Czech University of Life Sciences Prague
Faculty of Forestry and Wood Sciences

# The impact of natural disturbances and forest structure on the biodiversity of temperate spruce-dominated primary forests in the Western Carpathians

Dissertation thesis

Study programme: Forest Engineering
Field of study: Forest Biology

Author: RNDr. Matej Ferenčík
Supervisor: Ing. Martin Mikoláš, Ph.D.
Advisor: doc. RNDr. Jeňýk Hofmeister, Ph.D.

# CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Forestry and Wood Sciences

# Ph.D. THESIS ASSIGNMENT

RNDr. Matej Ferenčík

Forestry Engineering
Forest Biology

Thesis title

**The impact of natural disturbance and forest structure on the biodiversity of temperate spruce-dominated primary forests in the Western Carpathians**

---

**Objectives of thesis**

1) Identify the impact of historical natural disturbances on the species richness of saproxylic fungi.

2) Determine the structural attributes of primary forests that influence local species richness and the presence of threatened species across various taxa.

3) Examine the concordance in species composition among plots for multiple taxa and determine whether differences in species composition result from spatial species turnover or exhibit a nested structure.

4) Develop forest management recommendations aimed at enhancing biodiversity.

**Methodology**

Input data for forest structure and dendrochronology were collected during the REMOTE project, encompassing a total of 120 plots in spruce primary forests located in the Western Carpathians. Biodiversity data will be gathered from 58 plots distributed across five mountain ranges in Slovakia, focusing on the following taxonomic groups: birds, saproxylic beetles, lichens, and saproxylic fungi. Birds will be surveyed using the point count method (point transects) at a distance of 60 meters from the center of each research plot measuring 0.1 hectares, conducted during the peak of the breeding season (April-May). To collect data on saproxylic beetles, impact traps comprising two nested plastic glasses with a funnel and collection container in the lower part will be placed at the center of each plot from April to October, without the use of an attractant. Saproxylic fungi will be documented during 1.25-hour surveys by two mycologists, covering all types of dead wood objects selected based on their representation on each plot, during one visit in the months of September-October. Lichens will be recorded throughout the year without time limitations on five selected objects (two live trees, two fallen trees, and one standing dead tree or stump) for each research plot. Data analysis will be conducted using the R statistical software, primarily employing the ”nlme” and ”vegan” packages, along with the use of GLS models.

**The proposed extent of the thesis**

100

**Keywords**

primary forest, biodiversity, Western Carpathians, dendrochronology, forest structure

---

**Recommended information sources**

Abrego N, Salcedo J (2013) Variety of woody debris as the factor influencing wood-inhabiting fungi richness and assemblages: Is it a question of quantity or quality? Forest Ecol Manag 291:377-385

Bässler C, Müller J, Svoboda M, Lepšová A, Hahn CH, Holzer H, Pouska V (2012) Diversity of wood-decaying fungi under different disturbance regimes – a case study from spruce mountain forests. Biodivers. Conserv. 21:33-49

Hlmers 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(6):2756-2766

Janda P, Trotsiuk V, Mikoláš M, Bače R, Nagel TA, Seidl R, Seedre M, Morrissey RC, Kucbel S, Jaloviar P, Jasík M, Vysoký J, Šamonil P, Čada V, Mrhalová H, Lábusová J, Nováková MH, Rydval M, Matějů L, Svoboda M (2017) The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. Forest Ecol Manag 388:67-78

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in Deadwood. Cambridge University Press, Cambridge, p. 524

Thorn S, Bässler C, Brandl R, Burton PJ, Cahall R, Campbell JL, Castro J, Choi CY, Cobb T, Donato DC, Durska E, Fontaine JB, Gauthier S, Hebert C, Hothorn T, Hutto RL, Lee EJ, Leverkus AB, Lindenmayer DB, Obrist MK, Rost J, Seibold S, Seidl R, Thom D, Waldron K, Wermelinger B, Winter MB, Zmihorski M, Müller J (2018) Impacts of salvage logging on biodiversity: A meta-analysis. J Appl Ecol. 55(1):279-289

Zemanová L, Trotsiuk V, Morrissey RC, Bače R, Mikoláš M, Svoboda M (2017) Old trees as a key source of epiphytic lichen persistence and spatial distribution in mountain Norway spruce forests. Biodivers. Conserv. 26:1943-1958

**Expected date**

2023/24 WS – FFWS – State Doctoral Examinations

**The Dissertation Thesis Supervisor**

Ing. Martin Mikoláš, Ph.D.

**Supervising department**

Department of Forest Ecology

Electronic approval: 31. 01. 2024

**prof. Ing. Miroslav Svoboda, Ph.D.**

Head of department

Electronic approval: 01. 02. 2024

**prof. Ing. Milan Lstibůrek, MSc, Ph.D.**

Chairperson of Field of Study Board

Electronic approval: 21. 08. 2024

**prof. Ing. Róbert Marušák, PhD.**

Dean

Prague on 22. 08. 2024

I confirm that this Phd. thesis “The impact of natural disturbances and forest structure on the biodiversity of temperate spruce-dominated primary forests in the Western Carpathians” was elaborated independently with the usage of quoted literature and based on consultations and the recommendations of my supervisor.

I agree with publishing this PhD. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording. This agreement is independent from the results of defense.

September 2024, Prague

## Acknowledgements

Before starting my PhD in 2018, I had no idea how many adventures and fulfilling moments I would have the chance to experience during these six years.

I got to places I had only heard or read about - jewels of the Carpathian wilderness. However, the doctoral studies were about more than wild nature and forests. Working in a great team brought a lot of valuable experiences and friendships into my life, which, I believe, will last even after my mission at the Department of Forest Ecology is over. I will never forget the moments when we went through primary forests to work, forded rivers, got wet together many times, and spent long hours talking by the fire after work. This fantastic team became my second family.

My massive thanks belong to prof. Ing. Miroslav Svoboda, PhD., for the trust shown and the opportunity to become part of this amazing team. I also thank my supervisor, Ing. Martin Mikoláš, PhD. for expert guidance and support whenever I needed his help. Thanks to him also for his patience. Thanks go to my consultant doc. RNDr. Jeňýk Hofmeister, PhD. for his help and how much I could learn from him. The list of names would be much longer, so I would like to thank everyone who trusted, supported, and helped me during my studies, both professionally and personally. However, the most enormous thanks go to the Carpathian wilderness itself for always accepting me and allowing me to get to know its beauty and, along with it, myself.

My studies aimed to contribute to biodiversity knowledge in the spruce primary forests of the Western Carpathians. I believe I succeeded and, in a small way, contributed to understanding and protecting such unique and magnificent ecosystems.

# Abstract

Understanding the processes shaping the species assemblages at multiple spatial and temporal scales in response to natural disturbances and their legacies is crucial for preventing ongoing worldwide biodiversity loss, and for improving forest management practices aimed at mitigating accelerating changes in environmental conditions and enhancing forest resilience. Spruce primary forests are critical habitats for a wide spectrum of forest-dwelling taxa. However, because of the higher frequency and severity of natural disturbances in the last decades, and the subsequent salvage logging, these ecosystems are incredibly rare and are disappearing rapidly. Although we have sufficient evidence for the fundamental role of structural variables for forest biodiversity, the influence of long-term natural disturbance regimes - which are the primary driver of these variables - has not been sufficiently documented. To address this knowledge gap, we sampled four taxonomic groups: birds, epiphytic and epixylic lichens, saproxylic beetles, and deadwood-inhabiting fungi at 58 locations within ten of the best-preserved spruce primary forest stands distributed across the Western Carpathians Mountains and investigated the drivers of their assemblages.

Our dataset combines disturbance history variables (frequency and severity), forest structural variables (e.g. tree age, quantity and quality of deadwood, canopy openness), and biodiversity data. The four taxonomic groups were selected because of their particular sensitivity to forest management. We applied a dendroecological approach (using tree-ring data) to describe the effect of 250-years of historical natural disturbances on current species richness of deadwood-inhabiting fungi at a plot-level (local) and stand level (regional). The magnitude of inter-site differences in species assemblages for four taxonomic groups were used to quantify corresponding levels of total beta-diversity, which were then decomposed into nestedness and turnover components. We also assessed the degree of congruence among groups for beta-diversity metrics. Finally, using regression methods, we investigated relationships between habitat features and observed alpha-diversity and red-listed species incidence.

The main findings of this thesis are:

I) Historical disturbances shaped the contemporary local and regional species richness of deadwood-inhabiting fungi, with contrasting impacts of disturbance regime components at different spatial scales. While the local diversity of red-listed species increased due to higher disturbance frequency, the regional diversity of all species decreased due to the higher severity

of historical disturbances. The deadwood volume positively influenced the species richness of deadwood-inhabiting fungi, while canopy openness had a negative impact.

II) The number of species found exclusively at the respective stand and the total number of species were similar for all stands for fungi and lichens but varied more strongly for beetles and birds. Except for birds, the individual stands generally hosted less than half of the species identified in the total regional species pool. Thus, variability in species composition among stands was large relative to the number of species found exclusively at the respective stand in the beetle, fungi, and lichen groups.

III) We found evidence for a congruence among taxonomic groups in terms of total beta-diversity. All groups were significantly correlated with at least one other group. The bird group was congruent with all other groups, while beetles were correlated with birds only. In contrast, we did not find evidence for a significant correspondence between groups in terms of the two components of beta-diversity, namely turnover and nestedness. The single exception was a congruence of spatial turnover between fungi and lichens.

IV) For beetles and lichens, local species richness (alpha-diversity) was influenced by characteristics associated with both the living tree canopy and the local deadwood supply. Specifically, the richness of the beetle group increased with both canopy openness (light levels) and volume of relatively intact (decay stage 1) lying deadwood. For lichens, the mean age of the five oldest trees and the volume of standing deadwood promoted local alpha-diversity. The local diversity of both lichen and fungi red-listed species was positively affected by stand conditions. Again, the mean age of the oldest trees, as well as the volume of highly decomposed lying deadwood (decay stages 4 and 5), positively influenced the number of red-listed species for these two groups. The number of rare lichens also covaried with elevation.

V) Spatial turnover for all taxonomic groups was significantly higher than nestedness. Each primary forest stand had unique and unrepeatable species composition and contributed equally to the total regional species pool.

Our results bring new and valuable insight into forest dynamics and biodiversity patterning at the local and regional landscape scale in montane temperate spruce-dominated primary forests in the Western Carpathians. From a landscape perspective, we can conclude

that the distribution of species from the regional species pool is driven by past spatiotemporal patterns of disturbance events and by spatial turnover. Natural disturbances occurring at higher frequencies that create multiscale habitat patchiness through disturbance legacies are necessary for a wide range of biodiversity, especially for rare and endangered species. The high number of observed rare species also highlights the importance of primary forests for biodiversity conservation. Thus, both creating a network of strict forest reserves with sufficient area and landscape connectivity at the regional scale, as refuges and sources for management-sensitive forest-dwelling taxa, and forest management practices that emulate natural disturbance processes, are recommended to support habitats for biodiversity and their associated ecosystem functions.

**Keywords:** Natural disturbances, Old-growth forests, Forest-dwelling taxa, Beta-diversity, Forest structure, Dendrochronology, Species richness, Species turnover

# Table of contents

# List of figures and tables

**Table 1.** Selected environmental variables from measurements of forest structure and reconstructed chronologies of disturbance history.

**Table 2.** Selected environmental variables from measurements of forest structure.

**Table 3.** Significant linear models (stand scale) and linear mixed-effect models (plot scale) linking plot-level alpha diversity ($D_\alpha$) and stand-level gamma diversity ($D_\gamma$), respectively, to characteristics of historical disturbances and forest structure.

**Table 4.** Congruence between beta-diversity matrices of the taxonomic groups.

**Table 5.** Results of generalised least squares models (GLS) for species richness and number of red-listed species of the respective taxonomic groups in the plots.

**Table S1.** List of all recorded species of the four taxonomic groups with their IUCN red-list status and occurrences across all plots.

**Table S2.** Results of generalised least squares model (GLS) selection for species richness of the respective taxa in the plots.

**Table S3.** Results of generalised least squares model (GLS) selection for the number of red-listed species of the respective taxa in the plots.

# 1 Introduction

Primary forests are essential refuges for biodiversity, including many endemics and species of high conservation and functional value (Moning & Müller 2009; Wallenius et al. 2010; Paillet et al. 2015; Eckelt et al. 2018; Di Marco et al. 2019). These ecosystems provide not only habitats for a wide range of biodiversity, but they are also irreplaceable in terms of water retention, soil protection, carbon storage, and many other ecosystem services (Gibson et al. 2011; Potapov et al. 2017; Watson et al. 2018; Mackey et al. 2020). Primary forests are shaped by natural processes that generate high vertical and horizontal structural diversity and complexity (Meigs et al. 2017; Stiers et al. 2018), which in turn supports the incidence of many highly-specialized organisms and red-listed species (Kozák et al. 2021; Ferenčík et al. 2022; Zemlerová et al. 2023; Gloor et al. 2024). The long-term viability and continuity of species-rich communities supported by higher structural heterogeneity created by natural disturbances have been statistically correlated with an absence of anthropogenic disturbance (Di Marco et al. 2019). Given this correlation, studying primary forests is essential because they serve as benchmarks for understanding natural ecosystem processes, functions, and biodiversity. These benchmarks provide critical insights that can inform restoration and conservation efforts worldwide. We can consider these ecosystems as living laboratories for science, providing vast sources of long-term historical data about forest dynamics and development (Luick et al. 2021). A growing body of research comparing managed and primary forests in the last decades highlights their importance as reference ecosystems (Kuuluvainen & Aakala 2011), where the highest structural heterogeneity, resilience, adaptability, and species richness of many taxonomic groups were found especially in unmanaged, old-growth forests (Dvořák et al. 2017; Stiers et al. 2018; Thorn et al. 2018; Asbeck et al. 2022; Wang et al. 2022).

Primary forest structure is shaped by natural disturbances (Pickett & White 1985; Svoboda et al. 2014), which are considered as a key driver in forest ecosystem dynamics (Stephens et al. 2013; Seidl et al. 2014). The European bark beetle (*Ips typographus*) and wind are the major disturbance agents of European Norway spruce (*Picea abies*) forests (Temperli et al. 2013). They create multi-scale habitat patchiness with various successional stages (Hilmers et al. 2018) and heterogeneous structures through disturbance legacies such as quantity and variability (decay stages) of standing and lying deadwood, as well as canopy openness. This heterogeneity is ideal for studying forest biodiversity (Donato et al. 2012) and the applicability of the "habitat heterogeneity hypothesis," which posits that species richness is higher in heterogeneous systems than in homogeneous systems with the same amount of resources (Stein et al. 2014; Hamm & Drossel 2017). In the last decades, natural disturbances have tended to occur more often (frequency), and at larger spatial scales in forests around the world (Seidl et al. 2014). This increasing trend has been observed not only in commercial forests but also in large areas of intact and natural forests (Potterf et al. 2022). In connection with climate change and greater temperature extremes, it can be expected that these changes in environmental conditions will result in a significant die-off of stands in the future and, thus, a limitation of ecosystem services (Grossiord et al. 2014).

Biodiversity is known to play an essential role in the functioning of ecosystems (Balvanera et al. 2006; Hector & Bagchi 2007), including forests. The positive effect of biodiversity is primarily determined by mechanical processes directly under the influence of species interactions. Through ecological processes, ecosystem performance increases, and resources become more available as they are shared between coexisting species. The potential availability of resources thus increases (Loreau et al. 2001). In addition to increased performance due to higher biodiversity, terrestrial ecosystems also become more resistant to biotic stressors, which, in Central Europe, is mainly bark beetles (Zhu et al. 2008; Jactel & Brockerhoff 2007; Grossiord et al. 2014). Stress and drought also represent a significant abiotic stressor of forest ecosystems (Rennenberg et al. 2009). Such conditions can cause the death of not only individual trees but also entire stands (Griess & Knoke 2011). The resistance and resilience of the trees themselves to stress depends, among other factors, on the tree species, the competitive status of the tree in the stand (Zang et al. 2012), its age and size (Lloret et al. 2011), as well as from the environmental conditions of the site (Pretzch & Dieler 2011). Findings from research focused on the resistance and resilience of forests indicates that mixed and species-rich forest ecosystems have an advantage over species-poor forests, as their resistance and resilience are higher due to overall biodiversity (Pretzsch et al. 2013; Ding et al. 2017).

The results presented here tell the story of long-term interactions between biodiversity and forest dynamics and biodiversity patterning in spruce primary forests, and they brought new insight into this topic. Aside from this knowledge, we hope that our results help to understand the importance of the conservation of all existing primary forests and help to stop the rapid ongoing biodiversity loss.

# 2 Literature review

## 2.1 Primary forests - definition, area, distribution, and protection

There are a large number of definitions of the word primary forest, and they are often ambiguous. Many of us imagine a forest with an ancient appearance, majestic trees, lots of natural regeneration, and deadwood covered with moss or fungi (Wirth et al. 2009). In reality, however, it is only a late successional stage typical for temperate forests. Most definitions today use multiple criteria, and these can be divided into three basic groups. The first emphasizes structural and compositional properties, the second points to the gradual processes that led to the current stage, and the third summarizes criteria related to the activity of biochemical processes (Messier & Kneeshaw 1999; Kimmins 2003). In primary forests, the structure of the forest is conditioned by natural processes. However, a strict understanding of the primary forest as an ecosystem without human influence would lead us to the conclusion that almost no primary forests exist anymore (Jasík & Polák 2011). Mikoláš et al. (2019) defined a primary forest as an unmanaged forest with a natural species composition, a wide age range, a high proportion of old trees, a high diversity of horizontal and vertical structures, and a considerable amount and diversity of standing and lying dead trees in various decay stages.

For the purposes of the "Protection of Slovakia's primeval forests" project, the following definition was created: "Relatively untouched natural forest (signs of former human activity are not recorded, or are difficult to identify and little evident) with climax (original) tree composition, with the occurrence of typical species of the ecosystem, preserved natural age, vertical, horizontal and spatial structure, with an adequate presence of dead wood (standing and lying) in various stages of decomposition and with the presence of individuals of woody plants whose age is close to the physical age. The successional stage of the forest ecosystem is also considered a part of the primeval forest, which arose naturally (without human influence) after natural disturbances on the area of the primeval forest (which was not interfered with and is assumed to be left to natural development) (Križová 2011). In the scientific literature, there are several terms for the primeval forest. The most frequently used terms are "primeval forest", "virgin forest", "natural forest" or "old-growth forest". However, especially in the case of "old-growth forest", we can meet some authors with the designation for any forest that has been without human intervention for a long time and has reached an older age.

Primary forests are naturally regenerated forests made up of native species, showing minimal signs of past human activity. In these forests, ecological processes, including natural disturbances, occur dynamically with minimal human interference (Barton & Keeton 2018).

Globally, roughly one-third of all forests are classified as primary, with most found in remote tropical, boreal, or mountainous regions (Potapov et al. 2017). Primary forests still cover approximately 1.4 Mha of the European surface (Figure 1), although their area is rapidly decreasing, they are becoming fragmented (Sabatini et al. 2018), and due to omnipresent historical land use, these ecosystems are incredibly rare in Europe (Parmasto 2001; Sabatini et al. 2020). Since ancient times, these forests have been used for the acquisition of pastures through deforestation, fuel wood, and timber extraction. The result of this land use change is a landscape characterized by non-natural forests intensively managed by man (Veen et al. 2010).

Within this landscape, the Carpathian Mountains harbour the largest and most important tracts of remaining European temperate primary forests (Grodzińska et al. 2004; Kuemmerle et al. 2010; Veen et al. 2010; Sabatini et al. 2018; Mikoláš et al. 2019), around 80% of the European Union’s temperate primary forests (Luick et al. 2021). The remaining primary forests are distributed mainly on sites with higher elevations, steeper slopes, rugged terrain, and greater distances from roads and settlements (Mikoláš et al. 2019). Nonetheless, many of Europe’s primary forests remain unknown or unprotected (Sabatini et al. 2018; Sabatini et al. 2020), especially in the Carpathian region, and they are threatened by logging (Mikoláš et al. 2019; Mikoláš et al. 2023). The greatest portion of temperate European primary forests are situated in the Romanian part of the Carpathian Mountains. Based on the latest inventory, there are potentially more than 525,000 ha of old-growth and primary forests (Schickhofer & Schwarz 2019). There is no consensus on the total area of primary forests, and e.g. WWF (2016) estimates only 200,000 ha. The reality is that Romania officially protected only around 70,000 ha of these valuable ecosystems through the “Romanian National Catalogue of Virgin and Quasi-virgin Forests.”

Based on the latest precise mapping, the area of primary forests in Slovakia (our study area) is 10,583 ha, which represents 0.47% of the total Slovakian forest cover (Mikoláš et al. 2019). Thanks to the creation of the nature reserve “Primary Forests of Slovakia” in December 2021, 94.5% of these ecosystems are strictly protected.

Where primary forests remain, the top priority for conservation should be to protect a sufficiently large area. However, there is no clear agreement on the necessary amount of primary forest that needs to be conserved to ensure biodiversity (Visconti et al. 2019). Where protection is in place, it must be stringent enough to prevent primary forest degradation. Many protected areas permit human activities (e.g., salvage logging) that can disrupt natural forest dynamics, such as recovery from natural disturbances and the preservation of biological legacies (Thorn et al. 2018). To enable natural development, such activities should be prohibited in primary forests. Identifying areas that need stricter protection is thus a critical priority for the long-term conservation of primary forests (Sabatini et al. 2020).

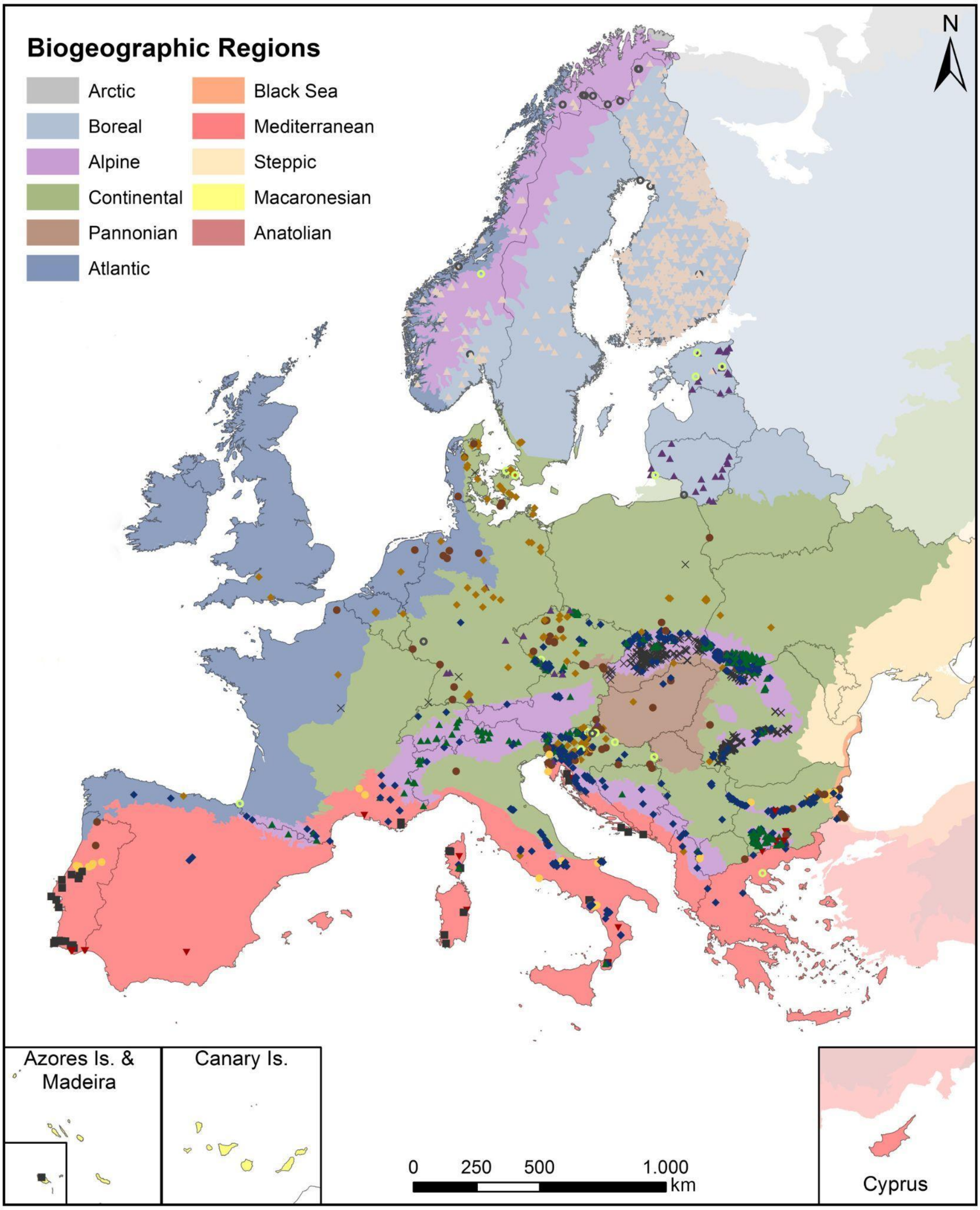


**Figure 1**. Spatial distribution of primary forest patches in Europe (Sabatini et al. 2018, edited).

## 2.2 Fragmentation and habitat loss

Habitat connectivity plays a key role in the regional viability of many taxonomic groups, while the effect of destruction and degradation of natural ecosystems on biodiversity can be considered the leading cause of ongoing worldwide biodiversity loss (e.g. Pimm et al. 2014; Maxwell et al. 2016; Rybicki et al. 2020; Semper-Pascual et al. 2019; Thorn et al. 2020). The study published by Haddad et al. (2015) showed that between the years 1980-2015, habitat loss and fragmentation reduced biodiversity by 13 to 75% across five continents. Currently, more than 70% of the world's remaining forests are now in close proximity to modified environments. Fragmentation and habitat loss reduce the availability of suitable habitats and resources for biota, create dispersion barriers, and influence the size and spatial configuration of habitat areas (Fahrig 1997). The vulnerability of some species to alteration of the environment is related to life history and ecological traits (Thornton et al. 2011). Therefore, it is expected that some evolutionary lineages are more sensitive and vulnerable than others to fragmentation and habitat loss.

Habitat loss has a strong negative impact on the species richness of forest-dwelling taxa (Fahrig 2013; Püttker et al. 2020), and the result is species extinction (Brooks et al. 2002). On the other hand, the influence of habitat fragmentation on biodiversity is not so clear.

A significant consequence of landscape modification is that, beyond reductions in habitat area, large expanses of natural habitats have been fragmented into smaller patches within a matrix of human-altered land use (Haddad et al. 2015). It is well established that habitat loss diminishes species diversity by decreasing the available area for species to inhabit (Keil et al. 2015). However, the impact of habitat fragmentation—distinct from habitat loss—remains less clear. Habitat fragmentation refers to the changes in spatial configuration of habitat, wherein remaining patches become smaller but more numerous, independent of habitat loss itself (Fahrig 2003). While the conservation literature has generally indicated that fragmentation is detrimental to biodiversity (Eigenbrod et al. 2017), there is ongoing debate regarding whether the effects of fragmentation on biodiversity are uniformly negative (Fletcher et al. 2018a) or if they can be insignificant or even positive (Fahrig 2017; Fahrig et al. 2019). In practice, fragmentation and habitat loss are closely interconnected (Fletcher et al. 2018). Nevertheless, distinguishing the impacts of fragmentation from those of habitat loss and determining under what conditions fragmentation influences species diversity are crucial for conservation strategies. This includes decisions on habitat network restoration (Isaac et al. 2018) and land management choices, such as whether to prioritize the conservation of multiple small patches versus fewer large ones (Tulloch et al. 2016), or to permit activities that might reduce habitat loss but increase fragmentation (Miller-Rushing et al. 2019). While there is speculation about the potential positive or negative effects of habitat fragmentation on biodiversity, these mechanisms need further theoretical exploration and empirical testing.

For instance, understanding how habitat fragmentation's positive and negative effects on biodiversity are influenced by species characteristics—such as ecological specializations and habitat affiliations—can inform landscape management strategies. It is commonly assumed that specialist species and those closely linked to the habitat undergoing fragmentation will experience adverse effects due to fragmentation (Halstead et al. 2019). Conversely, if fragmentation is reported to positively impact biodiversity, one explanation is that generalist species' richness and abundance may increase with fragmentation, leading to enhanced overall diversity (Hu et al. 2012). However, a review by Fahrig (2017) found that fragmentation positively affected the landscape-level (gamma) diversity of specialist, rare, or threatened species in 97% of the studies reviewed. This might be because fragmentation can segregate competing species among different habitat patches within a landscape (Ramiadantsoa et al. 2018). Nonetheless, this hypothesis needs further clarification, particularly regarding the distinction between specialists and generalists. Specialists and generalists are typically defined by their association with specific habitats, but being a generalist does not imply a lack of habitat preferences (Da Silveira et al. 2016). Research by Chetcuti et al. (2019) on beetle species revealed that most species had positive associations with multiple habitats, with only a few exhibiting substantial habitat restrictions. It is also frequently assumed that specialists are more competitive in their preferred habitats compared to generalists, while generalists tend to be more competitive across a broader range of habitats (Marvier et al. 2004). Specialists may outperform generalists in their optimal habitats but may be less competitive than generalists in other habitats, even if they share habitat preferences within a landscape.

Another challenge is linking patch-scale effects to landscape-scale impacts of fragmentation. Long-term manipulation experiments typically demonstrate that patch attributes associated with fragmentation (e.g., reduced patch size) decrease biodiversity at the patch scale, i.e., alpha-diversity (Haddad et al. 2015). However, mechanisms identified at the patch scale may sometimes translate to negative effects on biodiversity at the landscape scale (Fahrig 2017). Indeed, at the landscape scale, which includes multiple habitat patches, studies often report either neutral or positive responses of biodiversity (gamma-diversity) to fragmentation (Fahrig 2017). In contrast, the species-area relationship predicts that the negative impacts of fragmentation should reduce gamma-diversity compared to predictions based solely on the species-area relationship (Hanski et al. 2013). Yet, patch-scale studies and models describing the species-fragmented area relationship often overlook mechanisms that could lead to positive fragmentation effects, such as increased beta-diversity due to competitive release and enhanced habitat diversity (Fahrig et al. 2019; Rybicki et al. 2019). These mechanisms might increase beta-diversity, potentially leading to overall increases in gamma-diversity with fragmentation.

Separating the effects of habitat loss from those of fragmentation can be challenging, as highly fragmented habitats often consist of smaller patches (Fahrig 2003). Conducting landscape-scale manipulative studies is generally difficult, and controlling for habitat area is often impractical, leading to the conflation of fragmentation effects with habitat loss (Betts et al. 2019). Fahrig (2017), in the review, states that 76% of scientific papers (n=118) declared the positive effect of habitat fragmentation irrespective of how the authors controlled for habitat amount, the measure of fragmentation, the taxonomic group, the type of response variable or the degree of specialization or conservation status of the species or species group. The main assumptions of the positive effect of habitat fragmentation on biodiversity are mainly higher habitat heterogeneity with more available resources compared with adjacent and more homogenous landscapes (Öckinger et al. 2012), increased functional connectivity, and positive edge effects (Fahrig 2017). But it should be noted that species with differing life history strategies are differentially affected by habitat fragmentation (Ewers & Didham 2006), and some rare forest specialists, such as Western Capercaillie (*Tetrao urogallus*), are strongly negatively affected by habitat fragmentation (Virkkala 1987; Mikoláš et al. 2017; Klinga et al. 2019).

Habitat amount hypothesis (Fahrig 2013) claims that species richness depends on the total amount of habitat in a landscape. On the contrary, lots of empirical studies report contrasting patterns: some find positive and some negative effects of fragmentation on species richness. Explanation of these opposite results lies in the understanding of the complex effect of fragmentation and habitat loss on species diversity (Rybicki et al. 2020). In other words, it is necessary to observe this complex effect at a landscape scale. While for the landscape with a high area of suitable habitat may habitat fragmentation represents more or less positive effect through an increase of heterogeneity, for the landscape where the proportion of suitable habitat decreases, area and isolation effects start influencing the population size and species diversity (Fahrig 2013; Torrenta et al. 2018; Rybicki et al. 2020).

## 2.3 Natural disturbances

Natural disturbances represent key drivers in forest ecosystem dynamics (Franklin et al. 2002; Stephens et al. 2013; Seidl et al. 2014). These events play a fundamental role in shaping forest composition and structure through disturbance legacies. It is precisely the structure that plays a critical role in the whole ecosystem functioning, including habitat provisioning for biodiversity, and they are essential for the long-term health of forest ecosystems (Turner 2010). The European bark beetle (*Ips typographus*) can be considered one of the key factors determining the dynamics of European spruce-dominated forests (Temperli et al. 2013) and, together with wind, are the major disturbance agents in the Carpathians (Holeksa et al. 2017). The intensity and temporal scale of disturbances caused by bark beetle are influenced by direct and indirect interactions between insect and climate conditions (Jönsson et al. 2009; Jactel et al. 2012), wind events (Schroeder & Lindelöw 2002), and by forest sensitivity to disturbances (Netherer & Nopp-Mayr 2005). Forests in Central European conditions are dynamic ecosystems under the influence of natural disturbances with different frequencies and at different spatial scales. Disturbances create the mosaic landscape structure (Korpeľ 1995; Svoboda et al. 2014), prevent forests from remaining in the mature successional stage - climax (Ulanova 2000; Woods 2007), and we can consider them as a main driver of changes at the ecosystem level (Nagel et al. 2013). Based on the percentual removal of canopy openness, natural disturbances are classified into three classes of severity (Frelich 2002):

1) Low-severity disturbances: only a small part of the understory and overstory is affected by mortality. Smaller canopy gaps and a few larger dead trees are the result of its influence.
2) Moderate-severity disturbances: most of the overstory or understory trees are killed, but a significant number of mature trees and seedlings survive.
3) High-severity disturbances: most of the understory and overstory tree layers are killed.

Disturbances are complex mechanisms that form forest structure through mainly moderate, only occasionally high severity and large-scale events. Moderate-severity and high-severity disturbances occur mainly in conifer forests (Čada et al. 2013; Trotsiuk et al. 2014). Western Carpathian's spruce-dominated forests are characterized by a wide spectrum of disturbances with a predominance of moderate-severity events called "mixed-severity disturbance regime" (Svoboda et al. 2014; Janda et al. 2017; Meigs et al. 2017; Schurman et al. 2018), but there is also occurrence of high-severity disturbances (Figure 2) with short turnover time (Čada et al. 2016). In general, spruce-dominated forests are more prone to windstorms than mountain beech and beech-fir mixed forests. There are some exceptions to the occurrences of high-severity disturbances in mixed-beech forests (Nagel et al. 2017), usually caused by the synergy of strong wind and hail or strong wind and heavy snow.

**Figure 2.** Example of high-severity disturbance event in the spruce stand Zadné Meďodoly, High Tatras, Slovakia (photo Matej Ferenčík).

Despite the fact that disturbances are a key factor for creating a heterogeneous structure of forest (Turner et al. 1993), not only large-scale disturbances are important. Huge importance also have small-scale disturbances when several (3-5 or more) trees die and create patches (gaps). These patches are important refuges for light-loving species, which can also survive in the mosaic structure in the mature successional stage (Picket & White 1985). Creating patches increases forest heterogeneity, which creates conditions for a wide range of taxonomic groups with different life strategies.

Historical evidence shows that disturbances are an integral part of the forest ecosystems. Between 1950 and 2000, disturbances in European forests damaged an annual average of 35 million m³ of wood, though yearly variation was significant. Storms accounted for 53% of the total damage, fires for 16%, snow for 3%, and other abiotic factors for 5%. Biotic factors were responsible for 16% of the damage, with bark beetles causing half of this.

For 7% of the damage, no specific cause was identified, or multiple causes were involved. The 35 million m³ of damaged wood represents approximately 8.1% of the total fellings in Europe and about 0.15% of the total volume of growing stock (Schelhaas et al. 2003).

In recent decades, European forests have faced mounting pressure from natural disturbances, and most types of damage appear to be increasing. A database of >170,000 records of ground-based natural disturbance observations in European forests from 1950 to 2019 confirms a significant increase in forest disturbance in 34 European countries, causing an average of 43.8 million m3 of disturbed timber volume per year over the 70-year study period. In the last 20 years, disturbances, on average, accounted for 16% of the mean annual harvest in Europe. Wind was the most important disturbance agent over the study period (46% of total damage), followed by fire (24%) and bark beetles (17%), while bark beetle disturbance doubled its share of the total damage in the last 20 years (Patacca et al. 2023). The likely reasons for increased disturbance-related damage include changes in forest management and resulting changes in forest conditions (Schelhaas et al. 2003).

Forest disturbances can profoundly impact ecosystem services (e.g., climate change mitigation), affect regional forest resource provisioning, and consequently disrupt long-term management planning objectives and timber markets (Thom & Seidl 2016). For that reason, adaptation to changing disturbance regimes needs to be reflected in future forest management strategies and policy debates (Peltzer et al. 2009; Jactel et al. 2012; Patacca et al. 2023). Furthermore, a coherent and homogeneous monitoring system of natural disturbances is urgently needed in Europe to better observe and respond to the ongoing changes in forest disturbance regimes.

## 2.4 Forest biodiversity

Forest ecosystems are essential to human well-being, providing multiple ecosystem services and housing over 80 % of the terrestrial biodiversity (Aerts & Honnay 2011; Brockerhoff et al. 2017). Therefore, preserving forest biota is crucial for global biodiversity conservation. The conservation of biodiversity has become a major concern for resource managers and conservationists worldwide, and it is one of the foundation principles of ecologically sustainable forestry (Lindenmayer & Franklin 2013). Multi-scale habitat patchiness, which is in Central European primary forests created by natural disturbances, helps to increase the species richness and incidence of red-listed species of different taxonomic groups (Hilmers et al. 2018) through disturbance legacies such as quantity and variability (decay stages) of standing and lying deadwood, and canopy openness. Although different taxonomic groups have different and specific ecological requirements.

### 2.4.1 Deadwood-inhabiting fungi

Deadwood-inhabiting fungi are a very diverse and functionally important component of forest biodiversity and one of the main groups of organisms decomposing wood on dead or living trees worldwide. Many centuries of forest use have shaped the temperate forests in Central Europe, and natural or undisturbed, near-natural, and primary forests have become very rare (Sabatini et al. 2018). Fungi are important decomposition agents and are associated with fluxes of carbon and nutrients (Boddy et al. 2008; Stokland et al. 2012; Bradford et al. 2014; Krah et al. 2018a). A plentitude of deadwood substrates - an important disturbance legacy - and their variability in primary forests represent suitable conditions for species-rich assemblages of lignicolous fungi that are particularly sensitive to forest management (Penttilä et al. 2004; Hottola et al. 2009; Abrego & Salcedo 2013; Komonen & Müller 2018; Tomao et al. 2020). Natural forests consist of a mixture of different tree species, tree sizes, stand structures, and mortality agents. Together with higher deadwood volumes, it explains why natural forests are much more species-rich in saproxylic species than managed forests (Jonsson et al. 2005; Stokland et al. 2012). Due to specific habitat demands, fungi can be used as indicators of forest naturalness (Christensen et al. 2004; Stokland et al. 2012).

In mixed-species forests, the variability in stem quality traits can enhance fungal species diversity, as different tree species provide a variety of habitats for wood-inhabiting fungi (Brockerhoff et al. 2017). Consequently, mixed forests often exhibit higher fungal diversity than monocultures, promoting overall forest biodiversity. Fungal diversity is determined by site conditions, canopy closure, age structure, microclimatic conditions and, importantly, by the amount and diversity (e.g. log size, decay stage, tree species) of deadwood (Heilmann-Clausen & Christensen 2003; Seibold et al. 2016; Pouska et al. 2017; Hilmers et al. 2018; Tomao et al. 2020), all of which are significantly driven by natural disturbances (Meigs et al. 2017). Various abiotic and biotic factors affect wood-inhabiting fungi diversity, shaping fungal community structures. A larger contact area between wood and soil enhances fungal access to the logs (Rajala et al. 2012), while climatic factors like relatively high temperature and humidity facilitate fungal growth (Purahong et al. 2017). The assemblages of saproxylic fungi are influenced by site location and history, soil fertility (Wallander 1995), microclimates (Müller et al. 2020), and the surrounding vegetation cover and composition (Kubartová et al.

2012). The stem traits of the tree species play a crucial role, as they leave their legacy in the properties of dead wood. Physical defense traits such as a thick bark reduce log accessibility to fungi (Lee et al. 2019), while chemical defense traits such as phenols inhibit fungal growth (Kahl et al. 2017).

Conversely, high nutritional stem quality can stimulate fungal growth. In general, species that invest heavily in physical and chemical defense and exhibit slow growth are considered resource-conservative, while species with less defense investment that promotes rapid photo-assimilation, transport, and growth are seen as resource-acquisitive (Poorter et al. 2018). The heterogeneous bark structure creates diverse microhabitats with higher sugar and nutrient levels compared to wood tissues. Bark defences and protects logs from fungal attacks, influencing fungal communities in the bark and colonizing the wood beneath (Dossa et al. 2018). Thus, understanding fungal colonization on logs requires consideration of multiple stem traits, including wood and bark characteristics.

Fungal community assembly on dead wood is determined not only by initial stem traits but also by decay stages (Ruokolainen et al. 2018), as well as dispersal limitation. The identity of the initial colonizing fungi can influence their competition and inhibit with other fungal species or facilitate succession through substrate modification (Hiscox et al. 2015). As wood decays, substrate conditions change over time (Heilmann-Clausen 2001). There is a distinct succession where (semi)parasitic species colonize first, followed by polypores and agarics (Stokland et al. 2012). Early colonizers may disappear in later decay stages. At the same time, species like *Armillaria cepistipes*, *Fomitopsis pinicola*, and *Ganoderma lipsiense* persist through different decay stages due to their diverse enzyme complexes (Ruokolainen et al. 2018).

Fungal species richness reaches its maximum during succession at intermediate stages of decay (Renvall 1995). Initially, a variety of substrates is accessible to pioneer species, but as decay progresses, the substrate becomes more uniform, leading to intense interspecific competition (Huston & DeAngelis 1994) and a consequent reduction in species diversity. Other studies focusing on spruce and beech logs found that fungal richness increases and peaks in the most decayed logs (Fukasawa et al. 2009; Rajala et al. 2012), likely due to colonization by soil fungi that start to colonize the heavily decayed logs. The variation of fungal richness throughout the decay process remains a topic of debate, as successional trajectories can vary depending on the three species. Therefore, more tree species should be studied to develop broader generalizations on successional patterns of saproxylic fungal communities.

**Figure 3.** Primary colonizer *Fomitopsis pinicola* in disturbed spruce stand Piľsko, Oravské Beskydy, Slovakia (photo Matej Ferenčík).

From some studies, it becomes evident that even relatively high volumes of deadwood are not able to guarantee a high diversity of fungi (Hofmeister et al. 2015; Müller et al. 2020) unless there is sufficient variability in the size of deadwood, including large objects. In principle, large logs are accompanied by fine woody debris (Nordén et al. 2004; Küffer et al. 2008), but the variability of decomposition stages generally increases with the amount of deadwood (Küffer et al. 2008; Nordén et al. 2013). Wood in the latest decay stages has exclusive importance in maintaining some extremely rare fungal species (Jonsson et al. 2005; Abrego et al. 2014; Halme et al. 2013). Specifically, in the remnants of temperate primary forests in Central Europe, rare mycorrhizal fungi can colonize highly decayed deadwood (Holec & Kučera 2020). In general, natural disturbance legacies such as diversity of deadwood sizes and decomposition stages are positively related to fungal species richness, and with increasing management intensity, the diversity of the fungal community decreases (Tomao et al. 2020).

Within intact primary forests, natural processes generate temporal variation and spatial patchiness of resource supply, which in turn foster a high biodiversity potential. Distinctive features provisioned in naturally functioning forests include standing and downed deadwood, as well as large and old trees (Siitonen 2001; Schuck et al. 2004). The inherent complexity of these systems supports many deadwood-inhabiting fungi species with specialized, fine-scale habitat requirements. Different attributes of deadwood, such as size, volume, density, position (standing/lying), and decay stage, have been correlated with variation in the composition of lignicolous fungal communities and incidence of red-listed species (Ferenčík et al. 2022; Majdanová et al. 2023, Ferenčík et al. 2024).

### 2.4.2 Lichens

Lichens result from symbiotic interactions between the fungus and a phototroph. These organisms are prevalent across most terrestrial ecosystems and often are present as minor contributors. However, in certain forests, drylands, and tundra regions, they can constitute the majority of the ground layer biomass. Consequently, lichens dominate about 8% of the Earth's terrestrial surface. Despite their significant potential to influence ecosystem biogeochemistry, the impact of lichens on community dynamics and ecosystem functioning has been relatively understudied (Asplund & Wardle 2017).

Lichens are slow-growing, long-lived, and stress-tolerant, exhibiting a wide array of growth forms. They frequently dominate environments that are too nutrient-poor, too dry, or too cold to support a complete or permanent plant cover. Over 18000 lichen species exist globally, and at higher latitudes, the number of lichen species surpasses that of vascular plants (Nash 2008). Unlike plant-dominated communities, which primarily obtain nutrients from the soil or internal nutrient cycling, lichen-dominated ecosystems acquire a significant portion of their nutrients from external sources. This is because lichens have a lack roots and instead absorb considerable nutrient pools from wet and dry depositions originating outside the ecosystem. They accomplish this efficiently due to their large surface area relative to their biomass and the absence of cuticles and stomata on their surfaces, enhancing nutrient absorption. Moreover, lichens can accumulate nutrient concentrations far exceeding their physiological requirements. However, their ability to capture nutrients varies greatly depending on their specific characteristics. Certain lichen growth forms, particularly fruticose hair-like lichens (e.g. genus *Usnea*), are highly effective at capturing dew and fog, which often contain nutrient levels than rain (Nash 2008). Due to their nutrient uptake and accumulation capacity, lichens can store a substantial proportion of the total nutrients present in the ecosystem.

Because of their sensitivity to land-use and habitat changes, lichens serve as crucial environmental indicators in conservation planning. They reflect the cumulative effects of environmental changes through their current conservation status or trends in diversity, reproductive success, and abundance (Bartell 2006; Seaward 2008). Lichens also serve as indicators of forest ecosystem naturalness, where their species richness significantly correlates with the degree of forest naturalness as assessed by structural and historical features along the naturalness gradient (Czerepko et al. 2021). The primary causes of the decline in lichen species richness and the increase in threatened species are habitat degradation from human activities and air pollution (Boch et al. 2013). Between the 1950s and 1980s, certain regions of Europe experienced high levels of air pollution (e.g. Bege & Jakobsen 1998), particularly sulphur dioxide (SO2) deposition, which decreased bark pH and reduced regional lichen species pools (Gilbert 1992; Purvis 2010). Consequently, studying various regions is necessary to draw general conclusions about the effects of forest management on lichen diversity.

Temperate European forests have extensive histories of management, with forests free from human influence limited to remote or inaccessible regions (Parviainen et al. 2000). Hence, these forests are fragmented, and large areas are dominated by economically driven age-class forests. These forests consist of even-aged tree structures, typically resulting from clear-cutting or shelterwood logging. Recently, the extent of protected forest reserves in Europe has increased, mainly to conserve vulnerable and rare forest ecosystems and to create a network of reserves (Parviainen et al. 2000). However, nearly all of these forests have experienced varying degrees of intensive management in the past. Central European unmanaged forests are not comparable with natural forests in North America, Siberia, or some parts of Eastern and Northern Europe, which have remained largely untouched for centuries. The effectiveness of forest protection and various silvicultural systems in maintaining lichen diversity in temperate European forests remains poorly studied, calling for a comprehensive analysis.

Natural forest dynamics is crucial for the diversity and species composition of epiphytic and epixylic lichens. Dead-standing trees, as biological legacies of natural disturbances, enhance lichen species richness and the presence of threatened species, indicating better-growing conditions for both rare and common lichens during the early stages of post-disturbance recovery. However, high-severity disturbances negatively influence species richness. Both species richness and the number of old-growth specialists increase over time since disturbance, reflecting long-term uninterrupted succession (Langbehn et al. 2021). Lichen species richness also significantly increases with the openness of canopy (Gloor et al. 2024). This suggests that increased downed deadwood volume and dead tree basal area increased with the severity of disturbances, both positively influencing the species richness. However, maximum tree age and live tree diameter variability decrease with increasing disturbance severity (Janda et al. 2017).

**Figure 4.** *Lobaria pulmonaria* is a critically endangered lichen species in Slovakia (photo Matej Ferenčík).

Therefore, conservation of rare and endangered lichen species necessitates a deep understanding of their ecology (Scheidegger & Werth 2009). To stop ongoing lichen biodiversity loss, the main goal should be to establish large protected areas encompassing the full spectrum of successional stages. It is especially important to consider rare and threatened lichen species in conservation-oriented forest-management plans (Thor 1995; Gustafsson et al. 2004).

### 2.4.3 Saproxylic beetles

Saproxylic insects form a diverse, species-rich, and ecologically dominant group, reliant on dead wood and old trees. This group is particularly sensitive to forest management practices. Managed or secondary forests generally support fewer individuals, fewer species, and different community assemblages compared to old-growth or primary forests. Saproxylic species are among the most threatened taxa in many regions due to forest loss and intensive forestry practices (Seibold et al. 2015). Their sensitivity is a product of their association with a habitat that tends to diminish in managed forests.

Consequently, many saproxylic insects adapted to primary forest characteristics, such as abundant dead wood and overmature trees, may have become regionally extinct due to habitat loss. Remaining primary forests thus serve as refuges for these species, which cannot survive in managed forests due to their specific ecological requirements (Lachatt & Müller 2018). Additionally, many species have low dispersal abilities relative to human-induced habitat fragmentation, making breaks in habitat continuity particularly detrimental (Grove 2002). The importance of large logs for saproxylic beetles has been documented in several studies (e.g. Økland et al. 1996; Sverdrup-Thygeson 2001), where the local density of large logs significantly and positively predicted total species richness (Bouget et al. 2014). Beyond the quantitative impact of dead wood on bark beetle outbreaks and saproxylic diversity, the latter is enhanced by key dead-wood microhabitats such as large logs, snags, and sun-exposed coarse woody debris (Janssen et al. 2017). Besides large logs, deadwood diversity and canopy openness are crucial habitat features for higher species richness and the composition of beetle assemblages (Bouget et al. 2013).

In some cases, a high amount of deadwood increased species richness independent of the presence of large logs (Haeler et al. 2021). Characteristics of primary forests vital for saproxylic insects, distinguishing these forests significantly from managed ones, include the absence of habitat fragmentation, continuity, natural disturbance regimes, deadwood amount and quality, tree species composition, and the presence of habitat trees (Lachat & Müller 2018). These characteristics underscore the importance of primary forests for the conservation of saproxylic insects.

Dispersion is a critical trait of species necessary for maintaining gene flow between habitat patches. It also facilitates the colonization of new habitats, influencing population dynamics, extinction risk, and species distributions. Dispersal allows species to persist in changing environments. Saproxylic insects, which rely on deadwood during some stage of their life cycle, must offset local extinctions due to deadwood decay by colonizing new deadwood structures both locally and across the landscape. Their dispersal strategies are driven by factors such as the spatial and temporal variability of deadwood structures, feeding strategy, resource competition, kin competition, and inbreeding avoidance. The significance of each factor varies among species depending on their life history and environmental interactions, such as the longevity of the deadwood habitat used. Species inhabiting more transient habitats, like fresh deadwood, exhibit better dispersal abilities than those in more persistent habitats, like tree hollows, which may last for several decades. Understanding dispersal abilities is crucial for improving conservation strategies and forest management, particularly regarding the spatial distribution of suitable habitats to enhance species persistence (Feldhaar & Schauer 2018).

Similar to other investigated taxonomic groups in our study, saproxylic beetles are strongly linked to natural disturbances. However, our knowledge of how disturbance intensity alters the functional and phylogenetic diversity of saproxylic beetles remains incomplete. Various aspects of beetle communities, including abundance, taxonomic, phylogenetic, and functional diversity, respond differently to disturbance regime components. Past disturbance frequency is the most significant component affecting saproxylic beetle communities and habitats through multiple temporal and spatial pathways. The quantity of deadwood and its diameter positively influence saproxylic beetle abundance and functional diversity, while phylogenetic diversity is positively influenced by canopy openness. Current beetle diversity is dynamic, and the importance of various drivers may change during further successional development. Only forest landscapes large enough to encompass the full range of temporal and spatial disturbance patterns and post-disturbance development will support long-term species coexistence and their associated ecosystem functions (Kozák et al. 2021). Therefore, forest continuity and stand maturity may have additive effects on biodiversity. Understanding their relative influence on biodiversity is crucial for the conservation of a wide range of forest-dwelling taxa (Hilmers et al. 2018), including saproxylic fungi (Majdanová et al. 2023) and saproxylic beetles (Janssen et al. 2017). Stand maturity, related to deadwood resources, induces strong environmental filtering and shapes functional trait composition (Janssen et al. 2017).

Regardless of forest continuity, species preferring large wood in advanced stages of decay were more abundant in overmature stands. This finding contrasts with several studies from temperate forests in Europe (e.g., Winter et al. 2015; Lettenmaier et al. 2022; Perlík et al. 2023; Seibold et al. 2023). Additionally, overmature stands promoted the co-occurrence of various saproxylic beetles with differing resource requirements. The interaction between forest continuity and stand maturity induced both taxonomic and functional changes in communities. Compared to other forest types, overmature stands in ancient forests supported assemblages with more characteristic species, larger average body sizes, and a preference for large deadwood pieces. Furthermore, these forests exhibited a greater diversity of body sizes (Janssen et al. 2017).

### 2.4.4 Birds

Birds belong to taxonomic groups frequently used in conservation planning due to their easy observability. They are crucial elements of ecosystems, participating in significant processes such as decomposition, pollination, and seed dispersal (Sekercioglu et al. 2004). Due to their relatively large spatial requirements (Whelan et al. 2015), extensive forest areas are necessary to maintain viable bird populations. Therefore, safeguarding bird habitats is an effective strategy for comprehensive ecosystem and biodiversity management (Thom & Keeton 2020). Birds are sensitive to changes in forest structure, which affects various aspects of their ecology, including food availability, predation risk, and breeding site availability (Hanzelka & Reif 2016). Studying bird assemblages is complex, and to this end, umbrella, flagship, and keystone species are often employed as surrogate species. However, it is currently impossible to determine in advance where a given surrogate approach will be effective. Addressing this issue requires substantial further research. Surrogate species should be used critically to avoid mistakes in resource and biodiversity management (Lindenmayer & Westgate 2020).

A significant conservation challenge in mosaic landscapes is to understand how trait-specific responses to habitat edges influence bird communities, including potential cascading effects on bird functions that provide ecosystem services, such as pest control in forests. Positive responses to forest edges were observed in several forest bird species with unfavorable conservation status. These species were generally insectivores, understorey gleaners, cavity nesters, and long-distance migrants, all displaying higher abundance at forest edges compared to forest interiors or adjacent open habitats. Additionally, negative edge effects were noted in some forest specialist birds and most open-habitat birds, which showed increasing densities from edges to interior habitats (Terraube et al. 2016). Bird communities appear to respond to a complex set of forest habitat attributes, including growth stage and the structure and composition of understorey vegetation (Hewson et al. 2011). Consequently, the higher abundance of breeding birds at forest edges could be linked to differences in small-scale vegetation composition and structure affecting foraging efficiency (Van Wilgenburg et al. 2001). Regional variation in trait responses to landscape heterogeneity, driven by past environmental filtering and broad-scale climates, may also lead to differential community responses (Spake et al. 2020).

**Figure 5.** *Tetrao urogallus* is a critically endangered umbrella species in many European countries (photo Matej Ferenčík).

Relationships between bird assemblages and forest structure are well documented in scientific literature. Early successional species associated with more open habitats are positively influenced by disturbance-related structures (i.e., deadwood-related variables, canopy openness), though some species respond negatively. Meanwhile, overall abundance, species richness, and Shannon diversity of the bird assemblage remain unchanged under varying disturbance histories. This supports the view of primary spruce forests as highly dynamic ecosystems, hosting bird species at all successional stages despite significant structural changes and shifting patch mosaics over time due to natural disturbances (Kameniar et al. 2021). While no differences were found regarding disturbance regimes between forest types, significant differences were observed in forest structure and bird assemblages. Spruce-dominated forests exhibited significantly higher cavity densities and greater canopy openness, whereas beech-dominated forests had higher tree species richness and more intense regeneration. Bird assemblages showed higher species richness in beech forests but lower total abundance. Most bird species present in both forest types were more numerous in spruce-dominated forests, yet more species were found exclusively in beech forests. Additionally, some spruce-preferring species were found in naturally disturbed patches within beech forests. Although natural disturbances are crucial drivers of primary forest structures, the differences in bird assemblages in the explored primary forest types were largely independent of disturbance regimes (Kameniar et al. 2023). This can be explained by birds' high dispersal abilities and tolerance of natural disturbances.

### 2.4.5 Impact of natural disturbances on biodiversity

Understanding how biodiversity responds to forest disturbances is essential for preserving ecosystem integrity and key ecological functions (Bowd et al. 2021). Natural disturbances have a profound impact on biodiversity and can induce significant changes in forest communities (Lindenmayer et al. 2019). The frequency, extent, intensity, and severity of natural disturbances-such as wildfires, windstorms, and insect outbreaks are increasing globally due to land-use changes and climate change (Seidl et al. 2017). This trend is expected to continue, with forest disturbance regimes intensifying further in many regions as climate change progresses over the coming decades.

These evolving conditions pose a growing challenge to the primary goals of forest ecosystem management: sustainably providing ecosystem services to society and preserving forest biodiversity. The impact of natural disturbances on biodiversity remains unclear in the context of accelerating environmental changes. While disturbances generally have a negative impact on ecosystem services such as supporting, provisioning, regulating, and cultural services-indicators of biodiversity, including species richness, habitat quality, and diversity indices, are often positively influenced by disturbances (Thom & Seidl 2016). This phenomenon, known as the "disturbance paradox," illustrates that disturbances can jeopardize ecosystem services while simultaneously supporting biodiversity.

The increasing volume of research underscores the significance of disturbance impacts on forest ecosystems and lays the groundwork for a comprehensive global synthesis of these effects. The rising number of publications likely reflects the scientific community's response to the heightened frequency of disturbances observed in recent decades (Westerling et al. 2006; Seidl et al. 2014), indicating a deeper understanding of disturbance processes. Given the anticipated intensification of natural disturbance regimes due to climate change, it is likely that biodiversity will generally benefit from these changes. However, the sustainable provision of ecosystem services may face increased pressure. This underscores the need to emphasize disturbance risk and resilience in future ecosystem management strategies.

## 2.5 Deadwood in forest ecosystems

Deadwood serves as a vital source of life, offering habitat and substrate for a diverse array of organisms, including bacteria, fungi, plants, insects, and mammals (Stokland et al. 2012). It is one of the typical features of primary forests, while natural disturbances increase its amount and variability. (Lindenmayer et al. 2012). Importance of deadwood for the carbon cycle (Lombardi et al. 2008; Woodall & Liknes 2008), nutrient cycle (Paletto et al. 2014; Yuan et al. 2017), protection against erosion (Stevens et al. 1997), or as a habitat provisioning for biodiversity (e.g. Ódor & Standovár 2001; Lachat et al. 2013; Hofmeister et al. 2016; Jaroszewicz et al. 2021) is well documented in scientific literature. Deadwood plays a critical role in the maintenance of biodiversity and complex trophic chains, influencing natural tree regeneration and soil development (Harmon et al. 1986). Its functions in forests can be categorized into four interrelated areas (Parisi et al. 2018):

(1) Enhancing the tree productivity
(2) Providing habitats and structures to maintain and increase the biological diversity
(3) Reducing hydrological risk on steep slopes by controlling water run-off and stream flows
(4) Storing carbon over the medium-term perspective.

The importance of these functions varies across regions, influenced by types of natural disturbances, the intensity and type of silvicultural activities, and the moisture regime (Seibold et al. 2015).

All forest-dwelling taxa interact with deadwood to some extent, but saproxylic organisms, particularly fungi and beetles, depend heavily on woody resources to complete their life cycles. Biodiversity associated with deadwood alone accounts for about 30% of a forest's total biodiversity and can reach up to 50% in certain groups, such as Coleoptera. In Europe, approximately 1,500 fungi species and 4,000 Coleoptera species rely on deadwood (Stokland et al. 2012). The presence and continuity of deadwood are closely linked to local conditions and natural tree mortality caused by disturbances like fires, windstorms, and beetle outbreaks. Generally, natural and unmanaged forests, where wood harvesting is limited or absent, have significantly higher amounts of deadwood. These ecosystems are often found in mountainous and remote areas where human activities have been abandoned due to shifting cultural and economic interests (Palombo et al. 2013). Studying deadwood production and decomposition dynamics in these ecosystems can enhance our understanding of the potential impacts of global change on forest structure and related ecosystem services.

**Figure 6.** Quantity of deadwood 12 years after high severity disturbance event in the stand Piľsko, Oravské Beskydy, Slovakia (photo Matej Ferenčík).

Deadwood recycling is a lengthy process, taking hundreds of years and comprising three main phases (Speight 1989). In the initial colonization phase, saproxylic organisms, often beetles associated with fungi, invade the still-hard wood. During the decomposition phase, primary and secondary saproxylic organisms gradually consume the material partially processed by the colonizers. In the final humification phase, saproxylic organisms are gradually replaced by scavenging organisms that incorporate wood residues into the soil. The amount and quality of deadwood provide insights into the intensity of past anthropogenic and natural disturbances and the conditions for deadwood accumulation in the future (Woodall & Nagel 2006). In managed forests, the quantity of deadwood ranges from 2% to 30% of that in unmanaged forests (Fridman & Walheim 2000). Therefore, site-specific conditions affecting deadwood accumulation and degradation are considered important structural indicators of naturalness. The presence of large amounts of organic matter in various stages of decay creates numerous ecological niches. However, shorter harvesting rotations in modern forestry have reduced the quantity, variety, and age distribution of deadwood, which is crucial for many saproxylic species (Hunter 1990). Highly decayed deadwood is particularly scarce in managed forests, which may contribute to the absence of many rare macrofungal, beetle, and lichen communities (Lonsdale et al. 2007; Vítková et al. 2018). Recently, conservation-oriented silviculture has begun exploring the retention of suitable woody debris to promote biodiversity in forests.

Most studies on saproxylic organisms have primarily concentrated on coarse woody debris (CWD) due to its frequent removal by forest management practices (Siitonen 2001) and practical considerations related to fruit body surveys (Juutilainen et al. 2011). However, a thorough analysis of fungal richness and community diversity should also encompass fine woody debris (Blaser et al. 2013). Small deadwood pieces have a higher surface-to-volume ratio, which facilitates fungal colonization (Heilmann-Clausen & Christensen 2004). Conversely, larger-diameter debris persists longer on the forest floor due to slower decay rates, allowing for the coexistence and succession of a greater number of species with varying ecological requirements. Additionally, larger and older logs may indicate a longer infection history of specialized heart-rot pathogens that inhabit living sapwood (Ódor et al. 2006). Furthermore, both colonization and extinction patterns are influenced by deadwood size; local extinction rates are higher on small-diameter logs compared to larger ones (Jönsson et al. 2008). Different species exhibit varied preferences for wood dimensions. For example, common species show little preference for specific wood sizes (Lindhe et al. 2004), while some threatened or endangered species are more frequently found on larger substrates typical of old-growth forests. Generally, species dependent on stable microclimatic conditions prefer larger trunks, which provide such conditions. Numerous studies have reported a positive correlation between CWD size and saproxylic species richness (Heilmann-Clausen & Christensen 2004; Lindhe et al. 2004). Bässler et al. (2010) and Pouska et al. (2010) demonstrated that the number of threatened and specialized species increases with the mean diameter of logs in mountain spruce-dominated forests. A recent study (Abrego & Salcedo 2013) suggested that certain species or families prefer specific substrate diameters; notably, Polyporaceae and Botryobasidiaceae are classified as size specialists. However, Rajala et al. (2012), in their study on Norway spruce logs, found no significant relationship between species richness and log diameter, although community composition was influenced by log volume and diameter.

## 2.6 Beta-diversity, turnover, and nestedness components

The relationship between species diversity and spatial scale is a central topic in spatial community ecology (Su et al. 2024). Traditionally, diversity is categorized into three levels: α-, β-, and γ-diversity (Whittaker 1960). α-Diversity refers to species diversity at the local scale, while γ-Diversity represents species diversity at the regional scale. β-Diversity, on the other hand, denotes the variation among samples that reflects the heterogeneity of community structure within a region or other structural units (Anderson et al. 2011). It serves to differentiate between local factors (such as environmental conditions, species interactions, and disturbances) and larger-scale processes (such as dispersal limitations and historical factors) that influence species assemblages (Zhang et al. 2020). Analysing β-diversity patterns can help determine whether variations in community composition are driven primarily by local, habitat-specific factors or by species dispersal from a broader regional pool (Langenheder et al. 2012; Wang et al. 2017). Additionally, β-diversity can reflect the strength of ecological gradients, which are gradual changes in environmental conditions across different habitats or geographical locations (Wang et al. 2020).

By quantifying species composition variation, researchers can correlate these differences with specific environmental variables (e.g., latitude, longitude, or temperature) to gain insights into the mechanisms underlying species distribution and community assembly. For instance, the latitudinal gradient is a major driver of global biodiversity distribution due to its correlation with factors such as temperature, precipitation, habitat heterogeneity, and historical events. While some studies have reported a decrease in overall β-diversity with increasing latitude (Soininen et al. 2018; Cao et al. 2021). Insights regarding the stability of multiple ecosystem functions and how to conserve them may be advanced through an understanding of the processes shaping variation in the composition of communities at landscape scales (Socolar et al. 2016; Chase et al. 2020). A growing body of research has explored the utility of beta-diversity metrics in explaining mechanisms underpinning spatial patterns in biodiversity (e.g., Hill et al. 2017; Zellweger et al. 2017; Di Marco et al. 2019; LaManna et al. 2021). Beta-diversity metrics are derived from locally-collected biotic inventories and, though variously defined in the literature, describe the extent of change or dissimilarity in community composition across disjunct localities (Baselga 2010; Anderson et al. 2011). Conceptually, beta-diversity represents the portion of the total regional species pool that accumulates from differences between sites in terms of species assemblages and thereby provides an empirical relationship between local or alpha-diversity and regional or gamma-diversity (Whittaker 1960; Whittaker 1972).

Two fundamental processes, termed spatial turnover and nestedness, may differentially influence community richness patterns or beta-diversity (Baselga et al. 2007; Ruhi et al. 2017). Turnover describes the replacement or substitution of species along spatial gradients due to, for example, dispersal constraints or environmental heterogeneity that differentially filters species based on their unique niche requirements (Anderson et al. 2011). Nestedness describes differences in the richness of a set of communities attributed to the loss of some species from some sites (Baselga 2010). A hypothetical example is the extirpation of a species from a locality as a consequence of a transient disturbance event, such as an extreme drought episode. Discriminating the relative importance of turnover versus nestedness may contribute to a more comprehensive understanding of biodiversity maintenance mechanisms and provide criteria to guide conservation actions (Socolar et al. 2016). For instance, high levels of turnover within a metacommunity, reflecting substantial spatial variation in species assemblages, may indicate the need for a reserve design that protects multiple local communities since the constituent organisms potentially provide complementary or disparate ecosystem functions (Mori et al. 2018). In contrast, a highly nested community structure may reflect low inter-site complementarity and point to a need for prioritizing particular sites that support disproportionately diverse species assemblages (Gianuca et al. 2017).

Processes that regulate species assembly and, hence, beta-diversity include: (1) niche differentiation through habitat filtering or competitive exclusion, (2) long-distance species dispersal, and (3) demographic stochasticity or drift (Vellend 2010). These factors may independently influence nestedness and turnover processes (Ruhi et al. 2017). For example, turnover may be alternately promoted by resource heterogeneity or reduced by long-distance dispersal (Mouquet & Loreau 2003). Nestedness patterns may be increased by dispersal barriers that inhibit rescue effects, which could otherwise facilitate the recovery of a locally endangered population (Heino 2013). These relationships are context-dependent, varying with local environmental conditions, the functional traits of the dispersing species, or anthropogenic disturbances (Leibold et al. 2004).

Biotic differentiation refers to the increasing dissimilarity among biological assemblages over time. This phenomenon, characterized by changes in spatial dissimilarity among assemblages, has emerged as a significant indicator of broader biodiversity changes during the Anthropocene. Despite this, empirical evidence of both biotic homogenization and differentiation remains fragmented across various ecosystems. Most meta-analyses focus on quantifying the extent and direction of changes in beta-diversity, rather than elucidating the underlying ecological mechanisms driving these changes. By understanding the mechanisms that lead to either increased or decreased dissimilarity in ecological assemblages, environmental managers and conservation practitioners can make more informed decisions about necessary interventions to preserve biodiversity and anticipate the potential impacts of future disturbances (Rolls et al. 2023). Congruent beta-diversity dynamics among different groups of organisms may help identify critical environments or sites that disproportionately regulate regional patterns in community assembly, and that may, consequently, require priority safeguarding (Socolar et al. 2016).

# 3 Aims and overview of the dissertation thesis

Understanding the processes shaping the composition of assemblages at multiple spatial and temporal scales in response to natural disturbances and disturbance legacies is crucial for preventing ongoing worldwide biodiversity loss. This insight may help to improve current forest management practices aimed at mitigating accelerating changes in environmental conditions and enhancing forest resilience. The dissertation thesis summarized biodiversity and dendrochronological surveys conducted at 58 spruce-dominated primary forest research plots distributed across ten of the best-preserved stands in the Western Carpathians Mountains of Slovakia. This thesis focused on the impact of natural disturbances and forest structure on forest-dwelling taxa. Birds, epiphytic and epixylic lichens, saproxylic beetles, and deadwood-inhabiting fungi were selected as model taxonomic groups because they are particularly sensitive to forest management practices, and many of them are used as an indicator of the naturalness of forest ecosystems in conservation biology. Nowadays, spruce primary forests are incredibly rare, and in the world of accelerating changes in environmental conditions, they are becoming optimal reference ecosystems for studying natural processes.

The particular aims of the thesis are:

1. To investigate the influence of historical natural disturbances and forest structure on current communities of deadwood-inhabiting fungi.

2. To explore alpha and beta-diversity dynamics in spruce primary forests for the four taxonomic groups (birds, epiphytic and epixylic lichens, saproxylic beetles, and deadwood-inhabiting fungi).

3. To compare species dissimilarity, spatial species turnover, and nestedness components for these taxonomic groups.

4. To develop forest management recommendations aimed at enhancing biodiversity.

# 4 Material and methods

## 4.1 Spatial and temporal extents of natural disturbances differentiate deadwood-inhabiting fungal communities in spruce primary forest ecosystems

### 4.1.1 Study area

Our study area is situated in the spruce primary forests in the Slovakian part of the Western Carpathians (48°63’–49°52’ N, 19°30’–20°12’ E). The nine study stands are located in elevations from 1244 to 1534 m (Fig. 1). The mean area of primary forest stands was 185.4 ha, varying from 41 to 431 ha. Annual precipitation varies from 1205 to 1365 mm yr$^{-1}$ and annual mean temperatures range from 1.6 to 3.4 ºC. The dominant tree species in the study area is *Picea abies* (L.) Karst. (Norway spruce) with an admixture of *Sorbus aucuparia* L. (rowan), *Fagus sylvatica* L. (European beech), *Abies alba* Mill. (European silver fir), *Acer pseudoplatanus* L. (sycamore maple) and *Pinus cembra* L. (arolla pine), depending on specific location. The research stands were selected based on the national inventory of primary forests in Slovakia (Mikoláš et al. 2019). The stands are situated within four mountain ranges with the largest portion of spruce primary forests in Slovakia – the High Tatras (four stands), the Low Tatras (two stands), the Great Fatra Mountains (two stands), and the Orava Beskids (one stand). For the fungal surveys, we used plots previously established by Janda et al. (2017), and from the total 134 plots within the nine stands, 51 study plots were surveyed. Each plot measured 1000 m$^2$ (17.84 m radius from the plot centre). In each stand, study plots were selected to cover the whole gradient of disturbance severities and timing over the last 250 years. For this purpose, we split plots from Janda et al. (2017) according to disturbance event timing into three equally large time classes (83-year interval) from the 250-year disturbance chronology. We then selected two plots within each class in every stand, which experienced disturbances of differing severities when available. At the same time, we avoided locating any additional plots within a 150-m diameter around a given plot. The average distance among plots within the stands was 1.2 km (range 0.5–2.8 km).

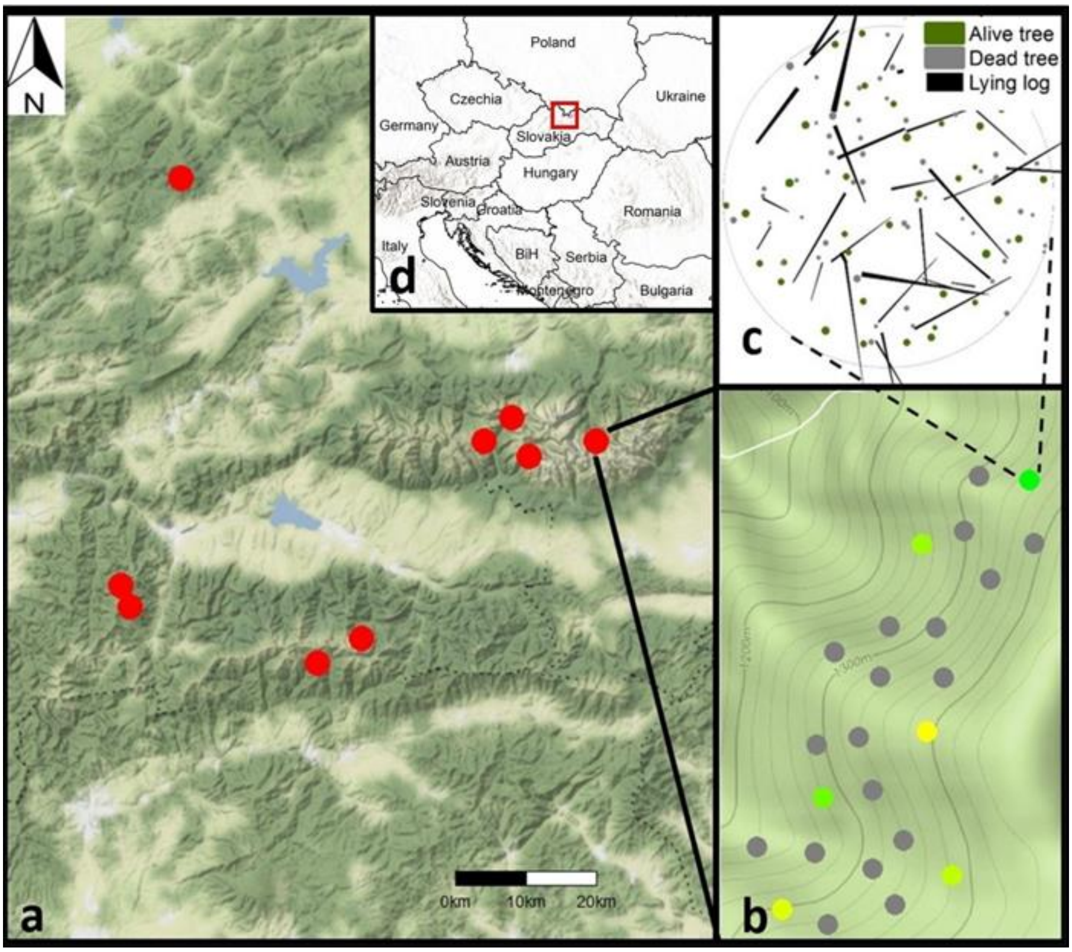
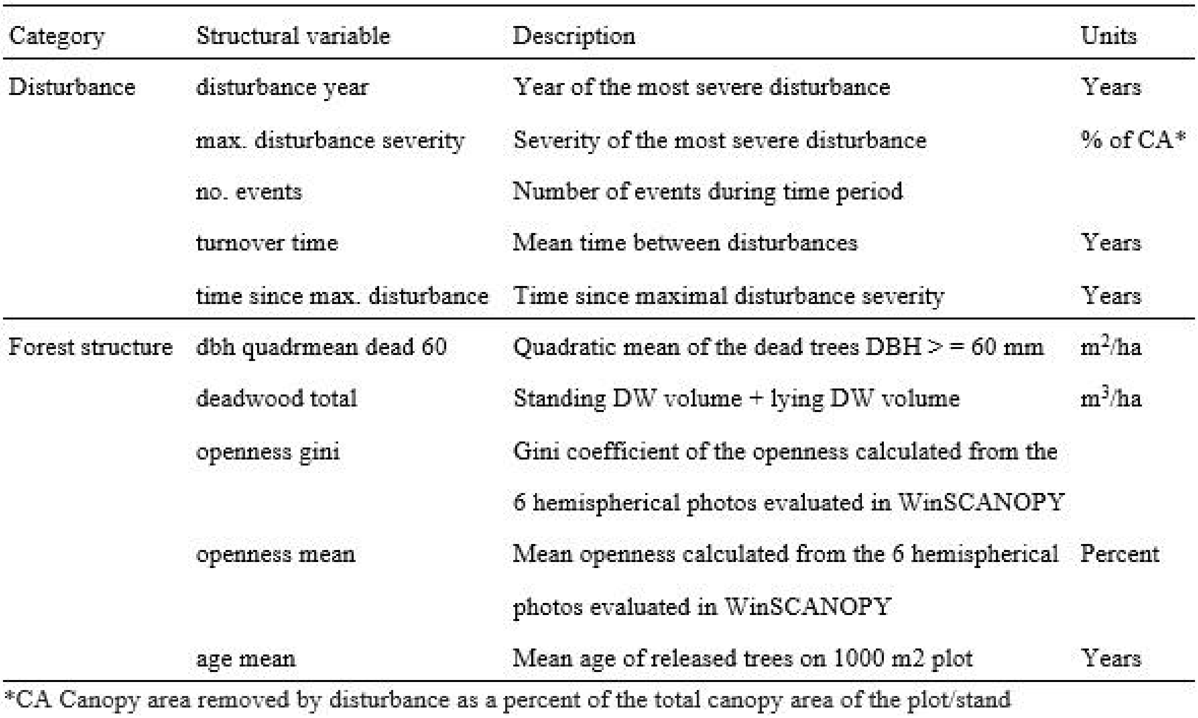


**Figure 7.** Distribution of the study sites in the landscape (a), example of plot locations within a stand (coloured plots were surveyed for fungi; b), tree and deadwood position within the plot (c), location of the study area within Western Carpathians (d).

### 4.1.2 Forest structure data

We collected structural data on all study plots in 2017. All live and dead trees with a diameter at breast height (DBH) ≥ 6 cm were numbered, and their DBH was measured and species recorded. Also, their position within the plot was precisely mapped using a laser with a compass and customised software FieldMap. The canopy position of each tree was assessed (suppressed: trees with crowns below the general canopy layer and receiving mostly diffuse light, and released: trees with crowns forming the general canopy layer and receiving at least 50% of full light). All downed deadwood with a thickness >10 cm was measured using the aforementioned FieldMap technology. The position of both ends was mapped with a laser with a compass, and their diameter was measured using a vernier caliper. The average decay stage (1–5) (Sippola & Renvall 1999) and tree species were also recorded for every deadwood object (Stokland et al. 2012). The height of standing deadwood with DBH > 6 cm was estimated in height categories (0–10 m; 10–20 m; 20–30 m). Subsequently, the volume of deadwood (standing and downed) was calculated. In each plot, six hemispherical photographs (one in the plot centre, and five distributed 12.1 m from the plot centre at 72° intervals around the plot) were taken 1.3 m above the ground using a circular fisheye lens (Sigma 4.5 mm F2.8 EX DC). The amount and variability of understorey light were analysed using WinSCANOPY software. Individual pixels were classified into sky- or leaf-dominated classes based on their spectral properties. Pixel classification results were aggregated to determine the overall mean sky fraction.

**Table 1.** Selected environmental variables from measurements of forest structure and from reconstructed chronologies of disturbance history.



| Category | Structural variable | Description | Units |
|---|---|---|---|
| Disturbance | disturbance year | Year of the most severe disturbance | Years |
| | max. disturbance severity | Severity of the most severe disturbance | % of CA* |
| | no. events | Number of events during time period | |
| | turnover time | Mean time between disturbances | Years |
| | time since max. disturbance | Time since maximal disturbance severity | Years |
| Forest structure | dbh quadrmean dead 60 | Quadratic mean of the dead trees DBH > = 60 mm | $m^2$/ha |
| | deadwood total | Standing DW volume + lying DW volume | $m^3$/ha |
| | openness gini | Gini coefficient of the openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY | |
| | openness mean | Mean openness calculated from the 6 hemispherical photos evaluated in WinSCANOPY | Percent |
| | age mean | Mean age of released trees on 1000 m2 plot | Years |

*CA Canopy area removed by disturbance as a percent of the total canopy area of the plot/stand

### 4.1.3 Disturbance history and age structure variables

We used an approximately 250-year long record of disturbance history together with the relationship between the past disturbance variability and patterns of fungal community diversity. Disturbance chronologies from Schurman et al. (2018) were utilized. Twenty-five living non-suppressed trees per plot were selected using a random number generator and were cored at 1 m height using an increment borer. One core per tree was extracted perpendicular to the slope direction and further processed by standard dendrochronological procedures. Tree-ring widths were measured with the LintabTM sliding-stage measuring device and TsapWin software (RINNTECH, http://www.rinntech.com). Finally, cores were visually cross-dated and verified using COFECHA (Holmes 1983). The mean age was calculated for each plot. Variables characterising the disturbance history covering the last 250 years of individual plots (maximum disturbance severity, year of maximum disturbance severity, time since the maximum disturbance, disturbance frequency, turnover time) were derived to describe the disturbance histories (their description and units are listed in Table 1). Historical disturbance variables were calculated exclusively from dendrochronological data according to the method of Schurman et al. (2018) and span the timeframe 1750–2000. Disturbance events were reconstructed based on the assumption that disturbances affect neighbourhood competition and, therefore, growth responses in extant individuals (Svoboda et al. 2014). Two types of growth responses to disturbance events were determined from the tree ring series: (1) gap recruitment - characterized by rapid initial growth rates, and (2) release from suppression - characterized by an abrupt increase in growth rates after the period of suppressed growth. Disturbance event severity was estimated using regression methods and allometric equations relating the aggregate present-day size of tree responders (individuals with a disturbance signal) to the original extent of the disturbance-inducted canopy gap (for details, see Lorimer & Frelich 1989; Trotsiuk et al. 2018). The annual values of the disturbed canopy area were smoothed using the kernel density function, and individual disturbance events were detected as peaks above the 10% severity threshold (Trotsiuk et al. 2018). More detailed information about the processing of dendrochronological data and disturbance analysis is published in Schurman et al. (2018).

Years since the maximal disturbance were calculated as the year of data collection minus the year of maximum severity. At the plot level, for recently disturbed plots - where the current canopy area disturbed was larger than dendrochronologically detected maximum disturbance severities - the severity was expressed by current canopy openness, and the year of the recent disturbance was determined from Google Earth satellite imagery. Current canopy openness was calculated as the difference between the mean canopy closure of the whole dataset and the current canopy closure of a given plot (Bače et al. 2017). At the stand scale, structural variables were represented by summary characteristics (mean values and coefficients of variation) from all plots (including plots besides the fungal surveys) established in each stand. Reconstruction of stand-level disturbance history was performed by averaging annual values of disturbed canopy area among all plots (Schurman et al. 2018), followed by the same kernel density estimation and peak detection approach as at the plot level. The mean number of plots in the stands was 15, with a total of 134 plots (see section 4.1.1 Study area).

### 4.1.4 Fungal data

Macrofungal inventories (i.e. sampling of fruit bodies visible to the naked eye) were conducted on 51 circular plots, each with an area of 0.1 ha in September and October 2017. All wood-inhabiting macrofungi (Ascomycota and Basidiomycota) were recorded by two skilled mycologists, with a maximum time of 1.25 hours on each plot. Initially, each plot was inspected, and deadwood was selected to represent all types of available objects as a combination of substrate type (dead standing trees, snags, logs, branches), diameter, stage of decay (1-5), and tree species using a printed map and list of deadwood objects previously recorded by FieldMap. This approach with precisely recorded deadwood objects will also allow us to repeat research on the same object in the future. They proceeded from the richest type of substrate to the least represented and recorded all species present on every selected object. A total of 563 individual deadwood objects were investigated. All the fruit bodies of the same species on one object were considered as one record. If the fungi could not be determined directly on the plot, a sample was taken, described, dried, and prepared for further microscopic determination. For the classification of red-listed species, we used three (German, Austrian, and Czech) national red lists (Binot-Hafke et al. 2011; Dämon & Krisai-Greilhuber 2016; Holec & Beran 2006). The species was considered red-listed if it had a category corresponding to the current IUCN categories CR, EN, VU, NT, or the German category R (very rare) at least in one national red list.

### 4.1.5 Statistical analysis

Fungal diversity was quantified at two spatial scales: (1) plot-level alpha diversity and (2) stand-level gamma diversity. Alpha diversity was calculated as the total number of species per plot. Gamma diversity was quantified as the total number of species per stand pooled across all plots within a given stand. Since the observed gamma diversity is an estimate of the overall stand-level diversity, we also calculated confidence intervals of the gamma diversity measures using an unconditional variance estimator based on a general binomial mixture model (Colwell et al. 2004). Both plot- and stand-level diversity measures were quantified for four subsets of species data: (1) all species (lignicolous saprotrophs and saproparasites, mycorrhizal symbionts) (2) all red-listed species (lignicolous saprotrophs and saproparasites, mycorrhizal symbionts) (3) all species excluding mycorrhizal symbionts and (4) all red-listed species excluding mycorrhizal symbionts. We hypothesized that historical disturbances and their legacies in forest structure shape the diversity of fungal communities. To assess the evidence supporting our hypotheses, we fitted stand- and plot-level diversity measures by linear models (LMs) and linear mixed-effect models (LMMs), respectively. A suite of models was formulated to evaluate the responses of four groups of fungal species. Disturbance parameters (Table 1) were used as explanatory variables to estimate their effects on the diversity of fungi. Additional models were formulated to estimate the effects of forest habitat on fungal diversity.

In the plot-level LMMs, stands were treated as random effects to account for the hierarchical nature of the sampling design (see Fig. 1). Full models were simplified in a backward elimination procedure based on F tests with Satterthwaite's approximation to degrees of freedom (Kuznetsova et al. 2017). Residuals of all models were checked for normality and homoscedasticity. Data on maximum disturbance severity, total deadwood, and Gini coefficient of openness were log-transformed to reduce skewness. We also evaluated the variance inflation factors (VIFs, Quinn & Keough 2002) of each model and did not find any serious multicollinearity patterns (all VIFs < 4). Marginal determination coefficients ($R^2_m$) were calculated to quantify the proportion of the total variance explained by the fixed effects (Nakagawa et al. 2017).

Given the restricted degrees of freedom (n = 9 stands) in the stand-level LMs, using the stepwise selection approach would be impractical in the analysis. Therefore, we fitted a separate model for each predictor variable to explore potential drivers of gamma diversity in primary forests. The LMs were inversely weighted by the variance of the gamma diversity estimates to account for differences in the precision of diversity estimates (Strutz 2011), i.e. stands with a more accurately estimated total number of species had greater weight in the analysis than those with higher uncertainty.

The analyses were conducted in R (R Core Team 2021) using the packages ggplot2 (Wickham 2016), iNEXT (Hsieh et al. 2020), lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017).

## 4.2 Exploring the multiple drivers of alpha and beta-diversity dynamics in Europe’s primary forests: Informing conservation strategies

### 4.2.1 Study area

The study region encompasses high-elevation monodominant spruce forests in the Western Carpathian Mountains of Slovakia (48º63’–49º52’ N, 19º30’–20º12’ E). Permanent field survey plots previously established under the REMOTE Primary Forests project (www.remoteforests.org) were resampled for biodiversity data collection. The REMOTE project monitors the development and integrity of remnant stands of primary forests in Central Europe through a network of forest inventory plots. We selected a subset of plots from the network located across five major mountain ranges and within the ten best-preserved primary forest stands of Slovakia (Jasík & Polák 2011): the Tatra mountains (N=4 stands), the Low Tatras (N=2 stands), the Great Fatra (N=2 stands), the Orava Beskyds (N=1 stand) and the Poľana mountains (N=1 stand). Abbreviations for respective stands used in the text are as follows: Bielovodská dolina (BEL), Bystrá (BYS), Ďumbier (DUM), Hlina (HLI), Jánošíková kolkáreň (JAK), Kôprová dolina (KOP), Piľsko (PIL), Poľana (POL), Smrekovica (SMR), and Tichá dolina (TIC). The areal extent of the selected stands is highly variable, ranging from 41-494 ha (mean 185.4 ha). Elevations span a gradient of 1244-1534 m (Figure 1). Total annual precipitation varies from 1205-1365 mm $yr^{-1}$ and mean annual temperatures range from 1.6 to 3.4 ºC. The underlying geology is intrusive and metamorphic acid bedrock with prevailing Cambic Podzols or Haplic to Humic Podzols, Dystric Cambisols, and Cambic Umbrisols. The dominant tree species is *Picea abies* (L.) Karst. (Norway spruce), representing >90% of total plot biomass. Other minor tree species include *Sorbus aucuparia* L. (rowan), *Acer pseudoplatanus* L. (sycamore maple), *Abies alba* Mill. (European silver fir), *Fagus sylvatica* L. (European beech), and *Pinus cembra* (arolla pine) (Janda et al. 2017). Within the ten selected stands, we resurveyed a total of 58 REMOTE plots for biodiversity analyses. Plots were circular in shape, 0.1 ha in size, and stratified along broad gradients in environmental conditions and forest developmental stages (Svoboda et al. 2014). The average distance between plots within a stand was 1.2 km (0.5-2.8 km).

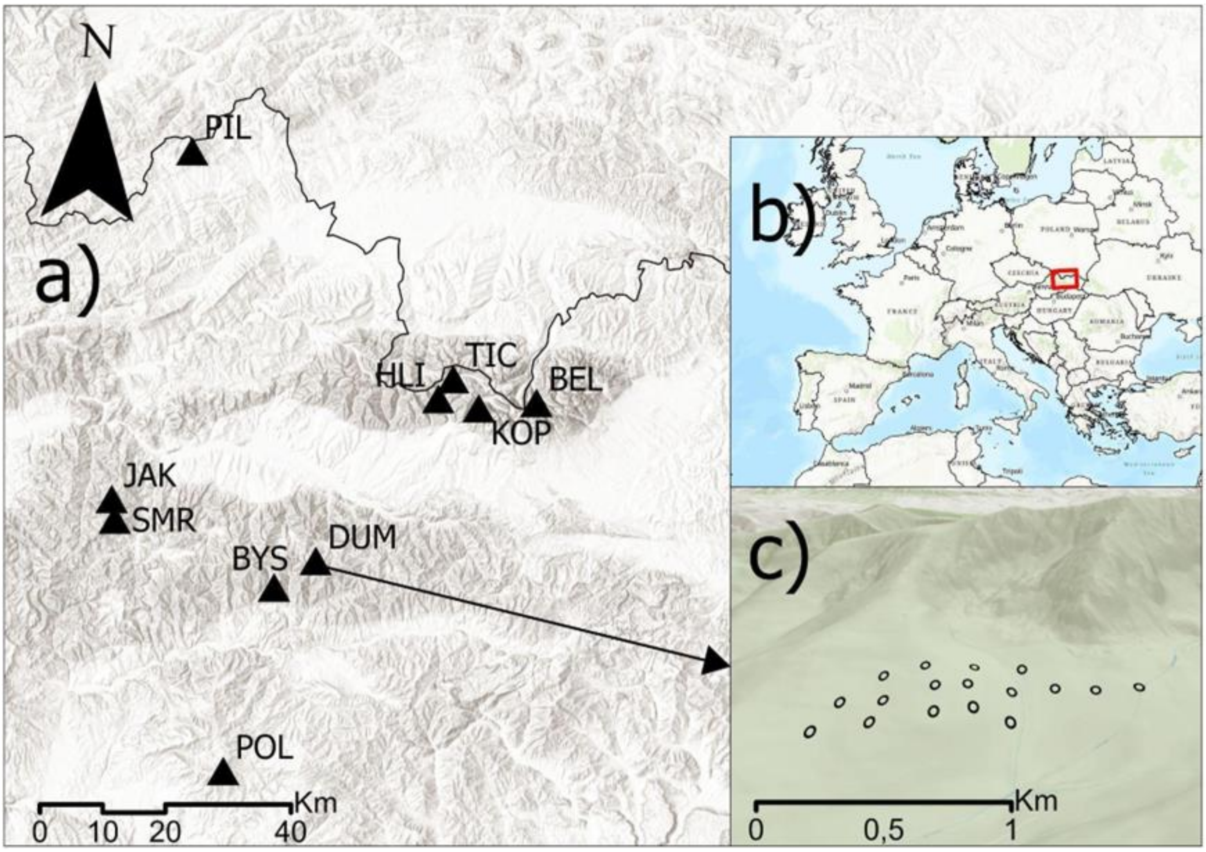


**Figure 8.** Distribution of the study sites in the landscape (a), location of the study area within Europe (b), example of plot locations within a stand (c).

### 4.2.2 Environmental variables

The structural attributes of forest plots were measured in 2017. We used a computer-aided data collection system (Field-Map; https://www.fieldmap.cz). We measured stem diameter at breast height (DBH at 1.3 m) for all living and dead plot trees above a minimum size threshold (DBH>6 cm). Tree taxonomy was identified at the species level. All trees were precisely mapped using a laser rangefinder and compass. Standing dead trees were visually categorized by height (0-10 m; 10-20 m; 20-30 m). All lying deadwood material with a thickness >10 cm was mapped by the aforementioned Field-map technology, and the diameter was measured at both ends with a vernier caliper. The decay stage (1-5) was classified based on Sippolla & Renvall (1999) and Stokland et al. (2012). To determine understory light levels, six hemispherical photographs were collected in predetermined locations: at the plot centre and 12.1 m from the plot centre on five different azimuths, each separated by 72°. The photos were taken 1.3 m above the ground using a wide-angle fisheye lens (Sigma 4.5 mm F2.8 EX DG). The images were subsequently analysed using WinSCANOPY software. Individual pixels were designated as sky or leaf-dominated based on associated spectral properties. Pixel classification results were aggregated to determine the overall mean sky fraction (canopy openness). Increment core samples from 25 randomly selected, living, non-suppressed trees were collected from all plots for age determination. A single core was extracted from each selected tree at a height of 1 m above the ground using a Pressler increment borer. Samples were processed using standard dendrochronological procedures. Annual growth increment was measured using a LintabTM sliding-stage and TsapWin software. Cores were visually cross-dated and verified using COFECHA (Holmes 1983). Selected environmental variables are shown in Table 2.

**Table 2.** Selected environmental variables from measurements of forest structure.

| Structural variable | Description | Units |
|---|---|---|
| Altitude | Elevation above sea level at the centre of the study plot | m.a.s.l |
| Canopy openness | Mean openness calculated from the 6 hemispherical photos | % |
| Mean age of the five oldest trees | Mean age of the five oldest trees on 1000 $m^2$ study plot | years |
| Total deadwood volume | Volume of standing and lying deadwood | $m^3$/ha |
| Standing deadwood volume | Volume of standing deadwood | $m^3$/ha |
| Lying deadwood (decay 1,2,3) | Volume of lying deadwood decay classes 1,2, and 3 | $m^3$/ha |
| Lying deadwood (decay 1) | Volume of lying deadwood decay class 1 | $m^3$/ha |
| Lying deadwood (decay 4, 5) | Volume of lying deadwood decay classes 4 and 5 | $m^3$/ha |

### 4.2.3 Deadwood-inhabiting fungi survey

Macrofungal inventories (sampling of fruit bodies visible to the naked eye) were conducted in September and October 2017. Two skilled mycologists identified all wood-inhabiting macrofungi (Ascomycota and Basidiomycota). To standardize sampling intensity across sites, surveys were restricted to a 1.5-hour window for each plot. Initially, a plot was inspected, and deadwood was selected to represent all types of available objects as a combination of substrate type (dead standing trees, snags, logs, branches), diameter, stage of decay (1-5), and tree species using a printed map and list of deadwood types previously recorded by FieldMap. Mycologists proceeded from the most common substrate type to the least represented, recording all fungal species present on every selected piece of deadwood. A total of 563 individual deadwood objects were investigated. All fruiting bodies of the same species on one object were considered as one record. If the fungal species could not be determined in the field, a sample was collected, described, dried, and prepared for further microscopic determination in the lab. For the identification of critically endangered (red-listed) fungi, we used three national (German, Austrian, and Czech) red lists (Binot-Hafke et al. 2011; Dämon & Krisai-Greilhuber 2017; Holec & Beran 2006). A fungal species was considered to be red-listed if it was classified by any single national red list as belonging to one of the following current IUCN (International Union for Conservation of Nature) categories: critically endangered (CR), endangered (EN), vulnerable (VU), or near threatened (NT).

### 4.2.4 Lichens survey

Surveys were conducted in 2017 and 2018. Within a given plot, all epiphytic and epixylic lichen occurrences associated with a selected subset of observed objects or substrates were recorded by an experienced lichenologist. We selected five representative objects in each plot for a detailed inspection: two living trees, two downed logs, and one standing dead tree or snag. If an object type did not occur within a plot, we sampled a replacement object(s) selected from the most abundant type to maintain consistent sample sizes across sites. We further sampled up to four additional objects (e.g. deadwood material in alternative stages of decay, alternate tree species) to capture the entire range of substrate variability within each plot. Lichens were recorded from the stem base up to a height of two metres for standing trees and two metres along downed logs (beginning at the wide end). We did not sample lichens associated with the forest floor, rocks, or fallen twigs. All lichens were identified to the species level based on the fungal component. Identification was performed either in the field or using a microscope in the laboratory. Red-listed categories were assigned according to Pišút et al. (2001), adjusted by Guttová et al. (2013). The species were designated as red-listed based on affiliation with one of the following IUCN categories: CR, EN, VU, and NT (as defined previously for fungi), as well as an additional extinct (EX) or regionally extinct (RE) category.

### 4.2.5 Saproxylic beetles survey

We investigated the saproxylic beetle assemblages using insect traps to characterise the taxonomic composition and species richness of local communities. We used flight intercept (window) traps to collect beetle specimens due to their efficacy in previous quantitative studies (Gossner et al. 2013; Hyvärinen et al. 2006; Økland 1996). Comparative analyses of trap performance have shown that window traps facilitate the collection of large sample sizes and a wide range of taxa compared with other methods (Alinvi et al. 2006). A single trap was installed on two metal rods 1 m above the ground at the centre of each plot. We avoided the use of insect bait to minimise the collection of random long-distance dispersers that would bias estimates of local species diversity. Traps were installed continuously from May to September 2017 and emptied monthly. Red-listed species were again identified based on IUCN categories (IUCN 2019) following Seibold et al. (2015) and Schmidl & Büche (2016). In addition to the standard IUCN categories, we used the German category R (very rare).

### 4.2.6 Avian survey

Data on bird assemblage composition were collected between the end of April and the end of June (i.e. during the peak of the breeding season). Every plot was visited three times per season in 2017 and 2018. Point counts were used as a field technique, with a census point located in the centre of each plot (Verner 1985). During each plot visit, all birds within a distance of 60 m from the observer were counted for 10 min. We identified the taxonomic identity of all birds based on acoustic signals, particularly birdsong diagnostic of territorial behaviour. After arriving at a plot, we waited silently for one minute before initiating surveys to minimize observer effects on bird activity (Sutherland 2006). Counts were performed in the early morning (5:00-10:00) and only during optimal weather conditions without heavy rain or strong wind (Moning & Müller 2009). Red-listed categories were assigned from Demko et al. (2013).

### 4.2.7 Data analysis

We quantified levels of multiple-site total beta-diversity, as well as two components of total beta-diversity (nestedness and turnover) for each of the four taxonomic groups. We followed methods in Baselga (2010), as they are widely used in the literature (Soininen et al.

2018). Sorensen’s dissimilarity index for multiple sites was used to compute total beta-diversity. Simpson’s multi-site dissimilarity, which is largely insensitive to local richness differences among sites (Baselga 2010; Leprieur & Oikonomou 2014), was used to estimate species turnover. Nestedness was determined from the component of total beta-diversity that was not accounted for by turnover. Beta-diversity metrics were calculated using the betapart package in R. We subsequently estimated the degree of congruence among the four taxonomic groups in terms of the three metrics of beta-diversity by computing Pearson’s correlations. Specifically, we constructed separate matrices for each diversity statistic for each group and then conducted partial Mantel tests to assess the strength of correspondence and the associated statistical significance. We defined individual components as follows: alpha-diversity ($\alpha$) is the mean number of species in the plots within the stand, beta-diversity ($\beta_1$) represents the number of species found exclusively at the respective stand, beta-diversity ($\beta_2$) represents variability in species composition among stands, and gamma-diversity ($\gamma$) is a total regional species pool.

We formulated a set of generalized least square models (GLS) to test for the potential importance of forest structural attributes in determining both species richness (alpha diversity) and the number of red-listed species for each of the four taxonomic groups. We evaluated the influence of the following explanatory variables: (i) canopy openness as an index of understory light levels, (ii) mean age of the five oldest plot trees as a measure of forest maturity or developmental stage, and (iii) total deadwood volume. In separate models, total deadwood volume was defined alternately as the volume of standing deadwood; the volume of lying deadwood in decay classes 1, 2, and 3; the volume of lying deadwood in decay classes 1; and the volume of lying deadwood in decay classes 4 and 5. We also tested models that included elevation as an additional covariate, based on an assumption that elevation may serve as a proxy for local climate or other abiotic factors. To account for potential spatial autocorrelation among plots within stands, we included an exponential covariogram in all models. Covariogram parameters were estimated via restricted maximum likelihood (REML). We compared the performance of competing models using the Akaike information criterion (AIC). The best-performing models were selected based on parsimony; specifically, the most parsimonious model minimized AIC by at least two units. All analyses were performed in R (R Core Team 2022), using the ‘nlme’ (Pinheiro et al. 2022) and ‘vegan’ packages (Oksanen et al. 2012).

## 4.3 Species dissimilarity, spatial species turnover, and nestedness of environmentally sensitive forest-dwelling taxa in the spruce-dominated primary forests across the Western Carpathian Mountains

### 4.3.1 Study area

The study area includes high-elevation spruce primary forests in Slovakia's Western Carpathian Mountains (48°63'–49°52' N, 19°30'–20°12' E). Biodiversity data were collected by sampling of permanent field survey plots originally established under the REMOTE Primary Forests project (www.remoteforests.org). This project monitors the development and integrity of remnant primary forest stands in Central Europe through a network of forest inventory plots. We selected a subset of plots from this network (from the total 145 plots), located across five major mountain ranges and within Slovakia's ten best-preserved primary forest stands (Jasík & Polák 2011): the Tatra Mountains (4 stands), the Low Tatras (2 stands), the Great Fatra (2 stands), the Orava Beskyds (1 stand), and the Poľana Mountains (1 stand) (Figure 9). Abbreviations for these stands used in the results are: Bielovodská dolina (BEL), Bystrá (BYS), Ďumbier (DUM), Hlina (HLI), Jánošíková kolkáreň (JAK), Kôprová dolina (KOP), Piľsko (PIL), Poľana (POL), Smrekovica (SMR), and Tichá dolina (TIC). The stands vary in size from 41 to 494 hectares (mean 185.4 ha), and elevations range from 1244 to 1534 meters. Annual precipitation ranges from 1205 to 1365 mm, and mean annual temperatures range from 1.6 to 3.4 ºC. The geology consists of intrusive and metamorphic acid bedrock with prevailing Cambic Podzols, Haplic to Humic Podzols, Dystric Cambisols, and Cambic Umbrisols. The dominant tree species is Norway spruce (Picea abies (L.) Karst.), which accounts for more than 90% of the total plot biomass. Minor tree species include rowan (Sorbus aucuparia L.), sycamore maple (Acer pseudoplatanus L.), European silver fir (Abies alba Mill.), European beech (Fagus sylvatica L.) and arolla pine (Pinus cembra) (Janda et al. 2017). Within the ten selected stands, we surveyed a total of 58 REMOTE plots for biodiversity investigation. These plots were circular, 0.1 hectares in size, and stratified across broad gradients of environmental conditions and forest developmental stages (Svoboda et al. 2014). The average distance between plots within a stand was 1.2 km (ranging from 0.5 to 2.8 km).

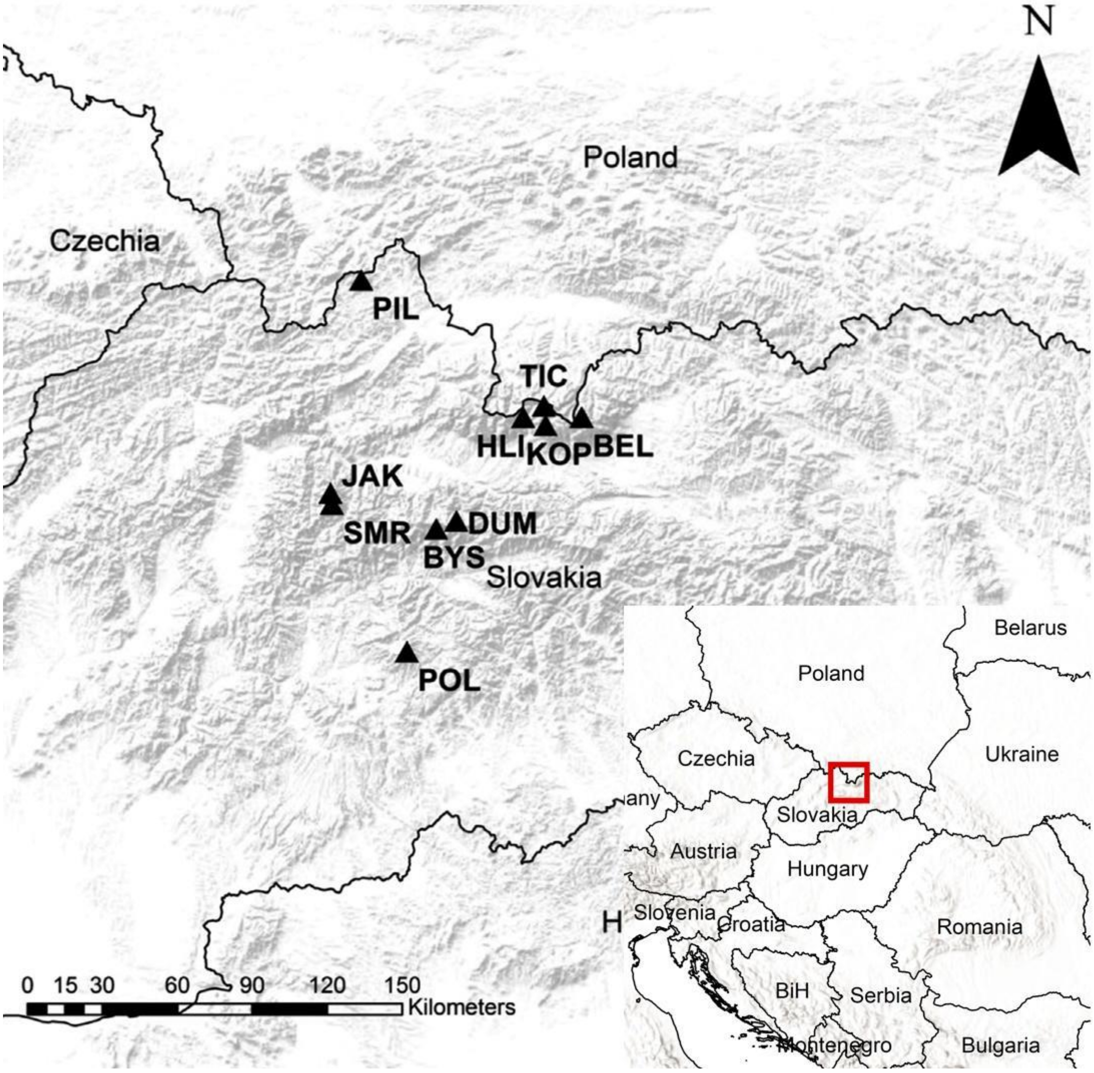


**Figure 9.** Distribution of the study sites in the landscape and location of the study area within Europe.

### 4.3.2 Deadwood-inhabiting fungi survey

Macrofungal surveys, involving the collection of visible fruiting bodies were carried out in September and October 2017. Two skilled mycologists identified all wood-inhabiting macrofungi (Ascomycota and Basidiomycota). To maintain consistent sampling efforts across different sites, each survey was limited to 1.5 hours per plot. Initially, a plot was examined, and deadwood was chosen to represent a variety of available types based on substrate type (dead standing trees, snags, logs, branches), diameter, decay stage (1-5), and tree species, guided by a printed map and a list of deadwood types previously recorded by FieldMap. The mycologists began with the most common substrate type and worked towards the least common, documenting all fungal species found on each piece of selected deadwood. In total, 563 individual pieces of deadwood were examined. All fruiting bodies of the same species on a single object were counted as one record. If a fungal species could not be identified in the field, a sample was collected, described, dried, and prepared for further microscopic identification in the laboratory.

### 4.3.3 Lichens survey

Surveys were conducted in 2017 and 2018. In each plot, an experienced lichenologist recorded all epiphytic and epixylic lichen occurrences associated with a selected subset of investigated objects or substrates. Five representative objects were chosen in each plot for detailed inspection: two living trees, two downed logs, and one standing dead tree or snag. If a specific object type was absent in a plot, a replacement object from the most abundant type was sampled to maintain consistent sample sizes across plots. Additionally, up to four more objects (e.g., deadwood in different stages of decay, alternate tree species) were sampled to capture the full range of substrate variability. Lichens were recorded from the stem base up to a height of two meters on standing trees and along two meters of downed logs, starting from the wide end. Lichens associated with the forest floor, rocks, or fallen twigs were not sampled. All lichens were identified to the species level based on the fungal component, either in the field or with a microscope in the laboratory. Difficult-to-determine lichens (mainly genus *Lepraria*) were determined using Thin Layer Chromatography (TLC).

### 4.3.4 Saproxylic beetles survey

We studied saproxylic beetle assemblages by using insect traps to analyze the taxonomic composition and species richness of local communities. Flight intercept (window) traps were chosen for collecting beetle specimens due to their proven effectiveness in past quantitative studies (Gossner et al. 2013; Hyvärinen et al. 2006; Økland 1996). Comparative analyses have demonstrated that window traps collect larger sample sizes, and a broader range of taxa compared to other methods (Alinvi et al. 2006). Each trap was mounted on two metal rods, positioned 1 meter above the ground at the center of each plot. To avoid attracting random long-distance dispersers that could skew local species diversity estimates, no insect bait was used. Traps were installed from May to September 2017 and were emptied monthly.

### 4.3.5 Avian survey

Data on bird assemblage composition were gathered from late April to late June, coinciding with the peak of the breeding season. Each plot was visited three times per season in both 2017 and 2018. Point counts, conducted at a census point in the center of each plot (Verner 1985), were used as the field technique. During each visit, all birds within a 60-meter radius of the observer were counted for 10 minutes. Birds were identified at the species level based on their acoustic signals, especially songs indicating territorial behaviour. To reduce observer impact on bird activity, we waited silently for one minute before starting the surveys (Sutherland, 2006). Counts took place in the early morning (5:00-10:00) and were conducted only under optimal weather conditions, avoiding heavy rain or strong winds (Moning & Müller 2009).

### 4.3.6 Data analysis

We quantified two components of total beta-diversity (nestedness and turnover) for each of the four taxonomic groups. We followed methods in Baselga (2010), as they are widely used in the literature (Soininen et al. 2018). The Sorensen dissimilarity index is one of the most used indices to quantify taxonomic homogenization using presence-absence data. This index not only expresses turnover but is also sensitive to differences in species richness among sites (Baeten et al. 2012). We used this index to compute total beta-diversity. Simpson’s multi-site dissimilarity, which is largely insensitive to local richness differences among sites (Baselga 2010; Leprieur & Oikonomou 2014), was used to estimate species turnover. Nestedness was determined from the component of total beta-diversity that was not accounted for by turnover. Beta-diversity metrics were calculated using the betapart package in R. All analyses were performed in R (R Core Team 2022) using the ‘vegan’ packages (Oksanen et al. 2012).

# 5 Results

## 5.1 Spatial and temporal extents of natural disturbances differentiate deadwood-inhabiting fungal communities in spruce primary forest ecosystems

We recorded a total of 204 species (from 1641 records) in the 51 study plots on 563 individual deadwood objects. Lignicolous saprotrophic fungi were the most abundant trophic group, represented by 165 species, followed by mycorrhizal symbionts (28 species), and 11 species were lignicolous saproparasites. Of these 204 fungal species, 55 were red-listed (for more details, see Supplement 1). The highest number of species per plot was observed in Hlina Valley in the High Tatras (n = 36) and the lowest number in Smrekovica in the Great Fatra mountains (n = 6). The most fungal species per stand (n = 83) were found in Kôprová Valley in the High Tatras.

### 5.1.1 Effect of disturbances

Among the investigated disturbance characteristics, the frequency of disturbances (number of events) was significantly related to both alpha diversity of all red-listed species and alpha diversity of red-listed species excluding mycorrhizal symbionts (Table 2). The number of red-listed species increased with the frequency of disturbance events (Fig. 2a). Gamma diversity of all species was significantly negatively influenced by the maximum disturbance severity (Fig. 2b). However, this negative effect was neither observed in all red-listed species nor in the dataset after exclusion of the mycorrhizal group. We did not find any significant effect of the remaining disturbance characteristics on fungal species diversity.

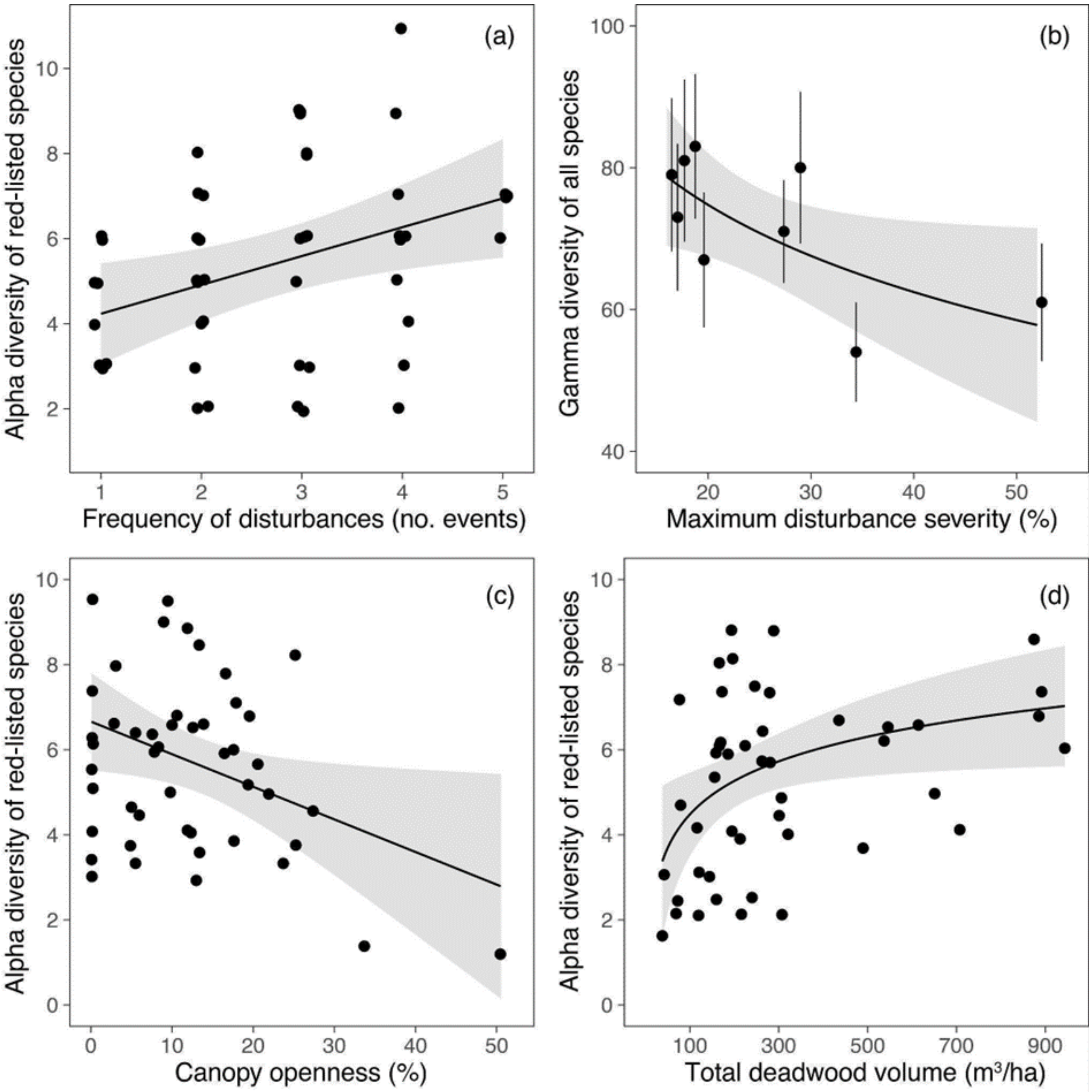
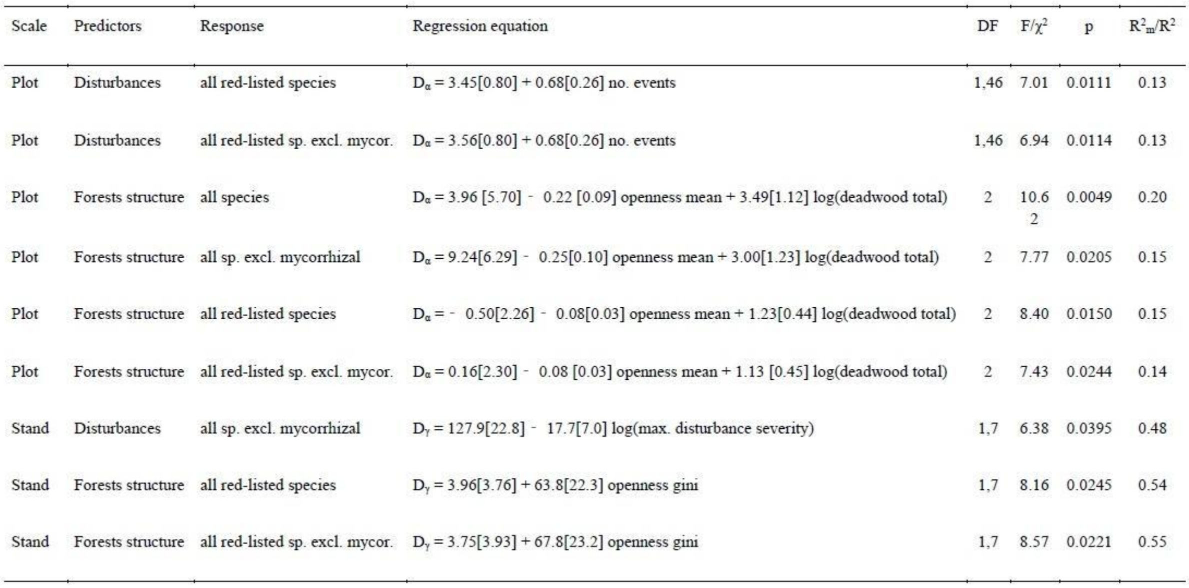


**Figure 10.** Significant influence of forest disturbance (a, b) and structural (c, d) characteristics on alpha and gamma diversity of all species of fungi recorded in primary temperate forests. The model-based predictions (lines) are displayed along with their 95% confidence intervals (grey bands). Observed values (a, b) and partial residuals (c, d) are shown as dots. Estimates of the gamma diversity (b) are plotted with their 95% confidence intervals (error bars). Note that the alpha diversity values (a) are slightly jittered to avoid overlap.

### 5.1.2 Effect of forest structure

The total deadwood volume and canopy openness showed a significant influence on alpha diversity in all investigated datasets (Table 2). The number of species per plot decreased with canopy openness and asymptotically increased with total deadwood volume (Fig. 2c, 2d). Gamma diversity of red-listed fungi was significantly positively linked with the Gini coefficient of the canopy openness regardless of whether we analyzed the set of all red-listed species or excluded the mycorrhizal group.

**Table 3.** Significant linear models (stand scale) and linear mixed-effect models (plot scale) linking plot-level alpha diversity ($D_\alpha$) and stand-level gamma diversity ($D_\gamma$), respectively, to characteristics of historical disturbances and forest structure. The regression equations show model coefficients and their standard errors in square brackets. Test statistics (F or $\chi^2$), degrees of freedom (numerator, denominator), probabilities (p), and (pseudo)determination coefficients ($R^2_m/R^2$) are displayed. Note that the results of likelihood ratio tests ($\chi^2$) are reported for multiple regression models. For abbreviations of predictor names, see Table 1.



| Scale | Predictors | Response | Regression equation | DF | $F/\chi^2$ | p | $R^2_m/R^2$ |
|---|---|---|---|---|---|---|---|
| Plot | Disturbances | all red-listed species | $D_\alpha = 3.45[0.80] + 0.68[0.26]$ no. events | 1,46 | 7.01 | 0.0111 | 0.13 |
| Plot | Disturbances | all red-listed sp. excl. mycor. | $D_\alpha = 3.56[0.80] + 0.68[0.26]$ no. events | 1,46 | 6.94 | 0.0114 | 0.13 |
| Plot | Forests structure | all species | $D_\alpha = 3.96\,[5.70] - 0.22\,[0.09]$ openness mean $+ 3.49[1.12]$ log(deadwood total) | 2 | 10.62 | 0.0049 | 0.20 |
| Plot | Forests structure | all sp. excl. mycorrhizal | $D_\alpha = 9.24[6.29] - 0.25[0.10]$ openness mean $+ 3.00[1.23]$ log(deadwood total) | 2 | 7.77 | 0.0205 | 0.15 |
| Plot | Forests structure | all red-listed species | $D_\alpha = - 0.50[2.26] - 0.08[0.03]$ openness mean $+ 1.23[0.44]$ log(deadwood total) | 2 | 8.40 | 0.0150 | 0.15 |
| Plot | Forests structure | all red-listed sp. excl. mycor. | $D_\alpha = 0.16[2.30] - 0.08\,[0.03]$ openness mean $+ 1.13\,[0.45]$ log(deadwood total) | 2 | 7.43 | 0.0244 | 0.14 |
| Stand | Disturbances | all sp. excl. mycorrhizal | $D_\gamma = 127.9[22.8] - 17.7[7.0]$ log(max. disturbance severity) | 1,7 | 6.38 | 0.0395 | 0.48 |
| Stand | Forests structure | all red-listed species | $D_\gamma = 3.96[3.76] + 63.8[22.3]$ openness gini | 1,7 | 8.16 | 0.0245 | 0.54 |
| Stand | Forests structure | all red-listed sp. excl. mycor. | $D_\gamma = 3.75[3.93] + 67.8[23.2]$ openness gini | 1,7 | 8.57 | 0.0221 | 0.55 |

## 5.2 Exploring the multiple drivers of alpha and beta-diversity dynamics in Europe’s primary forests: Informing conservation strategies

The number of species identified in individual plots varied considerably, both within and among taxonomic groups: 5-36 for beetles, 5-22 for birds, 6-38 for fungi, and 17-49 for lichens. Mean species richness within stands (Figure 11) varied more strongly for beetles and birds relative to fungi and lichens. At a stand level, both beta diversity ($\beta_1$-diversity, Figure 11) and the total number of species (sum of $\beta_1$-diversity and $\alpha$-diversity) were similar for all stands for fungi and lichens but varied more strongly for beetles and birds. Except for birds, the individual disjunct stands generally hosted less than half of the species identified in the total regional species pool ($\gamma$-diversity, Figure 11). Thus, levels of $\beta_2$-diversity were large relative to $\beta_1$-diversity for stands in the beetle, fungi, and lichen groups. These results reflect patterns of spatial turnover in species composition and indicate that all stands contributed substantially and approximately equally to the total regional species pool. A few stands contribute disproportionately to gamma-diversity (e.g., SMR in the bird group).

We found evidence for a congruence among taxonomic groups in terms of total beta-diversity. All groups were significantly correlated with at least one other group (Table 2). The bird group was congruent with all other groups, while beetles were correlated with birds only. In contrast, we did not find evidence for a significant correspondence between groups in terms of the two components of beta-diversity, namely turnover and nestedness. The single exception was a congruence of spatial turnover between fungi and lichens (Table 2).

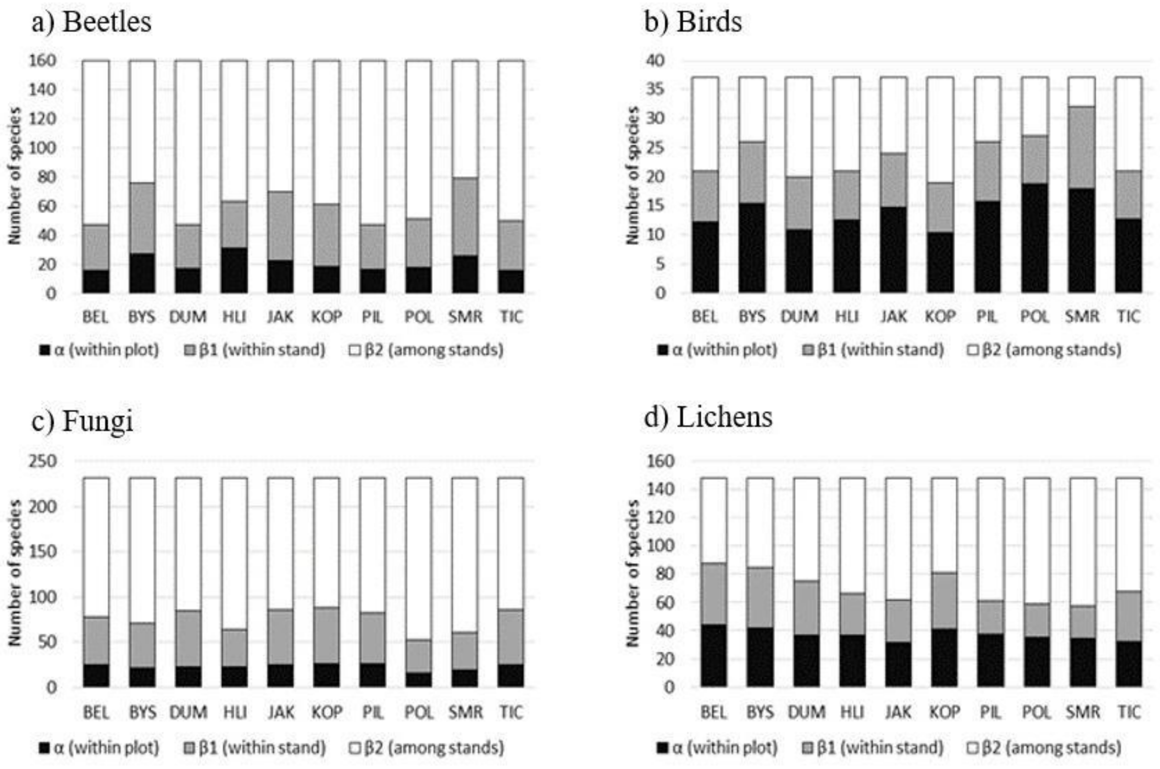
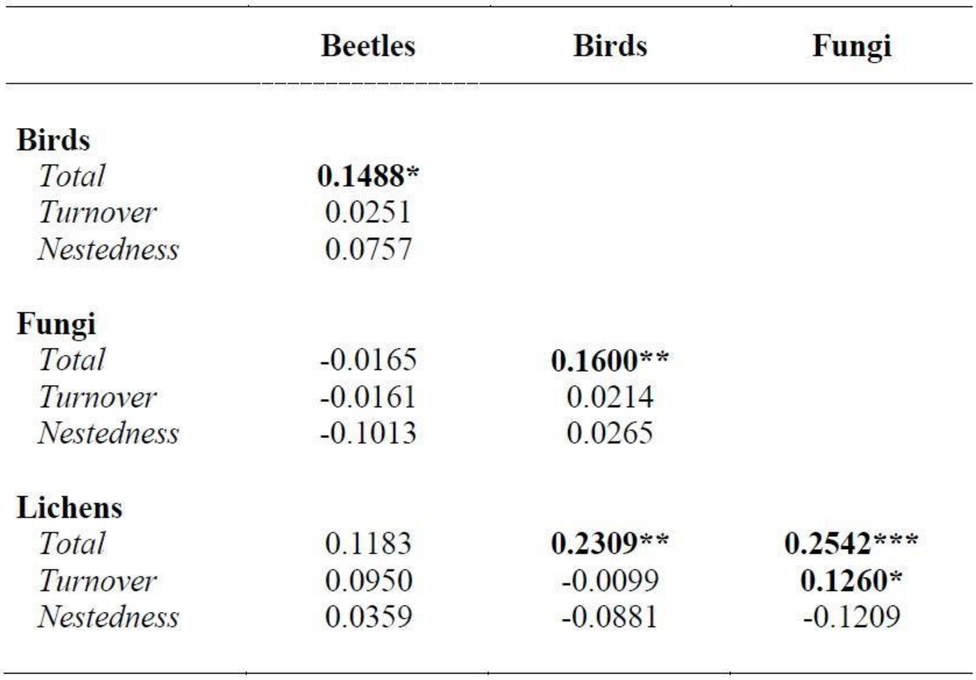


**Figure 11.** Proportion of γ-diversity due to α-diversity and the two components of β-diversity among the plots and the stands. The α-diversity is the mean number of species in the plots within the respective stand, $\beta_1$-diversity represents the dissimilarity in species composition within a respective stand, the sum of α-diversity and $\beta_1$-diversity represents the total number of species in the respective stand and $\beta_2$-diversity represents a measure of dissimilarity in species composition among stands.

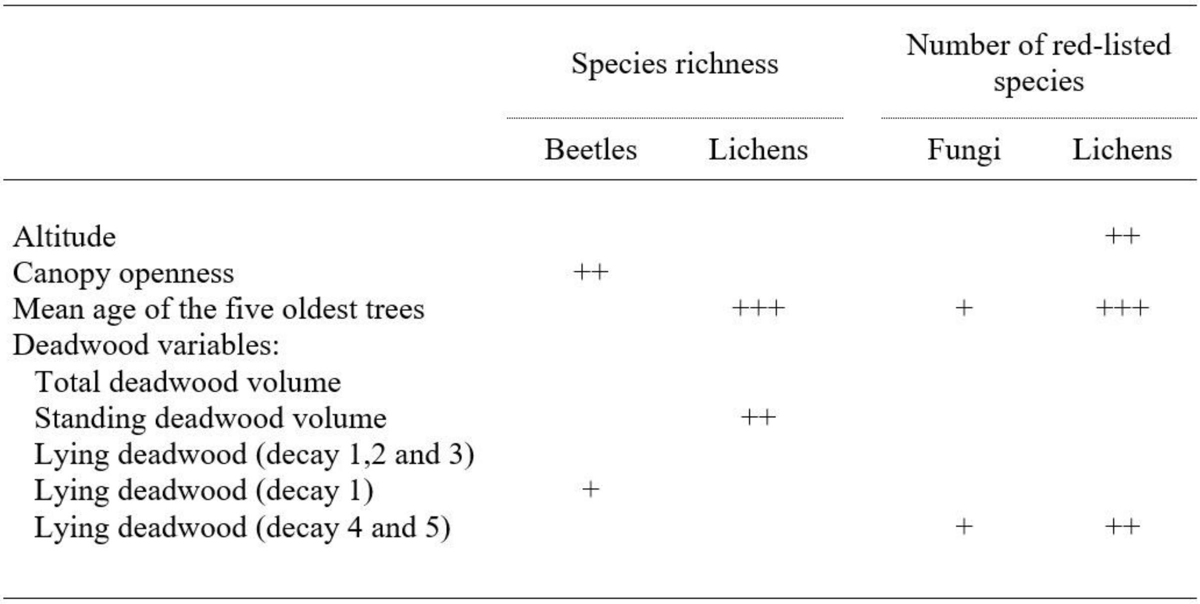
**Table 4.** Congruence between beta-diversity matrices of the taxonomic groups. The values of partial Mantel statistic r for matrices of Sørensen dissimilarity (as total beta-diversity), Simpson dissimilarity (as spatial turnover), and nestedness are given. The symbol * indicates significance level p < 0.05, symbol ** p < 0.01 and *** p < 0.001.



| | **Beetles** | **Birds** | **Fungi** |
|---|---|---|---|
| **Birds** | | | |
| *Total* | **0.1488*** | | |
| *Turnover* | 0.0251 | | |
| *Nestedness* | 0.0757 | | |
| **Fungi** | | | |
| *Total* | -0.0165 | **0.1600**** | |
| *Turnover* | -0.0161 | 0.0214 | |
| *Nestedness* | -0.1013 | 0.0265 | |
| **Lichens** | | | |
| *Total* | 0.1183 | **0.2309**** | **0.2542***** |
| *Turnover* | 0.0950 | -0.0099 | **0.1260*** |
| *Nestedness* | 0.0359 | -0.0881 | -0.1209 |

The results of the GLS models indicate that, for beetles and lichens, local species richness (alpha-diversity) was influenced by characteristics associated with both the living tree canopy and the local deadwood supply (Table 5). Specifically, the richness of the beetle group increased with both canopy openness (light levels) and volume of relatively intact (decay stage 1) lying deadwood. For lichens, the mean age of the five oldest trees and the volume of standing deadwood promoted local alpha-diversity. The regression models further reveal that the local diversity of red-listed species, at least within the fungal and lichen groups, was positively affected by stand conditions (Table 5). Again, the mean age of the oldest trees, as well as the volume of highly decomposed lying deadwood (decay stages 4 and 5) positively influenced the number of red-listed species for these two groups. The number of rare lichens also covaried with elevation.

**Table 5.** Results of generalised least squares models (GLS) for species richness and number of red-listed species of the respective taxonomic groups in the plots. Each model includes the same three explanatory variables (altitude, openness, age) and, additionally, one variable that characterised deadwood quantity and quality (total deadwood volume; standing deadwood volume; lying deadwood volume in decay classes 1, 2 and 3; lying deadwood volume in decay class 1; and lying deadwood volume in decay classes 4 and 5). The model selection procedure is documented in Table S2 and Table S3. The best models having at least two significant explanatory variables are presented here. The significant positive effects of explanatory variables in the models are indicated by symbol + at $p < 0.05$, ++ at $p < 0.01$, and +++ at $p < 0.001$.



| | Species richness | | Number of red-listed species | |
|---|---|---|---|---|
| | Beetles | Lichens | Fungi | Lichens |
| Altitude | | | | ++ |
| Canopy openness | ++ | | | |
| Mean age of the five oldest trees | | +++ | + | +++ |
| Deadwood variables: | | | | |
| Total deadwood volume | | | | |
| Standing deadwood volume | | ++ | | |
| Lying deadwood (decay 1,2 and 3) | | | | |
| Lying deadwood (decay 1) | + | | | |
| Lying deadwood (decay 4 and 5) | | | + | ++ |

## 5.3 Species dissimilarity, spatial species turnover, and nestedness of environmentally sensitive forest-dwelling taxa in the spruce-dominated primary forests across the Western Carpathian Mountains

We recorded a total of 158 lichen species on 479 investigated objects, 204 fungi species on 563 deadwood objects, 160 beetle species, and 37 bird species on 58 plots. According to the IUCN red-lists, three lichen species were considered extinct (EX) (*Usnea scabrata*, *Lecidea huxariensis*, *Fellhanera bouteillei*), 20 critically endangered (CR), nine endangered (EN) and eight vulnerable (VU). The four fungi species were considered CR, eight EN, and six VU, the one beetle species was EN, and 10 VU, and the one bird species was EN, and one VU. We found the most lichen species per stand (n = 89) in Kôprová Valley (KOP) in the High Tatras. This stand also hosted the most fungal species (n = 83). Most beetle species (n = 79) and bird species (n =32) were found in stand Smrekovica (SMR) in the Veľká Fatra Mountains.

### 5.3.1 Species dissimilarity

The dissimilarity of species composition was quite balanced among stands for each taxonomic group. Stands BEL and BYS show relatively higher median dissimilarity values in beetles (Figure 12a). It means that these stands tend to have a more distinct beetle species composition compared to others. On the opposite, stands SMR and PIL show relatively lower median dissimilarity, suggesting that the species composition in these stands is more similar to those in other stands. Stands DUM and JAK seem to have a higher median dissimilarity (around 0.4) compared to other stands (Figure 13a), indicating that the bird species composition in these stands is more different from other stands.

Conversely, stands like POL and TIC show lower median dissimilarity values (closer to 0.3), suggesting that their bird species composition is more similar to that of other stands. Stands DUM, HLI, and JAK show greater variability in dissimilarity values in fungi within those stands (Figure 14a). The overall dissimilarity seems relatively consistent across most stands, with the median dissimilarity values hovering around similar levels. However, stands JAK and TIC show a wider spread of values, indicating more variability in fungi species composition within these stands. Finally, stands BYS, HLI, and TIC show a slightly higher median dissimilarity of lichens (Figure 15a), suggesting that the species composition in these stands is somewhat more distinct compared to others. On the other hand, stands like DUM, PIL, and POL exhibit a slightly lower median dissimilarity, implying more similar species compositions across their respective plots.

### 5.3.2 Spatial species turnover

Most medians appear to be around 0.5, suggesting moderate turnover in beetle species composition (Figure 12b). BEL and JAK show a relatively high median turnover, suggesting higher dissimilarity in species composition across plots in these stands. SMR and TIC exhibit a lower median turnover, indicating more similar species composition across their plots. Stands like KOP and PIL have greater variability in turnover among their plots. BEL, BYS, and DUM show relatively lower median dissimilarity values of birds (Figure 13b), suggesting a more homogenous species composition across the plots within these stands. KOP and PIL have higher median values, indicating more heterogeneity in species composition across their plots. SMR and TIC exhibit a broader range of dissimilarity values, as evidenced by the presence of outliers, indicating a mix of both highly similar and highly dissimilar plots within these stands. The median spatial turnover values of fungi (Figure 14b) for the different stands are relatively similar, generally falling between 0.2 and 0.4. Stands such as BEL and SMR show a slightly lower median turnover compared to others like DUM or KOP. The presence of outliers suggests that in some plots within these stands, the dissimilarity in species composition of fungi is particularly high. Some stands, such as BEL, show relatively higher median turnover (Figure 15b), suggesting more significant variation in species composition of lichens across different plots within the stand. Other stands, like TIC, have lower median turnover values, indicating more homogeneity in species composition among plots.

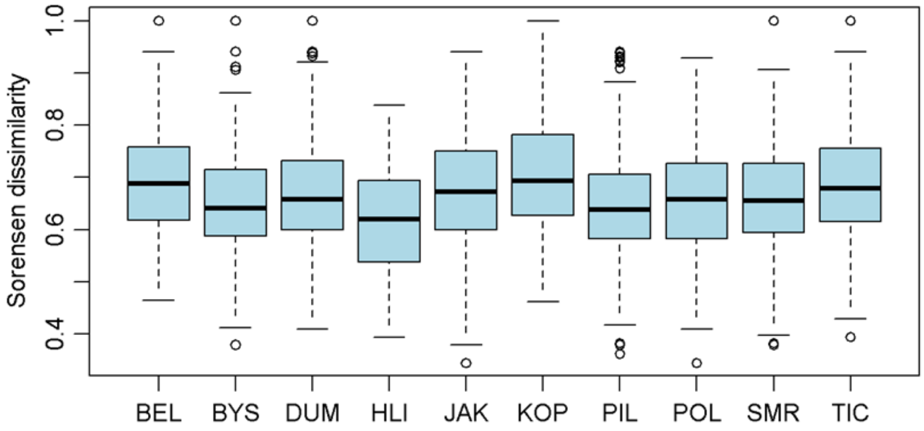
### 5.3.3 Nestedness

The nestedness values vary slightly across different stands, with most stands showing similar median values, typically around 0.2 to 0.3. Some stands, such as KOP and JAK, exhibit a wider range of nestedness values, indicating greater variability in how beetle communities are nested within these stands compared to others (Figure 12c). The presence of multiple outliers, particularly in KOP and JAK, suggests that in some plots within these stands, the beetle communities are either much more nested or less nested than the majority of the plots. The consistent median values across most stands suggest that beetle communities have a relatively uniform level of nestedness across these different environments. This could indicate similar ecological processes shaping the beetle communities in these stands. All stands exhibit varying degrees of nestedness, with the majority having nestedness values between 0.1 and 0.4 (Figure 13c). The stands show a relatively similar median nestedness, with no stand showing an exceptionally higher or lower median compared to others. However, there is some number of outliers, indicating differences in the consistency of species community nestedness among these stands. Stands like DUM and TIC have a slightly higher concentration of nestedness values around the median, suggesting more consistent nestedness within those stands compared to others like KOP and JAK, which show greater spread and more outliers.

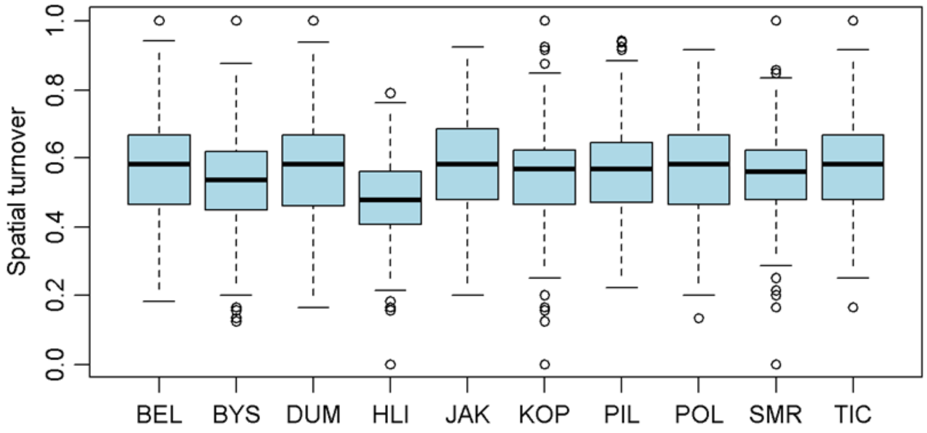
While the general trend suggests relatively low median nestedness values of fungal communities across all stands, specific stands might show slight differences in their distributions (Figure 14c). For example, stands like TIC and POL have more outliers, indicating some plots with more distinct community compositions or higher nestedness values. The observed patterns of nestedness across the stands indicate that while some fungal species communities are nested (i.e., some stands have species that are subsets of those in richer stands), there is also considerable species turnover between stands. The variability in nestedness of lichens differs across stands (Figure 15c). Some stands, like HLI and TIC, show higher median values and greater variability, indicating that the species composition in these stands might be more consistently nested across plots. In contrast, stands like KOP and PIL have lower median nestedness and less variability, suggesting a more uniform or less nested species distribution. The presence of outliers in multiple stands (e.g., BEL, HLI, SMR) indicates that there are individual plots within those stands where the nestedness is significantly higher or lower than in most other plots of the same stand.

**Figure 12.** Sørensen dissimilarity (a) and spatial species turnover (b) and nestedness (c) in species communities of beetles in the stands. Dissimilarity values with the plots of all stands (axis Y) are shown for particular stands (axis x).

a)



b)



c)

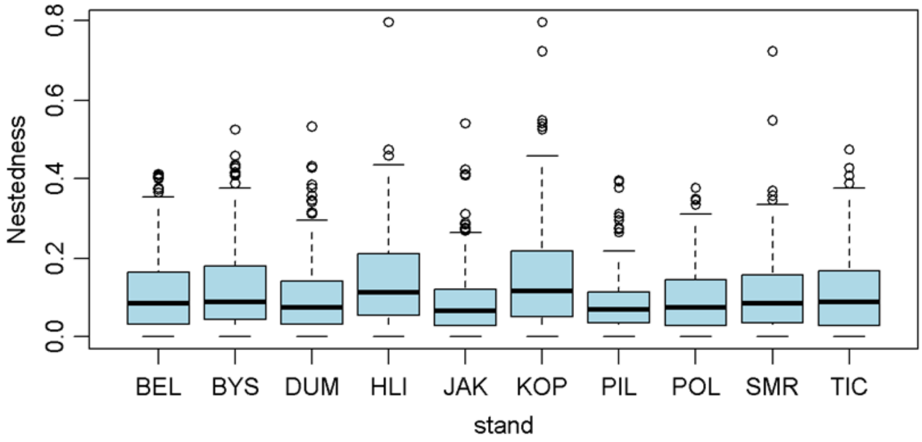


**Figure 13.** Sørensen dissimilarity (a) and spatial species turnover (b) and nestedness (c) in species communities of birds in the stands. Dissimilarity values with the plots of all stands (axis Y) are shown for particular stands (axis x).

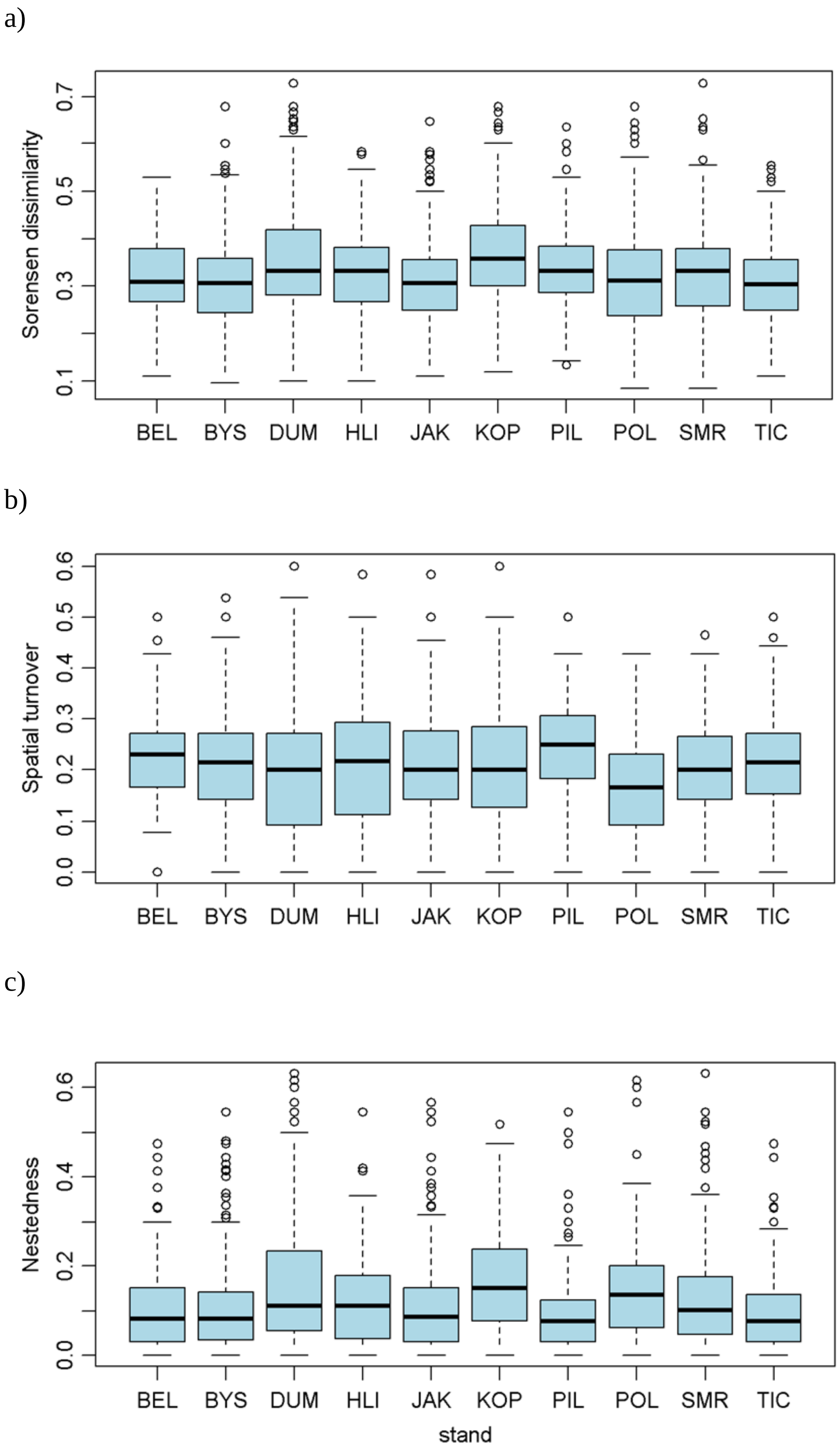
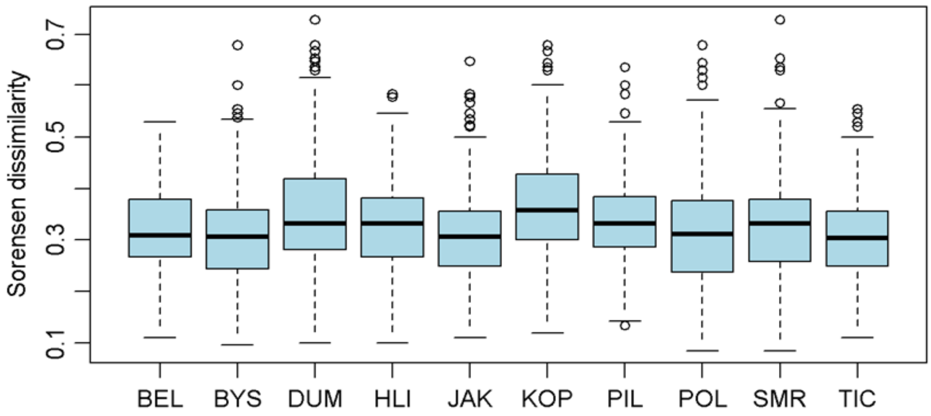
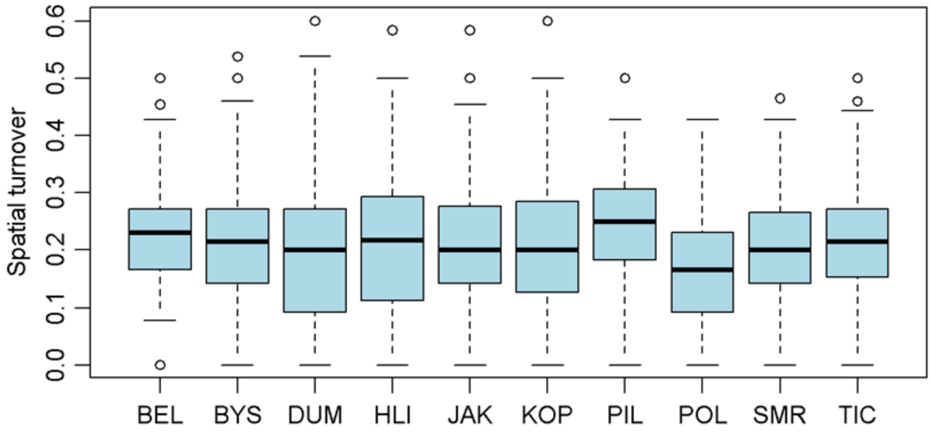


**Figure 14.** Sørensen dissimilarity (a) and spatial species turnover (b) and nestedness (c) in species communities of fungi in the stands. Dissimilarity values with the plots of all stands (axis Y) are shown for particular stands (axis x).

a)



b)



c)

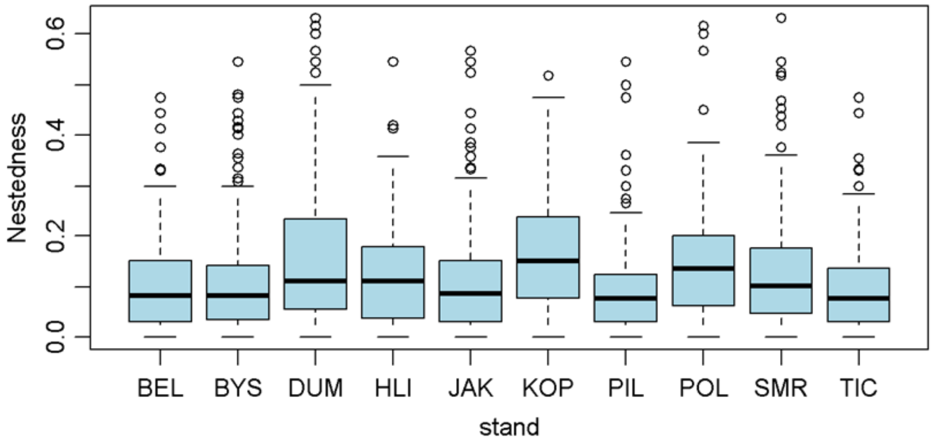
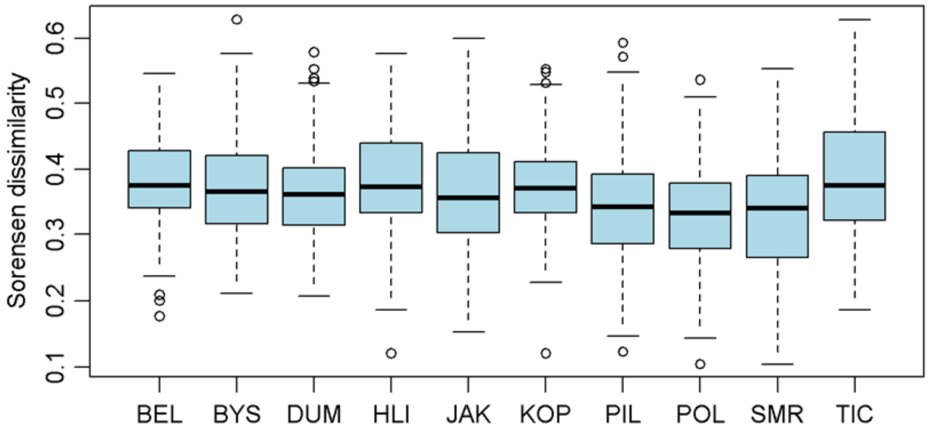
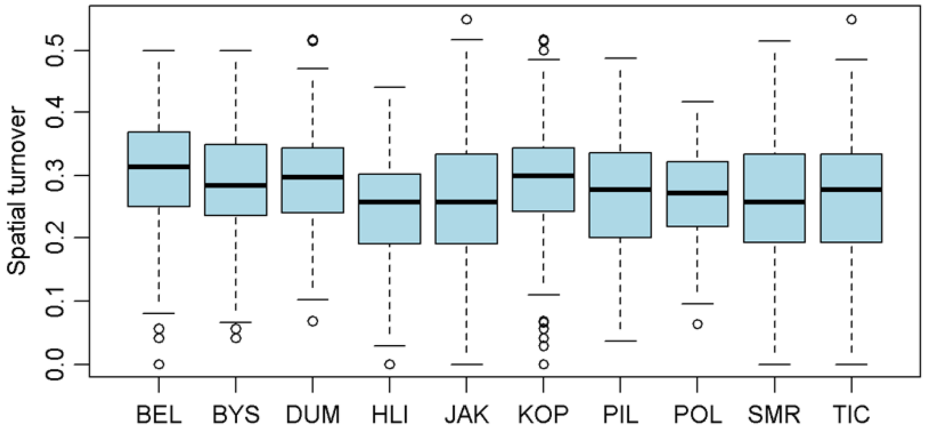


**Figure 15.** Sørensen dissimilarity (a) and spatial species turnover (b) and nestedness (c) in species communities of lichens in the stands. Dissimilarity values with the plots of all stands (axis Y) are shown for particular stands (axis x).

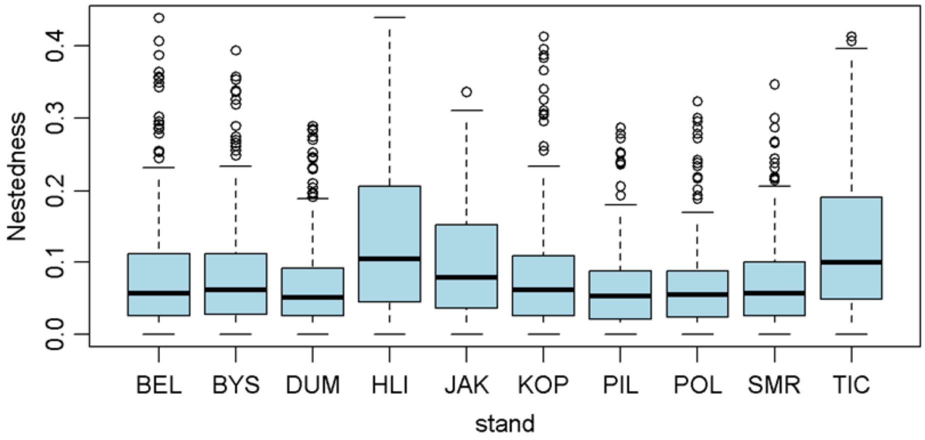
a)



b)



c)



# 6 Discussion

## 6.1 Spatial and temporal extents of natural disturbances differentiate deadwood-inhabiting fungal communities in spruce primary forest ecosystems

Understanding the processes shaping the composition of forest assemblages in response to disturbances is a key challenge in adaptive policies and strategies as natural disturbances change and forest management intensifies across the globe. Deadwood-inhabiting fungi represent an essential component of forest ecosystems, as they are associated with the cycling of wood nutrients and carbon, and can also be considered as indicators of the state of forest ecosystems (Stokland et al. 2012). We found many rare and endangered fungi in the studied primary forests, and our analyses revealed that natural disturbances have a long-term effect on present-day diversity of fungal communities. Interestingly, the effect of disturbances had different effects at different spatial scales, and the distribution of species from the regional species pool was driven by past spatiotemporal patterns of disturbance events.

### 6.1.1 Impact of forest structure on fungal communities

The heterogeneity–diversity hypothesis is a fundamental concept in ecology that explains the spatial patterns of biodiversity observed in natural environments. This hypothesis posits that an increase in spatial heterogeneity of abiotic and biotic factors results in an expansion of available niche space, thereby creating greater opportunities for a higher number of species to coexist (Zibold et al. 2024). The presence of deadwood is one of the characteristic attributes of natural forests, while natural disturbances increase its volume (Lindenmayer et al. 2012; Bässler et al. 2016; Thorn et al. 2017) and variability (Aakala 2010). The significance of deadwood in supporting biodiversity is well documented (e.g. Lassauce et al. 2011; Horák et al. 2016; Kubart et al. 2016; Doerfler et al. 2017; Thorn et al. 2018b; Jaroszewicz et al. 2021), which is in accordance with our results, where alpha-diversity of red-listed fungal species was positively influenced by higher deadwood volume. We detected a positive effect of forest structure (higher deadwood volume) on all deadwood-associated species regardless of their trophic category (including mycorrhizal species).

Conversely, we found a significant relationship between increasing canopy openness and decreasing alpha-diversity of red-listed species. Krah et al. (2018b) mentioned that the community composition of deadwood-inhabiting fungi is better explained by canopy openness than by the local amount or heterogeneity of deadwood. Yet, our results regarding the influence of canopy openness on red-listed fungi are instead in line with the findings of Bässler et al. (2010) and Thorn et al. (2018b), who showed that the diversity of deadwood-inhabiting fungi decreased with increased canopy openness. Canopy openness is associated with an increase in deadwood availability but also with changed microclimatic conditions such as increased insolation and desiccation, all of which affect fungal communities (Bässler et al. 2016; Thorn et al. 2017). Young forests with open canopies after a high-severity fire disturbance can be highly valuable for fungal biodiversity (Kouki & Salo 2020), and some threatened forest specialists, such as *Antrodiella citrinella,* were more abundant in more open stands, recently disturbed by the bark beetle, which agrees with findings of Bässler et al. (2012). However, the negative effects of canopy openness may be a transitional phase (temporary) since the dead wood in gaps will eventually become sheltered by the regeneration canopy during forest development (Meigs et al. 2017). In principle, a mosaic stand structure is largely driven by natural disturbances that generate higher structural heterogeneity, volumes of deadwood, and light availability, which are all key factors influencing fungal communities (Thorn et al. 2017).

### 6.1.2 Contrasting impact of disturbance regime components at different spatial scales (plots vs. stand)

The observed positive effect of disturbance frequency on local species richness of fungal assemblages highlighted how disturbance dynamics considerably modulate spatiotemporal distribution of species which form a regional community. The more frequent disturbance at a particular plot in the past, a higher variability of biological legacies (e.g. deadwood decay stage diversity) and environmental conditions can be expected (Kulakowski et al. 2017). Some studies suggest that for fungal species richness, the diversity and variability of deadwood is more significant than the amount of deadwood (Abrego & Salcedo 2013; Thorn et al. 2018a). According to the habitat heterogeneity theory, species richness is higher in heterogeneous systems than in homogeneous systems with the same total amount of resources (Stein et al. 2014; Stein & Kreft 2014; Hamm & Drossel 2017). The wide range of niches and sufficient amount of resources created by frequent disturbances are a prerequisite for species-rich fungal assemblages (Tomao et al. 2020). Hence, plots that cover broader gradients of regional environmental variability likely incept a bigger part of the regional species pool. From a landscape perspective, we can conclude that the distribution of species from the regional species pool is - at least to some extent - driven by a spatiotemporal pattern of disturbance events in the past. This result also explains why we did not detect the positive influence of disturbance frequency on species richness at the regional (stand) scale. However, maximum disturbance severity, another aspect of disturbance dynamics, appeared to contribute to both the constitution of and subsequent changes in the regional species pool of fungal communities. A high-severity disturbance occurring on a large scale led to regionally flattened forest structure and narrowed environmental conditions with a lack of less disturbed habitats (Senf et al. 2020). Regionally curtailed habitat heterogeneity predetermines spatial similarity in species composition of fungal communities. The severity of the disturbances regulates the amount and heterogeneity of resources (mainly deadwood) and modulates relationships among competitors (Meyer et al. 2021). Site-specific disturbance-related changes in the forest microclimate (Bässler et al. 2010) and regional habitat complexity and connectivity are also important factors for diverse fungal species composition (Abrego et al. 2017). Thus, effective protection of regionally species-rich fungal communities requires sufficiently large, unmanaged forest habitats, to allow for long-term spontaneous natural disturbance regimes.

## 6.2 Exploring the multiple drivers of alpha and beta-diversity dynamics in Europe’s primary forests: Informing conservation strategies

We studied the remaining fragments of spruce primary forests in the Western Carpathians that are key habitats for rare and endangered forest biodiversity (Kozák et al. 2021; Ferenčík et al. 2022). Based on a unique dataset covering spruce primary mountain forests in Central Europe, we quantified levels of multiple-site total beta-diversity, as well as two components of total beta-diversity (nestedness and turnover) of selected taxonomic groups assumed to be highly sensitive to environmental change: birds, epiphytic and epixylic lichens, saproxylic beetles, and deadwood-inhabiting fungi. We also quantified the effects of structural attributes of the forests on species richness and the number of red-listed species of particular taxonomic groups in the plots.

Our results show that levels of beta-diversity were high and predominantly driven by spatial turnover. This is especially true for dispersal-limited organisms having closer relationships with deadwood. In particular, the spatial turnover was strongest for lichens and fungi, including many habitat specialists and red-listed species, and relatively weak for highly mobile birds. This leads us to assume that niche specialization and dispersal limitation seem to be more important drivers of beta-diversity and turnover (valid particularly for lichens and fungi) than forest structural and environmental heterogeneity, which is opposite with e.g. Sabatini et al. (2014). Because the turnover components and total beta-diversity tend to increase with an increase in the spatial scale (Gabriel et al. 2006; Soininen et al. 2018), it becomes evident that for effective conservation of forest biodiversity, especially rare and endangered (red-listed) species, it is necessary to protect their habitats in sufficiently large areas (Abrego et al. 2014; Parmasto 2001). Nevertheless, our results documented that each studied stand (Fig. 11) had essentially unique and unrepeatable species composition irrespective of the size of the area, and was important for regional biodiversity.

Congruence in the similarity of species composition of the various taxonomic groups in our study (Table 4) indicates that the same environmental and structural attributes govern their spatial distribution, even if they have quite different ecological requirements. However, each taxonomic group could respond differently to environmental and structural heterogeneity, leading to variations in how species composition alternates (turnover) or how species are nested within sites (nestedness). Birds and beetles might have different habitat preferences and dispersal abilities compared to lichens and fungi, resulting in incongruent spatial turnover and nestedness patterns between these groups. This suggests that the underlying mechanisms driving beta-diversity components are not uniform and vary among taxonomic groups. Although the similarity of species composition was congruent among taxonomic groups (the bird group was congruent with all other groups, while beetles were correlated with birds only), neither spatial turnover nor nestedness appeared to be significant drivers of this spatial pattern. An absence of significant nested patterns in the species composition of any taxonomic group enables us to conclude that each plot in each stand contributed to the total (regional) species pool.

Multi-scale habitat patchiness, which is in Central European primary forests created by natural disturbances, helps to increase the species richness and incidence of red-listed species of different taxonomic groups (Hilmers et al. 2018) through disturbance legacies such as quantity and variability (decay stages) of standing and lying deadwood, and canopy openness. The influence of canopy openness and the presence of slightly decayed deadwood (decay stage 1) on the species richness of beetles presented here is expected and well-documented in scientific literature (e.g. Winter et al. 2015; Lettenmaier et al. 2022; Perlík et al. 2023; Seibold et al. 2023). The same is true for the relationship between forest maturity (age of the oldest trees), the volume of highly decomposed deadwood (decay stages 4 and 5), and the number of red-listed species of fungi and lichens (Dvořák et al. 2017; Halme et al. 2013; Majdanová et al. 2023). These results show that not only the volume of deadwood but also variability in size and decay stages is important for species diversity, incidence, and number of red-listed species of different taxonomic groups, which is following current knowledge (Hofmeister et al. 2015; Müller et al. 2020). Species richness of saproxylic species and the occurrence of rare saproxylic species are determined, among other factors, by the presence of deadwood, its size, and the decay stage (Heilmann-Clausen & Christensen 2004). Decaying wood is inhabited by a large number of fungi, lichens, and saproxylic insects, whose occurrence is influenced by the decay stage (Ódor & Standovár 2001; Penttilä et al. 2004). Particularly, highly decayed deadwood is largely missing in managed forests, which may be the reason for the absence of a substantial part of rare macrofungal and lichen communities in forestry-managed areas (Lonsdale et al. 2007; Vítková et al. 2018). Bird assemblage composition in the spruce primary forests of the Western Carpathians is most influenced (except for natural disturbances) by several structural variables such as density of cavities and canopy openness (Kameniar et al. 2023), volume of standing and lying deadwood, and by density of large dead trees (DBH ≥ 500 mm) (Kameniar et al. 2021). Conversely, we did not find any significant relationships between primary forest structure variables and the species richness of birds. It can be explained by the high dispersal abilities of birds and their ability to tolerate natural disturbances. Only several specialists and a high number of generalists recorded in our study may also influence the absence of significant relationships between the species richness of birds and structural variables of primary forests.

Many European primary forests are not protected and are still being lost at alarming rates (Sabatini et al. 2021). These ecosystems have evolved under a wide-range spectrum of natural disturbance regimes (Janda et al. 2017; Čada et al. 2020) without significant human impact in the past, which creates mosaic landscape structures suitable for studying forest biodiversity and forest structure through disturbance legacies (Donato et al. 2012). Our study suggests that long-term habitat continuity in primary forests (presence of trees ≥ 250 years), together with natural disturbance legacies (amount and heterogeneity of deadwood), provides a diverse range of habitat conditions for a wide range of different taxonomic groups and supports the diversity of red-listed species. The amount and heterogeneity of deadwood are the most important factors in determining assemblages of deadwood-inhabiting fungi and lichens, while assemblages of saproxylic beetles are most strongly influenced by canopy cover (Table 5). Although similar results were described in several studies from temperate forests in Europe (e.g. Seibold et al. 2016; Thorn et al. 2016; Thorn et al. 2017), our study brings new insight into biodiversity patterning at a regional scale and brings evidence that each fragment of primary forest harbours unique species composition contributing to the regional species pool. The high number of red-listed species (Table S1) across different taxonomic groups stresses the fundamental role of primary forests as biodiversity hotspots for the conservation of forest-dwelling taxa.

## 6.3 Species dissimilarity, spatial species turnover, and nestedness of environmentally sensitive forest-dwelling taxa in the spruce-dominated primary forests across the Western Carpathian Mountains

Understanding the patterns in species dissimilarity, turnover, and nestedness components of beta diversity is essential for effective conservation planning and conservation of biodiversity in ecosystems (Baselga 2010). Partitioning beta diversity into turnover (caused by the replacement of species from one site to another) and nestedness-resultant components (determined by species loss or gain in nested subsets) could provide a unique way to understand the variation of species composition, especially in fragmented habitats (Baselga & Reprieur 2015).

### 6.3.1 Species dissimilarity

The Sørensen dissimilarity index is a measure of how different two communities are in terms of species composition, with varying ranging from identical communities to completely dissimilar communities (Sørensen 1948). The differences in dissimilarity values across stands in our study could be indicative of varying degrees of habitat heterogeneity. Stands with high dissimilarity values (e.g., BEL, BYS) might be more ecologically distinct or isolated, leading to unique beetle communities. Conversely, stands with lower dissimilarity (e.g., SMR, PIL) might represent more homogeneous habitats or have more extensive species overlap with other stands. Identifying stands with high dissimilarity is crucial for conservation efforts as these stands may harbour unique species compositions that are not found in others, thereby contributing to the overall (regional) biodiversity species pool (Ferenčík et al. 2024). A lower Sørensen dissimilarity suggests that certain stands share more bird species in common, implying ecological similarities or shared environmental conditions. In contrast, higher dissimilarity indicates distinct bird communities, which could be a result of different habitat characteristics, or disturbance regimes (Drapeau et al. 2016). Although, the responses of bird assemblages to natural disturbances in spruce-dominated primary forests are more or less unbiased (Kameniar et al. 2021). Stands JAK and TIC show higher levels of variability, implying that these habitats may be more heterogeneous in terms of fungi species distribution, possibly due to varying environmental factors such as habitat structure, resource availability, or disturbance history (Hoppe et al. 2016) In contrast, stands with less variability might represent more uniform habitats where fungi species are distributed more evenly across plots.

Our results can be useful for understanding the degree of habitat differentiation and the potential drivers of biodiversity distribution across different stands. For instance, stands with higher dissimilarity may represent unique but also isolated habitats, potentially making them more important for biodiversity conservation. Conversely, stands with lower dissimilarity may be more integrated into the surrounding landscape, supporting communities of different taxonomic groups that are more typical for the region.

### 6.3.2 Spatial species turnover

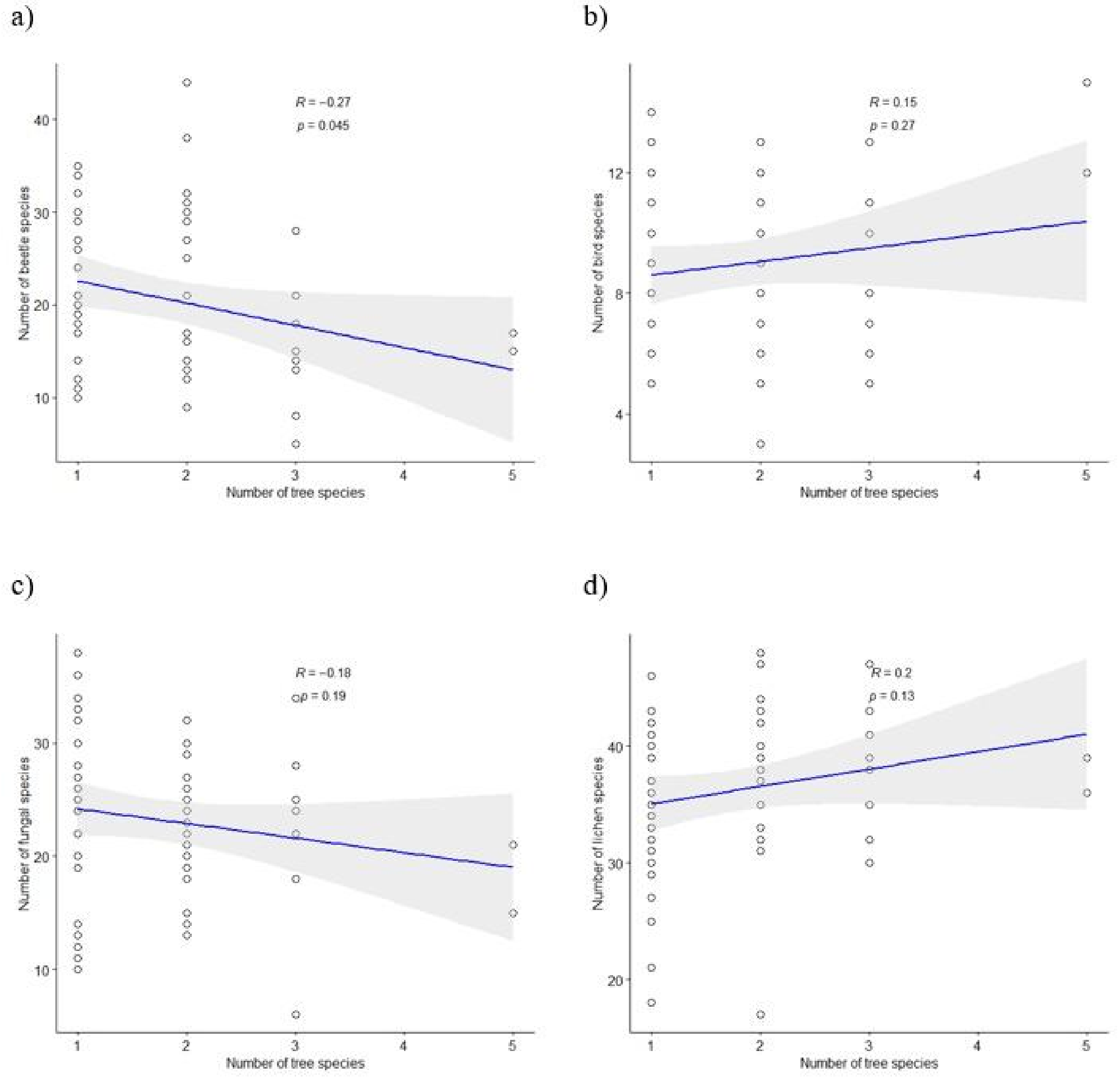
Spatial turnover implies the replacement of some species by others, as a consequence of environmental filtering or spatial and historical constraints (Qian et al. 2005). The variation in spatial turnover across stands in our study could be influenced by various ecological factors such as habitat heterogeneity, disturbance regimes, or environmental gradients within each stand. Stands with lower turnover in birds (e.g., BEL, BYS) might be more homogeneous in terms of habitat structure, leading to a more uniform bird species composition. Stands with higher turnover (e.g., KOP, PIL) might have more varied habitats and greater environmental heterogeneity, leading to a more diverse set of species compositions between plots.

The variation in spatial turnover among the stands indicates that fungal species composition varies to some degree across different plots within each stand. Stands with higher median dissimilarity values may have greater spatial heterogeneity in environmental conditions or may be influenced by factors like natural disturbances, microhabitat variation, or species dispersal limitations.

Dispersal limitations likely also play a role for the lichen group. In stands with high spatial turnover (e.g., BEL), the environmental conditions or disturbance regimes may be highly variable, leading to more diverse lichen communities between plots. The incidence of recent disturbances in this stand (Janda et al. 2017), followed by decrease of live tree density and increased canopy openness may be the main reason of higher turnover, as these conditions are known as key drivers of lichen assemblages (Langbehn et al. 2021). On the contrary, in stands with lower spatial turnover (e.g., TIC), the forest structure might be more homogeneous, resulting in a more uniform species composition. This stand was affected by higher severity disturbances in the last years (Janda et al. 2017), which may lead to more homogenous species composition of lichens. As lichens are sensitive to favourable light and moisture conditions, the dramatic environmental changes associated with high severity disturbance events may limit the colonisation ability of more sensitive species, whilst other species may be driven to extinction (Snäll et al. 2005). These results leads us to assume that dispersal limitation seems to be the more important driver of species turnover of fungi and lichens than niche specialization (Ferenčík et al. 2024). To confirm this theory, we compared the relationships between the number of tree species at research plots and species richness of all studied taxonomic groups (Figure 16). However, we did not find significant relationships between higher species richness of any taxonomic groups to a higher number of tree species. This result is opposite to Langbenh et al. (2021), where the authors found a pattern between increased species richness and the number of old-growth specialists of lichens with an admixture of tree species in spruce primary forests in the Western Carpathians.

The study of Kameniar et al. (2021) conducted at the same study area found that distinct bird assemblages (composition, diversity and overall abundance) were not influenced by structural characteristics of the forest. This may be explained by species turnover along disturbance gradients, but also by the prevalence of generalists recorded in this study. As we mentioned in chapter 2.4, multi-scale habitat patchiness, which in Central European primary forests is created by natural disturbances, helps to increase the species richness and incidence of red-listed species of different taxonomic groups (Hilmers et al. 2018) through disturbance legacies such as quantity and variability (decay stages) of standing and lying deadwood, and canopy openness. This was confirmed in the study of Ferenčík et al. (2022), where diversity of red-listed species of fungi increased due to higher disturbance frequency, mainly thanks to higher volume and variability of deadwood. We assume that the occurrence of natural disturbances with higher frequencies and different severities creates a mosaic landscape structure and higher resource availability, which is necessary not only for the diversity of fungal species, but also for a wide spectrum of other forest-dwelling taxa. This fact may be the explanation and also main driver of higher spatial species turnover (compared to nestedness) recorded in our study.

**Figure 16.** Relationships between number of tree species per plot and species richness in (a) beetles, (b) birds, (c) fungi, and (d) lichens; regression coefficients and p-values are shown in the graphs.



### 6.3.3 Nestedness

Nestedness of species assemblages occurs when sites with a smaller number of species are subset of richer sites, reflecting processes of species loss as a consequence of a large number of possible factors (Ulrich & Gotelli 2007). The variability of beetle communities in certain stands like KOP and JAK might be due to unique environmental conditions or differences in habitat heterogeneity, leading to a broader range of nestedness outcomes.

No single stand shows a significantly higher or lower median nestedness values compared to others, implying that the overall nestedness of beetle communities is consistent across the different stands sampled. However, the slight differences in outliers might be worth investigating further to understand any underlying factors that contribute to these differences. The consistency of nestedness across different stands implies a similar level of ecological processes influencing the species composition within these habitats. The presence of outliers might suggest some unique environmental factors or presence of natural disturbances in particular stands, which we explained in chapter 6.3.2.

The stands show a relatively similar median nestedness of bird communities, with no stand showing an exceptionally higher or lower median compared to others. However, there is some variation in the spread and the number of outliers, indicating differences in the consistency of species community nestedness among these stands. Stands like DUM and TIC have a slightly higher concentration of nestedness values around the median, suggesting more consistent nestedness within those stands compared to others like KOP and JAK, which show more outliers in bird communities.

The observed patterns of nestedness across the stands indicate that while some fungal species communities are nested (i.e., some stands have species that are subsets of those in richer stands), there is also considerable species turnover between stands. This could be due to environmental heterogeneity, differences in microhabitats, or other ecological factors leading to varied fungal communities. Low nestedness values, as seen in most stands, suggest that the fungal species compositions are not highly similar across the different stands. This can imply that each stand has a relatively distinct set of fungal species, potentially influenced by specific stand characteristics such as soil type, moisture levels, host tree species, or disturbance history. The results indicate a diverse fungal community structure across the studied stands, with relatively low nestedness, implying high species turnover and likely a rich diversity of fungal communities across different environmental conditions.

Stands with higher median nestedness, such as HLI and TIC, may have a core set of species that are widely shared across different plots, potentially indicating a stable lichen community. Conversely, stands with lower nestedness might have more heterogeneous species distributions, suggesting either a more diverse habitat or less predictable species associations. The results suggest that nestedness is not uniform across stands, highlighting that environmental factors or the specific characteristics of each stand may influence the structure of the fungal communities. Stands with similar nestedness patterns may share ecological similarities, while those with divergent patterns might differ significantly in terms of habitat, disturbance, or other ecological factors.

Human-induced habitat fragmentation undermines the preservation of biological communities, leading to a rapid decline in biodiversity. This decline occurs as species face increased local extinction risks due to habitat loss, which leaves forest-dwelling taxa in smaller habitats more vulnerable to extinction (Krauss et al. 2010). Consequently, smaller habitat patches are often deemed less critical for conservation efforts and receive minimal protection (Gibson et al. 2013). Additionally, habitat fragmentation frequently enhances beta-diversity by causing a patchy distribution of species due to varying local extinction rates across different fragments (Guadagnin et al. 2005). This fragmentation poses a conservation challenge. While the remaining smaller fragments may not suffice to sustain viable populations, they contribute significantly to the regional species pool (Kattan et al. 2006). Thus, the conservation potential of these small habitat remnants should not be underestimated. It is therefore important to determine if the compositional differences among fragments stem from species turnover or nestedness.

Our results showed that each stand had unique species composition and was important for regional biodiversity. Spatial turnover was significantly higher than nestedness and contributed more to total beta diversity than the nestedness. Turnover tends to increase with increasing of an area (Soininen et al. 2018). From that reason it becomes evident that effective conservation of sufficiently large areas supports the protection of wide spectrum of forest biodiversity, especially rare species and species with specific habitat requirements (Abrego et al. 2014). Our results documented unique species composition at each stand irrespective of the size of the area. This is true like for the smallest stand Tichá Dolina (TIC) with an area of primary forest 41 ha, as well as for the biggest stand Poľana (POL) with an area of 494 ha. However, our results showed slightly higher nested pattern in bird communities exactly in the smallest stands TIC, as well as in stand Ďumbier (DUM) (62 ha). And the opposite, stands with the higher area of primary forests, Kôprová dolina (KOP) (122 ha), or Piľsko (PIL) (431 ha) had higher median values, indicating more heterogeneity in species composition across their plots. The uniqueness of stand KOP, as a part of the large unmanaged protected area, is also supported by the highest recorded incidence of lichen and fungal species per stand (section 5.3).

The fundamental question what we should ask is, how the area of the respective stands, isolation, and landscape connectivity around them influences the species composition. Most of investigated stands in our study are highly isolated, what relates to wind and bark beetle outbreaks in the last several decades followed by salvage logging (Mikoláš et al. 2019). Habitat fragmentation is often defined as a process during which “a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original” (Wilcove et al. 1986). By this definition, a landscape can be qualitatively categorized as either continuous (containing continuous habitat) or fragmented, where the fragmented landscape represents the endpoint of the process of fragmentation (Fahrig et al. 2003), what is consequently connected with isolation of the fragments and potentially by the loss of biological and genetic diversity inside the fragments. This factor represents high risk especially for the dispersal limited organisms. The solution for the negative situation of abovementioned isolated fragments of primary forest in our study area is to directly stop the habitat loss and then to apply conservation and management strategies aimed foremost at habitat restoration (Fahrig 1997). Establishing a network of strict forest reserves with adequate area and landscape connectivity at a regional scale is crucial for conserving forest-dwelling taxa that are sensitive to management practices. Such reserves can serve as refuges and sources of biodiversity, allowing for the preservation of the highest tree ages and supporting a broad spectrum of species at the landscape level (Moning & Müller 2009; Gossner et al. 2013).

We believe that our kind of analysis and results may help in understanding the factors driving the diversity of different taxonomic groups, and the ecological processes that maintain this diversity in different forest stands. In conclusion, we suggest that management should recognize natural disturbances as a key part of ecosystem dynamics in the spruce-dominated mountain forests instead of aiming to eliminate them (through salvage logging) and should account for their occurrence in management planning as well as mimicking their patterns to foster biodiversity in forest landscapes.

# 7 Management implications

Our research was conducted in spruce-dominated primary forests, which are shaped by natural processes that generate high structural complexity and habitat heterogeneity. This complexity drives a high incidence of specialized organisms and consequently acts as refuges for biodiversity, hosting unique ecological interactions and evolutionary processes absent in managed ecosystems. Here, we present the implications for conservation management in forestry-managed landscapes, in order to conserve rare forest-dwelling taxa and stop the rapid loss of biodiversity in the managed forests of the Western Carpathian region.

To maximise forest biodiversity in managed forests it is necessary to diversify the forest management regimes, which will generate higher habitat heterogeneity at a landscape scale, and this will support numerous groups of species (Duflot et al. 2022). Both early and late successional stages support a wide range of taxa, hence a comprehensive conservation strategy has to maintain all successional stages in the landscape. However, for the conservation of regional biodiversity in multifunctional forests in the Western Carpathians, this would mean that the proportion of stands in early and late successional stages should be increased (Hilmers et al. 2018). Conservation activities aimed at a wide spectrum of taxonomic groups in temperate forests of the whole Carpathian's ecoregion should aim at increasing the amount and variability of standing and lying deadwood, creating sunny exposed areas, and trying to increase the age of the forests, as age is one of the parameters which can be most easily controlled by forest management (Lassauce et al. 2012). Mimicking natural forest structure and patch dynamics would improve structural heterogeneity and the functioning of forest ecosystems (Lindenmayer & Franklin 2013), yet the favoured close-to-nature forestry approach fails regularly to meet these expectations (Topercer & Maderič 2022). Creating a network of strict forest reserves with sufficient area and landscape connectivity at the regional scale, as refuges and sources for management-sensitive forest-dwelling taxa, is the most effective way to reach the highest tree age and to support and protect a wide range of biodiversity at the landscape scale (Gossner et al. 2013; Liu et al. 2022; Moning & Müller 2009). Rewilding of previously managed (secondary old-growth) forests creates mosaic structures with varying tree ages and canopy openness that support both, early- and late-successional biodiversity. These forests represent great potential for the conservation of biodiversity especially in the world of accelerating changes in environmental conditions. Finally, a crucial step is to identify all existing primary forests globally and stop the rapid loss and fragmentation of the remaining primary forests (Mikoláš et al. 2019; Mikoláš et al. 2023).

Deadwood is a vital source of life, offering habitat and substrate for a diverse array of forest-dwelling taxa (Stokland et al. 2012). Over 30% of a forest's total biodiversity is directly associated with deadwood in different tree species, diameters, and stages of decay. However, it remains unclear how deadwood can best be managed to most effectively promote the wide range of taxonomic groups. In managed forests, deadwood volume is generally low in comparison to natural forests (Siitonen et al. 2000; Nagel et al. 2017). This fact is caused by the harvesting of trees after they reach the target age for felling. This means that only a small amount of deadwood, usually stumps, twigs, and branches, is kept in forests, and large logs are absent (Kruys et al. 1999). Large logs are critically important for deadwood continuity because they remain longer in the forests as a habitat for organisms compared with small-deadwood dimension, which offers habitat only temporarily (Lachat et al. 2013), which may result in extinction, especially for species with unique niche requirements.

Each of our studied taxonomic groups is specific and has different and unique ecological and habitat requirements. Although there are some similarities, our recommendations are proposed for each taxonomic group separately.

## 7.1 Deadwood-inhabiting fungi

Deadwood-inhabiting fungi are important decomposition agents and are associated with fluxes of carbon and nutrients (Boddy et al. 2008; Stokland et al. 2012). Fungi, as a vital component of forest ecosystems, occupy a plenty of spatial and trophic groups (Persiani et al. 2010). Due to specific habitat requirements and sensitivity to forest management (Komonen & Müller 2018; Tomao et al. 2020), they are frequently used as indicators of forest naturalness (Christensen et al. 2004; Stokland et. al. 2012). In addition, conservation of fungal diversity is essential to maintaining the provisioning of ecosystem services essential to forest ecosystem functioning and human well-being (Heilmann-Clausen et al. 2014).

One of the most important forest attributes that influences the fungal communities is the tree age (Ferenčík et al. 2024), which is one of the parameters most easy to control with forest management (Lassauce et al. 2012). Tree cover significantly influences the diversity of wood-inhabiting fungi (Bässler et al. 2010) by altering microclimatic conditions. The openness of the canopy affects key factors such as temperature, temperature fluctuations, and moisture availability, which are crucial for the fungal decomposition of wood (Rayner & Boddy 1988). Although microclimate has been shown to have a lesser impact on fungal diversity compared to other factors, such as host tree diversity (Krah et al. 2018b). Bässler et al. (2010) emphasized the importance of microclimatic changes in shaping fungal richness and community composition, particularly on fine woody debris.

Deadwood constitutes a significant element of forest structure and is crucial for biodiversity conservation, as it offers habitats for numerous wood-dependent organisms (Parisi et al. 2018). Deadwood can be categorized into stumps, standing deadwood (including dead trees and snags), and lying deadwood (such as logs, branches, and twigs). Importance of large dimensions of woody debris is crucial for wood-inhabiting fungi and is well documented in scientific literature (Parisi et al. 2018). Large logs have the longer persistence on the forest floor because of a lower decomposition rate. Lack of these logs in managed forests may be the reason for the absence of rare fungal communities. Drawing from the extensive body of literature on deadwood as a crucial indicator of biodiversity and leveraging current expertise, several strategies have been identified to enhance the quantity and diversity of deadwood in managed forests. These strategies include retaining individual live trees or clusters of trees, as well as preserving snags and existing deadwood (Vítková et al. 2018). Adopting deadwood enhancement strategies can lead to greater diversity in deadwood, both in terms of decay stages and size variations, which plays a more crucial role in supporting biodiversity than merely increasing deadwood quantity (Rimle et al. 2017). It is essential to collaborate with natural processes that generate deadwood while also enhancing connectivity between existing deadwood structures by artificially creating additional deadwood and safeguarding what already exists (Humphrey & Bailey 2012). The beneficial impact of the quantity of deadwood, along with the diversity in deadwood size and decomposition stages, on the richness and community composition of wood-inhabiting fungi has also been documented in tropical ecosystems (Olou et al. 2019). This indicates a consistent pattern of diversity drivers for wood-inhabiting fungi across various ecosystems globally.

Timber harvesting following thinning, or regeneration cuts significantly impacts fungal occurrence. This process can alter the physical properties of the soil, leading to soil compaction and a consequent decrease in water retention capacity (Picchio et al. 2012). A study investigated tree harvesting after a natural disturbance, such as wind damage, in boreal ecosystems revealed that salvage logging can decrease macrofungal species richness and fruiting abundance (Ford et al. 2018). Notably, greater species richness was observed in plots where fallen trees were left undisturbed on the forest floor. This finding is attributed to a reduction in deadwood availability and changes in the ectomycorrhizal-associated plant community, driven by the loss of host trees and soil disturbance. If large-scale salvage logging is applied, increased isolation of individual forest fragments may affect the occurrence and distribution of fungi, especially species with specific requirements (e.g. Penttilä et al. 2004; Laaksonen et al. 2008; Nordén et al. 2013).

On the other hand, our results suggest that the predicted increase in disturbance severity could lead to stand scale homogenization and a consequent decrease in species richness of fungal communities. This effect will be especially pronounced in small and mutually isolated forests, because the smaller and more distant the fragments are, the higher is the probability of structural homogenization by a single high severity disturbance, and connectivity and possible colonization of new areas by fungi is more problematic (Berglund & Jonsson 2008). Based on current knowledge of primary forest dynamics, only large tracts of intact forest provide a sufficient range of seral stages under natural disturbance regimes (Mikoláš et al. 2021). Thus, effective protection of fungi, especially rare and endangered species, can only be achieved by protecting their habitats (Parmasto 2001) and it is necessary to implement such protection on sufficiently large areas (Abrego et al. 2014). In managed areas, forests must be allowed to attain older ages and higher deadwood volumes, if they are to reach higher fungal diversity (Dove & Keeton 2015). Our results can be applied in ecological forestry approaches. Mimicking natural forest structure and dynamics that would improve structural heterogeneity and late-successional forest characteristics can contribute to the maintenance of fungal diversity and the functioning of ecosystems in general (Lindenmayer & Franklin 2013).

## 7.2 Lichens

As we mentioned in chapter 2.4.2, the growing body of literature demonstrates the sensitivity of epiphytic lichens to forest management. Only a small area of the European forests is in old-growth (natural) conditions. The rest are managed forests for timber production. The forest management approaches, the most frequently used in the spruce-dominated forests are:
a) The shelterwood system, based on thinning and final harvest with a rotation cycle between 80-120 years; b) Selective cutting, while especially the shelterwood system, is a source of threat for many forest-dwelling lichens (Nascimbene et al. 2013). The last decades, the rotation cycle are becoming shorter because of higher incidence of natural disturbances followed by salvage logging.

Light conditions are crucial in determining the composition of lichen communities, and the advantages of selective cutting are likely linked to the sustained presence of canopy cover

over time. However, the majority of lichens found in European temperate forests thrive under moderate light conditions, avoiding both direct sunlight and deep shade. Consequently, excessive canopy closure can be harmful to epiphytic lichens in these forests (Moning et al. 2009; Nordén et al. 2012; Király et al. 2013). Nordén et al. (2012) highlight the positive impact of partial cutting on lichen conservation, while Moning et al. (2009) suggest that stands with less than 50% canopy cover are preferable. These conclusions are supported by Nascimbene et al. (2013), who observed more diverse lichen communities in selectively cut forests compared to abandoned silver fir-dominated forests with higher canopy cover, thereby recommending harvesting practices that maintain intermediate light conditions.

The impact of varying management intensities in coppice forests on epiphytic lichens remains insufficiently explored, particularly regarding the potential of traditional coppicing techniques for lichen conservation compared to other management practices or modern short-rotation coppicing methods (Verwijst et al. 2005). Existing studies reveal significant differences in species composition between short-rotation coppices and mature coppices (Giordani, 2012), corroborating earlier findings from boreal regions where Gustafsson (1986) reported a limited lichen flora in short-rotation coppices. Research examining the replacement of native coppice forests with monocultures managed under short rotation cycles indicates a reduction in lichen diversity and a trend towards species homogenization (Nascimbene & Marini 2010; Nascimbene et al. 2012a).

In the review of Nascimbene et al. (2013) authors state, that several studies provide specific recommendations for reducing the impact of forestry practices. Key suggestions include: (a) favouring selective cutting over the shelterwood system; (b) mitigating the shelterwood system’s adverse effects by extending the rotation period and preserving clusters of mature trees during the final harvest; (c) promoting the development of stands with moderate canopy openness; (d) retaining logs and snags in production forests; (e) conserving large old trees within production forests, with some left to decay naturally as "eternity trees"; (f) maintaining tree species diversity in mixed stands; (g) preserving forest fragments surrounding species-rich old-growth remnants to establish a network of set-aside areas; and (h) using indicator species for rapid assessments of forest sites with high conservation value.

One of the most important forest attributes that influences the lichen communities (species richness and the number of red-listed species) is the tree age. The next important attribute is a highly decomposed lying deadwood (decay stages 4 and 5). Both attributes are also important for the fungal communities (Ferenčík et al. 2024). These characteristics commonly occurred in natural forests. It should be the priority of close-to-nature forest management to mimic the natural dynamics to support the species richness and incidence of red-listed species of lichens.

## 7.3 Saproxylic beetles

The alteration of natural ecosystems has posed a global threat to biodiversity, with forests being particularly vulnerable. Efforts to mitigate biodiversity loss in forested areas frequently involve enhancing the availability of deadwood, an essential resource for numerous decomposer species (Gossner et al. 2016). Saproxylic beetles are among the most endangered taxonomic groups, significantly impacted by alterations in forest ecosystems. In addition to human-induced disturbances, such as forest fragmentation and a reduction in dead wood, the expansion of uniform, closed-canopy forests driven by natural succession poses a primary threat to numerous saproxylic species. This issue is particularly critical in key conservation regions across Europe (Jaworski et al. 2016). Many saproxylic species become threatened with extinction as a consequence of abovementioned factors (Eckelt et al. 2018). The quantity, spatial distribution, average size, and decomposition stage of deadwood play a critical role in shaping saproxylic communities, which rely on a diverse range of ecological niches to support various specialized species assemblages. However, when addressing specific conservation management objectives, a more comprehensive understanding of the population dynamics of threatened species is essential.

Red-listed species exhibit distinct habitat preferences (Heilmann-Clausen & Christensen 2004), highlighting the need for more focused research on their distribution patterns, especially in mountainous forests. Additionally, species that depend on rare substrates or have limited dispersal capabilities are particularly vulnerable to forestry practices that disrupt habitat continuity. Is important to stress the importance of preserving and enhancing mountain forests through sustainable management practices that prioritize the conservation of saproxylic species and their habitats at both local and regional levels. Ensuring the functionality and productivity of mountain ecosystems requires promoting structural heterogeneity and conducting precise evaluations of deadwood dynamics across various spatial and temporal scales. The significance of deadwood in supporting biodiversity within forest ecosystems is well-established. Recent research has further validated its critical role in sustaining species diversity, increasing carbon storage, and fostering biological activity in the soil (Blonska et al. 2017).

Drawing on the extensive body of literature highlighting deadwood as a critical indicator of biodiversity, as well as established expertise, several strategies have been identified to enhance the quantity and diversity of deadwood in managed forests. These include retaining individual living trees or groups of trees, as well as preserving snags and existing deadwood. While these methods align with research on the functional effectiveness of biodiversity-promoting measures (Hämäläinen et al. 2014), additional approaches can also be considered, such as leaving fallen logs post-harvest, retaining uprooted trees, or artificially creating deadwood through techniques like generating high stumps or tree girdling. Combining various deadwood management strategies is recommended to optimize both the volume and heterogeneity of deadwood (Ranius et al. 2005). Allowing individual trees or small clusters to naturally complete their life cycle is a beneficial strategy to enhance deadwood availability. These retained trees or groups may become veteran trees, which eventually develop into snags (unless they are toppled by wind) and will gradually decompose into coarse woody debris over time. The rate of decay accelerates under conditions such as increased air humidity, higher temperatures, and longer growing seasons. Priority should be given to the oldest and largest trees, particularly those that already host microhabitats, and those with some existing deadwood (Bouget et al. 2014). When selecting trees for retention and snag formation, priority should be given to those exhibiting microhabitats or structural defects within the lower 2 metres of the trunk. Healthy logs and stems with a diameter of less than 30 cm should only be retained if no other alternatives are available, as it is advantageous to preserve larger segments of deadwood, which have a longer decomposition period (Bače & Svoboda 2015).

Is important to retain sunny-exposed trees in gaps (similar case for lichens) or under more open canopy as a part of deadwood enhancing management (Gustafsson et al. 2010), and these microclimate conditions support the incidence especially saproxylic umbrella species (Buse et al. 2007). In addition, the sunny and warm conditions in gaps may attract beetle species that cannot tolerate shade, drawn more to the open environment than to the specific microhabitat of deadwood-bearing trees.

To effectively achieve deadwood management objectives, it is crucial to consider the diversity of deadwood types when selecting individual trees or tree groups for retention. In some cases, standing deadwood supports a greater diversity of saproxylic species than lying deadwood. For example, oak snags have been shown to harbour more saproxylic beetle individuals than fallen logs (Bouget et al. 2012). Conversely, lying deadwood often supports a higher abundance of fungi and bryophytes compared to standing deadwood (Jonsson et al. 2010). Furthermore, similar substrates in different locations, such as the forest floor, tree stems, or canopy branches, can create distinct ecological niches for different species. For instance, snags were found to accommodate species that were absent from lying logs (Bouget et al. 2012).

And finally, we cannot forget the importance of different decay stages for saproxylic beetles. The decomposition dynamics of deadwood differ depending on the type, with standing deadwood generally decaying at a slower rate compared to lying deadwood (Bouget et al. 2012). Therefore, it is essential for forest management practices to preserve or introduce various types of deadwood to maintain a continuum of decay stages, which provide habitat not only for saproxylic species but also for a broader range of organisms. In addition to its importance for saproxylic diversity, decaying wood plays a crucial role in natural regeneration, particularly in mountain forests. As a substrate, deadwood promotes the establishment and survival of naturally regenerating species such as Norway spruce (Zielonka 2006; Bujoczek et al. 2015).

## 7.4 Birds

Forest management affects conditions for early - and late-successional organisms, and forest managers and conservationists require information for balancing opposing habitat needs of both these guilds (Akresh et al. 2023). Birds are one of the most studied taxonomic groups (Collen et al. 2009), mainly due to their easy observability compared with other taxonomic groups. Production-focused silviculture typically results in a simplified forest structure, which reduces bird biodiversity by excluding species that rely on late-successional habitats or areas affected by natural disturbances (Paillet et al. 2010). There is no consensus, how forest management impacts bird biodiversity, and fundamental questions are mainly the area of forest stands, forest composition, type and intensity of forestry practices (Franklin et al. 2019; Paillet et al. 2010). Intensive tree harvesting decreases canopy cover, facilitating the growth of dense understory vegetation favoured by many shrubland and early-successional bird species (Smetzer et al. 2014). Conversely, unharvested forests or stands subjected to light thinning generally support bird species that require closed-canopy environments for nesting (Webb et al. 1977). It should be noted that species with differing life history strategies are differentially affected by forestry activities and habitat fragmentation (Ewers & Didham 2006) and some rare forest specialists, such as Western Capercaillie (*Tetrao urogallus*), are strongly negatively affected by forest management (Virkkala 1987; Mikoláš et al. 2017; Klinga et al. 2019).

Considering that Capercaillie is an umbrella species whose protection helps protect a wide spectrum of other species, our recommendations are formulated especially for this endangered species and its habitats.

A common approach to integrate conservational goals into forest management practices is to create environmental attributes considered suitable for a target species (Halme et al. 2013). For birds this may include retention of tree related microhabitats, deadwood (standing and lying), or understory composition and quality (Bauhus et al. 2009; Broome et al. 2014). The Capercaillie is considered an indicator for species-rich, open, structurally heterogeneous, mature conifer-dominated forests, and its occurrence is directly connected with natural disturbance events (Mikoláš et al. 2017, Mikoláš et al. 2019). Structural parameters typical for late-successional stages in natural forests and natural disturbance dynamics are often lacking in commercial forests focused on economic rentability (Bauhus et al. 2009). Today, central European forests are mostly continuously covered, which is associated with increasing tree density and closed canopy (Gustafsson et al. 2020). The light availability is crucial for Capercaillie through increasing blueberry growth and fruit development in general (Eckerter et al. 2019).

Habitat management for capercaillie conservation involves incorporating small clearings and selective canopy thinning into existing forestry operations, applied at varying intensities throughout the population's entire range. Active management needs to be used primarily to restore degraded habitats in locations with the presence of the Capercaillie. Forest stands up to 50 years old are especially suitable for this, where the structure of the stands can still be significantly changed without significant impact on their stability. They must also have the potential to quickly establish a rich blueberry understory after relighting. It is necessary to apply special management "capercaillie-friendly forest management" to newly created clearings, in worts and in stands intended for thinning. The goal is to quickly create habitats with a suitable age-species-spatial structure of forest stands for Capercaillie. In the wort, the existing open areas should be enlarged to a size of 20-30 m, separated by approx. 30-40 m. Trees should be removed in these gaps. These small open areas should be distributed unevenly along the stands and connected by 3-8 m wide lines. The crown cover should be reduced to 70% or less during thinning interventions. This thinning should not be distributed evenly over the entire area, but some areas should be taken over more than others so as to create small open areas - vegetation gaps. Preferably, more intensive thinning should be carried out in younger stands (up to 50 years old) and in areas with weaker growth (e.g. in wet areas). The result should be a mosaic of open gaps and relatively dark denser areas. Approach lines should be relatively wide (5-9 m) (ŠOP SR 2018).

Through the implementation of single-tree selection, group selection, conversion of spruce stands to mixed-species forests, increasing densities of large snags, and fostering multi-layered canopies at the stand level, foresters can expedite the development of suitable natural forest habitats (Franklin et al. 2002). Establishing sufficiently large areas of high-quality habitat, approximately 250 km², is crucial for sustaining viable capercaillie populations (Grimm and Storch, 2000). Therefore, management strategies to maintain viable populations must consider broader landscape-scale dynamics to create a mosaic of suitable habitats and ensure connectivity between habitat patches (Graf et al. 2009; Segelbacher et al. 2003). For the long-term conservation of capercaillie populations in the Carpathians, further evaluations of current habitat suitability are needed. This includes the development of habitat suitability models to determine the optimal extent of suitable habitats and their connectivity (Braunisch & Suchant 2008). These models should be regionally adapted, as species-habitat relationships can vary due to site-specific conditions, vegetation types, and successional processes (Graf et al. 2005), as demonstrated by differences in capercaillie habitat preferences between Norway and central Europe. Landscape-scale management should prioritize preserving old-growth forests and limiting fragmentation and large-scale deforestation to promote a more ecologically sustainable forestry model in central Europe.

# 8 Conclusions

Our findings provide a significant advancement in understanding how historical natural disturbances and multiple forest structural attributes influence alpha, beta, gamma-diversity, and the incidence of red-listed species for different taxonomic groups across varying temporal and spatial scales.

Disturbances have long-lasting impacts on fungal species diversity, with the attributes of these disturbances affecting different spatial scales in distinct ways. We emphasize the importance of incorporating this enhanced understanding of natural disturbances into forest management strategies, particularly as a conservation tool in protected areas. From the perspective of climate change, our results indicate that predicted shifts in disturbance regimes (Seidl et al. 2014) could potentially have a positive effect on fungal diversity, provided salvage logging is avoided and large forest landscapes remain strictly protected. It is also worth noting that the anticipated increase in disturbance frequency could support the diversity of red-listed species and contribute to habitat restoration in previously managed forests if salvage logging is discontinued (Thom et al. 2017). Almost all recent logging activities in primary and natural forests across Central Europe have been carried out as salvage logging, often justified as a protective measure against natural disturbances (Mikoláš et al. 2017; Mikoláš et al. 2019). However, our findings demonstrate that natural disturbances are integral to forest ecosystem dynamics, as disturbance frequency generates a wide range of habitat conditions that support diverse communities and enhance the diversity of red-listed species.

Additionally, our results show that beta-diversity levels across four taxonomic groups (birds, epiphytic and epixylic lichens, saproxylic beetles, and deadwood-inhabiting fungi) were high, primarily driven by spatial turnover. This was particularly evident for dispersal-limited organisms with close associations to deadwood. Specifically, spatial turnover was most pronounced for lichens and fungi, which include many habitat specialists and red-listed species, and relatively weaker for highly mobile birds. These findings suggest that niche specialization and dispersal limitation are more significant drivers of beta-diversity and turnover, especially for lichens and fungi, than forest structural and environmental heterogeneity. Given that both turnover components and overall beta-diversity tend to increase with spatial scale (Gabriel et al. 2006; Soininen et al. 2018), it becomes clear that effective conservation of forest biodiversity, particularly for rare and endangered (red-listed) species, requires the protection of their habitats across sufficiently large areas (Abrego et al. 2014; Parmasto 2001). Nevertheless, our results demonstrate that each studied stand exhibited a unique and irreplaceable species composition, irrespective of area size, highlighting their significance for regional biodiversity.

Congruence in the similarity of species composition of the various taxonomic groups in our study indicates that the same environmental and structural attributes govern their spatial distribution, even if they have quite different ecological requirements. Nevertheless, each taxonomic group may respond uniquely to environmental and structural heterogeneity, resulting in variations in species turnover (the replacement of species between sites) and nestedness (the degree to which species assemblages in smaller or less diverse sites are subsets of those in larger or more diverse sites). For example, birds and beetles, with their distinct habitat preferences and dispersal capacities, may exhibit different spatial turnover and nestedness patterns compared to lichens and fungi. This indicates that the mechanisms driving beta-diversity components are not consistent across taxonomic groups. While species composition similarity was generally congruent across groups (with birds showing congruence with all other groups and beetles correlating with birds), neither turnover nor nestedness significantly contributed to this spatial pattern. The lack of significant nestedness in any taxonomic group's species composition suggests that each plot within each forest stand adds uniquely to the total (regional) species pool.

Our study provides new insights into the effects of historical natural disturbances and forest structure on biodiversity within primary forests. Additionally, it sheds light on biodiversity patterns at both local and regional scales, highlighting that each fragment of primary forest harbours a distinct species composition that contributes to regional biodiversity. The high occurrence of red-listed species across various taxonomic groups underscores the critical role of primary forests as biodiversity hotspots essential for the conservation of forest-dwelling taxa. Establishing a network of strict forest reserves with adequate area and landscape connectivity at a regional scale is crucial for conserving forest-dwelling taxa that are sensitive to management practices. Such reserves can serve as refuges and sources of biodiversity, allowing for the preservation of the highest tree ages and supporting a broad spectrum of species at the landscape level (Gossner et al. 2013; Liu et al. 2022; Moning & Müller 2009). Rewilding previously managed (secondary old-growth) forests creates mosaic structures with varying tree ages and canopy openness, benefiting both early- and late-successional species. These forests offer substantial potential for biodiversity conservation, particularly in the face of accelerating environmental changes. Ultimately, the primary objective remains to identify and protect all existing primary forests globally, and halting their rapid loss and fragmentation (Mikoláš et al. 2019; Mikoláš et al. 2023).

# 9 Literature

Aakala, T. (2010). Coarse woody debris in late-successional *Picea abies* forests in northern Europe: Variability in quantities and models of decay class dynamics. *Forest Ecology and Management*, 260, 770-779.

Abrego, N., & Salcedo, I. (2013). Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? *Forest Ecology and Management*, 291, 377-385.

Abrego, N., Garcia-Baquero, G., Halme, P., et al. (2014). Community Turnover of Wood-Inhabiting Fungi across Hierarchical Spatial Scales. *PloS One*, 9(7), e103416.

Abrego, N., Christensen, M., Bässler, C., et al. (2017). Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models. *Fungal Ecology*, 27, 168-174.

Aerts, R., & Honnay, O. (2011). Forest restoration, biodiversity and ecosystem functioning. *BMC Ecology*, 11, 1-10.

Akresh, M. E., King, D. I., McInvale, S. L., et al. (2023). Effects of forest management on the conservation of bird communities in eastern North America: A meta-analysis. *Ecosphere*, 14(1), e4315.

Anderson, M. J., Crist, T. O., Chase, J. M., et al. (2011). Navigating the multiple meanings of β diversity: a roadmap for practicing ecologist. *Ecology Letters*, 14(1), 19-28.

Ansaldo, D., Vergara, P. M., Carvajal, M. A., et al. (2021). Tree decay modulates the functional response of lichen communities in Patagonian temperate forests. *Science of The Total Environment*, 771, 145360

Asplund, J., & Wardle, D.A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews*, 92(3), 1720-1738.

Bače, R., & Svoboda, M. (2015). Management mrtvého dřeva v hospodářských lesích - certifikovaná metodika (Deadwood management in production forests - certified methods).

Bače, R., Schurman, J.S., Brabec, M., et al. (2017). Long-term response of canopy-understorey interactions to disturbance severity in primary *Picea abies* forests. *Journal of Vegetation Science*, 28(6), 1128-1139.

Bader, P., Jansson, S., Jonsson, B.G. (1995). Wood-inhabiting fungi and substratum decline in selectively logged bereal spruce forests. *Biological Conservation*, 72(3), 355-362.

Baeten, L., Vangansbeke, P., Hermy, M., et al. (2012). Distinguishing between turnover and nestedness in the quantification of biotic homogenization. *Biodiversity and Conservation*, 21, 1399-1409.

Barlow, J., Lennox, G.D., Ferreira, J., et al. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, 535, 144-147.

Bartell, S. M. (2006). Biomarkers, Bioindicators, and Ecological Risk Assessment-A Brief Review and Evaluation. *Environmental Bioindicators*, 1(1), 60-73.

Barton, A.M., & Keeton, W.S. (2018). Ecology and recovery of eastern old-growth forests. Washington, DC, Island Press.

Baselga, A., Jiménez-Valverde, A., Niccolini, G. (2007). A multiple-site similarity measure independent of richness. *Biology Letters*, 3(6), 642-645.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134-143.

Baselga, A., & Leprieur, F. (2015). Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, 6(9), 1069-1079.

Basile, M., Parisi, F., Tognetti, R., et al. (2023). Diversity of beetle species and functional traits along gradients of deadwood suggests weak environmental filtering. *Forest Ecosystems*, 10, 100090.

Bässler, C., Müller, J., Dziock, F., et al. (2010). Effects of resource availability and climate on the diversity of wood-decaying fungi. *Journal of Ecology*, 98, 822-832.

Bässler, C., Müller, J., Svoboda, M., et al. (2012). Diversity of wood-decaying fungi under different disturbance regimes - a case study from spruce mountain forests. *Biodiversity and Conservation*, 21, 33-49.

Bässler, C., Müller, J., Cadotte, M.W., et al. (2016). Functional response of lignicolous fungal guilds to bark beetle deforestation. *Ecological Indicators*, 65, 149-160.

Bates, D., Maechler, M., Bolker, B., et al. (2015). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Bauhus, J., Puettmann, K., & Messier, C. (2009). Silviculture for old-growth attributes. *Forest Ecology and Management*, 258, 525-537.

Belote, R. T., Barnett, K., Dietz, M. S., et al. (2021). Options for prioritizing sites for biodiversity conservation with implications for “30 by 30”. *Biological Conservation*, 264, 109378.

Berge, E., & Jakobsen, H.A. (1998). A regional scale multi-layer model for the calculation of long-term transport and deposition of air pollution in Europe. *Tellus*, 50, 205-223.

Berglund, H., & Jonsson, B.G. (2008). Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented northern Swedish boreal forests. *Biological Conservation*, 141, 3029-3039.

Betts, M. G., Fahrig, L., Hadley, A. S., et al. (2014). A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, 37, 517-527.

Binot-Hafke, M., Balzer, S., Becker, N., et al. (2011). Rote liste gefährdeter tiere, pflanzen und pilze Deutschlands. Wirbellose Tiere (part 1). Bundesamt für Naturschutz.

Blaser, S., Prati, D., Senn-Irlet, B., et al. (2013). Effects of forest management on the diversity of deadwood-inhabiting fungi in Central European forests. *Forest Ecology and Management*, 304, 42-48.

Boddy, L., Frankland, J.C., Van West, P. (2008). Ecology of saprotrophic basidiomycetes. London, United Kingdom: Elsevier Academic Press.

Boch, S., Prati, D., Hessenmöller, D., et al. (2013). Richness of lichen species, especially of threatened ones, is promoted by management methods furthering stand continuity. *PloS One*, 8(1), e55461.

Blonska, E., Kacprzyk, M., Spólnik, A. (2017). Effect of deadwood of different tree species in various stages of decomposition on biochemical soil properties and carbon storage. *Ecological Research*, 32, 193-203.

Bouget, C., Nusillard, B, Pineau, X., et al. (2012). Effects of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. Insect *Conservation and Diversity*, 5(4), 264-278.

Bouget, C., Larrieu, L., Nusillard, B., et al. (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, 22, 2111-2130.

Bouget, C., Larrieu, L., Brin, A. (2014). Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, 36, 656-664.

Bowd, E., Blanchard, W., McBurney, L., et al. (2021). Direct and indirect disturbance impacts on forest biodiversity. *Ecosphere*, 12(12), e03823.

Bradford, M.A., Warren II, R.J., Baldrian, P., et al. (2014). Climate fails to predict wood decomposition at regional scales. *Nature Climate Change*, 4, 625-630.

Braunisch, V., & Suchant, R. (2008). Using ecological forest site mapping for long-term habitat suitability assessment in wildlife conservation - demonstrated for capercaillie (*Tetrao urogallus*). *Forest Ecology and Management*, 256, 1209-1221.

Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., et al. (2017). Forest biodiversity, ecosystem functioning and the provisioning of ecosystem services. *Biodiversity Conservation*, 26, 3005-3035.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., et al. (2002). Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology*, 16(4), 909-923.

Broome, A., Connolly, T., Quine, C. P. (2014). An evaluation of thinning to improve habitat for capercaillie (*Tetrao urogallus*). *Forest Ecology and Management*, 314, 94-103.

Bujoczek, L., Bujoczek, M., Banaš, J., et al. (2015). Spruce regeneration on woody microsites in a subalpine forest in the western Carpathians. *Silvia Fennica*, 49(3), 1-21.

Bujoczek, L., Bujoczek, M., Zięba, S (2021). Distribution of deadwood and other forest structural indicatiors relevant for bird conservation in Natura 2000 special protection areas in Poland. *Scientific Reports*, 11, 14937.

Čada, V., Svoboda, M., Janda, P. (2013). Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. *Forest Ecology and Management*, 295, 59-68.

Čada, V., Morrissey, R. C., Michalová, Z., et al. (2016). Frequent severe natural disturbances and non-equilibrium landscape dynamics shaped the mountain spruce forest in central Europe. *Forest Ecology and Management*, 363, 169-178.

Čada, V., Trotsiuk, V., Janda, P., et al. (2020). Quantifying natural disturbances using a large-scale dendrochronological reconstruction to guide forest management. *Ecological Applications*, 30(8), e02189.

Cao K, Condit R, Mi X, et al. (2021). Species packing and the latitudinal gradient in beta-diversity. *Proceedings of the Royal Society B*, 288, 20203045.

Ceballos, G., Ehrlich, P R., Barnosky, A. D., et al. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1(5), 1400253.

Ceballos, G., Ehrlich, P. R., Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the national academy of sciences*, 114(30), 6089-6096.

Collen, B., Loh, J., Whitmee, S., et al. (2009). Monitoring change in vertebrate abundance: the living planet index. *Conservation Biology*, 23, 317-327.

Colwell, R. K., Mao, C. X., Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85, 2717-2727.

Czerepko, J., Gawryś, R., Szymczyk, R., et al. (2021). How sensitive are epiphytic and epixylic cryptogams as indicators of forest naturalness? Testing bryophyte and lichen predictive power in stands under different management regimes in tie Białowieża forest. *Ecological Indicators*, 125, 107532.

Dämon, W., & Krisai-Greilhuber, I. (2017). Die Pilze Österreichs. Verzeichnis und Rote Liste 2016. Teil Makromyzeten. – Wien: Österreichische Mykologische Gesellschaft.

Da Silveira, N. S., Niebuhr, B. B. S., Muylaert, R. D. L., et al. (2016). Effects of land cover on the movement of frugivorous birds in a heterogeneous landscape. *PLoS One*, 11, e0156688.

Demko, M., Krištín, A., Puchala, P. (2013). Red list of birds in Slovakia. *Tichodroma*, 25, 69-78.

Di Marco, M, Ferrier, S., Harwood, T. D., et al. (2019). Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, 573(7775), 582-585.

Dirzo, R., Young, H. S., Galetti, M., et al. (2014). Defaunation in the Anthropocene. *Science*, 345(6195), 401-406.

Dobson, A., Lodge, D., Alder, J., et al. (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87(8), 1915-1924.

Doerfler, I., Müller, J., Gossner, M.M., et al. (2017). Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. *Forest Ecology and Management*, 400, 607-620.

Donato, D. C., Campbell, J. L., Franklin, J. F. (2012). Multiple successional pathways and precocity in forest development: can some forests be born complex? *Journal of Vegetation Science*, 23(3):576-584.

Dossa, G.G.O., Schaefer, D., Zhang, J.L., et al. (2018). The cover uncovered: Bark control over wood decomposition. *Journal of Ecology*, 106(6), 2147-2160.

Dove, N.C., & Keeton, W.S. (2015). Structural Complexity Enhancement increases fungal species richness in northern hardwood forests. *Fungal Ecology*, 13, 181-192.

Duflot, R., Fahrig, L., Mönkkönen, M. (2022). Management diversity begets biodiversity in production forest landscapes. *Biological Conservation*, 268, 109514.

Dvořák, D., Vašutová, M., Hofmeister, J., et al. (2017). Macrofungal diversity patterns in central European forests affirm the key importance of old-growth forests. *Fungal Ecology*, 27, 145-154.

Eckelt, A., Müller, J., Bense, U., et al. (2018). “Primeval forest relict beetles” of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. *Journal of Insect Conservation*, 22, 15-28.

Eckerter, T., Buse, J., Förschler, M., et al. (2019). Additive positive effects of canopy openness on European bilberry (*Vaccinium myrtillus*) fruit quantity and quality. *Forest Ecology and Management*, 433, 122-130.

Eigenbrod, F., Adams, W., Hill, C., et al. (2017). A review of large-scale conservation in England, Scotland and Wales. *Natural England Joint Publication*, 19, 227.

Ewers, R. M., & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews of the Cambridge Philosophical Society*, 81(1), 117-142.

Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management*, 61(3), 603-610.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487-515.

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40(9), 1649-1663.

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual Review of Ecology, Evolution, and Systematics* 48, 110316-122612.

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J. R., et al. (2019). Is habitat fragmentation bad for biodiversity? *Biological Conservation* 230, 179-186.

Feldhaar, H., & Schauer, B. (2018). Dispersal of saproxylic insect. *Zoological Monographs*, 515-546.

Ferenčík, M., Svitok, M., Mikoláš, M., et al. (2022). Spatial and temporal extents of natural disturbances differentiate deadwood-inhabiting fungal communities in spruce primary forest ecosystems. *Forest Ecology and Management*, 517, 120272.

Ferenčík, M., Hofmeister, J., Mikoláš, M., et al. (2024). Exploring the multiple drivers of alpha and beta-diversity dynamics in Europe's primary forests: Informing conservation strategies. *Forest Ecology and Management*, 571, 122229.

Fitting linear mixed-effects models Using lme4. *Journal of Statistical Software*, 67, 1-48.

Ford, S. A., Kleinman J. S., Hart, J. L. (2018). Effects of wind disturbance and salvage harvesting on macrofungal communities in a *Pinus* woodland. *Forest Ecology and Management*, 407, 31-46.

Franklin, J.F., Spies, T.A., Van Pelt, R., et al. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, 155(1-3), 399-423.

Franklin, C. M. A., Macdonald, S. E., Nielsen, S. E. (2019). Can retention harvests help conserve wildlife? Evidence for vertebrates in the boreal forests. *Ecosphere*, 10(3), e02632.

Franzén, M., & Molander, M. (2012). How threatened are alpine environments? a cross taxonomic study. *Biodiversity and Conservation*, 21, 517-526.

Frelich, L. E. (2002). Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press.

Fridman, J., & Walheim, M. (2000). Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management*, 131, 23-36.

Fukasawa, Y., Osono, T., Takeda, H. (2009). Microfungus communities of Japanese beech logs at different stages of decay in a cool temperate deciduous forest. *Canadian Journal of Forest Research*, 39(8), 1606-1614.

Gabriel, D., Roschewitz, I., Tscharntke, T., et al. (2006). Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. *Ecological Applications*, 16(6), 2011-2021.

Gianuca, A. T., Declerck, S. A., Lemmens, P., et al. (2017). Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of β-diversity. *Ecology*, 98(2), 525-533.

Gibson, L., Lee, T.M., Koh, L.P., et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378-381.

Gibson, L., Lynam, A. J., Bradshaw, C. J. A., et al. (2013). Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, 341, 1508-1510.

Gilbert, O.L. (1992). Lichen reinvasion with declining air pollution. In: Bates, J.W., & Farmer, A. Bryophytes and Lichens in a Changing Environment. Oxford: Clarendon Press, 159-177.

Giordani, P. (2012). Assessing the effects of forest management on epiphytic lichens in coppiced forests using different indicators. *Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology*, 146(3), 628-637.

Gjerde, I., Grytnes, J.A., Heegaard, E., et al. (2018). Red List updates and the robustness of sites selected for conservation of red-listed species. *Global Ecology and Conservation*, 16, e00454.

Gloor, R., Svitok, M., Mikoláš, M., et al. (2024). Sustaining forest biodiversity: Exploring the effect of long-term natural disturbance dynamics on contemporary lichen communities in primary forest ecosystems. *Forest Ecosystems*, 11, 100214.

Gossner, M. M., Lachat, T., Brunet, J., et al. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology*, 27(3), 605-614.

Graf, R. F., Bollmann, K., Suter, W., et al. (2005). The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. *Landscape Ecology*, 20, 703-717.

Graf, R. F., Mathys, L., Bollmann, K. (2009). Habitat assessment for forest dwelling species using LiDAR remote sensing: capercaillie in the Alps. *Forest Ecology and Management*, 257, 160-167.

Griess, V. C., & Knoke, T. (2011). Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. *Canadian Journal of Forest Research*, 41(6), 1141-1159.

Grimm, V., & Storch, I. (2000). Minimum viable population size of capercaillie *Tetrao urogallus*: results from a stochastic model. *Wildlife Biology*, 6, 219-225.

Grodzińska, K., Godzik, B., Frącek, et al. (2004). Vegetation of the selected forest stands and land use in the Carpathian Mountains. *Environmental Pollution*, 130(1), 17-32.

Grossiord, C., Granier, A., Ratcliffe, S., et al. (2014). Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences*, 111(41), 14812-14815.

Grove, S.J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology, Evolution, and Systematics*, 33, 1-23.

Guadagnin, D. L., Peter, Â. S., Perello, L. F. C., et al. (2005). Spatial and temporal patterns of waterbird assemblages in fragmented wetlands of southern Brazil. *Waterbirds*, 28, 261-272.

Gustafsson, L. (1986). Vegetation and flora of short-rotation willow stands from a conservation viewpoint. Dissertation. Swedish University of Agricultural Sciences, Upsala.

Gustafsson, L., Appelgren, L., Jonsson, F., et al. (2004). High occurence of red-listed bryophytes and lichens in mature managed forests in boreal Sweden. *Basic and Applied Ecology*, 5(2). 123-129.

Gustafsson, L., Kouki, J., Sverdup-Thygeson, A. (2010). Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. *Scandinavian Journal of Forest Research*, 25, 295-308.

Gustafsson, L., Bauhus, J., Asbeck, T., et al. (2020). Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. *Ambi*o, 49, 85-97.

Guttová, A., Lackovičová, A., Pišút, I. (2013). Revised and updated checklist of lichens of Slovakia (May 2013). *Biológia*, 68, 845-850.

Haddad, N. M., Brudvig, L. A., Clobert, J., et al. (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances*, 1(2), e1500052.

Haeler, E., Bergamini, A., Blaser, S., et al. (2021). Saproxylic species are linked to the amount and isolation of dead wood across spatial scales in a beech forest. *Landscape Ecology*, 26, 89-104.

Halme, P., Ódor, P., Christensen, M., et al. (2013). The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. *Biological Conservation*, 168, 24-30.

Halstead, K. E., Alexander, J. D., Hadley, A. S., et al. (2019). Using a species-centered approach to predict bird community responses to habitat fragmentation. *Landscape Ecology*, 34, 1919-1935.

Hämäläinen, A., Kouki, J., Löhmus, P. (2014). The value of retained Scots pines and their deadwood legacies for lichen diversity in clear-cut forests: the effects of retention level and prescribed burning. *Forest Ecology and Management*, 324, 89-100.

Hamm, M., & Drossel, B. (2017). Habitat heterogeneity hypothesis and edge effects in model metacommunities. *Journal of Theoretical Biology*, 426, 40-48.

Harmon, M.E., Franklin, J.F., Swanson, F.J., et al. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, 15, 133-302.

Hattori, T., Yamashita, S., Lee, S. (2012). Diversity and conservation of wood inhabiting polypores and other aphyllophoraceous fungi in Malaysia. *Biodiversity Conservation*, 21, 2375-2396.

Hanzelka, J., & Reif, J. (2016). Effects of vegetation structure on the diversity of breeding bird communities in forest stands of non-native black pine (*Pinus nigra* A.) and black locust (*Robinia pseudoacacia* L.) in the Czech Republic. *Forest Ecology and Management*, 379, 102-113.

Heilmann-Clausen, J., & Christensen, M. (2003). Fungal diversity on decaying beech logs – implications for sustainable forestry. *Biodiversity Conservation*, 12, 953-973.

Heilmann-Clausen, J., & Christensen, M. (2004). Does size matter?: On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *Forest Ecology and Management*, 201(1), 105-117.

Heilmann-Clausen, J., Aude, E., Christensen, M. (2005). Cryptogam communities on decaying deciduous wood – does tree species diversity matter? *Biodiversity Conservation*, 14, 2061-2078.

Heilmann-Clausen, J., Barron, E. S., Boddy, L., et al. (2014). A fungal perspective on conservation biology. *Conservation Biology*, 29(1), 61-68.

Heino, J. (2013). The importance of metacommunity ecology for environmental assessment research in the freshwater realm. *Biological Reviews*, 88(1), 166-178.

Hewson, C.M., Austin, G.E., Gough, S.J., et al. (2011). Species specific responses of woodland birds to stand-level habitat characteristics: the dual importance of forest structure and floristics. *Forest Ecology and Management*, 261, 1224-1240.

Hill, M. J., Heino, J., Thornhill, I., et al. (2017). Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos*, 126(11), 1575-1585.

Hilmers, T., Friess, N., Bässler, C., et al. (2018). Biodiversity along temperate forest succession. *Journal of Applied Ecology*, 55(6), 2756-2766.

Hiscox, J., Savoury, M., Müller, C.T., et al. (2015). Priority effects during fungal community establishment in beech wood. *The ISME Journal*, 9(10), 2246-2260.

Hofmeister, J., Hošek, J., Brabec, M., et al. (2015). Value of old forest attributes related to cryptogam species richness in temperate forests: a quantitative assessment. *Ecological Indicators*, 57, 497-504.

Hofmeister, J., Hošek, J., Malíček, J., et al. (2016). Large beech (*Fagus sylvatica*) trees as ‘lifeboat’ for lichen diversity in central European forests. *Biodiversity and Conservation*, 25, 1073-1090.

Holec, J., & Beran, M. [Eds] (2006). Červený seznam hub (makromycetů) České republiky [Red list of fungi (macromycetes) of the Czech Republic]. *Příroda*, 24, 1-282.

Holec, J., & Kučera, T. (2020). Richness and composition of macrofungi on large decaying trees in a Central European old-growth forest: a case study on silver fir (*Abies alba*). *Mycological Progress*, 19, 1429-1443.

Holeksa, J., Jaloviar, P. Kucbel, S., et al. (2017). Models of disturbance driven dynamics in the West Carpathian spruce Forests. *Forest Ecology and Management*, 15, 79-89.

Holmes, R.L. (1983). Analysis of tree rings and fire scars to establish fire history. *Tree-Ring bulletin*, 43, 51-67.

Hoppe, B., Purahong, W., Wubet, T., et al. (2016). Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Diversity*, 77, 367-379.

Horák, J., Kout, J., Vodka, Š., et al. (2016). Dead wood dependent organisms in one of the oldest protected forests of Europe: Investigating the contrasting effects of within-stand variation in a highly diversified environment. *Forest Ecology and Management*, 363, 229-236.

Hottola, J., & Siitonen, J. (2008). Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. *Biodiversity and Conservation*, 17, 2559-2577.

Hottola, J., Ovaskainen, O., Hanski, I. (2009). A unified measure of the number, volume and diversity of dead trees and the response of fungal communities. *Journal of Ecology*, 97, 1320-1328.

Howard, C., Flather, C. H., Stephens, P. A. (2020). A global assessment of the drivers of threatened terrestrial species richness. *Nature Communication*, 11, 993.

Hsieh, T.C., Ma, K.H., Chao, A. (2020). iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.20.

Hu, G., Wu, J., Feeley, K. J., et al. (2012). The effects of landscape variables on the species-area relationship during late-stage habitat fragmentation. *PLoS One*, 7, e0043894.

Humphrey, J., & Bailey, S. (2012). Life in the deadwood - A guide to managing deadwood in forestry commission forests. Forest Enterprise - Environment and Communications, Edinburgh.

Hunter, M.L. (1990). Wildlife, forest, and forestry. Principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs, NJ, USA.

Huston, M.A., & DeAngelis, D.L. (1994). Competition and coexistence: the effects of resource transport and supply rates. *The American Naturalist*, 144, 954-977.

Hyvärinen, E., Kouki, J., Martikainen, P. (2006). A comparison of three trapping methods used to survey forest-dwelling Coleoptera. *European Journal of Entomology*, 103(2), 397.

Chase, J. M., Blowes, S. A., Knight, T. M., et al. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, 584, 238-243.

Chetcuti, J., Kunin, W. E., Bullock, J. M. (2019). A weighting method to improve habitat association analysis: tested on British carabids. *Ecography*, 42, 1395-1404.

Christensen, M., Heilmann-Clausen, J., Walleyn, R., et al. (2004). Wood inhabiting fungi as indicators of nature value in European beech forest. *Monitoring and Indicators of Forest Diversity in Europe – From Ideas to Operationality*, 51, 229-237.

Isaac, N. J. B., Brotherton, P. N. M., Bullock, J. M., et al. (2018). Defining and delivering resilient ecological networks: Nature conservation in England. *Journal of Applied Ecology*, 55, 2537-2543.

Jactel, H., & Brockerhoff, E. G. (2007). Tree diversity reduces herbivory by forest insects. *Ecology Letters*, 10(9), 835-848.

Jactel, H., Petit, J., Desprez-Loustau, M., et al. (2012). Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*, 18, 267-276.

Janda, P., Trotsiuk, V., Mikoláš, M., et al. (2017). The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. *Forest Ecology and Management*, 388, 67-78.

Janssen, P., Fuhr, M., Cateau, E., et al. (2017). Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biological Conservation*, 205, 1-10.

Jaroszewicz, B., Cholewińska, O., Chećko, E., et al. (2021). Predictors of diversity of deadwood-dwelling macrofungi in a European natural forest. *Forest Ecology and Management*, 490, 119123.

Jasík, M., & Polák, P. (eds) (2011). Pralesy Slovenska. FSC Slovensko, Banská Bystrica.

Jaworski, T., Plewa, R., Tarwacki, G., et al. (2019). Ecologically similar saproxylic beetles depend on diversified deadwood resources: From habitat requirements to management implications. *Forest Ecology and Management*, 449, 117462.

Johansson, P. (2008). Consequences of disturbance on epiphytic lichens on boreal and near boreal forests. *Biological Conservation*, 141(8), 1933-1944.

Jonsson, B.G., Kruis, N., Ranius, T. (2005). Ecology of Species Living on Dead Wood – Lessons for Dead Wood Management. *Silva Fennica*, 39(2), 289-309.

Juutilainen, K., Halme, P., Kotiranta, H., et al. (2011). Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecology*, 4, 342-349.

Quian, H., Ricklefs, R. E., White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, 8, 15-22.

Quinn, G. P., & Keough, M. J. (2002). Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.

Kahl, T., Arnstadt, T., Baber, K., et al. (2017). Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecology and Management*, 391, 86-95.

Kameniar, O., Baláž, M., Svitok, M., et al. (2021). Historical natural disturbances shape spruce primary forest structure and indirectly influence bird assemblage composition. *Forest Ecology and Management*, 481, 118647.

Kameniar, O., Baláž, M., Svitok, M., et al. (2023). Spruce- and beech-dominated primary forests in the western carpathians differ in terms of forest structure and bird assemblages, independently of disturbance regimes. *European Journal of Environmental Sciences*, 13(1), 47-59.

Kattan, G. H., Franco, P., Saavedra-Rodríguez, C. A., et al. (2006). Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. *Conservation Biology*, 20, 1203-1211.

Kebrle, D., Zasadil, P., Hošek, J., et al. (2021). Large trees as a key factor for bird diversity in spruce-dominated production forests: Implications for conservation management. *Forest Ecology and Management*, 496, 119460.

Keil, P., Storch, D., Jetz, W. (2015). On the decline of biodiversity due to area loss. *Nature Communications*, 6, 8837.

Kimmins, J. P. (2003). Old-growth forest: An ancient and stable sylvan equilibrium, or a relatively transitory ecosystem condition that offers people a visual and emotional feast? Answer it depends. *The Forestry Chronicle*, 79(3), 429-440.

Király, I., Nascimbene, J., Tinya, F., et al. (2013). Factors influencing epiphytic bryophyte and lichen species richness at different spatial scales in managed temperate forests. *Biodiversity and Conservation*, 22, 209-223.

Klinga, P., Mikoláš, M., Smolko, P., et al. (2019). Considering landscape connectivity and gene flow in the Anthropocene using complementary landscape genetics and habitat modelling approaches. *Landscape Ecology*, 34, 521-536.

Komonen, A., & Müller, J. (2018). Dispersal ecology of deadwood organisms and connectivity conservation. *Conservation Biology*, 32(3), 535-545.

Korpeľ S. 1995. Die Urwälder der Westkarpaten. Stuttgart, Fischer.

Kouki, J., & Salo, K. (2020). Forest disturbances affect functional groups of macrofungi in young successional forests - harvests and fire lead to different fungal assemblages. *Forest Ecology and Management*, 463, 118039.

Kozák, D., Svitok, M., Wiezik, M., et al. (2021). Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests. *Ecosystems*, 24, 37-55.

Kozák, D., Svitok, M., Zemlerová, V., et al. (2023). Importance of conserving large and old trees to continuity of tree-related microhabitats. *Conservation Biology,* e14066.

Krah, F.S., Bässler, C., Heibl, CH., et al. (2018a). Evolutionary dynamics of host specialization in wood-decay fungi. *BMC Evolutionary Biology*, 18, 119.

Krah, F.S., Seibold, S., Brandl, R., et al. (2018b). Independent effects of host and environment on the diversity of wood-inhabiting fungi. *Journal of Ecology*, 106(4), 1428-1442.

Krauss, J., Bommarco, R., Guardiola, M., et al. (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters*, 13, 597-605.

Križová, E. (2011). Definície pralesa – prístupy, porovnania, základné pojmy. In: Jasík M., Polák P. (eds.) Pralesy Slovenska. FSC Slovensko, Banská Bystrica.

Kruys, N., Fires, C., Jonsson, B. G., et al. (1999). Wood inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. *Canadian Journal of Forest Research*, 29, 178-186.

Kubart, A., Vasaitis, R., Stenlid, J., et al. (2016). Fungal communities in Norway spruce stumps along a latitudinal gradient in Sweden. *Forest Ecology and Management*, 371, 50-58.

Kubartová, A., Ottosson, E., Dahlberg, A., et al. (2012). Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Molecular Ecology*, 21(18), 4514-4532.

Kuemmerle, T., Perzanowski, K., Chaskovskyy, O., et al. (2010). European Bison habitat in the Carpathian Mountains. *Biological Conservation*, 143(4), 908-916.

Küffer, N., Gillet, F., Senn-Irlet, B., et al. (2008). Ecological determinants of fungal diversity on deadwood in European forests. *Fungal Diversity,* 30, 83-95.

Kulakowski, D., Seidl, R., Holeksa, J., et al. (2017). A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management*, 388, 120-131.

Kuuluvainen, T., & Aakala, T. (2011). Natural forest dynamics in boreal Fennoscandia: a review and classification. *Silva Fennica*, 45(5), 823-841.

Kuznetsova, A., Brockhoff, P. B., Christensen, R. H. B. (2017). lmerTest Package: Tests in linear mixed effects models. *Journal of Statistical Software,* 82, 1-26.

Laaksonen, M., Peuhu, E., Várkonyi, G., et al. (2008). Effects of habitat quality and landscape structure on saproxylic species dwelling in boreal spruce-swamp forests. *Oikos*, 117(7), 1098-1110.

Lachat, T., Bouget, C., Bütler, R., et al. (2013). Deadwood: quantitative and qualitative requirements for the conservation of saproxylic biodiversity. *Integrative approaches as an opportunity for the conservation of forest biodiversity*, 92-102.

LaManna, J. A., Burkle, L. A., Belote, R. T., et al. (2021). Biotic and abiotic drivers of plant-pollinator community assembly across wildfire gradients. *Journal of Ecology*, 109(2), 1000-1013.

Langbehn, T., Hofmeister, J., Svitok, M., et al. (2021). The impact of natural disturbance dynamics on lichen diversity and composition in primary mountain spruce forests. *Journal of Vegetation Science*, 32(5), e13087.

Langenheder, S., Berga, M., Östman, Ö., et al. (2012). Temporal variation of β-diversity and assembly mechanisms in a bacterial metacommunity. *The ISME Journal*, 6, 1107-1114.

Lassauce, A., Paillet, Y., Jactel, H., et al. (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators*, 11(5), 1027-1039.

Lassauce, A., Larrieu, L., Paillet, Y., et al. (2012). The effects of forest age on saproxylic beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high forest. *Insect Conservation and Diversity*, 6(3), 396-410.

Leberger, R., Rosa, I. M., Guerra, C. A., et al. (2020). Global patterns of forest loss across IUCN categories of protected areas. *Biological Conservation*, 241, 108299.

Lee, M.R., Powell, J.R., Oberle, B., et al. (2019). Good neighbors aplenty: fungal endophytes rarely exhibit competitive exclusion patterns across a span of woody habitats. *Ecology*, 100(9), e02790

Leibold, M. A., Holyoak, M., Mouquet, N., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7(7), 601-613.

Lettenmaier, L., Seibold, S., Bässler, C., et al. (2022). Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. *Oecologia*, 198, 825-834.

Leprieur, F., & Oikonomou, A. (2014). The need for richness-independent measure of turnover when delineating biogeographical regions. *Journal of Biogeography*, 41(2), 417-420.

Lie, M. H., Arup, U., Grytnes, J. A., et al. (2009). The importance of host tree age, size and growth rate as determinants of epiphytic lichen diversity in boreal spruce forests. *Biodiversity and Conservation*, 18, 3579-3596.

Liu, J., Xia, S., Zeng, D., et al. (2022). Age and spatial distribution of the world's oldest trees. *Conservation Biology*, e13907.

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., et al. (2012). A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, 5(6), 421-431.

Lindenmayer, D., & Franklin, J.F. (2013). Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press.Lindenmayer, D., & Franklin, J.F. (2013). Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press.

Lindenmayer, D. B., Westgate, M. J., Scheele, B. C., et al. (2019). Key perspectives on early successional forests subject to stand-replacing disturbances. *Forest Ecology and Management, 454*, 117656.

Lindenmayer, D.B., & Westgate, M.J. (2020). Are flagship, umbrella and keystone species useful surrogates to understand to consequences of landscape change? *Current Landscape Ecology Reports*, 5, 76-84.

Lindhe, A., Asenblad, N., Toresson, H.G. (2004). Cut logs and high stumps of spruce, birch, aspen and oak - nine years of saproxylic fungi succession. *Biological Conservation*, 119, 443, 454.

Lloret, F., Keeling, E. G., Sala, A. (2011). Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12), 1909-1920.

Lombardi, F., Lasserre, B., Tognetti, R., et al. (2008). Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). *Ecosystems*, 11, 882-894.

Lonsdale, D., Pautasso, M., Holdenrieder, O. (2007). Wood-decaying fungi in the forests: conservation needs and management options. *European Journal of Forest Research*, 127, 1-22.

Loreau, M., Naeem, S., Inchausti, P., et al. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294(5543), 804-808.

Lorimer, C.G., & Frelich, L.E. (1989). A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*, 19(5), 651-663.

Luick, R., Reif, A., Schneider, E., et al. 2021. Virgin forests at the heart of Europe- The importance, situation and future of Romanian’s virgin forests. Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz 24.

Mackey, B., Kormos, C.F., Keith, H., et al. (2020). Understanding the importance of primary tropical forest protection as a mitigation strategy. *Mitigation and Adaptation Strategies for Global Change*, 25, 763-787.

Majdanová, L., Hofmeister, J., Pouska, V., et al. (2023). Old-growth forests with long continuity are essential for preserving rare wood-inhabiting fungi. *Forest Ecology and Management*, 541, 121055.

Marvier, M., Kareiva, P., Neubert, M. G. (2004). Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis: An International Journal*, 24, 869-878.

Maxwell, S. L., Fuller, R. A., Brooks, T. M., et al. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, 536(7615), 143-145.

Meigs, G.W., Morrissey, R.C., Bače, R., et al. (2017). More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. *Forest Ecology and Management*, 406, 410-426.

Messier, C., & Kneeshaw, D. D. (1999). Thinking and acting differently for sustainable management of the boreal forest. *The Forestry Chronicle*, 75(6), 929-938.

Meyer, P., Schmidt, M., Feldmann, E., et al. (2021). Long-term development of species richness in a central European beech (Fagus sylvatica) forest affected by windthrow—Support for the intermediate disturbance hypothesis? *Ecology and Evolution*, 11, 12801-12815.

Mikoláš, M., Tejkal, M., Kuemmerle, T., et al. (2017). Forest management impacts on Capercaillie (*Tetrao urogallus*) habitat distribution and connectivity in the Carpathians. *Landscape Ecology*, 32, 163-179.

Mikoláš, M., Ujházy, K., Jasík, M., et al. (2019). Primary forest distribution and representation in a Central European landscape: Results of a large-scale field-based census. *Forest Ecology and Management*, 449, 117466.

Mikoláš, M., Svitok, M., Bače, R., et al. (2021). Natural disturbance impacts on trade-offs and co-benefits of forest biodiversity and carbon. *Proceedings of The Royal Society B*, 288, 20211631.

Mikoláš, M., Piovesan, G., Ahlström, A., et al. (2023). Protect old-growth forests in Europe now. *Science*, 380(6644), 466.

Miller-Rushing, A. J., Primack, R. B., Devictor, V., et al. (2019). How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. *Biological Conservation*, 232, 271-273.

Moning, C., & Müller, J. (2009). Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. *Ecological Indicators*, 9(5), 922-932.

Moning, C., Werth, S., Dziock, F., et al. (2009). Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *Forest Ecology and Management*, 258, 745-751.

Mori, A. S., Isbell, F., & Seidl, R. (2018). β-diversity, community assembly, and ecosystem functioning. *Trends in Ecology & Evolution*, 33(7), 549-564.

Mouquet, N., & Loreau, M. (2003). Community patterns in source-sink metacommunities. *The American Naturalist*, 162(5), 544-557.

Müller, J., Ulyshen, M., Seibold, S., et al. (2020). Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos*, 129(10), 1579-1588.

Nagel, T. A., Zenner, E. K., Brang, P. (2013). Research in old-growth forests and forest reserves: implications for integrated forest management. *Integrative approaches as an opportunity for the conservation of forest biodiversity*.

Nagel, T. A., Mikac, S., Dolinar, M., et al. (2017). The natural disturbance regime in forests of the Dinaric Mountains: A synthesis of evidence. *Forest Ecology and Management*, 388, 29-42.

Nakagawa, S., Johnson, P. C., Schielzeth H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, 14, 20170213.

Nascimbene, J., & Marini, L. (2010). Oak forest exploitation and black locust invasion caused severe shifts in epiphytic lichen communities in northern Italy. *Science of the Total Environment*, 408, 5506-5512.

Nascimbene, J., Nimis, P. L., Benesperi, R. (2012). Mature non-native black-locust (*Robinia pseudoacacia* L.) forest does not regain the lichen diversity of the natural forest. *Science of the Total Environment*, 421, 197-202.

Nascimbene, J., Thor, G., Nimis, P. L. (2013). Effect of forest management on epiphytic lichens in temperate deciduous forests of Europe - A review. *Forest Ecology and Management*, 298, 27-38.

Nascimbene, J., Dainese, M., Sitzia, T. (2013). Contrasting response of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. *Forest Ecology and Management*, 289, 325-332.

Netherer, S., & Nopp-Mayr, U. (2005). Predisposition assessment systems (PAS) as supportive tools in forest management—rating of site and stand-related hazards of bark beetle infestation in the High Tatra Mountains as an example for system application and verification. *Forest Ecology and Management*, 207(1-2), 99-107.

Nordén, B., Götmark, F., Tönnberg, M., et al. (2004). Deadwood in semi-natural temperate broadleaved woodland: contribution of coarse and fine deadwood, attached deadwood and stump. *Forest Ecology and Management*, 194(1-3), 235-248.

Nordén, B., Paltto, H., Claesson, C., et al. (2012). Partial cutting can enhance epiphyte conservation in temperate oak-rich forests. *Forest Ecology and Management*, 270, 35-44.

Nordén, J., Penttilä, R., Siitonen, R., et al. (2013). Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology*, 101, 701-712.

Nordén, J., Åström, J., Josefsson, T., et al. (2018). At which spatial and temporal scales can fungi indicate habitat connectivity? *Ecological Indicators*, 91, 138-148.

Öckinger, E., Bergman, K. O., Franzén, M., et al. (2012). The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. *Landscape Ecology*, 27(1), 121-131.

Ódor, P., & Standovár, T. (2001). Richness of bryophyte vegetation in near-natural and managed beech stands: the effects of management-induced differences in dead wood. *Ecological Bulletins*, 49, 219-229.

Ódor, P., Heilmann-Clausen, J., Christensen, M., et al. (2006). Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. *Biological Conservation*, 131, 58-71.

Økland, B. (1996). A comparison of three methods of trapping saproxylic beetles. *European Journal of Entomology*, 93, 195-210.

Oksanen, J., Blanchet, F. G., Kindt, R. (2012) Package 'vegan'.

Paillet, Y., Berges, L., Hjältén, J., et al. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology*, 24, 101-112.

Paillet, Y., Pernot, C., Boulanger, V., et al. (2015). Quantifying the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology and Management*, 346, 51-64.

Paletto, A., De Meo, I., Cantiani, P., Ferretti, F. (2014). Effects of forest management on the amount of deadwood in Mediterranean oak ecosystems. *Annals of Forest Science*, 71, 791-800.

Palombo, C., Chirici, G., Marchetti, M., et al. (2013). Is island abandonment affecting forest dynamics at high elevation in Mediterranean mountains more than climate change? *Plant Biosystems*, 147, 1-11.

Parisi, F., Innangi, M., Tognetti, R., et al. (2021). Forest Stand structure and coarse woody debris determine the biodiversity of beetle communities in Mediterranean mountain beech forests. *Global Ecology and Conservation*, 28, e1637.

Parmasto, E., (2001). Fungi as indicators of primeval and old-growth forests deserving protection. In: Moore, D., Nauta, M.M., Evans, S.E. & Rotheroe, M. 2001. Fungal Conservation: Issues and Solutions, Cambridge University Press.

Parviainen, J., Bücking, W., Vandekerkhove, K., et al. (2000). Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-Action E4). *Forestry*, 73, 107-118.

Patacca, M., Lindner, M., Lucas-Borja, M.E., et al. (2023). Significant increase in natural disturbance impacts on European forests since 1950. *Global Change Biology*, 29(5), 1359-1376.

Peltzer, D.A., Allen, R.B., Lowett, G.M., et al. (2009). Effect of biological invasion of forest carbon sequestration. *Global Change Biology*, 16, 732-746.

Penttilä, R., Siitonen, J., & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. *Biological Conservation*, 117(3), 271-283.

Perlík, M., Kraus, D., Bußler, H., et al. (2023). Canopy openness as the main driver of aculeate Hymenoptera and saproxylic beetle diversity following natural disturbances and salvage logging. *Forest Ecology and Management*, 540, 121033.

Persiani, A. M., Audisio, P., Lunghini, O. (2010). Linking taxonomical and functional biodiversity of saproxylic fungi and beetles in broad-leaved forests in southern Italy with varying management histories. *Plant Biosystems,* 144(1), 250-261.

Picchio, R., Neri, F., Petrini, E., et al. (2012). Machinery-induced soil compaction in thinning two pine stands in central Italy. *Forest Ecology and Management*, 285, 38-43.

Pickett, S. T. A., & White, P. S. (1985). The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pimm, S. L., Jenkins, C. N., Abell, R., et al. (2014). The biodiversity of species and their rates of extinction, distribution, and protection Background Rates of Species Extinction. *Science*, 344(6187), 1246752.

Pinheiro, J., Bates, D., DebRoy, S., et al., EISPACK authors, Heisterkamp, S., Van Willigen, B., Ranke, J., R Core Team. (2022). Linear and nonlinear mixed effect models. Package ‘nlme’, version 3.1-160.

Pišút, I., Guttova, A., Lackovičová, A., et al. (2001). Red list of lichens of Slovakia (December 2001). Červený zoznam lišajníkov Slovenska (december 2001). *Ochrana prírody,* 20, 23-30.

Poorter, L., Castilho, C.V., Schietti, J., et al. (2018). Can traits predict individual growth performance? A test in a hyperdiverse propical forest. *New Phytologist*, 219(1), 109-121.

Potapov, P., Hansen, M.C., Laestadius, L., et al. (2017). The last frontiers of wilderness: Tracking loss of intact forest land-scapes from 2000 to 2013. *Science Advanced*, 3(1), e1600821.

Potterf, M., Eyvindson, K., Blattert, C., et al. (2022). Interpreting wind damage risk–how multifunctional forest management impacts standing timber at risk of wind felling. *European Journal of Forest Research*, 141(2), 347-361.

Pouska, V., Svoboda, M., Lepšová, A. (2010). The diversity of wood-decaying fungi in relation to changing site conditions in an odl-growth mountain spruce forest, Central Europe. *European Journal of Forest Research*, 129, 219-231.

Pouska, V., Macek, P., Zíbarová, L., et al. (2017). How does the richness of wood-decaying fungi relate to wood microclimate? *Fungal Ecology*, 27, 178-181.

Pretzsch, H., & Dieler, J. (2011). The dependency of the size-growth relationship of Norway spruce (Picea abies [L.] Karst.) and European beech (Fagus sylvatica [L.]) in forest stands on long-term site conditions, drought events, and ozone stress. *Trees*, 25, 355-369.

Pretzsch, H., Schütze, G., Uhl, E. (2013). Resistance of European tree species to drought stress in mixed versus monospecific forests: evidence of stress release by interspecific facilitation. *Plant Biology,* 15, 483-495.

Purahong, W., Pietsch, K.A., Lentendu, G., et al. (2017). Characterization of unexplored deadwood mycobiome in highly diverse subtropical forests using culture-independent molecular technique. *Frontiers in Microbiology*, 8, 574.

Purvis, O.W., Tittley, I., Chimonides, P.D.J., et al. (2010). Long-term biomonitoring of lichen and bryophyte biodiversity at Burnham Beeches SAC and global environmental change. *Systematics and Biodiversity*, 8, 193-208.

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., et al. (2020). Indirect effects of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species. *Biological Conservation*, 241, 108368.

R Core Team. (2021). R: *A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. (2022). R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rajala, T., Peltoniemi, M., Pennanen, T., et al. (2012). Fungal community dynamics in relation to substrate quality of decaying Norway spruce (Picea abies [L.] Karst.) logs in boreal forests. *FEMS Microbiology Ecology*, 81, 494-505.

Ramiadantsoa, T., Hanski, I., Ovaskainen, O. (2018). Responses of generalist and specialist species to fragmented landscapes. *Theoretical Population Biology,* 124, 31-40.

Ranius, T., & Jansson, N. (2000). The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biological Conservation*, 95(1), 85-94.

Ranius, T., Ekvall, H., Jonsson, M., et al. (2005). Cost-efficiency of measures to increase the amount of coarse woody debris in managed Norway spruce forests. *Forest Ecology and Management*, 206(1), 119-133.

Rayner, A. D. M., & Boddy, L. (1988). Fungal decomposition of wood: its biology and ecology. Bath Press, Bath, UK.

Rennenberg, H., Loreto, F., Polle, A., et al. (2006). Physiological responses of forest trees to heat and drought. *Plant Biology*, 8(5), 556-571.

Renvall, P. (1995). Community structure and dynamics of wood-rooting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia,* 35, 1-51.

Rolls, R. J., Deane, D. C., Johnson, S. E. (2023). Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver-response relationships to develop conceptual models across ecosystems. *Biological Reviews*, 98(4), 1388-1423.

Rybicki, J., Abrego, N., Ovaskainen, O. (2020). Habitat fragmentation and species diversity in competitive communities. *Ecology Letters*, 23(3), 506-517.

Rimle, A., Heiri, C., Bugmann, H. (2017). Deadwood in Norway spruce dominated mountain forest reserves is characterized by large dimensions and advanced decomposition stages. *Forest Ecology and Management*, 404, 174-183.

Ruhi, A., Datry, T., Sabo, J. L. (2017). Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conservation Biology*, 31(6), 1459-1468.

Ruokolainen, A., Shorohova, E., Penttilä, R., et al. (2018). A continuum of dead wood with various habitat elements maintains the diversity of wood-inhabiting fungi in an old-growth boreal forest. *European Journal of Forest Research*, 137, 707-718.

Sabatini, F. M., Burrascano, S., Tuomisto, H., et al. (2014). Ground layer plant species turnover and beta diversity in Southern-European old-growth forests. *PLoS One*, 9(4), e95244.

Sabatini, F.M., Burrascano, F., Keeton, W.S., et al. (2018). Where are Europe's last primary forests? *Diversity and Distribution*, 24, 1426-1439.

Sabatini, F.M., Keeton, W.S., Lindner, M., et al. (2020). Protection gaps and restoration opportunities for primary forests in Europe. *Diversity and Distributions*, 26(12), 1646-1662.

Sabatini, F.M., Bluhm, H., Kun, Z., et al. (2021). European primary forest database v2.0. *Scientific Data*, 8, 220.

Seaward, M.R.D. (2008). Environmental role of lichens. Cambridge: Cambridge University Press, 2, 274-298.

Segelbacher, G., Höglund, J., Storch, I. (2003). From connectivity to isolation: genetic consequences of population fragmentation in capercaillie across Europe. *Molecular Ecology*, 12, 1773-1780.

Seibold, S., Bässler, C, Brandl, R., et al. (2015). Experimental studies of dead-wood biodiversity - a review identifying global gaps in knowledge. *Biological Conservation*, 191, 139-149.

Seibold S., Brandl, R., Buse, J., et al. (2015). Association of extinction rosk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29(2), 382-390.

Seibold, S., Bässler, C., Brandl, R., et al. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, 53(3), 934-943.

Seibold, S., Weisser, W. W., Ambarli, D., et al. (2023). Drivers of community assembly change during succession in wood-decomposing beetle communities. *Journal of Animal Ecology*, 92(5), 965-978.

Seidl, R., Schelhaas, M. J., Rammer, W., et al. (2014). Increasing forest disturbances in Europe and their impact on carbon storage. *Nature climate change*, 4(9), 806.

Şekercioğlu, Ç.H., Daily, G.C., Ehrlich, P.R. (2004). Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences*, 101(52), 18042-18047.

Semper-Pascual, A., Decarre, J., Baumann, M., et al. (2019). Biodiversity loss in deforestation frontiers: Linking occupancy modelling and physiological stress indicators to understand local extinctions. *Biological Conservation*, 236, 281-288.

Senf, C., Buras, A., Zang, CH.S., et al. (2020). Excess forest mortality is consistently linked to drought across Europe. *Nature Communications*, 11, 6200.

Scheidegger, C., & Werth, S. (2009). Conservation strategies for lichens: insights from population biology. *Fungal Biology Reviews*, 23(3), 55-66.

Schelhaas, M.J., Nabuurs, G.J., Schuck, A. (2003). Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*, 9(11), 1620-1633.

Schickhofer, M., & Schwarz, U. (2019). Inventory of Potential Primary and Old-Growth Forest Areas in Romania (PRIMOFARO). Identifying the largest intact forests in the temperate zone of the European Union.

Schmidl, J., & Büche, B. (2016). Die Rote Liste und Gesamtartenliste der Käfer (Coleoptera, exkl. Lauf- und Wasserkäfer) Deutschlands im Überblick. Naturschutz und Biologische Vielfalt 70.

Schroeder, L. M., & Lindelöw, Å. (2002). Attacks on living spruce trees by the bark beetle Ips typographus (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. *Agricultural and forest entomology*, 4(1), 47-56.

Schuck, A., Meyer, P., Menke, N., et al. (2005). Forest biodiversity indicator: dead wood - a proposed approach towards operationalising the MCPEE indicator. *Monitoring and indicators of forest biodiversity in Europe-from ideas to operationality*, 51, 49-77.

Schurman, J.S., Trotsiuk, V., Bače, R., et al. (2018). Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. *Global Change Biology*, 24(5), 2169-2181.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11-41.

Sippola, A.L., & Renvall, P. (1999). Wood-decomposing fungi and seed-tree cutting: A 40-year perspective. *Forest Ecology and Management*, 115(2-3), 183-201.

Smetzer, J. R., King, D. I., Schlossberg, S. (2014). Management regime influences shrubland birds and habitat conditions in the Northern Appalachians, USA. *Journal of Wildlife Management*, 78, 314-324.

Snäll, T., Ehrlén, J., Rydin, H. (2005). Colonization-extinction dynamics of an epiphyte metapopulation in a dynamics landscape, *Ecology*, 86, 106-115.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., et al. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, 31(1), 67-80.

Soininen, J., Heino, J., Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27(1), 96-109.

Sørenser, T. A. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. *Biologiske skrifter*, 5, 1-34.

Spake, R., Soga, M., Kawamura, K., et al. (2020). Regional variability in landscape effects on forest bird communities. *Landscape Ecology*, 35, 1055-1071.

Speight, M.C. (1989). Saproxylic invertebrates and their conservation. Council of Europe, Strasbourg, France

Stein, A., & Kreft, H. (2014). Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Reviews*, 90(3), 815-836.

Stein, A., Gerstner, K., Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866-880.

Stephens, S.L., Agee, J.K., Fulé, P.Z., et al. (2013). Managing Forests and Fire in Changing Climates. *Science*, 342, 41-42.

St-Laurent, M., Dussault, C., Ferron, J., et al. (2009). Dissecting habitat loss and fragmentation effects following logging in boreal forest: conservation perspectives from landscape simulations. *Biological Conservation*, 142, 2240-2249.

Stokland, J.N., Siitonen, J., Jonsson, B.G. (2012). Biodiversity in deadwood. Cambridge: Cambridge University Press.

Strutz, T. (2011). Data fitting and uncertainty: A practical introduction to weighted least squares and beyond. Wiesbaden: Vieweg+Teubner Verlag | Springer Fachmedien Wiesbaden GmbH.

Su, J., Mazei, Y. A., Tsyganov, A. N., et al. (2024). Multi-scale beta-diversity patterns in testate amoeba communities: species turnover and nestedness along a latitudinal gradient. *Oecologia*, 1-17.

Sutherland, W. J. (Ed.) (2006). Ecological census techniques. Second edition. Cambridge University Press. Cambridge.

Svoboda, M., Janda, P., Bače, R., et al. (2014). Landscape-level variability in historical disturbance in primary *Picea abies* mountain forests of the Eastern Carpathians, Romania. *Journal of Vegetation Science*, 25, 386-401.

Temperli, CH., Bugmann, H., Elkin, CH. (2013). Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. *Ecological Monographs*, 83(3), 383-402.

Terraube, J., Archaux, F., Deconchat, M., et al. (2016). Forest edges have high conservation value for bird communities in mosaic landscapes. *Ecology and Evolution*, 6(15), 5178-5189.

Thom, D., & Seidl, R. (2016). Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*, 91(3), 760-781.

Thom, D., Rammer, W., Dirnböck, et al. (2017). The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology,* 54(1), 28-38.

Thom, D., & Keeton, W.S. (2020). Disturbance-based silviculture for habitat diversification: Effects on forest structure, dynamics, and carbon storage. *Forest Ecology and Management,* 469, 118-132.

Thor, G. (1995). Red Lists-aspects of their compilation and use in lichen conservation. Mitt Eidgenöss Forsch anst Wald Schnee Landsch 70, 29-39.

Thorn, S., Bußler, H., Fritze, M. A., et al. (2016). Canopy closure determines arthropod assemblages in microhabitats created by windstorms and salvage logging. *Forest Ecology and Management*, 381, 188–195.

Thorn, S., Bässler, C., Svoboda, M., et al. (2017). Effects of natural disturbances and salvage logging on biodiversity - Lessons from the Bohemian Forest. *Forest Ecology and Management,* 388, 113-119.

Thorn, S., Bässler, C., Brandl, R., et al. (2018a). Impacts of salvage logging on biodiversity: A meta-analysis. *Journal of Applied Ecology*, 55(1), 279-289.

Thorn, S., Förster, B., Heibl, C., et al. (2018b). Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. *Biodiversity and Conservation*, 27, 3119-3135.

Thorn, S., Seibold, S., Leverkus, A.B., et al. (2020). The living dead: acknowledging life after tree death to stop forest degradation. *Frontiers in Ecology and the Environment*, 18(9), 505-512.

Thornton, D., Branch, L., Sunquist, M. (2011). Passive sampling effects and landscape location alter associations between species traits and response to fragmentation. *Ecological Applications*, 21, 817-829.

Tikkanen, O. P., Punttila, P., Heikkilä, R. (2009). Species-area relationships of red-listed species in old boreal forests: a large-scale data analysis. *Diversity and Distributions*, 15(5), 852-862.

Tingstad, L., Grytnes, J. A., Sætersdal, M., et al. (2020). Using Red List species in designating protection status to forest areas: a case study on the problem of spatio-temporal dynamics. *Biodiversity and Conservation*, 29, 3429-3443.

Tomao, A., Bonet, J.A., Castaño, C., et al. (2020). How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. *Forest Ecology and Management*, 457, 117678.

Tomiałojć, L., & Wesołowski, T. (2004). Diversity of the Białowieża Forest avifauna in space and time. *Journal of Ornithology*, 145, 81-92.

Topercer, J., & Maderič, B. (2022). Nest-platform, nest-tree, nest-site, home-range and landscape characteristics of the Lesser Spotted Eagle (*Clanga pomarina*) in relation to its breeding performance in East Carpathians. *Forest Ecology and Management*, 520, 120350.

Torrenta, R., Lacoste, F., Villard, M. A. (2018). Loss and fragmentation of mature woodland reduce the habitat niche breadth of forest birds. *Landscape Ecology*, 33, 1865-1879.

Trotsiuk, V., Svoboda, M., Janda, P., et al. (2014). A mixed severity disturbance regime in the primary Picea abies (L.) Karst. forests of the Ukrainian Carpathians. *Forest Ecology and Management*, 334, 144-153.

Trotsiuk, V., Pederson, N., Druckenbrod, D.L., et al. (2018). Testing the efficacy of tree-ring methods for detecting past disturbances. *Forest Ecology and Management*, 425, 59-67.

Turner, M. G., Romme, W. H., Gardner, R. H., et al. (1993). A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape ecology*, 8, 213-227.

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, 91(10), 2833-2849.

Ulanova, N. G. (2000). The effects of windthrow on forests at different spatial scales: a review. *Forest ecology and management*, 135(1-3), 155-167.

Ulrich, W., & Gotelli, N. J. (2007). Null model analysis of species nestedness patterns. *Ecology*, 88, 1824-1831.

van Der Plas, F., Manning, P., Soliveres, S., et al. (2016). Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences*, 113(13), 3557-3562.

Van Wilgenburg, S.L., Mazerolle, F.F., Hobson, K.A. (2001). Patterns of anthropod abundance, vegetation and microclimate at boreal forest edge and interior in two landscapes: implications for forest birds. *Ecoscience*, 8, 454-461.

Veen, P., Fanta, J., Raev, I., et al. (2010). Virgin forests in Romania and Bulgaria: results of two national inventory projects and their implications for protection. *Biodiversity and Conservation*, 19, 1805-1819.

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85(2), 183-206.

Verner, J. (1985). Assessment of counting techniques. In: Johnston R. F. (ed). Current ornithology. Plenum Press, New York.

Verwijst, T., Ledin, S., Mirck, J., et al. (2005). Development of short-rotation willow coppice systems for environmental purposes in Sweden. *Biomass and Bioenergy*, 28, 219-228.

Virkkala, R. (1987). Effects of forest management on birds breeding in northern Finland. *Annales Zoologici Fennici*, 24(4), 281-294.

Visconti, P., Butchart, S.H.M., Brooks, T.M., et al. (2019). Protected area targets post-2020. *Science*, 364(6437), 239-241.

Vítková, L., Bače, R., Kjučukov, P., et al. (2018). Deadwood management in Central European forests: Key considerations for practical implementation. *Forest Ecology and Management*, 429, 394-405.

Vogel, S., Alvarez, B., Bässler, C., et al. (2017). The Red-belted Bracket (*Fomitopsis pinicola*) colonizes spruce trees early after bark beetle attack and persists. *Fungal Ecology*, 27, 182-188.

Wallander, H. (1995). A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply. *Developments in Plant and Soil Science*, 169, 243-248.

Wallenius, T., Niskanen, L., Virtanen, T., et al. (2010). Loss of habitats, naturalness and species diversity in Eurasian forest landscapes. *Ecological Indicators*, 10(6), 1093-1101.

Wang, X. B., Lü, X. T., Yao, J., et al. (2017). Habitat-specific patterns and drivers of bacterial β-diversity in China's drylands. *The ISME Journal*, 11, 1345-1358.

Wang, J., Legendre, P., Soininen, J., et al. (2020). Temperature drives local contributions to beta diversity in mountain streams: stochastic and deterministic processes. *Global Ecology and Biogeography*, 29, 420-432.

Watson, J.E.M., Shanahan, D.F., Di Marco, M., et al. (2016). Catastrophic declines in wilderness areas undermine global environment targets. *Current Biology*, 26(21), 2929-2934.

Watson, J.E.M., Evans, T., Venter, O., et al. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, 2, 599-610.

Webb, W. L., Behrend, D. F., Saisorn, B. (1977). Effect of logging in songbird populations in a Northern Hardwood Forest. *Wildlife Monographs*, 55, 3-35.

Westerling, A.L., Hildago, H.G., Cayan, D.R., et al. (2006). Warming and earlier spring increase western U.S. forest wildfire activity. *Science*, 313, 940-943.

Whelan, CH.J., Şekercioğlu, Ç.H., Wenny, D.G. (2015). Why birds matter: from economic ornithology to ecosystem services. *Journal of Ornithology*, 156, 227-238.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30(3), 279-338.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213-251.

Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Winter, M.B., Bässler, C., Bernhardt-Römermann, M., et al. (2017). On the structural and species diversity effects of bark beetle disturbance in forests during initial and advanced early-seral stages at different scales. *European Journal of Forest Research*, 136, 357-373.

Wirth, Ch., Gleixner, G., Heimann, M. (Eds.) (2009). Ecological studies. Springer-Verlag, Berlin.

Woodall, C., & Nagel, L. (2006). Coarse woody type: a new method for analyzing coarse woody debris and forest change. *Forest Ecology and Management*, 227, 115-121.

Woodall, C. W., & Liknes, G. C. (2008). Climatic regions as an indicator of forest coarse and fine woody debris carbon stocks in the United States. *Carbon balance and management*, 3, 1-8.

Woods, K. D. (2007). Predictability, contingency, and convergence in late succession: slow systems and complex data-sets. *Journal of Vegetation Science*, 18(4), 543-554.

Yuan, J., Hou, L., Wei, X., et al. (2017). Decay and nutrient dynamics of coarse woody debris in the Qinling Mountains, China. *PLoS One*, 12(4), e0175203.

Zang, C., Pretzsch, H., Rothe, A. (2012). Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees*, 26, 557-569.

Zellweger, F., Roth, T., Baugmann, H., et al. (2017). Beta diversity of plants, birds and butterflies is closely associated with .climate and habitat structure. *Global Ecology and Biogeography*, 26(8), 898-906.

Zemanová, L., Trotsiuk, V., Morrissey, R. C., et al. (2017). Old trees as a key source of epiphytic lichen persistence and spatial distribution in mountain Norway spruce forests. *Biodiversity and Conservation*, 26, 1943-1958.

Zemlerová, V., Kozák, D., Mikoláš, M., et al. (2023). Natural disturbances are essential determinants of tree-related microhabitat availability in temperate forests. *Ecosystems*, 26, 1260-1274.

Zhang, X., Liu, S., Wang, J., et al. (2020). Local community assembly mechanisms shape soil bacterial β diversity patterns along a latitudinal gradient. *Nature Communication*, 11,1-10.

Zhu, J., Rasmussen, J. G., Møller, J., et al. (2008). Spatial-temporal modeling of forest gaps generated by colonization from below-and above-ground bark beetle species. *Journal of the American Statistical Association*, 103(481), 162-177.

Zibold, M., Bässler, C., Hauck, M., et al. (2024). Fungi and deadwood diversity: A test of the area-heterogeneity trade-off hypothesis. *Journal of Ecology*, 112(8), 1701-1718.

Zumr, V., Nakládal, O., Bílek, L., et al. (2023). The diameter of beech snags is an important factor for saproxylic beetle richness: Implications for forest management and conservation. *Forest Ecosystems*, 10, 100143.

# Appendix

**Table S1:** List of all recorded species of the four taxonomic groups with their IUCN red-list status and occurrences across all plots.

| Taxonomic group | Species | Protection status | Occurrence |
|---|---|---|---|
| **beetles** | *Agathidium_nigripenne* | LC | 10 |
| | *Alosterna_tabacicolor* | LC | 33 |
| | *Ampedus_aethiops* | LC | 7 |
| | *Ampedus_auripes* | R | 28 |
| | *Ampedus_erythrogonus* | VU | 2 |
| | *Ampedus_nigrinus* | LC | 8 |
| | *Anaspis_frontalis* | LC | 3 |
| | *Anaspis_ruficollis* | LC | 1 |
| | *Anaspis_rufilabris* | LC | 47 |
| | *Anastrangalia_sanguinolenta* | LC | 4 |
| | *Anisotoma_castanea* | LC | 9 |
| | *Anisotoma_humeralis* | LC | 10 |
| | *Anisotoma_orbicularis* | LC | 1 |
| | *Anobium_emarginatum* | LC | 1 |
| | *Anostirus_castaneus* | LC | 1 |
| | *Anthaxia_helvetica* | LC | 4 |
| | *Arpidiphorus_orbiculatus* | LC | 1 |
| | *Atomaria_affinis* | DD | 1 |
| | *Atomaria_alpina* | LC | 10 |
| | *Atomaria_atrata* | DD | 2 |
| | *Atomaria_diluta* | LC | 1 |
| | *Atomaria_elongatula* | NA | 1 |
| | *Atomaria_ornata* | LC | 4 |
| | *Atomaria_procerula* | LC | 6 |
| | *Atomaria_turgida* | LC | 3 |
| | *Bitoma_crenata* | LC | 1 |
| | *Callidium_aeneum* | LC | 2 |
| | *Calopus_serraticornis* | LC | 12 |
| | *Calyptomerus_alpestris* | NA | 15 |
| | *Cerylon_ferrugineum* | LC | 11 |
| | *Cerylon_histeroides* | LC | 2 |
| | *Cis_bidentatus* | LC | 2 |
| | *Cis_boleti* | LC | 7 |
| | *Cis_dentatus* | LC | 25 |
| | *Cis_fagi* | DD | 1 |
| | *Cis_glabratus* | LC | 1 |
| | *Cis_hispidus* | LC | 1 |
| | *Cis_jacquemartii* | DD | 1 |
| | *Cis_micans* | LC | 2 |
| | *Cis_nitidus* | LC | 1 |
| | *Cis_punctulatus* | LC | 10 |
| | *Cis_quadridens* | LC | 1 |

| | | |
|---|---|---|
| *Cis_rugulosus* | LC | 1 |
| *Cis_setiger* | LC | 1 |
| *Corticaria_abietorum* | LC | 10 |
| *Corticeus_linearis* | DD | 2 |
| *Cortodera_femorata* | LC | 23 |
| *Corymbia_maculicornis* | LC | 3 |
| *Corymbia_rubra* | LC | 5 |
| *Cryphalus_abietis* | LC | 23 |
| *Cryptophagus_badius* | NA | 5 |
| *Cryptophagus_dorsalis* | LC | 2 |
| *Crypturgus_hispidulus* | LC | 20 |
| *Crypturgus_pusillus* | LC | 3 |
| *Curtimorda_maculosa* | LC | 8 |
| *Cychramus_variegatus* | LC | 1 |
| *Dasytes_cyaneus* | LC | 1 |
| *Dasytes_obscurus* | LC | 19 |
| *Dendrophagus_crenatus* | NA | 1 |
| *Denticollis_rubens* | VU | 23 |
| *Diacanthous_undulatus* | VU | 1 |
| *Dictyopterus_aurora* | LC | 13 |
| *Drapetes_cinctus* | VU | 1 |
| *Dryocoetes_autographus* | LC | 47 |
| *Dryophilus_pusillus* | LC | 2 |
| *Endomychus_coccineus* | LC | 1 |
| *Enicmus_frater* | DD | 11 |
| *Enicmus_fungicola* | LC | 22 |
| *Enicmus_testaceus* | LC | 10 |
| *Epuraea_angustula* | LC | 1 |
| *Epuraea_boreella* | LC | 6 |
| *Epuraea_fageticola* | NA | 1 |
| *Epuraea_longula* | LC | 9 |
| *Epuraea_marseuli* | LC | 17 |
| *Epuraea_oblonga* | LC | 2 |
| *Epuraea_pallescens* | LC | 2 |
| *Epuraea_pygmaea* | NA | 12 |
| *Epuraea_rufomarginata* | LC | 3 |
| *Epuraea_silacea* | LC | 7 |
| *Epuraea_terminalis* | LC | 2 |
| *Epuraea_thoracica* | LC | 1 |
| *Epuraea_variegata* | LC | 1 |
| *Ernobius_abietis* | LC | 10 |
| *Ernobius_mollis* | LC | 1 |
| *Evodinus_clathratus* | LC | 25 |
| *Gaurotes_virginea* | LC | 3 |
| *Glischrochilus_quadripunctatus* | LC | 1 |
| *Hallomenus_axillaris* | VU | 1 |
| *Hylastes_angustatus* | LC | 3 |
| *Hylastes_cunicularius* | LC | 44 |

|  |  |  |
|---|---|---|
| *Hylecoetus_dermestoides* | LC | 5 |
| *Hylis_foveicollis* | NT | 3 |
| *Hylis_olexai* | NT | 1 |
| *Hylobius_abietis* | LC | 1 |
| *Hylobius_piceus* | LC | 3 |
| *Hylurgops_glabratus* | LC | 31 |
| *Hylurgops_palliatus* | LC | 33 |
| *Ipidia_binotata* | R | 1 |
| *Ips_amitinus* | LC | 4 |
| *Ips_cembrae* | LC | 1 |
| *Ips_typographus* | LC | 32 |
| *Latridius_hirtus* | LC | 1 |
| *Leptophloeus_alternans* | LC | 1 |
| *Leptura_maculata* | LC | 2 |
| *Lepturobosca_virens* | VU | 3 |
| *Melanotus_rufipes* | LC | 4 |
| *Micrambe_bimaculatus* | DD | 1 |
| *Molorchus_minor* | LC | 2 |
| *Mycetina_cruciata* | LC | 3 |
| *Mycetophagus_quadriguttatus* | LC | 1 |
| *Nemosoma_elongatum* | LC | 1 |
| *Octotemnus_glabriculus* | LC | 1 |
| *Orchesia_minor* | LC | 2 |
| *Orchesia_undulata* | LC | 5 |
| *Orthocis_alni* | LC | 5 |
| *Ostoma_ferruginea* | VU | 3 |
| *Oxymirus_cursor* | LC | 5 |
| *Pachytodes_cerambyciformis* | LC | 12 |
| *Phthorophloeus_spinulosus* | LC | 8 |
| *Pissodes_gyllenhalii* | NA | 1 |
| *Pissodes_pini* | LC | 1 |
| *Pityogenes_chalcographus* | LC | 28 |
| *Pityophagus_ferrugineus* | LC | 5 |
| *Pityophthorus_pityographus* | LC | 12 |
| *Platycis_minutus* | LC | 2 |
| *Plegaderus_vulneratus* | LC | 1 |
| *Pogonocherus_fasciculatus* | LC | 1 |
| *Polygraphus_poligraphus* | LC | 17 |
| *Polygraphus_subopacus* | DD | 1 |
| *Pteryngium_crenatum* | LC | 9 |
| *Ptilinus_pectinicornis* | LC | 3 |
| *Pyropterus_nigroruber* | LC | 1 |
| *Pytho_depressus* | LC | 1 |
| *Rabocerus_foveolatus* | LC | 1 |
| *Rhagium_inquisitor* | LC | 3 |
| *Rhizophagus_bipustulatus* | LC | 3 |
| *Rhizophagus_dispar* | LC | 11 |
| *Rhizophagus_ferrugineus* | LC | 12 |

| | | | |
|---|---|---|---|
| | *Rhizophagus_nitidulus* | LC | 4 |
| | *Salpingus_ruficollis* | LC | 22 |
| | *Serropalpus_barbatus* | LC | 1 |
| | *Sphaerites_glabratus* | LC | 5 |
| | *Stenurella_melanura* | LC | 21 |
| | *Stephostethus_rugicollis* | LC | 5 |
| | *Sulcacis_affinis* | LC | 1 |
| | *Tetratoma_ancora* | LC | 9 |
| | *Tetropium_castaneum* | LC | 8 |
| | *Tetropium_fuscum* | LC | 1 |
| | *Thanasimus_femoralis* | LC | 7 |
| | *Thanasimus_formicarius* | LC | 6 |
| | *Thymalus_limbatus* | VU | 1 |
| | *Triplax_aenea* | VU | 13 |
| | *Triplax_scutellaris* | R | 7 |
| | *Xestobium_austriacum* | R | 1 |
| | *Xylechinus_pilosus* | LC | 18 |
| | *Xylita_laevigata* | VU | 2 |
| | *Xylita_livida* | EN | 11 |
| | *Xyloterus_laevae* | R | 1 |
| | *Xyloterus_lineatus* | LC | 43 |
| **birds** | *Aegolius funereus* | LC | 2 |
| | *Anthus trivialis* | LC | 6 |
| | *Aquila chrysaetos* | NT | 1 |
| | *Bonasa bonasia* | LC | 12 |
| | *Buteo buteo* | LC | 2 |
| | *Carduelis spinus* | LC | 21 |
| | *Certhia familiaris* | LC | 48 |
| | *Coccothraustes coccothraustes* | LC | 1 |
| | *Columba palumbus* | LC | 11 |
| | *Corvus corax* | LC | 1 |
| | *Cuculus canorus* | LC | 15 |
| | *Dendrocopos major* | LC | 1 |
| | *Dryocopus martius* | LC | 3 |
| | *Erithacus rubecula* | LC | 58 |
| | *Fringilla coelebs* | LC | 58 |
| | *Garrulus glandarius* | LC | 4 |
| | *Glaucidium passerinum* | LC | 3 |
| | *Lophophanes cristatus* | LC | 22 |
| | *Loxia curvirostra* | LC | 14 |
| | *Nucifraga caryocatactes* | NT | 13 |
| | *Periparus ater* | LC | 55 |
| | *Phoenicurus phoenicurus* | VU | 1 |
| | *Phylloscopus collybita* | LC | 50 |
| | *Phylloscopus trochilus* | LC | 16 |
| | *Picoides tridactylus* | LC | 26 |
| | *Prunella modularis* | LC | 53 |
| | *Pyrrhula pyrrhula* | NT | 41 |

|  |  |  |  |
|---|---|---|---:|
|  | *Regulus ignicapilla* | LC | 27 |
|  | *Regulus regulus* | LC | 51 |
|  | *Scolopax rusticola* | LC | 5 |
|  | *Sitta europaea* | LC | 9 |
|  | *Sylvia atricapilla* | LC | 48 |
|  | *Tetrao urogallus* | EN | 6 |
|  | *Troglodytes troglodytes* | LC | 50 |
|  | *Turdus merula* | LC | 23 |
|  | *Turdus philomelos* | LC | 34 |
|  | *Turdus torquatus* | NT | 29 |
| **fungi** | *Alutaceodontia alutacea* | LC | 2 |
|  | *Amphinema byssoides* | LC | 14 |
|  | *Amylocystis lapponica* | CR | 1 |
|  | *Amylostereum areolatum* | LC | 16 |
|  | *Amylostereum chailletii* | LC | 2 |
|  | *Amyloxenasma allantosporum* | LC | 1 |
|  | *Antrodia serialis* | LC | 23 |
|  | *Antrodia sinuosa* | LC | 2 |
|  | *Antrodiella citrinella* | EN | 4 |
|  | *Aphanobasidium pseudotsugae* | LC | 45 |
|  | *Arrhenia epichysium* | EN | 1 |
|  | *Ascocoryne sarcoides s.l.* | LC | 11 |
|  | *Athelia cf. singularis* | LC | 1 |
|  | *Athelia cystidiolophora* | LC | 1 |
|  | *Athelia decipiens* | LC | 14 |
|  | *Basidiodendron caesiocinereum* | LC | 3 |
|  | *Basidiodendron radians* | LC | 1 |
|  | *Basidiodendron rimosum* | LC | 1 |
|  | *Bertia moriformis s.l.* | LC | 10 |
|  | *Boidinia furfuracea* | NT | 5 |
|  | *Boletus badius* | LC | 1 |
|  | *Botryobasidium aureum* | LC | 3 |
|  | *Botryobasidium candicans* | LC | 7 |
|  | *Botryobasidium ellipsosporum* | VU | 1 |
|  | *Botryobasidium intertextum* | NT | 10 |
|  | *Botryobasidium medium* | EN | 2 |
|  | *Botryobasidium obtusisporum* | LC | 15 |
|  | *Botryobasidium subcoronatum* | LC | 31 |
|  | *Botryobasidium vagum* | LC | 19 |
|  | *Calocera cornea* | LC | 3 |
|  | *Calocera furcata* | LC | 5 |
|  | *Calocera viscosa* | LC | 37 |
|  | *Camarops cf. pugillus* | LC | 2 |
|  | *Camarops tubulina* | NT | 4 |
|  | *Cantharellus tubaeformis* | LC | 10 |
|  | *Ceraceomyces eludens* | LC | 7 |
|  | *Ceraceomyces serpens* | LC | 1 |
|  | *Ceratobasidium cf. cornigerum* | LC | 1 |

| | | |
|---|---|---|
| *Ceriporia viridans* | LC | 2 |
| *Chlorencoelia versiformis* | LC | 3 |
| *Cinereomyces lindbladii* | LC | 2 |
| *Clavulicium macounii* | EN | 2 |
| *Clavulina rugosa* | LC | 1 |
| *Climacocystis borealis* | LC | 4 |
| *Conferticium ochraceum* | LC | 6 |
| *Coniophora arida* | LC | 1 |
| *Coniophora olivacea* | LC | 17 |
| *Cortinarius bataillei* | LC | 3 |
| *Cortinarius cf. biformis* | LC | 1 |
| *Cortinarius cf. brunneus* | LC | 1 |
| *Cortinarius cf. lignicola* | LC | 1 |
| *Cortinarius flexipes s.l.* | LC | 2 |
| *Cortinarius sommerfeltii* | LC | 1 |
| *Crepidotus applanatus* | LC | 2 |
| *Crepidotus kubickae* | LC | 20 |
| *Crepidotus malachius* | LC | 1 |
| *Crepidotus stenocystis* | LC | 1 |
| *Crustoderma corneum* | LC | 1 |
| *Crustoderma dryinum* | LC | 1 |
| *Cystoderma amianthinum* | LC | 5 |
| *Dacrymyces chrysospermus* | LC | 4 |
| *Dacrymyces stillatus* | LC | 96 |
| *Dacryobolus karstenii* | LC | 1 |
| *Dacryobolus sudans* | LC | 3 |
| *Datronia mollis* | LC | 1 |
| *Dentipellis fragilis* | LC | 1 |
| *Exidia pithya* | LC | 13 |
| *Exidiopsis calcea* | LC | 3 |
| *Exidiopsis grisea* | LC | 1 |
| *Fomes fomentarius* | LC | 2 |
| *Fomitopsis pinicola* | LC | 151 |
| *Galerina calyptrata s.l.* | LC | 1 |
| *Galerina calyptrospora* | LC | 3 |
| *Galerina camerina* | LC | 11 |
| *Galerina marginata* | LC | 3 |
| *Galerina pruinatipes* | LC | 3 |
| *Galerina triscopa* | LC | 1 |
| *Gerronema chrysophyllum* | EN | 3 |
| *Globulicium hiemale* | CR | 42 |
| *Gloeocystidiellum cf. clavuligerum* | LC | 2 |
| *Gloeophyllum odoratum* | LC | 1 |
| *Gloeophyllum sepiarium* | LC | 30 |
| *Gloiothele citrina* | LC | 2 |
| *Gymnopilus bellulus* | VU | 11 |
| *Gymnopilus josserandii* | DD | 1 |
| *Gymnopilus picreus* | LC | 20 |

| | | |
|---|---|---|
| *Gymnopilus sapineus* | LC | 1 |
| *Gymnopus acervatus* | LC | 2 |
| *Gymnopus androsaceus* | LC | 34 |
| *Gymnopus perforans* | LC | 4 |
| *Hastodontia hastata* | LC | 3 |
| *Helicogloea lagerheimii* | LC | 1 |
| *Heterobasidion annosum* | LC | 10 |
| *Hydnum rufescens* | LC | 1 |
| *Hygrophorus olivaceoalbus* | LC | 14 |
| *Hymenochaete fuliginosa* | EN | 17 |
| *Hyphoderma argillaceum* | LC | 14 |
| *Hyphoderma cf. cryptocallimon* | LC | 1 |
| *Hyphoderma cremeoalbum* | LC | 1 |
| *Hyphoderma definitum* | LC | 2 |
| *Hyphoderma involutum* | LC | 1 |
| *Hyphoderma velatum nom. prov.* | LC | 1 |
| *Hyphodontia alutaria* | LC | 15 |
| *Hyphodontia pallidula* | LC | 23 |
| *Hypholoma capnoides* | LC | 1 |
| *Hypholoma marginatum* | LC | 12 |
| *Hypochnicium albostramineum* | LC | 1 |
| *Hypochnicium cymosum* | LC | 1 |
| *Hypochnicium geogenium* | LC | 1 |
| *Hypochnicium punctulatum s.str.* | LC | 3 |
| *Hypochnicium wakefieldiae* | LC | 21 |
| *Hypocrea pulvinata* | LC | 3 |
| *Hypomyces aurantius* | LC | 1 |
| *Inocybe napipes* | LC | 1 |
| *Inocybe ovatocystis* | LC | 2 |
| *Ischnoderma benzoinum* | LC | 5 |
| *Jaapia ochroleuca* | LC | 23 |
| *Kneiffiella cineracea* | LC | 2 |
| *Kneiffiella subalutacea* | LC | 6 |
| *Lactarius lignyotus* | LC | 2 |
| *Lactarius rufus* | LC | 5 |
| *Lactarius turpis* | LC | 1 |
| *Lentinellus castoreus* | VU | 1 |
| *Leptoporus mollis* | NT | 1 |
| *Litschauerella sp.* | LC | 1 |
| *Lobulicium occultum* | LC | 1 |
| *Mucronella bresadolae* | LC | 2 |
| *Mucronella calva* | DD | 1 |
| *Mycena amicta* | LC | 1 |
| *Mycena epipterygia s.l.* | LC | 10 |
| *Mycena galericulata* | LC | 1 |
| *Mycena galopus* | LC | 19 |
| *Mycena laevigata* | VU | 23 |
| *Mycena maculata* | LC | 3 |

| | | |
|---|---|---|
| *Mycena metata* | LC | 1 |
| *Mycena mirata* | LC | 1 |
| *Mycena purpureofusca* | LC | 12 |
| *Mycena rubromarginata* | LC | 9 |
| *Mycena stipata* | LC | 4 |
| *Mycena viridimarginata* | LC | 6 |
| *Mycena vitilis* | LC | 1 |
| *Mycoacia nothofagi* | LC | 1 |
| *Nectria fuckeliana* | LC | 1 |
| *Panellus violaceofulvus* | CR | 2 |
| *Paullicorticium allantosporum* | LC | 3 |
| *Paxillus involutus* | LC | 3 |
| *Peniophora piceae* | LC | 2 |
| *Peniophora pithya* | LC | 3 |
| *Peniophorella pallida* | LC | 2 |
| *Peniophorella praetermissa s.l.* | LC | 6 |
| *Peniophorella pubera* | LC | 2 |
| *Phaeotremella foliacea* | LC | 1 |
| *Phanerochaete cf. sordida* | LC | 1 |
| *Phellinus ferrugineofuscus* | CR | 2 |
| *Phellinus nigrolimitatus* | NT | 61 |
| *Phellinus viticola* | LC | 101 |
| *Phlebia centrifuga* | EN | 5 |
| *Phlebia cremeoalutacea* | LC | 1 |
| *Phlebia segregata* | LC | 2 |
| *Phlebia subulata* | LC | 1 |
| *Phlebiella cf. fibrillosa* | LC | 7 |
| *Phlebiella tulasnelloidea* | LC | 3 |
| *Phlebiella vaga* | LC | 27 |
| *Phlebiopsis gigantea* | LC | 2 |
| *Pholiota astragalina* | LC | 2 |
| *Pholiota flammans* | LC | 5 |
| *Pholiota scamba* | LC | 24 |
| *Pholiota squarrosa* | LC | 3 |
| *Pholiota subochracea* | VU | 7 |
| *Physisporinus sanguinolentus* | LC | 26 |
| *Physodontia lundellii* | LC | 1 |
| *Piloderma bicolor* | LC | 2 |
| *Piloderma byssinum* | LC | 8 |
| *Pleurotus cf. abieticola* | LC | 3 |
| *Pleurotus pulmonarius* | LC | 1 |
| *Pluteus atromarginatus* | LC | 2 |
| *Pluteus cervinus* | LC | 2 |
| *Pluteus plautus* | LC | 2 |
| *Pluteus pouzarianus* | LC | 6 |
| *Postia caesia* | LC | 9 |
| *Postia fragilis* | LC | 1 |
| *Postia undosa* | VU | 4 |

| | | |
|---|---|---|
| *Pseudohydnum gelatinosum* | LC | 25 |
| *Pseudotomentella mucidula* | LC | 1 |
| *Pseudoxenasma verrucisporum* | LC | 3 |
| *Resinicium bicolor* | LC | 11 |
| *Resinicium furfuraceum* | LC | 13 |
| *Resupinatus striatulus* | LC | 2 |
| *Rickenella fibula* | LC | 1 |
| *Rigidoporus undatus* | LC | 1 |
| *Russula emetica* | LC | 6 |
| *Russula ochroleuca* | LC | 2 |
| *Scytinostromella heterogenea* | LC | 1 |
| *Serpula himantioides* | LC | 6 |
| *Sistotrema aff. autumnale* | LC | 1 |
| *Sistotrema brinkmannii* | LC | 3 |
| *Sistotrema oblongisporum* | LC | 1 |
| *Sistotrema octosporum* | LC | 4 |
| *Sistotrema resinicystidium* | LC | 1 |
| *Skeletocutis carneogrisea* | LC | 4 |
| *Skeletocutis cummata* | LC | 1 |
| *Skeletocutis jelicii* | LC | 4 |
| *Stereum hirsutum* | LC | 1 |
| *Stereum rugosum* | LC | 7 |
| *Stereum sanguinolentum s.l.* | LC | 45 |
| *Stypella subgelatinosa* | LC | 1 |
| *Stypella vermiformis* | LC | 1 |
| *Thelephora terrestris f. resupinata* | LC | 2 |
| *Tomentella badia* | LC | 1 |
| *Trechispora farinacea* | LC | 10 |
| *Trechispora mollusca s.l.* | LC | 4 |
| *Trechispora stellulata* | LC | 1 |
| *Trechispora subsphaerospora* | LC | 2 |
| *Tremella encephala* | LC | 2 |
| *Trichaptum abietinum* | LC | 14 |
| *Trichaptum fuscoviolaceum* | LC | 26 |
| *Tricholomopsis decora* | LC | 18 |
| *Tubaria confragosa* | EN | 2 |
| *Tubulicium vermiferum* | LC | 1 |
| *Tubulicrinis borealis* | LC | 2 |
| *Tubulicrinis chaetophorus* | LC | 3 |
| *Tubulicrinis hirtellus* | LC | 1 |
| *Tubulicrinis subulatus* | LC | 16 |
| *Tulasnella subglobispora* | LC | 2 |
| *Tylospora asterophora* | LC | 2 |
| *Tylospora fibrillosa* | LC | 79 |
| *Veluticeps abietina* | LC | 29 |
| *Xerocomus pruinatus* | LC | 1 |
| *Xeromphalina campanella* | LC | 4 |
| *Xylodon asperus* | LC | 12 |

| | | | |
|---|---|---|---|
| | *Xylodon brevisetus* | LC | 14 |
| **lichens** | *Absconditella lignicola* | LC | 4 |
| | *Alectoria sarmentosa* | CR | 27 |
| | *Arthonia arthonioides* | VU | 1 |
| | *Arthonia atra* | EN | 1 |
| | *Arthonia cf.* | NA | 1 |
| | *Arthonia leucopellaea* | CR | 13 |
| | *Arthonia radiata* | CR | 2 |
| | *Arthonia ruana* | VU | 5 |
| | *Arthonia vinosa* | CR | 1 |
| | *Bacidia subincompta* | VU | 1 |
| | *Bacidina sulphurella* | LC | 1 |
| | *Baeomyces rufus* | LC | 5 |
| | *Biatora chrysantha* | VU | 2 |
| | *Biatora efflorescens* | VU | 28 |
| | *Biatora fallax* | EN | 4 |
| | *Biatora globulosa* | VU | 2 |
| | *Biatora helvola* | EN | 3 |
| | *Bryoria capillaris* | CR | 161 |
| | *Bryoria fuscescens* | VU | 154 |
| | *Bryoria nadvornikiana* | CR | 8 |
| | *Buellia disciformis* | VU | 1 |
| | *Buellia griseovirens* | LC | 11 |
| | *Calicium abietinum* | CR | 9 |
| | *Calicium glaucellum* | CR | 15 |
| | *Calicium salicinum* | EN | 5 |
| | *Calicium viride* | EN | 2 |
| | *Candelaria concolor* | NT | 1 |
| | *Chaenotheca brunneola* | CR | 43 |
| | *Chaenotheca chrysocephala* | VU | 127 |
| | *Chaenotheca ferruginea* | LC | 77 |
| | *Chaenotheca furfuracea* | NT | 24 |
| | *Chaenotheca sphaerocephala* | CR | 21 |
| | *Chaenotheca trichialis* | CR | 38 |
| | *Chaenotheca xyloxena* | VU | 5 |
| | *Chrysothrix chlorina* | LC | 2 |
| | *Cladonia bellidiflora* | VU | 1 |
| | *Cladonia borealis* | DD | 1 |
| | *Cladonia callosa* | NA | 1 |
| | *Cladonia cariosa* | EN | 2 |
| | *Cladonia cenotea* | LC | 1 |
| | *Cladonia chlorophaea* | LC | 8 |
| | *Cladonia coniocraea* | LC | 340 |
| | *Cladonia digitata* | LC | 372 |
| | *Cladonia fimbriata* | LC | 27 |
| | *Cladonia floerkeana* | LC | 1 |
| | *Cladonia macilenta* | LC | 2 |
| | *Cladonia ochrochlora* | LC | 104 |

| | | |
|---|---|---|
| *Cladonia pleurota* | NT | 3 |
| *Cladonia polydactyla* | NT | 140 |
| *Cladonia ramulosa* | NT | 1 |
| *Cladonia squamosa* | NT | 27 |
| *Cladonia sulphurina* | EN | 2 |
| *Cliostomum corrugatum* | CR | 4 |
| *Cliostomum griffithii* | RE | 4 |
| *Coenogonium pineti* | LC | 244 |
| *Evernia divaricata* | CR | 9 |
| *Evernia mesomorpha* | CR | 3 |
| *Evernia prunastri* | EN | 1 |
| *Fellhanera bouteillei* | EX | 2 |
| *Fellhanera subtilis* | NT | 1 |
| *Graphis scripta* | EN | 6 |
| *Gyalecta friesi* | RE | 5 |
| *Hertelidea botryosa* | CR | 1 |
| *Hypocenomyce caradocensis* | LC | 134 |
| *Hypocenomyce friesii* | EN | 18 |
| *Hypocenomyce scalaris* | LC | 202 |
| *Hypogymnia bitteri* | EN | 3 |
| *Hypogymnia farinacea* | VU | 261 |
| *Hypogymnia physodes* | LC | 389 |
| *Hypogymnia tubulosa* | NT | 28 |
| *Icmadophila ericetorum* | CR | 6 |
| *Imshaugia aleurites* | VU | 53 |
| *Japewia subaurifera* | NT | 34 |
| *Lecanactis abietina* | CR | 25 |
| *Lecanora albellula* | VU | 2 |
| *Lecanora chlarotera* | LC | 1 |
| *Lecanora conizaeoides* | LC | 93 |
| *Lecanora expallens* | LC | 1 |
| *Lecanora phaeostigma* | NA | 49 |
| *Lecanora pulicaris* | LC | 57 |
| *Lecanora saligna* | LC | 19 |
| *Lecanora subintricata* | NT | 4 |
| *Lecanora symmicta* | NT | 2 |
| *Lecidea huxariensis* | EX | 3 |
| *Lecidea leprarioides* | EN | 17 |
| *Lecidea nylanderi* | VU | 59 |
| *Lecidea pullata* | NT | 213 |
| *Lecidella elaeochroma* | NT | 3 |
| *Lepraria elobata* | LC | 333 |
| *Lepraria incana* | LC | 11 |
| *Lepraria lobificans* | LC | 5 |
| *Lichenomphalia hudsoniana* | EN | 4 |
| *Lichenomphalia umbellifera* | LC | 91 |
| *Lopadium disciforme* | CR | 1 |
| *Melanelixia fuliginosa* | LC | 6 |

| | | |
|---|---|---|
| *Melanohalea exasperatula* | LC | 3 |
| *Micarea botryoides* | LC | 1 |
| *Micarea cf_melaena* | LC | 3 |
| *Micarea cinerea* | RE | 5 |
| *Micarea denigrata* | LC | 16 |
| *Micarea lignaria* | LC | 11 |
| *Micarea melaena* | LC | 4 |
| *Micarea micrococca* | LC | 385 |
| *Micarea misella* | LC | 17 |
| *Micarea nitschkeana* | NT | 2 |
| *Micarea peliocarpa* | LC | 23 |
| *Micarea prasina* | LC | 3 |
| *Micarea tuberculata* | CR | 1 |
| *Microalicium disseminatum* | NA | 1 |
| *Microcalicium ahlneri* | NA | 5 |
| *Mycoblastus alpinus* | EN | 10 |
| *Mycoblastus fucatus* | LC | 12 |
| *Mycoblastus sanguinarius* | CR | 191 |
| *Ochrolechia androgyna* | VU | 83 |
| *Parmelia ernstiae* | DD | 1 |
| *Parmelia saxatilis* | NT | 39 |
| *Parmelia submontana* | CR | 4 |
| *Parmelia sulcata* | LC | 8 |
| *Parmeliopsis ambigua* | LC | 320 |
| *Parmeliopsis hyperopta* | VU | 257 |
| *Peltigera membranacea* | VU | 2 |
| *Peltigera praetextata* | NT | 1 |
| *Pertusaria albescens* | NT | 14 |
| *Pertusaria amara* | NT | 2 |
| *Pertusaria cf.* | NA | 1 |
| *Pertusaria multipuncta* | CR | 1 |
| *Pertusaria pupillaris* | VU | 3 |
| *Phlyctis argena* | LC | 2 |
| *Placynthiella dasaea* | LC | 17 |
| *Placynthiella icmalea* | LC | 249 |
| *Placynthiella oligotropha* | LC | 3 |
| *Platismatia glauca* | NT | 340 |
| *Porina aenea* | LC | 8 |
| *Porina leptalea* | EN | 3 |
| *Pseudevernia furfuracea* | NT | 349 |
| *Psilolechia clavulifera* | LC | 2 |
| *Ramalina farinacea* | EN | 2 |
| *Rinodina orculata* | EN | 1 |
| *Schismatomma pericleum* | VU | 1 |
| *Scoliciosporum chlorococcum* | LC | 22 |
| *Strangospora moriformis* | NT | 68 |
| *Strangospora pinicola* | NT | 143 |
| *Thelocarpon epibolum* | LC | 2 |

| | | |
|---|---|---|
| *Thelocarpon lichenicola* | NA | 1 |
| *Trapelia corticola* | EN | 9 |
| *Trapeliopsis flexuosa* | LC | 194 |
| *Trapeliopsis granulosa* | LC | 3 |
| *Trapeliopsis pseudogranulosa* | LC | 49 |
| *Tuckermannopsis chlorophylla* | NT | 91 |
| *Usnea diplotypus* | EN | 2 |
| *Usnea filipendula* | NA | 2 |
| *Usnea scabrata* | EX | 67 |
| *Usnea substerilis* | NA | 2 |
| *Vulpicida pinastri* | NT | 3 |
| *Xylographa parallela* | VU | 51 |
| *Xylographa soralifera* | NA | 2 |
| *Xylographa vitiligo* | EN | 7 |

**Table S2:** Results of generalised least squares model (GLS) selection for species richness of the respective taxa in the plots. For each model, the regression coefficients are listed for a set of explanatory variables. The variables with significant effect ($p < 0.05$) are highlighted in bold. The explanatory variables relating to the deadwood were sequentially substituted in the models, and the model Akaike information criterion (AIC) was compared. The parsimonious models with at least two significant explanatory variables are indicated by a grey background.

| Taxa / model number | Explanatory variables | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Altitude | Openness | Age | Total dead wood volume | Standing dead wood volume | Lying dead wood in decay classes 1,2 and 3 | Lying dead wood in decay class 1 | Lying dead wood in decay classes 4 and 5 | AIC | ΔAIC |
| **Beetles** | | | | | | | | | | |
| 1.1 | -1.4271 | **4.2769** | 0.5624 | -1.6382 | | | | | 389.85 | |
| 1.2 | -1.3292 | **2.6811** | 0.0999 | | **2.3595** | | | | | -1.00 |
| 1.3 | -1.0185 | **3.6865** | 0.5279 | | | -0.5748 | | | | +1.23 |
| 1.4 | -0.8767 | **2.8889** | 03080 | | | | **2.2700** | | | -2.44 |
| 1.5 | -1.5285 | **3.8434** | 0.3573 | | | | | -1.8722 | | -1.06 |
| **Birds** | | | | | | | | | | |
| 2.1 | 0.2144 | 0.0822 | 0.0639 | 0.0608 | | | | | 294.86 | |
| 2.2 | 0.0107 | 0.3338 | 0.0931 | | -0.5791 | | | | | -1.30 |
| 2.3 | 0.1763 | 0.1820 | 0.0988 | | | -0.1422 | | | | -0.11 |
| 2.4 | 0.2426 | 0.1477 | 0.0762 | | | | -0.3108 | | | -0.24 |
| 2.5 | 0.2148 | 0.0691 | 0.0492 | | | | | 0.1636 | | +0,34 |
| **Fungi** | | | | | | | | | | |
| 3.1 | -1.3649 | -1.7631 | 0.8895 | 1.5797 | | | | | 370.86 | |
| 3.2 | -1.5590 | -1.1190 | 0.8530 | | 0.4825 | | | | | +1.80 |
| 3.3 | -1.5634 | -1.2071 | 0.8985 | | | 0.4812 | | | | +1.62 |
| 3.4 | -1.5896 | -0.9341 | 0.9528 | | | | -0.1623 | | | +2.11 |
| 3.5 | -1.3506 | -1.3097 | 1.0465 | | | | | 1.5254 | | -0.39 |
| **Lichens** | | | | | | | | | | |
| 4.1 | 1.6754 | 0.2228 | **2.9663** | 1.3320 | | | | | 369.39 | |
| 4.2 | 1.1952 | 0.3024 | **2.8244** | | **1.9202** | | | | | -1.34 |
| 4.3 | 1.4560 | 0.6734 | **3.0013** | | | 0.4795 | | | | +1.34 |
| 4.4 | 1.3296 | 0.7655 | **3.0479** | | | | 0.9794 | | | +0.76 |
| 4.5 | 1.8282 | 0.5886 | **3.0197** | | | | | 1.3848 | | -0.47 |

**Table S3:** Results of generalised least squares model (GLS) selection for the number of red-listed species of the respective taxa in the plots. For each model, the regression coefficients are listed for a set of explanatory variables. The variables with significant effect ($p < 0.05$) are highlighted in bold. The explanatory variables relating to the deadwood were sequentially substituted in the models, and the model Akaike information criterion (AIC) was compared. The parsimonious models with at least two significant explanatory variables are indicated by a grey background.

| Taxa / model number | Explanatory variables | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Altitude | Openness | Age | Total dead wood volume | Standing dead wood volume | Lying dead wood in decay classes 1,2 and 3 | Lying dead wood in decay class 1 | Lying dead wood in decay classes 4 and 5 | AIC | ΔAIC |
| **Beetles** | | | | | | | | | | |
| 5.1 | -0.0814 | 0.1275 | 0.0437 | -0.0797 | | | | | 169.61 | |
| 5.2 | -0.0669 | 0.1530 | 0.0830 | | -0.2097 | | | | | -2.04 |
| 5.3 | -0.0478 | 0.0174 | 0.0263 | | | 0.1194 | | | | -0.40 |
| 5.4 | -0.0719 | 0.0570 | 0.0335 | | | | 0.1626 | | | -1.13 |
| 5.5 | -0.1479 | 0.1527 | 0.0163 | | | | | **-0.2990** | | -4.84 |
| **Fungi** | | | | | | | | | | |
| 6.1 | 0.2253 | -0.2065 | 0.3051 | 0.0921 | | | | | 206.52 | |
| 6.2 | 0.2122 | -0.2391 | 0.2524 | | 0.2424 | | | | | -1.24 |
| 6.3 | 0.2000 | -0.0957 | 0.3189 | | | -0.1136 | | | | -0.12 |
| 6.4 | 0.2174 | -0.1320 | 0.3132 | | | | -0.1581 | | | -0.28 |
| 6.5 | 0.2985 | -0.2756 | **0.4234** | | | | | **0.3852** | | -2.70 |
| **Lichens** | | | | | | | | | | |
| 7.1 | **1.9560** | 0.0700 | **1.7586** | 1.1971 | | | | | 312.21 | |
| 7.2 | **1.5928** | 0.8115 | **1.9743** | | -0.2879 | | | | | +3.85 |
| 7.3 | **1.7040** | 0.5329 | **1.8928** | | | 0.3325 | | | | +3.49 |
| 7.4 | **1.6361** | 0.6696 | **1.9466** | | | | 0.2054 | | | +3.90 |
| 7.5 | **1.9032** | 0.3761 | **1.8263** | | | | | **1.1327** | | +5.25 |