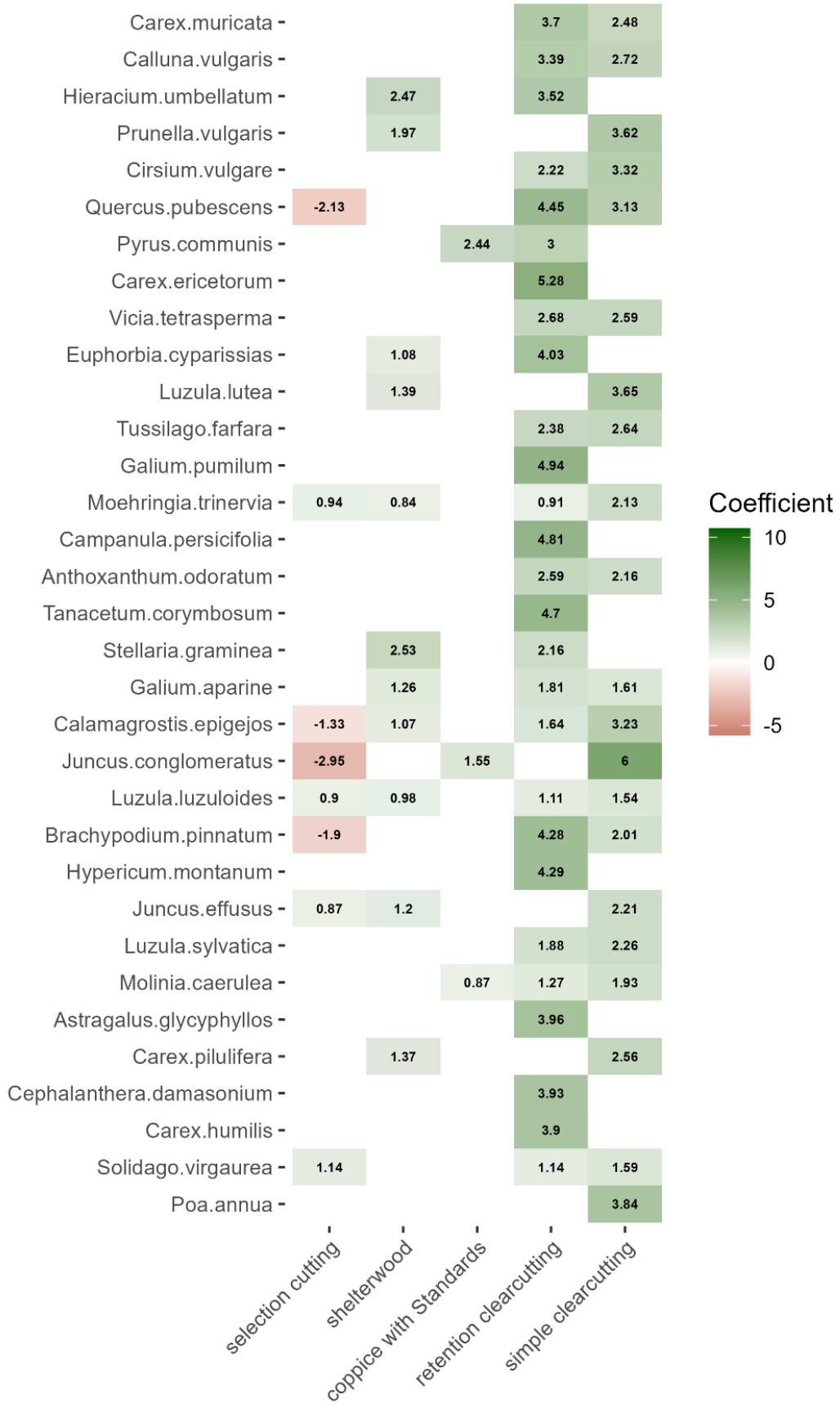

Scoliciosporum.chlorococcum
Lepraria.jackii
Lecanora.argentata
Lepraria.incana
Parmelia.sulcata
Punctelia.subrudecta
Parmelia.saxatilis
Buellia.griseovirens
Cladonia.coniocraea
Pertusaria.leioplaca
Physcia.adscendens
Coenogonium.pineti
Hypogymnia.physodes
Hypogymnia.farinacea
Opegrapha.vulgata
Chaenotheca.furfuracea
Biatora.chrysantha
Lecanora.saligna
Arthonia.didyma
Lecanora.chlarotera
Anisomeridium.polypori
Candelariella.xanthostigma
Micarea.peliocarpa
Ramalina.fraxinea
Calicium.salicinum
Biatora.efflorescens
Melanohalea.exasperata
Physcia.aipolia
Ricasolia.amplissima
Lecania.naegelii
1.84
1.61
0.8 0.78
1.27
1 1.68 -1.45
-3.48 4.27
2.51 -1.77
1.58 -1.69
-0.84 -1.28 1.99
-2.34 1.83
-2.76 1.92
-2.97 1.91
-1.81 0.73
-1.29
-1.31
-1.48
-1.67
-1.79
-1.83
-1.83
-1.88
-1.89
-2
-2.09
-2.45
-0.89 -1.61
-2.62
-2.64
-2.68
-2.71
selection cutting
shelterwood
coppice with Standards
simple clearcutting
Coefficient
4
2
0
-2

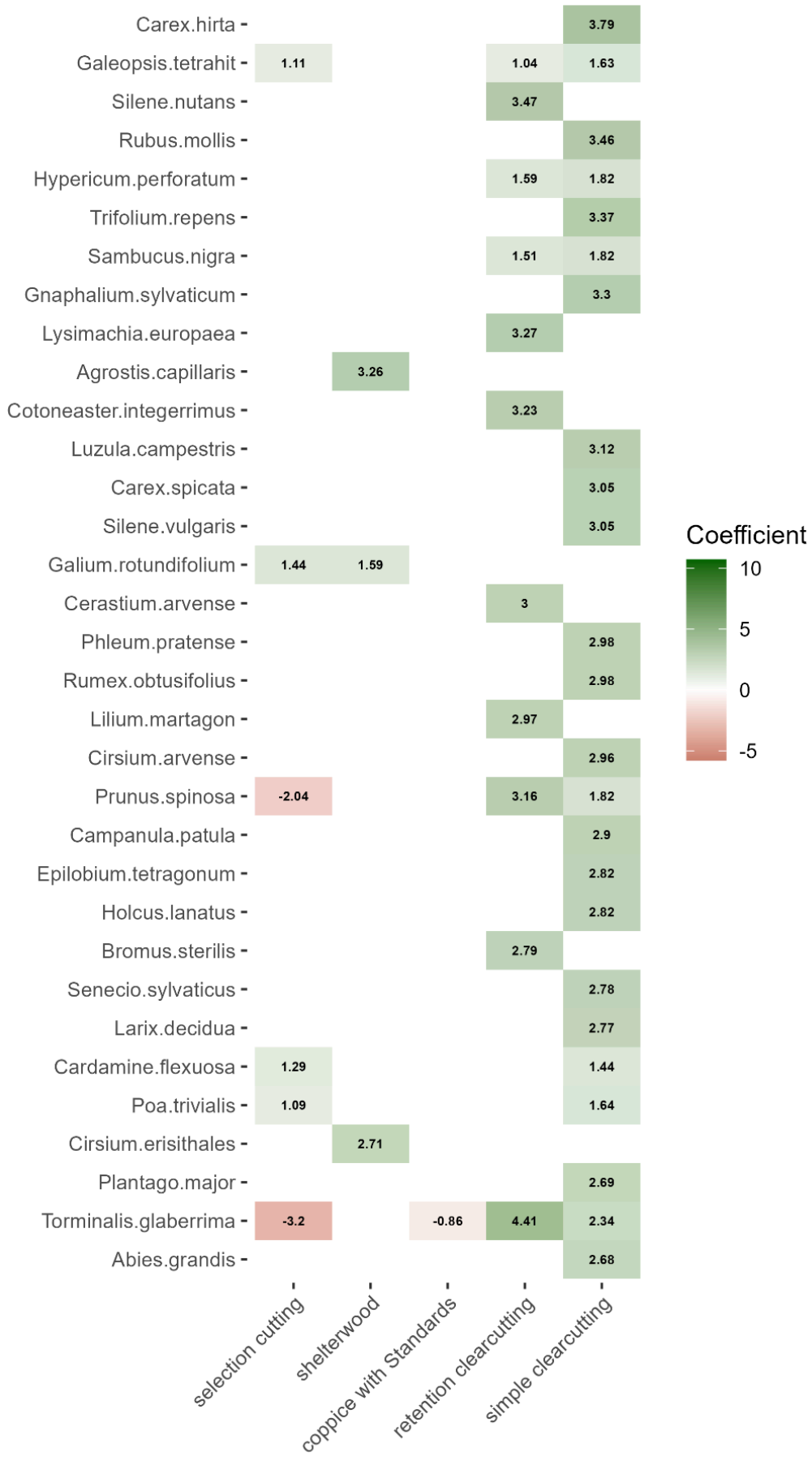


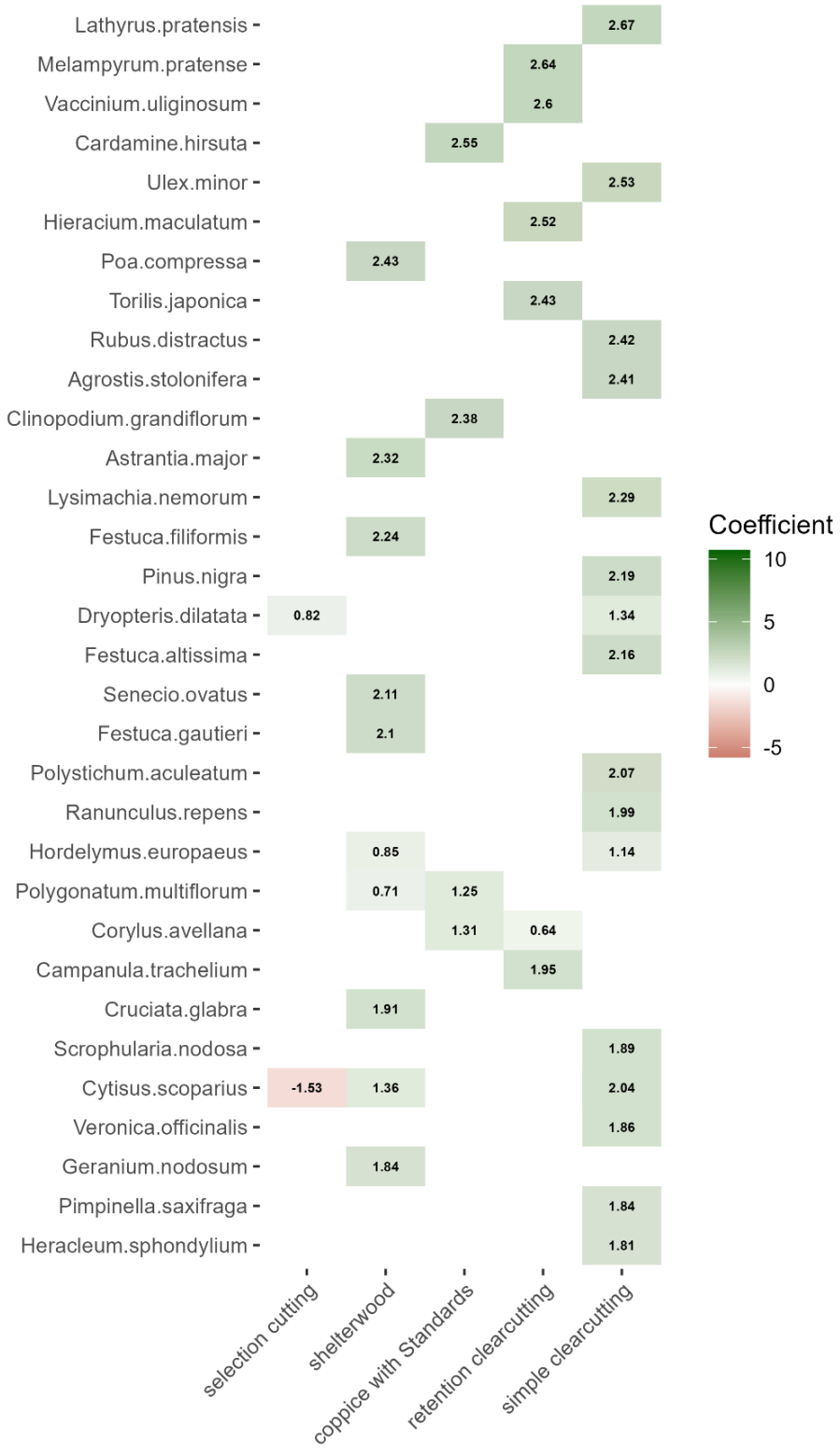
Supplementary Information 1.2 - Heatmap displaying significant lichen species coefficients across various management strategies, adapted from Trentanovi et al. (2023). Species are arranged in descending order from top to bottom, with those at the top exhibiting the highest cumulative positive coefficient values. Only significant coefficients are shown, providing insights into each species' response to management practices.

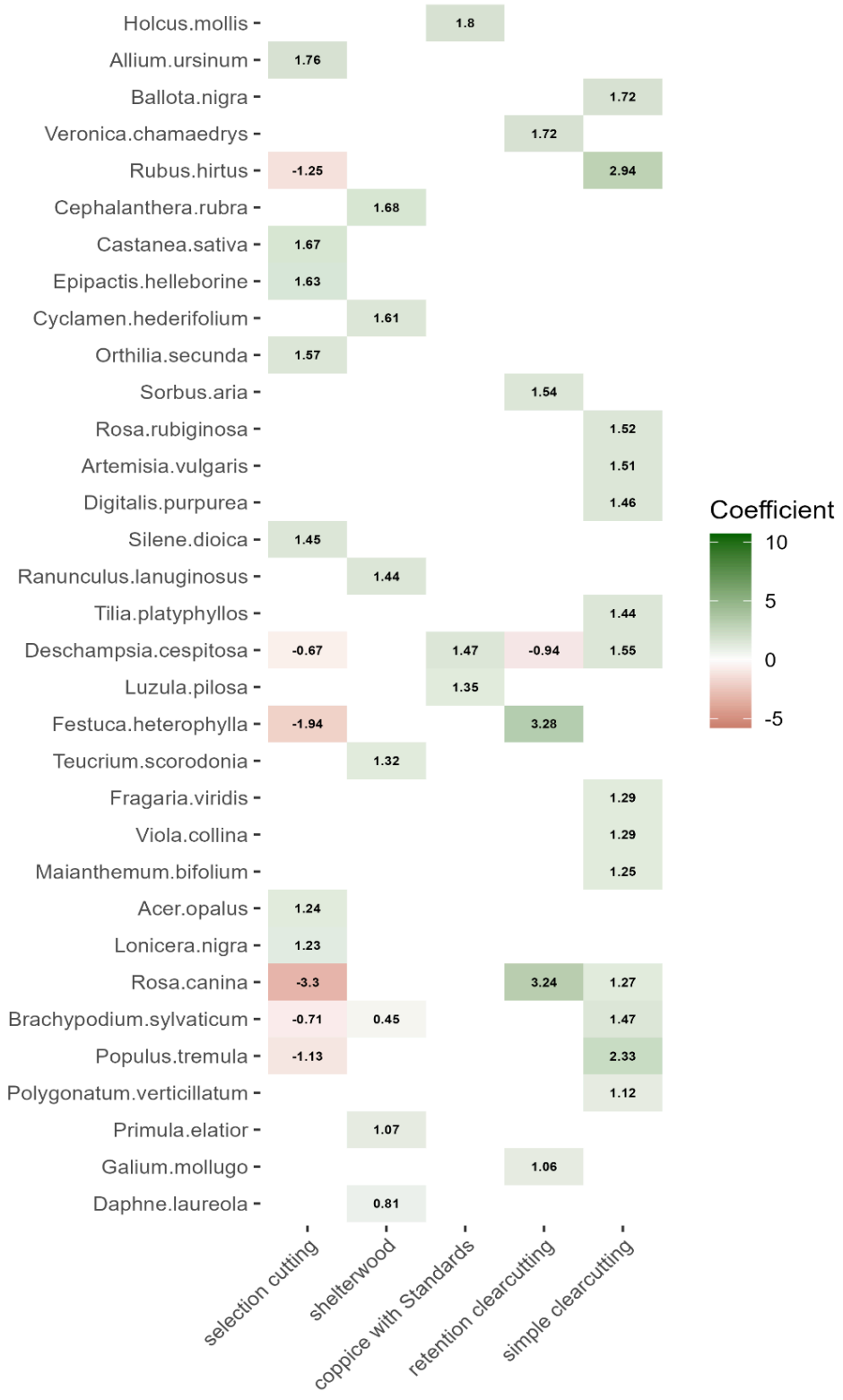
Supplementary Information 1.3

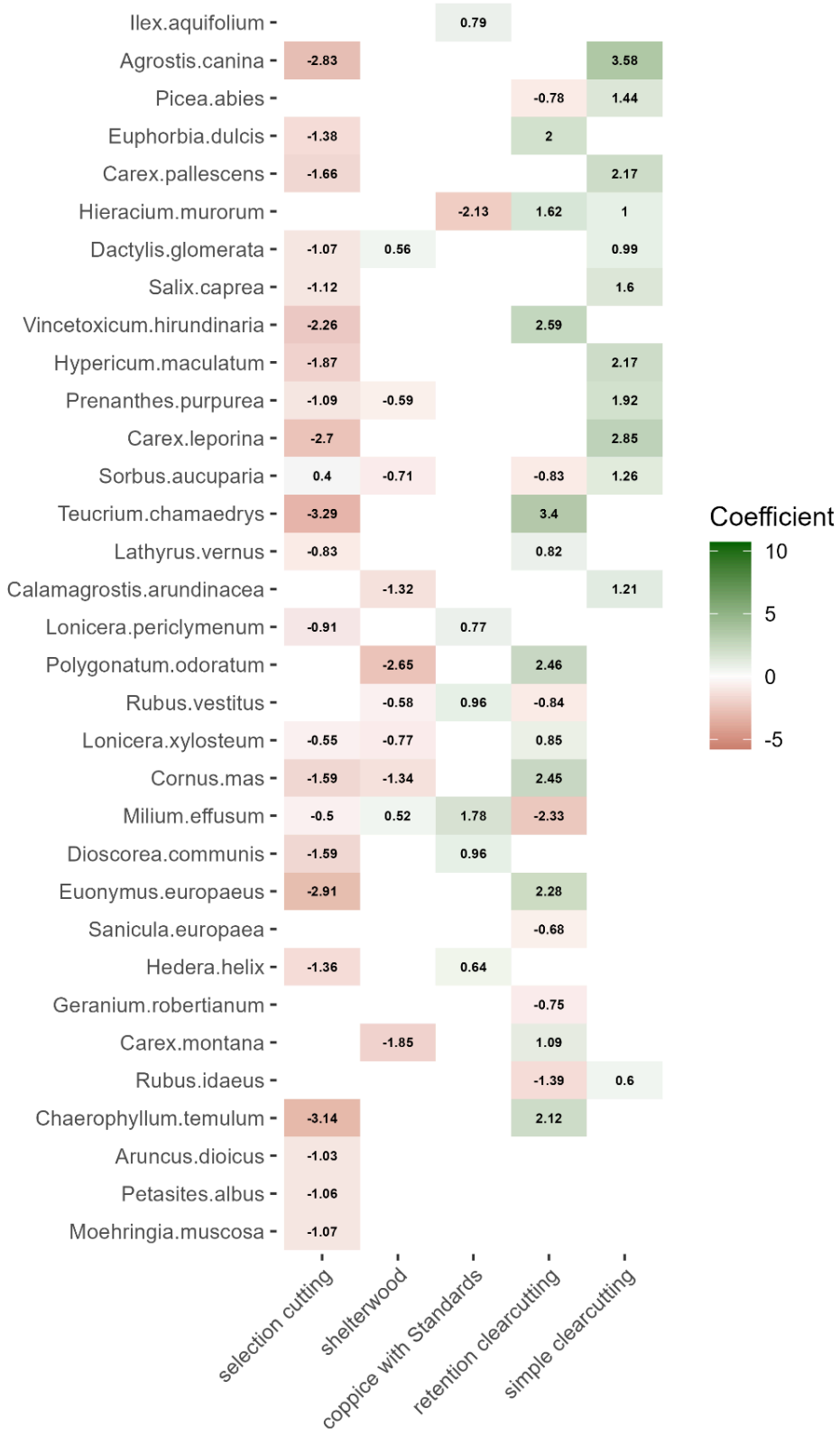


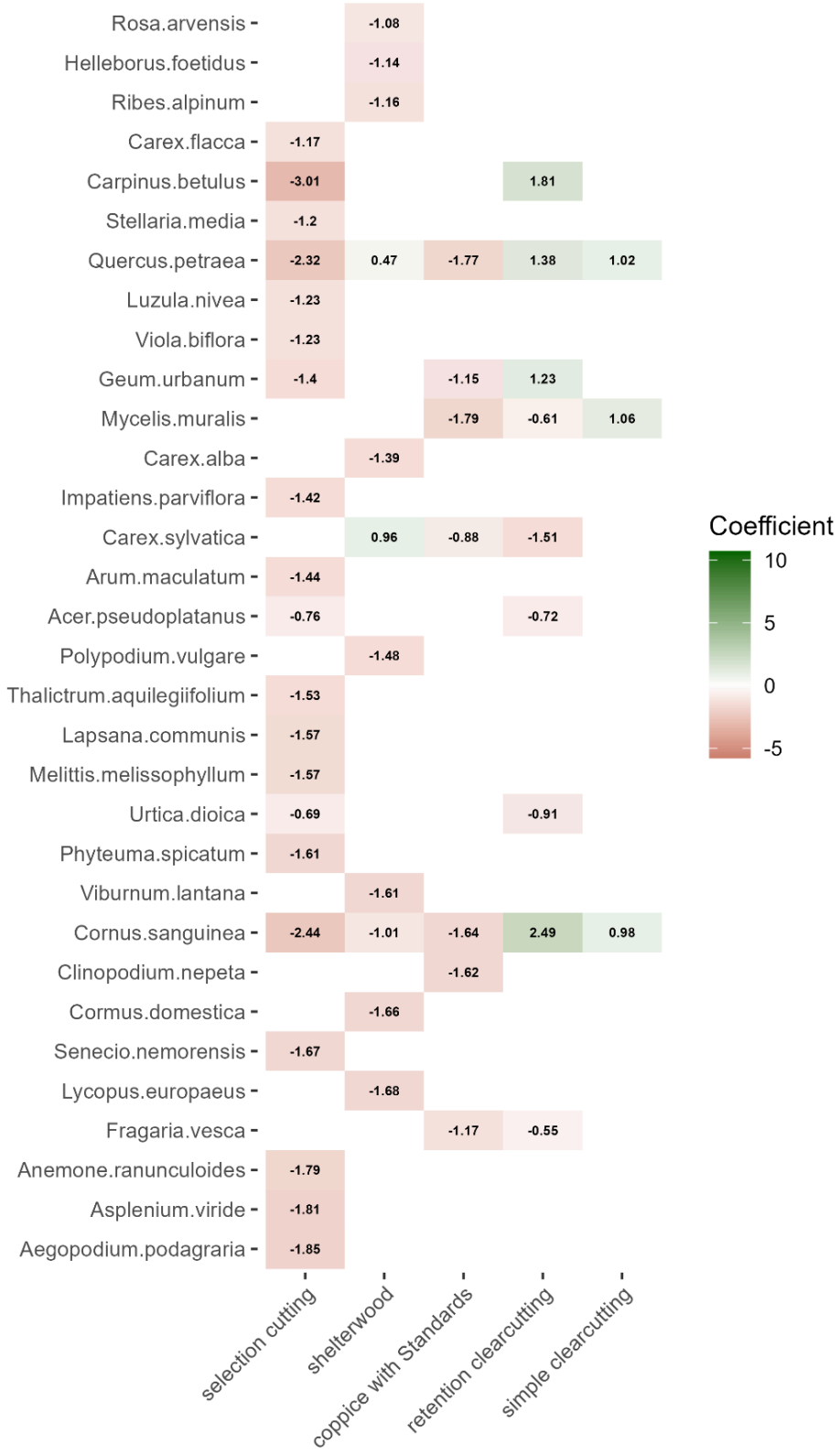

Carex.muricata
Calluna.vulgaris
Hieracium.umbellatum
Prunella.vulgaris
Cirsium.vulgare
Quercus.pubescens
Pyrus.communis
Carex.ericetorum
Vicia.tetrasperma
Euphorbia.cyparissias
Luzula.lutea
Tussilago.farfara
Galium.pumilum
Moehringia.trinervia
Campanula.persicifolia
Anthoxanthum.odoratum
Tanacetum.corymbosum
Stellaria.graminea
Galium.aparine
Calamagrostis.epigejos
Juncus.conglomeratus
Luzula.luzuloides
Brachypodium.pinnatum
Hypericum.montanum
Juncus.effusus
Luzula.sylvatica
Molinia.caerulea
Astragalus.glycyphyllos
Carex.pilulifera
Cephalanthera.damasonium
Carex.humilis
Solidago.virgaurea
Poa.annua
3.7 2.48
3.39 2.72
2.47 3.52
1.97 3.62
2.22 3.32
-2.13 4.45 3.13
2.44 3
5.28
2.68 2.59
1.08 4.03
1.39 3.65
2.38 2.64
4.94
0.94 0.84 0.91 2.13
4.81
2.59 2.16
4.7
2.53 2.16
1.26 1.81 1.61
-1.33 1.07 1.64 3.23
-2.95 1.55 6
0.9 0.98 1.11 1.54
-1.9 4.28 2.01
4.29
0.87 1.2 2.21
1.88 2.26
0.87 1.27 1.93
3.96
1.37 2.56
3.93
3.9
1.14 1.14 1.59
3.84
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5

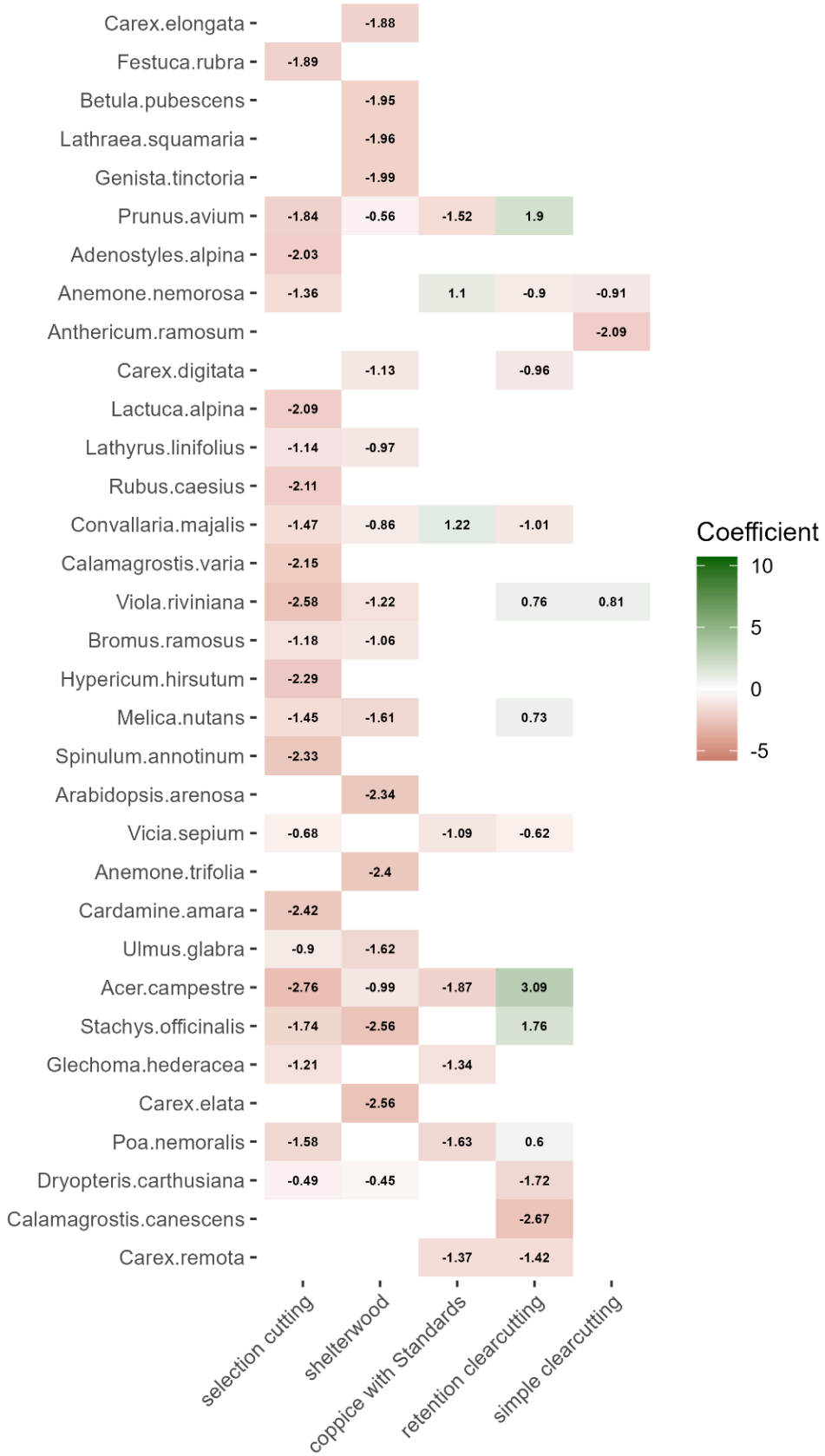

Carex.hirta
Galeopsis.tetrahit
Silene.nutans
Rubus.mollis
Hypericum.perforatum
Trifolium.repens
Sambucus.nigra
Gnaphalium.sylvaticum
Lysimachia.europaea
Agrostis.capillaris
Cotoneaster.integerrimus
Luzula.campestris
Carex.spicata
Silene.vulgaris
Galium.rotundifolium
Cerastium.arvense
Phleum.pratense
Rumex.obtusifolius
Lilium.martagon
Cirsium.arvense
Prunus.spinosa
Campanula.patula
Epilobium.tetragonum
Holcus.lanatus
Bromus.sterilis
Senecio.sylvaticus
Larix.decidua
Cardamine.flexuosa
Poa.trivialis
Cirsium.erisithales
Plantago.major
Torminalis.glaberrima
Abies.grandis
3.79
1.11
1.04
1.63
3.47
3.46
1.59
1.82
3.37
1.51
1.82
3.3
3.27
3.26
3.23
3.12
3.05
3.05
1.44
1.59
3
2.98
2.98
2.97
2.96
-2.04
3.16
1.82
2.9
2.82
2.82
2.79
2.78
2.77
1.29
1.44
1.09
1.64
2.71
2.69
-3.2
-0.86
4.41
2.34
2.68
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5

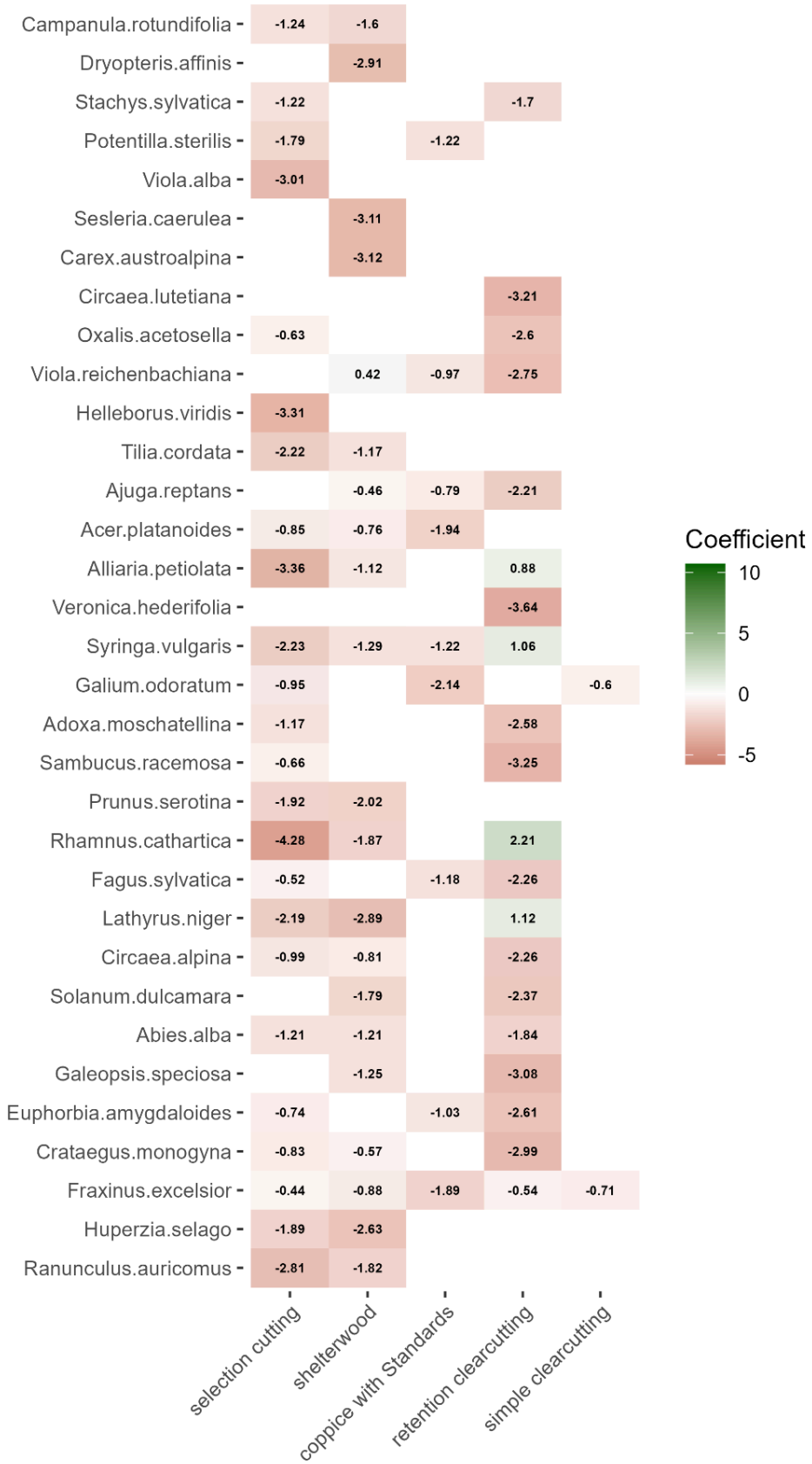

Lathyrus.pratensis
Melampyrum.pratense
Vaccinium.uliginosum
Cardamine.hirsuta
Ulex.minor
Hieracium.maculatum
Poa.compressa
Torilis.japonica
Rubus.distractus
Agrostis.stolonifera
Clinopodium.grandiflorum
Astrantia.major
Lysimachia.nemorum
Festuca.filiformis
Pinus.nigra
Dryopteris.dilatata
Festuca.altissima
Senecio.ovatus
Festuca.gautieri
Polystichum.aculeatum
Ranunculus.repens
Hordelymus.europaeus
Polygonatum.multiflorum
Corylus.avellana
Campanula.trachelium
Cruciata.glabra
Scrophularia.nodosa
Cytisus.scoparius
Veronica.officinalis
Geranium.nodosum
Pimpinella.saxifraga
Heracleum.sphondylium
2.67
2.64
2.6
2.55
2.53
2.52
2.43
2.43
2.42
2.41
2.38
2.32
2.29
2.24
2.19
0.82
1.34
2.16
2.11
2.1
2.07
1.99
0.85
1.14
0.71
1.25
1.31
0.64
1.95
1.91
1.89
-1.53
1.36
2.04
1.86
1.84
1.84
1.81
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5

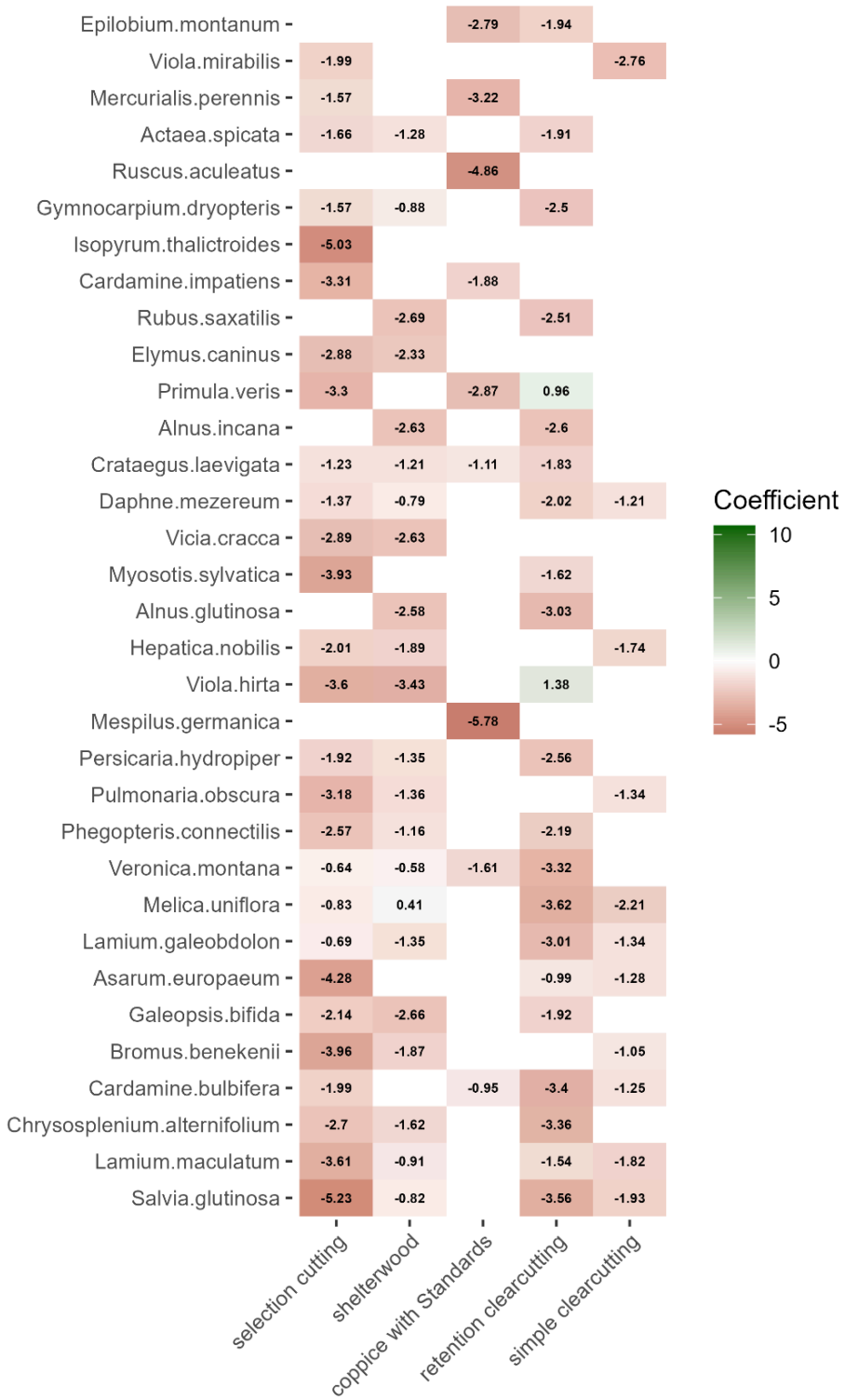

Holcus.mollis
Allium.ursinum
Ballota.nigra
Veronica.chamaedrys
Rubus.hirtus
Cephalanthera.rubra
Castanea.sativa
Epipactis.helleborine
Cyclamen.hederifolium
Orthilia.secunda
Sorbus.aria
Rosa.rubiginosa
Artemisia.vulgaris
Digitalis.purpurea
Silene.dioica
Ranunculus.lanuginosus
Tilia.platyphyllos
Deschampsia.cespitosa
Luzula.pilosa
Festuca.heterophylla
Teucrium.scorodonia
Fragaria.viridis
Viola.collina
Maianthemum.bifolium
Acer.opalus
Lonicera.nigra
Rosa.canina
Brachypodium.sylvaticum
Populus.tremula
Polygonatum.verticillatum
Primula.elatior
Galium.mollugo
Daphne.laureola
1.8
1.76
1.72
1.72
-1.25
2.94
1.68
1.67
1.63
1.61
1.57
1.54
1.52
1.51
1.46
1.45
1.44
1.44
-0.67
1.47
-0.94
1.55
1.35
-1.94
3.28
1.32
1.29
1.29
1.25
1.24
1.23
-3.3
3.24
1.27
-0.71
0.45
1.47
-1.13
2.33
1.12
1.07
1.06
0.81
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5


Ilex.aquifolium
Agrostis.canina
Picea.abies
Euphorbia.dulcis
Carex.pallescens
Hieracium.murorum
Dactylis.glomerata
Salix.caprea
Vincetoxicum.hirundinaria
Hypericum.maculatum
Prenanthes.purpurea
Carex.leporina
Sorbus.aucuparia
Teucrium.chamaedrys
Lathyrus.vernus
Calamagrostis.arundinacea
Lonicera.periclymenum
Polygonatum.odoratum
Rubus.vestitus
Lonicera.xylosteum
Cornus.mas
Milium.effusum
Dioscorea.communis
Euonymus.europaeus
Sanicula.europaea
Hedera.helix
Geranium.robertianum
Carex.montana
Rubus.idaeus
Chaerophyllum.temulum
Aruncus.dioicus
Petasites.albus
Moehringia.muscosa
0.79
-2.83 3.58
-0.78 1.44
-1.38 2
-1.66 2.17
-2.13 1.62 1
-1.07 0.56 0.99
-1.12 1.6
-2.26 2.59
-1.87 2.17
-1.09 -0.59 1.92
-2.7 2.85
0.4 -0.71 -0.83 1.26
-3.29 3.4
-0.83 0.82
-1.32 1.21
-0.91 0.77
-2.65 2.46
-0.58 0.96 -0.84
-0.55 -0.77 0.85
-1.59 -1.34 2.45
-0.5 0.52 1.78 -2.33
-1.59 0.96
-2.91 2.28
-0.68
-1.36 0.64
-0.75
-1.85 1.09
-1.39 0.6
-3.14 2.12
-1.03
-1.06
-1.07
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5


Rosa.arvensis
Helleborus.foetidus
Ribes.alpinum
Carex.flacca
Carpinus.betulus
Stellaria.media
Quercus.petraea
Luzula.nivea
Viola.biflora
Geum.urbanum
Mycelis.muralis
Carex.alba
Impatiens.parviflora
Carex.sylvatica
Arum.maculatum
Acer.pseudoplatanus
Polypodium.vulgare
Thalictrum.aquilegiifolium
Lapsana.communis
Melittis.melissophyllum
Urtica.dioica
Phyteuma.spicatum
Viburnum.lantana
Cornus.sanguinea
Clinopodium.nepeta
Cormus.domestica
Senecio.nemorensis
Lycopus.europaeus
Fragaria.vesca
Anemone.ranunculoides
Asplenium.viride
Aegopodium.podagraria
-1.08
-1.14
-1.16
-1.17
-3.01
1.81
-1.2
-2.32
0.47
-1.77
1.38
1.02
-1.23
-1.23
-1.4
-1.15
1.23
-1.79
-0.61
1.06
-1.39
-1.42
0.96
-0.88
-1.51
-1.44
-0.76
-0.72
-1.48
-1.53
-1.57
-1.57
-0.69
-0.91
-1.61
-1.61
-2.44
-1.01
-1.64
2.49
0.98
-1.62
-1.66
-1.67
-1.68
-1.17
-0.55
-1.79
-1.81
-1.85
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5


Carex.elongata
Festuca.rubra
Betula.pubescens
Lathraea.squamaria
Genista.tinctoria
Prunus.avium
Adenostyles.alpina
Anemone.nemorosa
Anthericum.ramosum
Carex.digitata
Lactuca.alpina
Lathyrus.linifolius
Rubus.caesius
Convallaria.majalis
Calamagrostis.varia
Viola.riviniana
Bromus.ramosus
Hypericum.hirsutum
Melica.nutans
Spinulum.annotinum
Arabidopsis.arenosa
Vicia.sepium
Anemone.trifolia
Cardamine.amara
Ulmus.glabra
Acer.campestre
Stachys.officinalis
Glechoma.hederacea
Carex.elata
Poa.nemoralis
Dryopteris.carthusiana
Calamagrostis.canescens
Carex.remota
-1.88
-1.89
-1.95
-1.96
-1.99
-1.84 -0.56 -1.52 1.9
-2.03
-1.36 1.1 -0.9 -0.91
-2.09
-1.13 -0.96
-2.09
-1.14 -0.97
-2.11
-1.47 -0.86 1.22 -1.01
-2.15
-2.58 -1.22 0.76 0.81
-1.18 -1.06
-2.29
-1.45 -1.61 0.73
-2.33
-2.34
-0.68 -1.09 -0.62
-2.4
-2.42
-0.9 -1.62
-2.76 -0.99 -1.87 3.09
-1.74 -2.56 1.76
-1.21 -1.34
-2.56
-1.58 -1.63 0.6
-0.49 -0.45 -1.72
-2.67
-1.37 -1.42
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5


Campanula.rotundifolia
Dryopteris.affinis
Stachys.sylvatica
Potentilla.sterilis
Viola.alba
Sesleria.caerulea
Carex.austroalpina
Circaea.lutetiana
Oxalis.acetosella
Viola.reichenbachiana
Helleborus.viridis
Tilia.cordata
Ajuga.reptans
Acer.platanoides
Alliaria.petiolata
Veronica.hederifolia
Syringa.vulgaris
Galium.odoratum
Adoxa.moschatellina
Sambucus.racemosa
Prunus.serotina
Rhamnus.cathartica
Fagus.sylvatica
Lathyrus.niger
Circaea.alpina
Solanum.dulcamara
Abies.alba
Galeopsis.speciosa
Euphorbia.amygdaloides
Crataegus.monogyna
Fraxinus.excelsior
Huperzia.selago
Ranunculus.auricomus
-1.24 -1.6
-2.91
-1.22 -1.7
-1.79 -1.22
-3.01
-3.11
-3.12
-3.21
-0.63 -2.6
0.42 -0.97 -2.75
-3.31
-2.22 -1.17
-0.46 -0.79 -2.21
-0.85 -0.76 -1.94
-3.36 -1.12 0.88
-3.64
-2.23 -1.29 -1.22 1.06
-0.95 -2.14 -0.6
-1.17 -2.58
-0.66 -3.25
-1.92 -2.02
-4.28 -1.87 2.21
-0.52 -1.18 -2.26
-2.19 -2.89 1.12
-0.99 -0.81 -2.26
-1.79 -2.37
-1.21 -1.21 -1.84
-1.25 -3.08
-0.74 -1.03 -2.61
-0.83 -0.57 -2.99
-0.44 -0.88 -1.89 -0.54 -0.71
-1.89 -2.63
-2.81 -1.82
selection cutting
shelterwood
coppice with Standards
retention clearcutting
simple clearcutting
Coefficient
10
5
0
-5



Supplementary Information 1.3 - Heatmap displaying significant vascular plant species coefficients across various management strategies, adapted from Trentanovi et al. (2023). Species are arranged in descending order from top to bottom, with those at the top exhibiting the highest cumulative positive coefficient values. Only significant coefficients are shown, providing insights into each species' response to management practices.

Bibliography

Alatalo, J. M., Jägerbrand, A. K., Erfanian, M. B., Chen, S., Sun, S.-Q., & Molau, U. (2020). Bryophyte cover and richness decline after 18 years of experimental warming in alpine Sweden. *AoB PLANTS*, *12*(6), plaa061. https://doi.org/10.1093/aobpla/plaa061

Angers, V. A., Messier, C., Beaudet, M., & Leduc, A. (2005). Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management*, *217*(2), 275–293. https://doi.org/10.1016/j.foreco.2005.06.008

Aragón, G., Martínez, I., Izquierdo, P., Belinchón, R., & Escudero, A. (2001). Effects of forest management on epiphytic lichen diversity in Mediterranean forests. *Applied Vegetation Science - APPL VEG SCI*, *13*. https://doi.org/10.1111/j.1654-109X.2009.01060.x

Bauhus, J., Puettmann, K., & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management*, *258*(4), 525–537. https://doi.org/10.1016/j.foreco.2009.01.053

Berg, Å., Gärdenfors, U., Hallingbäck, T., & Norén, M. (2002). Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden – analyses of data from a national survey. *Biodiversity & Conservation*, *11*(8), 1479–1503. https://doi.org/10.1023/A:1016271823892

Betts, M. G., Phalan, B. T., Wolf, C., Baker, S. C., Messier, C., Puettmann, K. J., Green, R., Harris, S. H., Edwards, D. P., Lindenmayer, D. B., & Balmford, A. (2021). Producing wood at least cost to biodiversity: Integrating Triad and sharing–sparing approaches to inform forest landscape management. *Biological Reviews*, *96*(4), 1301–1317. https://doi.org/10.1111/brv.12703

Blattert, C., Eyvindson, K., Mönkkönen, M., Raatikainen, K. J., Triviño, M., & Duflot, R.

(2023). Enhancing multifunctionality in European boreal forests: The potential role of Triad landscape functional zoning. *Journal of Environmental Management*, *348*, 119250. https://doi.org/10.1016/j.jenvman.2023.119250

Boch, S., Prati, D., Hessenmoeller, D., Schulze, E.-D., & Fischer, M. (2013). Richness of Lichen Species, Especially of Threatened Ones, Is Promoted by Management Methods Furthering Stand Continuity. *PLoS ONE*, *8*(1), e55461. https://doi.org/10.1371/journal.pone.0055461

Burnham, K. P., & Anderson, D. R. (Eds.). (2004). *Model Selection and Multimodel Inference*. Springer. https://doi.org/10.1007/b97636

Burrascano, S., Chianucci, F., Trentanovi, G., Kepfer-Rojas, S., Sitzia, T., Tinya, F., Doerfler, I., Paillet, Y., Nagel, T. A., Mitic, B., Morillas, L., Munzi, S., Van der Sluis, T., Alterio, E., Balducci, L., de Andrade, R. B., Bouget, C., Giordani, P., Lachat, T., … Ódor, P. (2023). Where are we now with European forest multi-taxon biodiversity and where can we head to? *Biological Conservation*, *284*, 110176. https://doi.org/10.1016/j.biocon.2023.110176

Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Gangale, C., Gargano, D., Gentilesca, T., Luzzi, G., Passalacqua, N., Pelle, L., Rivelli, A. R., Sabatini, F. M., Schettino, A., Siclari, A., Uzunov, D., & Blasi, C. (2018). It's a long way to the top: Plant species diversity in the transition from managed to old-growth forests. *JOURNAL OF VEGETATION SCIENCE*, *29*(1), 98–109. https://doi.org/10.1111/jvs.12588

Burrascano, S., Trentanovi, G., Paillet, Y., Heilmann-Clausen, J., Giordani, P., Bagella, S., Bravo-Oviedo, A., Campagnaro, T., Campanaro, A., Chianucci, F., De Smedt, P., García-Mijangos, I., Matošević, D., Sitzia, T., Aszalós, R., Brazaitis, G., Cutini, A., D'Andrea, E., Doerfler, I., … Ódor, P. (2021). Handbook of field sampling for multi-taxon biodiversity studies in European forests. *Ecological Indicators*, *132*, 108266. https://doi.org/10.1016/j.ecolind.2021.108266

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D.,

O'Hara, K., & Walters, B. (2006). Planted Forests and Biodiversity. *Journal of Forestry*, *104*(2), 65–77. https://doi.org/10.1093/jof/104.2.65

Chamberlain, S. A., & Szöcs, E. (2013). taxize: Taxonomic search and retrieval in R. *F1000Research*, *2*, 191. https://doi.org/10.12688/f1000research.2-191.v2

Chianucci, F., Napoleone, F., Ricotta, C., Ferrara, C., Fusaro, L., Balducci, L., Trentanovi, G., Bradley, O., Kovacs, B., Mina, M., Cerabolini, B. E. L., Vandekerkhove, K., De Smedt, P., Lens, L., Hertzog, L., Verheyen, K., Hofmeister, J., Hošek, J., Matula, R., … Burrascano, S. (2024). Silvicultural regime shapes understory functional structure in European forests. *Journal of Applied Ecology*, *61*(10), 2350–2364. https://doi.org/10.1111/1365-2664.14740

COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS EU Biodiversity Strategy for 2030 Bringing Nature Back into Our Lives (2020). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A52020DC0380

COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS New EU Forest Strategy for 2030 (2021). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A52021DC0572

Di Nuzzo, L., Benesperi, R., Nascimbene, J., Papini, A., Malaspina, P., Incerti, G., & Giordani, P. (2022). Little time left. Microrefuges may fail in mitigating the effects of climate change on epiphytic lichens. *SCIENCE OF THE TOTAL ENVIRONMENT*, *825*, 153943. https://doi.org/10.1016/j.scitotenv.2022.153943

Dias, A. C., & Arroja, L. (2012). Environmental impacts of eucalypt and maritime pine wood production in Portugal. *Journal of Cleaner Production*, *37*, 368–376. https://doi.org/10.1016/j.jclepro.2012.07.056

Directorate-General for Environment (European Commission), IUCN (International Union for Conservation of Nature), IUCN. Species Survival

Commission, Maxted, N., Bilz, M., Lansdown, R. V., & Kell, S. P. (2011). *European red list of vascular plants*. Publications Office of the European Union. https://data.europa.eu/doi/10.2779/8515

Dittrich, S., Jacob, M., Bade, C., Leuschner, C., & Hauck, M. (2014). The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecology*, *215*(10), 1123–1137. https://doi.org/10.1007/s11258-014-0371-6

Dormann, C. F., Bagnara, M., Boch, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., & Hartig, F. (2020). Plant species richness increases with light availability, but not variability, in temperate forests understorey. *BMC Ecology*, *20*(1), 43. https://doi.org/10.1186/s12898-020-00311-9

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

EEA. (2006). *European forest types—European Environment Agency*. https://www.eea.europa.eu/publications/technical_report_2006_9

Elith, J., & Franklin, J. (2013). Species distribution modelling. *Encyclopedia of Biodiversity*, 692–705.

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M. M., Peterson, A. T., … Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and

Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(Volume 40, 2009), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

European Environment Agency (EU body or agency). (2020). *State of nature in the EU: Results from reporting under the nature directives 2013 2018*. Publications Office of the European Union. https://data.europa.eu/doi/10.2800/088178

FAO. (2020). *Global Forest Resources Assessment 2020: Main report*. FAO. https://doi.org/10.4060/ca9825en

Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J. F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., & Gustafsson, L. (2014). REVIEW: Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, *51*(6), 1669–1679. https://doi.org/10.1111/1365-2664.12289

FOREST EUROPE. (2020). FOREST EUROPE, 2020: State of Europe's Forests 2020. *FOREST EUROPE, 2020: State of Europe's Forests 2020*.

Frego, K. A. (2007). Bryophytes as potential indicators of forest integrity. *Forest Ecology and Management*, *242*(1), 65–75. https://doi.org/10.1016/j.foreco.2007.01.030

Gaillard, M.-J., Sugita, S., Mazier, F., Trondman, A.-K., Broström, A., Hickler, T., Kaplan, J. O., Kjellström, E., Kokfelt, U., Kuneš, P., Lemmen, C., Miller, P., Olofsson, J., Poska, A., Rundgren, M., Smith, B., Strandberg, G., Fyfe, R., Nielsen, A. B., … Seppä, H. (2010). Holocene land-cover reconstructions for studies on land cover-climate feedbacks. *Climate of the Past*, *6*(4), 483–499. https://doi.org/10.5194/cp-6-483-2010

Gauslaa, Y., & Solhaug, K. A. (1999). High-light damage in air-dry thalli of the old forest lichen Lobaria pulmonaria—Interactions of irradiance, exposure duration and high temperature. *Journal of Experimental Botany*, *50*, 697–705. https://doi.org/10.1093/jxb/50.334.697

Guisan, A., Edwards, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: Setting the scene. *Ecological Modelling*,

157(2), 89–100. https://doi.org/10.1016/S0304-3800(02)00204-1

Gustafsson, L., Baker, S. C., Bauhus, J., Beese, W. J., Brodie, A., Kouki, J., Lindenmayer, D. B., Lõhmus, A., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W. J. A., Wayne, A., & Franklin, J. F. (2012). Retention Forestry to Maintain Multifunctional Forests: A World Perspective. *BioScience*, *62*(7), 633–645. https://doi.org/10.1525/bio.2012.62.7.6

Hanski, I. (2011). Habitat Loss, the Dynamics of Biodiversity, and a Perspective on Conservation. *Ambio*, *40*(3), 248. https://doi.org/10.1007/s13280-011-0147-3

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K., & Cummins, K. W. (1986). Ecology of Coarse Woody Debris in Temperate Ecosystems. In A. MacFadyen & E. D. Ford (Eds.), *Advances in Ecological Research* (Vol. 15, pp. 133–302). Academic Press. https://doi.org/10.1016/S0065-2504(08)60121-X

Hodgetts, N. (2019). *A miniature world in decline*. IUCN. https://doi.org/10.2305/IUCN.CH.2019.ERL.2.en

Hodgetts, N., Söderström, L., Blockeel, T., Caspari, S., Ignatov, N., Konstantinova, N., Lockhart, B., Papp, C., Schröck, M., Sim-Sim, D., Bell, N., Bell, H., Blom, M., Bruggeman-Nannenga, M., Brugués, J., Enroth, K., Flatberg, R., Garilleti, L., Hedenäs, D., & Roseggergasse, U. (2020). An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology*, *42*, 1–116. https://doi.org/10.1080/03736687.2019.1694329

Jolliffe, I. (2011). Principal Component Analysis. In M. Lovric (Ed.), *International Encyclopedia of Statistical Science* (pp. 1094–1096). Springer. https://doi.org/10.1007/978-3-642-04898-2_455

Kaplan, J. O., Krumhardt, K. M., & Zimmermann, N. (2009). The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, *28*(27), 3016–3034. https://doi.org/10.1016/j.quascirev.2009.09.028

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 170122. https://doi.org/10.1038/sdata.2017.122

Kass, J. M., Muscarella, R., Galante, P. J., Bohl, C. L., Pinilla-Buitrago, G. E., Boria, R. A., Soley-Guardia, M., & Anderson, R. P. (2021). ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution*, *12*(9), 1602–1608. https://doi.org/10.1111/2041-210X.13628

Kempeneers, P., Sedano, F., Seebach, L., Strobl, P., & San-Miguel-Ayanz, J. (2011). Data Fusion of Different Spatial Resolution Remote Sensing Images Applied to Forest-Type Mapping. *IEEE Transactions on Geoscience and Remote Sensing*, *49*(12), 4977–4986. IEEE Transactions on Geoscience and Remote Sensing. https://doi.org/10.1109/TGRS.2011.2158548

Kindt, R. (2020). WorldFlora: An R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. *Applications in Plant Sciences*, *8*(9), e11388. https://doi.org/10.1002/aps3.11388

Kiraly, I., Nascimbene, J., Tinya, F., & Odor, P. (2013). Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *BIODIVERSITY AND CONSERVATION*, *22*(1), 209–223. https://doi.org/10.1007/s10531-012-0415-y

Kirby, K., Buckley, G., & Mills, J. (2017). Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland. *Folia Geobotanica*, *52*. https://doi.org/10.1007/s12224-016-9252-1

Ladrón de Guevara, M., Gozalo, B., Raggio, J., Lafuente, A., Prieto, M., & Maestre, F. T. (2018). Warming reduces the cover, richness and evenness of lichen-dominated biocrusts but promotes moss growth: Insights from an 8 yr experiment. *New Phytologist*, *220*(3), 811–823. https://doi.org/10.1111/nph.15000

Lindenmayer, D. b., Franklin, J. f., Lõhmus, A., Baker, S. c., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., & Gustafsson, L. (2012). A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, *5*(6), 421–431. https://doi.org/10.1111/j.1755-263X.2012.00257.x

Müllerová, J., Hédl, R., & Szabó, P. (2015). Coppice abandonment and its implications for species diversity in forest vegetation. *Forest Ecology and Management*, *343*, 88–100. https://doi.org/10.1016/j.foreco.2015.02.003

Nascimbene, J., Marini, L., & Nimis, P. L. (2007). Influence of forest management on epiphytic lichens in a temperate beech forest of northern Italy. *Forest Ecology and Management*, *247*(1), 43–47. https://doi.org/10.1016/j.foreco.2007.04.011

Nascimbene, J., Marini, L., & Odor, P. (2012). Drivers of lichen species richness at multiple spatial scales in temperate forests. *PLANT ECOLOGY & DIVERSITY*, *5*(3), 355–363. https://doi.org/10.1080/17550874.2012.735715

Nordén, B., & Appelqvist, T. (2001). Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation*, *10*(5), 779–791. Scopus. https://doi.org/10.1023/A:1016675103935

Nordén, B., Dahlberg, A., Brandrud, T., Fritz, Ö., Ejrnæs, R., & Ovaskainen, O. (2014). Effects of Ecological Continuity on Species Richness and Composition in Forests and Woodlands: A Review. *Ecoscience*, *21*, 34–45. https://doi.org/10.2980/21-1-3667

Ódor, P., Király, I., Tinya, F., Bortignon, F., & Nascimbene, J. (2013). Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. *Forest Ecology and Management*, *306*, 256–265. https://doi.org/10.1016/j.foreco.2013.07.001

Ódor, P., & Van Hees, A. F. M. (2004). Preferences of dead wood inhabiting bryophytes for decay stage, log size and habitat types in Hungarian beech forests. *Journal of Bryology*, *26*(2), 79–95. https://doi.org/10.1179/037366804225021038

Peterson, A., Papes, M., & Eaton, M. (2007). Transferability and model evaluation in ecological niche modeling: A comparison of GARP and Maxent. *Ecography*, *30*, 550–560. https://doi.org/10.1111/j.0906-7590.2007.05102.x

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pommerening, A., & Murphy, S. T. (2004). A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry: An International Journal of Forest Research*, *77*(1), 27–44. https://doi.org/10.1093/forestry/77.1.27

Porfirio, L. L., Harris, R. M. B., Lefroy, E. C., Hugh, S., Gould, S. F., Lee, G., Bindoff, N. L., & Mackey, B. (2014). Improving the Use of Species Distribution Models in Conservation Planning and Management under Climate Change. *PLoS ONE*, *9*(11). https://doi.org/10.1371/journal.pone.0113749

Proposal for a REGULATION OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL on a Monitoring Framework for Resilient European Forests (2023). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=COM:2023:728:FIN

Pykälä, J. (2004). Immediate increase in plant species richness after clear-cutting of boreal herb-rich forests. *APPLIED VEGETATION SCIENCE*, *7*(1), 29–34. https://doi.org/10.1658/1402-2001(2004)007[0029:IIIPSR]2.0.CO;2

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, *41*(4), 629–643. https://doi.org/10.1111/jbi.12227

RStudio Team. (2020). *RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.*

Sabatini, F. M., Bluhm, H., Kun, Z., Aksenov, D., Atauri, J. A., Buchwald, E., Burrascano, S., Cateau, E., Diku, A., Duarte, I. M., Fernández López, Á. B., Garbarino, M., Grigoriadis, N., Horváth, F., Keren, S., Kitenberga, M., Kiš, A., Kraut, A., Ibisch, P. L.,

… Kuemmerle, T. (2021). European primary forest database v2.0. *Scientific Data*, *8*(1), Article 1. https://doi.org/10.1038/s41597-021-00988-7

Trentanovi, G., Campagnaro, T., Sitzia, T., Chianucci, F., Vacchiano, G., Ammer, C., Ciach, M., Nagel, T. A., del Río, M., Paillet, Y., Munzi, S., Vandekerkhove, K., Bravo-Oviedo, A., Cutini, A., D'Andrea, E., De Smedt, P., Doerfler, I., Fotakis, D., Heilmann-Clausen, J., … Burrascano, S. (2023). Words apart: Standardizing forestry terms and definitions across European biodiversity studies. *Forest Ecosystems*, *10*, 100128. https://doi.org/10.1016/j.fecs.2023.100128

Valladares, F., & Niinemets, Ü. (2008). Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. *Annual Review of Ecology, Evolution, and Systematics*, *39*(Volume 39, 2008), 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

Vellend, M. (2004). Parallel Effects of Land-Use History on Species Diversity and Genetic Diversity of Forest Herbs. *Ecology*, *85*(11), 3043–3055. https://doi.org/10.1890/04-0435

Warren, D. L., Wright, A. N., Seifert, S. N., & Shaffer, H. B. (2014). Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. *Diversity and Distributions*, *20*(3), 334–343. https://doi.org/10.1111/ddi.12160

Williams, M. (2000). Dark ages and dark areas: Global deforestation in the deep past. *Journal of Historical Geography*, *26*, 28–46. https://doi.org/10.1006/jhge.1999.0189

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., & Antonelli, A. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution*, *10*(5), 744–751. https://doi.org/10.1111/2041-210X.13152

Zuijlen, K. V., Nobis, M. P., Hedenäs, L., Hodgetts, N., Alarcón, J. A. C., Albertos, B., Bernhardt-Römermann, M., Gabriel, R., Gariletti, R., Lara, F., Preston, C. D., Simmel,

J., Urmi, E., Bisang, I., & Bergamini, A. (2023). *Bryophytes of Europe Traits (BET) dataset*. EnviDat. http://dx.doi.org/10.16904/envidat.348

Chapter 4. Guiding management practices to enhance multi-taxon diversity in Mediterranean forests

Guiding management practices to enhance multi-taxon diversity in Mediterranean forests

Lorenzo Balducci, Elisa Caprasecca, Francesco Di Pietro, Mirko Legnaro Diamanti, Giorgia Bertagni, The “GoProFor MED” Consortium, Sabina Burrascano.

Abstract: Mediterranean forests are biodiversity hotspots that provide essential ecosystem services, yet they face increasing pressures from changes in climate change and in human activities. In this study, we investigate the structural attributes that shape the species richness of three taxonomic/functional groups: vascular plants, epiphytic lichens, and saproxylic invertebrates. Using regression tree models, we identified habitat type, Leaf Area Index (LAI), basal area distribution across diameter classes, and deadwood quality (decay stage and diameter) as critical factors influencing biodiversity in these groups. Vascular plant species richness was primarily driven by light availability and reduced basal area in smaller diameter classes. Epiphytic lichen diversity was closely associated with habitat type and LAI, while saproxylic invertebrates were most affected by advanced decay stages and larger deadwood fragment sizes (≥13 cm). Our findings have direct implications for Sustainable Forest Management (SFM) practices, highlighting the need for strategies that retain large-diameter deadwood and maintain structural heterogeneity. These approaches support a wide range of species across different taxonomic groups. Furthermore, we emphasize the importance of integrating deadwood quality into SFM indicators, as current metrics often focus solely on deadwood volume, overlooking the relevance of decay stages and fragment size for biodiversity. By incorporating these findings, forest management can better align with the biodiversity conservation goals set forth in the EU Biodiversity Strategy for 2030 and the EU Forest Strategy for 2030.

keywords: biodiversity, forests, Europe, Mediterranean, SFM, multi-taxon

1. Introduction

The Mediterranean area is one of the regions most susceptible to climate changes, especially those involving increased temperatures, altered precipitation patterns, and prolonged droughts. Mediterranean forests are at risk of declining biodiversity due to these changes (EEA, 2020). The combination of rising temperatures and changes in seasonal rainfall can lead to shifts in species distributions and a decrease in overall ecosystem resilience (Acácio et al., 2017). These climatic pressures may exacerbate the existing threats to biodiversity and ecosystem services, emphasizing the urgent need for adaptive management strategies that consider these impacts. Mediterranean forests emerge as particularly vulnerable, with climate models predicting increased wildfire risk, drought, and shifts in dominant tree species ranges due to climate change (Hidalgo-Triana et al., 2023; Lionello & Scarascia, 2018).

On the other hand, the Mediterranean Basin is recognized as one of the world's 36 biodiversity hotspots (Myers et al., 2000). Despite covering only 1.5% of the Earth's land surface (Fady-Welterlen, 2005), it harbors 10% of the world’s biodiversity. Approximately 25,000 plant species are found in this region, with 13,000 of them being endemic (Médail & Quézel, 1999). This diversity extends beyond plant life: 35% of amphibians, 43% of reptiles, and 25% of mammals in the Mediterranean are considered endemic, highlighting the region's unique fauna. Within the Mediterranean Basin, around 10% of the area is classified as forest. The Mediterranean forest landscape has been heavily influenced by human activities over millennia, with constant exploitation of forest resources and conversion into agricultural and grazing lands. As a result, only an estimated 15% of the Mediterranean's original forest vegetation remains forest habitat (Quézel & Médail, 2003). In the Mediterranean Basin, more than 6,000 species (20% of known species) are at risk of extinction (IUCN, 2024). The decline of biodiversity within forest ecosystems, along with the over-alteration of communities, can negatively impact the ecosystem services provided by forests, with significant repercussions for both ecosystems and human well-being (Gamfeldt et al., 2013). Nonetheless, the Mediterranean Basin still hosts significant forest diversity, including 245 tree taxa, of which 210 are species and 35 subspecies. Notably, 46 of these species are endemic to the Mediterranean biogeographical region (Médail & Baumel, 2018). These forest types vary greatly depending on local environmental factors such as climate, geology, and soil types, as well as the varying degrees of human impact, both past and present (Vellend, 2004).

The distribution and composition of several taxonomic groups in Mediterranean forests are shaped by the interactions between physical, chemical, and biological factors (Palahi et al., 2008). At larger scales, macroclimatic conditions primarily drive the distribution of biological communities. Variables such as average precipitation, temperature, solar radiation, and humidity across vast geographic regions determine the presence of different vegetation physiognomies, from forests to grasslands

(Sayre et al., 2020). At smaller scales, physical factors such as local temperature, atmospheric humidity, and substrate type create environmental gradients that significantly influence the habitat availability for several taxonomic groups in these ecosystems. These microclimatic conditions can influence species diversity for several taxonomic groups, even within small areas. Vascular plant diversity is strongly affected by soil moisture, temperature, and light availability, particularly in the understory. For instance, small-scale variations in canopy cover and understory conditions can result in distinct microclimates, promoting changes in species composition, from shade-tolerant to light demanding species and vice-versa (Brunet et al., 2010). Also lichens are strongly influenced by microclimatic conditions, particularly humidity and light availability. Epiphytic lichens are sensitive to changes in microclimate (Ellis, 2009). Saproxylic insects, particularly beetles, are highly dependent on both microclimatic conditions and the availability of deadwood, which provides essential habitat.

Substrate availability is another key factor in determining species presence and diversity. Saproxylic insects and epiphytic lichens primarily rely on standing and lying deadwood as well as large living trees. Deadwood, in particular, provides microhabitats and resources for several taxonomic groups (Gibb et al., 2006; Parisi et al., 2018). Standing deadwood, e.g, snags, and lying deadwood provide different kinds of habitats for lichens, saproxylic insects and in general multiple taxonomic groups involved in the detritus food web (Stokland, 2012) that use it for nesting, shelter, and foraging (Dittrich et al., 2014; Dufour-Pelletier et al., 2020). For saproxylic insects, deadwood represents both a resource and a substrate with decaying wood that support different life stages of beetles (Stokland, 2012). The availability of different types and stages of deadwood decay can increase habitat heterogeneity, thus supporting a greater diversity of species (Larrieu et al., 2018). For epiphytic lichens, the presence of deadwood as a substrate supports species that may also colonize living trees, increasing the amount of surface available (Ellis, 2009), especially in the post-harvesting phases. Overall, deadwood significantly enhances habitat complexity, supporting a wider range of species across different taxonomic groups.

Forest management practices play a critical role in shaping microclimatic conditions and substrate availability through changes in forest structure. Changes in forest dynamics and structural characteristics, including tree size distribution and species composition, tree density, vertical stratification, deadwood amount affect key ecological factors such as light intensity, soil moisture, and temperature, ultimately impacting forest microhabitats, substrate availability and therefore the diversity of several taxonomic groups (LaRue et al., 2023; Prévost & Raymond, 2012). In Europe, and particularly in the Mediterranean, the majority of forests are managed under national or European regulations, often for timber production, but also for cork or non-timber products, and as forest pastures. However, only a small portion of Mediterranean forests (around 2%) remains untouched by human intervention

(Sabatini et al., 2021).

Current policies increasingly emphasize sustainable forest management (SFM), defined by the Helsinki Resolution (MCPFE, 1993), as a pathway to maintain forest biodiversity, productivity and regeneration capacity in these ecosystems. The EU's 2030 Forest Strategy, part of the European Green Deal, seeks to integrate biodiversity conservation into forest management while achieving climate neutrality by 2050 (European Commission, 2021). However, despite these policy efforts, there remain significant knowledge gaps regarding the impacts of different management practices on biodiversity, particularly for less-studied taxa and for Mediterranean forests (Burrascano et al., 2023). Effective forest management will require the development of more precise indicators of biodiversity to ensure long-term ecosystem resilience. SFM indicators monitor forest status and changes quantitatively, qualitatively, and descriptively (Forest Europe, 2020). While structural indices such as tree composition, microhabitat availability, and deadwood volume are widely used as biodiversity proxies (Larrieu et al., 2018), their indirect nature limits their effectiveness in capturing the complexities of forest biodiversity. Only two indicators (Threatened forest species and Common forest bird species) involve species other than trees. Novel measures, i.e., Index of Biodiversity Potential (IBP) (Larrieu & Gonin, 2008), try to bridge the gap between structural attributes and biodiversity indices by incorporating parameters directly linked to habitat quality and species requirements, including tree species richness, deadwood abundance, and habitat continuity, to evaluate biodiversity potential (Larrieu & Gonin, 2008). Even though previous research has demonstrated the potential of these indicators (Zeller et al., 2022) that could also simplify data collection, relying on habitat attributes and area-based metrics may overlook complex ecological processes. Additionally, most biodiversity indices lack validation, particularly in Mediterranean forest types, where research on their correlation with actual biodiversity is sparse (Gao et al., 2015). Moreover, existing biodiversity monitoring frameworks often neglect underrepresented taxa and are biased towards easily measurable indicators (Zeller et al., 2022). The lack of harmonization in biodiversity monitoring methods and poor data integration at the local scale have created significant informational gaps in biodiversity data at the continental level (Burrascano et al., 2023). These gaps are exacerbated by an uneven representation of forest categories, particularly the underrepresentation of Mediterranean forests (Burrascano et al., 2023; Tinya et al., 2023). Expanding research into various taxa and their interrelationships and responses to structural and environmental changes is becoming increasingly important. Given the current pressures on Mediterranean forests, it is crucial to identify and implement management practices that enhance multi-taxon biodiversity, with the aim of informing sustainable forest management. This may require setting new thresholds or ranges for sustainable forest management (Nocentini et al., 2022). Maintaining forest functions in the context of climate change also requires understanding the roles and the effect of management on different taxonomic groups at multiple levels (Golladay et al., 2016).

In this paper, we aimed to i) assess structural indicators driving species diversity for epiphytic lichens, vascular plants, saproxylic and phytophagous arthropods; ii) identifying thresholds for these attributes to iii) discuss these results in the perspective of sustainable forest management (SFM) goals.

2. Methods

2.1 Study area

The study area encompasses three countries along the Mediterranean coasts in Europe: Italy, Spain, France (Fig. 1). The investigated forest communities are referred to the forest habitats listed in Annex I of the Habitats Directive 92/43/EEC (European Commission, 1992), which are primarily associated with the Mediterranean Basin:

- Habitat 9330: *Quercus suber* forests, commonly known as cork oak forests.
- Habitat 9340: *Quercus ilex* and *Quercus rotundifolia* forests. These two species are morphologically similar and genetically related, the habitat is commonly referred to as holm oak forests.
- Habitat 9260: *Castanea sativa* forests, commonly known as European chestnut forests.
- Habitat 9530*: (Sub-) Mediterranean pine forests with endemic *Pinus nigra*, commonly known as black pine forests.

All the sampling areas are part of the Natura 2000 network and are located within Special Areas of Conservation (SAC). The study sites were selected as they are currently included in the framework of LIFE project GoProFor Med (LIFE21 NAT/IT/101074738), ensuring the availability of detailed data on the management practices applied to these areas.

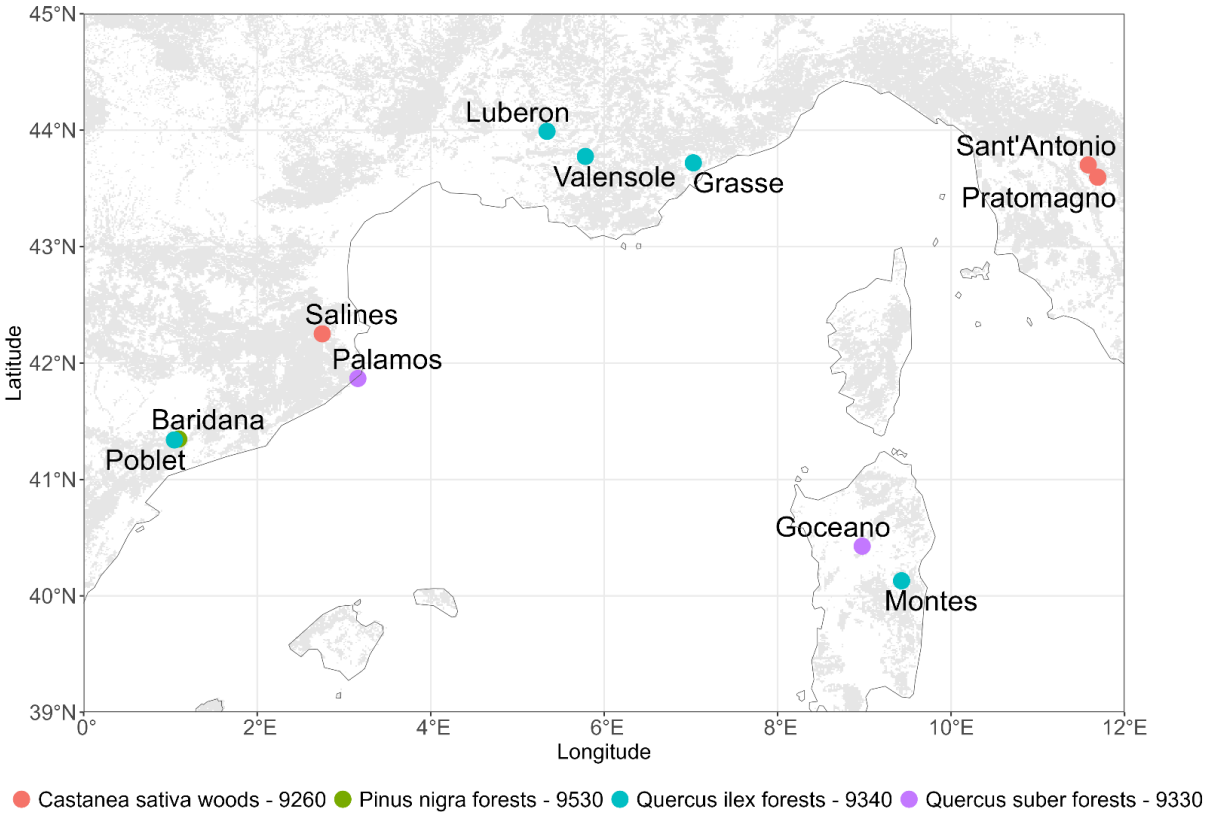


Figure 1. - Study sites. Habitat type 9260 (*Castanea sativa* forests) in red, habitat type 9340 (*Quercus ilex* and *Quercus rotundifolia* forests) in light blue, habitat type 9330 (*Quercus suber* forests) in purple, and habitat type 9530 (Sub-Mediterranean *Pinus nigra* forests) in green.

2.2 Sampling design

We collected data from 66 spatially distinct multi-taxon plots distributed across 11 sites (Fig. 1). For each sampling unit we collected biodiversity data on vascular plants, epiphytic lichens and saproxylic invertebrates; data on standing trees and deadwood for the forest structure, sampling protocols were based on standard approaches to allow integration and comparison with other databases (Burrascano et al., 2021).

2.2.1 Vascular plants

Vascular plants, such as trees, shrubs, and herbs, are the most frequently sampled taxonomic group in forests. This group is particularly suited for assessing forest biodiversity because it provides the physical structure for other organisms, constitutes the majority of forest primary productivity, and plays a crucial role in nutrient cycling. Vascular plants include a large number of habitat specialists distributed across broad environmental gradients, which are used to detect forest habitat diversity.

Each vascular plant species was will be recorded along with its estimated cover (%) inside 15x15 m square plots. Square sampling units have the advantage of allowing for an accurate delimitation of the sampling unit through a measuring tape starting from the coordinates of a vertex.

We strongly suggest recordeding separately species and abundance values for each of the three layers that are usually identified in European forests: overstorey, height greater than 3 meters; shrub, height between 1 and 3 meters; understorey, height below 1 meter.

2.2.2 Epiphytic lichens

For each plot, epiphytic lichens were sampled on three living trees. For each tree trunk, four 10x50 cm sampling grids (each split into 5 10x10cm quadrats) were located parallel to each trunk, at the four cardinal directions, between 100 and 150 cm from the ground. Epiphytic lichens were identified to the species level.

2.2.3 Saproxylic invertebrates

In each plot (15x15m), three logs (30-50 cm in length, 10-15 cm in diameter) were selected based on their decay class (one from each of the classes 2, 3, and 4). Preference was given to logs under partial or full tree cover. The logs were manually dissected to collect all the invertebrates within them (larvae, pupae, and adults). A total of 877 individuals were sampled. Taxonomic identification for each class or superclass was performed through the observation of diagnostic macroscopic and microscopic characteristics. Individuals were then associated to one of six functional groups: "Predators," "Detritivores," "Xylophages," "Phytophages," "Saprophages," and "Polyphages." Each individual was assigned to a specific functional group based on the feeding habits of its family, as determined through bibliographic research (Minelli et al., 2023).

2.2.4 Phytophagous arthropods sampling

The study also examined phytophagous arthropods. The sampling was carried out along a diagonal (21 metres) within a square plot, oriented in a northeast direction. The three vegetation layers (herbaceous, shrub and tree) were struck with a stick up to a height of 3 m, causing the insects to fall onto a white sheet (1.5 x 1.5 m). Each arthropod specimen arthropods was then collected with entomological tweezers and then stored in test tubes filled with pure ethanol. This procedure was repeated for each vegetation layer. Each test tube was labeled with a site code, plot code, vegetation layer and plant species. In the laboratory, the samples were are separated and placed in individual test tubes.

2.2.5 Forest structure

Standing trees, alive or dead, and stumps, were sampled in a circular area of 15 meters in diameter, with the same center of the sampling unit for biodiversity sampling (Fig. 2). Lying deadwood will be recorded along a transect corresponding to the diameter of the plot for standing trees.

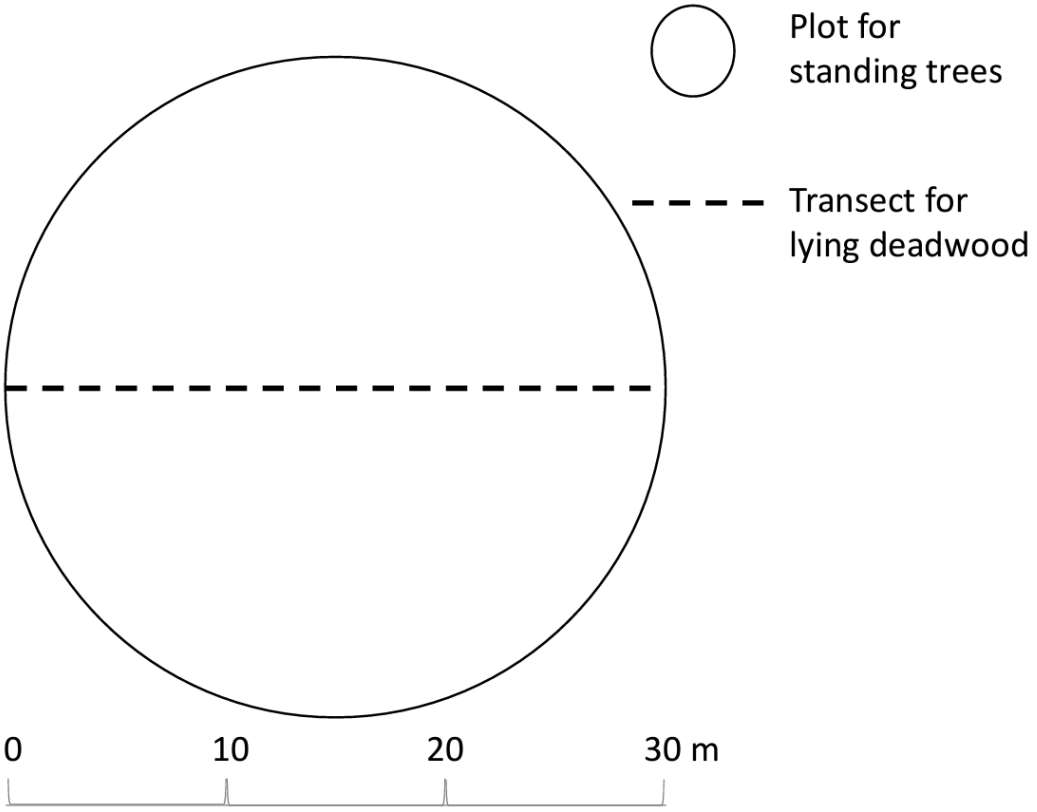


Figure 2. - Sampling unit used for standing trees and lying deadwood.

For each living tree, we measured tree height and diameter at breast height, defined as 1.3 meters from the highest point of ground at the tree base. All living and dead standing trees with a diameter > 7.5 cm were measured. In each sampling plot, we examined dead standing trees (diameter > 10 cm), snags (diameter > 10 cm, height > 1.3 m) and stumps (diameter > 10 cm, height < 1.3 m). The decay classes were established following Harmon et al. (2011), considering five classes.

We assigned species and decay class to each standing deadwood unit. For snags we measured diameter at breast height. For stumps, both top and bottom diameters, as well as height and the origin of the stumps were recorded or estimated. Lying deadwood length was measured along with decay class assigned following Harmon et al. (2011).

2.2.6 TreMs survey

For each standing tree within the sampling unit, the presence of tree-related microhabitats was observed and recorded using the categories and the codes referring to each specific microhabitat, also evaluating the size limits. For their description, size limits and macro-categories we followed Bütler et al. (2024):

- Cavities (CV): Woodpecker breeding cavities; Rot-holes; Insect galleries; Concavities.
- Tree injuries and exposed wood (IN): Exposed sapwood only; Exposed sapwood and heartwood.
- Crown deadwood (DE).
- Excrescences (EX): Twig tangles; Burrs and cankers.
- Fruiting bodies of saproxylic fungi and slime moulds (FU): Perennial fungal fruiting bodies; Ephemeral fungal fruiting bodies and slime moulds.
- Epiphytic and epixylic structures (EP): Epiphytic and parasitic crypto- and phanerogams; Nests; Microsoils.
- Exudates: Fresh exudates (ES).

2.2.7 IBP assessment

The IBP can be measured at the stand or stand type level using different survey methods: the simplest is the complete coverage method, where the entire stand is uniformly surveyed along regularly spaced transects using GPS in trace mode. Observations are made on strips typically 10-20 meters wide on either sides of the transect axis, ensuring no double counting between neighboring surveyors or adjacent strips. This method is suitable for small stands (less than 5 hectares).

For the present project, however, a partial coverage survey was adopted. It surveys a representative fraction of the stand such as every other strip, with rapid additional surveys in non-sampled areas. The IBP score is determined based on observations from the sampled areas.

From the start of the survey, we recorded all necessary elements such as tree species and deadwood. Data is collected through careful visual estimation rather than exhaustive inventory, ensuring precision in identifying elements necessary for IBP assessment. Estimate the percentage of cover for categories (like native tree species) by calculating the area in square meters or estimating the proportion of the stand they occupy. For factors requiring counts of trees in size categories, focus on the upper category and count the lower category only if the upper category is absent.

Standardize search effort to avoid overestimation, typically setting a maximum survey duration of 15-20 minutes per hectare per person, which may extend to 25-30

minutes in more difficult conditions. Preparation and data processing times must also be considered.

2.2.8 Canopy photography

For each plot, nine photographs were taken using a DSLR camera mounted on a tripod, positioned at a 90° angle with the base leveled horizontally (Pekin & Macfarlane, 2009). The photographs were processed and analyzed using the R package "coveR" (Chianucci et al., 2022), which follows the methodology of Macfarlane et al. (2007). This approach calculates various canopy metrics such as total cover, Leaf Area Index (LAI), and canopy gaps.

Images were converted to binary values (0-1) based on the contrast between canopy and sky pixels. Pixels representing the sky were assigned a value of 1, while those representing canopy were assigned 0. Gaps were classified by size, with large gaps defined as covering ≥1.3% of the image, and small gaps as <1.3% (Macfarlane et al., 2007; Pekin & Macfarlane, 2009). After classification, several canopy structural indices were calculated using the following equations:

- **Gap Fraction (GF):** Proportion of sky pixels in the image.

  $$GF = \frac{gT}{NR}$$

  where gT is the number of sky pixels, and NR is the total number of pixels.

- **Foliage Cover (FC):** Complement of the gap fraction.

  $$FC = \frac{1}{GF}$$

- **Crown Cover (CC):** Complement of the large gap fraction.

  $$CC = 1 - \frac{gl}{NR}$$

  where gLgLgL is the number of large gap pixels.

- **Crown Porosity (CP):** Fraction of small gaps within the canopy.

  $$CP = 1 - \frac{FC}{CC}$$

- **Leaf Area Index (LAI):** Calculated using the formula:

  $$L = -CC \cdot \left(log\frac{(CP)}{k}\right)$$

  where k=0.5 is the extinction coefficient.

2.3 Statistical analyses

In order to link the various structural parameters and indicators described in the previous sections, we modeled the response of different taxonomic groups to the total abundance of TreMs sampled in each plot, the number of TreM types found in each plot and the total IBP. We added to these indicators some structural variables that may be relevant to guide management strategies implemented within the framework of the project or in general for the target habitats.

The response variables were different across taxonomic groups:

- Vascular Plants - Cover of habitat diagnostic species;
- Epiphytic Lichens - Shannon index based on species frequency;
- Saproxylic Arthropods - Number of functional groups.
- Phytophagous Arthropods - Number of functional groups.

The calculation of each of these variables required specific methodologies and for each of them a specific set of explanatory variables were selected.

1. Vascular Plants: For the diagnostic species, we have included all the plant species of the herbaceous layer (height of individuals < 1m) and the shrub layer (height of individuals between 1m and 3m) that are listed in at least one of the four habitat interpretation manuals of the countries involved. We then summed the percentage cover of these species within each plot and divided it for the sum of the cover of all species in the same plot, therefore obtaining the relative cover of diagnostic species. The response variables for this first model were:

    - Site: the site column indicates the location of each sampling unit, reflecting geographical, environmental, and management differences.
    - Canopy Cover (CC): calculated following the methodology described by Chianucci et al. (2022), using hemispherical canopy photographs taken during the peak vegetative season. In this study, nine canopy photos were taken per sampling unit and analyzed to estimate the percentage of canopy cover. This metric provides insights into the light availability and forest structure.
    - Total IBP Score: The Index of Biodiversity Potential (IBP) is a composite indicator that reflects the capacity of a forest to support biodiversity (Larrieu & Gonin, 2008).
    - Abundance of TreMs: This metric quantifies the total number of tree-related microhabitats (TreMs) observed per plot.
    - Number of Types of TreMs: This variable measures the diversity of TreM types present within a plot, reflecting the range of habitat features available for different species.

- Basal Area Classes (BAXCD1 to BAXCD6): These variables represent the basal area (m²/ha) of trees divided into six diameter classes, which provide detailed information on forest stand structure and size distribution. The basal area classes capture the contributions of different tree size categories to overall stand structure, which is essential for understanding habitat availability for species dependent on large trees or specific structural conditions:

    - ➢ BAXCD1: Basal area of trees with diameters between 7.5 cm and 17.5 cm.
    - ➢ BAXCD2: Basal area of trees with diameters between 17.6 cm and 27.5 cm.
    - ➢ BAXCD3: Basal area of trees with diameters between 27.6 cm and 37.5 cm.
    - ➢ BAXCD4: Basal area of trees with diameters between 37.6 cm and 47.5 cm.
    - ➢ BAXCD5: Basal area of trees with diameters between 47.6 cm and 57.5 cm.
    - ➢ BAXCD6: Basal area of trees with diameters >57.5 cm.

2. Epiphytic lichens: we calculated the Shannon index, which represents the community biodiversity at plot level, taking into account both the number of species found and their evenness. In this case, evenness considers the frequencies of the species, meaning that the index value will be higher when the species found have similar frequencies. The response variables for this model were the same used for vascular plants.

3. Saproxylic arthropods**:** were divided into six categories: Predators, Detritivores, Xylophages, Phytophages, Saprophages, and Polyphages. The assignment of each individual to a specific functional category was based on the association between the individual's family and the feeding habit of that family.
    - Site.
    - Total IBP Score.
    - Abundance of TreMs.
    - Number of Types of TreMs.
    - Basal Area Classes (BAXCD1 to BAXCD6).
    - Decay class: state of decay of the deadwood unit where the functional group was found, following section 2.3.1.
    - Diameter: diameter (cm) of the deadwood unit where the functional group was found.

4. Phytophagous arthropods**:** individuals were partitioned into functional groups based on the functional traits pertaining the behavior and feeding habits of the identified families. The individuals were divided into three main categories: Saprophages, Non-saprophages, and Polyphages. Each of these main categories was further divided into subcategories based on more specific feeding habits. Specifically, the Saprophages were divided into Zoosaprophages, Phytosaprophages, and Polysaprophages. The Non-saprophages were further divided into the categories Predators/Parasitoids, Mycophages, and Phytophages. Within the Phytophages category, additional subcategories (Xylophages, Phyllophages, Spermophages, and Anthophages) were recognized based on the plant region the phytophages tend to feed on. The response variables for this model were:
    - Site.
    - Canopy Cover (CC).
    - Shrub Cover (SC): percentage of ground area covered by shrubs in each sampling unit.
    - Herb Cover (HC): percentage of ground area covered by herbaceous vegetation in each sampling unit.
    - Total IBP Score.
    - Abundance of TreMs.
    - Number of Types of TreMs.
    - Basal Area Classes (BAXCD1 to BAXCD6).

2.3.1 Boosted Regression Trees (BRTs)

We ran boosted regression trees (BRTs) for epiphytic lichens, vascular plants and phytophagous and saproxylic arthropods to assess the relationship between the response variable of each taxonomic/functional group and the predictor variables.

Boosted regression trees (BRTs) effectively model complex non-linear relationships, and enable reliable identification of relevant variables and interactions, with a strong predictive performance and robustness against overfitting, missing data, and collinearity (Elith, Leathwick, and Hastie, 2008). The model setting involves finding the optimal combination of four main parameters (number of trees, learning rate, tree complexity and bag fraction) to minimize predictive error: the number of trees refers to the total count of individual decision trees, influencing both predictive performance and model stability; the learning rate controls the contribution of each tree to the final model, providing a balance between accuracy and the risk of overfitting; tree complexity determines the maximum depth of each tree, affecting the model's ability to capture complex patterns in the data; and the bag fraction specifies the proportion

of the training set randomly selected for each iteration..
We used the gbm.step function from the ‘dismo’ package (Hijmans et al., 2022) to test various BRT settings by combining different learning rates (0.001, 0.0025, 0.005), tree complexity values (2, 3, 5), and bag fraction values (0.5, 0.75), and assess the relative importance (sum up to 100%) of each explanatory variable (Elith, Leathwick, and Hastie, 2008). We used the Gaussian error distribution.
We selected parameter combinations that resulted in models with over 1000 trees and evaluated their performance using three metrics, following the approach of Napoleone et al. (2021): (i) explained deviance (D^2), calculated as $D^2 = 1 - (\text{residual deviance/total deviance})$. This metric ranges from zero to one, where a value of one indicates a perfect fit, and is considered a generalization of the traditional R^2 used in regression analysis (Stojanova et al., 2010; Mouchet et al., 2015); (ii) the cross-validated mean correlation coefficient (CV), which measures the average correlation between the training and test datasets; and (iii) self-statistics (SS), which assesses the correlation between predicted and observed values. These correlation metrics are commonly used to evaluate the efficiency of Boosted Regression Trees (BRTs) (Szymura et al., 2018; Napoleone, Giarrizzo, and Burrascano, 2021).

3. Results

3.1 Results for vascular plants

The effect of the site, which also includes the differences across habitats, is the variable explaining most variance (Fig. 4). However, other structural variables resulted as importantly linked to the relative cover of diagnostic species. The habitat conservation state in terms of diagnostic species is maximised by a canopy cover greater than 50%, meaning that below this threshold the occurrence of heliophilous competitive species does not allow the full development of the habitat.
Interestingly, the abundance of TreMs was more relevant that their diversity (Fig. 4), i.e., the number of types of TreMs represented. This means that the occurrence of a high number of TreMs of few specific types is relevant also for the habitat conservation state as assessed through the composition of the understorey. In particular, the most abundant TreMs in the sampled plots, thus those causing this link, are:

- Epiphytic and epixylic structures - Bryophytes, lichens, Ivy and lianas, ferns, mistletoe;
- Crown deadwood - Dead branches, dead top, remnants of a broken limb
- Excrescences - Witches' broom and Epicormic shoots
- Tree injuries and exposed wood - Bark loss, fire scar, bark shelter, bark pockets
- Cavities - Insect galleries and bore holes.

These TreMs categories are in some cases abundant in those plots that are characterized by only a few types of TreMs, i.e., 1 to 4.
Some of these TreMs, when abundant, indicate the occurrence of a relevant number of senescent trees, e.g., crown deadwood and insect galleries, which are beneficial to the diversity of several taxonomic groups (Lindenmayer and Laurance, 2017). Others, like those related to epiphytic and epixylic structures may indicate a relatively high ecological continuity, which is also beneficial for forest biodiversity (Nordén, Dahlberg, Brandrud, Fritz, Ejrnaes, et al., 2014).
Interestingly, also the basal area of the smallest diameter class (7.5-17.5 cm) higher than 10 m^2/ha is relevantly linked to the abundance of diagnostic species. This value of basal area is very low, and, as such, witnesses the relevance of the younger age classes to be represented within the target habitats.
Overall the joint results on the abundance of TreMs related to senescing trees and on the smallest diameter class points to the relevance of maintaining a certain degree of unevenagedness at the stand scale.

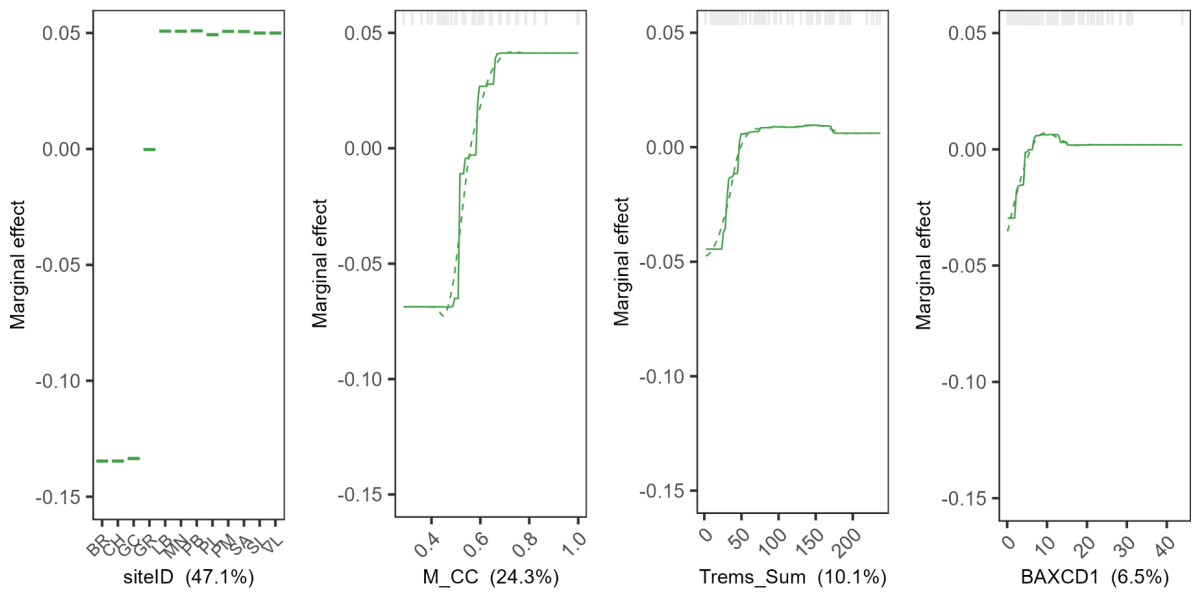


Figure 3. Partial dependence plots showing the marginal effect of site, canopy cover, abundance of TreMs, and basal area of the trees with DBH between 7.5 and 17.5 cm on the relative cover of diagnostic species. Grey stripes on the top of each graph represent the distribution of the data.

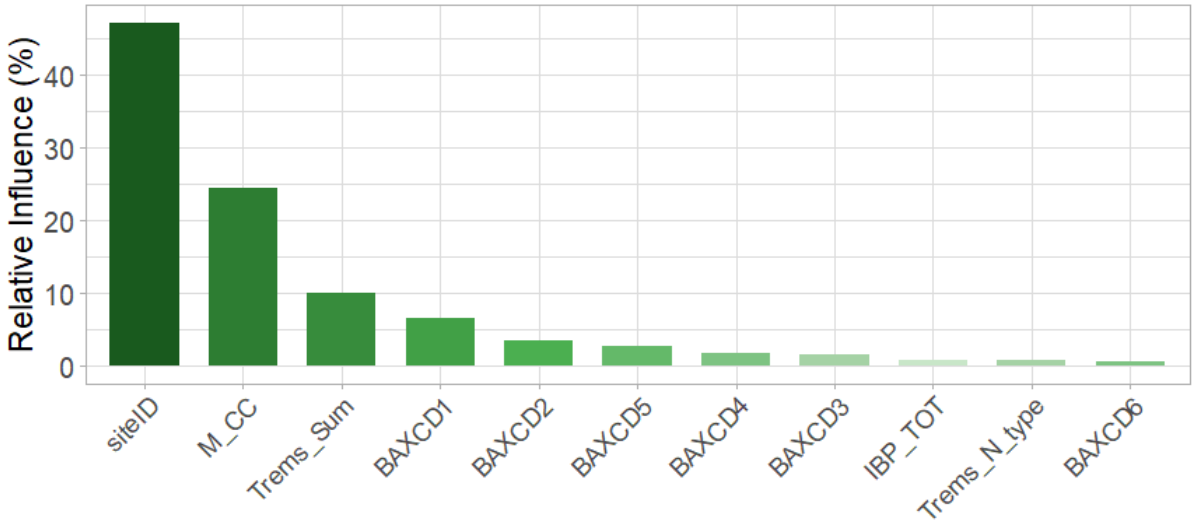


Figure 4. Relative influence of the predictor variables in determining the cover (%) of the diagnostic species of vascular plants per sampling unit.

3.2 Results for epiphytic lichens

Also in this case, the site had a great effect in explaining the changes in species diversity of epiphytic lichens. For this taxonomic group, however, a high tree density, especially in the diameter classes 7.5-17.5 cm and 27.5-37.5 cm that are the most

represented across the project sites, and a high degree of canopy closure have negative effects on this taxonomic group (Fig. 5).
Noteworthy, although less relevant,the abundance of TreMs showed positive links with the species diversity of epiphytic lichens (Fig. 6).

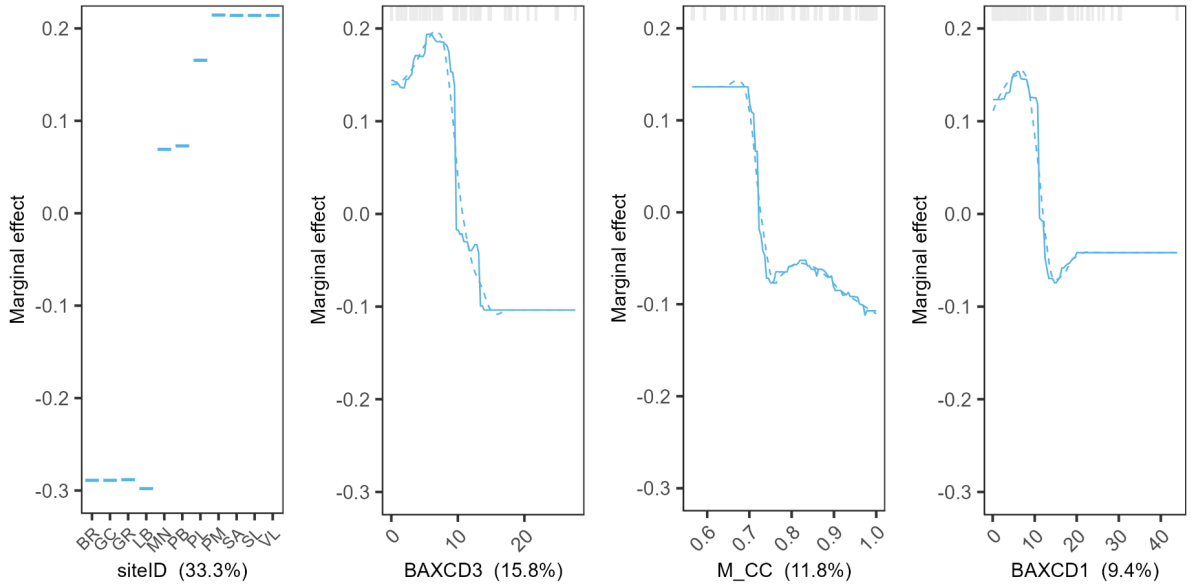


Figure 5. Partial dependency plots based on the Boosted Regression Trees modeling the Shannon index of epiphytic lichens against: site, basal area of the trees with DBH between 27.6 and 37.5 cm., canopy cover, and basal area of the trees with DBH between 7.5 and 17.5 cm.

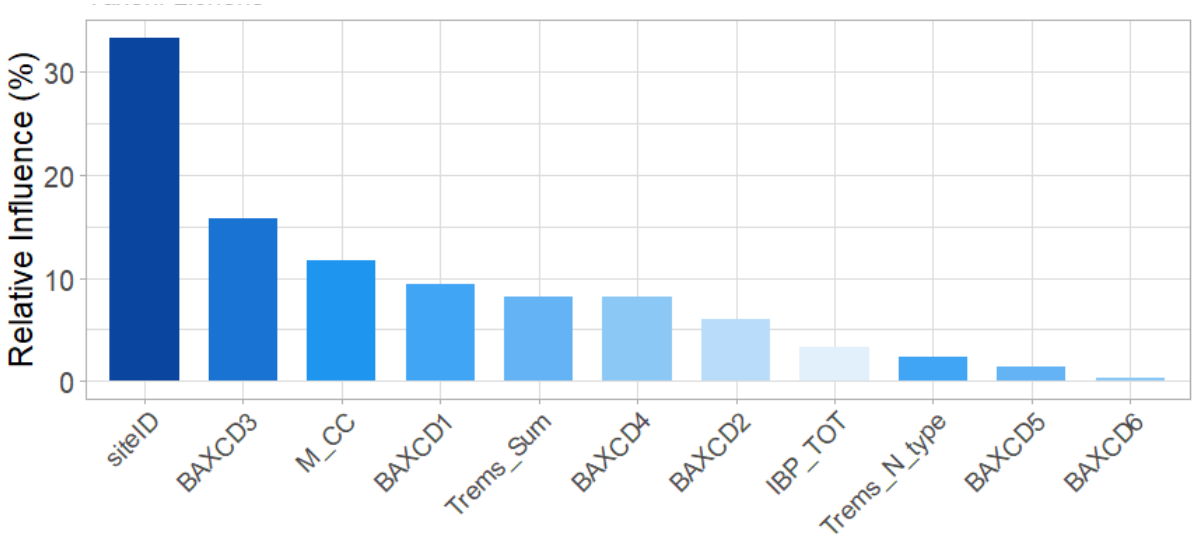


Figure 6. Relative influence of the predictor variables in determining the shannon index of epiphytic lichens per sampling unit according to BRTs.

3.3 Results for saproxylic arthropods

Also for this group we found the abundance of TreMs to be relevant rather than their diversity (Fig. 8). Again, it is important to underline that this abundance variable mainly derives from the categories of TreMs mentioned for vascular plants linked to senescing trees. Surprisingly, in this case, the distribution of TreMs across different types has a general negative effect on the richness of functional groups, with an increase only over a certain number (five) of TreMs' types represented.

Also the IBP is positively linked to the diversity of saproxylic beetles functional groups with an inflection point for IBP values around 30, i.e., between 27 and 35 (Fig. 7). Based on our interpretation, these values were mainly found in the habitat 9340 *Quercus ilex* and *Quercus rotundifolia* forests, with low scores for the factors of the IBP related to openness and large living trees. This indicates that, even in areas where standing and lying deadwood occurs, the lack of gaps or a very high canopy closure may limit the diversity of saproxylic arthropods functional groups.

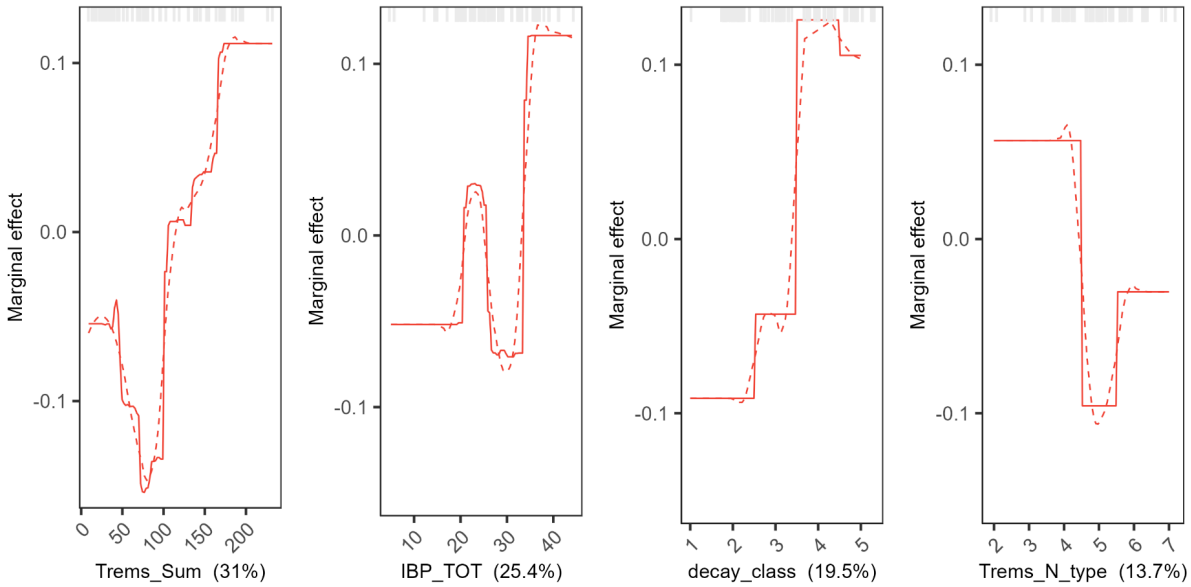


Figure 7. Partial dependence plots showing the marginal effect of abundance of Trems, total IBP score, decay class, and the number of types of Trems on the richness of functional groups of saproxylic arthropods. Grey stripes on the top of each graph represent the distribution of the data.

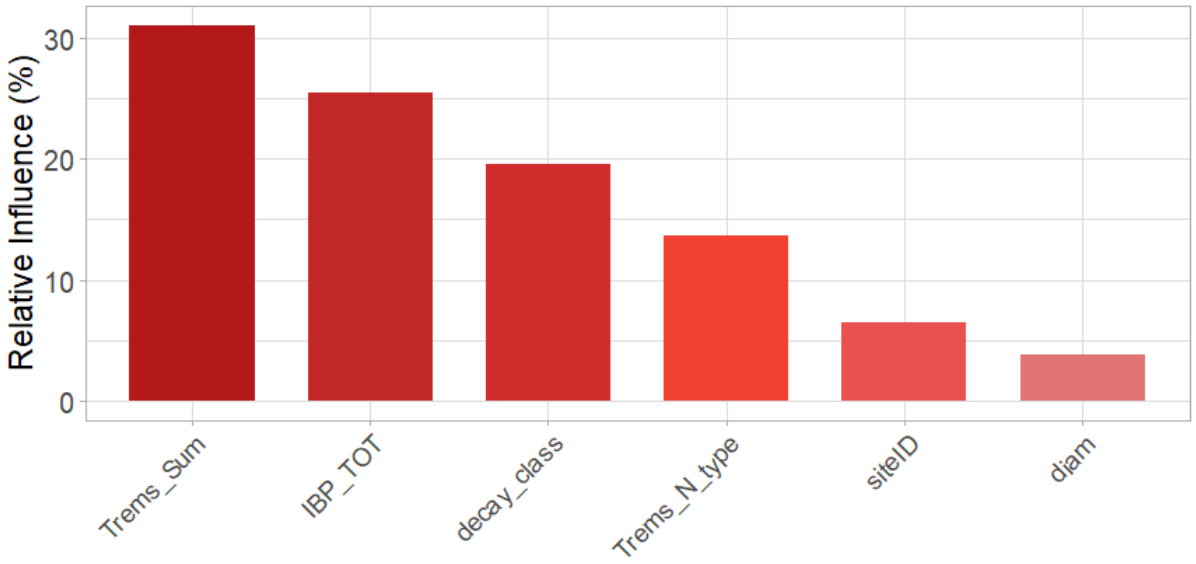


Figure 8. Relative influence of the predictor variables in determining the richness of functional groups for saproxylic arthropods per sampling unit according to BRTs.

3.4 Results for phytophagous arthropods

The results for phytophagous insects are partly in line with those for the other taxonomic groups. Also this group takes advantage of a lower density of trees in one of the most represented diameter classes (i.e., DBH between 27.6 and 37.5), and, accordingly, is favoured by a relatively high shrub cover, i.e., higher than 20% (Fig. 9). In this case the abundance of TreMs results as negatively related to the diversity of this group, however, this may be a spurious effect of the lower density of trees.

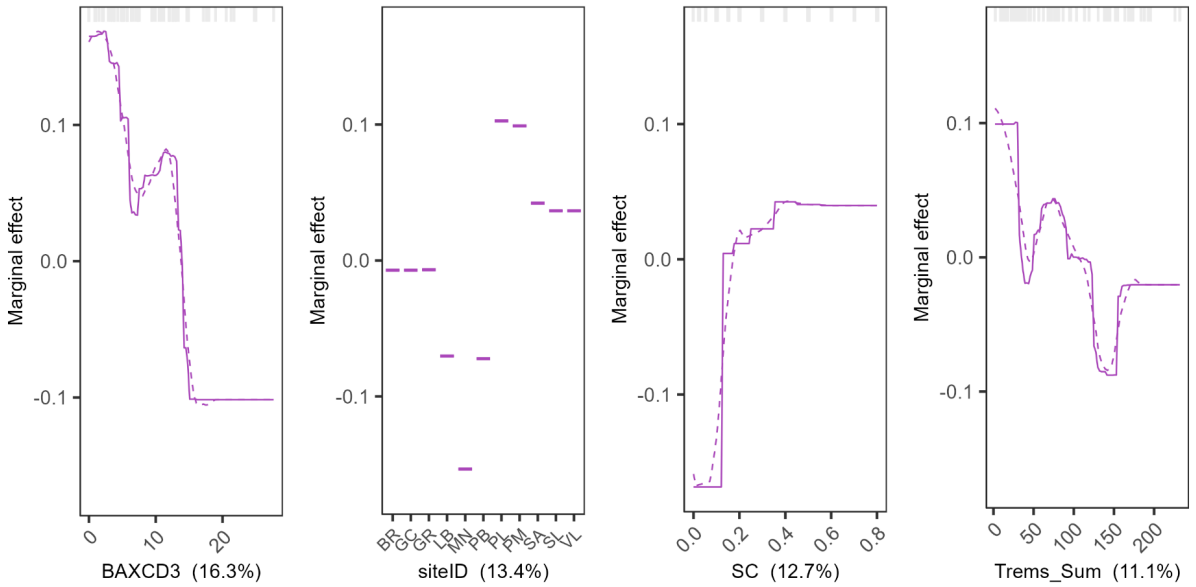


Figure 9. Partial dependence plots showing the marginal effect of basal area of the trees with DBH between 27.6 and 37.5 cm., site, shrub cover (%), and the

abundance of TreMs on the richness of functional groups of phytophagous arthropods. Grey stripes on the top of each graph represent the distribution of the data.

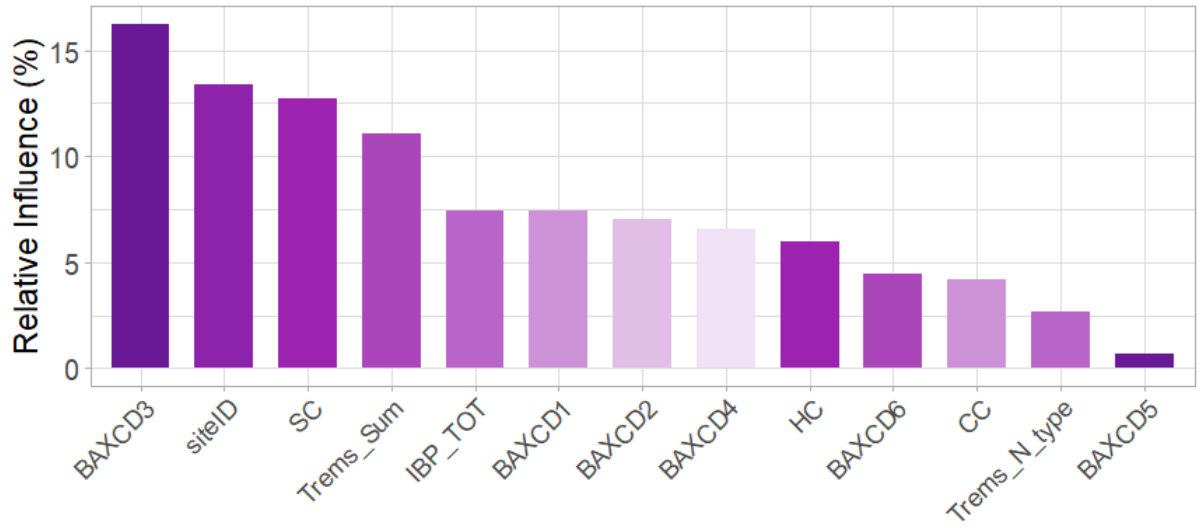


Figure 10. Relative influence of the predictor variables in determining the richness of functional groups for phytophagous arthropods per sampling unit according to BRTs.

4. Discussion

The work presented here is of primary relevance since it is the first comprehensive study modeling the diversity of multiple taxonomic groups against a series of structural variables relevant for management purposes and indicators of forest biodiversity within the Mediterranean context across four different countries and habitats. As such, the results here presented are novel and may significantly improve the management and monitoring of the habitats targeted by the project.
Below we summarise the insights for the target habitats' monitoring and management. Interestingly, these two sets of results are tightly intertwined, since the indicators that better describe the habitats' multi-taxon biodiversity correspond to those structural parameters that

4.1. Monitoring implications

4.1.1 IBP indicates the multi-taxon biodiversity of the habitats but should weigh more the openness factor

Overall, the IBP was positively correlated with the diversity values we used for different taxonomic groups. This was true for both saproxylic and phytophagous insects (see SM7) and more weakly for epiphytic lichens (see SM5). This effect on some specific taxonomic groups, with stronger links to arthropods is in line with a previous study linking IBP to field-sampled biodiversity in temperate forests (Zeller et al., 2022). However, it is important to underline how our results, especially for saproxylic arthropods, which are those showing the strongest response to IBP, show an inflection point that our interpretation associated with low openness values in forest stands with an average IBP value.
This insight is in line with our results for canopy cover (see section 4.2.1), and would support a revision of the scores for the openness factor of the IBP for Mediterranean forest habitats.

4.1.2 The abundance of some TreMs is more relevant than TreMs' diversification

When linking TreM related variables to the diversity of multiple taxonomic groups, we found the abundance of TreMs to be more relevant than their typological diversification. This is true for the habitat diagnostic vascular plant species and epiphytic lichens with similar thresholds indicated by the two models, and for saproxylic arthropods, although with a much greater threshold.
The general significance of the value of this indicator as compared to the number of TreMs type occurring within each sampling unit points to an general effect of the overall structure allowing for a high number of TreMs, rather than to a specific effect of individual TreMs for a set of species or functional groups. As a matter of fact, if

individual links between specific groups of saproxylic arthropods and individual TreMs' types were particularly influential, TreM diversification would have emerged as particularly significant. Our results point to the relevance of some TreMs' groups that arose to high abundance in numbers even in plots with a very low diversity. As a matter of fact, only for some of them a direct link with the diversity of the investigated taxonomic groups may be assumed, as it is for the epiphytic and epixylic structures, which directly include the abundance of epiphyte including lichens, and for insect galleries and bore holes, which are directly deriving by the population size of saproxylic communities.
Overall, however, the links between the abundance of the mentioned TreMs and the multi-taxon biodiversity suggests that a relatively high density of large habitat trees, bearing crown deadwood, injuries and excrescences is a general indicator of the habitat conservation status.
Noteworthy, epiphytic and epixylic structures more than other groups of TreMs also indicate a relatively long ecological continuity. This driver of forest biodiversity is inevitably linked to forest structural heterogeneity as well as with the abundance of habitat structures in forests (Nordén, Dahlberg, Brandrud, Fritz, Ejrnæs, et al., 2014). However, it should not be overlooked how allowing for continuous forest cover conditions has a crucial role in the colonization and long-term maintenance of several forest specialized taxa, as it was demonstrated in temperate oak forests (Mölder et al., 2019), and in Mediterranean forests, in a study including the Quercus ilex forests of Luberon (Abadie et al., 2021).

4.2. Management implications

4.2.1 The canopy cover strongly drives the diversity of multiple taxonomic groups

One of the variables that we found more relevant across different taxonomic groups is the canopy cover. This is unsurprising, since the intensity of the light passing through the canopy, determines the quantity of energy input for the understorey communities, as well as the microclimate to which they are subjected (De Frenne et al., 2021).
Based on our results the target canopy cover for the target habitats should be higher than 50% to allow for a relatively high abundance of diagnostic species in the understorey, but below 70% because this is a relevant negative threshold for epiphytic lichens. This means that the studied habitats benefit from relatively open conditions as compared to other forest habitats.
The target habitats, as many habitats within the Mediterranean biogeographical region, were longly subjected to human exploitment, both for timber and fodder. As such, often in space and time, these forests were characterized by a relatively low biomass level, as compared to other European forest habitats, e.g., within the continental biogeographical region. Such a low biomass level is also in line with the

relatively low productivity of these ecosystems, which are periodically subjected to a high level of stress linked to the summer drought.
This relatively low canopy cover is beneficial also to arthropods, as indicated by the inflection of the positive link with IBP in the *Quercus ilex forests* with very low openness scores for saproxylic species, and by the negative links between basal area in average diameter classes and phytophagous species. Based on the results for the latter group, it is also evident, how the degree of openness in the canopy would be beneficially occupied by shrub species, which, may support a functionally diverse community of phytophagous arthropods, and would likely make possible the occurrence of the many shrub diagnostic species of the habitats (see the report D.2.2 for the task 2.2.5 *Vegetation-based manual for the recognition and conservation state assessment of the target habitats*).
Therefore, our results give a clear indication on the range of canopy cover (50-70%) to be addressed when managing for a favorable conservation status of the habitat, and also indicate as advantageous to favour a shrub cover of at least 20%, especially referred to the habitats' diagnostic species.

4.2.2 TreMs related to senescent trees and ecological continuity are key for the diversity of multiple taxonomic groups

The TreM categories that often were highly abundant also in plots where very few TreMs' types were found were included in the groups epiphytic and epixylic structures, crown deadwood, excrescences, tree injuries and exposed wood, and, among cavities, insect galleries and bore holes.
These TreMs may be promoted within forest ecosystems by releasing the trees either in the larger size classes or showing some senescence signs (Larrieu et al., 2018). Another approach would include the active restoration of these structures. This was already attempted within the continental biogeographical region with positive outcomes in terms of TreMs abundance (Asbeck et al., 2023), but no examples are available to the best of our knowledge for the forests within the Mediterranean region.
Given the overall results of the models, our interpretation of biodiversity positive responses was focused on the general forest structure and ecological continuity rather than on specific species-TreM links. In this view, an intermediate approach based on individual tree selection with the release of large and potential habitat trees, with special attention to the forest ecological continuity will allow for a biodiversity increase in the target habitats in the mid- to long-term depending on the original habitat conditions.

4.2.3 The occurrence of deadwood in higher decay classes is crucial for saproxylic arthropods

As highlighted in a global meta-analysis (Parajuli & Markwith, 2023) and only partly confirmed in a European meta-analysis, deadwood decay stage is relevant for saproxylic organisms diversity.
This general positive trend for biodiversity as the decay process advances may be explained by the occurrence in deadwood referred to high decay classes of organisms that are specific to this stage. For beetles, it was demonstrated that the abundance of rare species increases in late successional stages (Traylor et al., 2023), supporting also the diversification in terms of functional groups that we observed.
Since deadwood diameter instead resulted in a neglectable response, in management terms, we would suggest the release of deadwood also in the lower diameter classes in order to facilitate a more rapid decay process towards the advanced stages.

4.3 Opportunities and limitations

The current work represents an unprecedented effort to study the biodiversity of Mediterranean forests, while also investigating its link with management related stand structural variables and structure-based indices of biodiversity potential. The lack of data for Mediterranean forests, with special reference to biodiversity and biodiversity indicators, was already highlighted in previous studies (Burrascano et al., 2023; Larrieu et al., 2018).
Given the high relevance for European forest diversity of Mediterranean forests and the massive threats posed to these ecosystems by climate changes these data and results are of primary relevance for the conservation of European biodiversity as a whole.
As expected, the novelty of this effort comes together with a series of limitations. The main one is the relatively low number of sampling units as compared to the great heterogeneity found across sites and habitats. Relying on a greater set of data for each individual habitat could have led to more specific outcomes for both the monitoring and the management implications. On the other hand, the target habitats have relevant commonalities in terms of human exploitation, and of relatively low productivity given the drought stress that affects these habitats. These commonalities allowed us to draw general, yet meaningful, conclusions, accounting for the differences across sites and habitats in the BRT models.

Bibliography

Abadie, J., Dupouey, J.-L., Salvaudon, A., Gachet, S., Videau, N., Avon, C., Dumont, J., Tatoni, T., & Bergès, L. (2021). Historical ecology of Mediterranean forests: Land use legacies on current understorey plants differ with time since abandonment and former agricultural use. *Journal of Vegetation Science*, *32*(1), e12860. https://doi.org/10.1111/jvs.12860

Acácio, V., Dias, F. S., Catry, F. X., Rocha, M., & Moreira, F. (2017). Landscape dynamics in Mediterranean oak forests under global change: Understanding the role of anthropogenic and environmental drivers across forest types. *Global Change Biology*, *23*(3), 1199–1217. https://doi.org/10.1111/gcb.13487

Asbeck, T., Benneter, A., Huber, A., Margaritis, D., Buse, J., Popa, F., Pyttel, P., Förschler, M., Gärtner, S., & Bauhus, J. (2023). Enhancing structural complexity: An experiment conducted in the Black Forest National Park, Germany. *Ecology and Evolution*, *13*(1), e9732. https://doi.org/10.1002/ece3.9732

Brunet, J., Fritz, Ö., & Richnau, G. (2010). Biodiversity in European beech forests—A review with recommendations for sustainable forest management. *Ecological Bulletins*, *53*, 77–94.

Burrascano, S., Chianucci, F., Trentanovi, G., Kepfer-Rojas, S., Sitzia, T., Tinya, F., Doerfler, I., Paillet, Y., Nagel, T. A., Mitic, B., Morillas, L., Munzi, S., Van der Sluis, T., Alterio, E., Balducci, L., de Andrade, R. B., Bouget, C., Giordani, P., Lachat, T., … Ódor, P. (2023). Where are we now with European forest multi-taxon biodiversity and where can we head to? *Biological Conservation*, *284*, 110176. https://doi.org/10.1016/j.biocon.2023.110176

Burrascano, S., Trentanovi, G., Paillet, Y., Heilmann-Clausen, J., Giordani, P., Bagella, S., Bravo-Oviedo, A., Campagnaro, T., Campanaro, A., Chianucci, F., De Smedt, P., García-Mijangos, I., Matošević, D., Sitzia, T., Aszalós, R., Brazaitis, G., Cutini, A.,

D'Andrea, E., Doerfler, I., … Ódor, P. (2021). Handbook of field sampling for multi-taxon biodiversity studies in European forests. *Ecological Indicators*, *132*, 108266. https://doi.org/10.1016/j.ecolind.2021.108266

Bütler, R., Lachat, T., Krumm, F., Kraus, D., & Larrieu, L. (2024). *Field Guide to Tree-related Microhabitats: Descriptions and size limits for their inventory in temperate and Mediterranean forests*.

Chianucci, F., Ferrara, C., & Puletti, N. (2022). *coveR: An R package for processing Digital Cover Photography images to retrieve forest canopy attributes* (p. 2022.01.13.475850). bioRxiv. https://doi.org/10.1101/2022.01.13.475850

COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS New EU Forest Strategy for 2030 (2021). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A52021DC0572

Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora, CONSIL, 206 OJ L (1992). http://data.europa.eu/eli/dir/1992/43/oj/eng

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., … Hylander, K. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, *27*(11), 2279–2297. https://doi.org/10.1111/gcb.15569

Dittrich, S., Jacob, M., Bade, C., Leuschner, C., & Hauck, M. (2014). The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. *Plant Ecology*, *215*(10), 1123–1137. https://doi.org/10.1007/s11258-014-0371-6

Dufour-Pelletier, S., A. Tremblay, J., Hébert, C., Lachat, T., & Ibarzabal, J. (2020). Testing the Effect of Snag and Cavity Supply on Deadwood-Associated Species in a

Managed Boreal Forest. *Forests*, *11*(4), Article 4. https://doi.org/10.3390/f11040424

Elith, J., & Leathwick, J. (2013). *Boosted Regression Trees for Ecological Modeling*.

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, *77*(4), 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Ellis, C. (2009). Changing climate and historic-woodland structure interact to control species diversity of the 'Lobarion' epiphyte community in Scotland. *Journal of Vegetation Science*, *18*, 725–734. https://doi.org/10.1658/1100-9233(2007)18[725:CCAHSI]2.0.CO;2

European Environment Agency (EU body or agency). (2020). *State of nature in the EU: Results from reporting under the nature directives 2013 2018*. Publications Office of the European Union. https://data.europa.eu/doi/10.2800/088178

Fady-Welterlen, B. (2005). Is there really more biodiversity in Mediterranean forest ecosystems? *TAXON*, *54*(4), 905–910. https://doi.org/10.2307/25065477

FOREST EUROPE. (2020). FOREST EUROPE, 2020: State of Europe's Forests 2020. *FOREST EUROPE, 2020: State of Europe's Forests 2020*.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*(1), 1340. https://doi.org/10.1038/ncomms2328

Gao, T., Nielsen, A. B., & Hedblom, M. (2015). Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, *57*, 420–434. https://doi.org/10.1016/j.ecolind.2015.05.028

Gibb, H., Hjältén, J., P. Ball, J., Atlegrim, O., Pettersson, R. B., Hilszczański, J., Johansson, T., & Danell, K. (2006). Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: A study using experimental logs for monitoring assemblages. *Ecography*, *29*(2), 191–204.

https://doi.org/10.1111/j.2006.0906-7590.04372.x

Golladay, S. W., Martin, K. L., Vose, J. M., Wear, D. N., Covich, A. P., Hobbs, R. J., Klepzig, K. D., Likens, G. E., Naiman, R. J., & Shearer, A. W. (2016). Achievable future conditions as a framework for guiding forest conservation and management. *Forest Ecology and Management*, *360*, 80–96. https://doi.org/10.1016/j.foreco.2015.10.009

Harmon, M. E., Woodall, C. W., Fasth, B., Sexton, J., & Yatkov, M. (2011). Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. *Res. Pap. NRS-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 40 p.*, *15*, 1–40. https://doi.org/10.2737/NRS-RP-15

Hidalgo-Triana, N., Solakis, A., Casimiro-Soriguer, F., Choe, H., Navarro, T., Pérez-Latorre, A. V., & Thorne, J. H. (2023). The high climate vulnerability of western Mediterranean forests. *Science of The Total Environment*, *895*, 164983. https://doi.org/10.1016/j.scitotenv.2023.164983

Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., & Hijmans, M. R. J. (2022). *Package 'dismo' Version 1.3-8*. https://CRAN.R-project.org/package=dismo

IUCN. (2024). *The IUCN Red List of Threatened Species. Version 2024-1. Https://www.iucnredlist.org. Accessed on 27/10/2024.*

Larrieu, L., & Gonin, P. (2008). L'indice de biodiversité potentielle (IBP): Une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. *Revue Forestière Française*, *60*(6), 727–748. https://doi.org/10.4267/2042/28373

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., & Vandekerkhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, *84*, 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051

LaRue, E. A., Knott, J. A., Domke, G. M., Chen, H. Y., Guo, Q., Hisano, M., Oswalt, C., Oswalt, S., Kong, N., Potter, K. M., & Fei, S. (2023). Structural diversity as a reliable

and novel predictor for ecosystem productivity. *Frontiers in Ecology and the Environment*, *21*(1), 33–39. https://doi.org/10.1002/fee.2586

Lindenmayer, D. B., & Laurance, W. F. (2017). The ecology, distribution, conservation and management of large old trees. *Biological Reviews*, *92*(3), 1434–1458. https://doi.org/10.1111/brv.12290

Lionello, P., & Scarascia, L. (2018). The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, *18*. https://doi.org/10.1007/s10113-018-1290-1

Macfarlane, C., Arndt, S. K., Livesley, S. J., Edgar, A. C., White, D. A., Adams, M. A., & Eamus, D. (2007). Estimation of leaf area index in eucalypt forest with vertical foliage, using cover and fullframe fisheye photography. *Forest Ecology and Management*, *242*(2), 756–763. https://doi.org/10.1016/j.foreco.2007.02.021

MCPFE. (1993). *Resolution H1: General Guidelines for the Sustainable Management of Forests in Europe. Second MCPFE 16–17 June 1993, Helsinki/Finland.*

Médail, F., & Baumel, A. (2018). Using phylogeography to define conservation priorities: The case of narrow endemic plants in the Mediterranean Basin hotspot. *Biological Conservation*, *224*, 258–266. https://doi.org/10.1016/j.biocon.2018.05.028

Médail, F., & Quézel, P. (1999). Biodiversity Hotspots in the Mediterranean Basin: Setting Global Conservation Priorities. *Conservation Biology*, *13*(6), 1510–1513. https://doi.org/10.1046/j.1523-1739.1999.98467.x

Minelli, A., Bologna, M., & Daniele, B. (2023). *Sistematica ed evoluzione degli esapodi*.

Mölder, A., Meyer, P., & Nagel, R.-V. (2019). Integrative management to sustain biodiversity and ecological continuity in Central European temperate oak (*Quercus robur, Q. petraea*) forests: An overview. *Forest Ecology and Management*, *437*, 324–339. https://doi.org/10.1016/j.foreco.2019.01.006

Mouchet, M., Levers, C., Zupan, L., Kuemmerle, T., Plutzar, C., Erb, K., Lavorel, S., Thuiller, W., & Haberl, H. (2015). Testing the Effectiveness of Environmental Variables to Explain European Terrestrial Vertebrate Species Richness across Biogeographical

Scales. *PLOS ONE*, *10*(7), e0131924. https://doi.org/10.1371/journal.pone.0131924

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Napoleone, F., Giarrizzo, E., & Burrascano, S. (2021). Habitat conservation state and plant diversity respond to different drivers in semi-natural grasslands. *Journal of Vegetation Science*, *32*(4), e13055. https://doi.org/10.1111/jvs.13055

Nocentini, S., Travaglini, D., & Muys, B. (2022). Managing Mediterranean Forests for Multiple Ecosystem Services: Research Progress and Knowledge Gaps. *Current Forestry Reports*, *8*(2), 229–256. https://doi.org/10.1007/s40725-022-00167-w

Nordén, B., Dahlberg, A., Brandrud, T. E., Fritz, Ö., Ejrnaes, R., & Ovaskainen, O. (2014). Effects of ecological continuity on species richness and composition in forests and woodlands: A review. *Écoscience*, *21*(1), 34–45. https://doi.org/10.2980/21-1-3667

Nordén, B., Dahlberg, A., Brandrud, T., Fritz, Ö., Ejrnæs, R., & Ovaskainen, O. (2014). Effects of Ecological Continuity on Species Richness and Composition in Forests and Woodlands: A Review. *Ecoscience*, *21*, 34–45. https://doi.org/10.2980/21-1-3667

Palahi, M., Mavsar, R., Gracia, C., & Birot, Y. (2008). Mediterranean forests under focus. *International Forestry Review*, *10*(4), 676–688. https://doi.org/10.1505/ifor.10.4.676

Parajuli, R., & Markwith, S. H. (2023). Quantity is foremost but quality matters: A global meta-analysis of correlations of dead wood volume and biodiversity in forest ecosystems. *Biological Conservation*, *283*, 110100. https://doi.org/10.1016/j.biocon.2023.110100

Parisi, F., Pioli, S., Lombardi, F., Fravolini, G., Marchetti, M., & Tognetti, R. (2018). Linking deadwood traits with saproxylic invertebrates and fungi in European forests—A review. *iForest - Biogeosciences and Forestry*, *11*(3), 423. https://doi.org/10.3832/ifor2670-011

Pekin, B., & Macfarlane, C. (2009). Measurement of Crown Cover and Leaf Area Index Using Digital Cover Photography and Its Application to Remote Sensing. *Remote*

Sensing. https://doi.org/10.3390/rs1041298

Prévost, M., & Raymond, P. (2012). Effect of gap size, aspect and slope on available light and soil temperature after patch-selection cutting in yellow birch–conifer stands, Quebec, Canada. *Forest Ecology and Management*, *274*, 210–221. https://doi.org/10.1016/j.foreco.2012.02.020

Quézel, P., & Médail, F. (2003). *Ecologie et biogéographie des forêts du bassin méditerranéen*. https://www.semanticscholar.org/paper/Ecologie-et-biog%C3%A9ographie-des-for%C3%AAts-du-bassin-Qu%C3%A9zel-M%C3%A9dail/cc4b22f11d5694af8cdeeeae43ada6c18a283832

Sabatini, F. M., Bluhm, H., Kun, Z., Aksenov, D., Atauri, J. A., Buchwald, E., Burrascano, S., Cateau, E., Diku, A., Duarte, I. M., Fernández López, Á. B., Garbarino, M., Grigoriadis, N., Horváth, F., Keren, S., Kitenberga, M., Kiš, A., Kraut, A., Ibisch, P. L., … Kuemmerle, T. (2021). European primary forest database v2.0. *Scientific Data*, *8*(1), Article 1. https://doi.org/10.1038/s41597-021-00988-7

Sayre, R., Martin, M., Karagulle, D., Frye, C., Breyer, S., Wright, D., Butler, K., VanGraafeiland, K., Boucher, T., McGowan, J., Touval, J., Wolff, N. H., Sotomayor, L., Game, E. T., & Possingham, H. (2020). World Terrestrial Ecosystems. In M. I. Goldstein & D. A. DellaSala (Eds.), *Encyclopedia of the World's Biomes* (pp. 31–34). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.12474-1

Stojanova, D., Panov, P., Gjorgjioski, V., Kobler, A., & Džeroski, S. (2010). 1 2 Estimating Vegetation Height and Canopy Cover from Remotely Sensed Data with Machine Learning 3 4 5. *Ecological Informatics*, *5*, 256–266. https://doi.org/10.1016/j.ecoinf.2010.03.004

Stokland, J. N. (2012). The saproxylic food web. In B. G. Jonsson, J. N. Stokland, & J. Siitonen (Eds.), *Biodiversity in Dead Wood* (pp. 29–57). Cambridge University Press. https://doi.org/10.1017/CBO9781139025843.004

Szymura, T. H., Szymura, M., Zając, M., & Zając, A. (2018). Effect of anthropogenic factors,

landscape structure, land relief, soil and climate on risk of alien plant invasion at regional scale. *Science of The Total Environment*, *626*, 1373–1381. https://doi.org/10.1016/j.scitotenv.2018.01.131

Tinya, F., Doerfler, I., de Groot, M., Heilman-Clausen, J., Kovács, B., Mårell, A., Nordén, B., Aszalós, R., Bässler, C., Brazaitis, G., Burrascano, S., Camprodon, J., Chudomelová, M., Čížek, L., D'Andrea, E., Gossner, M., Halme, P., Hédl, R., Korboulewsky, N., … Ódor, P. (2023). A synthesis of multi-taxa management experiments to guide forest biodiversity conservation in Europe. *Global Ecology and Conservation*, *46*, e02553. https://doi.org/10.1016/j.gecco.2023.e02553

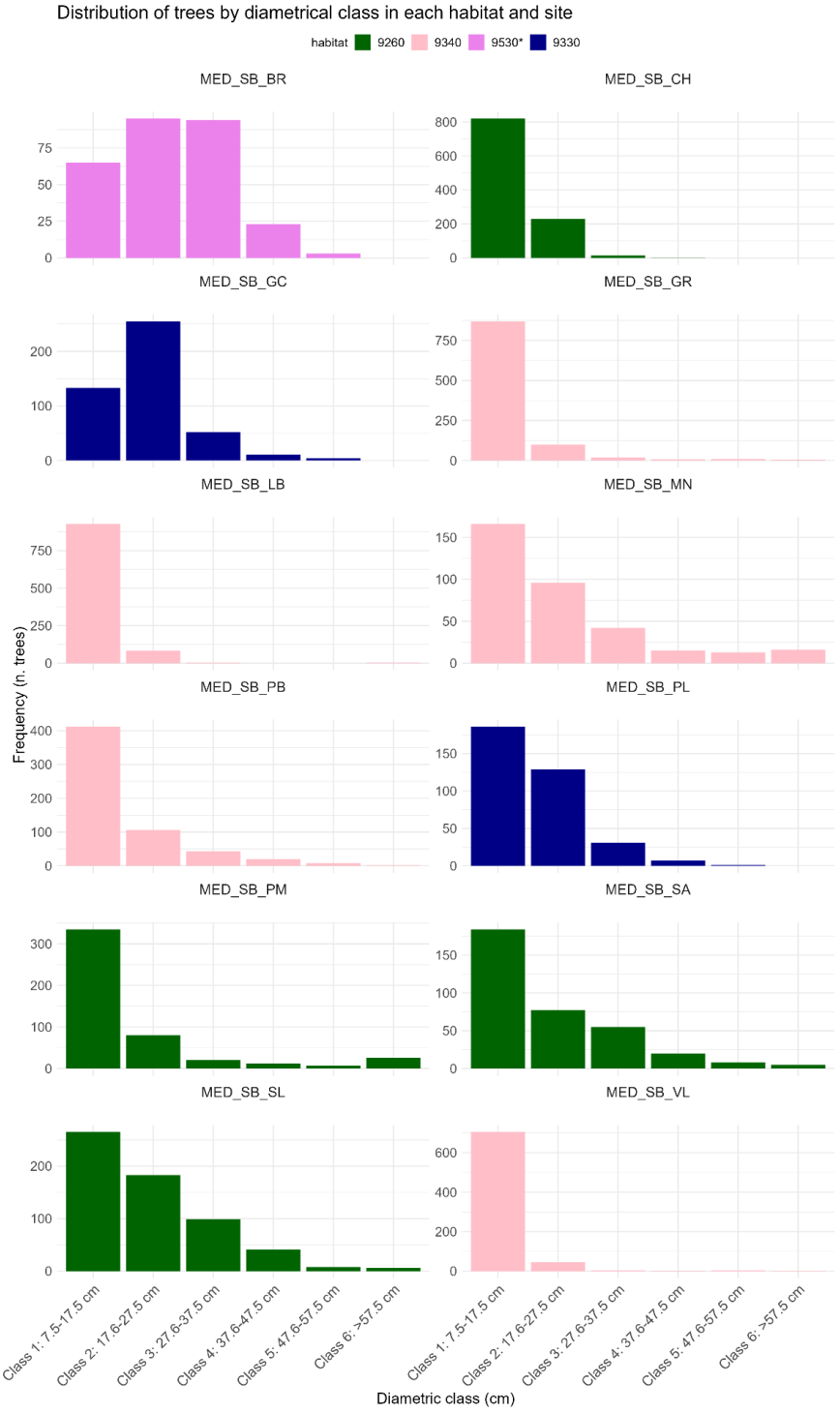
Traylor, C. R., Ulyshen, M. D., & McHugh, J. V. (2023). Forest age drives saproxylic beetle biodiversity in the southeastern United States. *Biological Conservation*, *285*, 110238. https://doi.org/10.1016/j.biocon.2023.110238

Vellend, M. (2004). Parallel Effects of Land-Use History on Species Diversity and Genetic Diversity of Forest Herbs. *Ecology*, *85*(11), 3043–3055. https://doi.org/10.1890/04-0435

Zeller, L., Baumann, C., Gonin, P., Heidrich, L., Keye, C., Konrad, F., Larrieu, L., Meyer, P., Sennhenn-Reulen, H., Müller, J., Schall, P., & Ammer, C. (2022). Index of biodiversity potential (IBP) versus direct species monitoring in temperate forests. *Ecological Indicators*, *136*, 108692. https://doi.org/10.1016/j.ecolind.2022.108692

Supplementary material

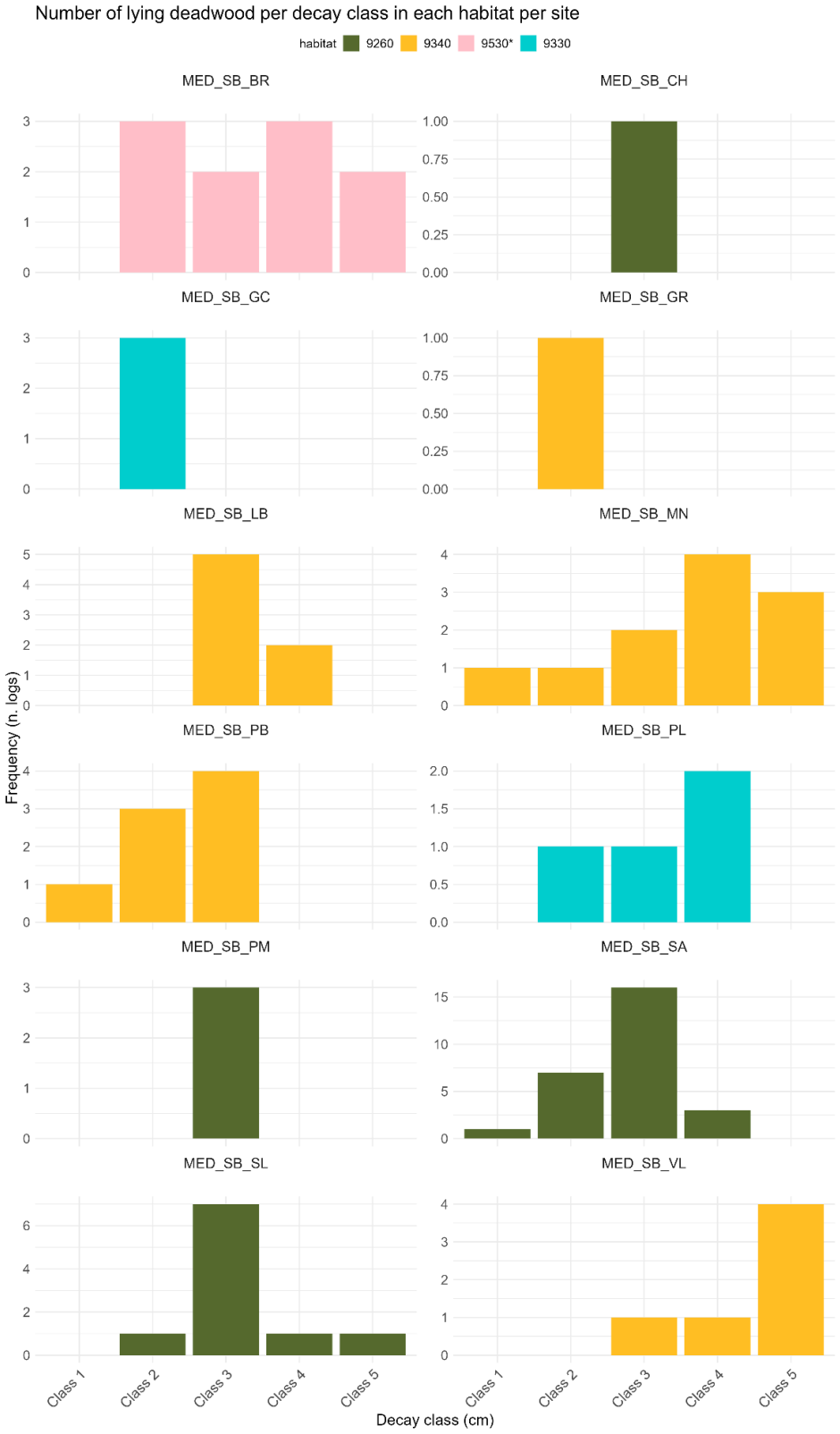
SM1. Tree diameter distribution across the project sites



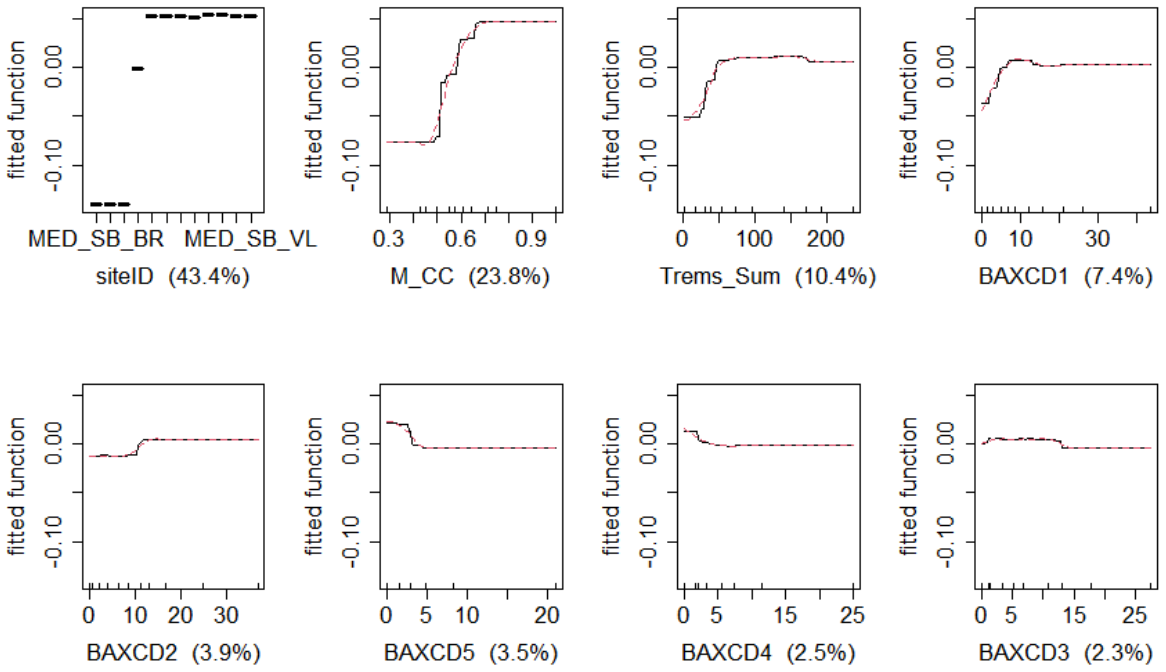
SM2. Lying deadwood diameter distribution across the project sites


Number of lying deadwood per diametrical class in each habitat per site
habitat 9260 9340 9530* 9330
MED_SB_BR
MED_SB_CH
MED_SB_GC
MED_SB_GR
MED_SB_LB
MED_SB_MN
MED_SB_PB
MED_SB_PL
MED_SB_PM
MED_SB_SA
MED_SB_SL
MED_SB_VL
Frequency (n. logs)
Class 1: 3-8 cm
Class 2: 9-14 cm
Class 3: 15-20 cm
Class 4: 21-26 cm
Class 5: 27-32 cm
Diametric class (cm)

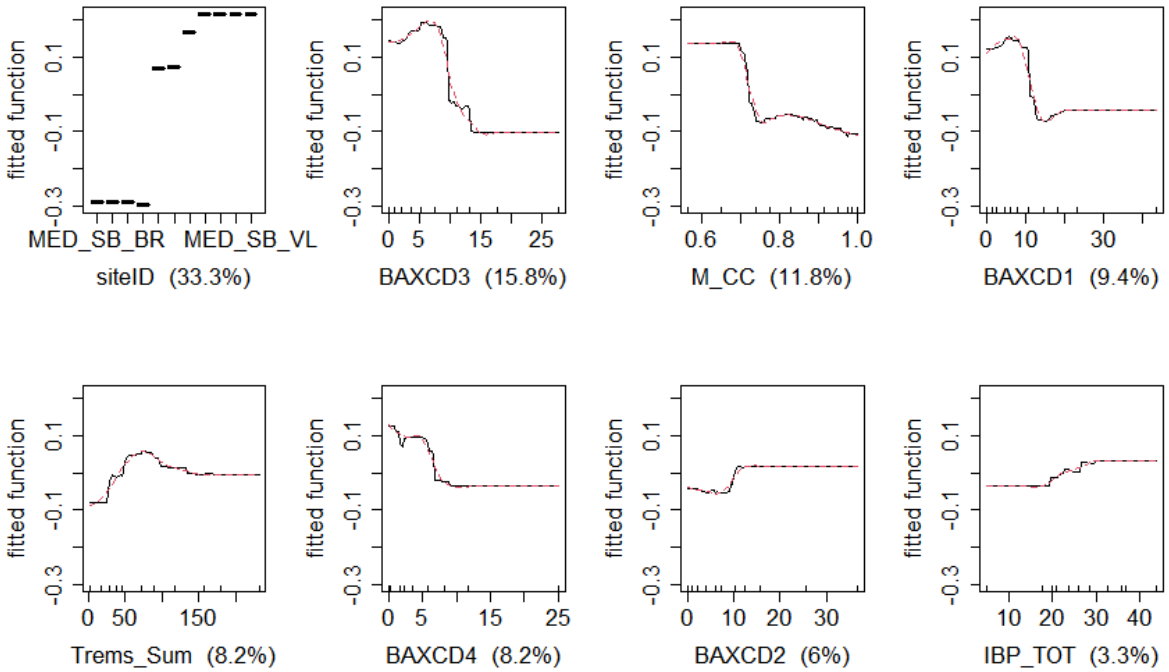
SM3. Distribution across decay classes of the lying deadwood sampled in the project site



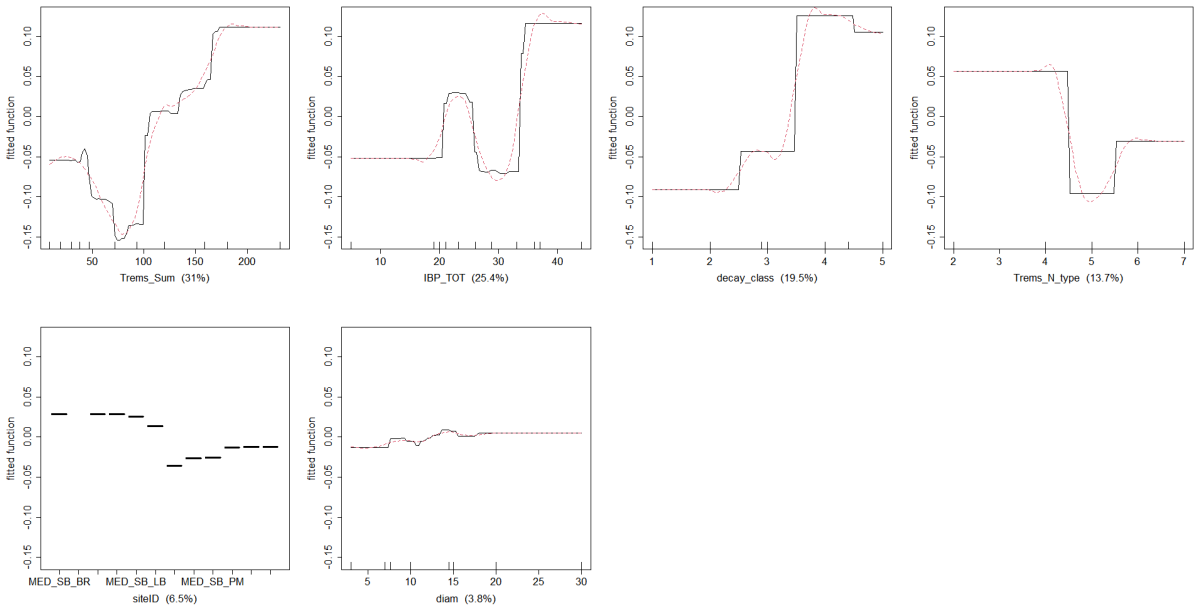
SM4. Partial dependency plots for all variables used in the vascular plants' BRT models



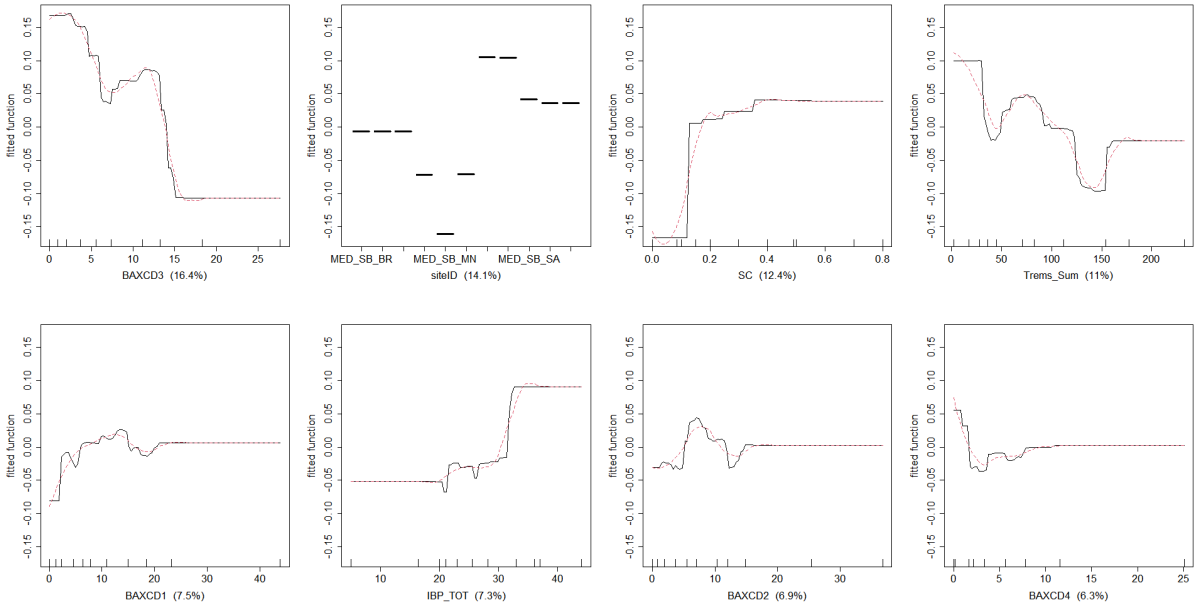
SM5. Partial dependency plots for all variables used in the epiphytic lichens' BRT models



SM6. Partial dependency plots for all variables used in the saproxylic arthropods' BRT models



SM7. Partial dependency plots for all variables used in the phytophagous arthropods' BRT models



Chapter 5. Towards an effective multi-taxon biodiversity assessment in European forests

Towards an effective in-situ biodiversity assessment in European forests

Authors:

Burrascano S., Chojnacki L., *Balducci L., Chianucci F., Haeler E., Kepfer-Rojas S., Paillet Y., Barreto de Andrade R., Boch S., De Smedt P., Fischer M., García-Mijangos, I., Heilmann-Clausen J., Hofmeister J., Hosek J., Kozak D., Kutszegi G., Lachat T., Mikolas M., Samu F., Ravera S., Schall P., Sitzia T., Svoboda M., Trentanovi G., Ujhazyova M., Vandekerkhove K., Tinya F., Odor P.

*Lorenzo Balducci. Tel.: +393343801066.
E-mail address: lorenzo.balducci@uniroma1.it.

Highlights:

The current information on forest multi-taxon biodiversity is deficient for most taxa

Existing data may help define an effective monitoring network for European forest

Sampling effort to assess species diversity varies across taxa and forest types

Sampling effort varies with the level of species diversity

Taxa may require different sampling efforts across species richness and composition

Abstract

Assessing multi-taxon biodiversity is crucial to understand forests' response to environmental changes and to inform management strategies. However, in Europe, forest biodiversity monitoring is still scattered and heterogeneous, although a comprehensive network has long

been advocated. Initiating such a network should start from the definition of the sampling effort, here intended as the number of sampling plots and sites.

We used a novel database of forest multi-taxon biodiversity as a pilot to: estimate the minimum sampling effort needed to assess species richness and variation in composition; compare these estimates with the efforts invested in the pilot database; discuss estimates' differences across taxonomic groups and forest categories.

We focused on six taxonomic groups (vascular plants, birds, epiphytic lichens and bryophytes, wood-inhabiting fungi and saproxylic beetles) across six forest categories. Based on 6,165 plots at 2,084 different locations across Europe, we estimated the effort to achieve a complete species richness sampling through interpolation/extrapolation curves, and evaluated the precision in species composition variation through multivariate standard error.

Our estimates differed widely, especially among taxonomic groups. For species richness, estimates range from 3 to 147 plots per site across 3 to 29 sites per forest category, with birds and epiphytic bryophytes requiring the least effort. For species composition, estimates range from 5 to over 25 plots per site across 5 to 20 sites per forest category, with saproxylic beetles, vascular plants, and fungi displaying the highest estimates.

The taxonomic groups requiring an effort comparable to the pilot database were the least diverse, all the others need further efforts, at least in some forest categories, either for species richness (e.g., saproxylic beetles) or species composition (e.g., vascular plants) or both (e.g., wood-inhabiting fungi). An effective monitoring network of European forests' biodiversity should thoroughly account for these figures and for their heterogeneity.

Keywords: birds, epiphytic lichens, epiphytic bryophytes, forest biodiversity, monitoring network, multivariate standard error, rarefaction curves, saproxylic beetles, vascular plants, wood-inhabiting fungi.

Introduction

Forests host about three-quarters of the global terrestrial plant, fungi and animal species (FAO, 2020), and have a great economical value, as well as a prominent role in climate regulation and human well-being (IPBES, 2019).

Implementing forest monitoring at different spatial scales is crucial to comprehend forest ecosystems' response to environmental changes (Senf et al., 2020), and to define pathways towards preserving biodiversity while profiting from forest resources in the framework of sustainable forest management (Aubin et al., 2013; Flensted et al., 2016). In this view, the European Union (EU) recently proposed a Forest Monitoring Law as a framework for the collection and reporting of forest data that integrates Earth observation and in-situ monitoring (EC, 2023). The EU Forest Strategy for 2030 (EC, 2021) defines the information on forest ecosystems as patchy, and advocates for an integrated forest monitoring framework with a special focus on biodiversity and forest management. In this view, the European Environmental Agency implemented the Forest Information System for Europe (FISE) (https://forest.eea.europa.eu/) to stimulate the integration of forest data, but still, biodiversity inventories are insufficient, even for forest habitats within Natura2000 sites (Alberdi et al., 2019). Although multi-taxon biodiversity assessments are recommended as a direct approach to comprehensively study and monitor forest biodiversity (Flensted et al., 2016; Schall et al., 2018), they are often replaced by indirect proxies, ranging from the extent

of forest or of protected forests at the broadest spatial scales, to the sampling of tree-related microhabitats at the finest scales. These indirect approaches are justified by the cost of the multiple hard skills needed for direct biodiversity data collection and management (Larrieu et al., 2019). For this reason, national forest inventories mostly do not include direct biodiversity sampling, but are rather focused on the measurement of structural variables, whose relation to biological diversity is still not broadly demonstrated (Gao et al., 2015; Penone et al., 2019; Zeller et al., 2022). Similarly, international forest monitoring networks (e.g., ICP - https://www.icp-forests.org) focus on forest health, i.e., crown condition, tree growth, and do not include comprehensive biodiversity assessments.

Species-based biodiversity surrogates (*sensu* Lindenmayer and Likens, 2011) give direct insights on biodiversity but cover only partially the wide range of forest organisms. These surrogates refer to individual species or groups of species that are either characteristics of certain habitat features, of conservation value, charismatic, or well known, e.g., indicator, umbrella, focal, and keystone species. Such partial assessments contribute only limitedly to defining the relationships between forest biodiversity and environmental conditions, including management regimes (Oettel and Lapin, 2021).

Multi-taxon surveys, even though challenging, allow for a comprehensive representation of the forest conservation status by giving insights on a wide range of ecological interactions at different scales (Burrascano et al., 2018; Pereira et al., 2013). Such surveys are still the exception rather than the rule in forest inventories, but they have been increasingly applied from local to national scales, especially to address research questions on the effect of management on forest biodiversity (Elek et al., 2018; Flensted et al., 2016). These efforts, however, may fail to provide answers to these relevant questions at the continental scale

(Burrascano et al., 2018; Chase et al., 2018), which is crucial for policies focused on the ongoing environmental crises (Pereira et al., 2013; Stadt et al., 2006). Since each taxonomic group reacts to environmental conditions at different spatial scales, and likely requires different sampling efforts to allow for broad scale assessments (Brunbjerg et al., 2019), taxon-specific sampling strategies should be adopted to optimize resources in the context of a broad-scale biodiversity assessment.

A comprehensive multi-taxon forest monitoring network at the European scale would allow to detect substantial changes in species richness and composition that may derive from changes in environmental conditions, e.g, climate change, nitrogen depositions, and/or in disturbance regimes, e.g., pathogens outbreaks, changes in harvesting intensity. The implementation of such a network is challenging. Lack of coordination in the definition of sampling designs and protocols still hamper such initiatives (Burrascano et al., 2021; Feld et al., 2009). Estimating beforehand the effort needed, here intended as the number of sites and plots, for an efficient inventory would play a key role to implement multi-taxon monitoring and demonstrate the effect of external variables (e.g., climate, forest management) on forest biodiversity (Hoffmann et al., 2019; Montes et al., 2021). An insufficient sampling effort could lead to a biased estimation of forest biodiversity due to low statistical power (Alessi et al., 2023; Underwood and Chapman, 2003). Conversely, an oversized inventory would waste time and resources, which are often limited for monitoring activities (Nuñez-Penichet et al., 2022). Thus, finding the right balance between obtaining a representative and cost-effective sample size is crucial in monitoring projects (Bruel and White, 2021; Gardner, 2010).

The increasing availability of biodiversity data from heterogeneous sources across large extents allows for ecological predictions at large scales; however, the upscaling issues of such

heterogeneous datasets are often neglected or only partly handled in modeling approaches (Ovaskainen and Abrego, 2020). For this reason, these datasets should not lead to abandoning the idea of targeted, soundly designed large-scale monitoring programmes, but rather underpin their development by making use of the acquired experience and data. In this view, investigating the effectiveness of local sampling intensities at broader spatial scales would represent a relevant asset for the development of a coordinated network for multi-taxon biodiversity assessment across European forests.

We used multi-taxon biodiversity data spread across 12 European countries (Burrascano et al., 2023) to link sampling effort to sampling completeness and precision for respectively the species richness and composition of six taxonomic groups. Our aims are to: i) estimate the minimum sampling effort needed to capture species richness and variation in species composition; ii) compare these estimates with the sampling effort of the pilot data; iii) discuss the estimates' differences across forest categories and taxonomic groups. Our ultimate goal is to inform the realization of a cooperative European forest biodiversity monitoring network in support of forest conservation and sustainable management policies.

Materials and methods

Biodiversity data

The data used in this study derives from the merging of 30 datasets (see Appendix A: Tab. 1) across 12 European countries (Burrascano et al., 2023). Each dataset includes forest multi-taxon biodiversity data for multiple plots, i.e., a concretely delimited sampling unit of known geographical coordinates, within one to 23 sites, i.e., an environmentally homogeneous forest area (Fig. 2). Here, we limited our analyses to the most commonly sampled taxonomic groups (vascular plants, birds,

epiphytic lichens and bryophytes, wood-inhabiting fungi and saproxylic beetles) rising to a total of 112,323 observations of 3,229 species in 6,165 plots (Fig. 3). By selecting this subset, we obtained a dataset in which not all but most plots have information on two or more taxonomic groups, resulting in a total of 2,084 spatially distinct sampling locations across 87 sites (Fig. 1), with each site having an average size of 106 km^2 containing at least 6 plots.

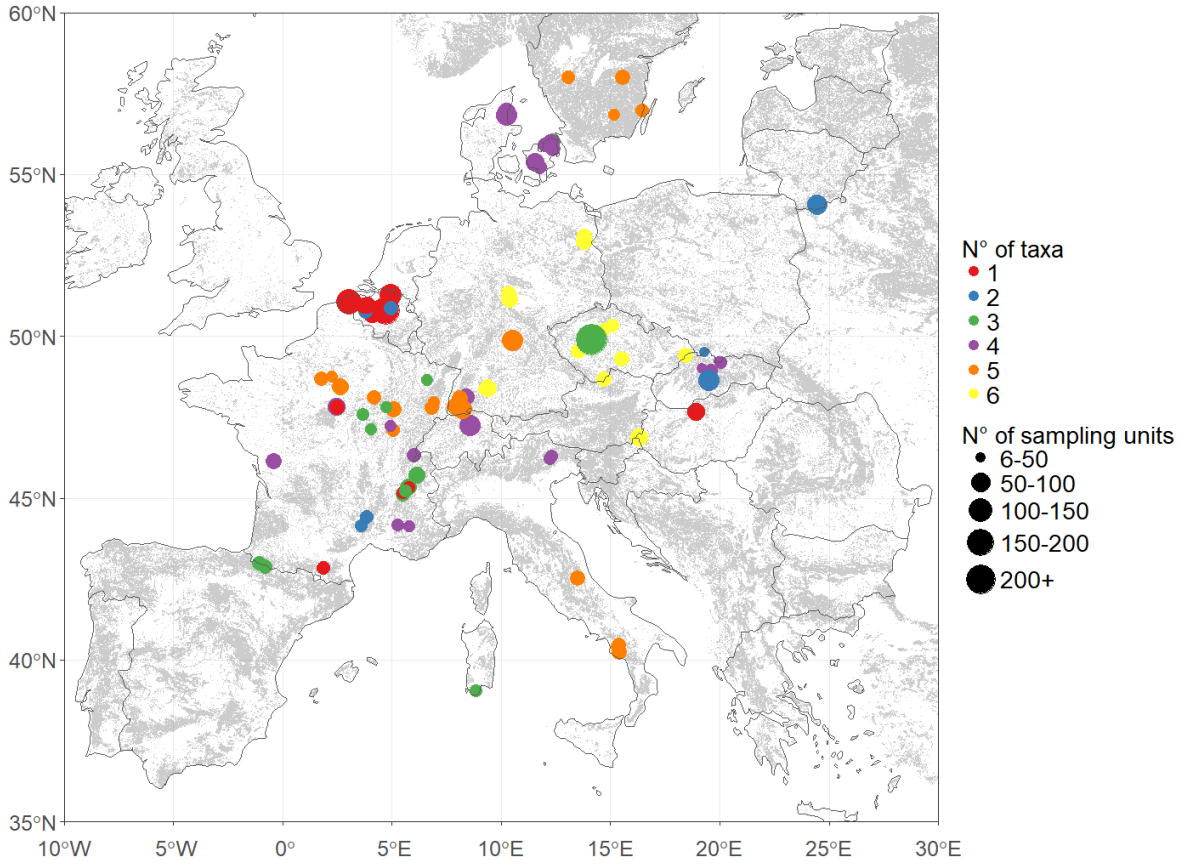


Fig. 1. Distribution of sites in Europe. Dot color and size indicate respectively the number of sampled taxonomic groups and of sampling units in each site. Gray areas are covered by forests with a tree cover greater than 40% according to Kempeneers et al. (2011).

Although extensive, the database is centered on central Europe, for this reason we limited our analyses to temperate forest categories, including also hemiboreal forests, although the latter are underrepresented as compared to the other categories.

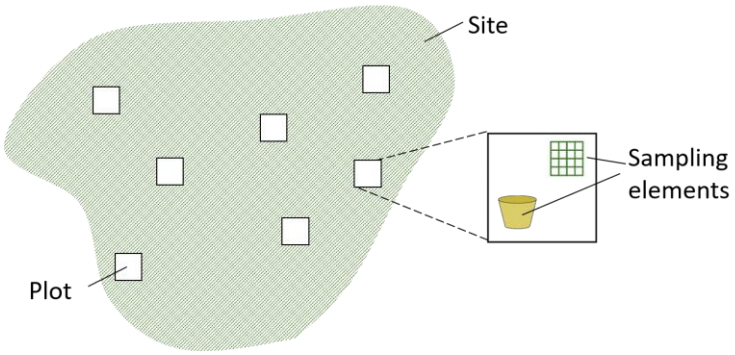


Fig. 2. Scheme representing the spatial structure of the database. Site is intended as an environmentally homogeneous forest area, plot is intended as a concretely delimited sampling unit of known geographical coordinates, within each plot different sampling elements were used for different taxonomic groups (in this case.

Sampling protocols vary across datasets but use similar sampling approaches locally adjusted to capture the species diversity of each site (see Burrascano et al., 2021 and Appendix A: Tab. 2): vascular plants and wood-inhabiting fungi were sampled in plots or blocks of plots rising to an overall sampling area mostly ranging from 78 to 1000 m^2; epiphytic lichens (called lichens henceforth) and epiphytic bryophytes (called bryophytes henceforth) were sampled respectively on two to 12, and five to 18 standing trees per plot, with complete censuses performed in very few studies; birds were sampled by point counts during time frames mostly ranging from 5 to 20 minutes, see e.g., Bouvet et al. (2016); saproxylic beetles were sampled with window-flight interception traps (1 to 6 in each plot), in some cases coupled with emerging traps and Winkler extractors (see e.g., Janssen et al. (2016).

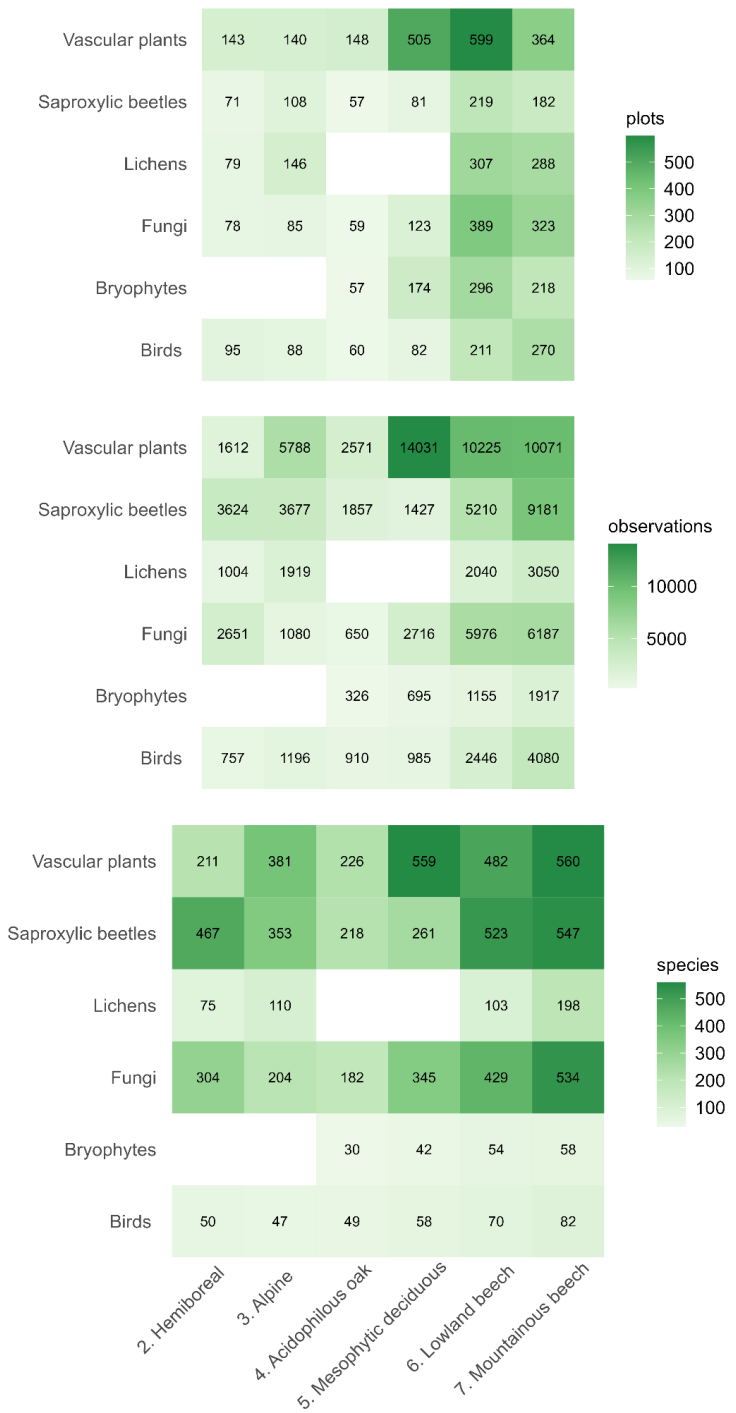
Species nomenclature was checked using the *gnr_resolve*() function in the 'taxize' package (Chamberlain and Szocs 2013) in R version 4.1.1 (R Core Team, 2021), with species names with scores lower than 0.9 corroborated by experts or checked against the GBIF.org (2023) database.

Plot-level metadata included spatial coordinates and forest compositional category. The latter refers to the classification into 14 categories of ecologically distinct forest communities in Europe dominated

by specific assemblages of tree species (EEA, 2007). These categories were designed to facilitate the interpretation and communication of indicators on the status and trends of forests in Europe (Barbati et al., 2014).

Following data availability, we focused on six forest categories, which according to Barbati et al. (2014), cover about 42% of European forest area: (2) ‘Hemiboreal’: hemiboreal forest and nemoral coniferous and mixed broadleaved-coniferous forest; (3) ‘Alpine’: alpine coniferous forests; (4) ‘Acidophilous oak’: acidophilous oak and oak-birch forests; (5) ‘Mesophytic deciduous’: mesophytic deciduous forests; (6) ‘Lowland beech’: beech forests; (7) ‘Mountainous beech’: mountainous beech forests.

The selection of the most commonly sampled taxonomic groups and forest categories ensured the broadest possible spatial overlap across taxonomic groups so that potential differences in sampling effort estimates among them would not depend on substantial differences in their sampling distribution.



186

187 Fig. 3. Heatmaps showing the distribution of plots (a), observations (b), and (c) species records across

188 taxonomic groups and forest categories according to EEA (2007).

Data visualization and statistical analysis

Data was analyzed at two different spatial scales: plot-grain/site-extent, henceforth plot scale, and site-grain/continental extent, henceforth site scale. Note that the heterogeneity in sampling protocols affected neither the plot scale, since the same sampling protocols were used within each site; nor the site scale for which plot data was pooled at the site level, thus blurring plot-scale differences potentially induced by varying sampling efforts. However, in order to exclude a substantial effect of the variables related to the sampling protocols we quantified the effort invested in terms of sampling protocols (e.g., area sampled, number of sampling elements) and showed that this is not related to the estimated species richness at the site level (Appendix A: Fig. 1).

Species diversity patterns across taxonomic groups and forest categories

Since we based our estimates of sampling effort on accurately capturing species diversity, which is deemed more informative than the mere extent of the area sampled (Chao & Jost, 2012), we visualized alpha, beta and gamma diversity of the pilot database at plot and site scale in two separate heatmaps using the forest category in the x axis and coloring the tiles based on the taxonomic group. At the plot scale, alpha was calculated as the average species richness per plot in each site, gamma as the overall richness per site, and beta as a ratio between gamma and alpha in each site following a multiplicative approach (Whittaker, 1972). For the site scale we calculated the average site alpha richness, the overall gamma richness per category, and the among-sites beta-diversity in each category through a multiplicative approach. Diversity values are showed into five separate classes (low; low-mid; mid; mid-high; high) based on the quantiles defined on the overall plot and site values' distribution.

The pilot database shows different patterns of species diversity especially across taxonomic groups, with slight differences across spatial scales (site or plot), and differences between forest categories emerging at the site scale (Fig. 4). At the plot scale, the only taxonomic groups reaching the mid-high and high diversity ranks are fungi, saproxylic beetles, vascular plants, and lichens, with the latter never

reaching the high diversity rank. Bryophytes diversity values are almost exclusively within the low rank, with few values in the mid class especially for beta and gamma diversity. Values for birds mostly occur at the low-mid and mid levels.

At the site scale, these patterns are more dramatic. Bryophytes are totally included in the low diversity class, and the mid-high and high classes exclusively occupied by fungi, saproxylic beetles and vascular plants. At this scale, differences across forest categories emerge. Vascular plants reach only mid values for hemiboreal, acidophilous oak and lowland beech forests, and high values in the remaining forest categories; while saproxylic beetles have a completely opposite pattern. Fungi have mid values for the alpine coniferous and acidophilous oak forests, mid-high values for the remaining categories, with high values only for the hemiboreal category.

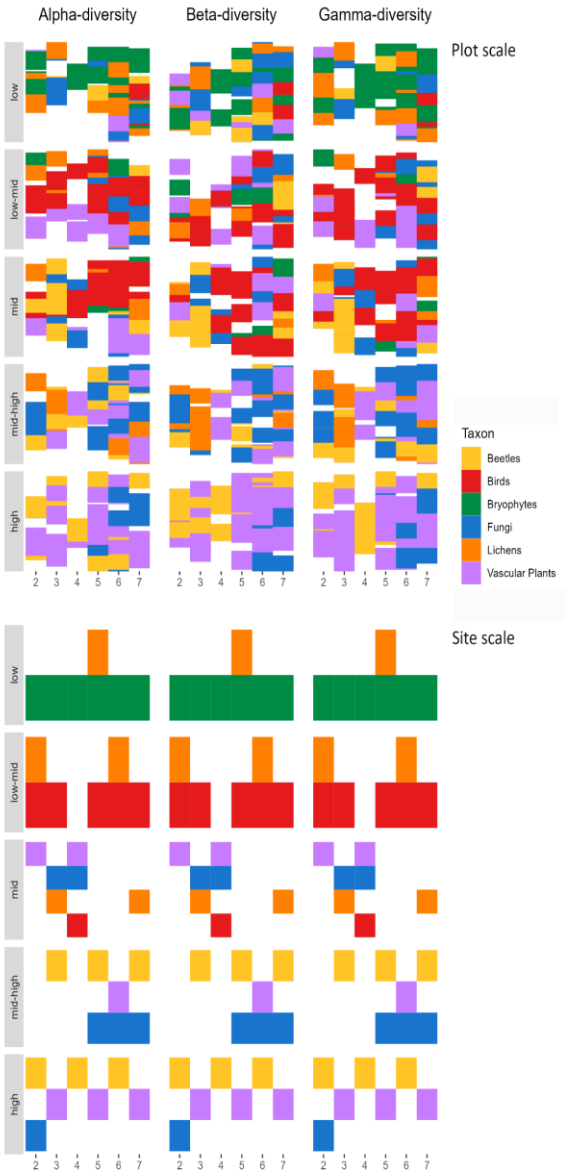


Fig. 4. Distribution of alpha, beta and gamma diversity at the plot and site scale. Diversity values were calculated for each taxonomic group in each plot and site and sorted in ascending order towards the bottom of the graphs. For the plot level, gamma diversity is the site asymptotic species, alfa is the plot richness standardized by gamma and beta is derived through a multiplicative approach. For the site scale, gamma is the overall species richness of a taxon in a forest category, alfa is the average species richness of a site and beta was calculated through a multiplicative approach. Diversity values were classified into five classes (low; low-mid; mid; mid-high; high) based on the quantiles of the overall plot and site values' distribution. The x axis distinguish the six forest categories: 2 = 'Hemiboreal'; 3 =

233 'Alpine'; 4 = 'Acidophilous oak'; 5 = 'Mesophytic deciduous'; 6= 'Lowland beech'; 7 = 'Mountainous
234 beech'.
235
236 ## *Estimates for species richness*
237 Rarefaction is traditionally used to compare the species richness values by down-sampling larger
238 samples up to the sampling effort of the smallest sample. Similarly, extrapolation estimates the
239 species richness associated with a larger sample (Chao and Jost, 2012). In this framework, sampling
240 completeness for species richness is the ratio of the observed species richness to the true richness,
241 i.e., observed plus undetected (Chao et al., 2020). We used rarefaction or extrapolation of our pilot
242 dataset (R package iNEXT, Hsieh et al., 2016) to calculate the number of sampling units needed for
243 each combination of taxonomic group and forest category to reach a desired sample completeness,
244 which we set at 90% as in several studies (Grey et al., 2018; Monleon-Getino and Frias-Lopez, 2020;
245 Nikkeshi et al., 2021). We tested the differences between the median number of plots per site
246 calculated on the iNext estimates and observed in the pilot database through the Mann-Whitney test.
247 Through this approach we estimated the sampling effort needed to detect 90% of the species richness
248 or more.
249
250 ## *Estimates for species composition*
251 Sampling designs often rely on the precision of the arithmetic mean of a response variable. This may
252 be estimated as the standard error of the mean of a previous pilot study from which the number of
253 replicates that are needed to improve that precision can be derived. Similarly, a multivariate pseudo
254 standard error (MultSE) can be used as a proxy for the precision in the assessment of the variation in
255 species composition (Anderson and Santana-Garcon, 2015). This approach has been improved
256 through simulations that allow to extrapolate the MultSE beyond the sampling effort of the pilot study
257 (Guerra-Castro et al., 2021).

We ran the simulations and MultSE calculations (R package SSP, Guerra-Castro et al., 2021) at both plot and site scale. For each forest compositional category, 10 data matrices were simulated based on the pilot dataset using the "sim.data" function, each matrix containing 25 virtual sites and 75 virtual plots per site.

A two-stage random sampling was performed using sites from 2 to 25 and plots from 2 to 25 with each combination repeated 10 times followed by the MultSE computation for each repeated combination. While this approach is usually aimed at defining optimal and suboptimal sampling efforts by analysing the pattern of MultSE as the sampling effort increases; here we focused on the minimum necessary sampling effort to assess species diversity in European forests since currently no pilot database may be assumed to encompass the total biodiversity of each forest category to assess an optimal sampling effort. In this perspective, we retrieved the sampling effort corresponding to a 0.1 multivariate standard error. Since the values of MultSE may vary across the dissimilarity measures used to compare sampling units, here we used the Jaccard index for all taxonomic groups and forest categories. Similarly, MultSE may vary depending on the number of variables, i.e., species (Anderson and Santana-Garcon, 2015), therefore should be discussed in relation to patterns of species diversity (Fig. 4). Through this approach we estimated the sampling effort needed to detect a change in species composition exceeding 0.1 multivariate standard error.

Results

Estimates of the minimum sampling effort

The minimum number of plots needed to assess species richness and variation in species composition for forest biodiversity varied widely (Tab. 1) primarily across taxonomic groups and secondarily across forest categories, with somewhat different results for species richness and species composition. For species richness, the taxonomic group requiring the highest number of plots was wood-inhabiting fungi, whose estimates for a 90% sampling completeness were highly variable across sites, ranging

283 from 7 to 147 plots (Appendix A: Fig. 2), with very high values occurring in sites across different forest
284 categories and regions. In contrast, birds required the lowest number of plots for the recovery of 90%
285 of species richness, from 2 to 17 depending on the site and forest category. Overall, all taxonomic
286 groups gave similar results for species richness and composition, with a comparable number of plots
287 and sites resulting from the two analyses, with some exceptions. The estimates for vascular plants for
288 species composition were much higher than for species richness (Tab. 1). Also for assessing species
289 composition, fungi were the taxonomic group that required the largest sampling effort in terms of
290 plots per site (over 25 which was the highest threshold for our modeling approach). Overall, the
291 number of plots per site to achieve a precise (multivariate standard error lower than 0.1) assessment
292 of variation in species composition (Tab. 1) was always higher than 12, with the lowest values for birds
293 in Alpine coniferous forests (12) and in mountainous beech forests (13), and for lichens in alpine
294 coniferous forests (14) (Appendix A: Fig. 3).
295 The estimates for the site scale were more homogeneous than those at the plot scale both across
296 forest categories and taxonomic groups, but with differences between species richness and species
297 composition values (Tab. 1). Interestingly, for species composition, besides birds and bryophytes, also
298 fungi resulted in low estimates for the number of sites. Indeed, within the estimated number of sites
299 to be sampled for fungi for each forest category ranges from 5 to 9, with values substantially lower
300 than those of vascular plants, ranging from 8 to 19 (Tab. 1).
301
302 Table 1. Estimates of the number of plots per site and the number of sites across Europe for each
303 forest category and taxonomic group to assess species richness with a 90% sampling completeness,
304 and the variation in species composition with a 0.1 multivariate standard error.

		Species richness		Species composition	
	Forest category	n° plots	n° sites	n° plots	n° sites
Beetles	2. Hemiboreal	8-14	7	24	11
	3. Alpine coniferous	8-29	11	23	12
	4. Acidophilous oak	8-14	7	22	5
	5. Mesophytic deciduous	7-16	13	23	14
	6. Lowland beech	6-34	19	>25	11
	7. Mountainous beech	7-32	27	21	19
Birds	2. Hemiboreal	3-12	4	23	5
	3. Alpine coniferous	2-8	3	12	4
	4. Acidophilous oak	3-5	3	15	2
	5. Mesophytic deciduous	4-7	4	19	4
	6. Lowland beech	3-8	5	18	2
	7. Mountainous beech	3-17	6	13	5
Bryophytes	2. Hemiboreal	-	-	-	-
	3. Alpine coniferous	-	-	-	-
	4. Acidophilous oak	3-18	8	19	4
	5. Mesophytic deciduous	3-21	7	25	7
	6. Lowland beech	2-28	13	22	8
	7. Mountainous beech	4-50	9	19	8
Lichens	2. Hemiboreal	3-17	5	16	9
	3. Alpine coniferous	2-11	9	14	11
	4. Acidophilous oak	-	-	-	-
	5. Mesophytic deciduous	-	-	-	-
	6. Lowland beech	5-39	13	21	9
	7. Mountainous beech	5-26	21	24	10
Fungi	2. Hemiboreal	10-16	6	>25	7
	3. Alpine coniferous	10-147	15	>25	8
	4. Acidophilous oak	23-58	11	>25	5
	5. Mesophytic deciduous	14-96	16	>25	9
	6. Lowland beech	7-42	17	>25	8
	7. Mountainous beech	9-56	12	>25	8
Vascular plants	2. Hemiboreal	6-18	11	21	19
	3. Alpine coniferous	4-12	12	22	8
	4. Acidophilous oak	8-20	12	>25	9
	5. Mesophytic deciduous	3-19	25	>25	11
	6. Lowland beech	3-46	21	>25	12
	7. Mountainous beech	6-34	17	>25	9

305
306

307

Comparison with current knowledge

Depending on the taxonomic group and forest category, the estimates for the number of plots per site to achieve a 90% sampling completeness for species richness were either higher or lower than the values in our pilot database (Appendix A: Fig. 2). For fungi the estimates were always higher than in the pilot database, while birds were sampled over the estimated minimum effort in terms of number of plots per site in the pilot dataset (Fig. 5). Vascular plants, bryophytes and lichens were sampled beyond the estimated minimum effort, although these differences have a lower degree of significance for most forest categories, except for vascular plants in mountainous beech forests.

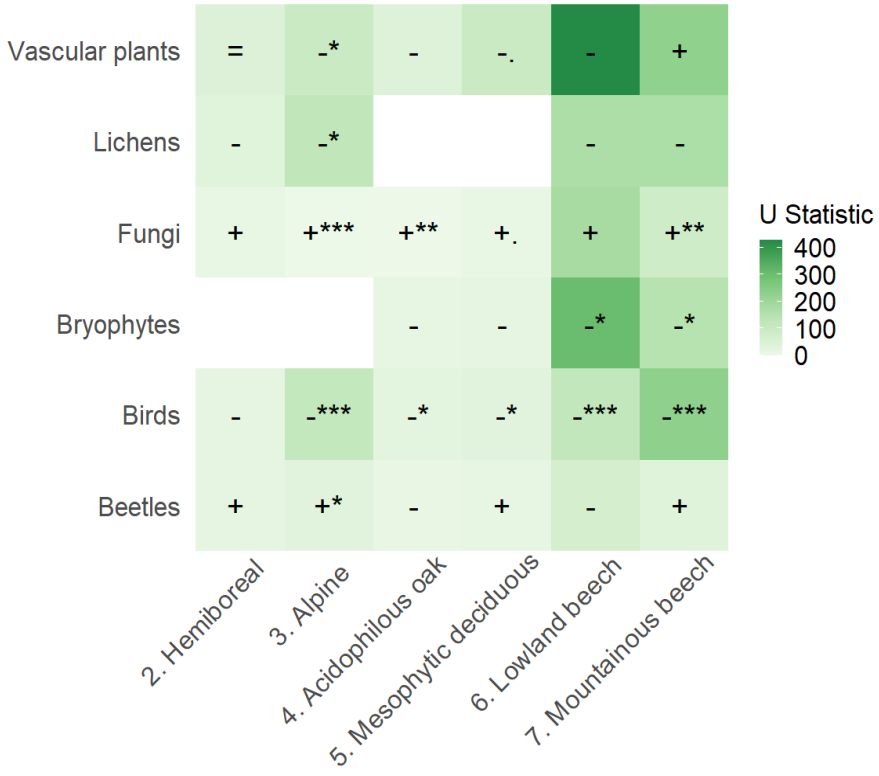


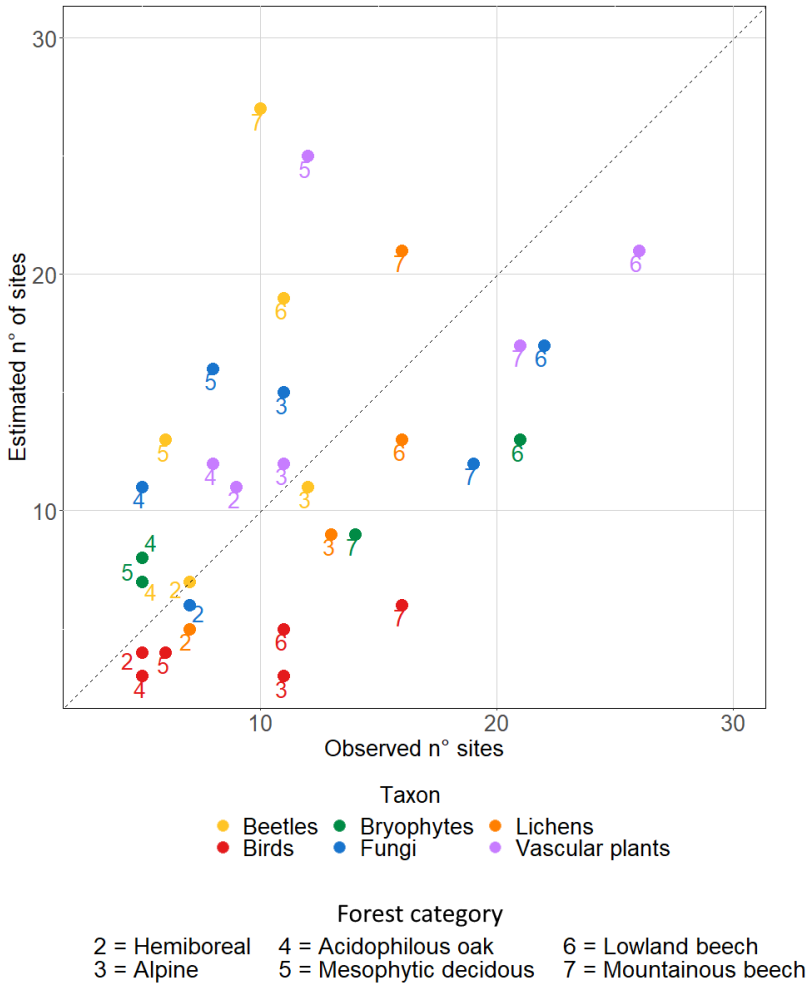
Fig. 5. Differences between the median of the number of plots per site in the pilot database and in the estimate for a sampling completeness of 90% (+: estimate>pilot; -: estimate < pilot; =: estimate equals pilot) and significance of the Mann-Whitney test between the pilot and estimated number of plots per site distributions (. p<0.1; * p<0.05; ** p< 0.001; *** p< 0.0005). The color intensity represents the U statistic from the Mann-Whitney U test, with darker shades indicating larger U statistics and thus

greater differences between the pilot and estimated distributions.

When pooling biodiversity information at the site scale, we found that the number of sites sampled in the pilot database was mostly not sufficient to reach a fair (90%) sample completeness for species richness within each forest category. Thus, the estimate for the minimum number of sites was mostly higher than the number of currently sampled sites (upper left part of the diagram in Figure 6). The highest gaps were found for vascular plants, saproxylic beetles, wood inhabiting fungi, and only in beech dominated forest categories for lichens. These results differ substantially from those obtained at the plot scale. Conversely, we obtained lower estimates of the number of sites for birds as compared to the pilot database across all forest categories.

We found different results for species composition (Fig. 7). The number of plots per site are generally high, always higher than 20 for fungi, vascular plants and beetles. At the site scale, except for saproxylic beetles that resulted as undersampled in all forest categories, only few combinations of forest categories and taxonomic groups required a substantially higher effort than the pilot database: vascular plants in hemiboreal and acidophilous oak forests, lichens in hemiboreal forests and bryophytes in mesophytic deciduous forests.

340



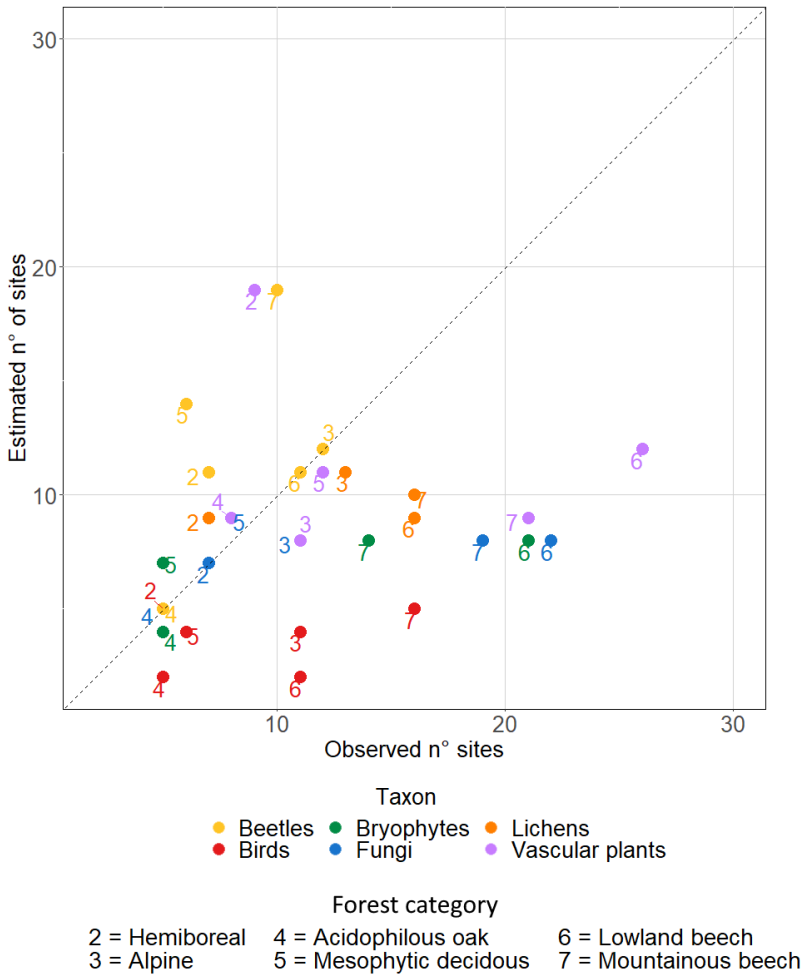
341

342 Fig. 6. Scatterplot of the number of sites across forest categories in the pilot database and estimated

343 to achieve a 90% sampling completeness for species richness. The dotted diagonal line separates the

344 taxon/category combinations that would and would not need further sampling effort based on the

345 pilot database.



346

347 Fig. 7. Scatterplot of the number of sites across forest categories in the pilot database and estimated
348 to achieve a 0.1 value of multivariate standard error when assessing variation in species composition.
349 The dotted diagonal line separates the taxon/category combinations that would and would not need
350 further sampling effort based on the pilot database.

351

352 # Discussion

353 ## *Setting the minimum threshold for forest biodiversity assessment*

354 Using a large pilot database with information deriving from multi-taxon sampling across Europe is a
355 novel and unique opportunity to estimate the sampling effort needed to cover European forest

biodiversity. Setting the minimum effort based on the existing knowledge means putting the basis for a coordinated European forest biodiversity assessment and long-term monitoring network, as advocated in the proposal for a EU Forest Monitoring Law (EC, 2023).

Once this minimum sampling effort is applied through data collection campaigns, it could be progressively refined through periodic assessments of sampling completeness and multivariate precision until an optimal sampling effort is achieved that could support evidence-based forest and conservation policies in the EU (Oettel and Lapin, 2021).

Initiating this process is highly relevant in the current political and environmental context. Biodiversity is listed among the priorities for sustainable forest management in the EU Taxonomy Regulation (2020/852), and for the enhancement of forest resilience to environmental changes and disturbance events in the European Forest Strategy for 2030 (EC, 2021); finally, biodiversity is in the focus of the proposal for a Forest Monitoring Law (EC, 2023). Nevertheless, none of these political documents, not even the latter, refers to an operational framework for a sound in-situ assessment of forest biodiversity, which is at the very base of developing forest policies and management strategies that comply with the definition of Sustainable Forest Management, and of detecting changes in forest biodiversity that derive from the increasingly impactful stresses (Senf et al., 2020) and disturbance events (Patacca et al., 2023) related to ongoing climate change.

Are we there yet?

As we may have expected, the short answer to this question is “no”.

This primarily derives from the relevant knowledge gaps for the biodiversity of several European forest categories (Burrascano et al., 2023). Based on the data availability, we were forced to limit our analyses to only six out of the 14 forest categories identified by the EEA (2007). This is particularly unfortunate since, among the forest categories that we could not include in our analyses, are those centered in the Mediterranean biogeographical region that likely display the highest forest biodiversity values for the European continent, e.g., thermophilous deciduous and broadleaved

evergreen forests (EEA, 2007). The high tree species richness of this region (Médail et al., 2019; Rivers et al., 2019) drives the occurrence of both several different forest types at the regional scale, and of a species-rich overstoreys at the local scale, with cascading positive effects on the diversity of forest-dwelling organisms (Groote et al., 2017; O'Brien et al., 2017; Vockenhuber et al., 2011). Southern Europe hosts the highest number of tree species threatened with extinction, mainly in direct or indirect relation to climate change (Rivers et al., 2019), which will impact especially this region through progressive subtropicalisation and desertification (Pörtner et al., 2022).

Also for the relatively well-studied categories, much work still must be done. Across the forest categories we analysed, we estimated a total need of 109 sites for reaching 90% sampling completeness in species richness, and of 71 sites to achieve a 0.1 multivariate standard error in species composition. The estimated number of plots per site goes beyond 20 to assess species composition variation in several taxonomic group/forest category combinations but is often lower than for species richness. As compared to the largest ongoing forest monitoring program, i.e., ICP forests (i.e., 6,000 first level plots across Europe), even if it does not comprehensively account for forest biodiversity, the overall number of sampling units needed for forest multi-taxon monitoring would be in the same order of magnitude, but different in its spatial structure. Although, this effort may seem insufficient to detect changes at the local or regional scales, at the continental scale it would contribute to detect broad-scale changes and to provide a data-driven dynamic benchmark for species richness and composition to be used also by national or local monitoring programs operating at finer scales.

Our results point to the relevance of an accurate sampling stratification across forest categories, since we found different estimates across forest categories, e.g., estimates for hemiboreal forests are often much lower than those for other categories. This stratification, however, is not suggested in the sampling design manuals of ICP forests (Ferretti et al., 2020), likely due to the lack of a reliable European map of forest categories, which would be extremely useful to design sound monitoring plans. Furthermore, we found very high estimates for the number of plots within a site, e.g., for fungi,

suggesting that a nested sampling design (i.e., several plots per site) is advisable when aiming at the analysis of forest biodiversity, whose patterns are also expressed at fine spatial scales (Burrascano et al., 2018).

Currently, the most relevant forest biodiversity coordinated monitoring in the European Union is the one put in place by Member States for the Habitats Directive obligations (Article 17). Although aimed at providing similar information, the monitoring programs to comply with Article 17 follow very different approaches among the Member States, e.g., some Member States established a special standardized monitoring program, while others use already existing data, e.g., habitat maps, forest inventories. Where in-situ monitoring is applied, data are collected through different protocols, which in many cases include lists of typical species, but seldom record complete plant species lists. Sampling of animal species is even rarer, and usually limited to few habitat types and taxonomic groups, i.e., birds and butterflies (Ellwanger et al., 2018).

Overall, the existing coordinated efforts for biodiversity assessment are strongly limited and need substantial investments at the European scale for improvement.

On which basis should we calibrate our sampling efforts?

A wide body of scientific literature studied the extent and pathways through which sampling effort influences biodiversity assessments (Gotelli and Colwell, 2001; Grey et al., 2018; Nuñez-Penichet et al., 2022). Within a certain habitat, an increasing sampling effort determines an initial increase in the observed species richness and in species composition precision, then levels off following respectively the general species-area relationship (Turner and Tjørve, 2005) and the decrease of the multivariate standard error (Guerra-Castro et al., 2021). As the share of species that are rare or hard to detect varies greatly across taxonomic groups and environmental contexts, so does the relationship between sampling effort and observed diversity (Anderson and Santana-Garcon, 2015; Chao and Jost, 2012; Coddington et al., 2009).

The other side of this evidence is that the more a taxonomic group in a certain context is rich with rare and hard to detect species, the higher sampling effort is needed to achieve a comprehensive assessment. This influences not only alpha-diversity, but also beta-diversity since rare and hard to detect species are more likely to vary across plots and sites either because they are linked to specific habitat features or because they were undetected in some sampling units (Pärtel et al., 2011). The variation of environmental conditions at different spatial scales, adds to the drivers of variation in species composition across plots and sites, and in turn to the patterns of beta-diversity (Graco-Roza et al., 2022).

Accordingly, our estimates reflect the diversity patterns of the different taxonomic groups in the first place, and, secondarily, of the different forest categories. It is important to underline that EU member states defined the sampling effort for habitat monitoring in the framework of the Habitats Directive mostly based on the habitat area or occurrences, but very rarely, the monitoring effort accounted for the habitat variability (Ellwanger et al., 2018). Based on our data, birds and bryophytes showed very low diversity levels across all forest categories and spatial scales. This is not surprising since the total number of species censused for these groups in Europe are relatively low, 912 for birds (Clements et al., 2023) and 1392 for bryophytes (Hodgetts et al., 2020). In European forests, these taxonomic groups would therefore achieve a relatively complete assessment of species richness and composition by applying a feasible sampling effort, which is similar to the one applied in the pilot database. Notwithstanding their similar diversity patterns, the amount of available data and conservation efforts for these two taxonomic groups is extremely different. Birds are among the most studied organisms globally, with species checklists updated annually (Clements et al., 2023), also through vast programs of citizen science (Sullivan et al., 2009; Jiguet et al., 2012), and have been protected in Europe since 1979 through an exclusive Directive (79/409/EEC) that was recently amended (2009/147/EC). Bryophytes are far less studied, especially in some European regions (Sabovljević et al., 2001) and

often marginal in conservation efforts (Vellak et al., 2010), not to mention their lower appeal for citizen science activities.

Given the relatively low effort and the large amount of available data, it is not surprising that birds, limited to 34 common bird species, were the only organisms (other than trees) included among the indicators for the maintenance, conservation and enhancement of biodiversity by Forest Europe (2020). However, we should question the informative value of this indicator, which is by definition focused on one of the least species rich taxonomic groups in European forests, and particularly on very common species whose abundance cannot say much on the temporal and spatial patterns of forest biodiversity, also in relation to their low congruence with the diversity of other taxonomic groups (Burrascano et al., 2018).

Alternative options exist but require a greater effort. We found very high diversity levels for wood-inhabiting fungi, with high levels of diversity at the plot scale. This means that very high numbers of fungi species may be found in one sampling unit, and that their species composition varies greatly among the plots within the same site, i.e., they may have very high levels of alpha and beta-diversity at the plot scale. This general pattern may be related to the amount and diversity of senescing and deadwood within a forest site, and thus make wood-inhabiting fungi particularly interesting as fine scale indicators of sustainable forest management. In general, fungi pose several challenges for sampling, since their surveys usually rely on reproductive structures that for most species are ephemeral and somewhat unpredictable (Lodge et al., 2004). This issue, however, is larger for soil fungi producing agaricoid reproductive structures than for saproxylic species (Runnel et al., 2015) often producing perennial reproductive structures, as in polypores (Halme & Kotiaho, 2012). These challenges are being progressively addressed by environmental DNA techniques (Burrascano et al., 2021; Leclerc et al., 2023), and are counterbalanced by the possibility of identifying complex spatial and temporal patterns of biodiversity as nuanced by the presence/absence of a wealth of species associated with different habitat features and ecological functions, e.g., deadwood decay.

At the site scale, fungi may be sampled through a relatively low effort as compared to other taxonomic groups, i.e., saproxylic beetles and vascular plants, both of which will have a particular relevance for forest monitoring.

The exact number of saproxylic beetle species in Europe is still unknown but has been estimated to about 4,000 (Bouget et al. 2008). Of these species, about 650 underwent a red list assessment: 20% of these resulted as threatened with extinction, and about a quarter as data deficient (Calix et al., 2018). Monitoring saproxylic beetles would provide crucial information on the distribution and abundance of a group that includes several species of conservation concern but for which a profound knowledge is missing. Furthermore, timber harvesting with deadwood release limited in quantity and diversity is by far the primary threat to the species within this group that could therefore give relevant and nuanced indications on the sustainability of forest management for biodiversity, as required by the aforementioned European policies and regulations.

Finally, vascular plants are also a well-studied group, whose species lists were used to gather information on the ecological patterns and community features since the early 1900. Our estimates for this group are intermediate as compared to other groups but reflect high levels of diversity across forest categories and spatial scales. Plants are the major structural and functional component of forest ecosystems and therefore influence forest structure and are the source of a diverse the producer-based food chain. They are renown as good surrogates, especially of spatial composition patterns in temperate forests (Blasi et al., 2010; Sætersdal et al., 2004), and are used by several conservation initiatives, including the Habitats Directive within the European Union and Natura2000 implementation, as a base for habitat interpretation and conservation status assessment (Burrascano et al., 2018).

Opportunities and limitations

We used the best available data to demonstrate that the efforts we are investing in monitoring biodiversity is not focused on the most diverse taxonomic groups and forest types. The current focus

504 on birds (e.g., by Forest Europe) and on vascular plants (e.g., by Habitat Directive) should be
505 coordinated and further implemented and should be complemented with assessment for saproxylic
506 fungi and beetles to test the sustainability of forest management in Europe. Other functional and
507 taxonomic groups, especially of arthropods, may also be suitable but were not analysed here due to
508 scarce and scattered available information. Further sampling effort should be directed towards
509 Mediterranean and thermophilous forests, which are currently underrepresented in multi-taxon
510 forest assessments, thus not included in our study.
511 Based on our results, we also learned that a nested sampling scheme will allow to better investigate
512 the within-site variation of species diversity for some taxonomic groups, i.e., wood-inhabiting fungi,
513 which could give fine-scale information on the effects of forest management activities on forest
514 ecosystems.
515 It is important to note, however, that our data derive from sampling performed through different
516 protocols and that further estimates based on standardized sampling strategies (Burrascano et al.,
517 2021) could give sounder insights for the implementation of a European forest biodiversity monitoring
518 network. It is also noteworthy that we did not account for the criteria through which the sites and
519 plots are selected and distributed across space and environmental gradients. In the datasets included
520 in the pilot database, these criteria derived from a trade-off between the project aims and local
521 constraints (e.g., ownership, stakeholder availability). When setting a European monitoring network,
522 the target spatial and environmental gradients should be defined at a broader scale, but the actual
523 network implementation would have to account anyway for these local constraints. Overall, these
524 considerations lead us to exclude the possibility that a purely probabilistic approach could be applied
525 for the site scale, i.e., that sites would be chosen through a pure random approach within a forest
526 category. We assumed the relevance of compositional categories, which are those designed to tune
527 forest indicators (EEA, 2007). However, the levels of species diversity may vary substantially across
528 areas under different management regimes, ranging from clearcut to no intervention. Further efforts

accounting for this additional classification could pay special attention to those forest areas in which management strategies allow for high levels of forest diversity and that could serve as a reference for forest biodiversity monitoring.

Author contribution

SB and LC designed the study, all authors contributed and/or harmonized the data, LB, LC, SB, FC and EH performed the data visualization and analysis, SB led the manuscript writing, to which all co-authors contributed.

Acknowledgments

This article was funded by the EU Framework Programme Horizon 2020 through the COST Association (www.cost.eu): COST Action CA18207: BOTTOMS-UP – Biodiversity Of Temperate forest Taxa Orienting Management Sustainability by Unifying Perspectives. The authors are thankful to all those experts and stakeholders contributing to the data collection. Part of the data for the Czech Republic were collected thanks to the funding of the Czech Science Foundation (grant GACR 22–31322S).

Data availability statement

The data used for this study are available upon request using the Data Explorer within the Cost Action website (https://www.bottoms-up.eu/en/results/data-explorer.html).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

References

Alberdi, I., Nunes, L., Kovac, M., Bonheme, I., Cañellas, I., Rego, F.C., Dias, S., Duarte, I., Notarangelo, M., Rizzo, M., Gasparini, P., 2019. The conservation status assessment of Natura 2000 forest habitats in Europe: capabilities, potentials and challenges of national forest inventories data.

552 Annals of Forest Science 76, 34. https://doi.org/10.1007/s13595-019-0820-4
553 Alessi, N., Bonari, G., Zannini, P., Jiménez-Alfaro, B., Agrillo, E., Attorre, F., Canullo, R., Casella, L.,
554 Cervellini, M., Chelli, S., Di Musciano, M., Guarino, R., Martellos, S., Massimi, M., Venanzoni,
555 R., Zerbe, S., Chiarucci, A., 2023. Probabilistic and preferential sampling approaches offer
556 integrated perspectives of Italian forest diversity. J Vegetation Science 34, e13175.
557 https://doi.org/10.1111/jvs.13175
558 Anderson, M.J., Santana-Garcon, J., 2015. Measures of precision for dissimilarity-based multivariate
559 analysis of ecological communities. Ecology Letters 18, 66–73.
560 https://doi.org/10.1111/ele.12385
561 Aubin, I., Venier, L., Pearce, J., Moretti, M., 2013. Can a trait-based multi-taxa approach improve our
562 assessment of forest management impact on biodiversity? Biodiversity and Conservation 22,
563 2957–2975. https://doi.org/10.1007/s10531-013-0565-6
564 Barbati, A., Marchetti, M., Chirici, G., Corona, P., 2014. European Forest Types and Forest Europe
565 SFM indicators: Tools for monitoring progress on forest biodiversity conservation. Forest
566 Ecology and Management, Mechanisms and predictors of ecological change in managed
567 forests: A selection of papers from the second international conference on biodiversity in
568 forest ecosystems and landscapes 321, 145–157.
569 https://doi.org/10.1016/j.foreco.2013.07.004
570 Bouget, C., Brustel, H., Zagatti, P., 2008. The French Information System on Saproxylic BEetle Ecology
571 (FRISBEE): an ecological and taxonomical database to help with the assessment of forest
572 conservation status. Revue d'Ecologie (suite de La Terre et la Vie) 10: 33–36.
573 Bouvet, A., Paillet, Y., Archaux, F., Tillon, L., Denis, P., Gilg, O., Gosselin, F., 2016. Effects of forest
574 structure, management and landscape on bird and bat communities. Environmental
575 Conservation 43, 148–160. https://doi.org/10.1017/S0376892915000363
576 Bruel, R., White, E.R., 2021. Sampling requirements and approaches to detect ecosystem shifts.

Ecological Indicators 121, 107096. https://doi.org/10.1016/j.ecolind.2020.107096

Brunbjerg, A.K., Bruun, H.H., Brøndum, L., Classen, A.T., Dalby, L., Fog, K., Frøslev, T.G., Goldberg, I., Hansen, A.J., Hansen, M.D.D., Høye, T.T., Illum, A.A., Læssøe, T., Newman, G.S., Skipper, L., Søchting, U., Ejrnæs, R., 2019. A systematic survey of regional multi-taxon biodiversity: evaluating strategies and coverage. BMC Ecology 19, 43. https://doi.org/10.1186/s12898-019-0260-x

Burrascano, S., Chianucci, F., Trentanovi, G., Kepfer-Rojas, S., Sitzia, T., Tinya, F., Doerfler, I., Paillet, Y., Nagel, T.A., Mitic, B., Morillas, L., Munzi, S., Van der Sluis, T., Alterio, E., Balducci, L., de Andrade, R.B., Bouget, C., Giordani, P., Lachat, T., Matosevic, D., Napoleone, F., Nascimbene, J., Paniccia, C., Roth, N., Aszalós, R., Brazaitis, G., Cutini, A., D'Andrea, E., De Smedt, P., Heilmann-Clausen, J., Janssen, P., Kozák, D., Mårell, A., Mikoláš, M., Nordén, B., Matula, R., Schall, P., Svoboda, M., Ujhazyova, M., Vandekerkhove, K., Wohlwend, M., Xystrakis, F., Aleffi, M., Ammer, C., Archaux, F., Asbeck, T., Avtzis, D., Ayasse, M., Bagella, S., Balestrieri, R., Barbati, A., Basile, M., Bergamini, A., Bertini, G., Biscaccianti, A.B., Boch, S., Bölöni, J., Bombi, P., Boscardin, Y., Brunialti, G., Bruun, H.H., Buscot, F., Byriel, D.B., Campagnaro, T., Campanaro, A., Chauvat, M., Ciach, M., Čiliak, M., Cistrone, L., Pereira, J.M.C., Daniel, R., De Cinti, B., De Filippo, G., Dekoninck, W., Di Salvatore, U., Dumas, Y., Elek, Z., Ferretti, F., Fotakis, D., Frank, T., Frey, J., Giancola, C., Gomoryová, E., Gosselin, M., Gosselin, F., Gossner, M.M., Götmark, F., Haeler, E., Hansen, A.K., Hertzog, L., Hofmeister, J., Hošek, J., Johannsen, V.K., Justensen, M.J., Korboulewsky, N., Kovács, B., Lakatos, F., Landivar, C.M., Lens, L., Lingua, E., Lombardi, F., Máliš, F., Marchino, L., Marozas, V., Matteucci, G., Mattioli, W., Møller, P.F., Müller, J., Németh, C., Ónodi, G., Parisi, F., Perot, T., Perret, S., Persiani, A.M., Portaccio, A., Posillico, M., Preikša, Ž., Rahbek, C., Rappa, N.J., Ravera, S., Romano, A., Samu, F., Scheidegger, C., Schmidt, I.K., Schwegmann, S., Sicuriello, F., Spinu, A.P., Spyroglou, G., Stillhard, J., Topalidou, E., Tøttrup, A.P., Ujházy, K., Veres, K., Verheyen, K., Weisser,

602 W.W., Zapponi, L., Ódor, P., 2023. Where are we now with European forest multi-taxon
603 biodiversity and where can we head to? Biological Conservation 284, 110176.
604 https://doi.org/10.1016/j.biocon.2023.110176
605 Burrascano, S., de Andrade, R.B., Paillet, Y., Ódor, P., Antonini, G., Bouget, C., Campagnaro, T.,
606 Gosselin, F., Janssen, P., Persiani, A.M., 2018. Congruence across taxa and spatial scales: Are
607 we asking too much of species data? Global Ecology and Biogeography 27, 980–990.
608 Burrascano, S., Trentanovi, G., Paillet, Y., Heilmann-Clausen, J., Giordani, P., Bagella, S., Bravo-
609 Oviedo, A., Campagnaro, T., Campanaro, A., Chianucci, F., De Smedt, P., García-Mijangos, I.,
610 Matošević, D., Sitzia, T., Aszalós, R., Brazaitis, G., Cutini, A., D'Andrea, E., Doerfler, I.,
611 Hofmeister, J., Hošek, J., Janssen, P., Kepfer Rojas, S., Korboulewsky, N., Kozák, D., Lachat, T.,
612 Lõhmus, A., Lopez, R., Mårell, A., Matula, R., Mikoláš, M., Munzi, S., Nordén, B., Pärtel, M.,
613 Penner, J., Runnel, K., Schall, P., Svoboda, M., Tinya, F., Ujházyová, M., Vandekerkhove, K.,
614 Verheyen, K., Xystrakis, F., Ódor, P., 2021. Handbook of field sampling for multi-taxon
615 biodiversity studies in European forests. Ecological Indicators 132, 108266.
616 https://doi.org/10.1016/j.ecolind.2021.108266
617 Calix, M., Alexander, K.N., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Vazquez-Albalate, X.,
618 Aleksandrowicz, O., Audisio, P., Istrate, P., 2018. European red list of saproxylic beetles.
619 Chamberlain, S., Szocs, E., 2013. taxize - taxonomic search and retrieval in R. F1000Research 2, 191.
620 https://doi.org/10.12688/f1000research.2-191.v2
621 Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by
622 completeness rather than size. Ecology 93, 2533–2547.
623 Chao, A., Kubota, Y., Zelený, D., Chiu, C.-H., Li, C.-F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C.-L.,
624 Costello, M.J., Colwell, R.K., 2020. Quantifying sample completeness and comparing
625 diversities among assemblages. Ecological Research 35, 292–314.
626 https://doi.org/10.1111/1440-1703.12102

627 Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., Knight, T.M., Purschke, O.,
628 Gotelli, N.J., 2018. Embracing scale-dependence to achieve a deeper understanding of
629 biodiversity and its change across communities. Ecology Letters 21, 1737–1751.
630 https://doi.org/10.1111/ele.13151
631 Clements, J. F., Rasmussen, P. C. , Schulenberg, T. S. , Iliff, M. J., Fredericks, T. A., Gerbracht, J. A.,
632 Lepage, D., Spencer, A., Billerman, S. M., Sullivan, B. L., Wood, C. L., 2023. The
633 eBird/Clements checklist of Birds of the World: v2023. Downloaded from
634 https://www.birds.cornell.edu/clementschecklist/download/
635 Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M., Hormiga, G., 2009. Undersampling bias: the
636 null hypothesis for singleton species in tropical arthropod surveys. Journal of Animal Ecology
637 78, 573–584. https://doi.org/10.1111/j.1365-2656.2009.01525.x
638 Drost, H.G., Gabel, A., Jiu, J., Quint, M., Grosse, I., 2018. myTAI: evolutionary transcriptomics with R.
639 Bioinformatics 34, 1589-1590. https://doi.org/10.1093/bioinformatics/btx835
640 EEA, 2007. European Forest Types. Categories and types for sustainable forest management,
641 reporting and policy. Technical Report 09/2006. Copenhagen.
642 Elek, Z., Kovács, B., Aszalós, R., Boros, G., Samu, F., Tinya, F., Ódor, P., 2018. Taxon-specific responses
643 to different forestry treatments in a temperate forest. Scientific Reports 8, 16990.
644 https://doi.org/10.1038/s41598-018-35159-z
645 Ellwanger, G., Runge, S., Wagner, M., Ackermann, W., Neukirchen, M., Frederking, W., Müller, C.,
646 Ssymank, A., Sukopp, U., 2018. Current status of habitat monitoring in the European Union
647 according to Article 17 of the Habitats Directive, with an emphasis on habitat structure and
648 functions and on Germany. Nature Conservation 29, 57–78.
649 https://doi.org/10.3897/natureconservation.29.27273
650 European Commission (EC), 2023. Proposal for a Regulation of the European Parliament and of the
651 Council on a monitoring framework for resilient European forests. COM(2023) 728 final,

652 2023/0413 (COD). Brussels.
653 European Commission (EC), 2021. New EU Forest Strategy for 2030, Brussels, 16.7.2021. COM(2021)
654 572 final.
655 FAO, 2020. Global Forest Resources Assessment 2020: Main report. FAO, Rome, Italy.
656 https://doi.org/10.4060/ca9825en
657 Feld, C.K., Martins da Silva, P., Paulo Sousa, J., De Bello, F., Bugter, R., Grandin, U., Hering, D.,
658 Lavorel, S., Mountford, O., Pardo, I., Pärtel, M., Römbke, J., Sandin, L., Bruce Jones, K.,
659 Harrison, P., 2009. Indicators of biodiversity and ecosystem services: a synthesis across
660 ecosystems and spatial scales. Oikos 118, 1862–1871. https://doi.org/10.1111/j.1600-
661 0706.2009.17860.x
662 Ferretti, M., Fischer, R., Mues, V., Granke, O., Lorenz, M., Seidling, W., Nicolas, M., 2020: Part II:
663 Basic design principles for the ICP Forests Monitoring Networks. Version 2020-2. Manual on
664 methods and criteria for harmonized sampling, assessment, monitoring and analysis of the
665 effects of air pollution on forests. Thünen Institute of Forest Ecosystems, Eberswalde,
666 Germany, 33 p + Annex.
667 Flensted, K.K., Bruun, H.H., Ejrnæs, R., Eskildsen, A., Thomsen, P.F., Heilmann-Clausen, J., 2016. Red-
668 listed species and forest continuity – A multi-taxon approach to conservation in temperate
669 forests. Forest Ecology and Management 378, 144–159.
670 https://doi.org/10.1016/J.FORECO.2016.07.029
671 Forest Europe, 2020. State of Europe's forests 2020. Ministerial conference on the protection of
672 forests in Europe. Liaison Unit Bratislava.
673 Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity
674 indicators for forest ecosystems in Europe. Ecological Indicators 57, 420–434.
675 https://doi.org/10.1016/j.ecolind.2015.05.028
676 Gardner, T., 2010. Monitoring Forest Biodiversity: Improving Conservation Through Ecologically

Responsible Management. Earthscan.

GBIF.org, 2023. GBIF Home Page. Available from: https://www.gbif.org

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4, 379–391.

Graco-Roza, C., Aarnio, S., Abrego, N., Acosta, A.T.R., Alahuhta, J., Altman, J., Angiolini, C., Aroviita, J., Attorre, F., Baastrup-Spohr, L., Barrera-Alba, J.J., Belmaker, J., Biurrun, I., Bonari, G., Bruelheide, H., Burrascano, S., Carboni, M., Cardoso, P., Carvalho, J.C., Castaldelli, G., Christensen, M., Correa, G., Dembicz, I., Dengler, J., Dolezal, J., Domingos, P., Erös, T., Ferreira, C.E.L., Filibeck, G., Floeter, S.R., Friedlander, A.M., Gammal, J., Gavioli, A., Gossner, M.M., Granot, I., Guarino, R., Gustafsson, C., Hayden, B., He, S., Heilmann-Clausen, J., Heino, J., Hunter, J.T., Huszar, V.L.M., Janišová, M., Jyrkänkallio-Mikkola, J., Kahilainen, K.K., Kemppinen, J., Kozub, Ł., Kruk, C., Kulbiki, M., Kuzemko, A., Christiaan le Roux, P., Lehikoinen, A., Teixeira de Lima, D., Lopez-Urrutia, A., Lukács, B.A., Luoto, M., Mammola, S., Marinho, M.M., Menezes, L.S., Milardi, M., Miranda, M., Moser, G.A.O., Mueller, J., Niittynen, P., Norkko, A., Nowak, A., Ometto, J.P., Ovaskainen, O., Overbeck, G.E., Pacheco, F.S., Pajunen, V., Palpurina, S., Picazo, F., Campos, J.A., Rodil, I.F., Sabatini, F.M., Salingré, S., De Sanctis, M., Segura, A.M., da Silva, L.H.S., Stevanovic, Z.D., Swacha, G., Teittinen, A., Tolonen, K.T., Tsiripidis, I., Virta, L., Wang, B., Wang, J., Weisser, W., Xu, Y., Soininen, J., 2022. Distance decay 2.0 – A global synthesis of taxonomic and functional turnover in ecological communities. Global Ecology and Biogeography 31, 1399–1421. https://doi.org/10.1111/geb.13513

Grey, E.K., Bernatchez, L., Cassey, P., Deiner, K., Deveney, M., Howland, K.L., Lacoursière-Roussel, A., Leong, S.C.Y., Li, Y., Olds, B., Pfrender, M.E., Prowse, T.A.A., Renshaw, M.A., Lodge, D.M., 2018. Effects of sampling effort on biodiversity patterns estimated from environmental DNA metabarcoding surveys. Sci Rep 8, 8843. https://doi.org/10.1038/s41598-018-27048-2

Groote, S.R.E.D., Lantman, I.M. van S., Sercu, B., Dekeukeleire, D., Boonyarittichaikij, R., Smith, H., Beelde, R.D., Ceunen, K., Vantieghem, P., Matheve, H., Neve, L., Vanhellemont, M., Baeten, L., Peña, E.D.L., Bonte, D., Martel, A., Verheyen, K., Lens, L., 2017. Tree species identity outweighs the effects of tree species diversity and forest fragmentation on understorey diversity and composition. Plant Ecology and Evolution 150, 229–239. https://doi.org/10.5091/plecevo.2017.1331

Guerra-Castro, E.J., Cajas, J.C., Simões, N., Cruz-Motta, J.J., Mascaró, M., 2021. SSP: an R package to estimate sampling effort in studies of ecological communities. Ecography 44, 561–573. https://doi.org/10.1111/ecog.05284

Halme, P., Kotiaho, J. S., 2012. The importance of timing and number of surveys in fungal biodiversity research. Biodiversity and Conservation 21, 205-219. https://doi.org/10.1007/s10531-011-0176-z

Hodgetts, N.G., Söderström, L., Blockeel, T.L., Caspari, S., Ignatov, M.S., Konstantinova, N.A., Lockhart, N., Papp, B., Schröck, C., Sim-Sim, M., Bell, D., Bell, N.E., Blom, H.H., Bruggeman-Nannenga, M.A., Brugués, M., Enroth, J., Flatberg, K.I., Garilleti, R., Hedenäs, L., Holyoak, D.T., Hugonnot, V., Kariyawasam, I., Köckinger, H., Kučera, J., Lara, F., Porley, R.D., 2020. An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. Journal of Bryology 42, 1–116. https://doi.org/10.1080/03736687.2019.1694329

Hoffmann, S., Steiner, L., Schweiger, A.H., Chiarucci, A., Beierkuhnlein, C., 2019. Optimizing sampling effort and information content of biodiversity surveys: a case study of alpine grassland. Ecological Informatics 51, 112–120. https://doi.org/10.1016/j.ecoinf.2019.03.003

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613

IPBES, 2019. Global assessment report of the Intergovernmental Science-Policy Platform on

727 Biodiversity and Ecosystem Services, Brondízio, E. S., Settele, J., Díaz, S., Ngo, H. T. (eds).
728 IPBES secretariat, Bonn, Germany. 1144 pages. ISBN: 978-3-947851-20-1
729 Janssen, P., Cateau, E., Fuhr, M., Nusillard, B., Brustel, H., Bouget, C., 2016. Are biodiversity patterns
730 of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in
731 unfragmented montane forests. Biodiversity and Conservation 25.
732 https://doi.org/10.1007/s10531-016-1116-8
733 Jiguet, F., Devictor, V., Julliard, R., & Couvet, D. (2012). French citizens monitoring ordinary birds
734 provide tools for conservation and ecological sciences. Acta Oecologica, 44, 58–66.
735 https://doi.org/10.1016/j.actao.2011.05.003
736 Kempeneers, P., Sedano, F., Seebach, L., Strobl, P., San-Miguel-Ayanz, J., 2011. Data Fusion of
737 Different Spatial Resolution Remote Sensing Images Applied to Forest-Type Mapping. IEEE
738 Transactions on Geoscience and Remote Sensing 49, 4977–4986.
739 https://doi.org/10.1109/TGRS.2011.2158548
740 Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Deconchat, M.,
741 Gosselin, M., Ladet, S., Savoie, J.-M., Tillon, L., Bouget, C., 2019. Assessing the potential of
742 routine stand variables from multi-taxon data as habitat surrogates in European temperate
743 forests. Ecological Indicators 104, 116–126. https://doi.org/10.1016/j.ecolind.2019.04.085
744 Leclerc, L., Calderón-Sanou, I., Martinez-Almoyna, C., Paillet, Y., Thuiller, W., Vincenot, L., Kunstler,
745 G., 2023. Beyond the role of climate and soil conditions: Living and dead trees matter for soil
746 biodiversity in mountain forests. Soil Biology and Biochemistry 187, 109194.
747 https://doi.org/10.1016/j.soilbio.2023.109194
748 Lindenmayer, D.B., Likens, G.E., 2011. Direct Measurement Versus Surrogate Indicator Species for
749 Evaluating Environmental Change and Biodiversity Loss. Ecosystems 14, 47–59.
750 https://doi.org/10.1007/s10021-010-9394-6
751 Lodge, D. J., Ammirati, J. F., O'Dell, T. E., Mueller, G. M., Huhndorf, S. M., Wang, C. J., Stokland, J. N.,

Schmit, J. P., Ryvarden, L., Leacock, P. R., Mata, M., Umaña, L., Wu, Q. F., Czederpiltz, D. L., 2004. Terrestrial and lignicolous macrofungi. biodiversity of fungi, inventory and monitoring methods, 127-158.

Médail, F., Monnet, A.-C., Pavon, D., Nikolic, T., Dimopoulos, P., Bacchetta, G., Arroyo, J., Barina, Z., Albassatneh, M.C., Domina, G., Fady, B., Matevski, V., Mifsud, S., Leriche, A., 2019. What is a tree in the Mediterranean Basin hotspot? A critical analysis. Forest Ecosystems 6, 17. https://doi.org/10.1186/s40663-019-0170-6

Monleon-Getino, T., Frias-Lopez, J., 2020. A priori estimation of sequencing effort in complex microbial metatranscriptomes. Ecology and Evolution 10, 13382–13394. https://doi.org/10.1002/ece3.6941

Montes, E., Lefcheck, J., Guerra-Castro, E., Klein, E., de Azevedo Mazzuco, A., Bigatti, G., Cordeiro, C., Simoes, N., Macaya, E., Moity, N., Londoño-Cruz, E., Helmuth, B., Choi, F., Soto, E., Miloslavich, P., Muller-Karger, F., 2021. Optimizing Large-Scale Biodiversity Sampling Effort: Toward an Unbalanced Survey Design. Oceanography 34. https://doi.org/10.5670/oceanog.2021.216

Nikkeshi, A., Hiraiwa, M.K., Ushimaru, A., Hoshizaki, K., Makita, A., Mizuki, I., 2021. Evaluation of sampling effort required to assess pollen species richness on pollinators using rarefaction. Appl Plant Sci 9, e11411. https://doi.org/10.1002/aps3.11411

Nuñez-Penichet, C., Cobos, M.E., Soberón, J., Gueta, T., Barve, N., Barve, V., Navarro-Sigüenza, A.G., Peterson, A.T., 2022. Selection of sampling sites for biodiversity inventory: Effects of environmental and geographical considerations. Methods in Ecology and Evolution 13, 1595–1607. https://doi.org/10.1111/2041-210X.13869

O'Brien, M.J., Brezzi, M., Schuldt, A., Zhang, J.-Y., Ma, K., Schmid, B., Niklaus, P.A., 2017. Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. Ecology and Evolution 7, 8753–8760. https://doi.org/10.1002/ece3.3411

Oettel, J., Lapin, K., 2021. Linking forest management and biodiversity indicators to strengthen sustainable forest management in Europe. Ecological Indicators 122, 107275. https://doi.org/10.1016/j.ecolind.2020.107275

Ovaskainen, O., Abrego, N., 2020. Joint Species Distribution Modelling: With Applications in R, Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781108591720

Pärtel, M., Szava-Kovats, R., Zobel, M., 2011. Dark diversity: shedding light on absent species. Trends in Ecology & Evolution 26, 124–128. https://doi.org/10.1016/j.tree.2010.12.004

Patacca, M., Lindner, M., Lucas-Borja, M.E., Cordonnier, T., Fidej, G., Gardiner, B., Hauf, Y., Jasinevičius, G., Labonne, S., Linkevičius, E., Mahnken, M., Milanovic, S., Nabuurs, G.-J., Nagel, T.A., Nikinmaa, L., Panyatov, M., Bercak, R., Seidl, R., Ostrogović Sever, M.Z., Socha, J., Thom, D., Vuletic, D., Zudin, S., Schelhaas, M.-J., 2023. Significant increase in natural disturbance impacts on European forests since 1950. Global Change Biology 29, 1359–1376. https://doi.org/10.1111/gcb.16531

Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M. R., Gossner, M. M., Seibold, S., Simons, N. K., Schall, P., van der Plas, F., Manning, P., Manzanedo, R. D., Boch, S., Prati, D., Ammer, C., Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., … Fischer, M. (2019). Specialisation and diversity of multiple trophic groups are promoted by different forest features. Ecology Letters, 22(1), 170–180. https://doi.org/10.1111/ele.13182

Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P., Freyhof, J., Gregory, R.D., Heip, C., Höft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch, M.A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013. Essential Biodiversity Variables. Science 339, 277–278. https://doi.org/10.1126/science.1229931

802 Pörtner, H.O., Roberts, D.C., Adams, H., Adler, C., Aldunce, P., Ali, E., Begum, R.A., Betts, R., Kerr,
803 R.B., Biesbroek, R. and Birkmann, J., 2022. Climate change 2022: impacts, adaptation and
804 vulnerability. IPCC.
805 R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for
806 Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.
807 https://doi:10.1093/bioinformatics/btx835
808 Rivers, M., Beech, E., Bazos, I., Bogunić, F., Buira, A., Caković, D., Carapeto, A., Carta, A., Cornier, B.,
809 Fenu, G., Fernandes, F., Fraga i Arguimbau, P., Garcia Murillo, P., Lepší, M., Matevski, V.,
810 Medina, F., Menezes de Sequeira, M., Meyer, N., Mikoláš, V., Montagnani, C., Monteiro-
811 Henriques, T., Naranjo Suárez, J., Orsenigo, S., Petrova, A., Reyes-Betancort, A., Rich, T.,
812 Salvesen, P.H., Santana López, I., Scholz, S., Sennikov, A., Shuka, L., Silva, L.F., Thomas, P.,
813 Troia, A., Villar, J.L., Allen, D. (2019). European Red List of Trees: European Red list
814 assessment review workshop: trees and shrubs. International Union for Conservation of
815 Nature and Natural Resources (IUCN). https://doi.org/10.2305/IUCN.CH.2019.ERL.1.en
816 Runnel, K., Tamm, H., Lõhmus, A., 2015. Surveying wood-inhabiting fungi: Most molecularly
817 detected polypore species form fruit-bodies within short distances. Fungal Ecology 18, 93-
818 99. https://doi.org/10.1016/j.funeco.2015.08.008
819 Sabovljević, M., Ganeva, A., Tsakiri, E., Ştefănuţ, S., 2001. Bryology and bryophyte protection in
820 south-eastern Europe. Biological Conservation 101, 73–84.
821 https://doi.org/10.1016/S0006-3207(01)00043-X
822 Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V.,
823 Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M.,
824 Müller, J., Overmann, J., Renner, S. C., … Ammer, C. (2018). The impact of even-aged and
825 uneven-aged forest management on regional biodiversity of multiple taxa in European
826 beech forests. Journal of Applied Ecology, 55(1), 267–278. https://doi.org/10.1111/1365-

827 2664.12950
828 Senf, C., Buras, A., Zang, C.S., Rammig, A., Seidl, R., 2020. Excess forest mortality is consistently
829 linked to drought across Europe. Nature Communications 11, 6200.
830 https://doi.org/10.1038/s41467-020-19924-1
831 Stadt, J.J., Schieck, J., Stelfox, H.A., 2006. Alberta Biodiversity Monitoring Program – Monitoring
832 Effectiveness of Sustainable Forest Management Planning. Environ Monit Assess 121, 33–46.
833 https://doi.org/10.1007/s10661-005-9075-7
834 Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., Kelling, S., 2009. eBird: a citizen-based bird
835 observation network in the biological sciences. Biological Conservation 142, 2282-2292.
836 Turner, W., Tjørve, E., 2005. Scale-dependence in Species–area relationships. Ecography 28, 721–
837 730. https://doi.org/10.1111/j.2005.0906-7590.04273.x
838 Underwood, A.J., Chapman, M.G., 2003. Power, precaution, Type II error and sampling design in
839 assessment of environmental impacts. Journal of Experimental Marine Biology and Ecology
840 296, 49–70. https://doi.org/10.1016/S0022-0981(03)00304-6
841 Vellak, K., Ingerpuu, N., Vellak, A., Pärtel, M., 2010. Vascular plant and bryophytes species
842 representation in the protected areas network on the national scale. Biodivers Conserv 19,
843 1353–1364. https://doi.org/10.1007/s10531-009-9766-4
844 Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tscharntke, T., 2011. Tree
845 diversity and environmental context predict herb species richness and cover in Germany's
846 largest connected deciduous forest. Perspectives in Plant Ecology, Evolution and Systematics
847 13, 111–119. https://doi.org/10.1016/j.ppees.2011.02.004
848 Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.
849 Zeller, L., Baumann, C., Gonin, P., Heidrich, L., Keye, C., Konrad, F., Larrieu, L., Meyer, P., Sennhenn-
850 Reulen, H., Müller, J., Schall, P., Ammer, C., 2022. Index of biodiversity potential (IBP) versus
851 direct species monitoring in temperate forests. Ecological Indicators 136, 108692.

852 https://doi.org/10.1016/j.ecolind.2022.108692

Appendix A.

Table 1. Table reporting general information on the datasets that compose the pilot database. A dataset may be reported in more than one line if it includes sites across multiple forest categories.

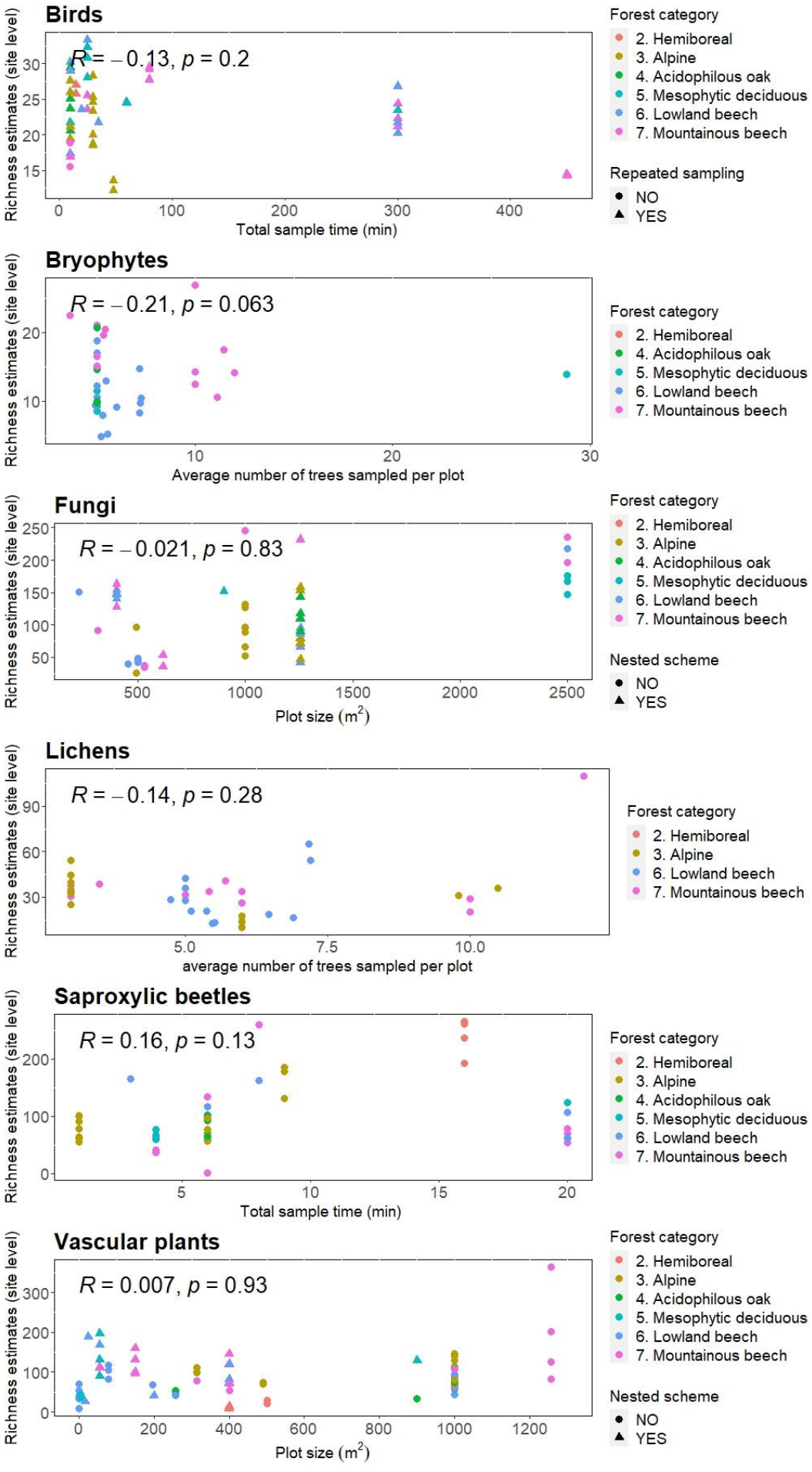
Country	Dataset ID	N of sites	Forest Category
Belgium	BE_KV1	1	4
Belgium	BE_KV1	2	5
Belgium	BE_KV1	2	6
Belgium	BE_PS1	2	5
Belgium	BE_PS2	2	4
Belgium	BE_PS2	2	6
Czech Republic	CZ_JH1	4	5
Czech Republic	CZ_JH1	3	6
Czech Republic	CZ_JH1	3	7
Czech Republic	CZ_JH2	1	5
Czech Republic	CZ_JH2	1	6
Denmark	DK_JC1	6	6
Denmark	DK_JC2	2	6
Denmark	DK_JC3	1	6
France	FR_AM	1	6
France	FR_JP	3	3
France	FR_NK	1	6
France	FR_YP	11	3
France	FR_YP	6	4
France	FR_YP	5	5
France	FR_YP	8	6
France	FR_YP	10	7
Germany	DE_ID	1	6
Germany	DE_JP	4	7
Germany	DE_PS	7	2
Germany	DE_PS	2	5
Germany	DE_PS	4	6
Germany	DE_PS	3	7
Hungary	HU_FT	1	5
Hungary	HU_PO1	1	5
Hungary	HU_PO2	1	5
Italy	IT_AC	1	7
Italy	IT_SB1	2	7
Italy	IT_SB2	2	7

Italy	IT_TS	2	3
Latvia	LT_GB	2	2
Slovakia	DK_SK	6	6
Slovakia	SK_DK	3	3
Slovakia	SK_MM	2	3
Slovakia	SK_MS	3	3
Slovakia	SK_MU	1	7
Spain	ES_IG	2	7
Sweden	SW_BN	4	2
Switzerland	CH_TL	1	7

856

857 Fig. 2. Standardized richness per site at 90% sample coverage in relation to the sampling intensity of
858 the different taxa along with the spearman rank correlation coefficient (R) and corresponding p-
859 values. Colors represent the forest category assigned to the sample plot and shapes indicate the

860 nestedness in the sampling design.


Birds
R = −0.13, p = 0.2
Richness estimates (site level)
Total sample time (min)
Bryophytes
R = −0.21, p = 0.063
Average number of trees sampled per plot
Fungi
R = −0.021, p = 0.83
Plot size (m2)
Lichens
R = −0.14, p = 0.28
average number of trees sampled per plot
Saproxylic beetles
R = 0.16, p = 0.13
Total sample time (min)
Vascular plants
R = 0.007, p = 0.93
Plot size (m2)
Forest category
2. Hemiboreal
3. Alpine
4. Acidophilous oak
5. Mesophytic deciduous
6. Lowland beech
7. Mountainous beech
Repeated sampling
NO
YES
Nested scheme
NO
YES

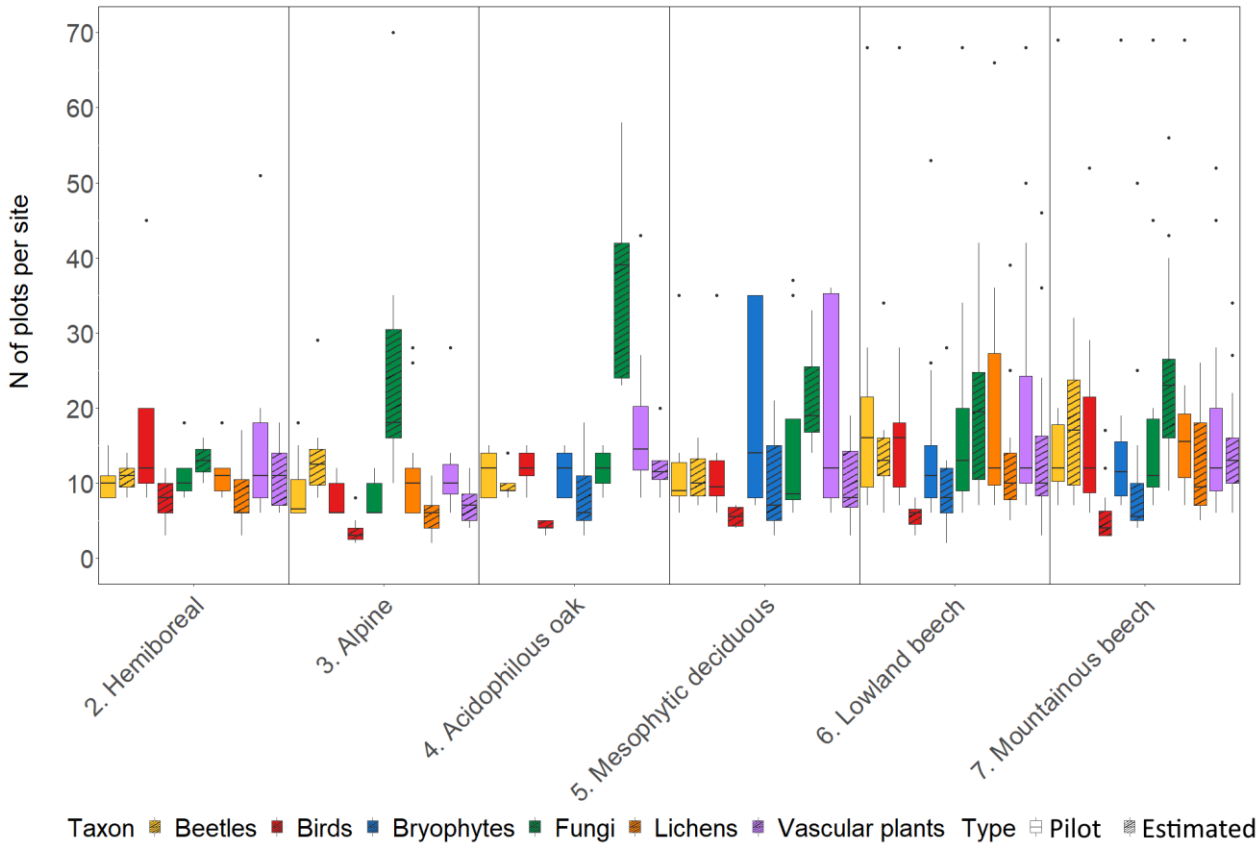
861

862 Table 2. Table reporting the sampling variable considered to investigate the influence of sampling
863 protocol on the richness estimates. “Repeated sampling” is a binary variable indicating whether the
864 total sampling time was split into multiple session. “Nested scheme” is a binary variable indicating
865 whether the total sample size was split into multiple sub-sampling unit.

Taxon	**Sampling variable considered**	**Range**
Birds	Total sample time per plot (min)	10 - 1980
	Repeated sampling	/
Bryophytes	Average number of tree sampled within plots of a same site	3,67 - 12
Lichens	Average number of tree sampled within plots of a same site	3 - 12
Fungi	Total sample size per plot (m^2)	100 - 20000
	Nested scheme	/
Saproxylic beetles	Total number of traps used within a plot	1 - 20
Vascular plants	Total sample size per plot (m^2)	1 - 20000
	Nested scheme	/

866

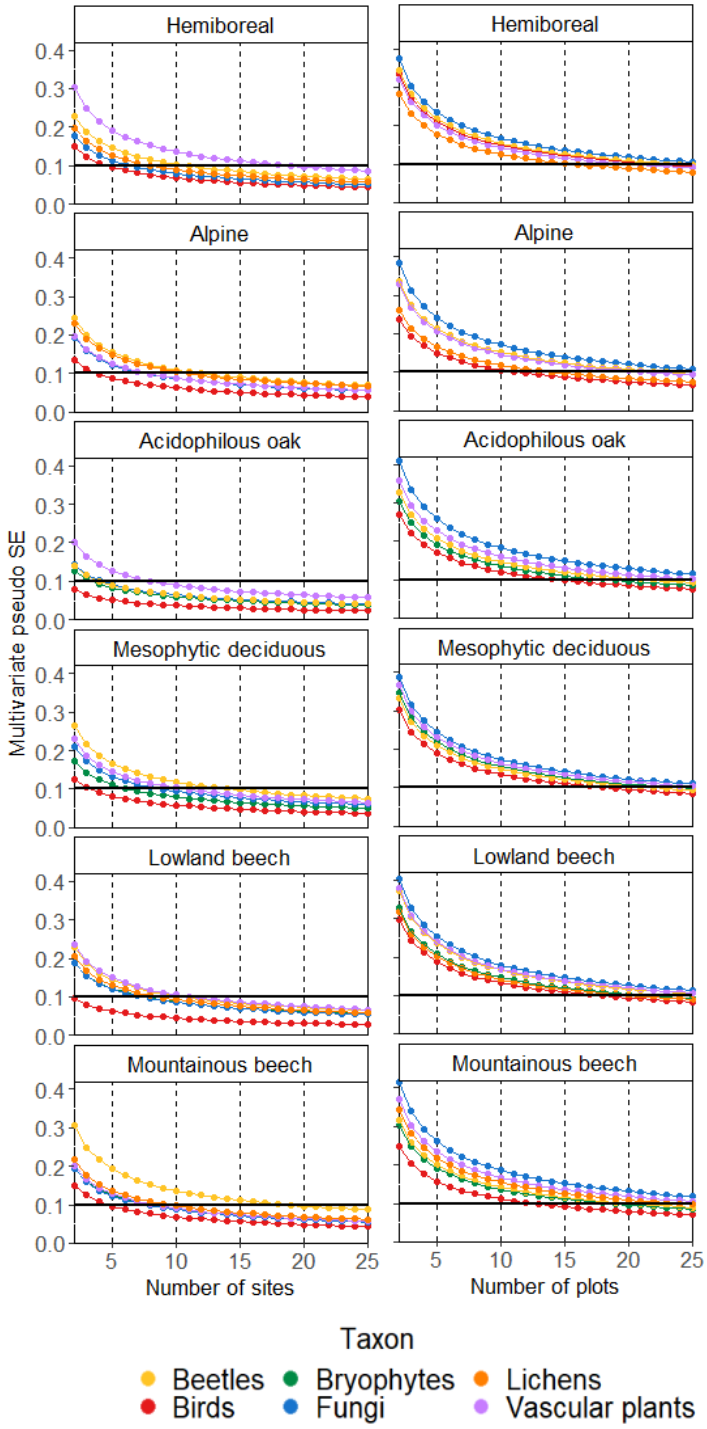
867 Fig. 3. Distribution of the pilot (plain) and estimated (diagonal lines) number of plots per site across
868 different taxonomic groups and forest categories. The estimated number of plots was assessed as to
869 reach a 90% coverage.


N of plots per site
70
60
50
40
30
20
10
0
2. Hemiboreal
3. Alpine
4. Acidophilous oak
5. Mesophytic deciduous
6. Lowland beech
7. Mountainous beech
Taxon Beetles Birds Bryophytes Fungi Lichens Vascular plants Type Pilot Estimated

870

871

872 Fig. 4. Values of multivariate pseudo standard errors representing the variability in species
873 composition for different sampling efforts in terms of number of sites per forest category (left column)
874 and number of plots per site (right column).



875

876

Conclusions

This PhD research contributes to a deeper understanding of the potential to achieve multifunctionality in European forests, emphasizing the complex interdependencies between biodiversity conservation, timber production, and climate change mitigation. By addressing key questions on the trade-offs between biodiversity conservation, forest management for timber production, and climate change mitigation, this work offers insights into the challenges of balancing these crucial forest functions.

- **Chapter 1. Where are we now with European forest multi-taxon biodiversity and where can we head to?**

  Through extensive collaboration within the COST Action CA18207 “Bottoms-Up”, this thesis built a novel Europe-wide, harmonized database covering biodiversity across multiple taxa and forest stand structural information.

- **Chapter 2. Do European forest carbon and biodiversity policies have a win-win potential?**

  This research addresses the often-overlooked complexity in carbon and biodiversity relationships, showing that focusing solely on living biomass carbon stocks does not adequately preserve biodiversity, particularly for deadwood-reliant taxa. Through analysis of deadwood carbon pools, the study demonstrates positive carbon-biodiversity relationships that are especially beneficial for wood-inhabiting fungi, saproxylic beetles, and epiphytic lichens. These findings stress that policies aimed at multifunctionality should consider the interconnections between carbon stocks in different forest carbon pools and biodiversity of multiple taxonomic groups. Deadwood emerges as a crucial resource, supporting both carbon sequestration and the diversity of several taxonomic groups, especially in managed forests where deadwood retention is typically reduced.

- **Chapter 3. Biodiversity at stake: winners and losers of forest management in Europe.**

  The impact of forest management practices on the occurrence of single species was evaluated across multiple taxonomic groups, revealing an heterogeneous response to management intensity and practices, depending on species-specific ecological needs. Bryophytes, for example, showed negative responses to most forms of management, indicating their reliance on stable, humid environments often provided by closed canopies and

deadwood. In contrast, vascular plants, particularly light-demanding species, benefitted from high-intensity management practices that increase light availability. Lichens presented a mixed response profile, with reactions influenced by both the type and intensity of management. The results suggest that a one-size-fits-all approach to forest management is inadequate for maintaining biodiversity across taxa, highlighting the need for species- and group-specific management approaches.

- **Chapter 4. Guiding management practices to enhance multi-taxon diversity in Mediterranean forests.**

  Mediterranean forests, with their unique ecological pressures, require tailored management practices. We identified deadwood quality, canopy openness, and basal area as key structural attributes impacting species richness and composition in Mediterranean forests. This work suggests that Sustainable Forest Management (SFM) practices in Mediterranean regions should prioritize large-diameter deadwood retention and structural diversity to support both biodiversity and carbon storage. These findings underscore the unique needs of Mediterranean ecosystems, which are underrepresented in broader forest biodiversity research, and emphasize the importance of adapting management practices to specific ecological conditions.

- **Chapter 5: Towards an effective multi-taxon biodiversity assessment in European forests.**

  Using the “Bottoms-Up” platform as a pilot, this chapter evaluates the effectiveness of in-situ biodiversity assessments, focusing on the varying sampling needs of different taxonomic groups. The study found that birds and epiphytic bryophytes require a moderate sampling effort to detect changes in species richness when compared to groups like saproxylic beetles, vascular plants, and fungi require more intensive efforts to monitor shifts in species composition. These results emphasize the necessity of a comprehensive monitoring network that can adapt to the specific sampling requirements of each group, providing accurate data to inform management practices. Insights from this research underscore the need for scalable, efficient biodiversity monitoring networks across Europe, especially in light of the new EU forest monitoring law.

Our findings reveal that although EU policies like the Biodiversity and Forest strategies for 2030 seek to support multifunctionality, the simultaneous achievement of these challenges remains a complex undertaking. Achieving forest multifunctionality in Europe requires integrating biodiversity conservation, timber production, and climate change mitigation within a single management framework. We underscore the limitations of current policies in addressing these interconnected

objectives. Despite their intentions, the complexity of interdependencies between biodiversity, carbon storage, and timber production makes the achievement of these aims a challenge (EEA, 2020; Forest Europe, 2020).

The path toward achieving multifunctionality in European forests needs a shift from broad, generalized strategies to adaptive management approaches that accounts for species-specific and habitat-specific responses. Forest policies must promote management techniques that maintain ecological niches for different species while supporting carbon storage and timber production. To do so, sustainable forest management (MCPFE, 1993) should embrace a landscape-level perspective, enabling the establishment of mosaics of habitats that support a wider range of taxonomic groups and forest-dependent species to enhance forest resilience (Blattert et al., 2023). In this framework, the development of biodiversity indicators that capture species-specific metrics, alongside traditional structural indicators (Forest Europe, 2020), will be crucial to accurately track biodiversity trends at the continental and scale level following increasing pressures on forest biodiversity in the upcoming years (Puumalainen et al., 2003). Policies must align with sustainable management goals from local to national scale and support practices such as variable retention harvesting, continuous cover forestry, and the retention of deadwood and mature trees (Lindenmayer et al., 2012; Pommerening & Murphy, 2004), that support a variety of less-studied taxonomic groups and single species requirements.

As anthropogenic pressures intensify, gathering data and integrating these methods across less-studied and threatened forest ecosystems is crucial (Palahi et al., 2008). Enhanced monitoring strategies that include less-studied taxonomic groups, particularly in underrepresented regions such as the Mediterranean, are vital to achieve this goal (Palahi et al., 2008). The proposed EU Biodiversity Monitoring Law offers a framework to address these data deficiencies by standardizing monitoring protocols across EU member states (European Commission, 2023). However, several challenges remain, including the need for harmonization of data collection methods, ensuring funding for implementation, and overcoming logistical barriers related to monitoring diverse forest ecosystems across heterogeneous landscapes. Achieving these goals will require not only policy alignment but also substantial investment in monitoring resources and technology. The establishment of the COST Action CA18207 “Bottoms-Up” database emerges as a critical foundation for these monitoring efforts. Based on our findings, we underscore the necessity of targeted sampling efforts for less-studied taxonomic groups at the continental level to accurately reflect their diversity. In particular, groups such as fungi and saproxylic beetles play essential roles in forest ecosystems yet remain poorly monitored (Stokland, 2012).

Ultimately, promoting forest multifunctionality in Europe requires not only advances in monitoring and management practices but also a reorientation of forest policies to

embrace the inherent trade-offs between biodiversity, timber, and climate goals. Current frameworks often favor win-win solutions that may overlook complex ecosystem interdependencies, particularly those between biodiversity conservation and carbon storage (Burton et al., 2013; Khamila et al., 2023) and biodiversity and timber production (Paillet et al., 2010). Achieving multifunctionality requires flexible policies that integrate these trade-offs while supporting adaptive management practices capable of responding to ecological and climatic changes.

In conclusion, this research provides a foundation for further research on European forests multifunctionality and emphasizes that addressing biodiversity, timber production, and carbon sequestration synergically is a difficult, yet essential, challenge to meet current objectives while sustaining their ecological integrity. The adoption of refined biodiversity indicators, enhanced monitoring, and a focus on policy integration across scales are crucial steps toward this vision, ensuring the resilience and sustainability of European forests for future generations.

Bibliography

Aitken, S. N., & Bemmels, J. B. (2016). Time to get moving: Assisted gene flow of forest trees. *Evolutionary Applications*, *9*(1), 271–290. https://doi.org/10.1111/eva.12293

Angers, V. A., Messier, C., Beaudet, M., & Leduc, A. (2005). Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *Forest Ecology and Management*, *217*(2), 275–293. https://doi.org/10.1016/j.foreco.2005.06.008

Asbeck, T., Großmann, J., Paillet, Y., Winiger, N., & Bauhus, J. (2021). The Use of Tree-Related Microhabitats as Forest Biodiversity Indicators and to Guide Integrated Forest Management. *Current Forestry Reports*, *7*(1), 59–68. https://doi.org/10.1007/s40725-020-00132-5

Aude, E., & Poulsen, R. S. (2000). Influence of Management on the Species Composition of Epiphytic Cryptogams in Danish Fagus Forests. *Applied Vegetation Science*, *3*(1), 81–88. https://doi.org/10.2307/1478921

Baessler, C., Mueller, J., Dziock, F., & Brandl, R. (2010). Effects of resource availability and climate on the diversity of wood-decaying fungi. *JOURNAL OF ECOLOGY*, *98*(4), 822–832. https://doi.org/10.1111/j.1365-2745.2010.01669.x

Barredo, J., Brailescu, C., Teller, A., Sabatini, F. M., Mauri, A., & Janouskova, K. (2021). *Mapping and assessment of primary and old-growth forests in Europe* (Scientific Analysis or Review, Anticipation and Foresight, Technical Guidance KJ-NA-30661-EN-N (online),KJ-NA-30661-EN-C (print)). Publications Office of the European Union. https://doi.org/10.2760/797591 (online),10.2760/13239 (print)

Bauhus, J., Puettmann, K., & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management*, *258*(4), 525–537. https://doi.org/10.1016/j.foreco.2009.01.053

Bełcik, M., Lenda, M., Amano, T., & Skórka, P. (2020). Different response of the taxonomic,

phylogenetic and functional diversity of birds to forest fragmentation. *Scientific Reports*, *10*(1), 20320. https://doi.org/10.1038/s41598-020-76917-2

Bernal, B., Murray, L., & Pearson, T. (2018). Global carbon dioxide removal rates from forest landscape restoration activities. *Carbon Balance and Management*, *13*. https://doi.org/10.1186/s13021-018-0110-8

BirdLife International, Directorate-General for Environment (European Commission), & IUCN. (2022). *European red list of birds 2021*. Publications Office of the European Union. https://data.europa.eu/doi/10.2779/959320

Blattert, C., Eyvindson, K., Mönkkönen, M., Raatikainen, K. J., Triviño, M., & Duflot, R. (2023). Enhancing multifunctionality in European boreal forests: The potential role of Triad landscape functional zoning. *Journal of Environmental Management*, *348*, 119250. https://doi.org/10.1016/j.jenvman.2023.119250

Bohada-Murillo, M., Castano-Villa, G. J., & Fonturbel, F. E. (2020). The effects of forestry and agroforestry plantations on bird diversity: A global synthesis. *LAND DEGRADATION & DEVELOPMENT*, *31*(5), 646–654. https://doi.org/10.1002/ldr.3478

Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P., & Sayer, J. (2008). Plantation forests and biodiversity: Oxymoron or opportunity? *Biodiversity and Conservation*, *17*(5), 925–951. https://doi.org/10.1007/s10531-008-9380-x

Brunet, J., Fritz, Ö., & Richnau, G. (2010). Biodiversity in European beech forests—A review with recommendations for sustainable forest management. *Ecological Bulletins*, *53*, 77–94.

Burrascano, S., Chianucci, F., Trentanovi, G., Kepfer-Rojas, S., Sitzia, T., Tinya, F., Doerfler, I., Paillet, Y., Nagel, T. A., Mitic, B., Morillas, L., Munzi, S., Van der Sluis, T., Alterio, E., Balducci, L., de Andrade, R. B., Bouget, C., Giordani, P., Lachat, T., … Ódor, P. (2023). Where are we now with European forest multi-taxon biodiversity and where can we head to? *Biological Conservation*, *284*, 110176. https://doi.org/10.1016/j.biocon.2023.110176

Burrascano, S., Trentanovi, G., Paillet, Y., Heilmann-Clausen, J., Giordani, P., Bagella, S.,

Bravo-Oviedo, A., Campagnaro, T., Campanaro, A., Chianucci, F., De Smedt, P., García-Mijangos, I., Matošević, D., Sitzia, T., Aszalós, R., Brazaitis, G., Cutini, A., D'Andrea, E., Doerfler, I., … Ódor, P. (2021). Handbook of field sampling for multi-taxon biodiversity studies in European forests. *Ecological Indicators*, *132*, 108266. https://doi.org/10.1016/j.ecolind.2021.108266

Burton, J. I., Ares, A., Olson, D. H., & Puettmann, K. J. (2013). Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests. *Ecological Applications*, *23*(6), 1297–1310. Scopus. https://doi.org/10.1890/12-1472.1

Cairns, M. A., Brown, S., Helmer, E. H., & Baumgardner, G. A. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, *111*(1), 1–11. https://doi.org/10.1007/s004420050201

Cálix, M., Alexander, K. N. A., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Vazquez-Albalate, X., Aleksandrowicz, O., Audisio, P., Istrate, P., Jansson, N., Legakis, A., Liberto, A., Makris, C., Merkl, O., Mugerwa Pettersson, R., Schlaghamersky, J., Bologna, M. A., Brustel, H., … Purchart, L. (2018). *European Red List of saproxylic beetles*. IUCN. https://portals.iucn.org/library/node/47296

Calviño-Cancela, M., Rubido-Bará, M., & van Etten, E. J. B. (2012). Do eucalypt plantations provide habitat for native forest biodiversity? *Forest Ecology and Management*, *270*, 153–162. https://doi.org/10.1016/j.foreco.2012.01.019

Cardellini, G., Valada, T., Cornillier, C., Vial, E., Dragoi, M., Goudiaby, V., Mues, V., Lasserre, B., Gruchala, A., Rørstad, P. K., Neumann, M., Svoboda, M., Sirgmets, R., Näsärö, O. P., Mohren, F., Achten, W. M. J., Vranken, L., & Muys, B. (2018). EFO-LCI: A New Life Cycle Inventory Database of Forestry Operations in Europe. *Environmental Management*, *61*(6), 1031–1047. https://doi.org/10.1007/s00267-018-1024-7

Carnus, J.-M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., & Walters, B. (2006). Planted Forests and Biodiversity. *Journal of Forestry*, *104*(2), 65–77. https://doi.org/10.1093/jof/104.2.65

Chaudhary, A., Burivalova, Z., Koh, L. P., & Hellweg, S. (2016). Impact of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs. *Scientific Reports*, *6*(1), 23954. https://doi.org/10.1038/srep23954

Christensen, M., Heilmann-Clausen, J., Walleyn, R., & Adamcik, S. (2005). Wood-inhabiting fungi as indicators of nature value in European beech forests. *Monitoring and Indicators of Forest Biodiversity in Europe–from Ideas to Operationality*, *229*. https://www.iufro.org/download/file/2220/75/80701-40205-40206-florence03.pdf/#page=229

COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS EU Biodiversity Strategy for 2030 Bringing Nature Back into Our Lives (2020). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A52020DC0380

COMMUNICATION FROM THE COMMISSION TO THE EUROPEAN PARLIAMENT, THE COUNCIL, THE EUROPEAN ECONOMIC AND SOCIAL COMMITTEE AND THE COMMITTEE OF THE REGIONS New EU Forest Strategy for 2030 (2021). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A52021DC0572

Crowther, T., Glick, H., Covey, K., Bettigole, C., Maynard, D., Thomas, S., Smith, J., Hintler, G., Duguid, M., Amatulli, G., Tuanmu, M.-N., Jetz, W., Salas-Eljatib, C., Stam, C., Piotto, D., Tavani, R., Green, S., Bruce, G., Williams, S., & Bradford, M. (2015). Mapping tree density at a global scale. *Nature*, *advance online publication*. https://doi.org/10.1038/nature14967

da Silva, L. P., Heleno, R. H., Costa, J. M., Valente, M., Mata, V. A., Gonçalves, S. C., da Silva, A. A., Alves, J., & Ramos, J. A. (2019). Natural woodlands hold more diverse, abundant, and unique biota than novel anthropogenic forests: A multi-group assessment. *European Journal of Forest Research*, *138*(3), 461–472. Scopus. https://doi.org/10.1007/s10342-019-01183-5

Dambrine, E., Dupouey, J. L., Laüt, L., Humbert, L., Thinon, M., Beaufils, T., & Richard, H.

(2007). Present forest biodiversity patterns in france related to former Roman agriculture. *Ecology*, *88*(6), 1430–1439. https://doi.org/10.1890/05-1314

De Vos, B., Cools, N., Ilvesniemi, H., Vesterdal, L., Vanguelova, E., & Carnicelli, S. (2015). Benchmark values for forest soil carbon stocks in Europe: Results from a large scale forest soil survey. *Geoderma*, *251–252*, 33–46. https://doi.org/10.1016/j.geoderma.2015.03.008

Dias, A. C., & Arroja, L. (2012). Environmental impacts of eucalypt and maritime pine wood production in Portugal. *Journal of Cleaner Production*, *37*, 368–376. https://doi.org/10.1016/j.jclepro.2012.07.056

Directive—EU - 2023/2413—EN - Renewable Energy Directive—EUR-Lex. (n.d.). Retrieved October 1, 2024, from https://eur-lex.europa.eu/eli/dir/2023/2413/oj

Ellis, C. (2009). Changing climate and historic-woodland structure interact to control species diversity of the 'Lobarion' epiphyte community in Scotland. *Journal of Vegetation Science*, *18*, 725–734. https://doi.org/10.1658/1100-9233(2007)18[725:CCAHSI]2.0.CO;2

European Environment Agency (EU body or agency). (2020). *State of nature in the EU: Results from reporting under the nature directives 2013 2018*. Publications Office of the European Union. https://data.europa.eu/doi/10.2800/088178

Eurostat. (2020). *Forestry statistics: Timber production and trade in the EU. Retrieved from https://ec.europa.eu/eurostat*.

FAO. (2020). *Global Forest Resources Assessment 2020: Main report*. FAO. https://doi.org/10.4060/ca9825en

Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J. F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., & Gustafsson, L. (2014). REVIEW: Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*, *51*(6), 1669–1679. https://doi.org/10.1111/1365-2664.12289

Felton, A., Lindbladh, M., Brunet, J., & Fritz, Ö. (2010). Replacing coniferous monocultures

with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. *Forest Ecology and Management*, *260*(6), 939–947. https://doi.org/10.1016/j.foreco.2010.06.011

FOREST EUROPE. (2020). FOREST EUROPE, 2020: State of Europe's Forests 2020. *FOREST EUROPE, 2020: State of Europe's Forests 2020*.

Fuller, R., & Warren, M. (1993). *Coppiced Woodlands: Their Management for Wildlife*.

Fyfe, R. M., Woodbridge, J., & Roberts, N. (2015). From forest to farmland: Pollen-inferred land cover change across Europe using the pseudobiomization approach. *Global Change Biology*, *21*(3), 1197–1212. https://doi.org/10.1111/gcb.12776

Gaillard, M.-J., Sugita, S., Mazier, F., Trondman, A.-K., Broström, A., Hickler, T., Kaplan, J. O., Kjellström, E., Kokfelt, U., Kuneš, P., Lemmen, C., Miller, P., Olofsson, J., Poska, A., Rundgren, M., Smith, B., Strandberg, G., Fyfe, R., Nielsen, A. B., … Seppä, H. (2010). Holocene land-cover reconstructions for studies on land cover-climate feedbacks. *Climate of the Past*, *6*(4), 483–499. https://doi.org/10.5194/cp-6-483-2010

Giuntoli, J., Barredo, J. I., Avitabile, V., Camia, A., Cazzaniga, N. E., Grassi, G., Jasinevičius, G., Jonsson, R., Marelli, L., Robert, N., Agostini, A., & Mubareka, S. (2022). The quest for sustainable forest bioenergy: Win-win solutions for climate and biodiversity. *Renewable and Sustainable Energy Reviews*, *159*, 112180. https://doi.org/10.1016/j.rser.2022.112180

Goded, S., Ekroos, J., Domínguez, J., Azcárate, J. G., Guitián, J. A., & Smith, H. G. (2019a). Effects of eucalyptus plantations on avian and herb species richness and composition in North-West Spain. *Global Ecology and Conservation*, *19*, e00690. https://doi.org/10.1016/j.gecco.2019.e00690

Goded, S., Ekroos, J., Domínguez, J., Azcárate, J. G., Guitián, J. A., & Smith, H. G. (2019b). Effects of eucalyptus plantations on avian and herb species richness and composition in North-West Spain. *Global Ecology and Conservation*, *19*, e00690. https://doi.org/10.1016/j.gecco.2019.e00690

González-Montelongo, C., & Pérez-Vargas, I. (2019). Looking for a home: Exploring the

potential of epiphytic lichens to colonize tree plantations in a Macaronesian laurel forest. *Forest Ecology and Management*, *453*, 117541. https://doi.org/10.1016/j.foreco.2019.117541

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology: The Journal of the Society for Conservation Biology*, *27*(3), 605–614. https://doi.org/10.1111/cobi.12023

Grassi, G., R, P., K, J., V, B., A, K., M, V., J, S. L., G, J., & M, A. (2021). *Brief on the role of the forest-based bioeconomy in mitigating climate change through carbon storage and material substitution* [Scientific analysis or review, Technical guidance]. European Commission.

Harris, N. L., Gibbs, D. A., Baccini, A., Birdsey, R. A., de Bruin, S., Farina, M., Fatoyinbo, L., Hansen, M. C., Herold, M., Houghton, R. A., Potapov, P. V., Suarez, D. R., Roman-Cuesta, R. M., Saatchi, S. S., Slay, C. M., Turubanova, S. A., & Tyukavina, A. (2021). Global maps of twenty-first century forest carbon fluxes. *Nature Climate Change*, *11*(3), Article 3. https://doi.org/10.1038/s41558-020-00976-6

Hedwall, P.-O., Nordin, A., Brunet, J., & Bergh, J. (2010). Compositional changes of forest-floor vegetation in young stands of Norway spruce as an effect of repeated fertilisation. *Forest Ecology and Management*, *259*, 2418–2425. https://doi.org/10.1016/j.foreco.2010.03.018

Hodgetts, N. (2019). *A miniature world in decline*. IUCN. https://doi.org/10.2305/IUCN.CH.2019.ERL.2.en

Hodgetts, N., Söderström, L., Blockeel, T., Caspari, S., Ignatov, N., Konstantinova, N., Lockhart, B., Papp, C., Schröck, M., Sim-Sim, D., Bell, N., Bell, H., Blom, M., Bruggeman-Nannenga, M., Brugués, J., Enroth, K., Flatberg, R., Garilleti, L., Hedenäs, D., & Roseggergasse, U. (2020). An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. *Journal of Bryology*, *42*, 1–116.

https://doi.org/10.1080/03736687.2019.1694329

Kaplan, J. O., Krumhardt, K. M., & Zimmermann, N. (2009). The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews*, *28*(27), 3016–3034. https://doi.org/10.1016/j.quascirev.2009.09.028

Keenleyside, C., & Tucker, G. (2010). Farmland abandonment in the EU: An assessment of trends and prospects. *London: WWF and IEEP (November*.

Khamila, C. N., Groen, T. A., Toxopeus, A. G., Santini, L., Neumann, M., Van Swaay, C., & Sierdsema, H. (2023). There is a trade-off between forest productivity and animal biodiversity in Europe. *Biodiversity and Conservation*, *32*(6), 1879–1899. https://doi.org/10.1007/s10531-023-02582-2

Kirby, K., Buckley, G., & Mills, J. (2017). Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland. *Folia Geobotanica*, *52*. https://doi.org/10.1007/s12224-016-9252-1

Konczal, A., Winkel, G., Derks, J., & de Koning, J. (2023). Integrating nature conservation measures in european forest management—An exploratory study of barriers and drivers in 9 european countries. *Journal of Environmental Management*, *325*, 116619. https://doi.org/10.1016/j.jenvman.2022.116619

Köster, K., Metslaid, M., Engelhart, J., & Köster, E. (2015). Dead wood basic density, and the concentration of carbon and nitrogen for main tree species in managed hemiboreal forests. *Forest Ecology and Management*, *354*, 35–42. https://doi.org/10.1016/j.foreco.2015.06.039

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., & Uotila, A. (2001). Forest Fragmentation in Fennoscandia: Linking Habitat Requirements of Wood-associated Threatened Species to Landscape and Habitat Changes. *Scandinavian Journal of Forest Research*, *16*(sup003), 27–37. https://doi.org/10.1080/028275801300090564

Kuuluvainen, T., & Gauthier, S. (2018). Young and old forest in the boreal: Critical stages of ecosystem dynamics and management under global change. *Forest Ecosystems*, *5*(1), 26. https://doi.org/10.1186/s40663-018-0142-2

Lachat, T., Wermelinger, B., Gossner, M., Bussler, H., Isacsson, G., & Müller, J. (2012). Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators*, *23*, 323–331. https://doi.org/10.1016/j.ecolind.2012.04.013

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., & Vandekerkhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. *Ecological Indicators*, *84*, 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051

Larsen, J., Angelstam, P., Bauhus, J., Carvalho, J., Diaci, J., Dobrowolska, D., Gazda, A., Gustafsson, L., Krumm, F., Knoke, T., Konczal, A., Kuuluvainen, T., Mason, B., Motta, R., Pötzelsberger, E., Rigling, A., & Schuck, A. (2022). *Closer-to-Nature Forest Management. From Science to Policy 12.* https://doi.org/10.36333/fs12

Lasanta, T., Arnáez, J., Pascual, N., Ruiz-Flaño, P., Errea, M. P., & Lana-Renault, N. (2017). Space–time process and drivers of land abandonment in Europe. *CATENA*, *149*, 810–823. https://doi.org/10.1016/j.catena.2016.02.024

Lefèvre, F., Koskela, J., Hubert, J., Kraigher, H., Longauer, R., Olrik, D. C., Schuler, S., & Bozzano, M. (2013). *Dynamic conservation of forest genetic resources in 33 European countries*. https://hdl.handle.net/10568/35562

Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, *131*(3), 433–445. https://doi.org/10.1016/j.biocon.2006.02.019

Lindenmayer, D. b., Franklin, J. f., Lõhmus, A., Baker, S. c., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., & Gustafsson, L. (2012). A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, *5*(6), 421–431. https://doi.org/10.1111/j.1755-263X.2012.00257.x

Lindenmayer, D., & Franklin, J. (2002). Conserving forest biodiversity: A comprehensive multiscaled approach. *Bibliovault OAI Repository, the University of Chicago Press*.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M., & Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, *259*, 698–709. https://doi.org/10.1016/j.foreco.2009.09.023

Lionello, P., & Scarascia, L. (2018). The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, *18*. https://doi.org/10.1007/s10113-018-1290-1

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., Ciais, P., & Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature*, *455*(7210), 213–215. https://doi.org/10.1038/nature07276

Maesano, M., Ottaviano, M., Lidestav, G., Lasserre, B., Matteucci, G., Scarascia Mugnozza, G., & Marchetti, M. (2018). Forest certification map of Europe. *iForest - Biogeosciences and Forestry*, *11*(4), 526. https://doi.org/10.3832/ifor2668-011

Mather, A. S. (1992). The Forest Transition. *Area*, *24*(4), 367–379.

Mather, A. S. (2001). The transition from deforestation to reforestation in Europe. *Agricultural Technologies and Tropical Deforestation*, 35–52. https://doi.org/10.1079/9780851994512.0035

MCPFE. (1993). *Resolution H1: General Guidelines for the Sustainable Management of Forests in Europe. Second MCPFE 16–17 June 1993, Helsinki/Finland.*

Messier, C., Bauhus, J., Doyon, F., Maure, F., Sousa-Silva, R., Nolet, P., Mina, M., Aquilué, N., Fortin, M.-J., & Puettmann, K. (2019). The functional complex network approach to foster forest resilience to global changes. *Forest Ecosystems*, *6*(1), 21. https://doi.org/10.1186/s40663-019-0166-2

Mohr, J., Thom, D., Hasenauer, H., & Seidl, R. (2024). Are uneven-aged forests in Central Europe less affected by natural disturbances than even-aged forests? *Forest Ecology*

and Management, *559*, 121816. https://doi.org/10.1016/j.foreco.2024.121816

Müller, J., Hothorn, T., & Pretzsch, H. (2007). Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica* L. *Forest Ecology and Management*, *242*(2), 297–305. https://doi.org/10.1016/j.foreco.2007.01.046

Müllerová, J., Hédl, R., & Szabó, P. (2015). Coppice abandonment and its implications for species diversity in forest vegetation. *Forest Ecology and Management*, *343*, 88–100. https://doi.org/10.1016/j.foreco.2015.02.003

Mund, M., & Ernst Detlef, S. (2006). Impacts of forest management on the carbon budget of European Beech (Fagus sylvatica) forests. *Allgemeine Forst Und Jagdzeitung*, *177*, 47–63.

Munteanu, C., Kuemmerle, T., Boltiziar, M., Butsic, V., Gimmi, U., Halada, L., Kaim, D., Király, G., Konkoly-Gyuró, É., Kozak, J., Lieskovsky, J., Mojses, M., Müller, D., Ostafin, K., Ostapowicz, K., Shandra, O., Stych, P., Walker, S., & Radeloff, V. (2014). Forest and agricultural land change in the Carpathian region—A meta-analysis of long-term patterns and drivers of change. *Land Use Policy*, *38*, 685–697. https://doi.org/10.1016/j.landusepol.2014.01.012

Nabuurs, G.-J., Lindner, M., Verkerk, P. J., Gunia, K., Deda, P., Michalak, R., & Grassi, G. (2013). First signs of carbon sink saturation in European forest biomass. *Nature Climate Change*, *3*(9), 792–796. Scopus. https://doi.org/10.1038/nclimate1853

Nabuurs, G.-J., Verkerk, P. J., Schelhaas, M.-J., Olabarria, J. R. G., Trasobares, A., & Cienciala, E. (2018). *Climate-Smart Forestry: Mitigation impacts in three European regions. From Science to Policy 6. European Forest Institute.*

Navarro, L. M., & Pereira, H. M. (2012). Rewilding Abandoned Landscapes in Europe. *Ecosystems*, *15*(6), 900–912. https://doi.org/10.1007/s10021-012-9558-7

Nocentini, S., Travaglini, D., & Muys, B. (2022). Managing Mediterranean Forests for Multiple Ecosystem Services: Research Progress and Knowledge Gaps. *Current Forestry Reports*, *8*(2), 229–256. https://doi.org/10.1007/s40725-022-00167-w

Ódor, P., Király, I., Tinya, F., Bortignon, F., & Nascimbene, J. (2013). Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. *Forest Ecology and Management*, *306*, 256–265. https://doi.org/10.1016/j.foreco.2013.07.001

O'Hara, K. L. (2016). What is close-to-nature silviculture in a changing world? *Forestry: An International Journal of Forest Research*, *89*(1), 1–6. https://doi.org/10.1093/forestry/cpv043

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., … Virtanen, R. (2010). Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. *Conservation Biology*, *24*(1), 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x

Palahi, M., Mavsar, R., Gracia, C., & Birot, Y. (2008). Mediterranean forests under focus. *International Forestry Review*, *10*(4), 676–688. https://doi.org/10.1505/ifor.10.4.676

Pan, Y., Birdsey, R. A., Phillips, O. L., & Jackson, R. B. (2013). The Structure, Distribution, and Biomass of the World's Forests. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 593–622. https://doi.org/10.1146/annurev-ecolsys-110512-135914

Pelli, P., Haapala, A., & Pykäläinen, J. (2017). Services in the forest-based bioeconomy – analysis of European strategies. *Scandinavian Journal of Forest Research*, *31*, 1–30. https://doi.org/10.1080/02827581.2017.1288826

Peterken, G. F. (George F. (with Internet Archive). (1996). *Natural woodland: Ecology and conservation in northern temperate regions*. Cambridge ; New York : Cambridge University Press. http://archive.org/details/naturalwoodlande0000pete

Pilli, R., Vizzarri, M., & Chirici, G. (2021). Combined effects of natural disturbances and management on forest carbon sequestration: The case of Vaia storm in Italy. *Annals of Forest Science*, *78*(2). Scopus. https://doi.org/10.1007/s13595-021-01043-6

Pommerening, A., & Murphy, S. T. (2004). A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry: An International Journal of Forest Research*, *77*(1), 27–44. https://doi.org/10.1093/forestry/77.1.27

Profft, I., Mund, M., Weber, G.-E., Weller, E., & Ernst Detlef, S. (2009). Forest management and carbon sequestration in wood products. *European Journal of Forest Research*, *128*, 399–413. https://doi.org/10.1007/s10342-009-0283-5

Proposal for a REGULATION OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL on a Monitoring Framework for Resilient European Forests (2023). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=COM:2023:728:FIN

Pukkala, T. (2014). Does biofuel harvesting and continuous cover management increase carbon sequestration? *Forest Policy and Economics*, *43*, 41–50. https://doi.org/10.1016/j.forpol.2014.03.004

Puumalainen, J., Kennedy, P., & Folving, S. (2003). Monitoring forest biodiversity: A European perspective with reference to temperate and boreal forest zone. *Journal of Environmental Management*, *67*(1), 5–14. https://doi.org/10.1016/S0301-4797(02)00183-4

Regulation (EU) 2021/2115 of the European Parliament and of the Council of 2 December 2021 Establishing Rules on Support for Strategic Plans to Be Drawn up by Member States under the Common Agricultural Policy (CAP Strategic Plans) and Financed by the European Agricultural Guarantee Fund (EAGF) and by the European Agricultural Fund for Rural Development (EAFRD) and Repealing Regulations (EU) No 1305/2013 and (EU) No 1307/2013, 435 OJ L (2021). http://data.europa.eu/eli/reg/2021/2115/oj/eng

Rio, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., & Ruiz-Peinado, R. (2017). A review of thinning effects on Scots pine stands: From growth and yield to new challenges under global change. *Forest Systems*, *26*, eR03S. https://doi.org/10.5424/fs/2017262-11325

Rodríguez-Soalleiro, R., Eimil-Fraga, C., Gómez-García, E., García-Villabrille, J. D., Rojo-Alboreca, A., Muñoz, F., Oliveira, N., Sixto, H., & Pérez-Cruzado, C. (2018). Exploring the factors affecting carbon and nutrient concentrations in tree biomass components in natural forests, forest plantations and short rotation forestry. *Forest Ecosystems*, *5*(1), 35. https://doi.org/10.1186/s40663-018-0154-y

Russell, M. B., Fraver, S., Aakala, T., Gove, J. H., Woodall, C. W., D'Amato, A. W., & Ducey, M. J. (2015). Quantifying carbon stores and decomposition in dead wood: A review. *Forest Ecology and Management*, *350*, 107–128. https://doi.org/10.1016/j.foreco.2015.04.033

Sabatini, F. M., Bluhm, H., Kun, Z., Aksenov, D., Atauri, J. A., Buchwald, E., Burrascano, S., Cateau, E., Diku, A., Duarte, I. M., Fernández López, Á. B., Garbarino, M., Grigoriadis, N., Horváth, F., Keren, S., Kitenberga, M., Kiš, A., Kraut, A., Ibisch, P. L., … Kuemmerle, T. (2021). European primary forest database v2.0. *Scientific Data*, *8*(1), Article 1. https://doi.org/10.1038/s41597-021-00988-7

Scharlemann, J. P., Tanner, E. V., Hiederer, R., & Kapos, V. (2014). Global soil carbon: Understanding and managing the largest terrestrial carbon pool. *Carbon Management*, *5*(1), 81–91. https://doi.org/10.4155/cmt.13.77

Scherrer, D., Baltensweiler, A., Bürgi, M., Fischer, C., Stadelmann, G., & Wohlgemuth, T. (2023). Low naturalness of Swiss broadleaf forests increases their susceptibility to disturbances. *Forest Ecology and Management*, *532*, 120827. https://doi.org/10.1016/j.foreco.2023.120827

Schütz, J.-P. (2011). Development of close to nature forestry and the role of ProSilva Europe. *Zbornnik Gozdarstva in Lesarstva*, *94*, 39–42.

Seidl, R., Schelhaas, M.-J., Rammer, W., & Verkerk, P. J. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*, *4*(9), Article 9. https://doi.org/10.1038/nclimate2318

Stokland, J. N. (2012). The saproxylic food web. In B. G. Jonsson, J. N. Stokland, & J. Siitonen (Eds.), *Biodiversity in Dead Wood* (pp. 29–57). Cambridge University Press.

https://doi.org/10.1017/CBO9781139025843.004

Svenning, J.-C., Lemoine, R. T., Bergman, J., Buitenwerf, R., Roux, E. L., Lundgren, E., Mungi, N., & Pedersen, R. Ø. (2024). The late-Quaternary megafauna extinctions: Patterns, causes, ecological consequences and implications for ecosystem management in the Anthropocene. *Cambridge Prisms: Extinction*, *2*, e5. https://doi.org/10.1017/ext.2024.4

Tinya, F., Doerfler, I., de Groot, M., Heilman-Clausen, J., Kovács, B., Mårell, A., Nordén, B., Aszalós, R., Bässler, C., Brazaitis, G., Burrascano, S., Camprodon, J., Chudomelová, M., Čížek, L., D'Andrea, E., Gossner, M., Halme, P., Hédl, R., Korboulewsky, N., … Ódor, P. (2023). A synthesis of multi-taxa management experiments to guide forest biodiversity conservation in Europe. *Global Ecology and Conservation*, *46*, e02553. https://doi.org/10.1016/j.gecco.2023.e02553

Trentanovi, G., Campagnaro, T., Sitzia, T., Chianucci, F., Vacchiano, G., Ammer, C., Ciach, M., Nagel, T. A., del Río, M., Paillet, Y., Munzi, S., Vandekerkhove, K., Bravo-Oviedo, A., Cutini, A., D'Andrea, E., De Smedt, P., Doerfler, I., Fotakis, D., Heilmann-Clausen, J., … Burrascano, S. (2023). Words apart: Standardizing forestry terms and definitions across European biodiversity studies. *Forest Ecosystems*, *10*, 100128. https://doi.org/10.1016/j.fecs.2023.100128

Turnock, D. (1998). Globalisation and the East European transition. *GeoJournal*, *45*(1), 129–140. https://doi.org/10.1023/A:1006946804157

Vellend, M. (2004). Parallel Effects of Land-Use History on Species Diversity and Genetic Diversity of Forest Herbs. *Ecology*, *85*(11), 3043–3055. https://doi.org/10.1890/04-0435

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., & Foster, D. R. (2003). Response of forest plant species to land-use change: A life-history trait-based approach. *Journal of Ecology*, *91*(4), 563–577. https://doi.org/10.1046/j.1365-2745.2003.00789.x

Vild, O., Roleček, J., Hédl, R., Kopecký, M., & Utinek, D. (2013). Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation

perspective. *Forest Ecology and Management*, *310*, 234–241. https://doi.org/10.1016/j.foreco.2013.07.056

Williams, M. (2000). Dark ages and dark areas: Global deforestation in the deep past. *Journal of Historical Geography*, *26*, 28–46. https://doi.org/10.1006/jhge.1999.0189