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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