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Faculty of Forestry and Wood Sciences

The effect of natural disturbances and forest structure on tree-related microhabitats and saproxylic beetles in primary mountain forests

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Objectives of thesis

Understanding the effects of historical disturbances and forest structure on biodiversity is crucial for the conservation and suitable management of forest ecosystems. Based on the data from up to 500 permanent study plots located across primary spruce and mixed forest landscapes we aim to enhance our knowledge of interactions between historical disturbance regimes, current forest structure and local biodiversity indicators. In particular, this dissertation thesis aims to evaluate the effects of historical natural disturbances and forest structure across primary forest landscapes on saproxylic beetles and tree related microhabitats. Saproxylic beetles are a diverse group of forest invertebrates representing a major component of biodiversity that is associated with the decomposition and cycling of wood nutrients and carbon in forest ecosystems. Tree related microhabitats are important structural features for the conservation of biodiversity, as they represent a substrates or life sites for species or communities to develop, feed, shelter or breed. Studies from primary forests are important reference baselines for forest management practices as they represent ultimate intact ecosystems, thus our results may serve to guide forest management and conservation in order to promote biodiversity in forest ecosystems.
Particular aims of the thesis are:

1. Investigate the influence of historical disturbances and forest structure on taxonomic, functional and phylogenetic diversity of current saproxylic beetle communities
2. Characterize the tree related microhabitats profile and evaluate the importance of local plot structure and spatial variability for tree related microhabitats density and diversity
3. Evaluate the effect of tree age and tree diameter on tree related microhabitats abundance and diversity

Methodology

The study will take place in the primary spruce and mixed forests in the Carpathian and Dinaric Mountains. Sample plots will be selected from the network of permanent research plots previously established using stratified random design. Field data will be collected to describe disturbance history, forest structure, associated tree-related microhabitats characteristics and saproxylic beetle communities. We will calculate various diversity indices for description of saproxylic beetle communities such as taxonomic richness, Shannon diversity, functional and phylogenetic diversity; and we will characterize tree related microhabitats profile using density and diversity of microhabitats per plot. On the tree level we will focus on abundance, diversity for overall microhabitat profile and specifically for different microhabitat types. Most of the statistical analyses will be performed using generalized linear mixed effect models or linear mixed effect models but we will also use techniques such as redundancy analysis or boosted regression trees.

The proposed extent of the thesis

100

Keywords

primary forests, natural disturbances, biodiversity indicators, saproxylic beetles, tree-related microhabitats, forest structure, disturbance legacies

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Recommended information sources

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I hereby confirm that this PhD. thesis “The effect of natural disturbances and forest structure on tree-related microhabitats and saproxylic beetles in primary mountain forests” 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.

December 10th, 2020, Prague

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Abstract

Natural disturbances shape forest structure, dynamics, ecosystem functions and services. Disturbance legacies such as deadwood, canopy gaps and habitat trees greatly influence the amounts of suitable habitats for forest dwelling species. Understanding the importance of disturbance legacies for supporting biodiversity is crucial in understanding any biotic responses in the face of the expected future intensification of forest disturbance as a consequence of ongoing anthropogenic climate change.

The main objective of this thesis is to observe how natural disturbances and current forest structure of primary mountain forests of Europe impacts forest habitats and forest dwelling species. We use tree-related microhabitats (TreMs) and saproxylic beetles as the objects of the study, since TreMs encompass a variety of habitats suitable for feeding, dwelling or shelter of forest species and saproxylic beetles because of their close relationship to deadwood substrate and forest structure conditions. Thus we first aimed to i) investigate the influence of historical disturbances and forest structure on the taxonomic, functional and phylogenetic diversity of current saproxylic beetle communities (Section 5.1), ii) characterize the TreM profile and evaluate the importance of local plot structure and spatial variability for TreM density and diversity (Section 5.2), iii) compare the TreM richness of primary and managed forests on a tree level (Section 5.3) and iv) evaluate the effect of tree age on TreM abundance and richness in primary spruce and beech-dominated forests (Section 5.4). For these aims we used a large database of permanent study plots from primary forests of Central, Eastern and Southeastern Europe and managed forests from the Black Forest region. We combined the dendroecological database from more than 350 plots with the survey of TreMs and samples of saproxylic beetles on a subset of plots.

The main findings of this thesis are:

i) Historical disturbances have significant effects on current beetle communities. Contrary to our expectations, different aspects of beetle communities, that is, abundance, taxonomic, phylogenetic and functional diversity, responded to different disturbance regime components. Past disturbance frequency was the most important component influencing saproxylic beetle communities and available habitats via multiple temporal and spatial pathways. The quantity of deadwood and its diameter positively influenced saproxylic beetle abundance and functional diversity, whereas phylogenetic diversity was positively influenced by canopy openness (Section 5.1).

ii) TreM density and diversity were significantly positively related with tree species richness and the proportion of snags. Root mean square of the tree diameters were significantly related to alpha and gamma diversity of TreMs. Both regions reached similarly high values of total TreM densities, and total TreM densities and diversity were not significantly different between the two regions. However, we observed significant differences between the two regions in regard to the densities of two TreM groups, conks of fungi and epiphytes. The density and diversity of TreMs were very high in beech-dominated primary forests, but their occurrence and diversity were highly variable within the landscape over relatively small spatial gradients (plot and stand levels; Section 5.2)

iii) We found congruent results based on the models for overall richness and the vast majority of TreM groups. Trees in primary forests hosted greater richness of all and specific types of TreMs than individuals in managed forests. The main driver of the difference was the long-term natural development with the absence of human management, followed by tree species and DBH.

iv) Tree diameter and age were the most important factors significantly increasing TreM abundance and richness, whereas tree species played a lesser but significant role in overall TreM abundance and richness across the primary forests. We observed the major role played by tree age in increasing the richness of specific TreM groups, such as concavities, insect galleries and exposed sapwood on studied trees.

Additionally, we provide general as well as specific recommendations for conservationists and forest managers based on our results, on how to conserve and increase the habitat amount and quality of forest stands in order to host a rich array of biodiversity.

Key words: natural disturbances, primary forest, biodiversity indicators, saproxylic beetles, tree-related microhabitats, forest structure, disturbance legacies

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1. Introduction

Biodiversity is considered a fundamental driver that shapes forest ecosystem functionality and facilitates key ecosystem processes and services. Forests support more than half of the world's terrestrial biodiversity and have the highest species diversity for many taxonomic groups (Lindenmayer et al. 2006). In a face of today's biodiversity crisis, conservation of forest biodiversity is therefore a critical task.

Forest ecosystems without human influence, also known as primary forests, have unique qualities that significantly contribute to biodiversity conservation (Lachat & Müller 2018). Primary forests serve as a refugia for rare or endangered forest specialists sensitive to human disturbance which cannot survive in managed forest stands (Peterken 1996). Thus, primary forests represent an important reference baseline which makes them extremely valuable for ecological research.

Primary forest ecosystems are characterized by natural disturbances of various intensities, frequencies and severities which have major effects on the quantity and quality of available habitats for forest taxa (Lachat & Müller 2018). The natural post-disturbance development and the various developmental pathways often result in high levels of structural heterogeneity (Meigs et al. 2017). Disturbance legacies such as large amounts of deadwood and senescent trees provide unique habitats for numerous species that have evolved in forest conditions regulated by natural processes (Franklin et al. 2007). Moreover, diverse deadwood substrates and senescent trees represent necessary habitats for saproxylic species which account for about one third of all forest species (Ulyshen et al. 2018).

Saproxylic beetles are a diverse group of forest invertebrates representing a major component of biodiversity that is associated with the decomposition and cycling of wood nutrients and carbon in forest ecosystems (Ulyshen et al. 2018). Due to their obligate and highly specific associations with particular substrate types (Grove 2002), many saproxylic beetles are indicator species. Along with other endangered saproxylic beetles, many of these indicator species are only found in primary forests (Lachat & Müller 2018), suggesting a dependence on structural legacies created by intermittent disturbance events.

Tree-related microhabitats (TreMs) are important structural features for biodiversity because they represent substrates or life sites for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed (Larrieu et al. 2018). TreMs are considered as structural indicators of biodiversity mostly due to their efficiency of indicating the presence of certain taxa (Winter & Möller 2008, Paillet et al. 2018), and for their relatively easy and time efficient assessments during field monitoring (Larrieu et al. 2018). There is evidence of several forest attributes influencing the occurrence of TreMs, such as tree diameter, vitality and species, but these observations were mostly in managed forests or previously managed forest reserves (Vuidot et al. 2011, Paillet et al. 2019, Asbeck et al. 2019). The studies of TreM profile across primary forests are scarce and only little is known on how tree and plot level primary forest structure influences the occurrence of specific TreM types.

Understanding the role of the natural disturbances and forest structure in maintaining the conditions to support a rich array of forest biodiversity is a critical issue in the face of the recent biodiversity crisis connected with species extinction worldwide. The results presented in this thesis can help guide forest management in understanding the natural processes behind the maintenance of species habitats and to implement the necessary practices to help conserve temperate forest biodiversity.

2. Literature review

2.1 Primary forests, natural disturbances and disturbance regimes

2.1.1 Primary forests

According to the Food and Agricultural Organization (FAO, 2015), primary forests refer to naturally regenerated forests of native species where there are no clearly visible indications of human activities, and where ecological processes are not significantly disturbed. However, this definition does not completely exclude human intervention in the distant past, which cannot always be known. Kraus & Krumm (2013) presented a definition based on natural processes: primary forests are forests that were initiated under a regime of natural disturbances and have developed with minimal human influence. A key factor of primary forests is the absence of human activities that could disturb ecological processes but, like all forests, primary ones are subject to indirect human impact, such as climate change, air pollution, and altered population densities of ungulates.

Primary forests can also be characterized as dynamic ecosystems driven by disturbances of various scales, diverse developmental pathways, shifting microenvironments, and competitive interactions governing spatial patterns of mortality and recruitment (Donato et al. 2012, Svoboda et al. 2012). These processes generate and maintain spatial heterogeneity, which in turn influences the spatiotemporal distribution of associated organisms – from large old trees to organisms not visible to the naked eye (Lindenmayer et al. 2006).

Primary forests contain substantially higher amounts of deadwood than managed forests (Siitonen 2001) leading to a higher diversity of deadwood substrates, particularly with respect to larger diameter deadwood, deadwood in later stages of decay and standing deadwood (Gibb et al. 2005). Moreover, primary forests contain large habitat trees that develop various microhabitats such as cavities and cracks (Commarmot et al. 2013). All of these structural features provide unique habitats for numerous species that have evolved in forest conditions regulated by natural processes (Korpel 1995). The continuous supply of high amounts of deadwood and senescent trees over several centuries or longer (habitat continuity) is an important driver that influences the presence of certain forest taxa (Buse 2012). Thus, primary forest attributes are of crucial importance for forest specialists and particularly for saproxylic taxa (Winter et al. 2005).

These irreplaceable primary forests have unique qualities that significantly contribute to biodiversity conservation (Lachat & Müller 2018), therefore their protection is a global concern (Mackey et al. 2015). They are also ecologically important in regions where forests are highly fragmented (Vandekerkhove et al. 2009). For instance, primary forests serve as refuges and reservoirs for rare or endangered species, especially for forest species sensitive to human disturbance which cannot survive in managed forests (Paillet et al. 2015, Peterken 1996).

Furthermore, primary forests serve as a model for understanding natural disturbances and successional dynamics (Kuuluvainen & Aakala 2011), especially in the face of climate change, and provide baselines for the delivery of ecosystem services under unmanaged conditions, including carbon stocks and sequestration (Burrascano et al. 2013). Finally, primary forests help us to evaluate human impacts on forest ecosystems and to understand the potential and limitations of forest management practices (Bauhus et al. 2009, Kuuluvainen & Aakala 2011).

Temperate zone forests of Europe have undergone a very complicated history. Since ancient times, they were used for various purposes including fuel wood, pasture, and timber extraction (Veen et al. 2010). In Europe, as in other human dominated regions, historical deforestation and forest exploitation came close to eliminating primary forests (Potapov et al. 2017), and the last remnants of primary forests are located in remote mountain regions of Eastern and Southeastern Europe. Even this little share of undisturbed forest is heavily fragmented, as no intact forest landscapes >500 km^2 exist outside European Russia and boreal Northern Europe (Potapov et al. 2017). Primary forests disproportionately occur in remote, sparsely populated regions, mostly in rugged mountain areas or at high latitudes (i.e. on land with low agricultural productivity or low profitability for forestry operations), where land-use history has been shorter and less intense than in the rest of Europe (Kulakowski et al. 2017). One of the largest continuous areas of forest cover in Europe occurs in the Carpathian Mountains, which harbors most of Europe's remaining temperate primary forests (Sabatini et al. 2018).

2.1.2. Natural disturbances and disturbance regimes

Disturbances are a key component of ecological systems and are the main drivers of spatial and temporal heterogeneity (Turner et al. 2010). Disturbance can be defined as any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment (White & Pickett 1985). In origin, disturbances may be abiotic and biotic, or combination of the two. In contrast to a disturbance event, a disturbance regime refers to the spatial and temporal dynamics of disturbances over a longer period. It includes characteristics such as the spatial distribution of disturbances, disturbance frequency, return interval, and rotation period, and disturbance size, intensity, and severity (Turner 2010). Natural disturbances are one of the most important drivers of primary forest dynamics. Due to disturbance processes of various spatial and temporal scales, forest ecosystems are dynamic; their composition and structure are in a continuous state of change (Kraus & Krumm 2013). Disturbances can, for instance, alter the age structure of forest landscapes, favor early seral species, and change the developmental trajectories of forest ecosystems, with effects that can persist for centuries after a disturbance event (Frelich 2002, Nagel et al. 2014).

Primary forest ecosystems are characterized by natural disturbances such as wildfires, insect outbreaks or windstorms (White & Picket 1985). The intensity, frequency and severity of natural disturbances in primary forests have a major effect on the quantity and quality of available habitats (Lachat & Müller 2018). Large disturbance events in particular can result in high deadwood volumes, and a high diversity of substrate types regarding e.g. tree diameter, sun exposure or tree species, and specific resource types, such as charred wood after fire, uprooted trees after windthrows or rot holes and other microhabitats in over-mature trees (Siebold et al. 2016). This variety of resource types and heterogeneity of microhabitats is crucial and widely beneficial for deadwood-dependent - saproxylic - species. Thus, disturbances play an important role in maintaining biodiversity in temperate forest ecosystems by creating biological legacies, such as deadwood and senescent trees, and increasing understory light level (Hanson & Lorimer 2007, Woods 2004). The combination of small gaps dynamics associated with the breakdown of a single tree, and disturbances affecting several square kilometers has shaped forest over millennia, which in turn has shaped the communities of species (Gauthier et al. 2015). Through co-evolution and selection processes, forest species are preadapted to the natural prevailing disturbance regime typical for their respective forest biome (McPeek & Holt 1992).

The most important type of disturbance in the temperate forests of Central Europe are blowdowns connected with the direct disturbance of the canopy trees (Ulanova 2000, Schelhaas et al. 2003). Studies in primary and natural beech and mixed forests indicate that periodic intermediate-severity damage from wind disturbances (i.e. single events that cause stand-level damage ranging from scattered single tree falls to larger openings several thousand square meters in size) is an important component of the disturbance regime in this region (Nagel et al. 2014). Montane coniferous forests are even more susceptible to severe blowdown than broadleaved stands (Baker et al. 2002). Central European montane spruce forests are also subject to wind disturbances, often with the probability of ongoing bark-beetle outbreaks. Windthrows significantly affect the composition of both the herb layer and seedlings, and at the same time, they influence the spatial variability of the forest floor and the diversity of decomposer communities (Šamonil et al. 2009). Wind disturbances also have long-term effects on forest structural composition, for example on the secondary succession of vegetation, canopy closure and the deadwood amount and decay. Perforation of closed canopy forests by windthrow creates open gaps with large amounts of sun exposed deadwood and habitat heterogeneity in time and space which acts as a source of regional biodiversity in forest ecosystems (Bouget & Duelli 2004). Changes in abundance and distribution patterns of resources on macro- and micro-habitat scales affects the abundance and distribution of forest taxa (Müller et al. 2008).

Another common disturbance driver in the Central European landscape are bark beetle outbreaks (mostly caused by the European spruce bark beetle *Ips typhographus*). They often start after windthrow events, which provide large amounts of breeding material (Wermelinger 2004). Bark beetle outbreaks create substantial amounts of deadwood and open the canopy across large areas (Schroeder 2007). Healthy spruce trees are generally resistant to bark beetle attacks through their resin defenses. However, if the defense system of the tree is weakened by drought or some other stress factor, or if there are a sufficient amount of adults boring into the trunk at the same time, the resin pressure is not sufficient to force them out (Stokland et al. 2012). Studies from recent years pointed out the ecological value of bark beetle related disturbances (Müller et al. 2008, Müller et al. 2010), using the terms “ecosystem engineer” and “keystone” species, through their role in driving forest regeneration, producing deadwood and rich patchiness in forest canopies (Jonášová & Pracha 2004). Apart from providing these ecosystem services, the arthropod communities associated with *I. typographus* includes more than 140 species and they significantly contribute to regional biodiversity (Müller et al. 2008). Bark beetle outbreaks cause major changes in forest structure, light regime and increase the deadwood amount in montane spruce forests, and such ecosystems are among the most species rich ecosystems in central Europe (Bouget & Duelli 2004).

2.2 Forest structure and biological diversity

Forests are important for the conservation of biodiversity because they host a substantial part of the terrestrial biodiversity (Lindenmayer et al. 2006). Biological diversity usually relates positively to habitat heterogeneity (Huston 1994). In forest ecosystems, habitat heterogeneity arises when either stand composition or structure varies over time and space (Franklin & Van Pelt 2004) and the provision of habitats within a forest are largely related to their structural richness or complexity. Thus, forest structure is identified as a key determinant of biodiversity and many other ecosystem services (McElhinny et al. 2005, Paillet et al. 2018).

Measuring biodiversity is a key step in preventing its further losses. It has been observed that single taxonomic groups are poor indicators of overall forest biodiversity (Jokela et al. 2018). Besides the limited indicating quality, taxonomic measures to assess biodiversity may be time-consuming and highly subjective to the knowledge of the observer and thus difficult to reproduce and can introduce biases into biodiversity assessment (Regnery et al. 2013). Thus, to enhance the conservation of biodiversity the emphasis has changed from inventorying single-species to measuring structural elements that support forest taxa on different scales ranging from landscape and stand-scale to fine-scale structures at the tree level (Ehbrecht et al. 2017, Paillet et al. 2018). Forest structural indicators of biodiversity use the relationship between habitat feature and the occurrence of forest-dwelling taxa instead (Lindenmayer et al. 2000, McElhinny et al. 2006). Several studies proposed using structure-based indicators such as deadwood, veteran trees or tree-related microhabitats (TreMs), (often called as old-growth forest attributes; Paillet et al. 2015) to assess biodiversity in forests (Winter & Möller 2008, Michel & Winter 2009). Such structural features are mostly legacies issued from natural disturbances and structural heterogeneity (Franklin et al. 2002), and thus are usually rare in managed forests.

2.2.1 Deadwood

Deadwood is a crucial element for biodiversity in forest ecosystems as the high amounts of nutrients, energy and habitat space formed by deadwood allowed a large number of species to evolve an association with deadwood including both saproxylic species (i.e. directly or indirectly dependent on dying or dead wood) and non-saproxylic species (Stokland et al. 2012). Besides this, deadwood also plays an important role in carbon sequestration and nutrient supply, and may also enhance natural regeneration, particularly in montane forests with perennial grasses.

In natural forest ecosystems, deadwood is frequently created by a complete or partial die-off of senescent and old trees, or by natural disturbances which can affect single trees or complete stands (White & Pickett 1985). Such events largely determine the spatial and temporal dynamics of deadwood in both broadleaved and coniferous forests (Šamonil et al. 2009, Seidl et al. 2014). As forementioned, both senescence and natural disturbances can result in high deadwood volumes, a high diversity of substrate types regarding, e.g. tree diameter, sun exposure or tree species, and specific resource types, such as charred wood after fire, uprooted trees after windthrows or rot holes in over mature trees (Seibold et al. 2015). This variety of resource types is crucial as it represents a wide range of habitats for saproxylic species.

A high amount of deadwood under natural conditions not only leads to a larger diversity of substrates but also to a higher deadwood surface area. According to the island theory (MacArthur & Wilson 1967), we can expect higher species richness on sampling units with a larger surface. Similarly, forests with high amounts of deadwood will generally harbor more saproxylic species than forests with low amounts of deadwood (Kraus & Krumm 2013).

Primary forests are important in maintaining a diversity of deadwood types. Although forest harvesting creates pulses of deadwood and habitats that might be similar to those created by disturbance events, it is not only the volume of deadwood that differs between managed forests and primary forests, but also the range of deadwood types. As proposed by Stokland et al. (2012), there are at least 4 important gradients of variation in deadwood types which needs to be considered:

1. In primary forests, deadwood input is relatively continuous, guaranteeing the local presence of dead trees at all stages of decay. Although mortality rates vary depending on tree size and age (Fraver et al. 2008), primary forests tend to produce dead trees of all dimensions.
2. There are a variety of mortality agents involved in tree deaths, each providing specific types of substrates for saproxylic species.
3. These substrates then undergo a decay succession, with the different decay stages each hosting partly different communities of saproxylic beetles.
4. Primary forests often include a larger set of tree species compared with managed stands, which are often monocultures.

These four types of variation – tree size, substrate type, decay stage and tree species – constitute the main deadwood diversity gradients. They may be viewed as a multidimensional space that sets the available niches (Stokland et al. 2012).

Recent conservation strategies emphasize biodiversity-related structures such as deadwood (e.g. Stokland et al. 2012) for which thresholds (Müller & Bütler 2010) and references have been published (e.g. Christensen et al. 2005, Paillet et al. 2015, Vandekerkhove et al. 2009). For example, deadwood volume has been used as a structural indicator for forest biodiversity monitoring in most European forest inventory protocols during the previous decades (Tomppo et al. 2010). Clear definitions and survey methods for assessing deadwood allow comparative studies (e.g. Christensen et al. 2005, Vandekerkhove et al. 2009), inventories and analyses to be carried out in harmonized way (Rondeux et al. 2012).

2.2.2 Tree-related microhabitats

Among the scientifically-based indirect structural indicators, tree-related microhabitats (TreMs) have been gaining attention in the recent decades in research and management (e.g. Larrieu & Cabanettes 2012, Michel & Winter 2009, Regnery et al. 2013, Vuidot et al. 2011), and some countries have already implemented TreMs assessment in forest management to identify habitat trees for retention (e.g. Forst 2015, Santopuoli et al. 2019).

TreMs have several advantages in terms of measurements, because they are simple (no specialized knowledge is required) and quick to measure (approximately 3 min per tree), and they provide a reliable measure of ecological niches for numerous forest species related to old-growth attributes. However, the links between trees, stand characteristics and TreMs are still only partially understood compared to other research areas related to biodiversity indicators (Michel & Winter 2009, Vuidot et al. 2011).

By definition, a TreM is a distinct, well-delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed. TreMs are specific above-ground tree morphological singularities which are not to be found on every tree. TreMs encompass both tree-originating modifications caused by biotic and abiotic impacts, such as intrusions, lesions and breakages, which expose sap and heartwood and initialize outgrowth structures and wood decay (saproxylic TreMs), as well as elements of external origin that are physically linked to the tree (epixylic TreMs). Although morphological singularities may also be observed on lying deadwood or roots, TreM are explicitly restricted to above-ground structures on standing trees, in order to avoid a too wide scope. Thus, this definition excludes features of lying deadwood such as root plates, pits and mounds and particular wood decay structures, as well as generic tree species-specific characteristics, such as rough bark on oak or larch, acid or alkaline bark conditions, in addition to peculiar tree growth forms (such as crooked, skewed or rotated trunks, low horizontal branching), resulting from specific abiotic conditions or hap-hazard growth (Larrieu et al. 2018).

Owing to their different origins, substrates, and positions on trees, TreMs represent an array of resources available for forest organisms and are of conservation relevance. TreMs strongly contribute to the internal heterogeneity of forest stands. They provide specific conditions, notably microclimatic conditions and substrates, where specialized taxa shelter, forage or breed. Therefore, there is a functional link between TreMs and species, ecological groups or guilds. In other words, TreMs constitute very small-scale habitats (or part of a habitat) for associated and specialized species or species assemblages (Larrieu et al. 2018, Michel & Winter 2009, Winter & Möller 2008). For example, dead branches are food source for saproxylic insects and fungi (Vanderwel et al. 2006). Cavities provide habitats for breeding birds, mammals, and invertebrates, and also lichens and bryophytes (Parsons et al. 2003, Ranius 2002). Many forest bats nest or roost behind cracked and loose bark. Other microhabitats, such as conks of fungi or ivy, are homes to insects and provide potential nesting and foraging sites for birds (Bässler et al. 2012). TreMs support a large food web and may have an important role in the functioning of forest ecosystems (Aitken & Martin 2007). Insect larvae or ants that live below the bark of recently dead trees constitute a non-negligible part of some birds' diet (Laiolo et al. 2004, Regnery et al. 2013). Some species linked to TreMs are also a major concern for biodiversity conservation, such as some saproxylic insects (e.g. *Limoniscus* *violaceus, Osmoderma eremita*), birds (e.g. *Dendrocopos leucotos*) and bats (e.g. *Barbastella barbastellus*) (Regnery et al. 2013).

Some TreM types (e.g. mould cavities) harbor high species richness and host many different taxonomic groups, while some TreM types (e.g. dendrothelms) harbor few species belonging to only a few taxonomic groups. Nevertheless, conservation value cannot only be defined by the number of species using a given TreM type, but one should also consider the occurrence of species exclusively conditioned to a single TreM type (Stokland et al 2012). Some specific interactions between forest-dwelling species and TreM types are well known. For instance, the relationship between living TreMs such as wood decaying fungi and woodpeckers (Cockle et al. 2012) or between invertebrates and lichens (Pettersson et al. 1995). Non-living TreMs, such as rot holes and cavities, are often used by forest species including lichens, bryophytes, bats and birds (Fritz & Heilmann-Clausen 2010, Tillon & Aulagnier 2014, Wesołowski & Maziarz 2012).

In recent years, attention has focused on specific TreM characteristics such as diversity or abundance, and their ability to predict the characteristics of specific forest taxa. For instance, some studies have found that birds and bats species richness was positively related to TreM diversity (Paillet et al. 2018, Regnery et al. 2013), while invertebrates showed positive associations with specific TreMs like fruiting bodies of fungi or cavities (Friess et al. 2019, Paillet et al. 2018). More specifically, abundance of rot holes had a positive effect on the abundance of Sternorrhyncha and bats (genus *Pipistrellus*; Basile et al. 2020a). The positive effect of rot holes on threatened epiphytes and saproxylic insects has also been demonstrated (Fritz & Heilmann-Clausen 2010, Müller et al. 2014).

These correlations indicate that it may be possible to predict the abundance and/or diversity of specific forest organisms from the occurrence of specific TreMs, however, not much research on this topic has been conducted yet, and a lot of studied correlations was insignificant or rather weak. Weak association between TreM occurrence and certain taxa might be caused by the implementation of inadequate sampling methods, or by the fact that many species might not be influenced by TreM occurrence, but for certain species TreMs still represent a necessary substrate (Paillet et al. 2018).

A recently developed hierarchical approach to typology (Larrieu et al. 2018) identifies seven general TreM forms that share the same physiognomy and functional characteristics:

1. <u>Cavities</u> are holes or shelters formed in the wood either by cavity builders (e.g. woodpeckers, saproxylic insects), decay processes (rot hole), morphological particularities on the trunk or collar (e.g. dendrothelms in forks or root-buttress shelters). They provide buffered climatic conditions and nesting sites for a wide array of species, from arthropods

to large mammals. They can be subdivided into cavities in which the entrance is smaller than its interior diameter, and galleries and concavities if the entrance is of the same or greater width than the interior.

2. Injuries expose sapwood and sometimes also heartwood, allowing access for colonizing taxa. They are mainly created by mechanical impacts such as trunk or crown breakage from wind, ice or snow, but may also be caused by lightning strikes and frost, and occasionally by forest fires. Exposed wood and injuries may evolve to rot holes over time if the tree is not able to seal the wound.
3. Crown deadwood consists of dead branches which most often occur at the top of a tree; this often provides open xero-thermophilous conditions due to the location in the canopy. Crown deadwood may also take the form of large broken branches where a thick dead branch section still remains. Dead treetops, generally sun-lit, expose the heartwood and offer a transition between the living tree and deadwood.
4. Excrescences are mainly caused by reactive growth in response to increased light availability or to a parasitic or microbial intrusion where the tree creates specific structures to isolate the pathogen (e.g. canker, burr).
5. Fungal fruiting bodies and slime moulds are the visible part of saproxylic fungi (or fungi-like organisms such as Myxomycetes) and are classified as perennial or ephemeral (lasting less than a year) structures.
6. Epiphytic and epixylic structures encompass a wide variety of structures in which the tree is merely the physical support on which the TreM grows or is located. These structures include different organisms growing on trees (cryptogams and phanerogams), vertebrate or invertebrate nests and also “perched” microsoils (developed from organic material such as leaves, bark, decaying bryophytes, etc.) either on the bark of a trunk, at fork intersections or on a flat area within the crown.
7. Exudates are sap runs or heavy resinosis.

At the tree scale, the link between TreM richness and/or diversity and tree characteristics (e.g. trunk diameter or tree vitality) has already been studied (Larrieu & Cabanettes 2012, Larrieu et al. 2014, Regnery et al. 2013, Paillet et al. 2019, Vuidot et al. 2011, Winter et al. 2015a, Winter & Möller 2008), and these tree characteristics have been shown as key factors for TreM presence and abundance. Larger trees are more likely to bear a TreM than smaller trees, as they have experienced more damages and microhabitats-creating events (e.g. woodpecker excavation, storms, snowfalls). Similarly, dead trees are more likely to bear more TreMs than living trees, due to the decomposition process and their role as habitat and food source for many microhabitat creating species (Stokland et al. 2012). In some cases, dead trees can bear up to 50 percent more TreMs than their living counterparts (Paillet et al. 2019), with increased numbers of individual types, such as woodpecker feeding holes or bark characteristics. However, the increased number of TreMs on dead trees varies across studied regions, from 1.2 times more TreMs in Mediterranean forests (Regnery et al. 2013), 1.3 times to 2 times more in French forests (Vuidot et al. 2011, Paillet et al. 2019) to 4 times more on habitat trees in south-western Germany (Johann & Schaich 2016). As living trees also bear microhabitats, many of them persist when the tree dies and continue to evolve, or even facilitate the development of other microhabitats linked with decay processes (Stokland et al. 2012). Injuries caused by logging, rockfall, treefall or branch break slowly rot and evolve into decayed cavities (Gouix & Brustel 2012, Larrieu et al. 2018) and these successions explain why these microhabitats are more numerous on dead trees. However, there are exceptions; epiphytes and forks with accumulated organic matter tend to be more numerous on living trees. Ivy, mosses and lichens benefit from bark characteristics and conditions which are likely to occur only on living trees (e.g. pH, Mežaka & Brumelis 2012). Moreover, epiphytes require a relative stable substrate to grow or anchor, especially when they have slow growth rates like some species of mosses or lichens (Ódor et al. 2014) and such a property is lost when tree dies; bark loosen and falls more rapidly than on living trees. Therefore, decay processes linked to tree death favors microhabitats that are linked to mortality (saproxylic TreMs) and disfavors those that are not linked to such phenomena (i.e. epixylic TreMs; Larrieu et al. 2018)

Larger (living) trees sometimes have a longer lifespan than smaller ones, and are consequently more prone to damages due to meteorological events (storms, snowfall), natural hazards (rockfalls) or attacks and use by a different tree- and wood-dependent species (woodpeckers, beetles, fungi; e.g. Bobiec 2002, Vuidot et al. 2011). For instance, dead branches are more prone to occur on large trees than smaller ones, as larger trees have more and often larger branches which are likely to die from competition with neighbors, especially broadleaves (Bouget et al. 2011). Cavity birds and bats are known to preferentially choose larger trees to nest or roost (Remm & Löhmus 2011, Tillon et al. 2016), since larger wood width around a cavity provides buffered and more stable conditions (Scheffers et al. 2014). The number and occurrence of TreMs also increases with diameter and sometimes at a higher rate for living trees than for their dead counterparts (Paillet et al. 2019).

Some studies at the plot scale investigated how TreM profiles are affected by the establishment of forest reserves, and by the time since management abandonment (e.g. Winter et al. 2005, Bouget et al. 2014, Larrieu et al. 2012, Paillet et al. 2017). There is a general trend towards higher densities of TreMs in strict reserves and when forests have been left unmanaged for a long time. For instance, Paillet et al. (2017) showed that the overall density of TreMs at the plot level was higher in strict forest reserves than in their managed counterparts, and that the magnitude of this difference varied with elevation. Moreover, Larrieu et al. (2012) found that despite a lower TreM diversity in managed forests, a number of certain TreM types (dendrothelms and missing bark) were favored by logging. To confirm these findings, reference studies in the rare primary temperate forests in Europe or elsewhere, are much needed (Larrieu et al. 2018). Studying primary forest remnants can also help to understand the spatial distribution of TreMs under natural conditions.

The study of TreM occurrence on a larger spatial scale (e.g. stand scale) is also important, since that is usually the scale on which silvicultural management occurs. Several TreMs - as well as any biotic agents that possibly create them - might depend on specific conditions influenced by the proportion of forest cover and its maturity in the surrounding landscape (Asbeck et al. 2019). One study found that on the stand scale, the abundance of TreMs increased with higher altitudes, and DBH was observed to positively influence not only the abundance but diversity of TreMs as well. Whilst a higher abundance of TreMs was observed in mono-dominated coniferous stands, TreM diversity was higher in mixed forests (Asbeck et al. 2019).

2.2.3 Saproxylic beetles

Deadwood is a key component for biodiversity in forest ecosystems as the high amount of nutrients, energy and habitat space provided by deadwood allowed many species to evolve an association with deadwood (Seibold 2015). Species dependent on deadwood are called saproxylic species (Speight et al. 1989), with this dependence being direct (obligatory) or indirect (facultative). Saproxylic organisms are species that depend on the phloem or wood of wounded, dying, or dead woody plants during some parts of their life cycle (Speight 1989, Alexander 2008, Stokland et al. 2012).

Saproxylic beetles are one of three diverse insect orders associated with deadwood representing about 30% of the total biodiversity in the temperate forests, and are one of the best studied taxa associated with deadwood (Grove 2002). In Central Europe, about 50% of all forest beetles are associated with deadwood (Seibold 2015). Habitat preferences of saproxylic beetle species differ between deadwood of different tree species, decay stages, wood diameter classes, microclimatic conditions and other deadwood criteria (Ulyshen & Hanula 2009, Gossner et al. 2013). Saproxylic beetles comprise a wide range of different functional groups including phloem- and wood-feeders, fungivores, predators or detritivorous species, and are thus involved in different ecosystem processes related to deadwood, such as wood decomposition, nutrient cycling and carbon sequestration (Seibold 2015). Due to their taxonomic and trophic diversity and sensitivity regarding deadwood quality and quantity, saproxylic beetles are considered indicators for forest habitat changes, naturalness and biodiversity (Siitonen 2001, Hjältén et al. 2012, Lachat & Müller 2018). Since deadwood is a resource patchily distributed and variable in time, saproxylic populations face variation in the availability of this resource driven by the dynamic mosaic of forest heterogeneity (Jonsson et al. 2005). Many saproxylic beetles are highly specialized to certain resource types or stages of wood decay (Stokland et al. 2012). For those species, the required type of deadwood represents an ephemeral habitat and its colonization requires high tracking and dispersal abilities (Ranius et al. 2011). Many saproxylic beetles can track deadwood, which is a spatio-temporally dynamic habitat (Seibold et al. 2017). Thus, many species can disperse over long distances as they are naturally adapted to search for their ephemeral resources, and even flightless species can disperse further than expected (Komonen & Müller 2018, De Gasperis et al. 2016). However, lower dispersal capacity was detected for red-listed species, which underlines the higher sensitivity of such species to fragmentation (Brunet & Isacsson 2009). Particularly specialized species with low mobility, such as some associated with tree cavities, might be sensitive to an interruption of habitat continuity because they are not able to find an alternative habitat within their distribution range at the right time (Ranius & Hedin 2001). Thus, not only spatial continuity but also temporal continuity of deadwood and senescent tree structures, such as TreMs, are important factors influencing saproxylic beetle communities.

At the local scale, habitat quality for saproxylic beetles is related to abiotic conditions (e.g. moisture and temperature conditions related to canopy closure) and available resources (Bouget et al. 2013). Resources not only include deadwood substrates, but also more cryptic biological legacies such as TreMs. The density and/or diversity of resources may underlie the resource-biodiversity relationship. Forest stands with a wider range of resources and/or higher density of substrates may be able to support a larger number of species due to demographic, stochastic and dispersal processes affecting local population dynamics (Päivinen et al. 2003).

3. Aims and overview of the dissertation thesis

Understanding the effects of historical disturbances and forest structure on biodiversity is crucial for the conservation and suitable management of forest ecosystems. Based on the data from up to 500 permanent study plots located across primary spruce and mixed forest landscapes, we aim to enhance our knowledge of interactions between historical disturbance regimes, current forest structure and local biodiversity indicators. In particular, this dissertation thesis aims to evaluate the effects of historical natural disturbances and forest structure across primary forest landscapes on saproxylic beetles and TreMs. As aforementioned, saproxylic beetles are a diverse group of forest invertebrates, representing a major component of biodiversity that is associated with the decomposition and cycling of wood nutrients and carbon in forest ecosystems. TreMs are important structural features for the conservation of biodiversity, as they represent important substrates or life sites for species or communities to develop, feed, shelter or breed. Studies from primary forests are important reference baselines for forest management practices as they represent ultimate intact ecosystems, thus our results may serve as a guidance for forest management and conservationists in order to promote biodiversity in temperate forest ecosystems.

Particular aims of the thesis are to:

1. Investigate the influence of historical disturbances and forest structure on the taxonomic, functional and phylogenetic diversity of current saproxylic beetle communities (Section 5.1)
2. Characterize the TreM profile and evaluate the importance of local plot structure and spatial variability for TreM density and diversity (Section 5.2)
3. Compare the TreM richness of primary and managed forests on a tree level (Section 5.3)
4. Evaluate the effect of tree age, diameter and other tree characteristics on TreM abundance and richness (Section 5.4)

4. Methods

4.1 Study area

This dissertation was realized within the REMOTE primary forests project (REsearch on MOuntain TEmperate forests; www.remoteforests.org). The project is a long-term international collaboration based on a network of permanent sample plots in the forests of Central, Eastern and Southeastern Europe. We refer to primary forest as a forest without signs of direct human impact, and where natural disturbances are the primary driver of forest structure and composition. These forests not only include old growth, but also the early seral stages of development.

The thesis was based on research carried out in two distinct regions: the Carpathian and Dinaric mountains. The Carpathian Mountains (hereafter Carpathians) span over 220 400 km^2 and they represent the second largest mountain range in Europe, stretching across eight European countries: Romania, Ukraine, Slovakia, Austria, Czech Republic, Poland, Hungary and Serbia. For a long time, forests in the Carpathians were protected from human influence due to their remote location and poor accessibility. Surrounding lowland forests - as well as forests located at lower elevations of the Carpathians - were cleared because of their suitability for human settlement and agriculture. This process took place in different regions of the Carpathians in various historical periods but mainly throughout the Middle Ages (between 500 and 1500 AD). The mountain forests located deep within steep valleys and on the ridges remained mainly intact at that time. Until a few decades ago, a relatively continuous mountain forest cover was maintained in the Romanian and Ukrainian (and partly also Slovakian) regions of the Carpathians because it was still not operationally or economically viable to conduct logging in these forests. Recently, however, due to the introduction of modern harvesting technologies, widespread destruction of many previously undisturbed sites has occurred across the Carpathians. As a result, primary forests are currently relatively rare in the Carpathians and they make up only a small proportion of the total forest cover. Despite their scarcity, the size of primary forests is still decreasing, mainly due the unawareness of their exact location (imprecise mapping) and the lack of effective protection measures. Our research in the Carpathians focuses on mixed beech-dominated and spruce forests, with more detailed description provided in Sections 5.1, 5.2, 5.3 and 5.4.

The Dinaric Mountains are approximately 700 km in length and 200 km in width; they range from the northwestern to the southeastern areas of the western Balkan Peninsula. The mountains are known for karst areas where a significant part of the mountains was formed by carbonate rocks (e.g., limestone) precipitously shaped by water. Although now the area is quite bleak, it was originally covered by forests. The Western Balkans have historically been a strategic location, even as far back as antiquity – important trade routes used to cross the land and several powerful states intersected there. The colonization and related deforestation in the region began around 6000 - 6500 BC. The original forests had undergone extraction and burning for settlement foundations, pasture, and metal mining (particularly iron). Ship construction was one of the main reasons for the disappearance of forests along coastal shores. We can trace the first attempts to protect these valuable forests back to the 12th century, but the measures were largely ineffective. Significant achievements in protecting and restoring forests occurred in the 19th century. However, the original forests have already been destroyed or at least completely changed since that time. The last of the true primary forests are scattered in the most isolated places throughout the Dinaric Mountains. It has been a long time since the forests formed continuous complexes, only residues are preserved nowadays. The forests are predominantly beech-fir forests, of which the largest and most famous are Peručica in Bosnia and Herzegovina (1434 ha) and Biogradska Gora (about 1600 ha) in Montenegro. Nowadays, there are even larger areas of critical forests unknown to the general population. Those areas are usually found outside protected areas, or they are poorly protected, and therefore in danger of deforestation. Our research in the Dinaric Mountains focused on mixed beech-dominated forests with detailed description provided in chapter 5.2.

4.2 Data collection and analysis

Data collection and analysis was the specific goal. The Western Carpathians were used as a study area within scope of goal 4.2.1. The study was carried out in the Dinaric Mountains and the Carpathians for the goal 4.2.2, and the Carpathians (Western and Southern) were chosen as an area of interest for the goal 4.2.3 and 4.2.4 (together with the data from Black forest) of the dissertation thesis.

4.2.1 Investigate the influence of historical disturbances and forest structure on taxonomic, functional and phylogenetic diversity of current saproxylic beetle communities

For this goal, the study region was restricted to primary forests in the Slovakian portion of the Western Carpathian Mountains. Field data were collected to describe disturbance history, forest structure, associated habitat characteristics, and beetle community demography. All data were collected within 0.1 ha circular plots (N = 57) with a minimum distance between selected plots of 300 m. Disturbance history was reconstructed using increment cores collected from the plot network and it described approximately a 250-year long record of disturbance history encompassing the study plots. These chronologies were derived from analyses of temporal patterns in interannual tree growth. Growth variation was quantified from measurements of annual radial increments in tree core samples. Disturbance events were reconstructed based on an assumption that disturbance processes affect levels of neighborhood competition and resource supply, and hence, growth responses in extant individuals (Svoboda et al. 2014). We used a reconstructed time series (Janda et al. 2017) of event occurrences and their associated severity estimates and derived a total of six disturbance-based metrics: time since maximum disturbance, severity of the maximum disturbance, time since last disturbance, severity of the last disturbance, disturbance frequency, and disturbance index (for a detailed description, see Table 1 in Section 5.1). To quantify and classify the forest structure, we collected comprehensive inventory data of 15 explanatory variables: mean tree age, deadwood root mean square (RMS) of the diameter at breast height (DBH), standing deadwood volume, TreM diversity, TreM density, mean canopy openness, Gini index of canopy openness, logs volume decay stage 1-5, logs volume, total deadwood volume (for a detailed description, see Table 1 in Section 5.1). We sampled the current saproxylic beetle populations in each survey plot using insect traps to characterize the taxonomic composition and species richness of local communities. For this purpose, we used flight intercept (window) traps to collect beetle specimens. Traps were installed continuously from May to September 2017 and emptied monthly. The taxonomic identity of all beetle specimens was determined to species level, excluding specimens in the family Staphylinidae, which were omitted from further analyses (Parmain et al. 2015). After the taxonomical classification of the remaining specimens, individual species were aggregated into four separate, non-mutually exclusive subgroups comprised of: (1) all taxa; (2) species only associated with coniferous trees; (3) endangered or red-listed species as classified by the International Union for Conservation of Nature (IUCN 2019); and (4) species that are both red-listed and conifer-tree specialists. To quantify the range of compositional (taxonomic) as well as functional and phylogenetic metrics we selected various standard diversity indices from the ecological literature, namely: overall abundance, species richness, Shannon diversity (Jost 2006), functional and phylogenetic diversity. We used the trap data to compute each of the selected diversity indices at a plot scale for each of the previously described species subgroups. Since sample sizes for beetle trap collections varied substantially among plots (N = 5-705 individuals/plot), we standardized all trap data before calculating diversity indices following protocols associated with a unified framework for extrapolation and rarefaction based on an effective number of species (Hill numbers; Chao and others 2014). The trap data of a plot were standardized based on the overall mean per plot sample size. We calculated functional and phylogenetic diversity (see Section 5.1 for full description), both based on proxy information, using the following approaches: (1) We acquired selected key ecological traits data to estimate the relative distribution of species in a composite traits or niche space and used species-specific mean niche positions within this construct to quantify an associated trait or functional diversity index; and (2) we compiled data describing phylogenetic relationships between surveyed beetle taxa and computed a diversity index based on the overall complexity and depth of the derived evolutionary tree. To test our hypotheses, we formulated a suite of linear mixed-effect models (LMMs) to quantify community responses in terms of the range of previously described indices of diversity, including the tree taxonomic-based measures, functional and phylogenetic diversity. Disturbance parameters were used as explanatory variables to estimate their direct effects on both forest structure (habitat) and, in an alternate model, beetle diversity. Additional models were formulated to estimate the effects of habitat on beetle diversity. Forest stands were treated as random effects in all models to account for the hierarchical nature of the sampling design (see Figure 1 in Section 5.1). To compare the relative importance of significant variables retained in the final LMMs, we calculated standardized regression coefficients and their 95% parametric bootstrap confidence intervals. Marginal (R^2_m) and conditional (R^2_c) determination coefficients were calculated for the final LMMs to quantify the proportion of the total variance explained by the fixed effects and by both fixed and random effects, respectively (Nakagawa et al. 2017). To further explore evidence for potential synergies or interactions between processes that shape current beetle communities, associations between disturbance effects and habitat condition, and relationships between habitat effects and beetle diversity, were integrated in a network of confirmatory path analysis (Shipley 2009).

4.2.2 Characterize the TreM profile and evaluate the importance of local plot structure and spatial variability for TreM density and diversity

For the second goal, we selected four primary European beech-dominated mountain forests from both regions – the Carpathian and Dinaric Mountains. Stands from the Carpathian Mountains spanned Slovakia and Romania, and those from the Dinaric Mountains were located in Croatia, Bosnia and Herzegovina, and Albania. There are broad environmental differences between the study sites that are pointed out in Table 1 in Section 5.2. We established 146 permanent sample plots nested within 73 pairs of plots across 8 forest stands. For each tree (with a DBH ≥ 6 cm), the status of all trees (live or snag), tree species. For all study plots, each tree, including stem and crown, was visually inspected for TreMs by two observers. Based on the typology of Vuidot et al. (2011), we created a list of 30 TreM types that we used to classify TreMs on our plots. All living trees with a DBH ≥ 6 cm and snags located within the plots were searched for presence of TreMs (see Appendix 2 in Section 5.2 for the complete list of all observed TreM types); we surveyed 13 640 living trees and snags in total. We arranged the TreM types into 12 groups for further analysis according to Paillet et al. (2017): crown deadwood, broken tops, conks of fungi, woodpecker cavities, non-woodpecker cavities, base cavities, bark characteristics, cracks, outgrowths, patches with exudates, epiphytes, and dendrothelms. All TreMs were surveyed in 2015 and 2016 during the period of June to September. We quantified diversity and density measures of TreMs for each sample plot. To reflect the diversity of TreM types, diversity was defined in terms of the number of TreM types occurring within the plots. Alpha diversity was defined as the average number of TreM types per tree in a given plot. Because the number of trees varied widely among plots (27-277 trees per plot), gamma diversity was calculated as the total number of TreM types per plot standardized by rarefaction to a common abundance level (N = 27 trees), to ensure comparability across plots (Chao et al. 2014). To identify TreM densities, we used the index proposed by Paillet et al. (2017), i.e. the density of TreM-bearing trees, which allowed us to compare the results with other studies that used the same indices. Density of TreMs was quantified as the sum of TreM-bearing trees extrapolated to one hectare (Paillet et al. 2017). To determine the number of trees per plot bearing a given TreM type, each TreM type found on a tree was counted only once, even if it was present in greater numbers. Diversity and density measures were also calculated for several broad groups of TreM types (see Table 2 in the Section 5.2), in which case the density defines the density of trees bearing a particular TreM type. Generalized linear mixed models (GLMMs) were used to assess the effect of local plot structure and spatial variability on the diversity and density characteristics of TreMs. Fixed effects included tree species richness (i.e., total number of tree species per plot), RMS DBH (root mean square diameter of trees at breast height in a given plot), proportion of snags (proportion of snags per plot versus total number of trees), and region (Dinarides and Carpathians). The random effects structure mirrored the spatial hierarchical nature of the sampling design, including plots nested within pairs of plots, which were nested within stands nested within regions. To compare the relative importance of the fixed effects, we calculated semi-partial marginal determination coefficients (R^2_m; Nakagawa et al. 2017) derived from a commonality analysis (Ray-Mukherjee et al. 2014). The intraclass correlation coefficients (ICC) were used to quantify the proportion of variance explained by each of the hierarchical spatial levels.

4.2.3 Compare the TreM richness of primary and managed forests on a tree level

For this goal, we used the data from the managed forests placed in one-hectare forest plots located on state land in the Black Forest region, Germany. The plot selection followed a landscape gradient of forest cover in the 25 km^2 surrounding the plots and a gradient of structural complexity indicated by the number of standing dead trees per plot (see Storch et al. 2020). We selected a subset of plots that were managed for timber production and excluded strict protected ones mentioned in Asbeck et al. 2019. We recorded the position of all inventoried trees, their DBH, species identity and TreMs in the snow-free and leaf-free period between fall 2016 and spring 2017. We collected additional data, including altitude and latitude per tree with the use of hand-held tablets.

For the primary forests, we collected the data in mixed forests of the Western (Slovakia, 210 plots) and Southern Carpathians (Romania, 190 plots). All data were collected within 0.15 ha circular plots randomly distributed across various environmental gradients. Across the primary forest plots, we recorded the positions of all living, adult trees (≥ 6 cm DBH), their DBH, species identity and TreM profile based on the methodology by Larrieu et al. (2018) during the vegetation season in 2018 and 2019. Altitude and latitude were measured at the center of the plot.

To decrease the observer effect (Paillet et al. 2015), inventories were carried out by the same team within each location. Three observers in the Black forests and two in the Carpathian region visually inspected the TreMs following the same hierarchical typology (Larrieu et al. 2018).

Since data for dead trees was not available for the Black Forest, we focused only on a comparison of living trees. We calculated the overall richness as the sum of different TreM groups per living tree. To model the richness as well as the groups of TreMs per living tree, we used generalized linear mixed effect models (GLMMs).

In combination with management, we tested the effects of the following covariates tree species, DBH, altitude and latitude on the overall richness and richness of Trem groups on individual living trees. These covariates were selected as they have previously been found to drive the richness and number of groups of TreMs per tree (Kozák et al. 2018, Asbeck et al. 2019). Tree DBH as well as species identity were included in the GLMMs as predictors. In addition to the three tree species, Norway spruce (*Picea abies, L.*), European beech (*Fagus sylvatica, L.*) and silver fir (*Abies alba, Mill.*), we included altitude and latitude as site factors as we have datasets from two different geographic regions. To prevent autocorrelation of trees within the same plot that might have more similar characteristics than individuals in different plots (Dormann 2013) we included plot-identity as a random factor. The computation of models was performed in R (R Core Team 2016). Since the richness data for TreMs were of count type, we built models with the glmmTMB function of the glmmTMB package (Brooks et al. 2017) with a negative binomial distribution due to overdispersion. To test for under- and overdispersion as well as zero-inflation models, we used the DHARMa package (Hartig 2018). Because of the large number of living trees that did not bear TreMs, there were signs of zero-inflation; however, models did not improve when considering this. We checked for correlations between the predictors in the final models by computing the variance inflation factors with the performance package (Lüdecke et al. 2020). Prior to running the models, we adjusted the continuous predictors due to the different scales using the default setting of the scale function in R, which calculates the mean and the standard deviation of the predictor and then scales each element by those values by subtraction of the mean and dividing by the standard deviation. We used the ggpredict function of the ggeffects package for plotting, which sets all other predictors, except the one for which the effect is shown, to the same value (Lüdecke et al. 2018).

4.2.4 Evaluate the effect of tree age, diameter and other tree characteristics on TreM abundance and richness

Within this particular goal of the dissertation thesis, we selected 379 primary European mixed-beech (n = 133) and spruce (n = 246) mountain forest plots in the Slovakian and Romanian parts of the Carpathian Mountains. Due to possible differences in topography and climatic conditions within the two studied forest types, which can not only influence the growth of the studied tree species, but also the occurrence and diversity of certain TreM types (Asbeck et al. 2019, Paillet et al. 2019), we divided our data in two subsets based on the forest type (mixed-beech and spruce). Field data were collected to describe tree and associated TreM characteristics. All data were collected within 0.1 ha circular plots on spruce dominated plots, and 0.15 ha on mixed beech-dominated plots. Firstly, we identified the coarse structure of plots by precisely mapping all standing trees using laser rangefinder and customized software (Field-map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic). As diameter of the tree has been recognized as important factor of TreM occurrence (Paillet et al. 2019), we measured the size (diameter at breast height, DBH) of all adult (≥ 6 cm DBH) trees, and determined ages for a subset of canopy trees (N = 15-30) based on increment core samples. Tree cores were randomly selected from individual trees contributing to canopy cover (Lorimer & Frelich 1989). These are individuals exhibiting potentially large variation in size and age, but with fully exposed canopies. Then, we identified occurrences of 47 distinct TreM types on all live trees based on the methodology by Larrieu et al. (2018) and particular types were pooled to TreM forms described by the same methodology. All trees were determined to species level. Due to the minor occurrences of other tree species in the dataset, we only used four major tree species in the analyses, namely: Norway spruce, European beech, silver fir and sycamore maple. The trees which were not cored - and therefore, without information about their age - were excluded from the final dataset. Cores were dried in the laboratory and cut by a core microtone (Gärtner & Nievergelt, 2010), crossdated and measured following standard dendrochronological methods (Stokes & Smiley, 1968). Annual rings were measured to the nearest 0.1 mm using a stereomicroscope and a Lintab^{TM} sliding-stage measuring device in conjunction with TSAP-WIN^{TM} software (http://www.rinntech.ds). Cores were first visually cross-dated using the marker year approach (Yamaguchi 1991), verified with PAST4^{TM} software (www.sciem.com), and then confirmed with COFECHA^{TM} software (Holmes 1983).

For the evaluation of the relative influence of the predictor variables (tree age, DBH, species, growth and region), we used Boosted Regression Trees (BRT, Elith et al. 2008). The measures are based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedmann & Meulman 2003). The relative influence (or contribution) of each variable is scaled so that the sum adds to 100, with higher numbers indicating stronger influence on the response. We fitted a BRT model using the function *gbm.step* from the *dismo* package (Hijmans et al. 2017) with the following parameters: tree complexity = 5, learning rate = 0.005, bag fraction = 0.5 (Elith et al. 2008). We repeated the same procedure for both the spruce and the beech datasets.

We used age and DBH as explanatory variables, since DBH is recognized as one of the most important factors influencing TreM occurrence and richness, and often has a relationship with tree age. As our study focused on tree level analyses, we did not include plot characteristics such as topography, climate and disturbance regime in the model. However, to account for the possible differences between study locations, we used region as an additional explanatory variable. As certain TreMs are known to differ between tree species, we used tree species as a categorical explanatory variable with four factors (beech, spruce, fir, maple) but we excluded tree species from models of spruce dataset, since there were very few tree species present other than spruce. We modelled the abundance, TreM richness and richness of TreM groups as a response variable with generalized linear mixed models (GLMMs). To prevent autocorrelation of trees within the same plot that might have more similar characteristics than trees in different plots, we included hierarchical spatial design of our study (plots nested in stands) as a random effect. Since the abundance and richness of TreMs are counts, we built models with the glmmTMB function from glmmTMB package (Brooks et al. 2017) with a Conway-Maxwell Poisson distribution because there were signs of underdispersion and zero-inflation. Additionally, we used a binomial distribution for models of the TreM groups richness which comprised of only presence and absence of one specific TreM (TreM groups such as insect galleries, twig tangles, perennial fungi). We scaled the continuous predictors using the default setting of the scale function in R. We used a stepwise model selection to select the best model using Akaike information criterion (AIC). All statistical analysis took place in R (R Core Team 2016).

5 Results

The dissertation thesis consists of two published manuscripts, one submitted manuscript and one soon-to-be submitted manuscript. The first part focuses on the influence of historical disturbances and forest structure on current saproxylic beetle communities (Section 5.1). The second part aims to evaluate the TreM profile across the European primary beech-dominated forests (Section 5.2). The third part presents a comparison of TreM richness in primary and managed forests (Section 5.3), and the fourth part focuses on disentangling the effect of tree age and other tree characteristics on TreM abundance and diversity (Section 5.4)

5.1 Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests

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Historical Disturbances Determine Current Taxonomic, Functional and Phylogenetic Diversity of Saproxylic Beetle Communities in Temperate Primary Forests

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ABSTRACT

The expected future intensification of forest disturbance as a consequence of ongoing anthropogenic climate change highlights the urgent need to more robustly quantify associated biotic responses. Saproxylic beetles are a diverse group of forest invertebrates representing a major component of biodiversity that is associated with the decomposition and cycling of wood nutrients and carbon in forest ecosystems. Disturbance-induced declines or shifts in their diversity indicate the loss of key ecological and/or morphological species traits that could change ecosystem functioning. Functional and phylogenetic diversity of biological communities is commonly used to link species communities to ecosystem functions. However, our knowledge on how disturbance intensity alters functional and phylogenetic diversity of saproxylic beetles is incomplete. Here, we analyzed the main drivers of saproxylic beetle abundance and diversity using a comprehensive dataset from montane primary forests in Europe. We investigated cascading relationships between 250 years of historical

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disturbance mechanisms, forest structural attributes and the taxonomic, phylogenetic and functional diversity of present-day beetle communities. Our analyses revealed that historical disturbances have significant effects on current beetle communities. Contrary to our expectations, different aspects of beetle communities, that is, abundance, taxonomic, phylogenetic and functional diversity, responded to different disturbance regime components. Past disturbance frequency was the most important component influencing saproxylic beetle communities and habitat via multiple temporal and spatial pathways. The quantity of deadwood and its diameter positively influenced saproxylic beetle abundance and functional diversity, whereas phylogenetic diversity was positively influenced by canopy openness. Analyzing historical disturbances, we observed that current beetle diversity is far from static, such that the importance of various drivers might change during further successional development. Only forest landscapes that are large enough to allow for the full range of temporal and spatial patterns of disturbances and post-disturbance development will enable long-term species coexistence and their associated ecosystem functions.

Key words: Disturbance processes; Climate change; Ecological traits; Phylogenetic diversity; Primary forest; Carpathians; Coleoptera.

HIGHLIGHTS

- Disturbance history determines current beetle diversity
- Deadwood amount and canopy openness play key roles
- Diversity measures respond to different disturbance characteristics
- Disturbance effects are diverse across temporal scales

INTRODUCTION

Anthropogenic climate change is expected to have substantial effects on future disturbance frequency and severity in Europe (Seidl and others 2011). The frequency, size and severity of disturbances are expected to increase with climate warming. Changes in disturbance regimes have the potential for both positive and negative effects on forest biodiversity and associated ecosystem function varying by species and their habitat preferences (Thom and others 2017). Scenarios may arise in which forest stands are impacted by multiple contemporaneous or synchronous events such as windthrows and subsequent insect outbreaks (Kulakowski and others 2011). The intensification and potential interaction of future disturbance processes highlights a critical need to better understand associated biotic responses, particularly relationships between species diversity and ecosystem functions (Loreau and others 2001; Thom and Seidl 2016).

Mixed-severity disturbances, characterized by substantial heterogeneity in frequency, size and severity, are predominant in temperate forest ecosystems of Europe (Nagel and others 2014). These processes strongly influence the physical attributes, light environment and associated species composition of forest ecosystems (Hanson and Lorimer 2007). Disturbances create key elements of forest structural complexity, such as canopy gaps, snags, habitat trees and forest-floor deadwood, which in turn provide a range of habitat substrates for specialized organisms including saproxylic insects (Lachat and others 2016). However, the abundance, distribution and persistence of these habitat features, often referred to as legacies of disturbance, are not static but continuously shaped by ongoing successional processes. A complex interplay of disturbance and succession generates an array of habitat conditions that may potentially support a diverse assemblage of invertebrate fauna ranging from early successional species adapted to high-light conditions (Franklin and others 2000) to late-successional, shade-tolerant taxa (Spies and others 2006).

Saproxylic beetle species are a functionally vital constituent of forest invertebrate communities. Many indicator species, due to their obligate and highly specified associations with particular substrate types (Grove 2002), and endangered taxa are only found in primary, unmanaged forests (Lachat and Müller 2018) suggesting a dependence on structural legacies created by intermittent disturbance events. Saproxylic species are, by definition, associated with decay processes and are thus dependent on the availability of deadwood (Alexander 2008). However, the assemblage of saproxylic beetle species at a given site varies according to the physical characteristics of available wood substrates, including size, density, volume and their spatial distribution (Lassauce and others 2011; Stokland and others 2012; Lachat and others 2016). Further, beetle species are differentially adapted to utilize deadwood in varying stages of decomposition (Ulyshen and Hanula 2009; Stokland and others 2012). They are additionally segregated by variation in understory light availability (Lindhe and others 2005). This divergence in habitat preferences indicates that beetle communities are dynamic, changing with stand age and the length of disturbance intervals.

Saproxylic beetle populations make up an important component of trophic food webs and provide an array of essential ecosystem functions including organic matter decomposition and nutrient cycling (Stokland and others 2012). As a consequence of trophic interactions, these functions may ultimately affect site productivity and regional-scale carbon budgets. The specific scope of functions provided by saproxylic beetles depends on the species composition of the respective communities (Pielou 1966). A single species can have strong effects on ecosystem processes by directly mediating energy and nutrient fluxes or by altering abiotic conditions that regulate the rate of these processes (Chapin and others 2000). Evidence suggests that a diverse assemblage of species is required to maintain ecosystem functions (Tilman 2001; Cadotte and others 2009) through either an aggregation of complementary traits associated with multiple taxa, or by functions provided by the presence of a few key species recruited from a regional species pool (Loreau and others 2001). In either case, the provision of ecosystem functions is related to phenotypical trait characters (Tilman 2001; Cadotte and others 2013). Phenotypes are determined, in part, by an individual's environment, but are also an expression of evolutionary ancestry. Thus, in studies exploring relationships between species richness and ecosystem processes, phylogenetic diversity is often used as an indicator and surrogate for the breadth of ecosystem functions provided by a taxonomic group (Ding and others 2012).

Relationships between species diversity, ecosystem functions, and abiotic factors constitute a major research challenge due in part to extensive data requirements (Seibold and others 2016a, b). Significant associations between the extant structural heterogeneity of forests and saproxylic beetle diversity have been previously established (for example, Gossner and others 2013; Seibold and others 2016a, b; Thorn and others 2018a). However, the more complex, long-term and dynamic effects of fluctuating resource availability driven by disturbance interactions with forest structure are less clear. A limited number of studies have documented short-term, decadal-scale effects of disturbance on beetle communities (Müller and others 2008; Winter and others 2015; Beudert and others 2015), but their limited temporal depth constrains the generality of those results.

The overall objective of this study was to determine the long-term, potentially interactive effects of forest disturbance and variation in stand structure on the taxonomic, functional and phylogenetic diversity of associated current saproxylic beetle communities. As disturbance processes potentially exert multiple direct and indirect effects on beetle populations, we collected a comprehensive, large-scale dataset quantitatively describing beetle community demography, structural characteristics of forest stands and the associated, centuries-long disturbance history of the surveyed primary forest locations. Tree core samples and dendrochronological analyses were used to quantify various aspects of past disturbance spanning an approximate 250-year period. We sampled current beetle communities using insect traps and identified the taxonomic composition of samples. We compiled data describing corresponding ecological traits and generated a phylogeny for the sampled communities and calculated functional and phylogenetic diversity indices. We restricted data collection to primary forests in montane regions of central Europe. As natural disturbance regimes are still prevalent in these systems (Svoboda and others 2012), we assume that statistical analyses are not confounded by management effects. Further, inferences gained from primary forests may serve as baseline data with which to assess biotic responses in other systems (Kuuluvainen and Aakala 2011; Kulakowski and others 2017).

We investigated evidence for three specific hypotheses: (1) Attributes of the long-term disturbance regime modulate the taxonomic, functional and phylogenetic composition of current beetle communities. (2) Fluctuating, nonsynchronous disturbance processes modulate current beetle populations by generating a spatial mosaic of forest conditions characterized by variable light environments and heterogeneous reservoirs of deadwood. Specifically, forest structure as the result of disturbance timing, severity and frequency in the past determine beetle taxonomic diversity. (3) Variability in the abundance, size and characteristics of deadwood along with heterogeneous light environments—both of which are legacies of the most recent disturbance event—determine the composition and diversity of current beetle communities due to niche specialization among divergent taxa irrespective of the historical disturbance regime.

Materials and Methods

Study Area

The study region was restricted to primary forests in the Slovakian portion of the Western Carpathian Mountains (Fig. 1; 48° 63′–9° 52′ N latitude, 19° 30′–20° 12′ E longitude). The Carpathian region supports a substantial component of all remnant primary forest area in Europe (Sabatini and others 2018; Mikoláš and others 2019). The climate is continental with four distinct seasons and a notably absent dry period. Annual precipitation ranges from 1205 to 1365 mm yr^{-1}, which is approximately evenly distributed across seasons. Mean annual temperatures range from 1.6 to 3.4°C. Field surveys were limited to high-elevation areas (1244 to 1534 m) that are occupied by broadly monodominant *Picea abies* (L.) Karst. (Norway spruce) forest. Minor tree species, in terms of abundance, include *Sorbus aucuparia* L.(rowan), *Abies alba* Mill. (silver fir), *Fagus sylvatica* L. (European beech) and *Acer pseudoplatanus* L. (sycamore maple).

Disturbance regimes are highly variable in terms of standard metrics of severity, size and return intervals (Janda and others 2017). Low- and

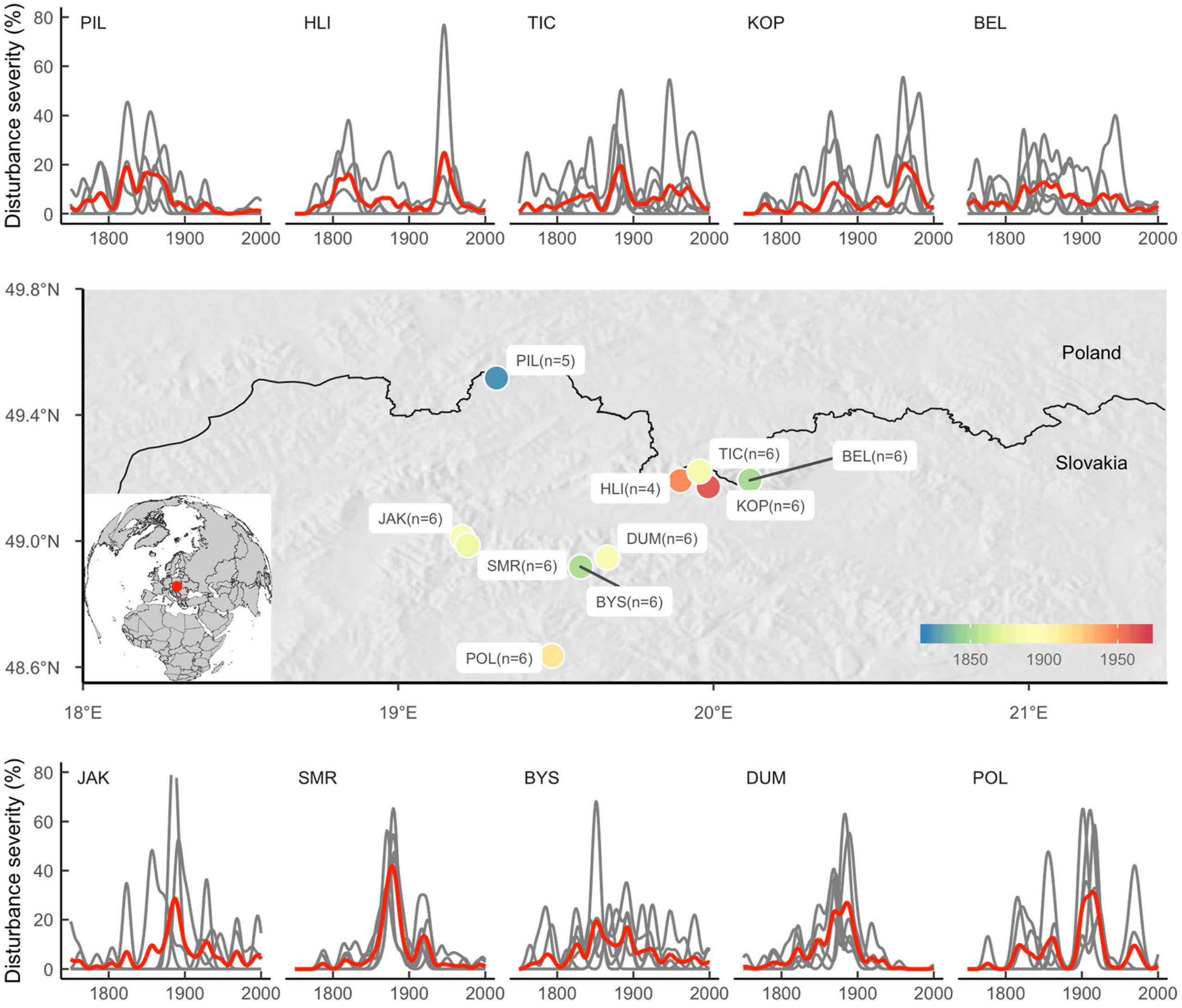

Fig. 1. Study area and plot locations. Data collection was based on a hierarchical stratified random sampling design. Forest stands (circles) were randomly distributed within remnant primary forest and across broad environmental gradients. Individual survey plots were located within stands (circles). Sample sizes (n) in terms of plot numbers within individual stands ranged from four to six. The color gradient indicates the maximum severity disturbance (color gradient) of the ten stands. The reconstructed disturbance history for all studied stands is based on the growth pattern of 15–25 trees per plot. Red line represents mean disturbance severity of given stands smoothed with kernel density function

moderate-severity gap-forming processes prevail in terms of frequency. At a landscape scale, disturbance processes require between 200 and 300 years (Janda and others 2017) to cause complete canopy replacement within a particular area of forest: a frequency metric termed disturbance rotation. At a plot scale, disturbance events re-occur with an average frequency of ~ 40 years (Fig. 1). Windstorms and population outbreaks of insects, particularly of the native saproxylic bark beetle, *Ips typographus* L., predominate as disturbance agents (Emborg and others 2000). Fire occurrence is notably rare in the historical record (Meigs and others 2017). Modern disturbance regimes appear to be essentially unaltered by modern management effects, and disturbance process variability remains within historical bounds (Janda and others 2017).

Field data were collected to describe disturbance history, forest structure, associated habitat characteristics, and beetle community demography. Survey locations were based on an existing international network of permanent inventory plots (REMOTE; https://www.remoteforests.org) that span primary forests in Central and Eastern Europe and that are randomly distributed across various environmental and climatic gradients (Meigs and others 2017). Disturbance history was reconstructed using increment cores collected from that plot network. Associated results have been previously published (Janda and others 2017) and are used in this study. Data describing beetle habitat and population demographics were collected within a selected subset ($N = 57$) of available REMOTE plots located within our target study region and distributed across gradients of disturbance severity and frequency as determined by Janda and others (2017). All data were collected within 0.1 ha circular plots, corresponding to the extent of the original REMOTE plots. Minimum distance between selected plots was 300 m.

Disturbance History

As described previously, we used data from a published, approximately 250-year long, record of disturbance history encompassing our study plots to infer relationships between the variability of past disturbance processes and current patterns of beetle community diversity. Specifically, we acquired disturbance chronologies from Janda and others (2017) that, both, delineate plot-scale past disturbance occurrences with high temporal resolution, and also estimate the magnitude of associated events. These chronologies were derived from analyses of temporal patterns in interannual tree growth. Growth variation was quantified from measurements of annual radial increment in tree core samples which were collected from the same survey plots used in this study. Disturbance events were reconstructed based on an assumption that disturbance processes affect levels of neighborhood competition and resource supply, and hence, growth responses in extant individuals (Svoboda and others 2014). In brief, statistically anomalous tree growth variation exceeding site-specific thresholds and sustained over minimum pre-defined temporal intervals was attributed to disturbance-driven gap formation events (Frelich 2002; Trotsiuk and others 2014). Corresponding event severity was defined in terms of the proportional area of tree canopy removed by the process, which 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-induced canopy gap (Lorimer and Frelich 1989). We used the resulting reconstructed time series of event occurrences and associated severity estimates (Table 1) to derive a total of six disturbance-based metrics that we hypothesized may influence current forest structure and the corresponding composition of saproxylic beetle species assemblages.

Forest Structure

We collected comprehensive inventory data to quantify and classify the variation and abundance of saproxylic beetle habitat comprising all study plots. Field measurements were used to parametrize a total of 15 explanatory variables, in addition to the disturbance-derived variables described previously, for use in statistical analyses (Table 1).

Firstly, we described the coarse structure of stands by precisely mapping all standing trees using laser rangefinders and customized software (Field-Map; Monitoring and Mapping Solutions, Jílové u Prahy, Czech Republic). As tree ontogeny has been associated with the character and availability of substrates (for example, cavities, cracks, bark decay) that potentially support invertebrate occurrence (Vuidot and others 2011), we measured the size (diameter at breast height; DBH) of all adult (> 6 cm DBH) trees and determined ages for a subset of canopy trees ($N = 15$–25) based on increment core samples. We identified occurrences of distinct substrate or tree-related microhabitat (TreM) types on all live and dead standing trees based on a previously defined typology created to

Table 1. Explanatory Variables Derived From Reconstructed Chronologies of Disturbance Events and Measurements of Structural Habitat

Category	Explanatory variable	Description	Units
Disturbance	Time since max dist	Time since the occurrence of the most severe disturbance event	Years
	Max dist severity	Maximum severity of any disturbance event in a chronology in terms of CA*	Percent
	Dist freq	Mean frequency of disturbance events	No. events
	Time since last dist	Time since most recent disturbance event	Years
	Last dist severity	Severity of most recent disturbance event in terms of CA	Percent
	Dist index	Shannon index based on the cumulative sum of CA per decade from 1800 to 1980	NA
Stand structure	Mean tree age	Mean age of all adult trees	Years
	DW RMS DBH	Root mean square of DBH for standing DW±	mm
	Standing DW BA	Basal area standing DW	m^2/ha
	Standing DW volume	Total volume standing DW	m^3/ha
	TreM Diversity	Shannon's diversity index for 11 microhabitat (TreM) types	NA
	TreM Density	Spatial density of TreM bearing trees	trees/ha
	Canopy openness mean	Mean canopy openness (see Methods)	Percent
	Canopy openness gini	Gini coefficient of openness (0–1)	NA
	Logs volume decay 1–5	Volume of lying DW calculated for 5 discrete decay classes (5 variables)	m^3/ha
	Logs volume	Total volume lying DW	m^3/ha
	total DW volume	Standing DW volume + lying DW volume	m^3/ha

Disturbance-based variables were computed for disturbance events with severities that exceeded a 15 percent threshold level in terms of percent canopy removed. Stand structural variables were derived from data for adult trees with a minimum DBH of 60 mm and minimum height of 1.3 m

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

± DW Standing dead trees (snags) or forest floor deadwood

standardize field inventories (Larrieu and others 2018). We subsequently aggregated observations of individual TreM types ($N = 29$) into broader categories (Table S1; $N = 11$; Paillet and others 2017) and then calculated two plot-scale indices (Table 1) of microhabitat diversity based on the relative abundance of aggregated TreM classes. Specifically, we calculated Shannon's diversity index, as well as a density metric based on the sample size (per ha) of all TreM-bearing trees on a plot (for example, Paillet and others 2017; Kozák and others 2018).

Forest canopy architecture and the associated understory light environment were quantified with 180°-field-of-view hemispherical photographs collected at six predetermined locations within each plot. The collected digital photographs were processed and analyzed using image processing software (WinSCANOPY; Regent Instruments, Ste-Foy, Quebec, Canada). Individual image 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 of a plot canopy and the spatial continuity or evenness of canopy openness.

Finally, we described the diversity, quantity and quality of habitat substrates available on the forest floor. All lying deadwood material was mapped and measured to determine size and volume. We categorized the associated structural integrity and state of decomposition of this material based on a hypothesis that variation in size and decay class segregates beetle taxa (Thorn and others 2018a). We used a five-category decay classification system (Stokland 2001) to categorize wood condition and computed the volume of wood in each class (Table 1).

Beetle Surveys

We sampled current saproxylic beetle populations in each survey plot using insect traps to characterize 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 (Hyvärinen and others 2006; Gossner and others 2013; 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 and others 2006). A single trap was mounted on two metal rods approximately 1 m above the ground at the center of each plot. We avoided the use of insect bait to minimize 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. The taxonomic identity of all beetle specimens was determined to species level, excluding specimens in the family Staphylinidae, which were omitted from further analysis following previous studies (Parmain and others 2015). After taxonomic classification of the remaining specimens, individual species were aggregated into four separate, nonmutually exclusive subgroups comprised of: (1) all taxa; (2) species only associated with coniferous trees; (3) endangered or red-listed species as classified by the International Union for Conservation of Nature (IUCN 2019); and (4) species that are both red-listed and conifer-tree specialists (Schmidl and Büche 2016; Seibold and others 2015).

Diversity Metrics

Our goal in this study was to understand the nature of disturbance and habitat effects on not only the composition of current saproxylic beetle communities, but also on the breadth of ecosystem functions provided by associated communities. Thus, we selected various standard diversity indices from the ecological literature to quantify a range of compositional (taxonomic) as well as functional and phylogenetic metrics that were subsequently used as response variables in regression models.

Compositional attributes of beetle communities were quantified using three diversity metrics: (1) overall abundance for all taxa combined; (2) species richness; and (3) Shannon diversity (Jost 2006). We used trap data to compute each of the selected diversity indices at a plot scale for each of the previously described species subgroups. However, since sample sizes for beetle trap collections varied substantially among plots ($N = 5$–705 individuals/plot), we standardized all trap data before calculating diversity indices following protocols associated with a unified framework for extrapolation and rarefaction based on an effective number of species (Hill numbers; Chao and others 2014). Trap data in a particular plot were standardized on the basis of the overall mean per plot sample size.

We calculated functional and phylogenetic diversity, both based on proxy information, using the following approaches: (1) We acquired selected key ecological traits data to estimate the relative distribution of species in a composite traits or niche space and used species-specific mean niche positions within this construct to quantify an associated trait or functional diversity index; and (2) we compiled data describing phylogenetic relationships between surveyed beetle taxa and computed a diversity index based on the overall complexity and depth of the derived evolutionary tree.

The functional diversity was derived from previously assembled and published comprehensive species-specific datasets representing life history and reproductive qualities for saproxylic beetles (Möller 2009; Gossner and others 2013; Seibold and others 2015). Specifically, we selected and acquired data for fundamental trait characteristics: mean body size, diameter of deadwood in which a species is known to occur, decay stage of deadwood, canopy cover and elevational distribution of forests in which the species is known to occur. Relative distributions of species across the five selected multivariate trait axes were computed using Gower distance (Gower 1971), which accounts for both categorical and continuous variable types.

The phylogenetic richness index was similarly generated using previously published data. We extracted phylogenetic relationships for sampled beetle species based on a comprehensive genetic phylogeny for all taxa within the order Coleoptera originally developed by Hunt and others (2007) and extended by Gossner and others (2013) and Seibold and others (2015). Observed, local phylogenetic richness was subsequently determined by summing total phylogenetic branch lengths (that is, Faith's D; Faith 1992).

Both the functional trait and phylogenetic richness metrics are correlated with species numbers (Winter and others 2013). Thus, we used null models that compare observed levels of diversity across multiple sampling locations to levels expected when species are randomly selected from a regional species pool (Gotelli 2000). Null models provide a standardized effect size which represents the difference between observed mean similarities and expected similarities for 999 artificial assemblages. The regional species pool of the present study was defined as all species recorded in our study. Resulting null model effect size values above 0 indicate higher diversity per number of species than expected by chance; effect size values below 0 indicate lower diversity per number of species than expected by chance (Pausas and Verdú 2010). Consequently, null model effects were used in subsequent modeling analyses to represent standardized species-specific functional and phylogenetic diversity metrics (Thorn and others 2018a).

Data Analysis

Our main hypothesis is that past disturbance frequency and magnitude indirectly modulate current beetle communities by shaping the physical structure of forests and availability of deadwood substrates for beetle colonization. We explored the strength of evidence supporting our hypotheses using linear mixed-effect models (LMMs). A suite of models was formulated to quantify community responses in terms of the range of previously described indices of diversity, including the three taxonomic-based measures (abundance, species richness and Shannon diversity), functional and phylogenetic diversity. Disturbance parameters (Table 1) were used as explanatory variables to estimate their direct effects on both forest structure (habitat) and, in alternate models, beetle diversity. Additional models were formulated to estimate the effects of habitat on beetle diversity. Forest stands were treated as random effects in all models to account for the hierarchical nature of the sampling design (see Fig. 1). Because a high degree of redundancy was observed among the 15 structural explanatory variables (Table S2), correlated terms were excluded from the analyses and a subset of seven parameters were used to formulate models (Table S1) to prevent multicollinearity problems. We evaluated variance inflation factors (VIFs, Quinn and Keough 2002) of each model and did not find any serious multicollinearity pattern (all VIFs < 3.5). Residuals of all models were checked for normality and homoscedasticity. Abundances were log-transformed to reduce skewness. Full models were simplified in a backward elimination procedure based on F tests with Satterthwaite approximation to degrees of freedom (Kuznetsova and others 2017). To compare the relative importance of significant variables retained in the final LMMs, we calculated standardized regression coefficients and their 95% parametric bootstrap confidence intervals. Marginal (R^2_{m}) and conditional (R^2_{c}) determination coefficients were calculated for the final LMMs to quantify the proportion of the total variance explained by the fixed effects and by both fixed and random effects, respectively (Nakagawa and others 2017). To further explore evidence for potential synergies or interactions between processes that shape current beetle communities, associations between disturbance effects and habitat condition, and relationships between habitat effects and beetle diversity, were integrated in a network of confirmatory path analysis (Shipley 2009).

All data management and analyses were conducted in R (R Core Team 2019). We used the function daisy from the cluster package to compute Gower distances. The function ses.mpd from the picante package (Webb and others 2002) was used to develop null models. Modeling analyses were performed using the R-dependent packages car (Fox and Weisberg 2011), iNEXT (Hsieh and others 2019), nlme (Pinheiro and others 2019).

Results

Disturbance and Current Beetle Communities

Modeling analyses reveal that historical disturbance processes had significant and strong effects on current beetle communities in addition to the interactions with habitat described previously. Associated LMMs explained between about 7 and 22 percent of variance according to marginal determination coefficients (Table 2). Time since disturbance was arguably the most important determinant of beetle community attributes having strong, inverse effects on the species richness of beetles in every species subgroup, except the red-listed conifer specialist assemblage. Although the severity of maximum disturbance event in the last 250 years negatively affected species richness of the current beetle community, the severity of the last disturbance event had a positive effect (Fig. 2).

Disturbance frequency also had similar unexpectedly negative direct effects on taxonomic diversity; more frequent disturbance occurrences were associated with fewer observed beetle taxa (Table 2). However, this pattern was only observed for conifer specialist species.

Functional and phylogenetic diversity was mostly not significantly affected by the range of disturbance processes that were modeled. A single significant effect was identified; functional diversity was found to decline with the magnitude of the last severe disturbance in the historical record. The corresponding effect size was among the lowest of any disturbance variable tested (0.27; Table 2) and significant only for conifer specialist beetles.

Table 2. Summary Statistics for Final LMMs that Estimated the Direct Effects From 5 Alternate Disturbance Metrics on Beetle Community Diversity

Species subgroup	**Model response (Beetle diversity index) diversity index**	**Time since max. disturbance**			**Max. disturbance severity**			**Disturbance frequency**		
		β (95%CL)	F	p	**β (95%CL)**	F	p	**β (95%CL)**	F	p
All species	Richness	0.40 (0.05, 0.75)	5	0.03	− 0.40 (− 0.79, − 0.02)	4.1	0.049			
	Shannon diversity									
	Functional trait diversity									
	Phylogenetic diversity									
	Abundance									
Conifer specialists	Richness	0.35 (0.01, 0.64)	4.2	0.046				− 0.39 (− 0.69, − 0.09)	6.7	0.012
	Shannon diversity	0.33 (0.01, 0.66)	4.2	0.047				− 0.55 (− 0.87, − 0.27)	14.1	< 0.001
	Functional diversity									
	Phylogenetic diversity									
	Abundance									
All red-listed species	Richness									
	Shannon diversity									
	Abundance									
Conifer red-listed specialists	Richness									
	Shannon diversity							− 0.27 (− 0.55, − 0.01)	4.07	0.049
	Abundance									

Species subgroup	Model response (Beetle diversity index) diversity index	Time since last disturbance			Last disturbance severity			Stand		R_m^2/R_c^2
		β (95%CL)	F	p	β (95%CL)	F	p	χ^2	p	
All species	Richness	− 0.54 (− 0.87, − 0.21)	10.5	0.002	0.49 (0.07, 0.91)	5	0.03	2.1	0.147	18.2/31.5
	Shannon diversity	− 0.31 (− 0.58, − 0.04)	5.58	0.022				0.2	0.693	9.2/12.8
	Functional trait diversity							1.1	0.304	–/9.6
	Phylogenetic diversity							0.6	0.448	–/11.2
	Abundance							0.7	0.393	–/7.9

Table 2. continued

Species subgroup	Model response (Beetle diversity index) diversity index	Time since last disturbance			Last disturbance severity			Stand		R^2_m/R^2_c
		β (95%CL)	F	p	β (95%CL)	F	p	χ^2	p	
Conifer specialists	Richness	− 0.45 (− 0.80, − 0.05)	5.9	0.019				1	0.33	13.9/24.8
	Shannon diversity	− 0.57 (− 0.94, − 0.18)	10.1	0.003				2.9	0.087	22.3/43.0
	Functional diversity				− 0.27 (− 0.54, − 0.02)	4.41	0.04	1.8	0.182	7.1/20.6
	Phylogenetic diversity							0.2	0.646	–/4.3
	Abundance							1.3	0.248	–/13.5
All red-listed species	Richness							0.3	0.514	–/6.3
	Shannon diversity	− 0.29 (− 0.55, − 0.01)	5	0.03				< 0.1	0.975	8.3/8.5
	Abundance							0.8	0.38	–/9.9
Conifer red-listed specialists	Richness							< 0.1	1	–/< 0.1
	Shannon diversity							< 0.1	0.985	6.9/7.1
	Abundance							1.2	0.277	–/12.8

Alternate models were fit to quantify disturbance effects on both taxonomic and functional (traits and phylogenetic) based measures of diversity. Independent models were fit for 4 species subgroups. Forest stand was used as a random effect. Shown are standardized regression coefficients (β) along with their 95% parametric bootstrap confidence limits (95% CL), test statistics (F, χ^2), and significance values (p) for all significant effect terms. Marginal (R^2_m) and conditional (R^2_c) determination coefficients were computed for each model. Note that the disturbance index (dist index in Table 1) was not a significant predictor for any subgroup and is not shown

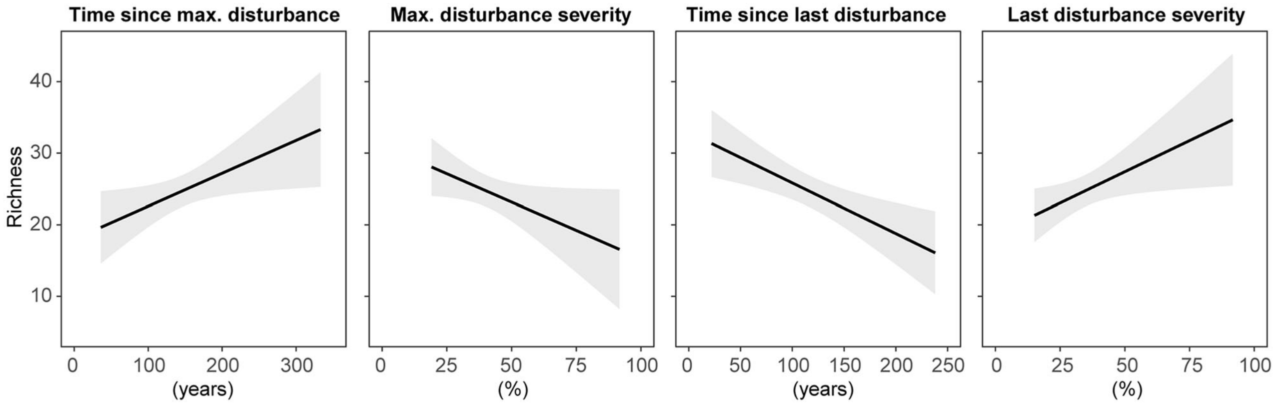

Fig. 2. Magnitude of disturbance effects on the taxonomic richness of current beetle communities based on linear mixed effects models. Each effect plot shows expected response to a particular variable keeping other variables constant at their mean value. Gray shading delineates 95% confidence limits

Disturbance and Forest Structure

Results from regression analyses reveal a range of important disturbance effects on various structural attributes of sampled forest stands, specifically deadwood amounts and canopy openness. Fixed effects in associated models explained between about 10 and 22 percent of relative variance in the observational data, excluding the forest age model which was much stronger (Fig. 3). Frequency was arguably the most important attribute of the disturbance regime, influencing the temporal and spatial heterogeneity of beetle habitat in several ways. For example, increases in disturbance event frequency were positively related to both the volume of logs on the forest floor and total volume of all (standing and lying) deadwood with relatively large positive standardized regression coefficients of 0.33 and 0.56, respectively (Table S4). Canopy openness declined with disturbance frequency, though this was perhaps a minor effect ($\beta = -0.26$).

In addition to disturbance occurrence frequency, the length of disturbance-free intervals significantly influenced forest structure. Canopy openness decreased with time since the last disturbance ($\beta = -0.28$) due to promoted growth of the trees and associated canopy gaps filling. Also, the mean size of standing deadwood varied as, over time, standing dead trees deteriorated and fell to the forest floor. Positive relationships ($\beta = 0.31$) indicate that larger diameter dead trees persisted for longer periods as compared with smaller snags. The total reservoir of deadwood increased with time in the absence of disturbance.

Disturbance severity had strong effects on the amount of deadwood supplies. The overall volume of deadwood strongly covaried with event severity ($\beta = 0.59$); in other words, stronger disturbances (last disturbance severity; Table S4) caused greater tree mortality and produced more deadwood. Negative relationships ($\beta = -0.27$) between the most severe events (maximum disturbance severity; Table S4) at our study plots and the mean size of the standing reservoir of deadwood suggest that a majority of these events happened several decades ago (mean time since maximum severity disturbance was 147 years; Table S5) and due to post-disturbance development, the snags most likely decayed and forest patches affected with historical high severity events became relatively homogenous with a poor deadwood pool. This effect was, however, only marginally significant ($p = 0.049$; Table S4).

We did not detect evidence for a corresponding increase in microhabitat (TreM) diversity associated with the frequency or severity of disturbances.

Habitat and Current Beetle Communities

Modeling results reveal that a range of forest stand structural attributes significantly influenced the current saproxylic beetle communities in this study, consistent with our hypotheses. Depending on the species subgroup and response variable, alternate models having significant fixed effects explained between about 8 and 16 percent of the variance in the observational data according to marginal determination coefficients. Our model selection process resulted in single-factor models for all diversity-based response variables (Table S3). A total of four different explanatory variables were important in the final most parsimonious models. All selected variables had positive effects on corre-

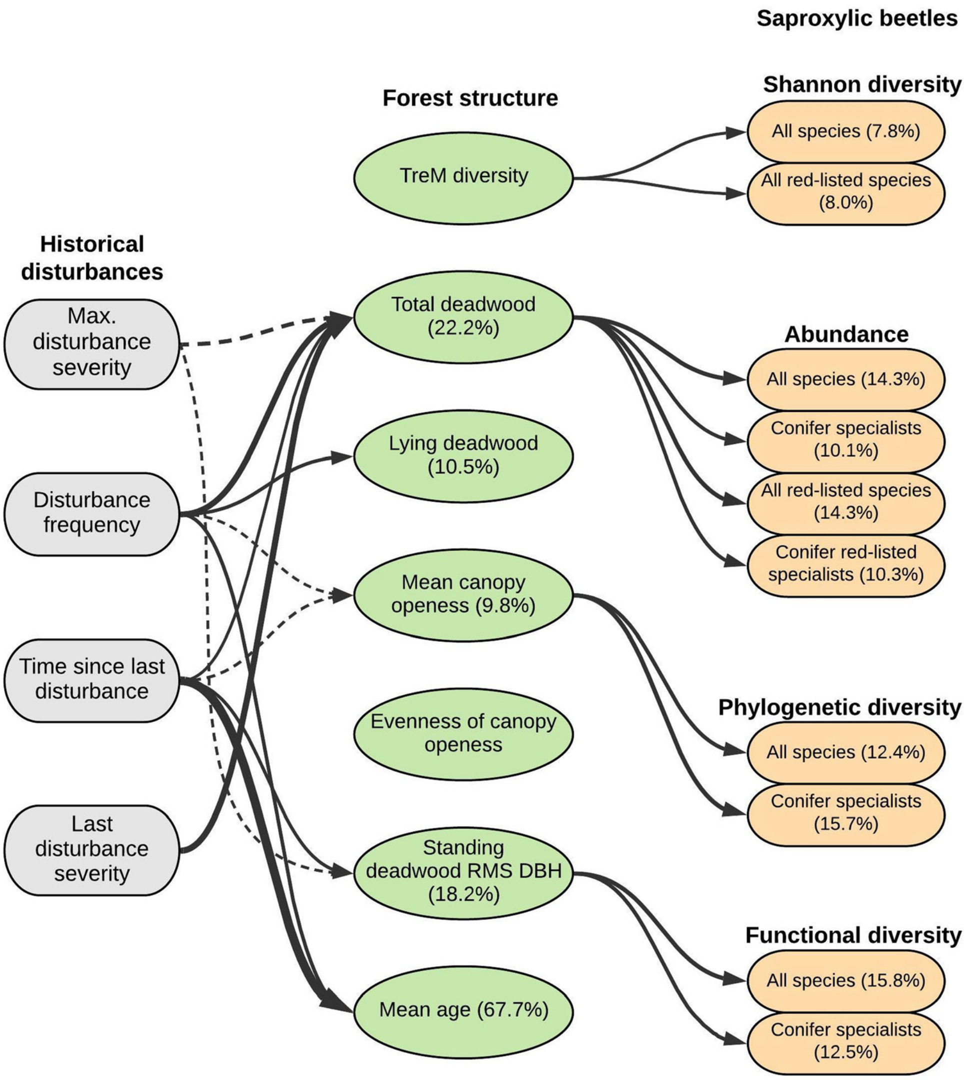

Fig. 3. Directed acyclic graph of confirmatory path analysis linking historical disturbances and forest structure with abundance and diversity of current saproxylic beetle communities. Models were fit with data from four subgroups. Arrows represent significant ($p < 0.05$) positive (solid line) and negative (dashed line) relationships between predictors and responses. Width of the arrows is proportional to standardized regression coefficients. Relative proportion of variance explained by fixed effects (R^2_m) is given in parentheses. Note that variables without any significant link are omitted for brevity. Further details can be found in Tables S1 and S2

sponding diversity measures (Fig. 3). Different aspects of beetle community diversity, that is, total abundance, taxonomic richness, phylogenetic and functional diversity, responded to different, unique features of the environment. For example, the volume of deadwood on the plot and the length of disturbance-free intervals (Table S4) were the consistent predictors of beetle abundance, influencing abundance in each subgroup ($\beta = 0.34$–0.41). Models indicate that species diversity was associated only with the range of microhabitats available at a site. This TreM relationship was valid for the all-inclusive species subgroup and not for conifer specialist species (Table S3). The diversity of TreM types was not significantly determined by any disturbance process (Fig. 3), thus indicating that, at least for the variables tested, we did not detect a common indirect disturbance effect that could result in covariation between abundance and species diversity.

Similarly, model results show that phylogenetic diversity was significantly influenced only by canopy openness. Lastly, the functional diversity was associated only with the mean size of standing dead trees. In this case, attributes of the disturbance regime, specifically disturbance-free interval length and maximum event severity, may similarly influence both functional trait diversity and total species abundance through congruent indirect effects on forest structure (Fig. 3).

DISCUSSION

Elucidating mechanisms of how disturbance influences structure of ecological communities and facilitates species coexistence and associated ecosystem functions is central to ecological theory (Shea and others 2004). Our comprehensive dataset covering 250 years of disturbance history and associated changes in forest structure expanded the current knowledge about the effect of disturbance regimes on current beetle communities. Disturbances played an important role in determining the diversity of saproxylic beetle communities, with the frequency and time since disturbance as the most important factors. Our results further demonstrate that the dynamics of natural disturbance determine heterogeneity in resources, most importantly deadwood supplies and canopy openness, which positively contributed to the maintenance of diverse beetle assemblages.

Effect of Natural Disturbances on Saproxylic Beetle Communities

We demonstrated that the more recently the disturbance occurred, the more species-rich the current communities of saproxylic beetles were. This effect was observed for the diversity of all beetles and for conifer specialists separately. The observed pattern might be an effect of higher canopy openness immediately following a disturbance event as saproxylic beetle communities are often more species-rich in gaps than under a closed canopy (Seibold and others 2016a, b). Another possibility is that this observation is a transient effect and caused by the higher proportion of fast-developing freshwood dwellers present in post-disturbance beetle communities, such as bark beetles and species associated with them (Saint-Germain and others 2007). Decreasing amounts of nutrients in decaying woody debris decreases the attractiveness of deadwood over time (especially coniferous wood; Saint-Germain and others 2007) for saproxylic beetles (Kopf and Funke 1998). Similar findings were observed by Winter and others (2015) with the highest numbers of saproxylic beetles preferring wood of early decay stages in the initial early-seral stage following the availability of fresh deadwood. As observed by Gossner and others (2016), for *Picea abies*, species richness of saproxylic beetles was highest in the first year of decay followed by a decrease in species richness. Moreover, species richness increased with the severity of the last disturbance, probably as a result of deadwood pool enrichment across disturbed plots (Table S4).

The severity of the last historical disturbance (events occurred on average 120 years ago; Table S5) negatively affected functional diversity of conifer specialists. This finding might be explained by the post-disturbance development and highlights the need to understand long-term disturbance effects on biological communities. Gaps or patches after high-severity disturbance close between 50 and 100 years following a disturbance (Svoboda and others 2014), and as a result, forest stands become more homogenous and the structural elements, for example deadwood, decline. Thus, altered environmental conditions may exclude functionally diverse early and mid-successional species and lead to the co-occurrence of functionally similar species that are adapted to changing habitat conditions (Winter and others 2017; Thorn and others 2018a). Our findings agree with the results of Hilmers and others (2018) which showed a U-shaped response of beetle communities to forest succession.

Predicting the effect of future disturbance regimes on forest diversity, Thom and others (2017) observed that an increase in disturbance frequency and severity had consistently positive effects on biodiversity. High disturbance severity and increasing disturbance frequency create a complex pattern of open areas, forest edges and remaining closed canopy forests, increasing the variation in environmental conditions (Perry and others 2011; Lehnert and others 2013). However, these findings only partially match ours, which could be because Thom and others (2017) did not specifically focus on spruce-dominated forests. Although the severity of the last disturbance was associated with an increase in species richness for all species, the increases in the maximum detected disturbance severity were related to declines in species richness. The high-severity disturbances cause higher tree mortality which might lead to more homogenous forest structure with limited amounts of forest edges and old-growth structures (Svoboda and others 2014), making such a forest unfavorable for certain beetle species.

We observed a negative impact of disturbance frequency on conifer specialist species richness and diversity. Higher disturbance frequencies generate more gaps that support more diverse tree species, including broad-leaved species, which might cause a decline of conifer specialists as the deadwood pool contains more diverse tree species composition. Environmental changes such as the removal of the overstory forest canopy and the subsequent effect on the light regime may favor some species, while creating suboptimal or intolerable conditions for other species (Swanson and others 2011): for example, species that prefer shaded deadwood (Lachat and others 2016). Devictor and Robert (2009) showed that generalist species might benefit strongly from disturbance events while specialists and late-seral species could be affected negatively. Possibly, other drivers not included in our data, such as microclimate, shrub and herb layer vegetation, and fungal occurrence may explain diversity patterns of beetle communities present at the studied plots.

Effect of Disturbance-Related Structural Characteristics on Saproxylic Beetles

Saproxylic beetle communities are largely reliant on structural characteristics created by natural disturbance. Our results support previous findings that beetle abundance and diversity are associated with heterogeneous and dynamic forests with high amounts of deadwood and canopy gaps (for example, Wermelinger and others 2002; Müller and others 2010).

Deadwood is an important component of forest ecosystems, biogeochemical cycles, trophic chains and provides key niches for many species (Vandekerkhove and others 2009). The total amount of deadwood was the most important structural characteristic, positively influencing the abundance of all studied subgroups. Similarly, Müller and others (2010) observed a positive response of beetle populations to deadwood amount which was also true for the specialized and red-listed species.

Mean canopy openness positively influenced the phylogenetic diversity of all beetles and conifer specialists. Mountain spruce forests of the Carpathians are characterized by mixed-severity disturbance dynamics (Svoboda and others 2011, 2014) of wind and bark-beetle origin, which provide periodically a large amount of freshly killed trees with lots of canopy openings and thus might have favored the evolution of species adapted to utilize sun-exposed deadwood (Gossner and others 2016). Another possibility is that changed light conditions in canopy gaps attract more flower-visiting beetles and higher temperatures of sun-exposed deadwood allow emergence of beetles from different phylogenetic lineages.

Amount of deadwood, particularly of large diameter and in a late decay stage, influences the functional composition of saproxylic beetles (Gossner and others 2013). We observed that functional diversity of all saproxylics and conifer specialists was positively influenced by the diameter of standing deadwood. These findings confirm the importance of the high-diameter standing deadwood for saproxylic beetles as they can provide diverse habitats for functionally diverse assemblages (Stokland and others 2012; Larrieu and others 2012; Martikainen and others 2000). Moreover, our results support earlier findings which emphasize the positive effect of bark-beetle infestations on saproxylic beetle communities (Müller and others 2010). Finally, we observed the significant positive influence of tree-related microhabitat diversity on overall and red-listed beetle diversity. This finding is consistent with studies emphasizing the role of tree-related microhabitats as important habitat for saproxylic beetles (Parisi and others 2019).

Effect of Natural Disturbances on Forest Structure

We observed a significant influence of historical disturbance variables on structural characteristics in terms of deadwood volume and canopy openness. Such observation suggests that the effect of historical disturbance regimes on forest structure persists in the form of structural characteristics and may still be visible after several decades or even centuries from the disturbance event. These findings are consistent with the findings of Winter and others (2015) that structural changes such as reduced canopy cover and high volumes of deadwood after windthrow and bark-beetle outbreak remain high or even higher after multiple decades of succession, suggesting persistence of early-seral heterogeneity into succession.

We found a positive effect of the time since last disturbance on total deadwood volume and diameter of standing deadwood, suggesting that trees dying during a disturbance event are available habitat for several decades, as was observed by Spies and Franklin (1988), or even for a century. The observed increases in total deadwood volume during disturbance-free periods further suggest that decay processes in spruce wood are comparatively gradual, at least relative to decomposition rates in angiosperm-derived substrates (Weedon and others 2009) and that disturbance impacts on deadwood supply have substantial temporal persistence.

In primary forests, post-disturbance succession is frequently influenced by other disturbances of various severities which can continuously replenish the deadwood pool (Hansen and others 1991). Our results support those findings, since disturbance frequency positively influenced the total deadwood volume and lying deadwood volume. However, mean canopy openness decreased with increasing disturbance frequency and with longer times since disturbance, probably as part of the canopy trees survived frequent disturbance events and partly due to conditions favoring seedling recruitment and growth after disturbance events (Winter and others 2015).

Finally, natural disturbance characteristics did not significantly affect the tree-related microhabitat diversity. This supports the findings of Larrieu and others (2014) that tree-related microhabitat availability remained stable throughout the forest succession, both in terms of their quantity and diversity.

Varying Responses of Different Diversity Metrics to Disturbance History

Our studied diversity metrics of current saproxylic beetle communities responded to different disturbance and structural characteristics. Each historical disturbance characteristic influenced at least a part of the current beetle diversity, with frequency and time since the last disturbance event being the most important factors. With respect to saproxylic beetle richness, we observed contrasting effects between maximum disturbance severity (negative) and severity of the last disturbance (positive); a contrast was also observed between the effects of time since most recent disturbance (negative) and time since maximum disturbance (positive). Disturbances, habitat fluctuations and changes in environmental conditions cause variations in ecosystem properties and variable responses of different components of biodiversity (Cadotte 2007). Thus, the observed influence of disturbance on current beetle diversity may be caused by beetle species inhabiting temporary niches created by forest succession after disturbance. Saproxylic beetle communities show pronounced successional changes with ongoing decay of deadwood material (Jonsell 2008) due to changes in the physical structure and nutritional quality of deadwood (Wende and others 2017). For instance, the presence of late-successional species often depends upon earlier colonists creating suitable conditions by initiating deadwood decomposition (Jacobsen and others 2015).

Composition of a saproxylic beetle communities also depends on the ratio of different functional groups such as xylophages, fungivores and predators. For example, xylophages are highly abundant in early successional phases of deadwood colonization, whereas fungivores and predators are commonly present later in the successional food chain (Grove 2002). Thus, the heterogeneous arrangement and decomposition of deadwood resources, both spatially and temporally, might influence taxonomic and functional diversity of the current saproxylic beetle communities.

Implications for Forest Management

Our results demonstrate that natural disturbances are an indispensable part of forest ecosystems and provide a diverse range of habitat conditions for the beetle community. Saproxylic beetles provide important ecosystem functions that depend on the species composition of the beetle community (Pielou 1966). Evidence suggests that a diverse assemblage of species is required to maintain ecosystem functions (Tilman 2001; Cadotte and others 2009). Thus, our results further suggest that diverse natural disturbance components that act across different timescales are necessary to create heterogeneous habitats and maintain taxonomic, functional and phylogenetic diversity and consequently the ecosystem functioning. The disturbance regime influences the spatiotemporal variation of deadwood, on both the stand and landscape scale (Jonsson and others 2005), and this variation may influence the occurrence of saproxylic beetle species (Stokland and others 2012).

Various species have different habitat requirements and thus need to be able to disperse across the landscape when an area is no longer suitable (Jonsson and others 2005). Previous studies suggest that total amount of deadwood available within a given landscape is the main driver of the number of saproxylic beetle species and that the spatial arrangement of deadwood, that is, connectivity, plays no or only a minor role (Seibold and Thorn 2018). In our study, we focused on plot-scale effects of disturbance on alpha diversity of saproxylic beetles. However, when we consider the stand-scale or landscape perspective, shifting mosaics of forest structures developing after disturbance in space and time may lead to high species turnover (Gossner and Müller 2011). Some species require open areas with high amounts of deadwood and thus have a rapid increase in their population following a high-severity disturbance. Subsequently, a major decline follows in conjunction with succession in disturbed patches, but species should be able to persist when a nearby forest stand undergoes natural disturbance.

The adverse effect of homogenized forest structure on forest biodiversity and survival of specialized forest species has strong implications on active forest management. Large-scale homogenization and simplification of forest structure, and consequent biodiversity decline, is often a characteristic feature of intensive forestry practices (but see Schall and others 2018). This is particularly relevant following large-scale clearing of disturbance legacies due to salvage and sanitary logging after wind and insect disturbance (Thorn and others 2017, 2018b). In the Carpathian region, the situation is especially critical and controversial because such treatments regularly occur in protected areas, such as national parks (Mikoláš and others 2017a), which have presumably been established to protect native biodiversity and maintain natural processes.

CONCLUSIONS

Our study documented that disturbance-created structures promote species-rich communities of saproxylic beetles. Species-rich beetle communities were favored by the structure created by historical disturbances that increase the structural heterogeneity, whereas historical disturbances which homogenized the forest environment appear to have unfavorable present-day forest structure. Present-day forest structure such as the amount and diameter of deadwood and changed light conditions positively influenced the abundance and diversity of beetle communities. We should acknowledge that current beetle diversity is far from temporally static so that the importance of these aspects might be changed during further successional development. Ongoing climate change will likely increase disturbance frequency and severity in many parts of the world (Thom and others 2017). Our results suggest that climate-induced changes in natural disturbance regimes may temporarily impact saproxylic beetle communities, whereas these changes are highly dependent on post-disturbance successional pathways. The timescale and long-term post-disturbance development trajectories may pose a challenge for local conservation planning. Therefore, we emphasize the importance of setting aside large areas (strictly protected forest landscapes) where wide range of timing and severity of disturbance can act and create a heterogeneous environment that can support a full array of biodiversity (Mikoláš and others 2017b; Nagel and others 2017; Watson and others 2018). When the area on which natural disturbances operate is too small, large-scale disturbances may change the habitat across small protected forests to conditions that are not appropriate for certain species.

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5.2 Profile of tree-related microhabitats in European primary beech-dominated forests

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Profile of tree-related microhabitats in European primary beech-dominated forests

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ABSTRACT

Tree-related microhabitats (TreMs) are important features for the conservation of biodiversity in forest ecosystems. Although other structural indicators of forest biodiversity have been extensively studied in recent decades, TreMs have often been overlooked, either due to the absence of a consensual definition or a lack of knowledge. Despite the increased number of TreM studies in the last decade, the role of drivers of TreM profile in primary forests and across different geographical regions is still unknown. To evaluate the main drivers of TreM density and diversity, we conducted the first large-scale study of TreMs across European primary forests. We established 146 plots in eight primary forests dominated by European beech (*Fagus sylvatica* L.) in the Carpathian and Dinaric mountain ranges. Generalized linear mixed effect models were used to test the effect of local plot characteristics and spatial variability on the density and diversity (alpha, beta, and gamma) of TreMs. Total TreM density and diversity were significantly positively related with tree species richness and the proportion of snags. Root mean square tree diameters were significantly related to alpha and gamma diversity of TreMs. Both regions reached similarly high values of total TreM densities and total TreM densities and diversity were not significantly different between the two regions; however, we observed between the two regions significant differences in the densities of two TreM groups, conks of fungi and epiphytes. The density and diversity of TreMs were very high in beech-dominated mountain primary forests, but their occurrence and diversity was highly

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variable within the landscapes over relatively short spatial gradients (plot and stand levels). Understanding these profile provides a benchmark for further comparisons, such as with young forest reserves, or for improving forest management practices that promote biodiversity.

1. Introduction

The natural development and the varied timing and intensity of disturbances within primary forests often results in high levels of structural heterogeneity (Bauhus, 2009). Certain structural elements, such as high volumes of accumulated standing and lying deadwood (Nagel et al., 2017), large canopy (veteran) trees (Commarmot et al., 2013), and a diverse array of tree-related microhabitats (TreMs; Larrieu et al., 2018), are often abundant in primary forests. These structural elements are important features for the maintenance and conservation of biodiversity (Lindenmayer et al., 2006), and they are widely recognized as an important feature of conservation management plans (Kraus and Krumm, 2013). Although structural indicators of forest biodiversity have been a major research topic in recent decades, TreMs have often been overlooked, either due to the absence of a consensual definition or a lack of knowledge (Paillet et al., 2017). Larrieu et al. (2018) defined TreMs as a distinct, well-delineated structure occurring on living or standing dead trees that constitute a particular and essential substrate or life site for species or communities to develop, feed, shelter, or breed during at least a part of their life cycle. They are specific aboveground tree morphological singularities that are not found on every tree. The origins of TreMs encompass both endogenous modifications, caused by biotic and abiotic factors, such as intrusions, lesions, and breakages that expose sap and heartwood and initialize outgrowth structures and wood decay (saproxylic TreM), as well as exogenous elements that are physically linked to the tree (epixylic TreM).

Many recent TreM studies have largely been conducted in managed forests or forest reserves historically influenced by harvesting (e.g., Paillet et al., 2017; Regnery et al., 2013a; Vuidot et al., 2011), and studies have been largely restricted to a few distinct forest types in the Mediterranean, Western Europe, and the USA (Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Regnery et al., 2013b; Winter, 2015). Forest management often encourages the production of uniform stands through the logging of high value trees and the removal of damaged or large trees with limited economic value. Conventional forest management systems sometimes create TreMs, such as dendrothelms or bark loss, due to damage during harvesting operations (Larrieu et al., 2012; Vuidot et al., 2011). However, most of the TreM types are typically removed or never develop (Paillet et al., 2017). It is widely documented that TreMs are more abundant and diverse in unmanaged stands (e.g., Paillet et al., 2017; Winter and Moller, 2008; Winter, 2015). The negative effects of forest management on the occurrence of TreMs can largely be explained by the lack of structural features and differences in tree species composition (Keren et al., 2017). Many of these structural components, such as snags and large trees, are considered to be important drivers of TreM diversity and abundance (Keren and Diaci, 2018; Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Vuidot et al., 2011). Only a few studies have been conducted in forests that have developed naturally for at least a century (Larrieu et al., 2014a,b; Courbaud et al., 2017). Primary forests may serve as suitable reference points compared to forests with former management because they tend to have more complex structure and are thus more favorable for many forest-dwelling species (Hunter, 1999; Peterken, 1996).

The importance of studies carried out in primary forests has increasingly been recognized (Commarmot et al. 2013), however, the temperate forests of Europe have a complex land use history, as they have been used for a variety of purposes, such as for fuel wood, pasture, and timber extraction, since ancient times (Sabatini et al., 2018; Veen et al., 2010). Despite extensive forest exploitation in the middle ages and intensive commercial forest management more recently, large patches of primary forests were spared in some remote mountainous areas of central, eastern, and southeastern European countries (Veen et al., 2010). Within Europe, the southeastern European mountain ranges (Carpathians, Dinarides) contain some of the largest areas of well-preserved primary forests, primarily in old-growth stages of development, dominated by European beech (*Fagus sylvatica* L.) (Meyer et al., 2003; Standovár and Kenderes, 2003). There are currently few censuses of TreMs from primary forests because these forests are rare in Europe and they are usually located in remote mountain regions (Parviainen, 2005; Sabatini et al., 2018).

Despite the increased number of TreM studies in the last decade, the role of drivers of TreM densities and diversity is still unknown at the plot and stand scales across different geographical regions (Paillet et al., 2017). Differences in precipitation, temperature, topography, soils, and bedrock play an important role in the development of forest structure, and TreMs develop at differing rates (Paillet et al., 2017). Natural disturbance regimes are another important driver of stand structure in primary forests (Schurman et al., 2018), and studying remnants of primary forests may help us understand the spatial distribution of TreMs under natural conditions (Larrieu et al. 2018). External biotic factors, such as population dynamics of woodpeckers that create cavities, may also influence the production of certain TreMs (Remm and Lõhmus 2011).

This study examines TreM profile from temperate primary forests dominated by European beech in two distinct mountainous regions – the Carpathians and Dinarides. Our objectives were: (i) to provide reference values of TreM density and diversity measures in mountainous mixed beech primary forests and (ii) to evaluate the importance of local plot structure and spatial variability for TreM density and diversity.

2. Material and methods

2.1. Study area and site selection

We refer to "primary forest" as a forest without signs of direct human impact (Fig. 1, Table 1), and where natural disturbances are the primary driver of forest structure and composition. These forests not only include old growth, but also the early seral stages of development. Potential study forests were selected using previous inventories of primary forest remnants when available (e.g., Veen et al., 2010), searching the available archival information, and historical data regarding the land use history of these areas. Almost all study forests are parts of formally protected areas (i.e., national parks, natural parks, strict forest reserves, UNESCO World Heritage sites), or they are proposed to soon be part of protected areas (i.e., Curai i Eperm, Ramino Korito). During the initial field surveys, all forests were inspected for various indicators of naturalness (e.g., coarse woody debris in various stages of decay, pit-and-mound topography, large trees, natural tree species composition) and signs of human impact; forests with evidence of past logging and grazing and those in close proximity (ca. 500 m) to formerly grazed areas were avoided. Preliminary dendrochronological analysis of selectively chosen tree cores from the study stands (30–40 trees per stand) revealed that a significant number of trees in each stand were older than 350 years, and one tree was even more than 450 years old (located at Perućica).

We selected four primary European beech-dominated mountain forests from both regions. Stands from the Carpathian Mountains spanned Slovakia and Romania, and those from the Dinarides were located in Croatia, Bosnia and Herzegovina, and Albania. The dominant

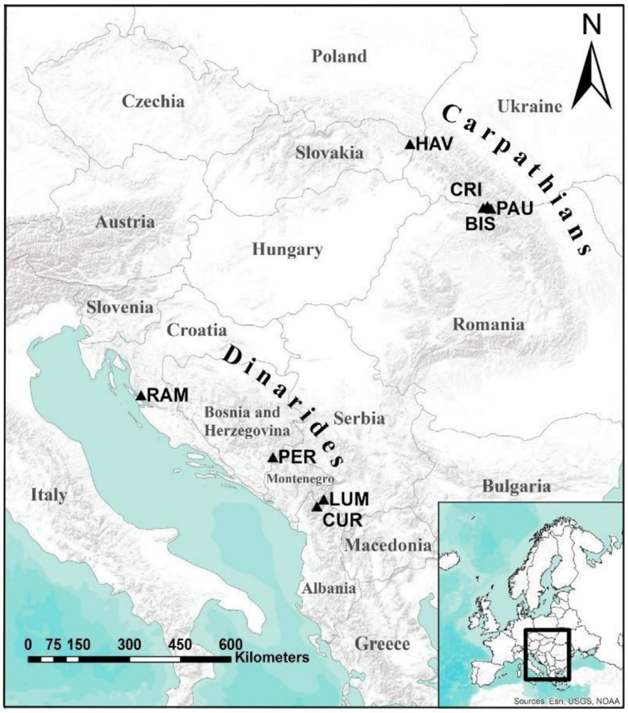

Fig. 1. Locations of primary forest study areas in the Carpathians and Dinarides.

tree species in these forests was European beech, mixed with mainly silver fir (*Abies alba* Mill.), maples (*Acer* spp. L.), and ashes (*Fraxinus* spp. L.).

In the Carpathians, the Slovakia Havešová (HAV) study site was located in the Bukovské Mountains. Havešová lies within Poloniny National Park and it is part of the UNESCO World Heritage - Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany. In Romania, the selected study forests, Bistra Valley (BIS), Criva (CRI), and Paulic (PAU), were located in the Maramures Mountains, which are formally protected within Maramures Natural Park, located on the Romanian-Ukrainian border.

In the Dinarides, the Ramino Korito (RAM) study site is situated in Velebit Nature Park in the Velebit Mountains of Croatia. The Curraj i Eperm (CUR) and Lumi i Gashit (LUM) sites are part of Nikaj-Mërtur Regional Nature Park located in the Albanian Alps. Lumi i Gashit (Gashi River) is also part of the UNESCO World Heritage - Primeval Beech Forests of the Carpathians and Other Regions of Europe. The site in Bosnia and Herzegovina was located in the Perućica primary forest (PER), which is part of Sutjeska National Park.

There are broad environmental differences between our study sites of the Eastern Carpathians and the Dinarides that are important to point out (Table 1). The average annual precipitation and temperature are higher in the Dinaric region compared to the Carpathian sites. Bedrock in the Dinaric sites is primarily limestone, while in the Carpathians sites it is primarily flysch and gneiss. The sites in the Carpathians were also located on steeper slopes.

2.2. Stand structural data

For the selection of permanent study plots, a polygon network (10 ha each) was created using the ArcView 9.3 Environment (ESRI ArcGIS, 2011). Within each 10-ha polygon we generated a random point to establish sampling points where we established two plots. The paired plots consisted of two 1500 m^2 circular plots (radius of 21.85 m); each plot center was located 40 m in opposite directions from the random sample point and parallel to the slope contour (Appendix 1). We established 146 permanent sample plots nested within 73 pairs of

Table 1
Study stand characteristics from the Dinaric (CUR, LUM, PER, RAM) and Carpathian (CRI, HAV, BIS, PAU) mountain ranges. Climate characteristics were obtained using the KNMI Climate Explorer (Van Oldenborgh et al., 2009). Mean temperature and mean annual precipitation were calculated using measurements from 1901 to 2016.

Country	Forest	Number of plots	Elevation range (m a.s.l.)	Mean annual precipitation (mm)	Mean temperature range (°C)	Average slope (°)	DBH mean (DBH max) (cm)	Broadleaved-Coniferous ratio (%)	Snags (% from all trees)	Mean number of trees per ha (DBH > 6 cm)	Mean number of TreM-bearing trees per ha
	Dinarides										
Albania	Curraj i Eperm (CUR)	14	1019–1287	1237	7.1–8.4	19.6	24.9 (124.1)	99:1	13	878	306.7
Albania	Lumi i Gashit (LUM)	14	1223–1682	1162	5.9–7.9	27.4	26.1 (135)	58:42	8	820	247.6
Bosnia	Perućica (PER)	48	1057–1450	1157	5–7.2	24.7	24.4 (134.5)	60:40	12	951	321.4
Croatia	Ramino Korito (RAM)	16	820–984	1299	8.1–8.9	15.4	32.1 (97.9)	91:9	16	518	281.6
	Carpathians										
Romania	Criva (CRI)	14	874–1147	862	4.2–5.6	34.7	28.1 (120)	77:23	7	533	311.4
Romania	Paulic (PAU)	12	942–1097	830	4.4–5.2	33.7	32.2 (163)	76:24	17	559	350.6
Romania	Bistra (BIS)	14	959–1154	830	4.1–5.1	35.4	32.2 (107.6)	69:31	9	477	176.7
Slovakia	Havešová (HAV)	14	615–710	815	6–6.5	23.4	25.5 (130)	100:0	13	572	226.7

plots across 8 forest stands. For each tree with diameter at breast height (DBH) ≥6 cm, the status of all trees (live or snag), tree species, and TreM presence/absence were recorded.

2.3. TreM data

For all study plots, each tree, including the stem and crown, was visually inspected for TreMs by two observers. Based on the typology of Vuidot et al. (2011), we created a list of 30 TreM types that we used to classify TreMs on our plots. All living trees with a DBH > 6 cm and snags located within the plots were searched for presence of TreMs (Appendix 2); we surveyed 13,640 living trees and snags in total. We arranged the TreM types into 12 groups for further analysis according to Paillet et al. (2017): crown deadwood, broken tops, conks of fungi, woodpecker cavities, non-woodpecker cavities, base cavities, bark characteristics, cracks, outgrowths, patches with exudates, epiphytes, and dendrothelms. All TreMs were surveyed in 2015 and 2016 during the period of June to September.

2.4. TreM characteristics

Diversity and density measures of TreMs were quantified for each sample plot. To reflect the diversity of TreM types, diversity was defined in terms of the number of TreM types occurring within the plot. Alpha diversity was defined as the average number of TreM types per tree in a given plot. Because the number of trees varied widely among plots (27–277 trees per plot), gamma diversity was calculated as the total number of TreM types per plot standardized by rarefaction to a common abundance level (n = 27 trees) to ensure comparability across plots (Chao et al., 2014). Beta diversity was defined as the ratio of gamma to alpha diversity, as originally proposed by Whittaker (1960); this ratio measures the degree to which TreM composition changes from tree to tree within a given plot.

To identify TreM densities, we used the index proposed by Paillet et al. (2017), i.e. the density of TreM-bearing trees, which allowed us to compare our results with other studies that used the same indices. Density of TreMs was quantified as the sum of TreM-bearing trees extrapolated to one hectare (Paillet et al., 2017). To determine the number of trees per plot bearing a given TreM type, each TreM type found on a tree was counted only once, even if it was present in greater numbers. Diversity and density measures were also calculated for several broad groups of TreM types (Table 2), in which case when we refer to density, it defines the density of trees bearing a particular TreM type. A major advantage of this sampling design was the minimal amount of time an observer needed to access TreMs in the field. Although we did not record the true abundance of all TreM types, our approach allowed us to compare our TreM data with other studies that used the same method (e.g., Paillet et al., 2017; Vuidot et al. 2011).

2.5. Data analyses

Generalized linear mixed models (GLMMs) were used to assess the effect of local plot structure and spatial variability on diversity and density characteristics of TreMs. Fixed effects included tree species richness (i.e., total number of tree species per plot), RMS DBH (root mean square diameter of trees at breast height in a given plot), proportion of snags (proportion of snags per plot versus total number of trees), and region (Dinarides and Carpathians). The random effects structure mirrored the spatial hierarchical nature of the sampling design, including plots nested within pairs of plots, which were nested within stands nested within regions. In the models of TreM density, the tree density per plot was treated as a nuisance variable to account for a trivial positive relationship between tree density and TreM density. Because diversity and density of TreMs are strictly positive and continuous variables, we used GLMMs with a gamma error distribution and log link function (McCullagh and Nelder, 1989). Model parameters were estimated using Laplace approximation and their significance was tested using likelihood ratio tests (Bolker et al., 2009). There was no serious multicollinearity observed in the models (all VIFs < 2.3). To compare the relative importance of the fixed effects, we calculated semi-partial marginal determination coefficients (R^2_m; Nakagawa et al., 2017) derived from a commonality analysis (Ray-Mukherjee et al., 2014). The intraclass correlation coefficients (ICC) were used to quantify the proportion of variance explained by each of the hierarchical spatial levels. All analyses were performed in R language version 3.4.3 (R Core Team, 2017) using the lme4 library (Bates et al., 2015).

3. Results

3.1. Total TreM densities

Total mean density of TreM-bearing trees (number of trees bearing at least one TreM) was similar in the Carpathians (266.4 bearing-trees ha^{-1}) and Dinarides (289.3 bearing-trees ha^{-1}). The average density of TreM-bearing trees for all stands was 277.8 TreM-bearing trees ha^{-1}. Epiphytes (128.8 bearing-trees ha^{-1}), bark characteristics (101.2 bearing-trees ha^{-1}), base cavities (65.2 bearing-trees ha^{-1}), and non-woodpecker cavities (41.3 bearing-trees ha^{-1}) had the highest TreM densities in both regions (Table 2). The lowest densities were observed for outgrowths (9.9 bearing-trees ha^{-1}) and dendrothelms (4.6 bearing-trees ha^{-1}). In the Carpathians, bark characteristics (112.7 bearing-

Table 2

Tree-related microhabitat densities for different TreM groups for the Carpathian and Dinaric mountain ranges, including total, living trees, and snags. All densities are presented as ha^{-1} values.

TreM group	Total TreM density	Carpathians	Dinarides	Snags total	Snags Carpathians	Snags Dinarides	Living trees total	Living trees Carpathians	Living trees Dinarides
Crown deadwood	33.1	31.6	33.9	1.5	2.8	0.7	31.6	28.8	33.3
Broken tops	17.3	29.6	10.1	3.8	6.9	2.0	13.5	22.7	8.1
Conks of fungi	21.8	33.1	15.2	17.7	26.4	12.6	4.1	6.7	2.6
Woodpecker cavities	13.3	15.9	11.7	11.1	12.5	10.3	2.2	3.5	1.4
Non-woodpecker cavities	41.3	28.8	48.7	10.2	7.2	12.0	31.1	21.6	36.7
Base cavities	65.7	98.9	46.2	8.0	10.5	6.5	57.7	88.4	39.7
Bark characteristics	101.2	112.7	94.4	59.1	53.6	62.3	42.1	59.1	32.1
Cracks	30.3	23.7	34.2	7.9	10.4	6.4	22.5	13.3	27.8
Outgrowth	9.9	14.8	7.0	0.8	0.7	0.8	9.1	14.1	6.2
Patches with exudates	16.0	28.5	8.6	1.1	1.5	0.9	14.8	27.0	7.7
Epiphytes	128.8	60.7	168.7	15.8	11.5	18.3	113.0	49.3	150.4
Dendrothelms	4.2	1.6	5.8	0.2	0.0	0.3	4.1	1.6	5.5
SUM	482.9	480.0	484.6	137.1	144.0	133.0	345.8	336.0	351.6

Table 3

Summary of GLMMs relating diversity (alpha, beta, gamma) and density of microhabitats to fixed and random effects. Likelihood ratio test statistics (χ^2), probabilities (p), semi-partial marginal determination coefficients (R^2_m [%]), and intra-class correlation coefficients (ICC [%]) are displayed. Significant positive/negative partial relationships (r) are designated by +/− signs, respectively; inequality signs are used for comparisons between Carpathians (C) and Dinarides (D). Model parameters were considered significant at 5% and are highlighted in bold.

	Fixed effects																Random effects								
	Tree species richness				RMS DBH				Proportion of snags				Region				Stand			Paired plots			Plot		
Model	χ^2	p	R^2_m	r	χ^2	p	R^2_m	r	χ^2	p	R^2_m	r	χ^2	p	R^2_m	r	χ^2	p	ICC	χ^2	p	ICC	χ^2	p	ICC
Alpha diversity	**6.3**	**0.0121**	**0.6**	+	**64.3**	**< 0.0001**	**12.2**	+	**41.8**	**< 0.0001**	**7.2**	+	0.3	0.6152	1.4		**8.6**	**0.0034**	**9.4**	**84.3**	**< 0.0001**	**23.0**	**107.9**	**< 0.0001**	**48.0**
Beta diversity	**9.9**	**0.0016**	**2.2**	+	1.5	0.2223	< 0.1		**12.4**	**0.0004**	**4.6**	+	2.8	0.0962	9.0		2.2	0.1395	11.7	**64.3**	**< 0.0001**	**24.3**	**74.5**	**< 0.0001**	**42.1**
Gamma diversity	**10.5**	**0.0012**	**0.2**	+	**52.9**	**< 0.0001**	**13.2**	+	**16.5**	**0.0001**	**2.6**	+	1.0	0.3176	5.5		**11.8**	**0.0006**	**13.6**	**62.9**	**< 0.0001**	**25.2**	**63.5**	**< 0.0001**	**36.5**
Density																									
All microhabitats	**10.6**	**0.0011**	**7.3**	+	< 0.1	0.8353	< 0.1		**29.7**	**< 0.0001**	**14.4**	+	0.1	0.7811	< 0.1		**4.7**	**0.0294**	**5.7**	**100.9**	**< 0.0001**	**33.8**	**85.7**	**< 0.0001**	**44.0**
Crown deadwood	0.4	0.5135	0.2		**15.2**	**0.0001**	**7.2**	–	**4.4**	**0.0367**	**1.9**	+	0.1	0.7995	< 0.1		**8.1**	**0.0044**	**12.0**	3.5	0.0601	18.0	0.0	0.9708	0.0
Broken tops	**4.3**	**0.0376**	**< 0.1**	+	**5.6**	**0.0181**	**1.5**	–	1.0	0.3063	< 0.1		3.2	0.0727	13.9		**10.3**	**0.0013**	**19.7**	**50.0**	**< 0.0001**	**26.3**	**28.2**	**< 0.0001**	**32.8**
Conks of fungi	0.4	0.5268	< 0.1		**15.3**	**0.0001**	**7.4**	+	**11.8**	**0.0006**	**6.1**	+	**5.6**	**0.0178**	**13.3**	**C > D**	**5.4**	**0.0203**	**18.3**	**10.5**	**0.0012**	**12.6**	**15.6**	**0.0001**	**41.1**
Woodpecker cavities	0.1	0.7610	0.0		< 0.1	1.0000	< 0.1		**21.5**	**< 0.0001**	**9.9**	+	0.1	0.6993	0.8		**8.4**	**0.0038**	**11.7**	**60.6**	**< 0.0001**	**29.5**	**50.1**	**< 0.0001**	**39.4**
Non-woodpecker cavit.	0.6	0.4444	1.4		0.8	0.3672	0.5		3.2	0.0715	2.1		2.2	0.1419	10.5		**6.6**	**0.0103**	**10.3**	**29.7**	**< 0.0001**	**14.8**	**55.7**	**< 0.0001**	**56.2**
Base cavities	0.2	0.6821	0.7		**6.4**	**0.0112**	**4.6**	+	3.1	0.0769	4.8		0.8	0.3585	5.7		**18.9**	**< 0.0001**	**18.7**	**14.0**	**0.0002**	**17.3**	2.9	0.0910	40.6
Bark characteristics	0.8	0.3864	0.4		1.3	0.2631	< 0.1		**50.9**	**< 0.0001**	**18.8**	+	0.8	0.3583	2.1		**5.4**	**0.0206**	**7.1**	**70.6**	**< 0.0001**	**25.8**	**99.3**	**< 0.0001**	**50.6**
Cracks	2.8	0.0932	3.4		< 0.1	0.8959	< 0.1		1.0	0.3172	0.9		1.5	0.2140	2.4		0.2	0.6855	1.6	**26.0**	**< 0.0001**	**16.0**	**32.2**	**< 0.0001**	**62.6**
Outgrowth	0.1	0.7428	0.7		**7.0**	**0.0082**	**1.6**	+	**7.6**	**0.0058**	**1.2**	–	3.8	0.0507	8.3		3.7	0.0529	13.6	**20.3**	**< 0.0001**	**22.4**	**12.5**	**0.0004**	**31.3**
Patches with exudates	**10.2**	**0.0014**	**4.3**	+	0.3	0.6099	< 0.1		**4.7**	**0.0299**	**1.2**	+	1.6	0.2124	8.1		**22.5**	**< 0.0001**	**25.8**	**53.4**	**< 0.0001**	**17.8**	**66.8**	**< 0.0001**	**40.3**
Epiphytes	**11.4**	**0.0007**	**8.9**	+	**5.4**	**0.0204**	**0.5**	+	0.5	0.4768	0.9		**6.4**	**0.0116**	**13.9**	**C < D**	< 0.1	0.9968	5.6	**51.1**	**< 0.0001**	**37.1**	**19.9**	**< 0.0001**	**27.6**
Dendrothelms	< 0.1	0.9658	< 0.1		2.1	0.1446	1.0		2.5	0.1146	1.2		2.6	0.1098	6.9		1.3	0.2572	10.9	**42.2**	**< 0.0001**	**26.0**	**35.6**	**< 0.0001**	**33.2**

trees ha^{-1}) and base cavities (98.9 bearing-trees ha^{-1}) had the highest densities, and dendrothelms (1.6 bearing-trees ha^{-1}) had the lowest density. The Dinarides were characterized by high TreM densities of epiphytes (168.7 bearing-trees ha^{-1}) and non-woodpecker cavities (48.7 bearing-trees ha^{-1}), and low densities of patches with exudates (8.6 bearing-trees ha^{-1}), outgrowths (7 bearing-trees ha^{-1}), and broken tops (10.1 bearing-trees ha^{-1}).

3.2. Key factors to the diversity of TreMs

Tree species richness, RMS DBH, and the proportion of snags showed significant relationships to TreM alpha diversity (i.e., the mean number of TreM types per tree), and gamma diversity (i.e., the total number of TreM types per plot; Table 3). All these habitat properties were positively correlated with the TreM diversity measures (Fig. 2). RMS DBH displayed a relatively strong relationship with TreM alpha (R^2_m = 12.2%) and gamma diversity (R^2_m = 13.2%), but the effect of tree diversity was rather negligible ($R^2_m \leq$ 0.6%). In contrast, beta diversity, the TreM turnover among trees, was unaffected by tree DBH. Considering spatial variability, alpha, beta, and gamma diversity of TreMs varied widely within paired plots (ICC > 35%) and also among pairs within stands (ICC ~ 23–25%). The contribution of stands to the observed variation was less obvious, but still important (ICC ~ 9–14%), with the exception of beta diversity, where the between-stand component of variance was not significant. We did not find any significant differences in TreM diversity between the Carpathians and Dinarides.

3.3. Key factors to the density of TreMs

Total density of TreMs was significantly and positively correlated with tree species richness and the proportion of snags in plots; RMS DBH showed no significant relationship with total TreM density (Fig. 2). Total TreM density significantly varied among plots, pairs of plots, and stands, but there was no significant difference in overall TreM density between regions (Table 3).

The density of broken tops, patches with exudates, and epiphytes displayed a significant and positive relationship with tree species richness. RMS DBH was positively related with density of conks of fungi, base cavities, epiphytes, and outgrowths, and it was negatively related with crown deadwood and density of broken tops. The density of most TreMs was significantly correlated with the proportion of snags, both positively (crown deadwood, conks of fungi, woodpecker, bark characteristics, patches with exudates) and negatively (outgrowth). Significant differences between regions were observed for the density of conks of fungi and epiphytes; the first group showed higher densities in the Carpathians, while the latter group was higher in Dinarides. There was also a higher density of outgrowths and broken tops in the Carpathians, although the relationships were marginally non-significant (Table 3). These large-scale geographic trends were accompanied by high similarity of TreM densities among stands within

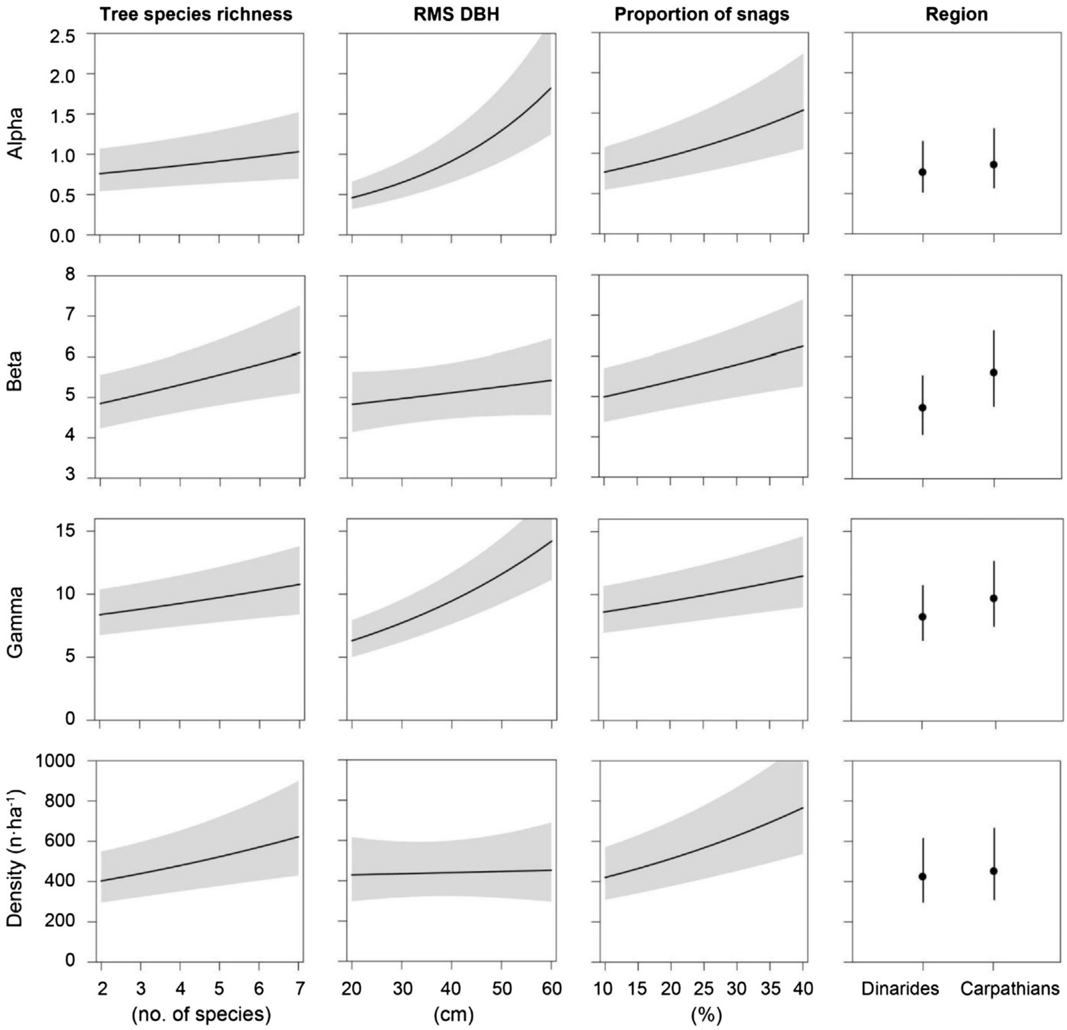

Fig. 2. Effect plots showing the results of GLMMs testing for the effect of tree species richness, RMS DBH, proportion of snags, and region on diversity (alpha, beta and gamma) and density of TreMs. Predicted values (lines, circles) are displayed along with 95% confidence intervals (gray polygons, error bars).

regions (non-significant stand effects). In contrast, densities of the other TreM groups varied considerably at smaller spatial scales (plots, pairs of plots, stands), and consistent large-scale differences between regions were not evident.

4. Discussion

Preserving the diversity of organisms that rely on specific forest structures is a key conservation challenge as forest management intensifies across the globe (Hansen et al., 2013; Mori and Kitagawa, 2014). Our assessment of TreM densities in primary forests provides a valuable benchmark for forest managers and policy makers that seek to implement structures that will benefit a host of species of conservation concern (Vuidot et al., 2011). We performed the first quantitative TreM analyses and comparison of TreM diversity in primary mixed beech-dominated forests in two distinct mountainous regions — the Carpathians and Dinarides. The primary drivers of TreM density (number of trees bearing a particular TreM per hectare) and diversity (richness of TreM types) at the plot scale in these forests were structural characteristics, such as RMS DBH, tree species composition, and proportion of snags. Geographical distance between regions did not play an important role in TreM densities and diversity, either at the alpha, beta, or gamma levels. Our study highlights that TreM densities observed in the primary forests were significantly higher in comparison to densities presented in studies from managed forests (e.g., Larrieu et al. 2012; Paillet et al., 2017).

We observed a significant increase in total TreMs density and alpha and gamma diversity of TreM types with an increased proportion of snags and tree species richness. Several studies have already observed the importance of snags, large living trees, and different tree species for densities of TreM types (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011). Tree diameter has also been recognized as an important factor in TreM dynamics across different forest types; it has been observed to influence the abundance of TreMs (Larrieu and Cabanettes, 2012), the diversity of TreM types (Larrieu et al. 2014a; Vuidot et al., 2011), or the occurrence of some TreM types, such as bark characteristics (Michel and Winter, 2009). Large diameter trees were also important in our study, especially for alpha and gamma diversity of TreMs, and densities of some TreM types. We did not find a significant relationship between DBH and total TreM density; most studies that observed a significant relationship between tree diameter and TreM used the DBH of the individual tree bearing the TreM. In contrast, we used RMS DBH of the trees on a plot, which likely introduced noise into the relationship given the mixed severity disturbance regimes of the region, and we also counted only one TreM type on each TreM-bearing tree, which may also further mask any relationship between diameter and density of TreMs. Tree species composition is another factor that has been observed to influence total TreM density and diversity (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011). Tree species diversity has also been observed to positively influence densities of some specific TreMs, such as broken tops, patches with exudates, and epiphytes. Patches with exudates, such as sap-runs and gummosis, are more likely to be found on deciduous trees (Siitonen, 2012), while the excurrent growth habit of conifers makes them more susceptible to broken tops. The proportion of snags had a significant effect on TreM diversity at the alpha, beta, and gamma levels, and also on the overall density of TreMs (Table 3). However, we observed that all TreM types were present within the living trees and snags as well, which may be due to partial mortality, whereby dead wood occurs on living trees, which is characteristic of very large trees (Siitonen, 2012) that could bear TreMs normally present on dead trees in managed forests (e.g., woodpecker feeding holes). Our findings emphasize the importance of snags in broadleaved stands because they promote increased TreM diversity and densities within beech-dominated primary forests. We also observed higher densities of certain TreM types that are rarer on living trees than on snags (woodpecker cavities, conks of fungi, and bark characteristics), which is consistent with the findings of Vuidot et al. (2011) and Larrieu and Cabanettes (2012), whereas the presence of conks of fungi and woodpecker cavities were significantly higher on snags than on living trees (Appendix 3). Woodpeckers generally prefer to nest and roost in snags, and fungi play an important role in the excavation of woodpecker cavities (Zahner et al. 2012), and woodpeckers are often suggested as a vector for the fungus (Jackson and Jackson, 2004). After the tree dies, the decay process promotes conditions that influence the occurrence of other TreM types, such as bark characteristics and non-woodpecker cavities (Vuidot et al., 2011). Although snags represented only 7–17% of all trees per stand, they accounted for one-third of the density of all TreMs tallied in our study (Table 2). Our results generally agree with prior TreM research conducted in different regions, and it highlights the positive effects of high levels of structural heterogeneity (e.g., large trees, and high tree species richness and proportions of snags) to support a diverse array of TreMs. Finally, our results showed higher densities of TreMs associated with certain taxa compared to published conservation guidelines: a minimum of 40 cavities per hectare for the conservation of cavity dwelling birds (Blondel, 2005) or a network of 7–10 live cavity- or crack-bearing trees per hectare for bats (Meschede and Heller, 2003). Our data support these findings and demonstrate that the primary forests can reach very high TreM levels.

Here, we compared for the first time TreM densities and diversity between primary forests of the Carpathian and Dinarides mountain ranges. Although precipitation and temperature differ among the regions (Table 1), we did not observe significant differences in total TreM densities or TreM diversity between the regions. Both of the regions had similarly high diversity values (Table 2). However, we observed significant differences in densities of several TreM types between the regions, including densities of conks of fungi and epiphytes (Table 3), which could potentially be influenced by large-scale climatic differences or soil properties (Ding et al., 2016). However, our results suggested significant variability between TreM densities and diversity on relatively small spatial gradients (stand and plot levels). We observed TreM densities almost two times greater than that of Paillet et al. (2017) in strict mixed mountain forest reserves of France (Table 2; Appendix 2). They determined that strict forest reserves had higher TreM densities, both total and individual densities, than comparable adjacent managed forests. This general trend has also been observed in several other European forests (Winter and Moller, 2008; Winter, 2015). Although Paillet et al. (2017) sampled strict forest reserves, the mean time since any previous harvesting was only 48 years; it is impossible to identify the structure of the stands at the beginning of the set-aside period or how intensively the stands were managed prior to their strict reserve designation. We analyzed TreMs exclusively from remote primary forests with very limited access, and it is likely that these stands were never managed; some of the oldest trees are more than 450 years old. Compared to the findings of Paillet et al. (2017), we observed the density of broken tops was more than 10 times higher on average, and almost 20 times higher in the Carpathians. The higher densities of broken tops may be attributable to the natural disturbance regime that influences structural dynamics in primary forests (Meigs et al., 2017), as well as the high proportion of live trees bearing polypores, such as *Fomes fomentarius* or *Fomitopsis pinicola*, which make beech stems more prone to breakage (Zeibig et al., 2005*)*. In addition, taller trees with larger primary branches may be more prone to partial crown loss. Similar conclusions can be drawn for higher densities of other TreM groups. High volumes and diversity of deadwood, which are typical of primary forests (Nagel et al., 2017), may influence the presence of conks of fungi and even woodpeckers (Jackson and Jackson, 2004). We also observed much higher densities of base cavities compared to Paillet et al. (2017); because large cavities take more time to develop, higher rates of occurrence on very old trees would be expected, thus many primary forests would have higher numbers of older trees with longer periods of time since the last severe disturbance (Siitonen, 2012). In contrast, we found lower densities of outgrowths and bark characteristics in the Dinaric dataset compared to the French strict forest reserves (Paillet et al., 2017); outgrowths and bark characteristics tend to occur more frequently on oaks (*Quercus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.) compared to beech (Vuidot et al., 2011). However, higher densities of outgrowths and bark characteristics were found in the Carpathian dataset than in the Dinarides dataset.

5. Conclusions

We conducted the first assessment of tree-related microhabitats in beech-dominated primary forests of the Carpathian and Dinaric mountain ranges; these sites represent some of the last remnants of primary forests in Europe. Our study provides an empirical analysis of TreM variability and reference values from these primary forests, both of which will help inform forest managers, conservation strategies, and policy decisions. These reference values provide a means to assess the influence of forest management on the TreM profile. However, our study sites represent a relatively small fraction of these two vast mountain ranges. To improve our understanding of TreM dynamics, we suggest a more thorough survey of primary forest study areas across the Dinaric and Carpathian Mountains, as well as other mountain ranges where similar forest types occur. Climate characteristics, topographical features, such as the presence of cliffs that can increase the occurrence of certain TreMs, such as bark loss, by rock falls, or biotic factors, such as woodpecker density (or diversity) or the presence of large ungulates, may also play an important role in the availability of TreMs. A potentially important driver of TreM density and diversity may be the natural disturbance regime that may play an important role in creation and maintenance of TreMs. Future research will include the analysis of disturbance history variables in relation to TreMs. In particular, a dendroecological approach could be used to link natural disturbance history with TreM diversity and density, and to assess how forest development influences the distribution of TreMs. Finally, our results show that primary forests maintain high TreM diversity, and that they may significantly contribute to the overall species diversity across forested landscapes. Although our paper did not directly compare primary forests with managed forests under similar environmental conditions, we also plan to establish plots in managed forests near primary forests in future studies to better understand TreM dynamics and the critical role of protected areas to maintain and enhance biodiversity in our modern world.

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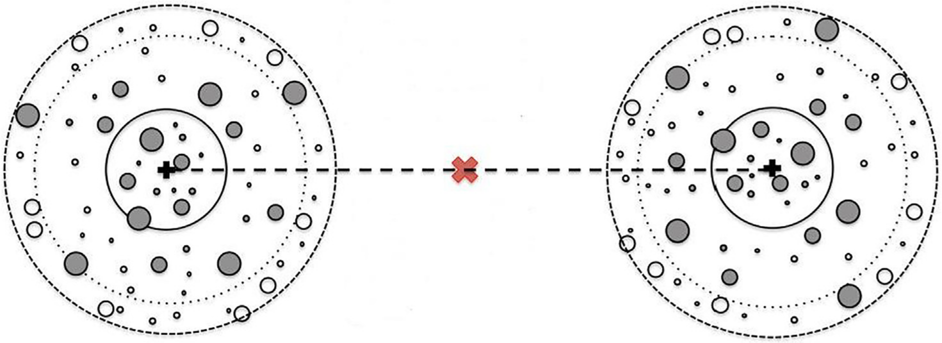
Appendix 1

Example of the nested plot structure. The red cross indicates the randomly generated navigation point used to locate the pair of circular sample plots.



Appendix 2

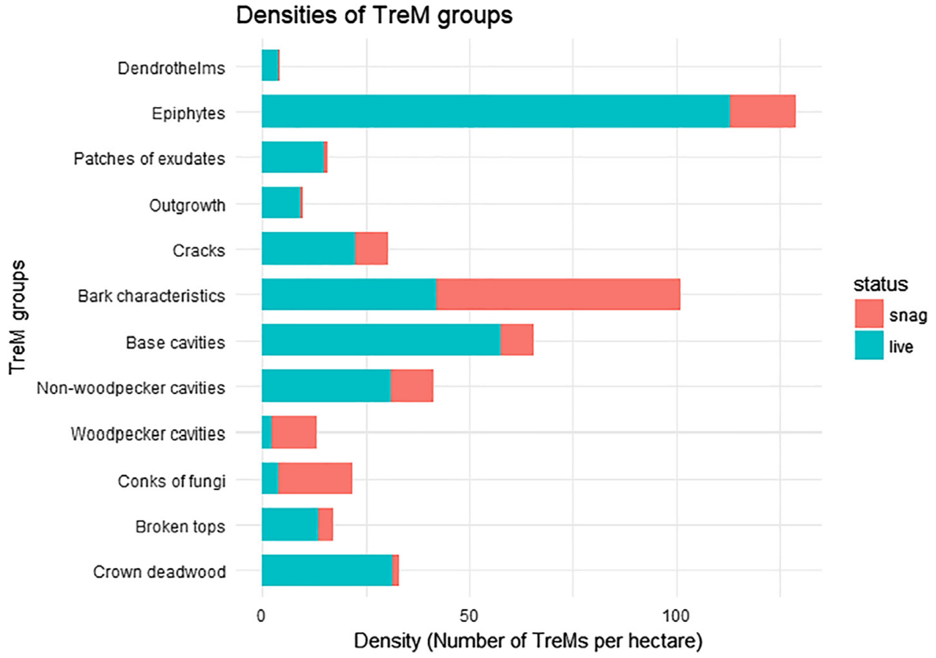
Tree-related microhabitat densities for all surveyed TreM types for the Carpathian and Dinaric mountain ranges, including total, living trees, and snags. All densities are presented as ha^{-1} values.

TreM group	Correlation with typology from Larrieu et al. (2018)	TreM type	Total number of TreMs	Total TreM density	Total Carpathians	Total Dinarides	Total snags	Carpathians snags	Dinarides snags	Total living trees	Carpathians living trees	Dinarides living trees
Woodpecker cavities	X	Woodpecker cavities with > 2 cm aperture, woodpecker breeding or feeding holes	289	13.2	15.9	11.6	11.1	12.5	10.2	2.1	3.5	1.4
Non-woodpecker cavities	X (partially)	Non-woodpecker cavities with > 5 cm aperture anywhere on the trunk: formed after injury, branch fall	744	34.0	22.7	40.6	4.1	2.6	4.9	29.9	20.1	35.7
Non-woodpecker cavities	X	Cavity string: at least three woodpecker cavities in a stem with a maximum distance of two meters between two cavity entrances. Cavity strings are an important starting point for the development of deep and long lasting stem cavities	161	7.4	6.0	8.1	6.1	4.6	7.0	1.2	1.5	1.1
Woodpecker cavities		Shallow cavities in the bark arranged in a ring; usually woodpecker	2	0.1	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1
Base cavities	X	Deep stem cavities: a tubular cavity in the base of the tree without mold	884	40.4	62.3	27.5	2.4	3.6	1.7	38.0	58.8	25.8
Base cavities	X	Deep stem cavities: a tubular cavity in the base of the tree with mold	525	24.0	35.9	17.0	5.4	6.8	4.6	18.6	29.1	12.4
Base cavities	X	Tree with hollow > 30 cm aperture	30	1.4	0.6	1.8	0.2	0.1	0.3	1.1	0.5	1.5
Dendrothelms	X	Dendrothelms with > 5 cm aperture. Water-filled holes in wood	93	4.2	1.6	5.8	0.2	0.0	0.3	4.1	1.6	5.5
Patches with exudates	X	Sap or resin drop: Only a few sap or resin drops (shorter than 30 cm or < 6 flows) indicating a minor injury	264	12.1	20.9	6.9	0.9	1.2	0.7	11.2	19.6	6.2
Patches with exudates	X	Heavy sap or resin: fresh heavy flow of sap or resin at least 30 cm long or > 5 flows of sap or resin of smaller size	86	3.9	7.7	1.7	0.3	0.2	0.3	3.7	7.4	1.4
Conks of fungi	X (partially)	Conks of fungi (both perennial and annual; including agarics). Fruiting bodies, diameter > 5 cm	285	13.0	18.0	10.1	10.1	13.6	8.0	2.9	4.4	2.0
Conks of fungi	X (partially)	Conks of fungi (both perennial and annual; including agarics). Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies	193	8.8	15.1	5.1	7.6	12.8	4.6	1.2	2.2	0.6
Bark characteristics	X	Bark loss: patches with bark loss of at least 5 * 5 cm mainly caused by felling, natural falling of trees and rock falls	1768	80.7	95.6	72.0	45.9	44.4	46.8	34.8	51.1	25.2
Bark characteristics	X (partially)	Bark burst: black burst of bark at least 2 cm wide often with resin indicating injury/disease	41	1.9	2.7	1.4	0.1	0.1	0.1	1.8	2.6	1.3

Bark characteristics		Gnaw and peeling by ungulates	20	0.9	1.5	0.6	0.3	0.1	0.4	0.6	1.4	0.1
Broken tops	X (partially)	Splintered stem: the split-up results in numerous scales (minimum 5) of wood > 50 cm long; caused by another tree fall etc.	70	3.2	4.2	2.6	2.1	3.0	1.5	1.1	1.2	1.1
Cracks	X	Lightning scar: a crack caused by lightning; at least 3 m long and reaching the sapwood	4	0.2	0.0	0.3	0.0	0.0	0.1	0.1	0.0	0.2
Cracks	X	Cracks: cleft into the sapwood > 25 cm long along the stem and at least 2 cm deep in the sapwood	660	30.1	23.7	33.9	7.8	10.4	6.3	22.3	13.3	27.6
Bark characteristics	X	Bark pocket: space between loose bark and the sapwood with a minimum extension of 5 * 5 * 2 cm	357	16.3	11.4	19.2	11.9	7.7	14.4	4.4	3.7	4.8
Bark characteristics	X	Bark pocket with mold: same structure and size as Bark loss but with mold.	30	1.4	1.6	1.2	0.8	1.2	0.6	0.5	0.4	0.7
Crown deadwood	X (partially)	Between 10% and 25% of dead crown: one or more main branches are dead. The living crown represents 75% of the former total crown	434	19.8	16.8	21.6	0.0	0.0	0.1	19.8	16.8	21.5
Crown deadwood	X (partially)	Between 25% and 50% of dead crown: one or more main branches are dead. The living crown represents between 50 and 75% of the former total crown	127	5.8	6.8	5.2	0.0	0.0	0.1	5.8	6.8	5.1
Crown deadwood	X (partially)	More than 50% of dead crown: one or more main branches are dead. The living crown seems to be < 50% of the former total crown	163	7.4	8.0	7.1	1.4	2.8	0.5	6.1	5.2	6.6
Broken tops	X	Broken stem: the primary crown is totally absent with or without presence of a secondary crown. Main parts of the tree stem are already dead with decomposing processes	265	12.1	25.1	4.5	1.7	4.0	0.4	10.4	21.1	4.1
Broken tops	X	Broken fork: complete fracture of one of the two forking branches; the loss of one forking branch results in a severe damage of the main stem	44	2.0	0.4	3.0	0.0	0.0	0.0	2.0	0.4	3.0
Outgrowth	X	Canker: proliferation of cell growth; irregular cellular growth on stems or branches, which is caused by bark-inhabiting fungi, viruses and bacteria. We recorded areas of canker > 10 cm in diameter	211	9.6	14.7	6.7	0.8	0.7	0.8	8.9	14.0	5.9
Outgrowth	X	Witch broom: dense agglomeration of branches from a parasite or epicormic branching	6	0.3	0.1	0.4	0.0	0.0	0.0	0.3	0.1	0.4
Epiphytes	X	Bryophytes developed on > 50% of the base or trunk area (height < 1 m)	2762	126.1	57.2	166.6	15.5	11.5	17.9	110.6	45.7	148.7
Epiphytes	X	Ivy developed on > 50% of the base or trunk area (height < 1 m)	18	0.8	0.0	1.3	0.2	0.0	0.4	0.6	0.0	0.9
Epiphytes	X	Mistletoe: presence of a hemiparasitic plants (e.g. Viscum spp., Arceuthobium oxycedri, Loranthus europaeus)	40	1.8	3.6	0.8	0.0	0.0	0.1	1.8	3.6	0.7
		SUM	10,576	482.9	480.0	484.6	137.1	144.0	133.0	345.8	336.0	351.6

Appendix 3

Comparison of densities of TreM groups between snags and living trees.



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5.3 Primary forests provide more tree-related microhabitats than managed ones underlining the need of their conservation

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Primary forests provide more tree-related microhabitats than managed ones underlining the need of their conservation

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Key words:

- Integrative conservation approaches
- Old-growth elements
- Natural disturbances and dynamics
- Black Forest
- Carpathians

Highlights:

- Trees provide more microhabitats in primary forests than in managed ones
- The conservation of primary forests is essential for providing tree microhabitats
- Selecting habitat trees that provide microhabitats is crucial in managed forests

Abstract

The impact of forest management on biodiversity is difficult to scrutinize along gradients of management. A step towards analyzing the impact of forest management on biodiversity are comparisons between managed and primary forests. The standardized typology of tree-related microhabitats (TreMs) is a multi-taxon indicator used to quantify forest biodiversity. We aim to disentangle the influence of forest management on the occurrence of specific groups of TreMs by comparing primary and managed forests. We collected data from the managed forests in the Black Forest region and from the primary forests in the Western (Slovakia) and Southern Carpathians (Romania). To model the richness and the different groups of TreMs per tree, we used generalized linear mixed models with primary vs. managed, diameter at breast height (DBH), tree species, altitude and latitude as predictors. We found congruent results based on the models for overall richness and the vast majority of TreM groups. Trees in primary forests hosted a greater richness of all and specific types of TreMs than individuals in managed forests. The main driver of the difference is the long-term natural development with absence of human management, followed by tree species and DBH. We recommend forest and nature conservation managers to: 1) focus on the conservation of remaining primary forests and 2) focus approaches of biodiversity-oriented forest management on the selection of high-quality habitat trees that already provide a high number of TreMs in managed forests based on the comparison with primary forests.

Introduction

To tackle the biodiversity and the climate crisis that forests face (Schelhaas and others 2003; Hanewinkel and others 2013; Seidl and others 2014, 2017) a great number of approaches including adaptive strategies, retention forestry, close-to-nature forest management or ecological forestry have been developed (Bauhus and others 2009, 2013; Messier and others 2019; Gustafsson and others 2020; Čada and others 2020). Yet, the impact of altered management approaches on biodiversity is difficult to scrutinize on large spatial scales as well as along gradients of management (Paillet and others 2010; Bruelheide and others 2020). One major step towards analyzing the impact of management on biodiversity are comparisons between types of managed and unmanaged forests, including sites where management has ceased relatively recently and to a lesser extent, primary forests (Paillet and others 2010; Schall and others 2018). However, when it comes to summarizing the margins of influence of management on biodiversity, the results may vary greatly according to the time of absence or type of management (Paillet and others 2015b; Schall and others 2020). Therefore, remnants of primary forests deliver a unique source of information to address the question of influence of management or natural disturbances and dynamics on biodiversity (Kozák and others 2020), however these remnants are rare and difficult to locate (Sabatini and others 2018; Mikoláš and others 2019). Another challenge in assessing differences between managed and primary forests is the comparability of datasets, for instance the collection of data on taxonomic groups might not always be comparable across sites (Bruelheide and others 2020). To overcome this problem partially, a multi-taxon indicator beyond single-species information has been widely implemented and used for quantifying forest biodiversity, namely the standardized, hierarchical typology of tree-related microhabitats (e.g. Larrieu and others 2012, 2018; Paillet and others 2018; Asbeck and others 2020a; Basile and others 2020a; Jahed and others 2020). The most common definition for a tree-related microhabitat (TreM) is "a distinct, well delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed" (Larrieu and others 2018). The hierarchical TreM typology distinguishes 15 groups of TreMs in seven forms:

- Cavities: woodpecker breeding cavities, rot holes, concavities, insect galleries and bore holes;
- Tree injuries and exposed wood: exposed sapwood and/or exposed heartwood;
- Crown deadwood in different forms;
- Excrescences: twig tangles (witches broom), cankers and burrs;
- Fruiting bodies of saproxylic fungi and slime molds: perennial and ephemeral fungi fruiting bodies;
- Epiphytic, epixylic and parasitic structures: epiphytic crypto- and phanerogams, nests of vertebrates and invertebrates, micro soils
- Fresh exudates such as sap run and heavy resinosis.

A variety of taxonomic groups have been linked to the different levels of the hierarchical typology of TreMs based on literature and empirical data and include invertebrates such as insects, arachnids and gastropods as well as vertebrates such as birds, rodents, bats and carnivores (Larrieu and others 2018; Paillet and others 2018; Basile and others 2020a).

Based on this standardized typology, datasets from primary (Kozák and others 2018) as well as managed forests (Asbeck and others 2019) provided first analyses of driving factors of TreM richness in temperate mountain forests in Central and Eastern Europe. The identification of these drivers of TreM abundance and richness still deserves further attention as most studies have only been able to identify that DBH and tree species are most important for living trees (Larrieu and Cabanettes 2012; Paillet and others 2019). As TreMs are considered a biodiversity indicator that could guide the selection of retention elements in managed forests, one major open question is the impact of management and the natural life cycle of trees in primary forests on the richness of TreMs (Larrieu and others 2012, 2014; Asbeck and others 2020b). Here, we aim to disentangle the influence of management on the richness and occurrence of specific groups of TreMs compared to primary forests for the first time. This might deliver valuable information for the development of evidence-based management strategies to provide old-growth elements and small-scale retention elements throughout managed forests and as well address the importance of primary forests for the conservation of biodiversity (Bauhus and others 2009; Asbeck and others 2020b; Basile and others 2020b; Gustafsson and others 2020). Old-growth elements are largely absent in managed forests, but provide valuable and rare habitats for the conservation of dependent species and increase the connectivity and dispersal ability of these species (Baguette and others 2013; Kraus and Krumm 2013). We aim to give a first overview how managed forests differ in TreM richness compared to primary forests to: 1) highlight the importance of the primary forests for the conservation of biodiversity, and 2) identify focal points for forest management to increase these habitats for the conservation of forest dwelling species.

Material and Methods

Data collection

We collected data for the managed forests placed in one-hectare forest plots located on state land in the Black Forest region (Latitude: 47.6°- 48.3°N, Longitude: 7.7°-8.6°E, WGS 84). The plot selection followed a landscape gradient of forest cover in the 25 km² surrounding the plots and a gradient of structural complexity indicated by the number of standing dead trees per plot: for details of plot selection see Storch and others, 2020. A full inventory of all living trees and their TreMs on all plots of 1 ha would have been beyond the capacity of this project, hence we pre-selected living trees based on their crown radius from GIS in different classes to get individuals of all dimensions. We selected a subset of plots that were managed for timber production and excluded strict-protected ones mentioned in Asbeck and others, 2019. We recorded the position of all inventoried trees, their diameter at breast height (DBH), species identity and TreMs in the snow-free and leaf-free period between fall 2016 and spring 2017. We collected additional data, including altitude and latitude per tree with the use of hand-held tablets.

For the primary forests, we collected the data in mixed forests of Western (Slovakia, 210 plots) and Southern Carpathians (Romania, 190 plots), for details of the mapping and selection of these primary forests see Mikoláš and others (2019). Surveyed plots were based on an existing international network of permanent inventory plots (REMOTE, www.remoteforests.org), encompassing primary forests in Central and Eastern Europe. All data were collected within 0.15 ha circular plots randomly distributed across various environmental gradients (but see Kozák and others, 2018 for details of plot selection). Across the primary forest plots, we recorded the positions of all living, adult trees (≥ 6 cm DBH), their DBH, species identity and TreM profile based on methodology by Larrieu et al. (2018) during the vegetation season in 2018 and 2019. Altitude and latitude were measured at the center of the plot.

In order to decrease the observer effect (Paillet and others 2015a), inventories were carried out by the same team within each location. Three observers in the Black Forest and two in the Carpathian region visually inspected the TreMs following the same hierarchical typology (Larrieu and others 2018).

Statistical analyses

In our analyses we focused only on a comparison of living trees, since data for dead trees was not available for the Black Forest and from a management perspective, the selection of high quality living habitat trees is more complex than the one of standing dead trees (Asbeck and others 2020b). We calculated the overall richness as the sum of different TreM groups per living tree. To model the richness as well as the groups of TreMs per living tree, we used generalized linear mixed models (GLMMs).

In combination with management, we tested the effects of the co-variates tree species, DBH, altitude and latitude on the richness and groups of TreMs on individual living trees. These co-variates drive the richness and number of groups of TreMs per tree (Kozák and others 2018; Asbeck and others 2019). Tree DBH as well as species identity were included in the GLMMs as predictors. In addition to the three tree species, Norway spruce (*Picea abies (L.)*), European beech (*Fagus sylvatica (L.))* and silver fir (*Abies alba (Mill.)*), we included altitude and latitude as site factors as we have datasets from two different geographic regions.

To prevent autocorrelation of trees within the same plot that might have more similar characteristics than individuals in different plots (Dormann 2013), we included plot-identity as random factor. The computation of models was performed in R (R Core Team 2016). Since the richness data for TreMs were of count type, we built models with the “glmmTMB function” of the “glmmTMB package” (Brooks and others 2017) with a negative binominal distribution to solve overdispersion. To test for under- and overdispersion as well as zero-inflation in the models, we used the “DHARMa package” (Hartig 2018). Obviously, with a large number of living trees that do not bear TreMs, there were signs of zero-inflation; however, models did not improve when considering this. We checked for correlations between the predictors in the final models by computing the variance inflation factors with the “performance package” (Lüdecke and others 2020).

The full models consisted of these predictors:

- Managed vs. primary + DBH + tree species + altitude + latitude + (1|PlotID)

Prior to running the models, we adjusted the continuous predictors due to the different scales using the default setting of the scale function in R, which calculates the mean and the standard deviation (sd) of the predictor and then scales each element by those values by subtraction of the mean and dividing by the sd. We re-run the final models with the unscaled data for plotting the effects of the significant predictors. We used the “ggpredict” function of the ggeffects package for plotting, which sets all other predictors, except the one for which the effect is shown, to the same value (Lüdecke 2018).

Results

Raw inventory data at the tree level in managed and primary forests

We restricted the analyses to living individuals of the three main tree species that were Norway spruce, European beech and silver fir in both data sets. Across all tree species, the individuals in the primary forests provided a greater richness of TreMs per living tree compared to the managed ones (Table 1).

Results of the statistical analyses

We found congruent results of TreM richness and among the vast majority of groups across the studied forests. First, the latitude included in the models was not the predictor with the greatest magnitude of influence. This allowed us to identify that the main driver of difference is indeed the absence of management (Table 2, Figure 1). This holds true for 10 out of the 16 models. Only epiphytes and fresh exudates are found more frequently in managed forests (Table 2, Figure 1). Altitude as a proxy of the site conditions was the most important driving factor for epiphytes (Table 2). All groups increased significantly with increasing DBH, despite diameter being less important than absence of management (Table 2, Figure 2). For woodpecker cavities, rot holes and annual fungi, tree species was the most important driver, as they increased with the greatest magnitude in beech trees, whilst exposed sapwood and twig tangles occurred in significantly lower numbers in Norway spruce (Table 2, Figure 3).

Discussion

The increasing importance of primary forests as key habitats for the conservation of biodiversity recently inspired silvicultural approaches that emphasize the role of old-growth attributes and natural disturbance legacies in management activities (Keeton 2006; Lindenmayer and others 2006; Bauhus and others 2009; Nagel and others 2014; Thom and others 2019; Čada and others 2020). Our novel approach compared the tree-level TreM richness of primary forests in the Carpathians with managed forests in the Black forest to disentangle the role of management for the provisioning of specific habitats. We consider our data sets comparable, as the latitude included in the models was not the predictor with the greatest magnitude of influence; hence, our results are robust across the inventoried geographic locations. Trees in primary forests hosted a more diverse array of TreMs in terms of overall richness and specific types of TreMs compared to their counterparts in managed forests.

The most prominent result is that we observed higher numbers of TreMs on living trees located in primary forests compared to those in managed ones. Previous studies were not able to extract this information as congruent as we did, for instance Vuidot and others (2011) did not find this difference when comparing managed and unmanaged forests on the tree level. Our findings might be influenced by the time that management is absent as in the mentioned study the unmanaged forests were left without timber extraction for a maximum of 150 years and logged previously. In contrast, we are the first to analyze primary forest plots without any traces of human activities due to difficulty of accessibility. Conventional forest management creates structurally uniform and highly productive stands with limited longevity of the trees. On the other hand, trees in primary forests often grow slowly, competing with other individuals under the vertically diverse canopy with longevity multiple times higher than the trees in managed stands (Bigler and Veblen 2009; Di Filippo and others 2012). Suboptimal tree growing conditions, such as poor soil conditions or suppression were connected to the formation of certain TreMs, such as cracks, bark lesions and rot holes (Jönsson 2000; Fritz and Heilmann-Clausen 2010). Such conditions are more likely to be found in primary forests because forest management is often avoided on nutrient poor and inaccessible sites. In addition, suppressed trees are systematically removed in most silvicultural practices. In this context, tree senescence is considered to play an important role for the occurrence of TreMs, but so far has only been included in one cross-sectional (Courbaud and others 2017) and one empirical study (Puverel and others 2019). We assume that the abundance and richness of TreMs increases with tree senescence, which might be the main reason for trees in primary forests bearing more TreMs, as they could be older compared to individuals of similar dimensions in managed forests.

Increased richness of specific TreM groups such as crown deadwood, exposed sapwood and heartwood, perennial polypores and insect galleries on primary forest trees implies the importance of natural disturbances for the formation of certain TreMs. The most important natural disturbances in Central and Eastern European mountain forests are wind, bark beetle outbreaks, snow and ice (Nagel and others 2014; Svoboda and others 2014; Janda and others 2017; Kulakowski and others 2017). The importance of effects from large-scale cyclones and convective instabilities on dynamics of these mountain forests has recently been recognized (Pettit and others in review).

Wind can cause damage either directly by breaking the stem or limb of a tree, or indirectly through trees damaging each other when breaking or uprooting. Forest management may substitute the role of wind as damage caused during felling operations whichcould create similar TreMs (Vuidot and others 2011). Such practices may be effective in mimicking the natural creation of TreMs in managed stands (Fritz and Heilmann-Clausen 2010). Besides wind damage, galleries from wood drilling insects resulting from insect outbreaks of various severities are common in primary forests. This group of TreMs is highly unfavorable in managed forests because of its negative impact on timber value combined with imminent large-scale insect outbreaks that hit the Central European region and became more severe recently (Schelhaas and others 2003; Seidl and others 2017). Management practices also tend to remove trees with signs of other timber damaging pathogens, such as fungi. Increased richness of perennial polypores on trees in primary forests is thus not surprising. This removal is not restricted to individuals bearing polypores, but for all trees bearing TreMs that are considered “defects” in forest management. Moreover, the presence of fungi combined with senescence may increase the probability of stem breakage during windstorms, especially in beech trees (Zeibig and others 2005), making it partially responsible for increased richness of exposed sap and heartwood TreMs in primary forests.

We demonstrated a positive effect of tree diameter on overall TreM richness and a consistent effect across the studied TreM groups (except twig tangles). As observed in previously, the diameter of the living trees is an important factor influencing the presence of TreMs across tree species, forest types and environmental conditions (Larrieu and Cabanettes 2012; Kozák and others 2018; Asbeck and others 2019; Paillet and others 2019).

Our results are also in line with observed patterns of increased TreM numbers in broadleaves (Larrieu and Cabanettes 2012; Regnery and others 2013; Paillet and others 2019), as we found the highest overall TreM richness on European beech. Specifically, a higher richness of woodpecker cavities, rot holes and annual fungi was observed on beech trees. Woodpeckers serve as a vector for the fungal infection and often prefer beech trees with rotten heartwood for the excavation of woodpecker cavities (Jackson and Jackson 2004; Zahner and others 2012). Woodpeckers are opportunistic in their choice of suitable trees for cavity establishment (Basile and others 2020b); whenever snags are available in lower quantities, which is the case in managed forests compared to primary ones, they select living trees to excavate their cavities. This is the reason for the non-significant effect of absence of management on woodpecker cavities, as we included only living trees in the analyses. We observed a lower richness of epiphytes in primary forests compared to managed ones and the most important predictor for an increase of this TreM group was an increase in altitude. Similarly, a higher altitude was responsible for increased abundance of epiphytic TreMs

(Asbeck and others 2019) and diversity of epiphytes (Ding and others 2016), which is possibly due to an increased precipitation or humidity in higher altitudes.

Uncertainties in our results might be caused by the variation in sampling design, as we selected living trees for the TreM survey based on the size of their crown area in managed forests (Asbeck and others 2019), whereas the primary forest plots did not include only old-growth successional phases but also early seral ones (Kozák and others 2018). However, we included the diameter as predictor in our models and thus took the difference in diameter into account; hence our results should be robust concerning this difference in sampling methods.

Conclusion

We were able to identify for the first time that the main driver of differences in richness and occurrence of TreMs between primary and managed forests is the absence of management. Our study suggests that primary forests are essential in providing habitats for forest-dwelling species through a high richness of TreMs. However, many complexes of primary forests are being lost due to poor mapping and lack of protection status (Knorn and others 2013; Sabatini and others 2018; Mikoláš and others 2019). This allows salvage logging operations, which can lead to extraction of trees with high potential to bear or develop TreMs, representing a threat to the ecosystem itself and the function it fulfills for biodiversity conservation (Thorn and others 2018). Hence, our results highlight the importance of primary forests for biodiversity conservation but have as well several implications for forest management. First, the constant removal of trees or parts of trees that show “defects”, such as exposed sap- and heartwood or crown deadwood created by natural disturbances, needs to be decreased to some extent in managed forests to provide these important TreMs as resources. This could be implemented by focusing the selection of retention elements such as habitat trees on individuals that provide these obvious and easily identifiable TreMs. Secondly, the increase of beech and other broadleaf species will increase the number of habitats available for forest dwelling species. Overall, we recommend forest and nature conservation managers to focus their approaches on: 1) protecting the remaining primary forests and 2) selecting high-quality habitat trees that already provide a high number of microhabitats in managed forests based on the comparison with primary ones.

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Data sharing

All data used in this article is available and has been published previously in Kozák and others 2018 and Asbeck and others 2019.

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Tables

Table 1 - Comparison of the main attributes of the inventoried living trees and sites in the inventoried managed and primary forests.

Managed forests

Tree species	N of trees	Share (%)	DBH (cm)			Mean (SD)	
			Min	Max	Mean (SD)	Altitude (m)	TreM richness/ living tree
European beech	877	26.4	7	128	36 (21)	750 (202)	1.9 (1.1)
Norway spruce	1788	53.7	7.5	115	46.5 (15)	910 (178)	1.6 (0.7)
Silver fir	662	19.9	8	137	56 (20)	849 (140)	1.9 (0.9)
Total	3327				46 (19)	856 (190)	1.7 (0.9)

Primary forests

Tree species	N of trees	Share (%)	DBH (cm)			Mean (SD)	
			Min	Max	Mean (SD)	Altitude (m)	TreM richness/ living tree
European beech	4045	27.1	6	129	36 (21)	1135 (112)	3.2 (1.5)
Norway spruce	9570	67.4	6	117	35 (17)	1440 (135)	3.0 (1.0)
Silver fir	1295	9.1	6	119	32 (24)	1154 (133)	2.8 (1.2)
Total	14910				35 (19)	1333 (194)	3.0 (1.1)

Table 2 - Results of the generalized linear mixed models indicating the magnitude of influence and the significance[a] of the scaled predictors. Positive values show an increase in the group of tree-related microhabitats. The bold letters indicate the predictor with the greatest influence on the respective TreM group. The managed forests and silver fir are represented in the intercept.

	Intercept	Site	DBH (cm)	Tree species		Latitude	Altitude
		Primary forest		European beech	Norway Spruce		
Overall TreM richness [b]	0.59***	**0.37*** **	0.16***	0.19***	0.00	-0.05***	0.09***
Woodpecker cavities [b]	-9.99***	-1.46	0.75***	**1.79* **	0.41	0.10	0.64
Rot holes [b]	-4.84***	0.38	0.50***	**2.82*** **	-0.35	0.01	0.06
Insect galleries [c]	-8.47***	**3.34*** **	0.44***	0.29	-0.34	0.47***	-0.64**
Concavities [b]	-2.47***	**1.56*** **	0.60***	0.89***	0.91***	-0.19***	0.03
Exposed sapwood only [b]	-2.31***	0.51***	0.05*	0.03	**-0.71*** **	0.28***	-0.32***
Exposed sap- and heartwood [c]	-5.06***	**1.21*** **	0.17***	0.97***	0.02	0.07	0.05
Crown deadwood [c]	-3.97***	**3.04*** **	0.32***	-0.26**	0.47***	-0.59***	-0.16
Twig tangles [c]	-2.10***	-2.40***	0.06	-3.05***	**-4.49*** **	0.53*	1.27***

Burrs and cankers [b]	-5.89***	**2.39*** **	0.65***	0.97***	-0.14	-0.03	-0.31*
Perennial fungi [c]	-7.33***	**1.79***	0.50***	0.46	-1.02*	0.29*	0.19
Annual fungi [c]	-8.49***	1.24	0.56***	**2.65*** **	0.36	-0.13	0.61
Epiphytes [c]	1.71***	-1.61***	0.50***	0.01	-1.24***	-0.06	**1.99*** **
Nests [b]	-10.15***	**4.08*** **	0.50***	0.32***	0.24*	-0.53**	-2.50***
Microsoils [c]	-9.95***	**4.07*** **	1.14***	1.65***	0.54**	-0.28*	-0.72**
Fresh exudates [c]	-4.84***	**-4.15*** **	0.35***	-1.76**	2.80*	-0.36	-0.28

[a] Significance codes: ‘***’ 0.001; ‘**’ 0.01; ‘*’ 0.05; [b] Models with a negative binomial distribution; [c] Models with a binomial distribution

Figures

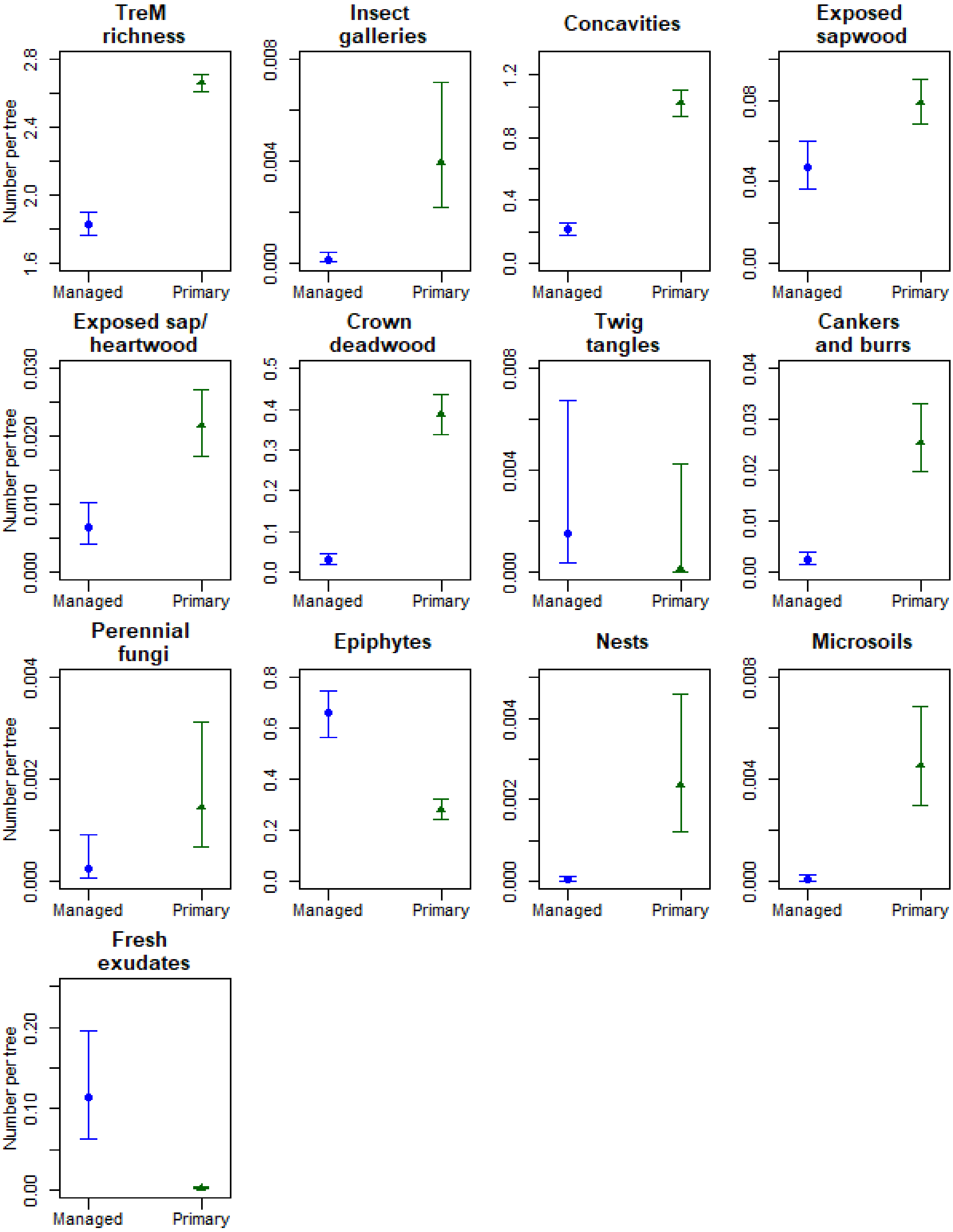

Figure 1 - Effect plots of the significant influence of managed versus primary forest sites for TreM richness and groups from the generalized linear mixed models. The error bars of the predictor indicate the 95%-confidence interval.

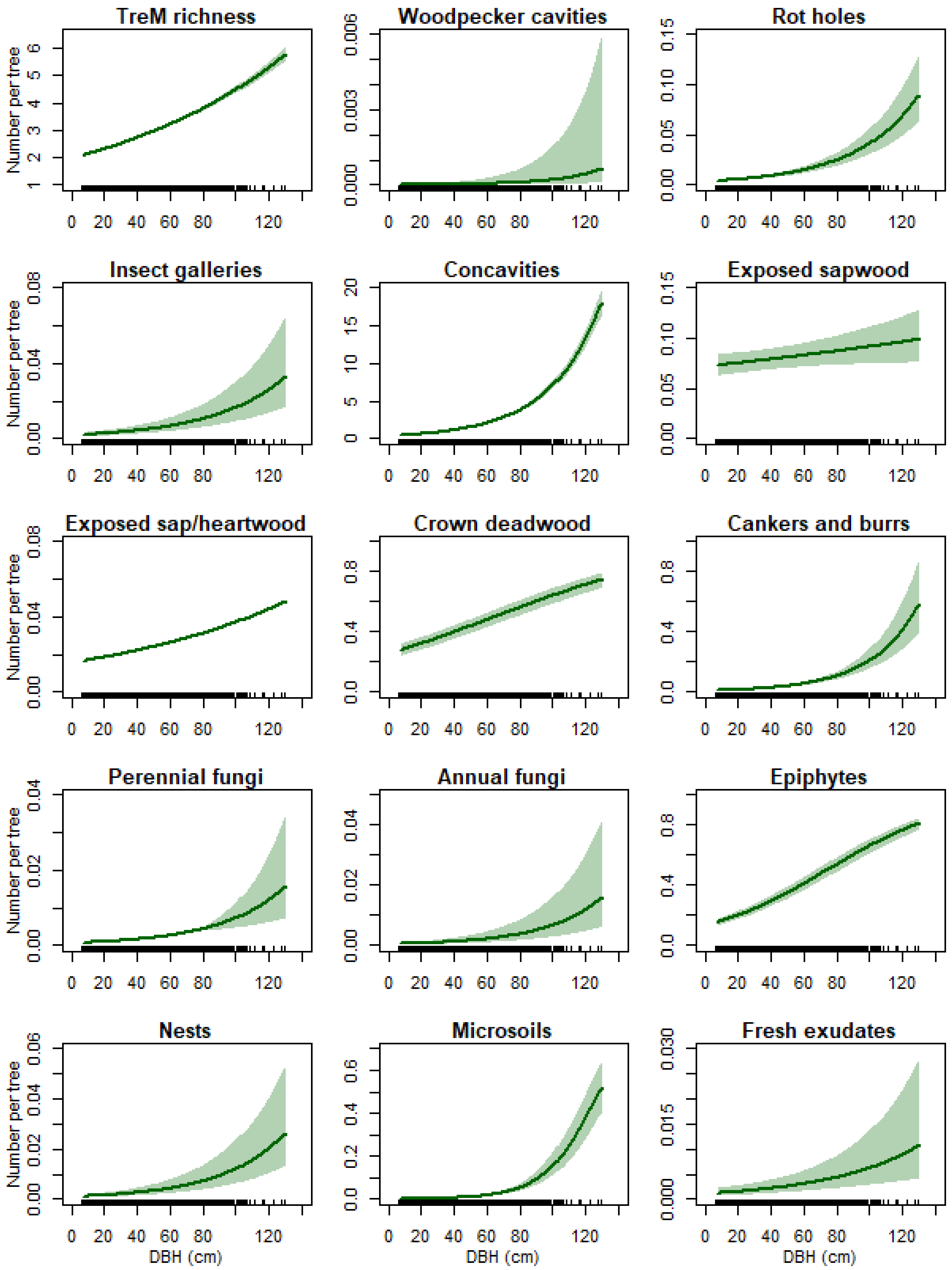

Figure 2 - Effect plots of the significant influence of the diameter at breast height (DBH) for TreM richness and groups from the generalized linear mixed models. The light color bands indicate the 95%-confidence interval. The rug plot shows the DBH range of the inventoried trees.

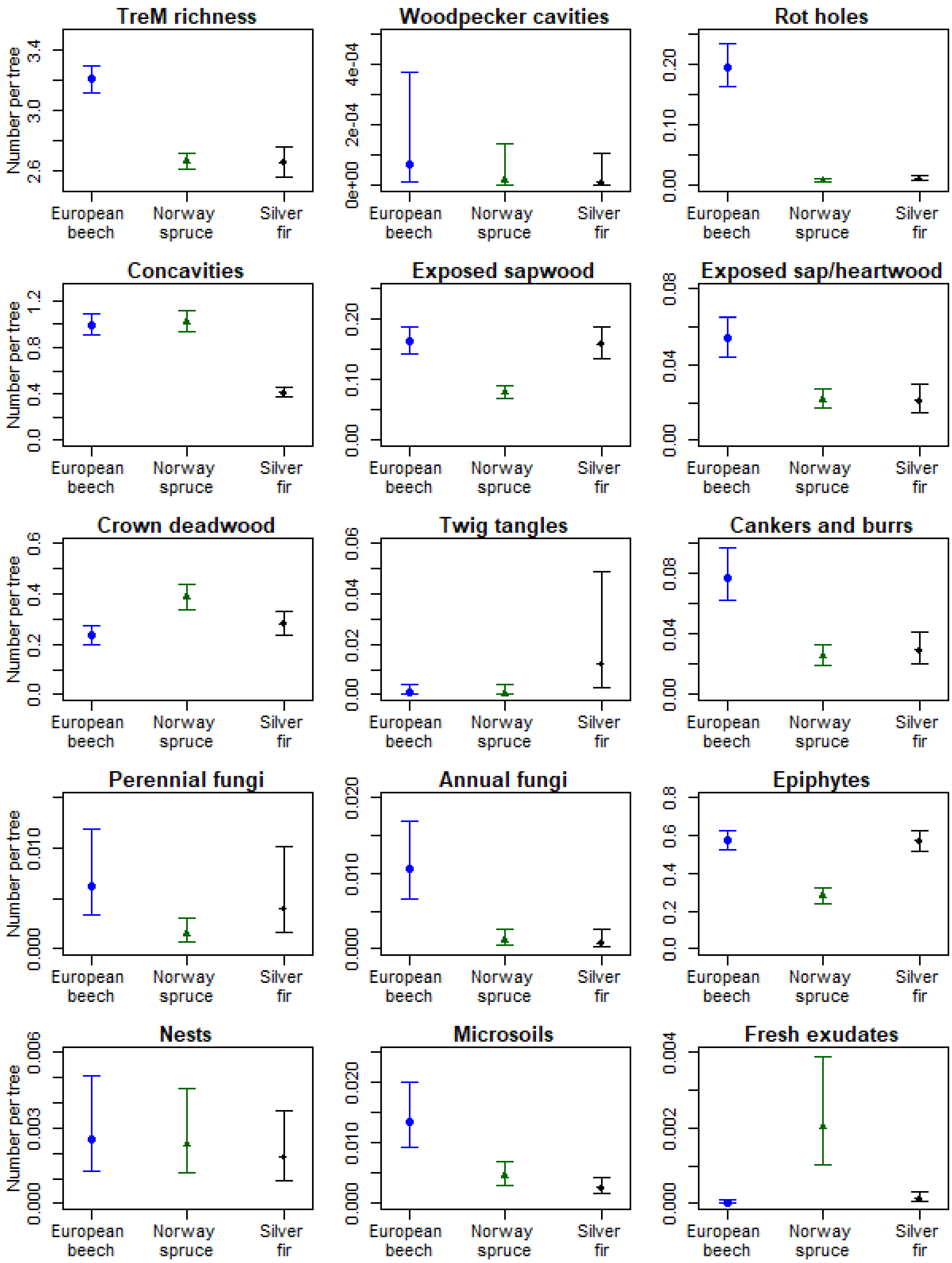

Figure 3 - Effect plots of the significant influence of tree species for TreM richness and groups from the generalized linear mixed models. The error bars of the predictor indicate the 95%-confidence interval.

5.4 Influence of tree age on tree-related microhabitats abundance and richness: comparison of mixed-beech and spruce mountain primary forests

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Influence of tree age on tree-related microhabitats abundance and richness: comparison of mixed-beech and spruce mountain primary forests

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Abstract

Tree characteristics such as diameter, species and live status greatly impacts the occurrence of tree-related microhabitats (TreMs), a structural indicator used to quantify forest biodiversity. However, our knowledge on how tree senescence influences TreM profile and thus, potential biodiversity habitats, is relatively understudied on the tree level. Older trees have higher likelihood to be damaged by biotic and abiotic factors and thus are more prone to TreM formation. Here we focused on disentangling the effect of tree age, diameter and other tree characteristics on TreM abundance and richness. We collected tree level data from >350 plots located in spruce and mixed beech dominated primary forests in the Western and Southern Carpathians, in Slovakia and Romania respectively. We used tree cores from 15-30 living trees per plot and calculated their age using dendrochronological methods. For the data analyses we firstly used boosted regression trees to assess the relative importance of the studied variables on the TreM profile, and then generalized linear mixed models to analyze TreM abundance, richness and the richness of 15 TreM groups with tree age, tree diameter, tree species and region as predictors. We observed that tree diameter and age were the most important factors significantly increasing TreM abundance and richness, whereas tree species played a lesser but still significant role in overall TreM abundance and richness across the studied primary forests. Interestingly, we observed a major role of tree age in increasing the richness of specific TreM groups, such as concavities, insect galleries and exposed sapwood on the studied trees. To protect the most valuable habitat trees, we recommend forest and nature managers to focus on

the conservation of forest stands where trees can reach their maximal potential longevity, and the retention of old trees within biodiversity-oriented forest stands.

Introduction

As complete biodiversity inventories are hardly feasible across forest stands due to time and economic constraints, much attention from scientists and forest managers in the past decade has focused on tree-related microhabitats (hereafter TreMs), mostly due to their suitability as a structural indicators of biodiversity for certain taxa such as insects, birds or bats (Buse et al. 2007, Winter & Möller 2008, Paillet et al. 2019). Quite recently, a new methodology for TreM assessment was presented by Larrieu et al. (2018) in order to ensure comparability across studied forest types and biogeographical regions. Here, we refer to TreMs as distinct, well delineated structures occurring on living trees or snags and they serve as a substrate or life site for species or communities during at least part of their life cycle to develop, feed, shelter or breed (Larrieu et al. 2018).

Our understanding of TreM dynamics and driving factors on the tree scale has highly increased over the last few years (Paillet et al. 2019). For instance, snags often contribute more to the TreM supply when compared with living trees, mostly due to the decompositional processes that favors the development of TreMs. Another largely important factor is the diameter of the tree, as the occurrence and diversity of the TreMs has been found to increase with tree diameter (Winter & Möller 2008). Additionally, tree species appears to play a role, as broadleaved tree species accumulate slightly higher microhabitat levels than coniferous ones (Paillet et al. 2019)

TreMs are important structural indicators of biodiversity within the concept of close-to-nature forestry, where the retention of habitat trees and the conservation of certain areas for biodiversity (Bauhus et al. 2009, Kraus & Krumm 2013) is a key concern. Within this scope, in areas set aside for conservation, forest management should be omitted or reduced only to the selection of certain valuable timber trees. The process of felling can cause tree damage and injuries which can lead to occurrence of certain TreM types such as wounds, stem decay or resinosis (Michel et al. 2011). Therefore, understanding TreM occurrence in areas where forest management has been absent for a long period or never occurred, can provide a reference point and help us understand the pattern of TreM development, and this knowledge can then be used in new set-aside areas without management, such as forest reserves and other special protected areas. Thus, primary forests represent the ultimate intact habitat (Ulyshen et al. 2018) for biodiversity studies and they often contain an abundant and diverse array of TreMs (Kozák et al. 2018).

As certain TreMs take time to develop or often develop after a tree is sufficiently large (Michel et al. 2011), the age of a tree may play an important role facilitating the occurrence and diversity of certain TreMs. Tree age is often in a close relationship with tree size however, this relationship is not always straightforward as the largest trees are not always the oldest (Issartel & Coiffard 2011). Trees can grow in the lower, shaded parts of the canopy for centuries with relatively small diameter increments and only after the removal of the upper canopy layers are they able to exploit the available light conditions and undergo increased growth rates. In contrast, trees in the upper parts of the canopy often grow faster and can reach large diameters without exceeding the life expectancy of their understory counterparts (Issartel & Coiffard 2011). This effect can lead to substantially different TreM occurrence between large and old trees, as certain conditions for TreM occurrence might relate to a large diameter but not necessarily with higher age and vice versa.

To address this knowledge gap, we aimed to distinguish the effect of the tree diameter and tree age on TreM occurrence using dendroecological methods on a comprehensive number of study plots in the Carpathian primary beech-dominated and spruce forests.

Specifically, our research hypotheses are: 1) Tree age, together with other tree characteristics such as diameter, position in the canopy and tree species will influence abundance and diversity of TreMs and 2) certain TreM types will increase with increasing senescence of the tree whereas other will remain unaffected by the senescence process.

Materials and methods

Study area

The study area was restricted to primary forests in two regions: the Western Carpathians (Slovakia) and the Southern Carpathians (Romania). The Carpathian Mountains support a substantial part of all remnant primary forest area in Europe (Sabatini et al. 2018, Mikoláš et al. 2019). We refer to “primary forest” as a forest without signs of direct human impact and where natural disturbances are the primary driver of forest structure and composition. These forests not only include old growth, but also the early seral stages of development. The study forests were selected using previous inventories of primary forest remnants when available (e.g. Veen et al. 2010, Mikoláš et al. 2019), and through searching the available archival information and historical data regarding the land use history of these areas. During the initial field survey, all forests were inspected for various indicators of naturalness (e.g. deadwood in various stages of decay, pit-and-mound topography, large trees, natural tree species composition) and signs of human impact; forests with evidence of past logging and grazing and those in close proximity (ca. 500 m) to formerly grazed areas were avoided.

We selected 379 primary European mixed-beech (n = 133) and spruce (n = 246) mountain forest plots in the Western and Southern Carpathian Mountains. Due to possible differences in topography and climatic conditions within the two studied forest types, which can not only differently influence the growth of the studied tree species but also the occurrence and diversity of certain TreM types (Asbeck et al. 2019, Paillet et al. 2019), we divided our data in two subsets based on the forest type (mixed-beech and spruce).

The dominant tree species in mixed-beech forests was European beech (*Fagus sylvatica* L.) together with mainly Norway spruce (*Picea abies* Karst.), silver fir (*Abies alba* Mill.) and sycamore maple (*Acer pseudoplatanus* L.). Spruce forests were mostly mono-dominated by Norway spruce with minor tree species admixtured, including rowan (*Sorbus aucuparia* L.), beech, silver fir, sycamore maple and stone pine (*Pinus cembra* L.).

Field data were collected to describe the tree and associated TreM characteristics. Survey locations were based on an existing international network of permanent inventory plots (REMOTE, https://www.remoteforests.org) that span primary forests in Central, Eastern and Southeastern Europe, and that are randomly distributed across various environmental and climatic gradients (Meigs et al. 2017). All data were collected within 0.1 ha circular plots on spruce dominated plots and 0.15 ha circular plots on mixed-beech plots, corresponding to the extent of the original REMOTE plots.

TreMs and forest structure

We collected comprehensive inventory data to quantify and classify the abundance and richness of TreMs across all study plots. We identified the coarse structure of plots by precisely mapping all standing trees using laser rangefinders and customized software (Field-map; Monitoring and Mapping Solutions, Jílove u Prahy, Czech Republic). As tree diameter has been recognized an important factor for TreM occurrence (Paillet et al. 2019), we measured the size (diameter at breast height, DBH) of all adult (≥ 6 cm DBH) trees, and determined ages for a subset of canopy trees (N=15-30) based on increment core samples. Tree cores were randomly selected from individual trees contributing to canopy cover (Lorimer & Frelich 1989). These are individuals exhibiting a potentially large variation in size and age, but with fully exposed canopies. We identified occurrences of 47 distinct TreM types on all live trees based on the methodology by Larrieu et al. (2018) and particular types were pooled to TreM groups described by the same methodology. All trees were identified to species level. Due to the minor occurrence of other tree species in the dataset we only used four major tree species in the analyses, namely: beech, fir, maple and spruce. Trees which were not cored, and therefore we do not have the information about their age, were excluded from the final dataset.

Tree age data

Cores were dried in the laboratory and cut by a core microtone (Gärtner & Nievergelt, 2010), cross-dated and measured following standard dendrochronological methods (Stokes & Smiley, 1968). Annual rings were measured to the nearest 0.1 mm using a stereomicroscope and a Lintab^{TM} sliding-stage measuring device in conjunction with TSAP-WIN^{TM} software (http://www.rinntech.ds). Cores were first visually cross-dated using the marker year approach (Yamaguchi 1991), verified with PAST4^{TM} software (www.sciem.com), and then confirmed with COFECHA^{TM} software (Holmes 1983).

Statistical analyses

For the evaluation of the relative influence of the predictor variables (tree age, its diameter, species, growth and region) we used Boosted Regression Trees (BRT, Elith et al. 2008). The measures of the relative influence were based on the number of times a variable was selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedmann & Meulman 2003). The relative influence (or contribution) of each variable was scaled so that the sum added to 100, with higher numbers indicating a stronger influence on the response variables. We fitted a BRT model using the function *gbm.step* from the *dismo* package (Hijmans et al. 2017) with the following parameters: tree complexity = 5, learning rate = 0.005, bag fraction = 0.5 (Elith et al. 2008). We repeated the same procedure for both the spruce and beech datasets.

We used age and DBH as explanatory variables, since DBH is recognized as one of the most important factors influencing TreM occurrence and richness and is often related to tree age. Because our study is focused on tree level analyses, we did not include plot characteristics such as topography, climate and disturbance regime in the model. However, to account for the possible differences between study locations, we used region as an additional explanatory variable. As certain TreMs are known to differ between tree species, we used tree species as a categorical explanatory variable with four factors (beech, spruce, fir, maple), but we excluded tree species from the models of the spruce dataset, since there were very few tree species present other than spruce. We modelled the abundance, TreM richness and richness of TreM groups as the response variable using generalized linear mixed models (GLMMs). To prevent the autocorrelation of trees within the same plot that might have more similar characteristics than trees in different plots, we included the hierarchical spatial design of our study (plots nested in stands) as a random effect. Since the abundance and richness of TreMs are counts, we built models with the glmmTMB function from glmmTMB package (Brooks et al. 2017) with a Conway-Maxwell Poisson distribution, because there were signs of underdispersion and zero inflation. Additionally, we used binomial distribution to model TreM groups which consisted of only one specific TreM (i.e. insect galleries, twig tangles, perennial fungi). We scaled the continuous predictors using the default setting of the scale function. We used a stepwise model selection to select the best model using Akaike information criterion (AIC). All statistical analysis took place in R (R Core Team 2017).

Results

The variable importance analyses revealed that DBH was the most influential factor for TreM richness and abundance in both the beech (56.5% and 60.4% respectively; Figure S1 and Figure S2) and spruce (51% and 54.1% for richness and abundance respectively; Figure S3 and Figure S4) datasets. Tree age was the second most important factor with a relative influence of 27.4% for abundance (Figure S1) and 24% for richness (Figure S2) in beech-dominated forests and 27.2% for TreM richness in spruce forests (Figure S4). The regions in which the plots were located had a higher relative importance in spruce forests (17.3% on TreM richness and 22.3% for abundance, Figure S3 and S4), and was of only minor importance in beech-dominated forests. Tree species were also of minor importance for the richness and abundance of TreMs in beech-dominated forests, and an even lower importance was observed in spruce forests. Position of the tree in the canopy (variable “growth”) was the least important factor with less than 1% of influence on TreM characteristics and therefore this variable was omitted from further analyses.

Congruent to the results of the variable importance analyses, the modeling results showed that DBH was the most important variable, and had a positive influence on TreM richness and abundance (Figure 1 and 2) and a similar pattern was observed for several TreM groups (Table 1 and 2). While a significant positive effect of tree age on TreM characteristics was also found, it proved itself as the most important variable only in case of certain TreM groups; concavities, burrs and cankers in beech-dominated forests; insect galleries, exposed sapwood, burrs and cankers in spruce forests (Table 1 and 2). Tree species was the most important factor for 6 out of the 15 TreM groups; twig tangles were found in higher frequencies on maples, and a lower occurrence of exposed sapwood was observed on spruce trees. Insect galleries and exudates were observed in lower magnitudes on beeches, while rot holes and annual fungi were found in higher magnitudes.

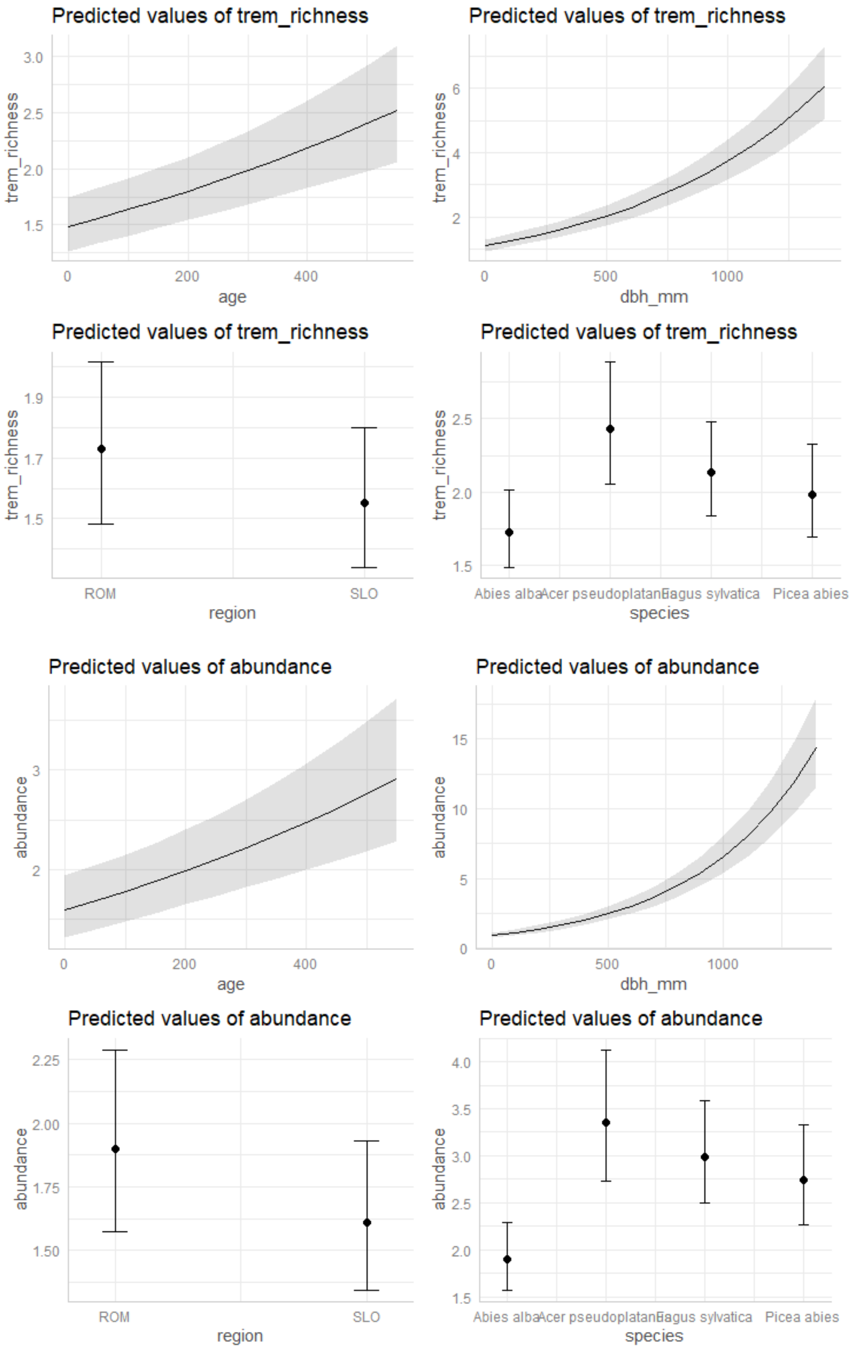

Figure 1: Effects of DBH on abundance and richness of TreMs in beech-dominated forests from the generalized linear mixed effect models. The grey bands indicate the 95%- confidence interval. Abbreviations represent the studied regions (ROM - Romania, Southern Carpathians; SLO - Slovakia, Western Carpathians).

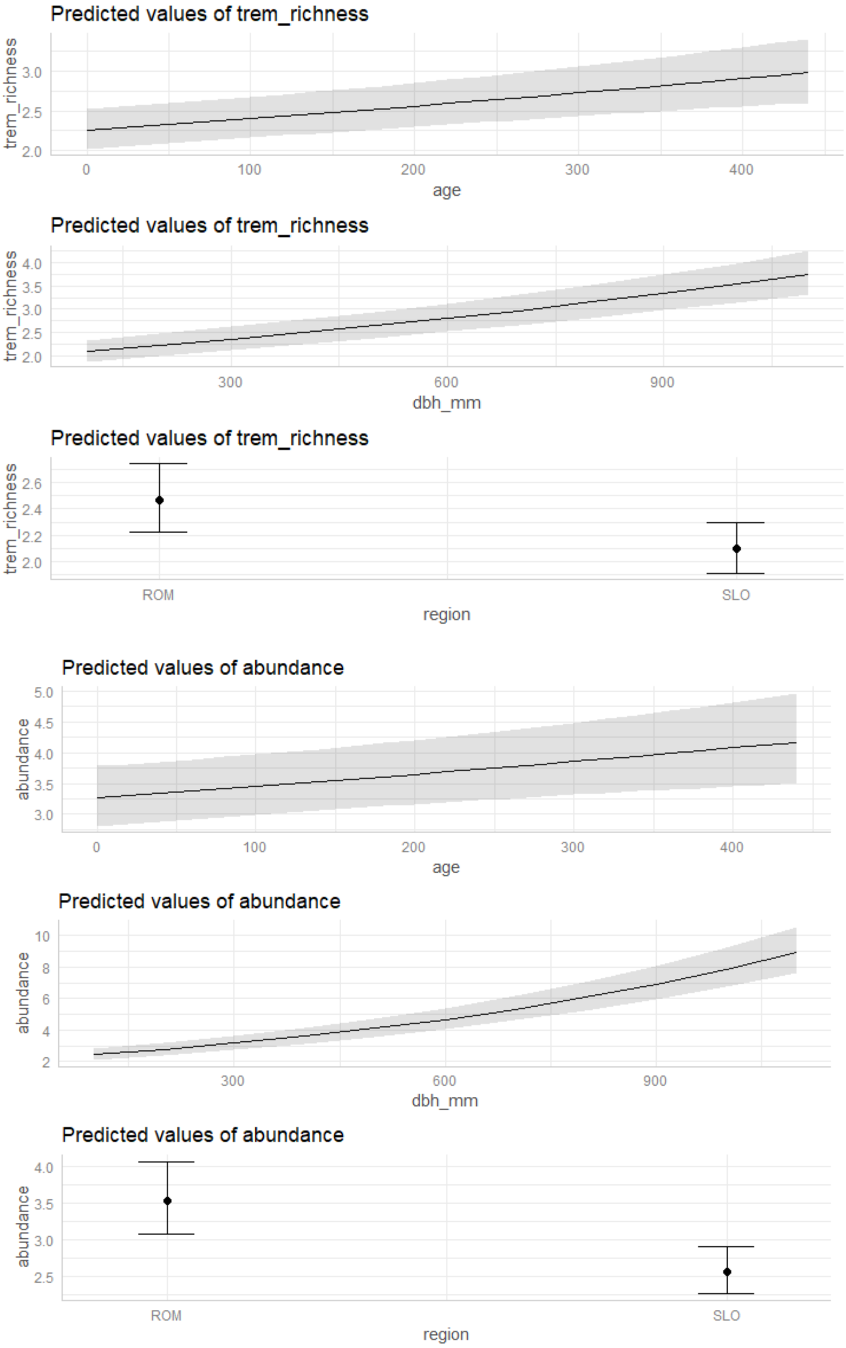

Figure 2: Effects of DBH on abundance and richness of TreMs in spruce forests from the generalized linear mixed effect models. The grey bands indicate the 95%- confidence interval.

Abbreviations represent studied regions (ROM - Romania, Southern Carpathians; SLO - Slovakia, Western Carpathians).

Table 1 and 2: Results of the generalized linear mixed effect models indicating the magnitude of influence and the significance (‘***’ 0.001, ‘**’ 0.01, ‘*’ 0.05) of the scaled predictors. Positive values show an increase in the richness/abundance of TreMs or TreM groups. The bold letters indicate the predictor with the greatest influence on the respective TreM group. Romania and silver fir are represented in the intercept.

	Intercept		**DBH**		**Age**		**Region**	
Spruce forest	**z value**	**p**	**z value**	**p**	**z value**	**p**	**z value**	**p**
Abundance	17.602	***	**23.22**	*******	3.225	***	-3.349	***
TreM richness	8.364	***	**12.97**	*******	4.574	***	-2.28	*
Woodpecker cavities	-8.467	***	0.992		1.331		0.185	
Rot holes	-11.562	***	1.023		1.619		0.351	
Insect galleries	-8.787	***	1.678		**3.549**	***	2.871	**
Exudates	-9.798	***	**5.606**	***	-1.302		-3.605	***
Concavities	-4.452	***	**9.663**	*******	-0.362		-1.383	
Exposed sapwood	-11.21	***	0.44		**3.113**	******	1.298	
Exposed sapwood & heartwood	-17.163	***	-0.96		-0.715		0.163	
Crown deadwood	-3.716	***	**5.806**	*******	1.405		-2.359	*
Twig tangles	-2.18	***	0.365		0.184		0.44	
Burrs & cankers	-15.805	***	2.644	**	**3.906**	*******	-1.054	
Perrenial fungi	-8.281	***	1.268		1.81	.	-0.562	
Annual fungi	-8.255	***	**2.357**	*****	0.57		0.299	
Epiphytes	-3.451	***	0.96		-0.879		-1.598	
Nests	-7.325	***	**4.236**	*******	-1.01		0.177	
Microsoils	-12.417	***	**4.409**	*******	1.864	.	-0.141	

	Intercept		DBH		Age		Region		Maple		Beech		Spruce	
Beech forest	**z value**	**p**	**z value**	**p**	**z value**	**p**	**z value**	**p**	**z value**	**p**	**z value**	**p**	**z value**	**p**
Abundance	6.71	***	**30.61**	*******	5.627	***	-1.285		9.412	***	13.612	***	8.701	***
TreM richness	6.979	***	**21.815**	*******	5.747	***	-1.036		6.908	***	7.869	***	3.938	***
Woodpecker cavities	-3.952	***	0.038		0.857		-0.898		1.486		0.195		-0.099	
Rot holes	-13.287	***	3.82	***	1.962	*	-2.636	**	6.653	***	**7.966**	*******	0.125	
Insect galleries	-12.114	***	0.491		1.58		1.404		-0.771		**-2.325**	*****	-0.734	
Exudates	-14.194	***	1.687		-1.673		1.607		-2.494	*	**-6.98**	*******	5.205	***
Concavities	-14.361	***	1.024		**14.188**	*******	-3.088	**	-0.967		9.67	***	8.151	***
Exposed sapwood	-10.635	***	1.034		-1.814	.	1.432		1.781	.	-1.829	.	**-3.371**	*******
Exposed sapwood & heartwood	-12.7	***	**2.544**	*****	-1.929	.	0.808		0.4		3.248	**	0.134	
Crown deadwood	-5.501	***	**5.531**	*******	0.002		0.105		-0.827		-3.916	***	2.342	*
Twig tangles	-5.79	***	0.05		1.395		-1.12		**2.745**	******	0.003		-0.001	
Burrs & cankers	-12.304	***	2.751	**	**5.702**	*******	1.278		3.259	**	3.151	**	1.404	
Perrenial fungi	-10.459	***	1.268		1.81	.	-0.562		0.969		1.026			
Annual fungi	-9.303	***	-0.442		1.233		-2.628	**	2.266	*	**3.347**	***	-0.204	
Epiphytes	-3.653	***	**8.591**	*******	6.598	***	-0.223		4.484	***	-1.663	.	-8.199	***
Nests	-6.009	***	**8.862**	*******	2.063	*	-0.64	***	-0.733		2.589	**	2.706	**
Microsoils	-10.485	***	**11.857**	*******	-0.144		-1.054		2.661	**	5.844	***	3.236	**

Discussion

Based on the comprehensive dataset covering the Western and Southern Carpathian's spruce and beech-dominated primary mountain forests we were able to elucidate the effects of tree diameter, age, and species on the TreM profile. We assessed living habitat trees across >350 plots and used dendrochronological methods to examine tree age, and its importance in TreM occurrence on the respective trees. Tree age played an important role in determining the richness and abundance of TreMs, and its role was specifically important for the richness of concavities, insect galleries, exposed sapwood, burrs and cankers. Tree diameter was recognized as the most important factor for the overall TreM profile, so for the richness of specific TreM groups. Our results further demonstrated that any potential differences between the two separate regions only played a minor role in influencing the TreM profile, while tree species showed a significant effect.

Tree diameter was the most important factor influencing diversity and abundance of TreMs, as well as almost all specific TreM groups. Our results confirmed the previously well-documented trend (Michel and Winter 2009, Winter and Moller 2008, Vuidot et al. 2011, Paillet et al. 2019), that a diverse and abundant TreM profile is linked to larger tree diameters. In addition to the effects of tree diameter, tree age also had a significant effect on TreM profile, but with a lower magnitude. Previously, it was considered that large trees are more prone to biotic and abiotic damage (Bobiec et al.2002, Vuidot et al. 2011) because they generally have longer lifespans and thus longer exposure to damaging elements which can lead to TreM formation (Paillet et al. 2019). However, trees can grow suppressed in the lower parts of the canopy for long time periods with relatively short diameter increments, attaining long lifespans with relatively smaller diameters compared to the trees in the upper parts of the canopy (Issartel & Coiffard 2011). Our results showed that richness of certain TreM groups are exclusively connected to tree age without a significant effect of tree diameter: concavities (beech-dominated forests), insect galleries and exposed sapwood (spruce forests). Higher richness of concavities among older trees in beech-dominated forests is not surprising, since it takes a long time for cavities to develop, especially when one keeps in mind the relatively long time period required for the decomposition of beech wood. The wood quality of beech trees also influences the preferences of woodpeckers, which are more likely to create cavities on individuals infected with heart rot, or on dead trees (Jackson and Jackson 2004, Asbeck et al. in review). In the case of exposed sapwood, TreM types belonging to this group (bark loss, bark shelter, bark pocket, fire scar) are almost exclusively connected to tree injuries. The likelihood of the damage occurring through abiotic or biotic factors rises with time, therefore a higher richness of this TreM group on older trees was of no surprise. On the other hand, large trees have bigger surface area and therefore have a higher chance of being damaged by abiotic factors such as storms, snowfall or rockfall, thus we would expect a higher richness of these TreM groups however, our results do not support this fact.

Broadleaved species (beech and maple) had higher TreM abundance and diversity compared with conifers (spruce and silver fir). These results are consistent with previous observations where broadleaved species showed higher TreM accumulation (Paillet et al 2019, Larrieu et al. 2014, Vuidot et al. 2011). However, this pattern varied for studied TreM groups. For example, richness of rot holes was significantly higher on beech trees and tree species, beech in this case, was the most important factor influencing the richness of this TreM group. Presence of cavities is rare in live conifers (Drapeau et al. 2005) and mostly linked to beech trees (Larrieu and Cabanettes 2012). On the other hand, lower richness among broadleaves than conifers were observed in case of exudates and crown deadwood.

We observed differences between the studied regions as the overall abundance and richness of TreMs in spruce forests was significantly higher in Southern Carpathians than in the Western part of the mountain range. The possible explanation might be the altitude, which was observed as the influential factor of TreM abundance (Asbeck et al. 2019), and so connected differences in precipitation or temperature (Jahed et al. 2020). Interestingly, we observed the distinctive pattern in regional differences between specific TreM groups among the studied forest types. Differences in precipitation patterns may also lead to increased richness of specific TreM groups, such as rot holes, concavities and annual fungi in Southern Carpathians as observed in beech-dominated forests. Increased presence of insect galleries in Western Carpathians, on the other hand, might be connected to bark-beetle outbreaks in the previous decades (Seidl et al. 2020), which may lead to colonization of the tree by other xylophagous insects more likely (Hagge et al. 2019)

It is also important to state here that one of the potential limitations of our study is that the threshold of tree age calculation was set for 20 missing tree rings. Trees with more missing rings, which were excluded from the dataset, have usually rotten heartwood, and can potentially host TreMs such as cavities and rot holes (Zahner et al. 2011).

Conclusions and management implications

Our study highlights the importance of old and large trees in temperate forest ecosystems as essential structures which facilitate the formation of biodiversity habitats. Tree age played a major role in increasing the abundance and richness of certain TreM groups, but our results also highlight the important role of tree diameter for TreM occurrence. These findings not only fill a gap in the current knowledge pertaining to TreM occurrence, but they may also find use in management of the forests where retention of habitat trees is the main objective. In Europe, the current forest landscapes are dominated by commercial forestry therefore, old and large trees have become extremely rare across the European temperate forests (Kraus & Krumm 2013). Considering such a situation, the retention of high diameter trees or fast-growing species might be the suitable management practice in order to reach an abundant and rich TreM profile. However, as our results imply, certain TreMs groups are highly dependent on senescent trees and thus, allowing trees to reach old age is also essential to facilitate the continuation of forest biodiversity. Nonetheless, for a better understanding of the effect of tree age on TreM occurrence further studies from different regions, forest types and under various management intensity are needed.

Acknowledgements

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Supplementary material

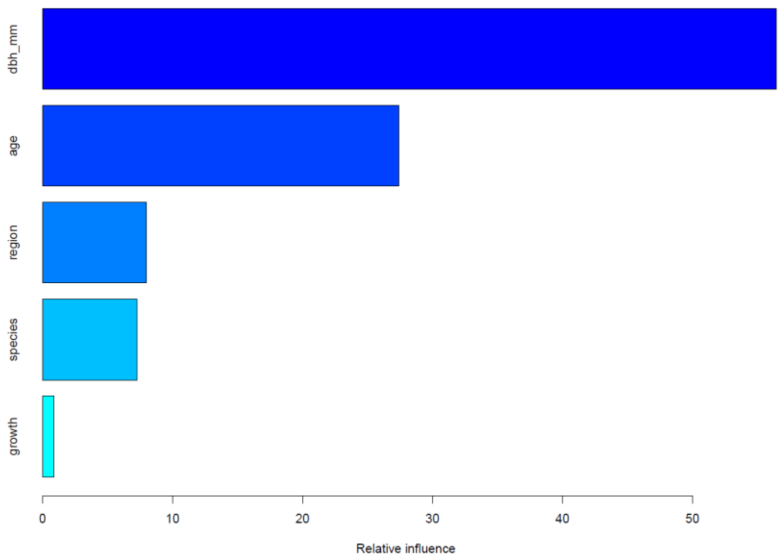

Figure S1. The relative influence of studied variables on TreM richness per tree in beech-dominated forests. (DBH – 56.5%; Age – 27.4%; Region – 8%; Species – 7.2%; Growth – 0.9%)

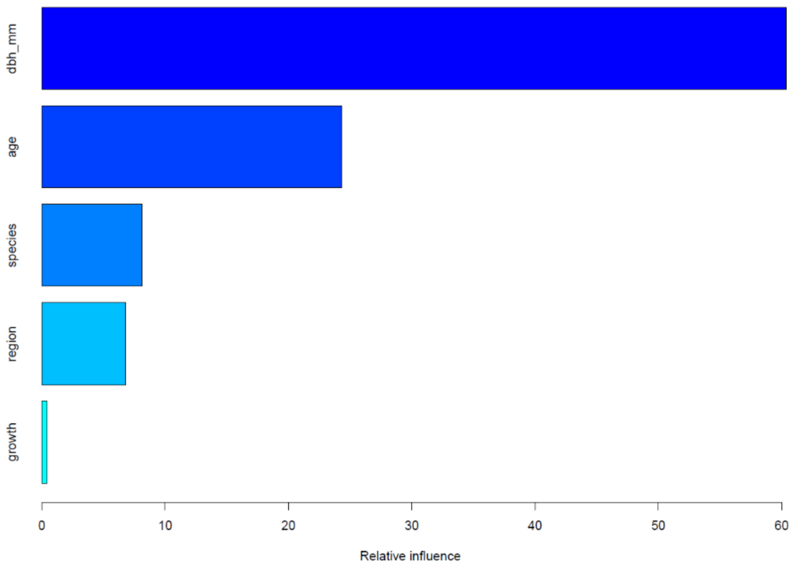

Figure S2. The relative influence of studied variables on TreM abundance per tree in beech-dominated forests. (DBH – 60.4%; Age – 24.3%; Species – 8.1%; Region – 6.8%; Growth – 0.4%)

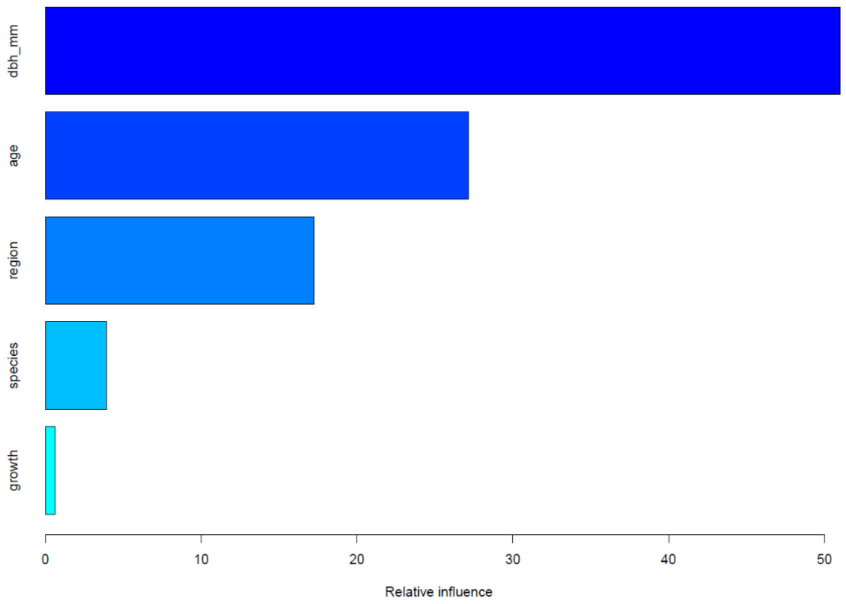

Figure S3. The relative influence of studied variables on TreM richness per tree in spruce forests. (DBH – 51%; Age – 27.2%; Region – 17.3%; Species – 3.9%; Growth – 0.6%)

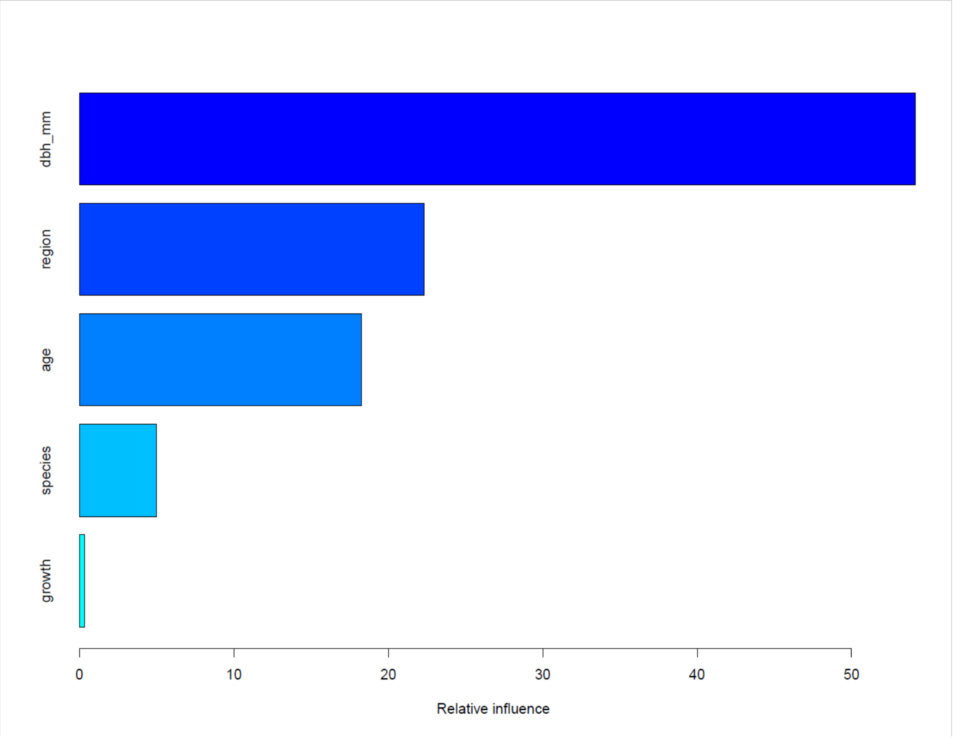

Figure S4. The relative influence of studied variables on TreM abundance per tree in spruce forests. (DBH – 54.1%; Region – 22.3%; Age – 18.3%; Species – 5%; Growth – 0.3%)

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6 Discussion

6.1 Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests

With the use of a comprehensive dataset covering 250 years of disturbance history and associated changes in forest structure, we have expanded the current knowledge about the effect of disturbance regimes on current beetle communities. Disturbances played an important role in determining the diversity of saproxylic beetle communities, with the frequency and time since disturbance as the most important factors. Our results further demonstrate that the dynamics of natural disturbances determine heterogeneity in resources, most importantly deadwood supplies and canopy openness, which positively contributed to the maintenance of diverse beetle assemblages.

We demonstrated that the more recently the disturbance occurred, the more species-rich the current communities of saproxylic beetles were. This effect was observed for the diversity of all beetles, and for conifer specialists separately. The observed pattern might be an effect of higher canopy openness immediately following a disturbance event, as saproxylic beetle communities are often more species-rich in gaps than under a closed canopy (Seibold et al. 2016). Another possibility is that this observation is a transient effect and caused by the higher proportion of fast-developing fresh-wood dwellers present in post-disturbance beetle communities, such as bark beetles and species associated with them (Saint-Germain et al. 2007). Decreasing amounts of nutrients in decaying woody debris decreases the attractiveness of deadwood over time (especially coniferous wood; Saint-Germain et al. 2007) for saproxylic beetles (Kopf & Funke 1998). Similar findings were observed by Winter et al. (2015), with the highest numbers of saproxylic beetles preferring wood of early decay stages in the initial early-seral stage following the availability of fresh deadwood. As observed by Gossner et al. (2016), for *Picea abies*, species richness of saproxylic beetles was highest in the first year of decay followed by a decrease in species richness. Moreover, species richness increased with the severity of the last disturbance, probably as a result of deadwood pool enrichment across disturbed plots.

The severity of the last historical disturbance (events that occurred on average 120 years ago) negatively affected the functional diversity of conifer specialists. This finding might be explained by the post-disturbance development and highlights the need to understand long-term disturbance effects on biological communities. Gaps or patches after a high severity disturbance close between 50 and 100 years of following a disturbance (Svoboda et al. 2014), and as a result, forest stands become more homogenous and the structural elements, for example deadwood, decline. Thus, altered environmental conditions may exclude functionally diverse early and mid-successional species and lead to the co-occurrence of functionally similar species that are adapted to changing habitat conditions (Winter et al. 2017, Thorn et al. 2018a). Our findings agree with the results of Hilmers et al. (2018) which showed a U-shaped response of beetle communities to forest succession.

Predicting the effect of future disturbance regimes on forest diversity, Thom et al. (2017) observed that an increase in disturbance frequency and severity had consistently positive effects on biodiversity. High disturbance severity and increasing disturbance frequency create a complex pattern of open areas, forest edges and remaining closed canopy forests, increasing the variation in environmental conditions (Perry et al. 2011, Lehnert et al. 2013). However, these findings only partially match ours, which could be because Thom et al. (2017) did not specifically focus on spruce-dominated forests. Although the severity of the last disturbance was associated with an increase in species richness for all species, the increases in the maximum detected disturbance severity were related to declines in species richness. The high-severity disturbances cause higher tree mortality which might lead to more homogenous forest structure with limited amounts of forest edges and old-growth structures (Svoboda et al. 2014), making such forest unfavorable for certain beetle species.

We observed a negative impact of disturbance frequency on conifer specialist species richness and diversity. Higher disturbance frequencies generate more gaps that support more diverse tree species, including broad-leaved species, which might cause a decline of conifer specialists as the deadwood pool contains more diverse tree species composition. Environmental changes such as the removal of the overstory forest canopy and the subsequent effect on the light regime may favor some species, while creating suboptimal or intolerable conditions for other species (Swanson et al. 2011): for example, species that prefer shaded deadwood (Lachat et al. 2016). Devictor & Robert (2009) showed that generalist species might benefit strongly from disturbance events while specialists and late-seral species could be affected negatively. Possibly, other drivers not included in our data, such as microclimate, shrub and herb layer vegetation, and fungal occurrence may explain diversity patterns of beetle communities present at the studied plots.

Saproxylic beetle communities are largely reliant on structural characteristics created by natural disturbance. Our results support previous findings that beetle abundance and diversity are associated with heterogeneous and dynamic forests with high amounts of deadwood and canopy gaps (for example, Wermelinger et al. 2002, Müller et al. 2010).

Deadwood is an important component of forest ecosystems, biogeochemical cycles, trophic chains and provides key niches for many species (Vandekerkhove et al. 2009). The total amount of deadwood was the most important structural characteristic, positively influencing the abundance of all studied subgroups. Similarly, Müller et al. (2010) observed a positive response of beetle populations to deadwood amount which was also true for the specialized and red-listed species.

Mean canopy openness positively influenced the phylogenetic diversity of all beetles and conifer specialists. Mountain spruce forests of the Carpathians are characterized by mixed-severity disturbance dynamics (Svoboda et al. 2012, 2014) of wind and bark-beetle origin, which provide periodically large amounts of freshly killed trees with lots of canopy openings and thus might have favored the evolution of species adapted to utilize sun-exposed deadwood (Gossner et al. 2016). Another possibility is that changed light conditions in canopy gaps attract more flower-visiting beetles, and higher temperatures of sun-exposed deadwood allows the emergence of beetles from different phylogenetic lineages.

Amount of deadwood, particularly of large diameter and in a late decay stage, influences the functional composition of saproxylic beetles (Gossner et al. 2013). We observed that functional diversity of all saproxylics and conifer specialists was positively influenced by the diameter of standing deadwood. These findings confirm the importance of high diameter standing deadwood for saproxylic beetles as they can provide diverse habitats for functionally diverse assemblages (Stokland et al. 2012, Larrieu et al. 2012, Martikainen et al. 2000). Moreover, our results support earlier findings which emphasize the positive effect of bark-beetle infestations on saproxylic beetle communities (Müller et al. 2010). Finally, we observed the significant positive influence of TreMs as important habitat for saproxylic beetles (Parisi et al. 2019).

We observed a significant influence of historical disturbance variables on structural characteristics in terms of deadwood volume and canopy openness. Such observation suggests that the effect of historical disturbance regimes on forest structure persists in the form of structural characteristics and may still be visible after several decades or even centuries from the disturbance event. These findings are consistent with the findings of Winter et al. (2015) that structural changes such as reduced canopy cover and high volumes of deadwood after windthrow and bark-beetle outbreak remain high or even higher after multiple decades of succession, suggesting persistence of early-seral heterogeneity into succession.

We found a positive effect of the time since the last disturbance on both total deadwood volume and diameter of standing deadwood, suggesting that trees dying during a disturbance event provide available habitats lasting for several decades, as was observed by Spies & Franklin (1988), or even for a century. The observed increases in total deadwood volume during disturbance-free periods further suggest that decay processes in spruce wood are comparatively gradual, at least relative to decomposition rates in angiosperm-derived substrates (Weedon et al. 2009) and that disturbance impacts on deadwood supply have substantial temporal persistence. In primary forests, post-disturbance succession is frequently influenced by other disturbances of various severities which can continuously replenish the deadwood pool (Hansen et al. 1991). Our results support those findings, since disturbance frequency positively influenced the total deadwood volume and lying deadwood volume. However, mean canopy openness decreased with increasing disturbance frequency and with longer times since disturbance, probably as part of the canopy trees survived frequent disturbance events and partly due to conditions favoring seedling recruitment and growth after disturbance events (Winter et al. 2015b).

Finally, natural disturbance characteristics did not significantly affect the TreM diversity. This supports the findings of Larrieu et al. (2014) that TreM availability remained stable throughout the forest succession, both in terms of their quantity and diversity.

Our studied diversity metrics of current saproxylic beetle communities responded to different disturbance and structural characteristics. Each historical disturbance characteristic influenced at least a part of the current beetle diversity, with frequency and time since the last disturbance event being the most important factors. With respect to saproxylic beetle richness, we observed contrasting effects between maximum disturbance severity (negative) and severity of the last disturbance (positive). Disturbances, habitat fluctuations and changes in environmental conditions cause variations in ecosystem properties and variable responses of different components of biodiversity (Cadotte 2007). Thus, the observed influence of disturbance on current beetle diversity may be caused by beetle species inhabiting temporary niches created by forest succession after a disturbance. Saproxylic beetle communities show pronounced successional changes with ongoing decay of deadwood material (Jonsell 2008) due to changes in the physical structure and nutritional quality of deadwood (Wende et al. 2017).

For instance, the presence of late-successional species often depends upon earlier colonists creating suitable conditions by initiating deadwood decomposition (Jacobsen et al. 2015).

Composition of a saproxylic beetle communities also depends on the ratio of different functional groups such as xylophages, fungivores and predators. For example, xylophages are highly abundant in early successional phases of deadwood colonization, whereas fungivores and predators are commonly present later in the successional food chain (Grove 2002). Thus, the heterogeneous arrangement and decomposition of deadwood resources, both spatially and temporally, might influence taxonomic and functional diversity of the current saproxylic beetle communities.

6.2 Profile of tree-related microhabitats in European primary beech dominated forests

Preserving the diversity of organisms that rely on specific forest structures is a key conservation challenge as forest management intensifies across the globe (Hansen et al. 2013, Mori & Kitagawa 2014). Our assessment of TreM densities in primary forests provides a valuable benchmark for forest managers and policy makers that seek to implement structures that will benefit a host of species of conservation concerns (Vuidot et al. 2011). We performed the first quantitative TreM analyses and comparison of TreM diversity in primary mixed beech-dominated forests in two distinct mountainous regions – the Carpathians and Dinarides. The primary drivers of TreM density (number of trees bearing a particular TreM per hectare) and diversity (richness of TreM types) at the plot scale in these forests were structural characteristics, such as RMS DBH, tree species composition, and the proportion of snags. Geographical distance between regions did not play an important role in TreM densities and diversity, either at the alpha, beta, or gamma levels. Our results highlight that TreM densities observed in the primary forests were significantly higher in comparison to densities presented in studies from managed forests (e.g., Larrieu et al. 2012, Paillet et al. 2017).

We observed a significant increase in total TreMs density and alpha and gamma diversity of TreM types with an increased proportion of snags and tree species richness. Several studies have already observed the importance of snags, large living trees, and different tree species for densities of TreM types (Larrieu & Cabanettes 2012, Larrieu et al. 2014, Vuidot et al. 2011). Tree diameter has also been recognized as an important factor in TreM dynamics across different forest types; it has been observed to influence the abundance of TreMs (Larrieu & Cabanettes 2012), the diversity of TreM types (Larrieu et al. 2014, Vudiot et al. 2011), or the occurrence of some TreM types, such as bark characteristics (Michel & Winter 2009). Large diameter trees were also important in our study, especially for alpha and gamma diversity of TreMs, and densities of some TreM types. We did not find a significant relationship between DBH and total TreM density; most studies that observed a significant relationship between tree diameter and TreM used the DBH of the individual tree bearing the TreM. In contrast, we used RMS DBH of the trees on a plot, which likely introduce noise into the relationship given the mixed severity disturbance regimes of the region, and we also counted only one TreM type on each TreM-bearing tree, which may also further mask any relationship between diameter and density of TreMs. Tree species composition is another factor that has been observed to influence total TreM density and diversity (Larrieu & Cabanettes 2012, Larrieu et al. 2014, Vuidot et al. 2011). Tree species diversity has also been observed to positively influence densities of some specific TreMs, such as broken tops, patches with exudates, and epiphytes. Patches with exudates, such as sap-runs and gummosis, are more likely to be found on deciduous trees (Siitonen, 2012), while the excurrent growth habit of conifers makes them more susceptible to broken tops.

The proportion of snags had a significant effect on TreM diversity at the alpha, beta, and gamma levels, and also on the overall density of TreMs. However, we observed that all TreM types were present within the living trees and snags as well, which may be due to partial mortality, whereby dead wood occurs on living trees, which is characteristic of very large trees (Siitonen, 2012) that can bear TreMs normally present on dead trees in managed forests (e.g., woodpecker feeding holes). Our findings emphasize the importance of snags in broadleaved stands because they promote increased TreM diversity and densities within beech-dominated primary forests. We also observed higher densities of certain TreM types that are rarer on living trees than on snags (woodpecker cavities, conks of fungi, and bark characteristics), which is consistent with the findings of Vuidot et al. (2011) and Larrieu & Cabanettes (2012), whereas the presence of conks of fungi and woodpecker cavities were significantly higher on snags than on living trees (Appendix 3 in Section 5.2). Woodpeckers generally prefer to nest and roost in snags, and fungi play an important role in the excavation of woodpecker cavities (Zahner et al. 2012), and woodpeckers are often suggested as a vector for the fungus (Jackson & Jackson 2004). After the tree dies, the decay process promotes conditions that influence the occurrence of other TreM types, such as bark characteristics and non-woodpecker cavities (Vuidot et al. 2011). Although snags represented only 7-17% of all trees per stand, they accounted for one-third of the density of all TreMs tallied in our study (Table 2 in Section 5.2).

Our results generally agree with prior TreM research conducted in different regions, and it highlights the positive effects of high levels of structural heterogeneity (e.g., large trees, and high tree species richness and proportions of snags) to support a diverse array of TreMs. Finally, our results showed higher densities of TreMs associated with certain taxa compared to published conservation guidelines: a minimum of 40 cavities per hectare for the conservation of cavity dwelling birds (Blondel 2005) or a network of 7-10 live cavity- or crack-bearing trees per hectare for bats (Meschede & Heller 2003). Our data support these findings and demonstrate that primary forests can reach very high TreM levels.

We compared for the first time TreM densities and diversity between primary forests of Carpathian and Dinarides mountain ranges. Although precipitation and temperature differ among the regions (Table 1 in Section 5.2), we did not observe significant differences in total TreM densities or TreM diversity between the regions, including densities of conks of fungi and epiphytes (Table 3 in Section 5.2), which could potentially be influenced by large-scale climatic differences or soil properties (Ding et al. 2016). However, our results suggested significant variability between TreM densities and diversity on relatively small spatial gradients (stand and plot levels). We observed TreM densities almost two times greater than that of Paillet et al. (2017) in strict mixed mountain forest reserves of France (Table 2; Appendix 2 in Section 5.2). They determined that strict forest reserves had higher TreM densities, both total and individual densities, than comparable adjacent managed forests. This general trend has also been observed in several other European forests (Winter & Möller 2008, Winter et al. 2015a). Although Paillet et al. (2017) sampled strict forest reserves, the mean time since any previous harvesting was only 48 years, and it is impossible to identify the structure of the stands at the beginning of the set-aside period or how intensively the stands were managed prior to their strict reserve designation. We analyzed TreMs exclusively from remote primary forests with very limited access, and it is likely that these stands were never managed; some of the oldest trees are more than 450 years old. Compared to the findings of Paillet et al. (2017), we observed the density of broken tops was more than 10 times higher on average, and almost 20 times higher in the Carpathians. The higher densities of broken tops may be attributable to the natural disturbance regime that influences the structural dynamics in primary forests (Meigs et al. 2017), as well as the high proportion of live trees bearing polypores, such as *Fomes fomentarius* or *Fomitopsis pinicola*, which make beech stems more prone to breakage (Zeibig et al. 2005). In addition, taller trees with larger primary branches may be more prone to partial crown loss.

Similar conclusions can be drawn for higher densities of other TreM groups. High volumes and diversity of deadwood, which are typical of primary forests (Nagel et al. 2017), may influence the presence of conks of fungi and even woodpeckers (Jackson and Jackson 2004). We also observed much higher densities of base cavities compared to Paillet et al. (2017); because large cavities take more time to develop, higher rates of occurrence on very old trees would be expected, thus many primary forests would have higher numbers of older trees with longer periods of time since the last severe disturbance (Siitonen 2012). In contrast, we found lower densities of outgrowths and bark characteristics in the Dinaric dataset compared to the French strict forest reserves (Paillet et al. 2017); outgrowths and bark characteristics tend to occur more frequently on oaks (*Quercus* spp.), firs (*Abies* spp.), and spruces (*Picea* spp.) compared to beech (Vuidot et al. 2011). However, higher densities of outgrowths and bark characteristics were found in the Carpathian dataset than in the Dinarides dataset.

6.3 Primary forests provide more tree-related microhabitats than managed ones underlining the need of their conservation

The increasing importance of primary forests as key habitats for the conservation of biodiversity recently inspired silvicultural approaches that emphasize the role of old-growth attributes and natural disturbance legacies in management activities (Keeton 2006; Lindenmayer and others 2006; Bauhus and others 2009; Nagel and others 2014; Thom and others 2019; Čada and others 2020). Our novel approach compared the tree-level TreM richness of primary forests in the Carpathians with managed forests in the Black forest to disentangle the role of management for the provisioning of specific habitats. We consider our data sets comparable, as the latitude included in the models was not the predictor with the greatest magnitude of influence; hence, our results are robust across the inventoried geographic locations. Trees in primary forests hosted a more diverse array of TreMs in terms of overall richness and specific types of TreMs compared to their counterparts in managed forests.

The most prominent result is that we observed higher numbers of TreMs on living trees located in primary forests compared to those in managed ones. Previous studies were not able to extract this information as congruent as we did, for instance Vuidot and others (2011) did not find this difference when comparing managed and unmanaged forests on the tree level. Our findings might be influenced by the time that management is absent as in the mentioned study the unmanaged forests were left without timber extraction for a maximum of 150 years and logged previously. In contrast, we are the first to analyze primary forest plots without any traces of human activities due to difficulty of accessibility.

Conventional forest management creates structurally uniform and highly productive stands with limited longevity of the trees. On the other hand, trees in primary forests often grow slowly, competing with other individuals under the vertically diverse canopy with longevity multiple times higher than the trees in managed stands (Bigler and Veblen 2009; Di Filippo and others 2012). Suboptimal tree growing conditions, such as poor soil conditions or suppression were connected to the formation of certain TreMs, such as cracks, bark lesions and rot holes (Jönsson 2000; Fritz and Heilmann-Clausen 2010). Such conditions are more likely to be found in primary forests because forest management is often avoided on nutrient poor and inaccessible sites. In addition, suppressed trees are systematically removed in most silvicultural practices. In this context, tree senescence is considered to play an important role for the occurrence of TreMs, but so far has only been included in one cross-sectional (Courbaud and others 2017) and one empirical study (Puverel and others 2019). We assume that the abundance and richness of TreMs increases with tree senescence, which might be the main reason for trees in primary forests bearing more TreMs, as they could be older compared to individuals of similar dimensions in managed forests.

Increased richness of specific TreM groups such as crown deadwood, exposed sapwood and heartwood, perennial polypores and insect galleries on primary forest trees implies the importance of natural disturbances for the formation of certain TreMs. The most important natural disturbances in Central and Eastern European mountain forests are wind, bark beetle outbreaks, snow and ice (Nagel and others 2014; Svoboda and others 2014; Janda and others 2017; Kulakowski and others 2017). The importance of effects from large-scale cyclones and convective instabilities on dynamics of these mountain forests has recently been recognized (Pettit and others in review). Wind can cause damage either directly by breaking the stem or limb of a tree, or indirectly through trees damaging each other when breaking or uprooting. Forest management may substitute the role of wind as damage caused during felling operations which could create similar TreMs (Vuidot and others 2011). Such practices may be effective in mimicking the natural creation of TreMs in managed stands (Fritz and Heilmann-Clausen 2010). Besides wind damage, galleries from wood drilling insects resulting from insect outbreaks of various severities are common in primary forests. This group of TreMs is highly unfavorable in managed forests because of its negative impact on timber value combined with imminent large-scale insect outbreaks that hit the Central European region and became more severe recently (Schelhaas and others 2003; Seidl and others 2017). Management practices also tend to remove trees with signs of other timber damaging pathogens, such as fungi. Increased richness of perennial polypores on trees in primary forests is thus not surprising. This removal is not restricted to individuals bearing polypores, but for all trees bearing TreMs that are considered “defects” in forest management. Moreover, the presence of fungi combined with senescence may increase the probability of stem breakage during windstorms, especially in beech trees (Zeibig and others 2005), making it partially responsible for increased richness of exposed sap and heartwood TreMs in primary forests.

We demonstrated a positive effect of tree diameter on overall TreM richness and a consistent effect across the studied TreM groups (except twig tangles). As observed in previously, the diameter of the living trees is an important factor influencing the presence of TreMs across tree species, forest types and environmental conditions (Larrieu and Cabanettes 2012; Kozák and others 2018; Asbeck and others 2019; Paillet and others 2019).

Our results are also in line with observed patterns of increased TreM numbers in broadleaves (Larrieu and Cabanettes 2012; Regnery and others 2013; Paillet and others 2019), as we found the highest overall TreM richness on European beech. Specifically, a higher richness of woodpecker cavities, rot holes and annual fungi was observed on beech trees. Woodpeckers serve as a vector for the fungal infection and often prefer beech trees with rotten heartwood for the excavation of woodpecker cavities (Jackson and Jackson 2004; Zahner and others 2012). Woodpeckers are opportunistic in their choice of suitable trees for cavity establishment (Basile and others 2020b); whenever snags are available in lower quantities, which is the case in managed forests compared to primary ones, they select living trees to excavate their cavities. This is the reason for the non-significant effect of absence of management on woodpecker cavities, as we included only living trees in the analyses. We observed a lower richness of epiphytes in primary forests compared to managed ones and the most important predictor for an increase of this TreM group was an increase in altitude. Similarly, a higher altitude was responsible for increased abundance of epiphytic TreMs (Asbeck and others 2019) and diversity of epiphytes (Ding and others 2016), which is possibly due to an increased precipitation or humidity in higher altitudes.

Uncertainties in our results might be caused by the variation in sampling design, as we selected living trees for the TreM survey based on the size of their crown area in managed forests (Asbeck and others 2019), whereas the primary forest plots did not include only old-growth successional phases but also early seral ones (Kozák and others 2018). However, we included the diameter as predictor in our models and thus took the difference in diameter into account; hence our results should be robust concerning this difference in sampling methods.

6.4 Influence of tree age on tree-related microhabitats abundance and richness: a comparison of mixed-beech and spruce mountain primary forests

Based on the comprehensive dataset covering the Western and Southern Carpathian’s spruce and beech-dominated primary mountain forests we were able to elucidate the effects of tree diameter, age, and species on the TreM profile. We assessed living habitat trees across >350 plots and used dendrochronological methods to examine tree age, and its importance in TreM occurrence on the respective trees. Tree age played an important role in determining the richness and abundance of TreMs, and its role was specifically important for the richness of concavities, insect galleries, exposed sapwood, burrs and cankers. Tree diameter was recognized as the most important factor for the overall TreM profile, so for the richness of specific TreM groups. Our results further demonstrated that any potential differences between the two separate regions only played a minor role in influencing the TreM profile, while tree species showed a significant effect.

Tree diameter was the most important factor influencing diversity and abundance of TreMs, as well as almost all specific TreM groups. Our results confirmed the previously well-documented trend (Michel and Winter 2009, Winter and Moller 2008, Vuidot et al. 2011, Paillet et al. 2019), that a diverse and abundant TreM profile is linked to larger tree diameters. In addition to the effects of tree diameter, tree age also had a significant effect on TreM profile, but with a lower magnitude. Previously, it was considered that large trees are more prone to biotic and abiotic damage (Bobiec et al.2002, Vuidot et al. 2011) because they generally have longer lifespans and thus longer exposure to damaging elements which can lead to TreM formation (Paillet et al. 2019). However, trees can grow suppressed in the lower parts of the canopy for long time periods with relatively short diameter increments, attaining long lifespans with relatively smaller diameters compared to the trees in the upper parts of the canopy (Issartel & Coiffard 2011). Our results showed that richness of certain TreM groups are exclusively connected to tree age without a significant effect of tree diameter: concavities (beech-dominated forests), insect galleries and exposed sapwood (spruce forests). Higher richness of concavities among older trees in beech-dominated forests is not surprising, since it takes a long time for cavities to develop, especially when one keeps in mind the relatively long time period required for the decomposition of beech wood. The wood quality of beech trees also influences the preferences of woodpeckers, which are more likely to create cavities on individuals infected with heart rot, or on dead trees (Jackson and Jackson 2004, Asbeck et al. in review). In the case of exposed sapwood, TreM types belonging to this group (bark loss, bark shelter, bark pocket, fire scar) are almost exclusively connected to tree injuries. The likelihood of the damage occurring through abiotic or biotic factors rises with time, therefore a higher richness of this TreM group on older trees was of no surprise. On the other hand, large trees have bigger surface area and therefore have a higher chance of being damaged by abiotic factors such as storms, snowfall or rockfall, thus we would expect a higher richness of these TreM groups however, our results do not support this fact.

Broadleaved species (beech and maple) had higher TreM abundance and diversity compared with conifers (spruce and silver fir). These results are consistent with previous observations where broadleaved species showed higher TreM accumulation (Paillet et al 2019, Larrieu et al. 2014, Vuidot et al. 2011). However, this pattern varied for studied TreM groups. For example, richness of rot holes was significantly higher on beech trees and tree species, beech in this case, was the most important factor influencing the richness of this TreM group. Presence of cavities is rare in live conifers (Drapeau et al. 2005) and mostly linked to beech trees (Larrieu and Cabanettes 2012). On the other hand, lower richness among broadleaves than conifers were observed in case of exudates and crown deadwood.

We observed differences between the studied regions as the overall abundance and richness of TreMs in spruce forests was significantly higher in Southern Carpathians than in the Western part of the mountain range. The possible explanation might be the altitude, which was observed as the influential factor of TreM abundance (Asbeck et al. 2019), and so connected differences in precipitation or temperature (Jahed et al. 2020). Interestingly, we observed the distinctive pattern in regional differences between specific TreM groups among the studied forest types. Differences in precipitation patterns may also lead to increased richness of specific TreM groups, such as rot holes, concavities and annual fungi in Southern Carpathians as observed in beech-dominated forests. Increased presence of insect galleries in Western Carpathians, on the other hand, might be connected to bark-beetle outbreaks in the previous decades (Seidl et al. 2020), which may lead to colonization of the tree by other xylophagous insects more likely (Hagge et al. 2019)

It is also important to state here that one of the potential limitations of our study is that the threshold of tree age calculation was set for 20 missing tree rings. Trees with more missing rings, which were excluded from the dataset, have usually rotten heartwood, and can potentially host TreMs such as cavities and rot holes (Zahner et al. 2011).

7 Management implications

Based on the results presented in the thesis there are three main points upon which we can imply specific management recommendations: i) the conservation of primary forest remnants and setting aside large enough areas of forests without management, ii) the retention or creation of saproxylic beetle habitats such as deadwood and canopy openings in forests management, and iii) the retention of TreM bearing trees.

Granting strict protection to primary forests should be a conservation priority, because of their important role in maintaining biodiversity. As our results highlight, primary forests can support a higher portion of biodiversity (in terms of TreMs) both on plot and tree level than their managed counterparts. Therefore, strict conservation of remaining primary forests and restoration of natural forests should be a main interest of nature conservation managers (Sabatini et al. 2020). Secondly, such areas should be large enough to be able to maintain suitable habitats in certain areas even when large-scale high severity disturbances occur. Natural disturbances can temporarily alter forest structure making it unsuitable for certain species or communities and thus large-scale protected areas are needed to avoid local extinctions until the suitable conditions occur again. This is clearly shown in our study of saproxylic beetles (Section 5.1), where a decreased richness was found with certain disturbance regimes. Larger areas of intact primary forest should therefore be maintained to enable natural dynamics, such as the minimum size of 500 km^2 set by the concept of intact forest landscapes (Potapov et al. 2017). According to Carbiener (1996), only surface areas of several thousand hectares can harbor all forest developmental phases, including the variability of natural disturbances and the associated fauna.

Our results imply that saproxylic beetle diversity is linked to natural disturbance legacies such as large amounts of lying and standing deadwood (especially those of large diameters), and variable light conditions associated with canopy openings. Current forest management concepts often do not sufficiently consider measures to integrate saproxylic biodiversity protection, maintenance, or enhancement into commercial forest management (Kraus & Krumm 2013). In Europe, many saproxylic species are rare or endangered because of thousands of years of human impacts on forest ecosystems. Intensive forest management approaches applied for timber production represents one of the main threats for saproxylic taxa (Stokland et al. 2012), dramatically reducing the amount and diversity of deadwood. In forests managed for commercial purposes, the maintenance of deadwood in terms of quantity and quality (such as tree species, diameter or decay stage) should be carefully assessed, in order to find a compromise between economic benefit and biodiversity conservation (New 2010). Depending on the forest type, deadwood quantities in managed forest should range from 20 to 50 m^3/ha (with amounts increasing with altitude of the forest stand) to maintain the threshold for the majority of saproxylic species (Kraus & Krumm 2013). However, some species are highly demanding, requiring very high amounts of deadwood (>100 m^3/ha) and such requirements are difficult to meet within forest management practices. In that case, areas such as strict forest reserves, or forests on steep slopes or water catchments where timber extraction is not a main goal, can serve as a refugia and should be equally distributed across the landscape to allow dispersal (Kraus & Krumm 2013). The occurrence of deadwood should also be more evenly distributed on the stand scale, to ensure ecological successions of saproxylic communities. Ideal conditions for saproxylic taxa include complex forest structures, gap occurrence and availability of deadwood (standing or lying) at different stages of wood degradation because these features guarantee optimal ecological conditions for many of them and thus high species richness (Telnov 2002). Management practices that promote deadwood should be organized on large scales as the influence of deadwood on saproxylic species increases with increasing spatial scales. The temporal dimensions should also be considered because the continuity of forest cover and deadwood availability might play a major role in the protection of saproxylic beetles (Kraus & Krumm 2013).

We observed higher TreM densities and richness within the primary forests compared to managed ones, thus the retention of habitat trees should be an essential part of management practices when focusing on increasing biodiversity habitats. Based on the results presented in the thesis, when selecting habitat trees for the retention, large trees are particularly important and should have special attention in forest management. Diameter of the trees was by far the most important factor positively influencing TreM profile on plot level (Table 3, Section 5.2) and on a tree level for overall abundance and diversity of TreMs but also for the majority of the specific TreM types (Table 1 and 2, Section 5.4). Additionally, snags host a more abundant and diverse array of TreMs therefore their retention is preferable over living trees. Besides the rich TreM profile found on the snags, they are important habitats for saproxylic species which can utilize the deadwood substrate. However large living habitat trees with a lot of TreMs are also valuable for retention as the number of TreM will possibly increase throughout the senescence process and after the tree death. Although the economic value of such habitat trees is often lower as they may contain “defects” such as cavities, bark anomalies or heart rot, they are highly valuable for certain forest taxa. Furthermore, when considering the retention of the specific tree species, broadleaves are in general preferable over coniferous species. Yet although our results showed that broadleaved species had a more abundant and diverse TreM profile (see Table 1 and 2 in Section 5.4 but also Table 2 in Section 5.3), the diversity and density of TreMs increased with the number of tree species per plot (Fig. 2, Section 5.2). A similar trend was observed in managed forests (Asbeck et al. 2019) therefore we recommend a mixture of species (with prevalence of broadleaves) left for retention when managing mixed forests. Spruce mountain forests are often naturally monodominant therefore its reasonable that majority of retention trees will include spruce specimens with some portion of broadleaved such as pioneer species (e.g. rowan and birch) or other broadleaves if they are present (e.g. beech or acer). In summary, the retention of large living and dead trees of several tree species appears as an ideal and quite universal way to promote TreMs and enhance potential substrates to support forest biodiversity.

Moreover, forest management should focus on the retention of such habitat trees equally across the different spatial scales (plot, stand and landscape) and ensure connection between forest reserves (Kraus & Krumm 2013) because one must also keep in mind that even if specific TreMs are present, this does not guarantee that they are used if the relevant taxa cannot colonize them (Asbeck et al. 2019).

8 Conclusions

The findings of the presented dissertation thesis contribute to the scientific knowledge on the effects of disturbance regimes and forest structure on saproxylic beetle communities and TreMs in primary mountain forests. Particularly, the thesis provides emphasis on: i) the influence of historical disturbances and forest structure on current saproxylic beetle communities, ii) the characteristics of the TreM profile in primary beech-dominated forests, iii) comparison of TreM richness of primary and managed forests on a tree level, and iv) the effect of tree age, diameter and other tree characteristics on TreM abundance and richness.

We documented that disturbance-created structures promote species-rich communities of saproxylic beetles. Species-rich beetle communities were favored by the structures created by historical disturbances that increase structural heterogeneity, whereas historical disturbances which homogenized the forest environment appeared to have been unfavorable for present-day beetle communities. Present-day forest structure such as the amount and diameter of deadwood and changed light conditions positively influenced the abundance and diversity of beetle communities. However, disturbance regimes and their influence on beetle communities is far from temporally static so the importance of these aspects might change during further successional development. Ongoing climate change will likely increase disturbance frequency and severity in many parts of the world. The presented findings suggest that any potential climate-induced changes in natural disturbance regimes may temporarily impact saproxylic beetle communities, however these changes are highly dependent on post-disturbance successional pathways. Therefore, the timescale and long-term post-disturbance development trajectories may pose a challenge for local conservation planning. The results of this thesis emphasize the importance of setting aside large areas (strictly protected forest landscapes) where a wide range of timing and severity of disturbances can occur and create a heterogeneous environment that can support a full array of biodiversity (Mikoláš et al. 2017, Nagel et al. 2017, Peterken 1996, Watson et al. 2018). When the area on which natural disturbances operate is too small, large-scale disturbances may change the habitat across the entire area of such small protected forests to conditions that are not appropriate for certain species.

We conducted the first assessment of TreMs in beech-dominated primary forests of the Carpathian and Dinaric mountain ranges, with these sites representing some of the last remnants of primary forests in Europe. The results provide an empirical analysis of TreM variability and reference values from these primary forests, both of which will help inform forest managers, conservation strategies, and policy decisions. These reference values provide a means to assess the influence of forest management on the TreM profile. However, the results focus only on a relatively small fraction of these two vast mountain ranges. To improve the understanding of TreM dynamics, we suggest a more thorough survey of primary forest study areas across the Dinaric and Carpathian Mountains, as well as other mountain ranges where similar forest types occur. Other factors, such as climate characteristics or topographical features (for example the presence of cliffs that can increase the occurrence of certain TreMs, such as bark loss by rock falls), or biotic factors, such as woodpecker density or diversity or the presence of large ungulates, may also play important roles in the availability of TreMs. A potentially important driver of TreM density and diversity may be natural disturbance regimes, through their possible role in the creation and maintenance of TreMs. Future research should include the analysis of disturbance history variables in relation to TreMs. In particular, a dendroecological approach could be used to link natural disturbance history with TreM diversity and density, and to assess how forest development influences the distribution of TreMs. To summarize, our results show that primary forests maintain high TreM diversity, and that they may significantly contribute to the overall species diversity across forested landscapes.

We were also able to identify for the first time that the main driver of differences in the richness and occurrence of TreMs between primary and managed forests is the absence of management. Our study suggests that primary forests are essential in providing habitats for forest-dwelling species through a high richness of TreMs. However, many complexes of primary forests are being lost due to poor mapping and the subsequent lack of protection status (Knorn et al. 2013, Sabatini et al. 2018, Mikoláš et al. 2019). This allows salvage logging operations, which can lead to extraction of trees with high potential to bear or develop TreMs, which represent a threat to the ecosystem itself and the function it provides for biodiversity conservation (Thorn et al. 2018b). Hence, our results not only highlight the importance of primary forests for biodiversity conservation, but they also have several implications for forest management. First, the constant removal of trees or parts of trees that show "defects" - such as exposed sap- and heartwood or crown deadwood created by natural disturbances - needs to be decreased to some extent in managed forests to allow the development of these important TreMs as resources. This could be implemented by focusing on the selection and retention of the individuals - such as habitat trees - that provide these obvious and easily identifiable TreMs. Secondly, the increase of beech and other broadleaf species will increase the number of habitats available for forest dwelling species. Overall, we recommend forest and nature conservation managers to focus their approaches on: 1) protecting the remaining primary forests and 2) selecting high-quality habitat trees that already provide a high number of microhabitats in managed forests based on the comparison with primary ones.

This presented study also highlights the importance of old and large trees in temperate forest ecosystems as essential structures which facilitate the formation of biodiversity habitats. Tree age played a major role in increasing the abundance and richness of certain TreM groups, but our results also highlight the important role of tree diameter for TreM occurrence. These findings not only fill a gap in the current knowledge pertaining to TreM occurrence, but they may also find use in management of the forests where retention of habitat trees is the main objective. In Europe, the current forest landscapes are dominated by commercial forestry therefore, old and large trees have become extremely rare across the European temperate forests (Kraus & Krumm 2013). Considering such a situation, the retention of high diameter trees or fast-growing species might be the suitable management practice in order to reach an abundant and rich TreM profile. However, as our results imply, certain TreMs groups are highly dependent on senescent trees and thus, allowing trees to reach old age is also essential to facilitate the continuation of forest biodiversity. Nonetheless, for a better understanding of the effect of tree age on TreM occurrence further studies from different regions, forest types and under various management intensity are needed.

9 Literature

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