142. Jahrgang (2025), Heft 1, S. 61–86

Austrian Journal of Forest Science
Centralblatt für das gesamte Forstwesen

# The occurrence and diversity of tree-related microhabitats in Dinaric mixed beech-fir old growth forest Ravna Vala in Bosnia and Herzegovina

# Vorkommen und Vielfalt von baumbezogenen Mikrohabitaten im dinarischen Buchen-Tannen-Urwald Ravna Vala in Bosnien und Herzegowina

Ćemal Višnjić[1], Besim Balić[1], Mehmed Čilaš[1*], Sead Vojniković[1]

**Keywords:** biodiversity, habitat tree, mixed forest, species diversity

**Schlüsselbegriffe:** Biodiversität, Habitatbaum, Mischwald, Artenvielfalt

## Abstract

The aim of this study was to investigate the influence of tree species characteristics on the occurrence and diversity of tree-related microhabitats in the mixed beech–silver fir Dinaric old-growth forest of Ravna Vala, located on Bjelašnica Mountain. We evaluated microhabitats in living trees of silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* Karst) and sycamore (*Acer pseudoplatanus* L.) with diameters at breast height (dbh) exceeding 40 cm. The microhabitats were systematically recorded using circular concentric plots distributed throughout the forest. Our findings revealed that deciduous tree species support a higher abundance and diversity of microhabitats per living tree compared to coniferous species. Sycamore and beech trees harbored a greater number and variety of microhabitats than silver fir and Norway spruce, consistently exhibiting higher amounts and diversity of microhabitat types per tree. In particular, even sycamore trees in the smaller dbh class (40–60 cm) exhibited microhabitat diversity comparable to larger trees (>80 cm dbh) of other species. These results underscore the significant role of sycamore as an auxiliary species in mixed beech and silver fir forests, which contributes substantially to the occurrence and diversity of microhabitats. Based on these findings, we suggest that forest management

[1] Faculty of Forestry, University of Sarajevo, Sarajevo, Bosnia & Herzegovina
*Corresponding author: Mehmed Čilaš, m.cilas@sfsa.unsa.ba

practices should prioritize the conservation and promotion of deciduous species such as sycamore and beech to enhance the diversity of the microhabitat. Maintaining a heterogeneous forest structure with a mix of species and tree sizes can serve as an effective strategy for biodiversity conservation, using old-growth forests like Ravna Vala as a blueprint for sustainable management.

## Zusammenfassung

Ziel dieser Studie war es, den Einfluss von Baumartenmerkmalen auf das Vorkommen und die Vielfalt von baumbezogenen Mikrohabitaten im dinarischen Buchen-Tannen-Urwald von Ravna Vala auf dem Bjelašnica-Gebirge zu untersuchen. Wir untersuchten die Mikrohabitate an lebenden Bäumen von Weißtanne (*Abies alba* Mill.), Rotbuche (*Fagus sylvatica* L.), Gemeine Fichte (*Picea abies* Karst) und Bergahorn (*Acer pseudoplatanus* L.) mit einem Brusthöhendurchmesser (dbh) von über 40 cm. Die Mikrohabitate wurden systematisch auf konzentrisches Kreißen erfasst. Unsere Ergebnisse zeigen, dass Laubbaumarten im Vergleich zu Nadelbaumarten eine größere Anzahl und Vielfalt an Mikrohabitaten pro lebenden Baum aufweisen. Bergahorn und Buche wiesen eine größere Anzahl und Vielfalt an Mikrohabitaten auf als Weißtanne und Fichte. Bemerkenswert ist, dass selbst Bergahorne der kleineren Durchmesser-Klasse (40-60 cm dbh) eine vergleichbare Vielfalt an Mikrohabitaten aufwiesen wie größere Bäume (>80 cm dbh) anderer Arten. Diese Ergebnisse unterstreichen die bedeutende Rolle des Bergahorns für die Habitatqualität von Buchen-Tannen-Mischwäldern. Unsere Ergebnisse weisen daraufhin, dass bei der Waldbewirtschaftung der Erhaltung und Förderung von Laubbaumarten wie Bergahorn und Buche Vorrang eingeräumt werden sollte, um die Vielfalt der Mikrohabitate zu erhöhen. Die Erhaltung einer heterogenen Waldstruktur mit einer Mischung von Arten und Baumgrößen kann eine wirksame Strategie zur Erhaltung der biologischen Vielfalt sein, wobei Urwälder wie Ravna Vala als Vorbild für eine nachhaltige Bewirtschaftung dienen können.

## 1 Introduction

Forest ecosystems currently cover approximately 31% of Earth's land area, provide habitats for two-thirds of terrestrial species and host 80 to 90% of the world's biodiversity (FAO, 2020; World Bank, 2008). Habitat trees are highly relevant for forest biodiversity, as they harbor many endangered and specialized species of flora and fauna. Habitat trees are defined as living or dead trees standing providing ecological niches (microhabitats) such as cavities, bark pockets, large dead branches, epiphytes, cracks, sap runs, or trunk rot (Großmann *et al*., 2018; Asbeck *et al*., 2022; Hämäläinen *et al*., 2023).

A tree-related microhabitat is typically defined as a distinct, well-delineated structure found on living trees as well as on snags. This structure provides a crucial substrate or life site for specific species or communities, supporting key aspects of their life cycle, such as development, feeding, sheltering, or breeding (Larrieu *et al*., 2018). At least 25% of forest species depend on or benefit from dead wood and habitat trees (Bütler *et al*., 2013). Trees provide shelter and food to many vertebrates, including amphibians, the most endangered class worldwide, even in forest ecosystems (Stuart *et al*., 2004; Wells, 2007).

Specific characteristics of living trees, such as species, age and the presence of microhabitats, determine how species use trees for food, nesting places or as growing substrates (Hämäläinen *et al*., 2023). The relationship between the occurrence of microhabitats and tree attributes across different tree species has been studied to some extent (Winter & Möller, 2008; Vuidot *et al.*, 2011; Larrieu & Cabanettes, 2012; Parisi, 2016; Winter, 2014; Großmann *et al*., 2018). The main factors identified to influence the frequency of microhabitats are the diameter of the tree at breast height (dbh), the species of the tree, the thickness of the bark, the vitality and therefore the age of the tree (Vuidot *et al*., 2011; Larrieu & Cabanettes, 2012; Bütler *et al*., 2013; Großmann *et al*., 2018). The number of microhabitats per tree increases with increasing dbh (Vuidot *et al*., 2011; Regnery *et al.*, 2013; Winter, 2014; Paillet *et al*., 2017; Großmann *et al*., 2018; Asbeck *et al*., 2022).

Stand structure is also essential for biodiversity. In pure, even-aged forests, fewer forest-dwelling species are encountered, while mixed forests with diverse structures and the presence of large trees are associated with a greater number of forest-dwelling species (Scherzinger, 1996; Višnjić *et al*., 2017; Hämäläinen *et al*., 2023). Old-growth structures provide habitats and niches that many forest-dwelling species require (Winter & Brambach, 2011; Asbeck *et al*., 2022). Deciduous trees generally provide more microhabitats than conifers (Vuidot *et al*., 2011; Winter, 2014; Großmann *et al*., 2018). Furthermore, the richness of tree species is essential for the diversity of forest-dwelling species, as many are associated with particular tree species. The specific bark characteristics of tree species are crucial for epiphytes (Ellis, 2012) and bark-dwelling invertebrates (Nicolai, 1986).

Many species throughout the boreal region, particularly epiphytes and cavity nesting birds, are associated with aspens, which provide these taxa with more favorable habitats than the more common coniferous trees (Boudreault *et al.*, 2000; Cadieux & Drapeau, 2017; Kivinen *et al*., 2020; Hämäläinen *et al.*, 2023). However, in most previous studies, the number of microhabitats has been considered in managed forests (Paillet *et al*., 2017; Vuidot *et al*., 2011; Larrieu *et al*., 2018; Großmann *et al*., 2018) and, to a lesser extent, in old-growth forests in the boreal zone (Martin *et al*., 2021; Hämäläinen *et al*., 2023) and temperate old-growth forests (Larrieu *et al*., 2014; Kozak *et al*., 2018; Sever & Nagel, 2019; Asbeck *et al*., 2022).

This study aims to investigate the occurrence and diversity of microhabitats in living trees of four key species: beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* L.) and sycamore (*Acer pseudoplatanus* L.) within the old-growth forest reserve Ravna Vala, located on the Bjelanica mountain. This reserve represents a mixed coniferous and broad-leaved forest typical of the Dinaric region. The forest exhibits a highly heterogeneous structure, where tree species are mixed individually and vary significantly in age, size, and dbh distribution. Multiple canopy layers are present, contributing to the high textural diversity of the forest, along with a significant amount of dead wood standing and lying (Višnjić *et al*., 2015, 2017; Čilaš & Višnjić, 2024). These structural characteristics create a rich environment for microhabitats, making Ravna Vala an ideal location to study the development of natural microhabitats. Bosnia has a long tradition of implementing the single-tree selection system, a silvicultural practice that has contributed to the preservation of natural forests (Čilaš et al., 2023). Ravna Vala, with its structure and species composition, closely resembles these managed forests, making it a valuable baseline for comparative analysis (Čilaš & Višnjić, 2024). By examining the natural occurrence and diversity of microhabitats in this unmanaged, old-growth context, we can gain valuable insights into forest management practices that promote biodiversity conservation. Understanding which tree species favor the development of microhabitats will offer crucial guidelines for future forest management, particularly in identifying species that should be prioritized to enhance biodiversity. This knowledge can inform more effective conservation strategies, particularly in managed forests, ensuring the preservation of vital ecological characteristics while maintaining productive forest ecosystems.

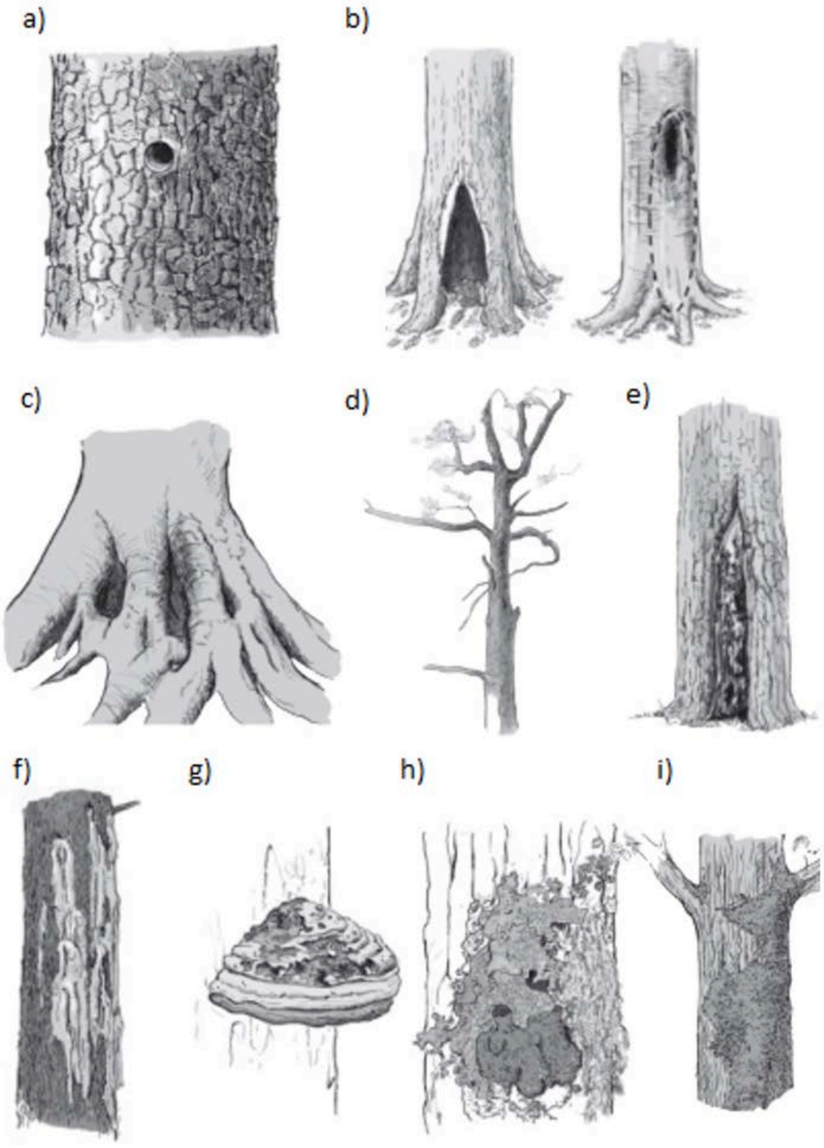


*Figure 1: An example of different types of microhabitat, where: a) woodpacker cavities, b) trunk rot holes, c) root-buttress cavities, d) dead branches, e)cracks, f) resin and sap flows, g) fungal fruiting bodies, h) epiphytic lichens, i) bryophytes (examples taken from Larrieu et al. 2018).*

Abbildung 1: Ein Beispiel für verschiedene Mikrohabitattypen: a) Spechthöhlen, b) Stammfäulnislöcher, c) Wurzelanlaufhöhlen, d) tote Äste, e) Risse, f) Harz- und Saftfluss, g) Pilzfruchtkörper, h) epiphytische Flechten, i) Moose (Beispiele stammen aus Larrieu et al. 2018).

## 2 Materials and methods

### 2.1 Study area

The study was carried out in the Ravna Vala old growth forest, located approximately 25 km southwest of Sarajevo, Bosnia and Herzegovina (Figure 2). Covering an area of 45 hectares, the forest reserve is anchored by a parent substrate predominantly composed of limestone, dolomite, and moraine deposits. These geological features facilitate the development of diverse mosaic soils characterized by rendzinas, calcomelanosols, and calcocambisols (Višnjić *et al*., 2015). The regional climate, characterized as continental with significant mountain influence (Beus & Vojniković, 2002), exhibits an average annual temperature of 6 ° C and an annual precipitation sum of 1600 mm. The elevation of the mountain range where our study is located ranged from 1400 to 1600 m. It is a typical uneven-aged mountain Dinaric mixed forest dominated by European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) with sporadic occurrence of Norway spruce (*Picea abies*) and sycamore (*Acer pseudoplatanus*). It represents a typical *Abieti* - F*agetum Illyricum* community (Fukarek & Stefanović, 1958). Interestingly, there is a conspicuous absence of signs for historic management interventions in this forest. The characteristics of structural and tree species, texture, dead wood, and diversity of vascular plants, lichens, and bryophytes in old-growth forest were described by many authors (Beus & Vojniković, 2002; Weckesser & Visnjic, 2005; Vojniković *et al*., 2006; Višnjić *et al*., 2015, 2017, Čilaš and Višnjić, 2024).

*Table 1: Stand information based on sample points per hectare, Nha is average number of trees per ha, BA is basal area, and share in BA is basal area proportion.*

Tabelle 1: Bestandsinformationen auf der Grundlage der Stichprobenpunkte pro Hektar, Nha ist die durchschnittliche Anzahl der Bäume pro Hektar, BA ist die Grundfläche, and der share in BA is der Anteil an der Grundfläche.

| Tree species | dbh class | | | | | | | | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 40-60 | | | 60-80 | | | >80 | | | | |
| | $N_{ha}$ | BA ($m^2$/ha) | share in BA / ha (%) | $N_{ha}$ | BA ($m^2$/ha) | share in BA / ha (%) | $N_{ha}$ | BA ($m^2$/ha) | share in BA / ha (%) | BA ($m^2$/ha) | share in BA / ha (%) |
| Beech | 31 | 5.94 | 21.77 | 9 | 3.32 | 12.17 | 2 | 1.56 | 5.70 | 10.8 | 39.7 |
| Fir | 32 | 5.73 | 20.99 | 9 | 3.15 | 11.55 | 4 | 2.89 | 10.61 | 11.8 | 43.2 |
| Spruce | 4 | 0.71 | 2.62 | 3 | 0.99 | 3.64 | 1 | 0.82 | 3 | 2.53 | 9.27 |
| Sycamore | 3 | 0.69 | 2.52 | 2 | 0.84 | 3.09 | 1 | 0.63 | 2.3 | 2.16 | 7.92 |
| All | 71 | 13.1 | 47.9 | 23 | 8.3 | 30.5 | 9 | 5.9 | 21.6 | 27.29 | 100 |

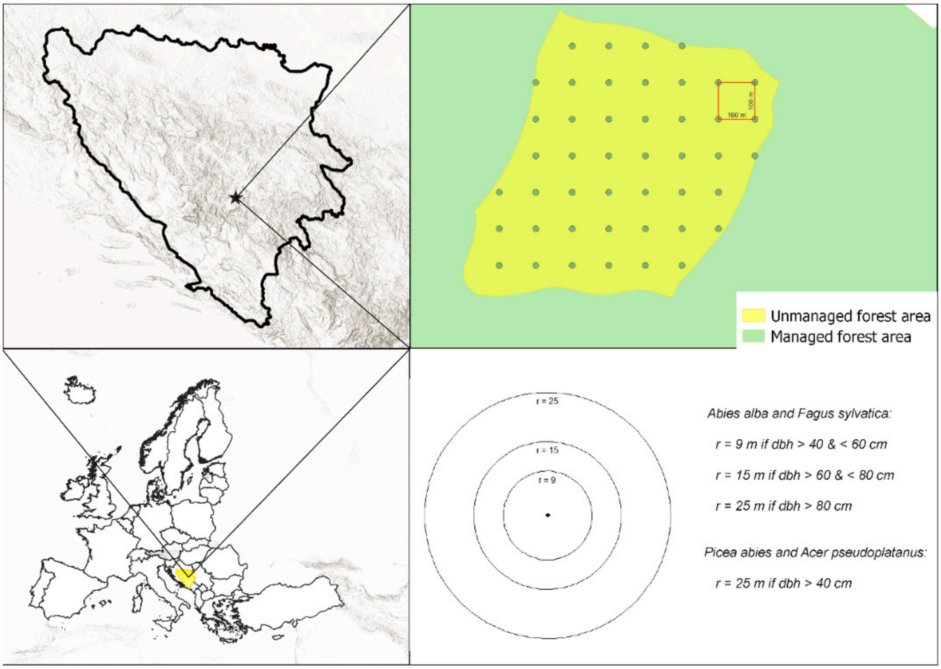


*Figure 2: Map of the study area and sample design layout within the old-growth forest of Ravna Vala, Bosnia and Herzegovina.*

Abbildung 2: Karte des Untersuchungsgebiets und Anordnung der Probenahme im Urwald von Ravna Vala, Bosnien und Herzegovina.

## 2.2 Sample Design and Data Collection

The presence of microhabitats was determined on living trees of silver fir, beech, Norway spruce and sycamore, with a diameter at breast height (dbh) greater than 40 cm. A systematic sampling approach was employed by establishing a 100 × 100 m grid across the forest, with circular experimental plots placed at grid intersections. For silver fir and beech trees, microhabitats were assessed using concentric circular plots of varying radii: trees with a dbh of 40–60 cm were examined within plots of 9 m radius; those with a dbh of 60.1–80 cm within plots of 15 m radius; and trees with a dbh exceeding 80.1 cm within plots of 25 m radius. In contrast, for Norway spruce and sycamore, we used circular plots with a fixed radius of 25 m to assess microhabitats. In total, 45 plots were established (Figure 2). This variation in the sampling approach was due to the lower abundance of Norway spruce and sycamore in the old-growth forest, which required larger plots to include sufficient numbers of these species. For each tree, we measured the dbh and recorded microhabitats using the field guide by Larrieu *et al.* (2018) for identification. To mitigate potential observer bias (Paillet *et al.*, 2015), the inventory was conducted by a single individual during the fall of 2023. This timing was chosen after vegetation had subsided, making microhabitats in the crown more visible. For taller trees, binoculars were used, with an average observation time of approximately 10 minutes per tree. The microhabitats were grouped into nine types: woodpecker cavities (all sizes), trunk rot holes (trunk base rot hole, trunk rot hole, semi-open trunk rot hole, chimney trunk base rot hole, chimney trunk rot hole, hollow brunch), root-buttress cavities (dendrotelm, root-buttress cavities, trunk bark-lined concavity), dead branches (crown deadwood), cracks (stem breakage, limb breakage, fork split, lighting scar cracks), resin and sap flows, fungal fruiting bodies, epiphytic lichens, and bryophytes. Microsoils, nests, and excrescences were not considered in this study. An example of microhabitats is shown in Figure 1. For countable microhabitats (*e.g.* woodpecker cavities, trunk rot holes), the number of occurrences was recorded. The presence and distribution of epiphytic lichens and bryophytes were recorded on a scale of 0 to 4, where 0 indicated absence, and the numbers 1 to 4 reflected their vertical distribution in the tree:

1 - present at the base;
2 - present up to half of the tree height;
3 - present up to two thirds of the tree height; and
4 - present in the entire tree.

An overview of the sampled trees is given in Table 2.

*Table 2: Overview of trees analyzed, where dbh is diameter at breast height, N is the number of trees, the share in BA represents the percentage share of trees in the basal area, and Nz represents the number of trees without a microhabitat.*

Tabelle 2: Übersicht über die untersuchten Bäume, wobei dbh der Brusthöhendurchmesser, N die Anzahl der Bäume, Anteil an BA der prozentuale Anteil der Bäume an der Grundfläche, and Nz die Anzahl der Bäume ohne Mikrohabitat ist.

| Tree species | dbh class | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 40-60 | | | | 60-80 | | | | >80 | | | |
| | dbh (cm) | N | share in BA (%) | Nz | dbh (cm) | N | share in BA (%) | Nz | dbh (cm) | N | Share in BA (%) | Nz |
| Beech | 48 ± 6 | 36 | 5.93 | 0 | 66±5 | 30 | 9.21 | 0 | 90±10 | 21 | 11.98 | 0 |
| Fir | 47 ± 5 | 37 | 5.72 | 0 | 67±5 | 28 | 8.74 | 0 | 96±16 | 34 | 22.3 | 0 |
| Spruce | 49 ±6 | 33 | 5.51 | 0 | 68±5 | 24 | 7.65 | 0 | 84±4 | 13 | 6.31 | 0 |
| Sycamore | 50±6 | 30 | 5.3 | 0 | 67±6 | 21 | 6.5 | 0 | 84±3 | 10 | 4.84 | 0 |
| All | 49 ± 6 | 136 | 22.5 | 0 | 67 ± 5 | 103 | 32.1 | 0 | 91 ± 13 | 78 | 52.1 | 0 |

### 2.3 Data analysis

Following field data collection, all recorded observations were transferred to an Excel database, where systematic, logical checks were performed to ensure data integrity. The data set was subsequently organized by tree species (*i.e.*, beech, silver fir, Norway spruce, sycamore maple) and classified according to the corresponding diameter classes (40 to 60 cm, 60 to 80 cm and over 80 cm). The influence of two independent variables (tree species and dbh) on the frequency of occurrence of tree-related microhabitats and the diversity of the microhabitats was analyzed. Analysis of variance was used to determine statistically significant differences in the frequency of occurrence of microhabitats between individual tree species, and the Tukey HSD test was used to test differences.

Microhabitat diversity for each tree was calculated employing the Shannon diversity index formula, Eq. 1 (Shannon, C.E. 1948).

$$H' = -\sum_{\bar{\iota}=1}^{S} p_{\bar{\iota}} \ln p_{\bar{\iota}} = -\sum_{\bar{\iota}=1}^{S} \left[\frac{n_{\bar{\iota}}}{N} \cdot \ln\left(\frac{n_{\bar{\iota}}}{N}\right)\right] \qquad (1)$$

The numbers were S - the number of different types of microhabitats, pi - the contribution of individual habitats to the total sum of microhabitats, ni - the number of one type of microhabitat on a single tree, N - the sum of different types of all inventoried microhabitats on a single tree.

Furthermore, the influence of tree species and dbh on microhabitat diversity was examined using ANOVA, followed by Tukey HSD test for a comprehensive assessment. For all tests, significance was considered when the associated critical value (p) was less than 0.05.

Regression analyzes were used to determine the relationship between the diameters of the trees of different species, the frequencies of occurrence of microhabitats, and the diversity of the microhabitat. The calculations and statistical analysis were performed in R (R Core Team, 2022).

## 3 Results

### 3.1 The occurrence of different types of microhabitats

This study indicates that all trees with a dbh greater than 40 cm harbored at least one type of microhabitat, regardless of species. However, the occurrence and type of microhabitats varied between tree species (Table 3). Beech trees predominantly harbored cavities (mean occurrence of 1.97), lichens (2.15), and fungal fruiting bodies

(0.19). In contrast, sycamore trees exhibited a higher prevalence of bryophyte species (3.89). Norway spruce trees showed a notable abundance of dead branches (1.73) and fresh exudates (0.19), while silver fir trees had a significant occurrence of trunk cracks (0.92).

*Table 3: The average number of microhabitat types per tree species. Homogeneous groups within each microhabitat type are indicated by letters (a, b, c, and d) based on Tukey's HSD test results.*

Tabelle 3: Die durchschnittliche Anzahl der Mikrohabitattypen nach Baumarten. Homogene Gruppen innerhalb jedes Mikrohabitattyps sind durch Buchstaben (a, b, c, d) auf der Grundlage der Ergebnisse des Tukey-HSD-Tests gekennzeichnet.

| Tree species | Cavities | Trunk cracks | Dead branches | Fungal Fruiting Body | Bryophytes | Lichens | Fresh exudates |
|---|---|---|---|---|---|---|---|
| Beech | $1.97^{a}$ | $0.26^{a}$ | $1.31^{ab}$ | $0.19^{a}$ | $1.44^{a}$ | $2.15^{a}$ | $0.05^{b}$ |
| Fir | $1.49^{a}$ | $0.92^{c}$ | $1.5^{b}$ | $0.06^{a}$ | $1.92^{b}$ | $2.11^{a}$ | $0.02^{b}$ |
| Spruce | $0.54^{b}$ | $0.34^{bc}$ | $1.73^{a}$ | $0.06^{a}$ | $0.89^{c}$ | $1.27^{b}$ | $0.19^{a}$ |
| Sycamore | $1.50^{a}$ | $0.68^{ab}$ | $1.53^{ab}$ | $0.14^{a}$ | $3.89^{d}$ | $1.47^{b}$ | $0^{b}$ |

Across all species, fungal fruiting bodies were relatively infrequent, whereas bryophytes and lichens were the most common microhabitats in living trees. Analysis of the frequency of microhabitats across different tree species showed some variations. Sycamore and beech exhibited the highest average number of different microhabitat types (4.3), followed by silver fir (4.2) and Norway spruce (3.6). Similar values were observed when considering the average number of microhabitats per tree, sycamore showing the highest average (9.2), followed by beech (8.0), silver fir (7.2), and Norway spruce (5.0).

The results of Tukey's Honest Significant Difference (HSD) test revealed distinct patterns in the distribution of microhabitat types among the studied tree species. There was no significant difference in the occurrence of different types of microhabitats or in the total number of microhabitats between beech and sycamore. In contrast, significant differences were found between Norway spruce and beech and sycamore. The microhabitat occurrences and total numbers for silver fir did not significantly differ from those of either the beech and sycamore group or the Norway spruce group, as indicated by the homogeneous groups in Tukey's HSD test.

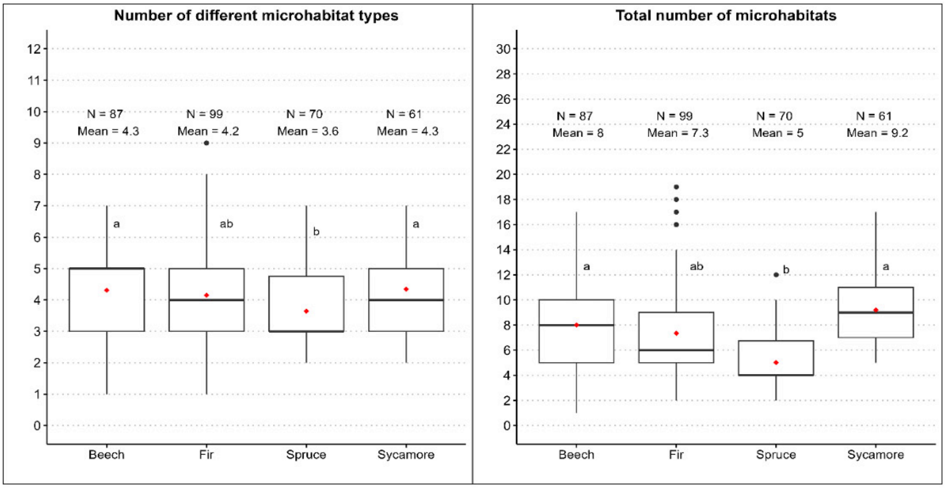


*Figure 3: Number of different types of microhabitat and total microhabitat counts per tree species, with corresponding homogeneous groups. N represents the number of trees analyzed and red dots the mean value.*

Abbildung 3: Anzahl der verschiedenen Mikrohabitattypen und Gesamtzahl der Mikrohabitate pro Baumart, mit den entsprechenden homogenen Gruppen. N steht für die Anzahl der untersuchten Bäume und die roten Punkte für den Mittelwert.

## 3.2 The Influence of tree diameter on number and occurrence of microhabitats

The results revealed a consistent increase in the average number of microhabitats per tree with increasing dbh in all tree species. A significant correlation was observed between the dbh classes and the average number of microhabitats per tree and the average number of different types per tree for all tree species ($p < 0.05$) (Table 4). Specifically, for Norway spruce, silver fir, and sycamore, the average number of microhabitats exhibited a gradual increase from diameter classes of 40-60 cm to 60-80 cm, followed by an increase in trees larger than 80 cm. For all tree species, significant differences were found between the dbh classes except beech, where no significant differences were found between the dbh class 60-80 and >80 (Figure 4).

The Tukeys HSD test reveals a clear pattern of the occurrence of different types of microhabitats when tested on all tree species and dbh classes (Table 5). Trees within identical dbh categories were predominantly aggregated into singular homogeneous groups based on Tukey's HSD test; however, exceptions were noted; for example, sycamore and silver fir trees in the >80 cm DBH class did not conform to this pattern. Additionally, a transitional grouping phenomenon was identified, exemplified by Norway spruce trees in the 60-80 cm dbh range exhibiting similarities to sycamore and beech trees within the 40-60 cm dbh interval.

*Table 4: Summary of different microhabitat types for each tree species, categorized by dbh class, along with the corresponding homogeneous groups across all tree species and dbh classes. N represents the number of trees analyzed, mean refers to the average number of different types of microhabitat per tree, and SD indicates the standard deviation.*

Tabelle 4: Zusammenfassung der verschiedenen Mikrohabitattypen für jede Baumart, kategorisiert nach dbh-Klasse, zusammen mit den entsprechenden homogenen Gruppen über alle Baumarten und dbh-Klassen. N steht für die Anzahl der untersuchten Bäume, der Mittelwert bezieht sich auf die durchschnittliche Anzahl der verschiedenen Mikrohabitattypen pro Baum, und SD bezeichnet die Standardabweichung.

| Tree species | dbh class | N | mean | SD | Tukeys HSD groups | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sycamore | > 80 | 10 | 5.9 | 0.74 | a | b | | | | | |
| Fir | > 80 | 34 | 5.74 | 1.42 | a | | | | | | |
| Beech | > 80 | 21 | 5.38 | 0.74 | a | b | | | | | |
| Spruce | > 80 | 13 | 5 | 1 | a | b | c | | | | |
| Beech | 60-80 | 30 | 4.8 | 0.81 | | b | c | | | | |
| Sycamore | 60-80 | 21 | 4.76 | 1.09 | | b | c | | | | |
| Fir | 60-80 | 28 | 4.25 | 0.93 | | | c | d | | | |
| Spruce | 60-80 | 24 | 3.92 | 1.21 | | | c | d | e | | |
| Sycamore | 40-60 | 30 | 3.53 | 0.82 | | | | d | e | f | |
| Beech | 40-60 | 36 | 3.28 | 1.23 | | | | | e | f | g |
| Spruce | 40-60 | 33 | 2.91 | 0.95 | | | | | | f | g |
| Fir | 40-60 | 37 | 2.62 | 0.68 | | | | | | | g |

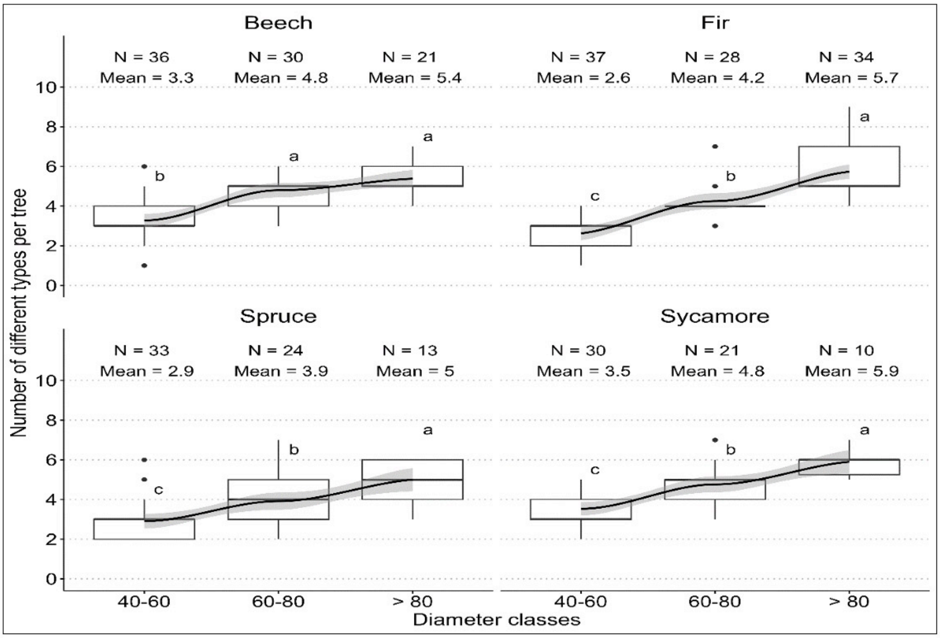


*Figure 4: The average number of different types of microhabitat for each dbh class, categorized by tree species, with corresponding homogeneous groups. N represents the number of trees analyzed and the mean indicates the average occurrence of different microhabitat types per tree.*

Abbildung 4: Durchschnittliche Anzahl der verschiedenen Mikrohabitattypen für jede dbh-Klasse, kategorisiert nach Baumarten, mit entsprechenden homogenen Gruppen. N steht für die Anzahl der untersuchten Bäume, und der Mittelwert gibt das durchschnittliche Vorkommen der verschiedenen Mikrohabitattypen pro Baum an.

A significant increase in the number of microhabitats for beech was observed from 40 to 80 cm in diameter, followed by gradual saturation beyond 80 cm. In the largest diameter classes (>80 cm), the mean number of microhabitats per tree was 13.4 for sycamore, 11.8 for beech, 11.0 for silver fir, and 7.6 for Norway spruce. For all tree species, a trend of increasing numbers was evident in microhabitat types with dbh, although the rate of increase is slower and follows an almost linear pattern. In particular, beech trees exhibit a slightly slower increase in microhabitats above 80 cm dbh compared to other tree species. The total number of microhabitats differs statistically between the dbh classes for all tree species (Figure 5). The analysis employing Tukey's HSD test indicates a pattern in the total number of microhabitats that is similar to that of microhabitat types, but with notable exceptions. For example, sycamore trees within the 40-60 cm dbh class are aggregated with other tree species within the higher 60-80 cm dbh class. On the contrary, Norway spruce trees are associated with tree species in lower dbh classes (Table 5).

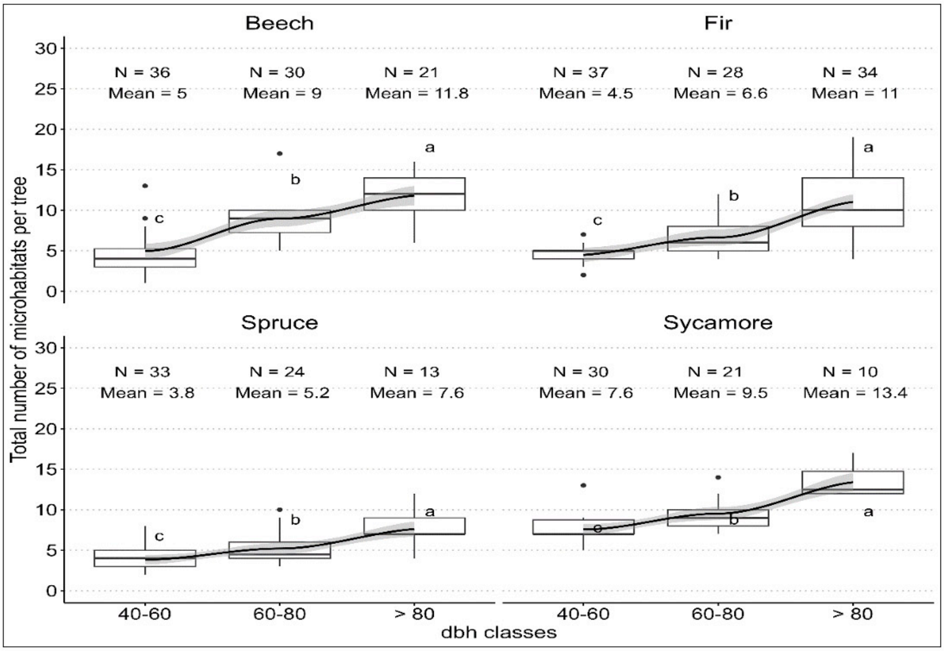


*Figure 5: Total number of microhabitats per tree across different dbh classes, classified by tree species, with corresponding homogeneous groups. N represents the number of trees analyzed and the mean indicates the average occurrence of microhabitats per tree.*

Abbildung 5: Gesamtzahl der Mikrohabitate pro Baum in verschiedenen dbh-Klassen, kategorisiert nach Baumarten, mit entsprechenden homogenen Gruppen. N steht für die Anzahl der untersuchten Bäume, und der Mittelwert gibt das durchschnittliche Vorkommen von Mikrohabitaten pro Baum an.

*Table 5: Summary of the total number of microhabitats per tree species, categorized by dbh class, along with the corresponding homogeneous groups across all tree species and dbh classes. N represents the total number of trees analyzed, mean refers to the average number of microhabitats per tree, and SD indicates the standard deviation.*

Tabelle 5: Zusammenfassung der Gesamtzahl der Mikrohabitate pro Baumart, kategorisiert nach dbh-Klasse, zusammen mit den entsprechenden homogenen Gruppen über alle Baumarten und dbh-Klassen. N steht für die Gesamtzahl der analysierten Bäume, der Mittelwert bezieht sich auf die durchschnittliche Anzahl der Mikrohabitate pro Baum, und SD bezeichnet die Standardabweichung.

| Tree species | dbh class | N | mean | SD | Tukeys HSD groups | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sycamore | > 80 | 10 | 13.4 | 1.78 | a | | | | | | |
| Beech | > 80 | 21 | 11.81 | 2.99 | a | b | | | | | |
| Fir | > 80 | 34 | 11.03 | 3.97 | a | b | | | | | |
| Sycamore | 60-80 | 21 | 9.52 | 1.6 | | b | c | | | | |
| Beech | 60-80 | 30 | 8.97 | 2.53 | | | c | | | | |
| Spruce | > 80 | 13 | 7.62 | 1.98 | | | c | d | e | | |
| Sycamore | 40-60 | 30 | 7.57 | 1.94 | | | c | d | | | |
| Fir | 60-80 | 28 | 6.64 | 2.06 | | | | d | e | f | |
| Spruce | 60-80 | 24 | 5.21 | 1.84 | | | | | e | f | g |
| Beech | 40-60 | 36 | 4.97 | 2.83 | | | | | | f | g |
| Fir | 40-60 | 37 | 4.49 | 1.24 | | | | | | | g |
| Spruce | 40-60 | 33 | 3.85 | 1.39 | | | | | | | g |

### 3.3 Microhabitat diversity

The diversity of microhabitats per tree varied between tree species. Beech exhibited the highest average diversity of microhabitats (1.3), followed by sycamore (1.3), Norway spruce (1.2), and silver fir (1.2). (Figure 6). According to the results of the Tukey HSD test, no statistically significant differences were observed between all tree species across all dbh classes. Different patterns in microhabitat diversity were observed in different diameter classes for each tree species (Figure 7). For beech, the diversity index increased from 1.05 (±0.05) in the 60-80 cm dbh class to 1.47 (±0.05) at 80 cm, with a slower increase afterward to 1.55 (±0.06) for trees above 80 cm. Similarly, silver fir exhibited an increase from 0.81 (±0.05) in the 40-60 cm dbh class to 1.38 (±0.05) at 60-80 cm, with a slight increase to 1.49 (±0.05) for trees above 80 cm. Sycamore showed an increase of 1.08 (±0.05) in the 40-60 cm dbh class to 1.36 (±0.06) at 60-80 cm, followed by a slower increase of 1.50 (±0.09) for trees greater than 80 cm. In contrast, Norway spruce exhibited a consistent increase, with diversity indices of 0.99 (±0.49) in the 40-60 cm dbh class, 1.26 (±0.06) at 60-80 cm, and 1.53 (±0.08) for trees greater than 80 cm. For beech and silver fir, there were no significant differences between dbh classes 60- 80 and >80, where for sycamore and Norway spruce, the differences between all dbh classes were statistically significant.

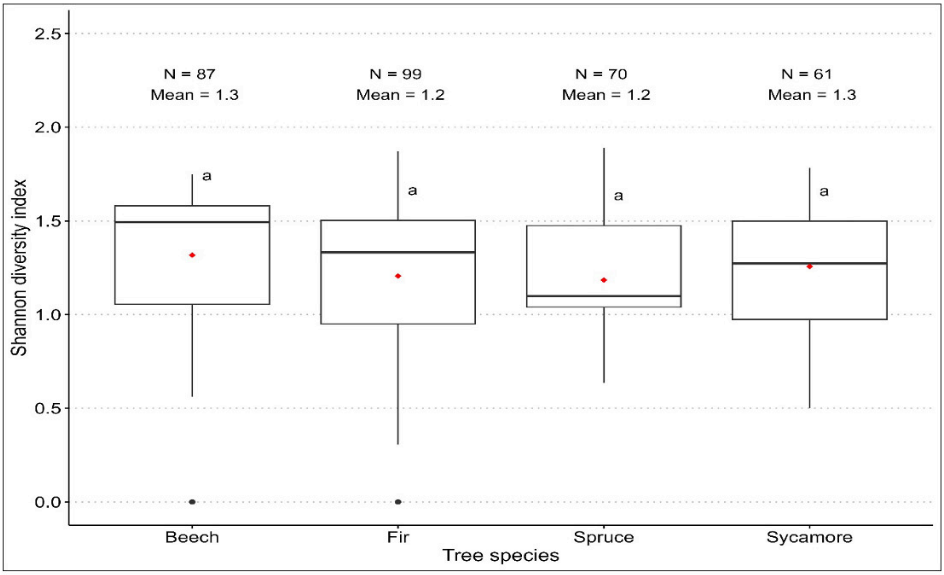


*Figure 6: Average diversity of microhabitats per tree species, with the corresponding homogeneous groups. N represents the number of analyzed trees, and mean indicates the mean value of the Shannon diversity index.*

Abbildung 6: Durchschnittliche Vielfalt der Mikrohabitate pro Baumart, mit entsprechenden homogenen Gruppen. N steht für die Anzahl der untersuchten Bäume, und der Mittelwert gibt den Mittelwert des Shannon-Diversitätsindex an.

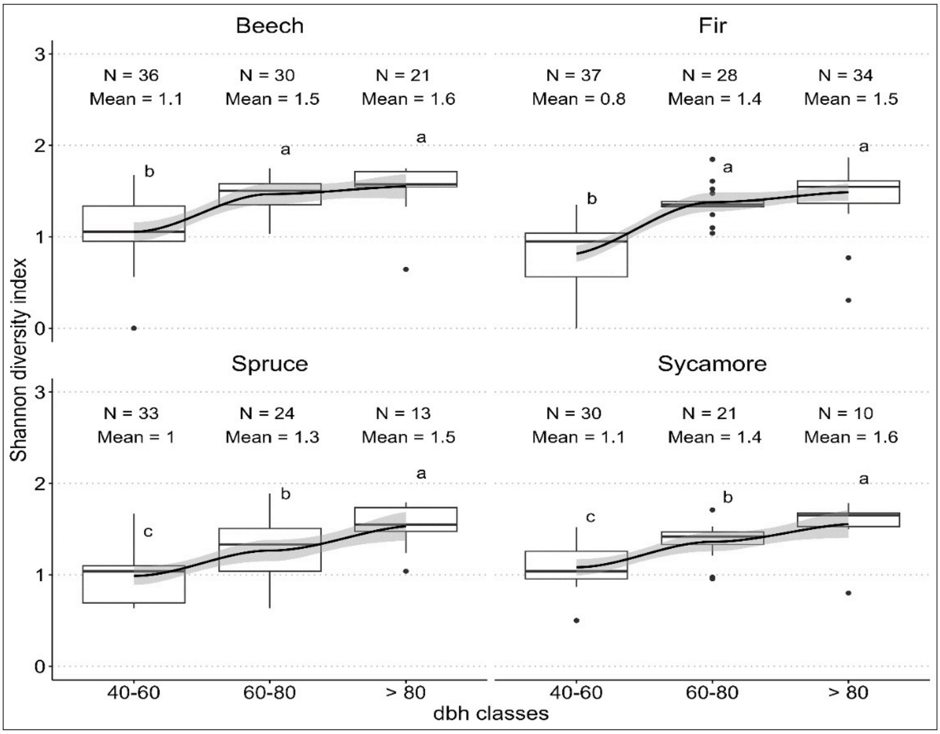


*Figure 7: Average diversity of microhabitats for each dbh class, categorized by tree species, with corresponding homogeneous groups. N represents the number of trees analyzed and the mean indicates the mean value of the Shannon diversity index.*

Abbildung 7: Durchschnittliche Vielfalt der Mikrohabitate für jede dbh-Klasse, aufgeschlüsselt nach Baumarten, mit entsprechenden homogenen Gruppen. N steht für die Anzahl der untersuchten Bäume, und der Mittelwert gibt den Mittelwert des Shannon-Diversitätsindex an.

# 4 Discussion

## 4.1 Importance of tree species on the occurrence of microhabitat types

The importance of tree-related microhabitats as crucial elements of forest biodiversity has led to numerous studies in both primary and managed forests throughout Europe. Generally, these studies have focused on the influence of two main drivers - tree species and diameter at breast height (dbh) - on the number and occurrence of microhabitat types (Vuidot *et al*., 2011; Larrieu & Cabanettes, 2012; Regnery *et al*., 2013; Paillet *et al*., 2019; Großmann *et al*., 2019; Sever & Nagel, 2019; Asbeck *et al*., 2021, 2022). The results consistently suggest that tree species are determining factors of microhabitat abundance and richness. The dbh emerges as a prominent determinant of the occurrence of tree-related microhabitats in various studies (Bütler *et al*., 2013; Larrieu *et al*., 2014; Großmann *et al*., 2019; Asbeck, 2021). Larger trees tend to harbor higher abundance and diversity of microhabitats, regardless of species (Asbeck *et al*., 2022; Großmann *et al*., 2019; Jahed *et al*., 2020; Paillet *et al*., 2019).

Our study observed that the diversity of tree species within the forest significantly influences the presence and abundance of various microhabitats. Each species showed a preference for a specific type of microhabitat. Our findings reveal that the most prevalent types of microhabitats in live trees were epiphytes (lichens and mosses), cavities (woodpecker cavities and rot holes), and dead branches. On the contrary, fungal fruiting bodies, trunk cracks, and fresh exudates were observed, but were notably less frequent. Epiphytes, including lichens and mosses, are highly abundant in mixed Dinaric and Alpine forests and are essential components of their biodiversity. They are crucial as nesting materials for birds and mammals (Hayward & Rosentreter, 1994; Wesołowski & Wierzcholska, 2018). Furthermore, they offer shelter and nesting sites for insects, predominantly beetles and moths (Asbeck et al., 2022). Epiphytic lichens and bryophytes also provide habitats for various invertebrates, including spiders, mites, and tardigrades (Ellis, 2012), and host lichenivorous fungi and epibryophytic lichens (Hämäläinen *et al*., 2023). Weckesser and Višnjić (2005) documented 35 species of lichens, 12 species of liverworts, and 17 species of mosses in the Dinaric old-growth forest "Ravna Vala," underscoring the importance of epiphytes as crucial biodiversity components within forest ecosystems. The abundance and diversity of lichens and mosses are influenced by factors such as the variety of tree species present, the structural complexity of the forest, and the unique habitat conditions within these forests. The presence of different epiphyte species is related to specific tree species and their location on the tree (Ellis, 2012; Kuusinen, 1996). Lichens are more prevalent in coniferous trees and can be found in both the trunk and the crown. Mosses are found almost exclusively on trunks, more so on deciduous trees than on conifers (Weckesser & Višnjić, 2005; Vuidot et al., 2011; Marmor *et al*., 2013; Tarasova *et al*., 2017). These studies reveal a similar trend: mosses are more abundant on sycamore and beech trees, while lichens are more commonly found on silver fir. Furthermore, the presence of bryophytes increases more rapidly with the diameter of the tree in beech and silver fir compared to Norway spruce. Interestingly, in sycamore trees, no significant correlations were found between dbh and the occurrence of epiphytes per tree. Mosses, often coexisting with lichens, contribute to complex epiphytic communities (Weckesser & Višnjić, 2005). Studies conclude that in old beech and sycamore trees, epiphytes are part of species-rich communities such as Lobario–Antitrichion, whereas these communities tend to be less diverse in younger trees with smoother and thinner bark. Dead branches of living trees serve as vital substrates for various organisms, including saproxylic insects, fungi, and lichens (Larrieu *et al*., 2018). In managed conifer-dominated boreal forests, these dead branches can account for up to half of the total tree surface area (Svensson *et al*., 2014). Dead branches were abundant in all tree species, exhibiting an exceptionally high abundance in Norway spruce (1.73) and sycamore (1.53). This can be attributed to structural characteristics similar to those of uneven-aged managed forests. In such environments, due to competition from neighboring trees, the branches in the crown, especially in the lower parts, tend to die off faster in Norway spruce compared to silver fir and beech, which exhibit greater tolerance to shade than Norway spruce and sycamore. Consequently, a higher incidence of dead branches was observed in thinner Norway spruce trees.

Trunk cracks can occur due to frost, lightning, or mechanical pressure from neighboring trees falling due to age or wind. These cracks serve as nesting and hiding sites for various invertebrates, including spiders and flat bugs, while larger cracks can also accommodate birds and bats (Michel & Winter, 2009). In our study, cracks in the trunk were more frequent in deciduous tree species than in conifers and were observed more frequently in larger trees than in smaller ones. These findings partially align with those of Vuidot *et al*. (2011), who found no significant differences in the probability of crack occurrence among tree species. Cavities are formed by excavating birds (woodpeckers) or by wood-decaying fungi. In this study, all cavities (woodpecker cavities and rot holes) were considered a single microhabitat due to the small number of woodpecker cavities in live trees. The presence of woodpecker cavities is a reliable indicator of tree vitality, with a significantly higher probability of occurrence in standing dead trees (snags) compared to live trees (Vuidot *et al*., 2011). Woodpecker-excavated cavities tend to be more abundant in large broadleaf trees, while decay-induced cavities are commonly found in older trees (Andersson *et al*., 2018; Parsons *et al*., 2003; Sever & Nagel, 2019). These cavities serve as habitats for numerous insects and other invertebrates and as nesting and sheltering sites for various birds and certain mammals, including bats (Esseen *et al*., 1997). The highest average number of cavities was found in silver fir and the lowest in Norway spruce. The highest concentration of cavities was at the base of old trees. Furthermore, we found a significantly higher occurrence of cavities in silver fir, sycamore, and beech compared to Norway spruce. Significant correlations were found between dbh and the average number of cavities per tree for silver fir, sycamore, beech and Norway spruce, consistent with the findings of Vuidot *et al*. (2011). Studies by Sever and Nagel (2019) and Asbeck *et al.* (2022) have also highlighted a substantial increase in cavities within old-growth forests compared to managed forests. This outcome is expected, given that in old-growth forests, live trees frequently sustain various types of damage from natural disturbances such as wind, snow, ice, and bark beetles, leading to cavity formation through decay processes.

Fungal fruiting bodies serve as habitats or food sources for insects, notably beetles (Jonsell *et al*., 2001). Their presence is closely related to tree vitality, with a higher probability of occurrence in standing dead trees (snags) compared to living trees (Vuidot, 2011; Großmann *et al*., 2018). In this study, the presence of this microhabitat was only evaluated in live trees, resulting in a relatively low average number of fungal fruiting bodies per tree. Silver fir and sycamore had a higher number of fungal fruiting bodies compared to beech and Norway spruce. There was no correlation between dbh and the average number of fungal fruiting bodies. Furthermore, Larrieu et al. (2012) identified dbh thresholds associated with the occurrence of fungal fruiting bodies in both beech and silver fir. Fresh exudates, which offer benefits to various insect species (Hämäläinen *et al*., 2023) and birds (Bütler *et al*., 2013), appear predominantly on injured sections of tree trunks. In our study, Norway spruce demonstrated a higher prevalence of fresh exudates compared to silver fir, beech, and sycamore, where its occurrence was notably infrequent. There was no correlation between dbh and the presence of fresh exudates. Despite its ecological importance, this microhabitat remains relatively understudied, which underscores the need for further research to delineate its significance for biodiversity.

### 4.2 Importance of tree species and dbh on the number and diversity of microhabitats

Our analysis revealed that tree characteristics mainly influence the number, occurrence, and diversity of microhabitat types. Consistent with previous studies conducted in Central Europe (Winter *et al.*, 2008; Regnery *et al*., 2013; Vuidot *et al*., 2011; Paillet *et al*., 2019; Asbeck *et al*., 2021, 2022), we found that tree species are a crucial determinant of tree-related microhabitat abundance and richness. Our investigation observed that sycamore, beech, and silver fir live trees provide a significantly greater abundance of tree-related microhabitats compared to Norway spruce. These results are consistent with previous research indicating a higher occurrence of microhabitats in deciduous tree species compared to coniferous (Larrieu *et al*., 2012; Großmann *et al*., 2018; Asbeck *et al.*, 2019; Asbeck *et al*., 2021). Furthermore, our study highlights the crucial role of sycamore in shaping the occurrence and richness of tree-related microhabitats within mixed Dinaric forests, where sycamore is typically found individually or in small groups alongside beech and silver fir.

Interestingly, sycamore trees with a smaller dbh (40-60 cm) showed a substantial abundance of microhabitats compared to other tree species with larger diameters (60-80 cm). Therefore, the contribution of sycamore to the biodiversity of these forests is invaluable.

Our findings underscore the crucial role of well-structured and mixed forests (deciduous and coniferous) in supporting forest-dwelling species' biodiversity and overall forest biodiversity. Each tree species within these communities has specific bioecological and morphological characteristics that favor the creation and maintenance of microhabitats. These results are consistent with similar findings reported by Kozak *et al*. (2018) and Sever and Nagel (2019).

The microhabitat diversity index was generally higher for beech (1.31), sycamore (1.26), and silver fir (1.21) than for Norway spruce (1.18); however, no statistically significant differences were found in the average diversity index among the tree species studied. Our findings align with those of Großmann *et al*. (2018) on the average microhabitat diversity index, particularly for beech (1.32). However, for silver fir (1.48) and sycamore (1.45), their reported values were higher, suggesting a potential correlation between microhabitat diversity and geographical factors, altitude, historical and contemporary habitat conditions, as well as anthropogenic influences. Consequently, comparability between regions is limited and evaluations should be carried out locally. Our study also indicates that there are no significant discrepancies in the average diversity index of microhabitats between the tree species investigated.

Consistent with previous research findings (Vuidot *et al*., 2011; Larrieu & Cabanettes, 2012; Kozak *et al.*, 2018; Paillet *et al.*, 2019; Sever & Nagel, 2019; Asbeck *et al*., 2019, 2022), our study indicates a positive correlation between the diameter of the tree at breast height (dbh) and the presence of microhabitats associated with trees, as well as the diversity of microhabitats per tree, across all examined tree species (beech, silver fir, sycamore, and Norway spruce). Generally, larger trees exhibit a higher abundance of microhabitats, a more comprehensive array of microhabitat types, and increased diversity across the spectrum of tree species (see Table 4, 5, 6). Asbeck et al. (2021) state that it is not fully understood whether tree species or diameter at breast height (dbh) is more decisive, but both are usually the two most important drivers of tree-related microhabitat occurrence. Other authors also indicate the importance of tree species and tree diameter in the abundance and richness of microhabitats (Sever & Nagel, 2019; Vuidot, 2011; Larrieu *et al*., 2014; Asbeck, 2022).

The mean diversity index values per tree were meticulously organized into diameter classes in all tree species, unequivocally affirming dbh as the primary predictor of microhabitat diversity (see Table 6). Our findings elucidate that different tree species exhibit preferences for specific types of microhabitats, underscoring the significance of tree species diversity in influencing the frequency of microhabitats, particularly in mixed forests that house both conifers and broadleaves. These observations are closely related to the findings of Kozlak *et al*. (2018). Furthermore, our study underscores that tree species and their dbh in mixed, uneven-aged forests are intricately intertwined. In particular, thinner suppressed trees, in some cases, harbor more microhabitats than larger ones, suggesting that the importance of these quantitative indicators is contingent on microsite characteristics and the structural complexity of the forest, which can exhibit considerable variation within a confined area.

*Table 6: Summary of the diversity of microhabitats for each tree species, categorized by dbh class, along with the corresponding homogeneous groups across all tree species and dbh classes. Mean represents the average value of the Shannon diversity index, and SD denotes the standard deviation.*

Tabelle 6: Zusammenfassung der Mikrohabitatvielfalt für jede Baumart, kategorisiert nach dbh-Klasse, zusammen mit den entsprechenden homogenen Gruppen über alle Baumarten und dbh-Klassen. Der Mittelwert stellt den Durchschnittswert des Shannon-Diversitätsindexes dar, und SD bezeichnet die Standardabweichung.

| Tree species | dbh class | N | mean | SD | Tukeys HSD groups | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sycamore | > 80 | 10 | 1.56 | 0.28 | a | | | | | | |
| Beech | > 80 | 21 | 1.55 | 0.24 | a | b | | | | | |
| Spruce | > 80 | 13 | 1.53 | 0.23 | a | b | | | | | |
| Fir | > 80 | 34 | 1.49 | 0.3 | | b | c | | | | |
| Beech | 60-80 | 30 | 1.47 | 0.21 | | | c | | | | |
| Fir | 60-80 | 28 | 1.38 | 0.18 | | | c | d | e | | |
| Sycamore | 60-80 | 21 | 1.36 | 0.19 | | | c | d | | | |
| Spruce | 60-80 | 24 | 1.27 | 0.31 | | | | d | e | f | |
| Sycamore | 40-60 | 30 | 1.08 | 0.25 | | | | | e | f | g |
| Beech | 40-60 | 36 | 1.06 | 0.4 | | | | | | f | g |
| Spruce | 40-60 | 33 | 0.99 | 0.28 | | | | | | | g |
| Fir | 40-60 | 37 | 0.82 | 0.31 | | | | | | | g |

Based on our findings, forest management should prioritize the conservation of beech and sycamore trees, as they host the highest number and diversity of microhabitats crucial for biodiversity. In particular, sycamore trees in the 40–60 cm dbh class exhibit microhabitat diversity comparable to larger trees (>80 cm dbh) of other species; therefore, preserving these smaller sycamores can significantly enhance habitat availability. Furthermore, retaining large-diameter trees of all species is essential, since the number and diversity of microhabitats increases with tree size. Promoting a heterogeneous forest structure - with a mix of species, varying tree sizes, and multiple canopy layers - will further support biodiversity conservation.

## Authors' contributions

Conceptualization, V.Ć., B.B. and V.S.; methodology, V.Ć.; formal analysis, B.B and Č.M.; investigation, B.B. and Č. M.; writing—original draft preparation, V.Ć and V.S writing—review and editing, Č.M.; visualization, Č.M. All authors have read and agreed to the published version of the manuscript.

## Declarations

The authors declare no competing interests. The authors declare that they have no known conflicts of interest.

## References

Andersson, J., Domingo Gómez, E., Michon, S., Roberge, J.-M., 2018. Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scand. J. For. Res. 33, 233- 244. https://doi.org/10.1080/02827581.2017.1360389

Asbeck, T., Großmann, J., Paillet, Y., Winiger, N., Bauhus, J., 2021. The Use of Tree-Related Microhabitats as Forest Biodiversity Indicators and to Guide Integrated Forest Management. Curr. For. Rep. 7, 59–68. https://doi.org/10.1007/s40725-020-00132-5

Asbeck, T., Kozák, D., Spînu, A.P., Mikoláš, M., Zemlerová, V., Svoboda, M., 2022. Tree-related microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed Temperate Mountain Forests. Ecosystems 25, 712–726. https://doi.org/10.1007/s10021-021-00681-1

Asbeck, T., Pyttel, P., Frey, J., Bauhus, J., 2019. Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes. For. Ecol. Manag. 432, 400–408. https://doi.org/10.1016/j.foreco.2018.09.043

Basile, M., Asbeck, T., Pacioni, C., Mikusiński, G., Storch, I., 2020. Woodpecker cavity establishment in managed forests: relative rather than absolute tree size matters. Wildl. Biol. 2020. https://doi.org/10.2981/wlb.00564

Beus, V., Vojniković, S. (2002): Floristical characteristics of the virgin forest of beech and fir in Ravna Vala on mountain Bjelašnica. Razp. IV. razreda SAZU. XLIII, Ljubljana, 63-78.

Beus, V., Vojniković, S. (2006): Floristički diverzitet prašume i gospodarske šume u Ravnoj vali na Bjelašnici; Zbornik radova: Gazdovanje šumskim ekosistemima nacionalnih parkova i drugih zaštićenih područja, Jahorina – Tjentište, str. 55-66.

Bütler R, Lachat T, Larrieu L, Paillet Y. 2013. Habitat trees: key elements for forest biodiversity. In: Kraus D, Krumm F, editors. Integrative approaches as an opportunity for the conservation of forest biodiversity. Joensuu: European Forest Institute. p. 284.

Ellis, C.J., 2012. Lichen epiphyte diversity: A species, community, and trait-based review. Perspect. Plant Ecol. Evol. Syst. 14, 131–152. https://doi.org/10.1016/j.ppees.2011.10.001

Esseen, P.-A., 1997. Boreal forests, in: Ecol. Bull. pp. 16–46.

FAO – Food and Agriculture Organization of The United Nations, 2006. Global Forest Resources Assessment 2005: Progress Towards Sustainable Forest Management. Rome. Forestry, n. 147

Fukarek, P., Stefanović, V., 1958. Prašuma Perućica i njena vegetacija. Rad. Šumar. Fak. Univ. U Sarajevu 6, 93–146. https://doi.org/10.54652/rsf.1958.v6.i3.399

Großmann, J., Schultze, J., Bauhus, J., Pyttel, P., 2018. Predictors of Microhabitat Frequency and Diversity in Mixed Mountain Forests in South-Western Germany. Forests 9, 104. https://doi.org/10.3390/f9030104

Hämäläinen, A., Runnel, K., Mikusiński, G., Himelbrant, D., Fenton, N.J., Lõhmus, P., 2023. Living Trees and Biodiversity, in: Girona, M.M., Morin, H., Gauthier, S., Bergeron, Y. (Eds.), Boreal Forests in the Face of Climate Change: Sustainable Management. Springer International Publishing, Cham, pp. 145–166. https://doi.org/10.1007/978-3-031-15988-6_5

Hayward, G.D., Rosentreter, R., 1994. Lichens as Nesting Material for Northern Flying Squirrels in the Northern Rocky Mountains. J. Mammal. 75, 663–673. https://doi.org/10.2307/1382514

Jahed, R.R., Kavousi, M.R., Farashiani, M.E., Sagheb-Talebi, K., Babanezhad, M., Courbaud, B., Wirtz, R., Müller, J., Larrieu, L., 2020. A Comparison of the Formation Rates and Composition of Tree- Related Microhabitats in Beech-Dominated Primeval Carpathian and Hyrcanian Forests. Forests 11, 144. https://doi.org/10.3390/f11020144

Johann, F., Schaich, H., 2016. Land ownership affects diversity and abundance of tree microhabitats in deciduous temperate forests. For. Ecol. Manag., Special section: Drought and US Forests: Impacts and Potential Management Responses 380, 70–81. https://doi.org/10.1016/j.foreco.2016.08.037

Jonsell, M., Nordlander, G., Ehnström, B., 2001. Substrate Associations of Insects Breeding in Fruiting Bodies of Wood-Decaying Fungi. Ecol. Bull. 49, 173–194. https://doi.org/10.2307/20113275

Koch, F., 1998. Scherzinger, W. (1996): Naturschutz im Wald: Qualitätsziele einer dynamischen

Waldentwicklung. Praktischer Naturschutz. – Stuttgart (Verlag Eugen Ulmer). – 447 S., 51 Farbabb., 119 s/w-Abb., 36 Tab. ISBN 3-8001-3356-3. Zoosystematics Evol. 74, 149–149. https://doi.org/10.1002/mmnz.19980740118

Kraus, D., Bütler, R., Krumm, F., Lachat, T., Larrieu, L., Mergner, U., Paillet, Y., Rydkvist, T., Schuck, A., Winter, S., 2016. Catalogue of tree microhabitats – Reference field list. https://doi.org/10.13140/RG.2.1.1500.6483

Kuusinen, M., 1996. Epiphyte flora and diversity on basal trunks of six old-growth forest tree species in southern and middle boreal Finland. The Lichenologist 28, 443–463. https://doi.org/10.1006/lich.1996.0043

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests1. Can. J. For. Res. 42, 1433–1445. https://doi.org/10.1139/x2012-077

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

Lindenmayer, D., Laurance, W., 2016. The ecology, distribution, conservation and management of large old trees. Biol. Rev. Camb. Philos. Soc. 92. https://doi.org/10.1111/brv.12290

Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E., Bible, K.J., 2013. The Importance of Large- Diameter Trees to Forest Structural Heterogeneity. PLOS ONE 8, e82784. https://doi.org/10.1371/journal.pone.0082784

Marmor-Ohtla, L., Tõrra, T., SAAG, L., LEPPIK, E., Randlane, T., 2013. Lichens on Picea abies and Pinus sylvestris - From tree bottom to the top. The Lichenologist 45. https://doi.org/10.1017/S0024282912000564

Martin, M., Paillet, Y., Larrieu, L., Kern, C.C., Raymond, P., Drapeau, P., Fenton, N.J., 2022. Tree-Related Microhabitats Are Promising Yet Underused Tools for Biodiversity and Nature

Conservation: A Systematic Review for International Perspectives. Front. For. Glob. Change 5. https://doi.org/10.3389/ffgc.2022.818474

Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. For. Ecol. Manag. 257, 1453–1464. https://doi.org/10.1016/j.foreco.2008.11.027

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., Guilbert, E., 2017. Snags and large trees drive higher tree microhabitat densities in strict forest reserves. For. Ecol. Manag. 389, 176–186. https://doi.org/10.1016/j.foreco.2016.12.014

Paillet, Y., Coutadeur, P., Vuidot, A., Archaux, F., Gosselin, F., 2015. Strong observer effect on tree microhabitats inventories: A case study in a French lowland forest. Ecol. Indic. 49, 14–23. https://doi.org/10.1016/j.ecolind.2014.08.023

Paillet, Y., Debaive, N., Archaux, F., Cateau, E., Gilg, O., Guilbert, E., 2019. Nothing else matters? Tree diameter and living status have more effects than biogeoclimatic context on microhabitat number and occurrence: An analysis in French forest reserves. PLOS ONE 14, e0216500 https://doi.org/10.1371/journal.pone.0216500

Parsons, S., Lewis, K.J., Psyllakis, J.M., 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. For. Ecol. Manag. 177, 559–570. https://doi.org/10.1016/S0378-1127(02)00448-6

Piraccini, R., Cammarano, M., Costa, A., Basile, M., Posillico, M., Boitani, L., Bascietto, M., Matteucci, G., De Cinti, B., Romano, A., 2016. Habitat trees and salamanders: Conservation and management implications in temperate forests. For. Ecol. Manag. 384, 17–25.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. Available online at https://www.r-project.org/

Regnery, B., Couvet, D., Kubarek, L., Julien, J.-F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Indic. 34, 221–230. https://doi.org/10.1016/j.ecolind.2013.05.003

Shannon, C.E. 1948: A Mathematical Theory of Communication. Bell Syst. Tech. J. 27, 623–656.

Sever, K., Nagel, T., 2019. Patterns of tree microhabitats across a gradient of managed to old-growth conditions: a case study from beech dominated forests of South-Eastern Slovenia. Acta Silvae Ligni 118, 29–40. https://doi.org/10.20315/ASetL.118.3

Svensson, M., Dahlberg, A., Ranius, T., Thor, G., 2014. Dead branches on living trees constitute a large part of the dead wood in managed boreal forests, but are not important for wood-dependent lichens. J. Veg. Sci. 25, 819–828. https://doi.org/10.1111/jvs.12131

Tarasova, V., Obabko, R., Himelbrant, D., Boychuk, M.A., Stepanchikova, I., Borovichev, E., 2017. Diversity and distribution of epiphytic lichens and bryophytes on aspen (*Populus tremula*) in the middle boreal forests of Republic of Karelia (Russia). Folia Cryptogam. Est. 54, 125–142. https://doi.org/10.12697/fce.2017.54.16

The World Bank. 2008. Forests Sourcebook: Practical Guidance for sustaining forests in development cooperation, Agriculture and Rural Development. https://doi.org/10.1596/978-0-8213-7163-3

Višnjić, Ć., Balić, B., Vojniković, S., Mekić, F., Uzunović, A., 2015. Structural characteristics, dynamics and texture development of virgin forest Ravna vala on Bjelašnica. Rad. Šumar. Fak. Univ. U Sarajevu 45, 100–112 https://doi.org/10.54652/rsf.2015.v45.i2.88

Višnjić, Ć., Solaković, S., Mekić, F., Balić, B., Vojniković, S., Dautbašić, M., Gurda, S., Ioras, F., Ratnasingam, J., Abrudan, I.V., 2013. Comparison of structure, regeneration and dead wood in virgin forest remnant and managed forest on Grmeč Mountain in Western Bosnia. Plant Biosyst. - Int. J. Deal. Asp. Plant Biol. 147, 913–922. https://doi.org/10.1080/11263504.2012.751064

Višnjić, Ć., Vojniković, S., Balić, B., Mekić, F., Ivojević, S., 2017. Stand structure, dead wood, and floristic composition of a pristine forest stand of beech and fir compared to a managed forest in the Dinaric mountain Bjelašnica. Rad. Šumar. Fak. Univ. U Sarajevu 47, 13–31. https://doi.org/10.54652/rsf.2017.v47.i1.64

Višnjić, Ć., Vojnikovic, S., Ioras, F., Mirza, D., Abrudan, I., Gurean, D.-M., Lojo, A., Trestic, T., Ballian, D., Bajric, M., 2009. Virgin Status Assessment of Plješevica Forest in Bosnia -Herzegovina. Not. Bot. Horti Agrobot. Cluj-Napoca 37. https://doi.org/10.15835/nbha3723308

Višnjić, Ć., Mekić, F., Balić, B., Memišević, M. 2020: Inventory, marking, and proposal for the protection of habitat trees in beech and fir forests in the Bosnian-Podrinje Canton. Final Report, Faculty of Forestry University of Sarajevo, 1-28.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biol. Conserv. 144, 441–450. https://doi.org/10.1016/j.biocon.2010.09.030

Winter, S., Brambach, F., 2011. Determination of a common forest life cycle assessment method for biodiversity evaluation. For. Ecol. Manag. 262, 2120–2132. https://doi.org/10.1016/j.foreco.2011.07.036

Winter, S., Höfler, J., Michel, A.K., Böck, A., Ankerst, D.P., 2015. Association of tree and plot characteristics with microhabitat formation in European beech and Douglas-fir forests. Eur. J. For. Res. 134, 335–347. https://doi.org/10.1007/s10342-014-0855-x

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manag. 255, 1251–1261. https://doi.org/10.1016/j.foreco.2007.10.029

Čilaš, M., Leiter, M., Višnjić, Ć., Hasenauer, H., 2023. Adapting the tree growth model MOSES to manage uneven-aged mixed species forests in Bosnia & Herzegovina. Trees For. People 14, 100433. https://doi.org/10.1016/j.tfp.2023.100433

Čilaš, M., Višnjić, Ć., 2024. Recent structural changes, species composition and interaction in an old-growth forest – an example from Bjelašnica MT. J. Agric. For. 70, 71–84. https://doi.org/10.17707/AgricultForest.70.3.05