

Raznolikost epifitskih mahovina u Park šumi Maksimir

Rumin, Paola

Master's thesis / Diplomski rad

2024

Degree Grantor / Ustanova koja je dodijelila akademski / stručni stupanj: **University of Zagreb, Faculty of Science / Sveučilište u Zagrebu, Prirodoslovno-matematički fakultet**

Permanent link / Trajna poveznica: <https://um.nsk.hr/um:nbn:hr:217:095916>

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Download date / Datum preuzimanja: **2025-03-31**



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University of Zagreb
Faculty of Science
Department of Biology

Paola Rumin

**The diversity of epiphytic mosses in
Maksimir Forest Park**

Master thesis

Zagreb, 2024.

Sveučilište u Zagrebu
Prirodoslovno-matematički fakultet
Biološki odsjek

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This master thesis was produced at the Division of Botany of the Faculty of Science in Zagreb, under the supervision of mentor Prof. Antun Alegro, PhD and co-mentor Anja Rimac, PhD. The work was submitted for evaluation to the Biology Department of the Faculty of Science, University of Zagreb, in order to obtain the title of Master of Experimental Biology.

Huge thanks to my co-mentor Anja Rimac on all the help with collecting and identifying bryophytes and writing this thesis, and thanks to my mentor Antun Alegro on advice and guidance.

I owe a thank you to Goran Rumin for putting up with my work (sacrificing his car once) and helping out on the field, and to everyone else who supported me during my studies.

I also want to take this opportunity to express gratitude for everyone who made working with bryophytes such a pleasure for me along the way.

BASIC DOCUMENTATION CARD

University of Zagreb
Faculty of Science
Department of Biology

Master thesis

The diversity of epiphytic mosses in Maksimir Forest Park

Paola Rumin

Rooseveltova trg 6, 10000 Zagreb, Croatia

Epiphytic bryophyte flora of Maksimir Forest Park was researched during the winter of 2023 and spring of 2024. Five tree species were sampled: sessile oak, hornbeam, beech, black locust and spruce. A total of 35 bryophyte taxa were recorded, of which 31 were mosses and 4 were liverworts. The tree species harbouring the highest bryophyte diversity was beech, while the most frequent and abundant bryophyte was *Hypnum cupressiforme*. During the research, a NATURA 2000 target species *Dicranum viride* was found on beech and oak. The predominant life form on all tree species was the smooth mat, while the most common life strategy was stress-tolerant perennial. Biogeographically, the majority of recorded species belonged to the temperate major biome element and circumpolar eastern limit element. Multivariate analyses were used to investigate bryophyte community composition on different tree species, with average Ellenberg indicator values for light, moisture, nitrogen and pH reaction and recorded environmental parameters passively projected as vectors over the ordination to assess the possible environmental gradients.

Keywords: epiphytes, bryophytes, life forms, life strategies, biogeographical elements, Ellenberg indicator values, ecological parameters

(44 pages, 20 figures, 5 tables, 52 references, original in: English)

Thesis is deposited in Central Biological Library.

Mentor: Prof. Antun Alegro, PhD

Co-mentor: Anja Rimac, PhD

Reviewers:

Prof. Antun Alegro, PhD

Prof. Zlatko Liber, PhD

Asst. Prof. Dario Hruševar, PhD

Thesis accepted: 7/11/2024

TEMELJNA DOKUMENTACIJSKA KARTICA

Sveučilište u Zagrebu
Prirodoslovno-matematički fakultet
Biološki odsjek

Diplomski rad

Raznolikost epifitskih mahovina u Park šumi Maksimir

Paola Rumin

Rooseveltov trg 6, 10000 Zagreb, Hrvatska

Epifitska flora mahovina Park šume Maksimir istraživana je tijekom zime 2023. i proljeća 2024. Uzorkovano je pet vrsta drveća: hrast kitnjak, grab, bukva, bagrem i smreka. Zabilježeno je 35 svojti mahovina, od kojih 31 prava mahovina i 4 jetrenjarke. Najveća raznolikost zabilježena je na bukvi, dok je najučestalija mahovina s najvišim pokrovnostima bila vrsta *Hypnum cupressiforme*. Tijekom istraživanja je na bukvi i hrastu pronađena NATURA 2000 ciljna vrst *Dicranum viride*. Obzirom na spektar životnih oblika, na svim vrstama drveća prevladavale su mahovine koje rastu u glatkim sagovima, a obzirom na životnu strategiju trajnice otporne na stres. Većina vrsta bila je temperatna s obzirom na pripadnost glavnim biomima, odnosno cirkumpolarna s obzirom na istočnu granicu pojavljivanja. Multivarijantnim analizama istražen je sastav epifitskih zajednica na različitim vrstama drveća, a u DCA analizi su dodatno srednje vrijednosti ekoloških indikatorskih vrijednosti i prikupljenih okolišnih parametara pasivno projicirani kao vektori kako bi se istražili eventualni okolišni gradijenti.

Ključne riječi: epifiti, briofiti, životni oblici, životne strategije, biogeografski elementi, Ellenbergove indikatorske vrijednosti, ekološki parametri
(44 stranice, 20 slika, 5 tablica, 52 literaturna navoda, jezik izvornika: Engleski)
Rad je pohranjen u Središnjoj biološkoj knjižnici

Mentor: prof. dr. sc. Antun Alegro
Komentor: dr. sc. Anja Rimac

Ocjenitelji:
prof. dr. sc. Antun Alegro
prof. dr. sc. Zlatko Liber
doc. dr. sc. Dario Hruševan

Rad prihvaćen: 7.11.2024.

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1 INTRODUCTION

1.1 BRYOPHYTES

Bryophytes are land plants whose life cycle is dominated by haploid stage – gametophyte, unlike all other land plants' life cycle whose dominant stage is diploid – sporophyte. They are the only land plants whose gametophyte is well-developed, branched and morphologically vastly diverse (Figure 1). In stark contrast to spermatophytes, the bryophytes' sporophyte grows on maternal gametophyte and is completely dependent on it for nutrients and water (Figure 1). It produces a single sporangium. Furthermore, bryophytes are usually tiny, up to a few centimeters (although exceptions do exist) and they require high levels of humidity due to their water-dependent reproduction. Namely, bryophytes' sperm cells are flagellated, meaning they require water to swim to the egg. They can also reproduce asexually by leaf fragments or by specialized structures such as gemmae and bulbils. Another major characteristic of bryophytes is that they do not possess a vascular system found in vascular plants (Vanderpoorten and Goffinet 2009). Phylogenetically, bryophytes are a monophyletic sister group to vascular plants. It splits into three lineages: Anthocerotophyta or hornworts, Marchantiophyta or liverworts and Bryophyta s.s. or mosses (de Sousa et al. 2018, Su et al. 2021).



Figure 1: *Hypnum cupressiforme* with some gametophytes and sporophytes marked.
(Author: Paola Rumin)

Anthocerotophyta are characterised by a thalloid gametophyte without any leaves. There are no specialised cells in the tissue for conducting water. The sporophyte is elongated but lacks seta. Basal meristem adds new cells to the base of the sporangium during maturation, thus elongating it. The sporangium opens via two longitudinal lines, exposing spores on an axial columella. It also harbours pseudo-elaters which facilitate the dispersal of spores (Vanderpoorten and Goffinet 2009).

Marchantiophyta are either thalloid or composed of leaves arranged in parallel rows on a stem (Figure 2). Some taxa have specialised water-conducting cells, but only in the gametophyte. Their sporophytes have a seta that grows by cell elongation, not cell division, with a capsule on top. The capsule usually opens via four vertical lines, exposing spores and elaters, specialised cells which facilitate the dispersal of spores. There is no columella in the sporangium (Vanderpoorten and Goffinet 2009).

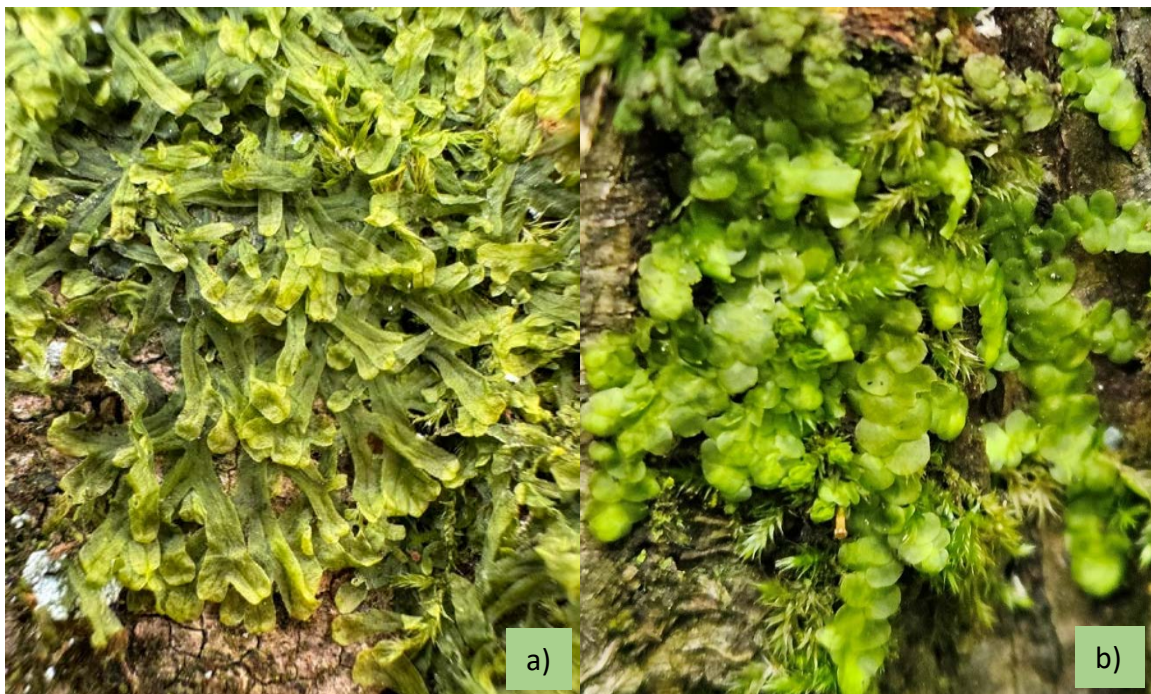


Figure 2: Thalloid *Metzgeria furcata* (a) and leafy *Radula complanata* (b).
(Authors: Margarita Delles and Paola Rumin)

Bryophyta s. s. always have stems and leaves. Axial water-conducting strands occur in both generations of many taxa. Sporophytes have a seta that grows by cell division, and a capsule on top. The capsule usually opens by shedding an operculum. Axial columella exists in most taxa.

Sporangium produces spores, but not elaters (Vanderpoorten and Goffinet 2009). They can be either acrocarpous or pleurocarpous (Figure 3). Acrocarpous mosses, which have terminal perichaetia and sporophytes, usually form cushions or turfs as their gametophyte's main axis is

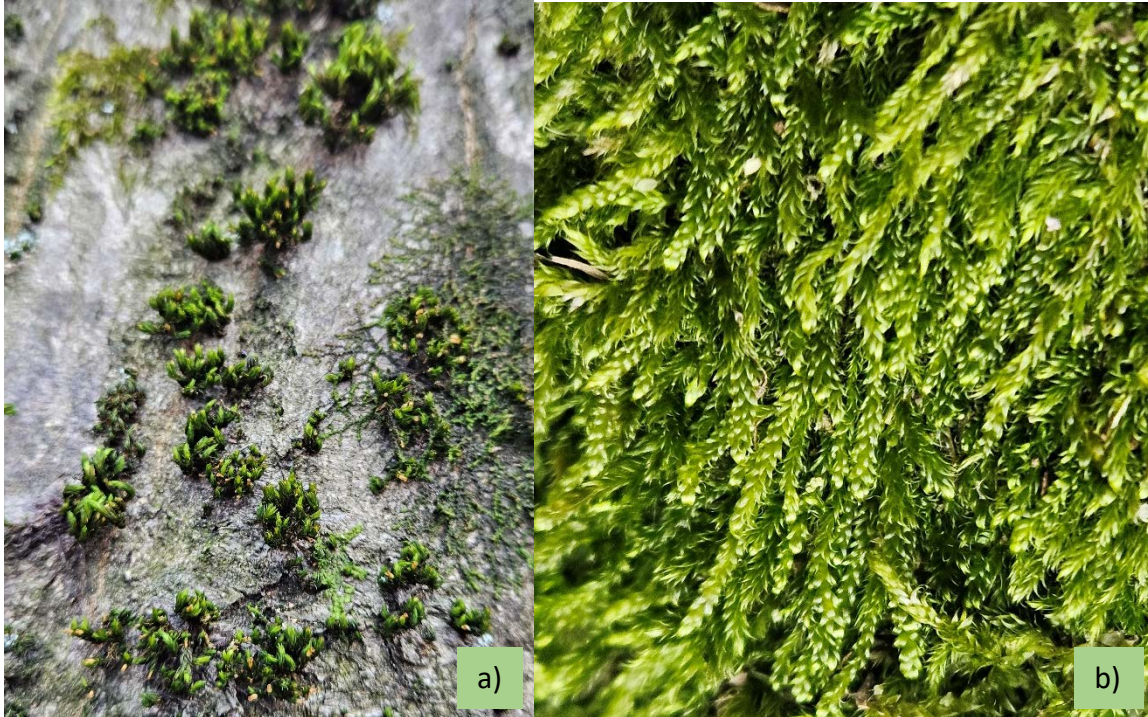


Figure 3: acrocarpous *Orthotrichum* sp. (a) and pleurocarpous *Hypnum cupressiforme* (b).
(Author: Paola Rumin)

erect. They can also appear scattered on a surface they inhabit, which is usually the case with epiphytes. On the other hand, pleurocarpous mosses, which have perichaetia and sporophytes in lateral buds or on short side branches, usually form prostrate mats, sometimes with ascending secondary shoots (Smith 2004, Glime 2017).

1.1.1 EPIPHYTIC BRYOPHYTES

Epiphytic bryophytes grow on the surface of a tree's or shrub's bark, without parasitizing on it. They can be obligate, meaning a certain species grows only on bark, or facultative, meaning they can be found on more than one substrate type. Obligate epiphytic bryophytes are usually monoecious. A monoecious plant can produce both male and female gametes. On the other hand, facultative epiphytic bryophytes are usually dioecious, meaning male gamete production and female gamete production happen in different individuals (Smith 1982). In general, roughly 70% of liverworts, 60% of mosses and 40% of hornworts are dioecious. Predominant monoecy in

obligate epiphytic bryophytes can be explained by the fact that a piece of bark is a rather small habitat which lowers the odds of both female and male spores landing in close proximity. Furthermore, competition for space and nutrients often arises even though the two bryophytes are of the same species, leading to cases in which only one sex develops into a fully grown gametophyte. With that in mind, it is clear that a monoecious bryophyte will have a higher rate of sexual reproduction than a dioecious one, because a single monoecious individual can „self“ or reproduce sexually with its own male and female gametes. Although the act of selfing produces spores that are virtually clones of their parent, the chance of an individual's descendants spreading further from them is higher than in the case of vegetative reproduction, which is the only available option for dioecious individuals without a partner (Haig 2016).

Unlike most bryophytes, the peristome of some epiphytic bryophytes opens while it is moist, instead of dry, so the rain can help disperse spores. Another interesting feature epiphytic bryophytes display is vertical zonation across the tree. The base of the tree is usually colonised by facultative epiphytes, the trunk and larger branches are colonised by both facultative and obligate epiphytes, while smaller upper branches are colonised by obligate epiphytic species (Smith 1982).

1.2 PHOROPHYTES AND MICROCLIMATE CONDITIONS

The term „phorophyte“ refers to a plant on which epiphytes grow. It has been previously shown that most epiphytic bryophytes occur in greater abundance on certain tree species than on other or even not occur at all on some, thus exhibiting host specificity (Szövényi et al. 2004, Mežaka et al. 2012). Whether a certain bryophyte will occur abundantly on a certain phorophyte will depend on the bryophyte's ecological demands and the microclimate conditions a phorophyte will have provided. Some of the ecological factors that form the microclimate are pH of the tree's bark, diameter of the tree at the height of 1.3 m, which directly corresponds with the area available for colonisation, bark crevices, the tree's age, tree inclination and water availability (Mežaka et al. 2012). Tree inclination and water availability are interlinked as less water will run off from inclined trees, and bryophytes tend to grow in habitats with high water availability. Furthermore, high sun exposure will decrease the amount of water on the bark so bryophytes will be more commonly found in shade (Ranius et al. 2008). The pH of the tree's bark varies among tree species as it depends on the chemical composition of the bark. Higher pH seems to benefit the richness of bryophyte species, while lower pH benefits the richness of lichen species. The amount of bark crevices, as well as diameter, depend on the tree's age. Older and bigger trees tend to have richer epiphytic

bryophyte flora than younger and smaller ones (Mežaka et al. 2012). Ranius et al. (2008), however, found that barks with deeper crevices harbour less epiphytic bryophytes, which could be explained by the fact that the chemical composition of bark changes with its age (Ranius et al. 2008).

1.3 BRYOPHYTES AS INDICATORS OF ENVIRONMENTAL HEALTH

Forest integrity is a term that refers to the overall health of the forest, including its ability to keep its biodiversity and ability to store carbon. The criteria showing forest integrity, such as species composition, ecological organization, disturbance regime or continuity, are oftentimes hard or expensive to measure, especially because focusing on only one could provide false insights. Hence, the need for surrogates arises - indicators that will provide insight into the state of many of the above-mentioned criteria. One such potential surrogate is bryophytes. They exhibit greater sensitivity to forest management activities than vascular plants, especially liverworts. Furthermore, a correlation between bryophyte richness and diversity and that of birds, vascular plants and lichens has been observed. The spatial scale on which such researches were made, however, impacted the correlation. The presence or abundance of certain bryophyte species appears to be a good indicator of forest integrity, except on forest edges where air pollution can negatively affect the appearance of some species. On the other hand, a valid critique of using bryophytes as surrogates for determining forest integrity is that determining bryophyte species is usually harder and requires a microscope, unlike vascular plant determination, thus making it more expensive and limited with the low number of experts (Frego 2007). Bryophytes' species richness, cover and life form composition have been used to assess the atmospheric purity and it is known that nitrogen content in bryophytes strongly correlates with atmospheric nitrogen concentration (Oishi and Hiura 2017).

2 RESEARCH GOALS

As epiphytic bryophytes are an important component of forest ecosystems and contribute to their stability, while changes in their composition reflect changes in the quality of the environment, knowledge on their diversity and ecology is of great importance in understanding the dynamics of forest ecosystems as well as for their application in monitoring of these ecosystems. Since the epiphytic bryoflora in the area of the city of Zagreb is poorly known, the goals of this work are:

1. to determine the total diversity of epiphytic bryophytes on selected tree species,
2. analyze the diversity of bryophyte species related to tree species,
3. analyze the ecology of epiphytic bryophyte assemblages present on different tree species based on measured parameters and ecological indicator values of bryophytes,
4. analyze the life strategies of epiphytic communities of bryophytes present on different tree species,
5. analyze the biogeographical structure of epiphytic communities of bryophytes present on different tree species and
6. propose a monitoring plan for epiphytic bryophytes in the researched area.

3 MATERIALS AND METHODS

3.1 RESEARCH AREA

Maksimir Forest Park was chosen as a research area for this thesis, because it is easily accessible, and is one of the biggest and the least anthropogenically affected parks in Zagreb (Figure 4). Furthermore, it bears the status of protected cultural property in Croatia due to its long history and magnificent park architecture (Web Registar kulturnih dobara RH 2024).



Figure 4: Aerial view of a part of Maksimir Forest Park.
(downloaded from the city of Zagreb's website <https://aktivnosti.zagreb.hr/maksimir/151>)

3.1.1 GEOGRAPHICAL POSITION

Maksimir Forest Park is situated in the southeastern part of the Maksimir city district in the city of Zagreb (Figure 5). It is surrounded by an urban area. The park's total area amounts to 316 ha, including forests, meadows, lakes, creeks and a zoo. Its elevation spans from 120 to 167 m above sea level (Priroda Grada Zagreba 2024).

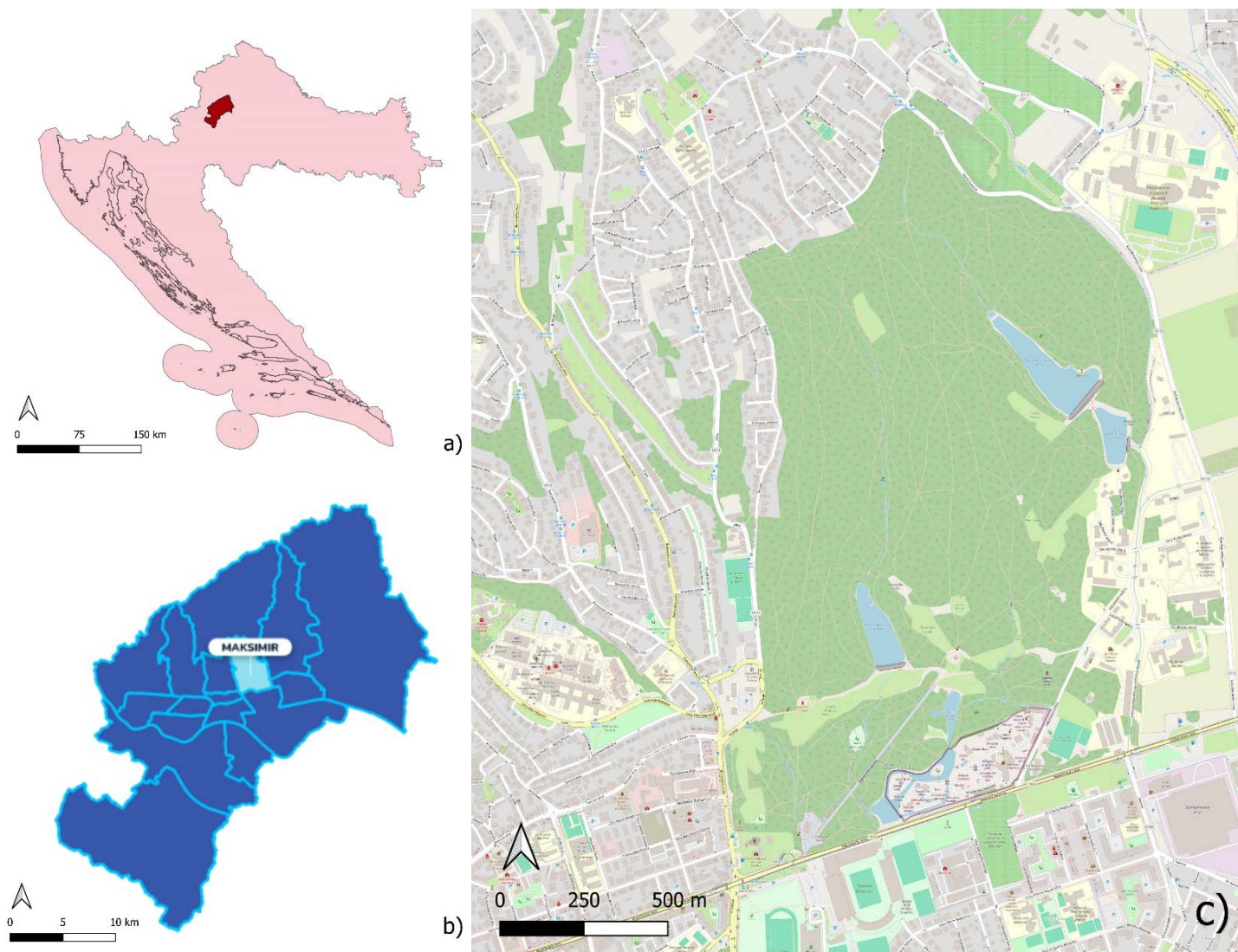


Figure 5: Map of Croatia with the city of Zagreb highlighted in red (a), map of Zagreb with visible division into city districts, Maksimir district is highlighted (b), open street map of the Maksimir Forest Park with surrounding urban areas (c).

All maps were created using QGIS 3.34.6 software. The template for city districts of Zagreb was downloaded from the city of Zagreb's webpage <https://aktivnosti.zagreb.hr/gradske-cetvrti-19/gradske-cetvrti-19/maksimir/151>.

3.1.2 CLIMATE

Zagreb belongs to the continental climate area and according to the Köppen climate classification, it has a moderately warm humid climate with warm summer. Main climate characteristics of Maksimir Forest Park are (Priroda Grada Zagreba 2024):

- the temperature of the coldest month is higher than $-3\text{ }^{\circ}\text{C}$ and lower than $18\text{ }^{\circ}\text{C}$,

- average annual temperature is around 11 °C, average winter temperature around 1 °C, spring 11 °C, summer 20 °C and autumn 11 °C,
- the temperature of the warmest month is around 21 °C, and the coldest month around 0 °C,
- annual precipitation amounts to about 870 mm (distribution within a year: winter 21%, spring 22%, summer 30% and autumn 27%),
- the most common wind directions are north and northeast.

3.1.3 VEGETATION

Oak forests are characteristic for the planar and colline belt of the continental part of Croatia, so naturally Maksimir Forest Park is dominated by *Quercus* species – *Quercus robur* (pedunculate oak) in more waterlogged parts and *Quercus petraea* (sessile oak) in higher elevated parts. Where the two intermix, *Quercus cerris* (Turkey oak) can be found as well. *Quercus robur* comes with *Carpinus betulus* (common hornbeam) and also *Alnus glutinosa* (black alder), *Salix alba* (white willow), *Fraxinus excelsior* (common ash), *Ulmus minor* (field elm), *Populus alba* (white poplar) and *Tilia cordata* (small-leaved lime) can be found closer to the lakes. *Quercus petraea*, on the other hand, comes with *Fagus sylvatica* (beech) and *Robinia pseudoacacia* (black locust). In such forest stands, *Castanea sativa* (chestnut), *Prunus padus* (bird cherry) and *Corylus avellana* (hazel) can also be found (Priroda Grada Zagreba 2024). In some places, black locust comes in greater abundance as it is an invasive species in Croatia (Boršić et al. 2008). At the time of the establishment, more than 300 foreign species were planted in the Maksimir Forest Park. However, most of them have been lost until now. In that manner some gymnosperm trees were introduced, such as *Picea abies* (European spruce), *Pinus sylvestris* (European red pine) and *Pinus nigra* (black pine). Other than forest, Maksimir Forest Park has grassland and swamp vegetation as well. Swamp vegetation is characterised by various *Carex* and *Juncus* species (Priroda Grada Zagreba 2024), while the forest ground vegetation can harbour some protected and endangered species such as *Lilium martagon* (martagon lily) which is vulnerable (VU) according to the Regulation on strictly protected species (OG 144/13, 73/16).

3.1.4 MANAGEMENT

The area Maksimir Forest Park nowadays occupies used to be a simple oak forest that belonged to the central episcopal property. In 1787 Maksimilijan Vrhovec made the decision to turn it into a park, and seven years later it became open to the public. However, the true creator of

the park as we know it, was bishop Juraj Haulik in 1838. According to his ideas, numerous pavilions, romantic bridges, numerous rest areas, corners for solitude, reading poetry, lakes and watercourses were added. During that time, many new species of plants were introduced into the park, such as *Dahlia* sp., *Hortensia* sp. (hydrangea), *Ilex aquifolium* (common holly), *Buxus sempervirens* (boxwood), *Rhus typhina* (staghorn sumac), *Prunus laurocerasus* (cherry laurel), *Juniperus virginiana* (red cedar), *Picea abies* (European spruce), *Picea pungens* (blue spruce), *Pinus nigra* (black pine), *Pinus strobus* (white pine), etc. Ever since, many of the park's facilities have decayed or have been removed, e.g. some statues have been transferred to the museum of the city of Zagreb for safekeeping, and many paths have overgrown with vegetation (Priroda Grada Zagreba 2024).

In the present day, Maksimir Forest Park is managed by Nature of the city of Zagreb, a public institution for the management of protected areas of the city. Along with the day-to-day management of the Forest Park, they have renewed some historical contents as well (Priroda Grada Zagreba 2024). The public institution has lately been sowing oak seeds to restore the natural forest which is threatened by the spread of invasive black locust.

3.1.5 PREVIOUS RESEARCH DONE IN MAKSIMIR FOREST PARK

Bryological research of Maksimir Forest Park has never been abundant. There are only 24 historical records of bryophyte species from three sources: Heinz (1888), Horvat (1932) and Pavletić (1955). Very few of the recorded species are epiphytes, one of which is *Dicranum viride* (Horvat 1932). *Dicranum viride* is a NATURA 2000 target species (Council Directive 92/43/EEZ) which makes this record very valuable, especially because *D. viride* hasn't been found for over ninety years in Maksimir Forest Park, until recent rediscovery (Rimac et al. 2023).

3.2 FIELD RESEARCH

Epiphytic bryophytes were collected from five individuals of five tree species: *Quercus petraea* (sessile oak), *Carpinus betulus* (common hornbeam), *Fagus sylvatica* (European beech), *Robinia pseudoacacia* (black locust) and *Picea abies* (European spruce). This set of species included the dominant species of autochthonous forest vegetation (sessile oak, common hornbeam and European beech), the most common foreign invasive species (black locust) and the most common planted species in the area (European spruce). Altogether, I sampled 25 trees from 25 localities (Figure 6). During the field research, only trees within the forest were considered for the

sampling to avoid the anthropogenic influence, as well as the influence of higher insolation and light intensity along the paths and the Forest Park margins.

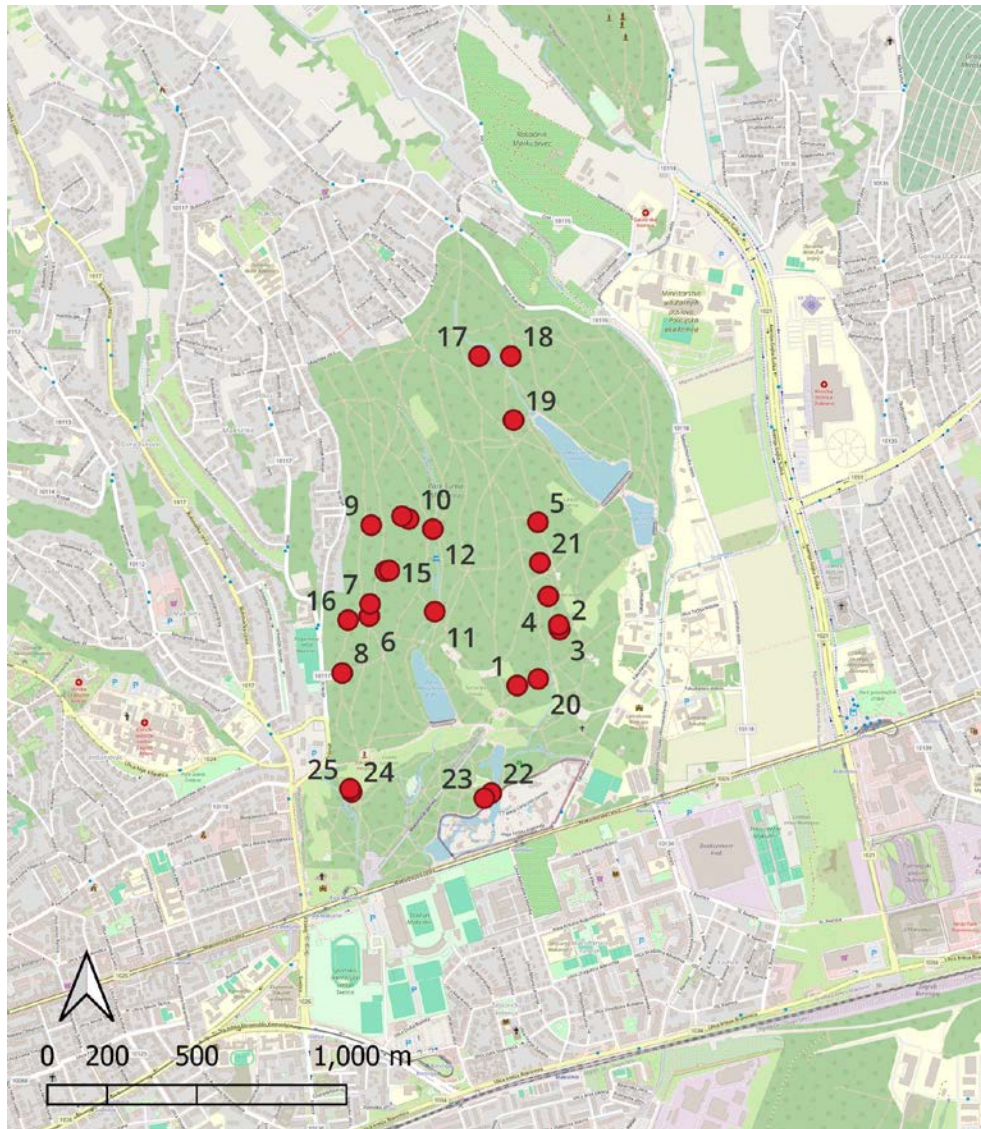


Figure 6: Open street map of the Maksimir Forest Park with indicated localities on which samples were collected. Map was created using QGIS 3.34.6 software.

I collected the samples in Maksimir Forest Park during the winter of 2023 and spring of 2024. I sampled the trees up to approximately 2 m in height. All bryophytes were collected for further identification in the laboratory. For each sampled tree I noted its coordinates, measured the

circumference at the height of 1.3 m and approximated the total coverage of epiphytic bryophytes, dominant species coverage and bark roughness. I estimated the bark roughness using a 3-degree scale (1 – smooth, 2 – relatively rough, 3 – rough).

I identified the collected bryophytes using the stereomicroscope and microscope and the following identification keys for bryophytes: Caparrós et al. 2016, Frey et al. 2006, Hallingbäck et al. 2008, Lara et al. 2009, Luth 2019 and Smith 2004. The samples will be stored at the Herbarium Croaticum and records added to the Flora Croatica Database (Nikolić 2005. -).

3.3 DATA ANALYSIS

I obtained data on growth forms and life strategies from BET data set (van Zuijlen et al. 2023). Growth forms describe the morphological organisation of a single shoot, rather than a whole colony (La Farge-England 1996). The following are listed in BET data set: acrocarpous, foliose, pleurocarpous, Sphagnum and thalloid. Life strategies, on the other hand, denote the species' adaptive traits to its habitat (During 1979). For them, I used the extended form available in BET data set, which are: annual shuttle, colonist, ephemeral colonists, pioneer colonists, fugitive, long-lived shuttle, perennial, competitive perennial, stress-tolerant perennials and short-lived shuttle.

I obtained data on life forms, biogeographical elements and Ellenberg indicator values from BRYOATT data set (Hill et al. 2017). Life forms are terms used to describe a species' colony organisation morphologically (Bates 1998). In van Zuijlen et al. (2023) the following are listed: annual, cushion, dendroid, mat, rosette, turf and weft. Biogeographical elements describe the distribution of a particular species with regard to the major biomes of the Earth, and with regard to the eastern limit of distribution seen from the Atlantic coast of Europe (Hill et al. 2017). Biogeographical elements listed in BRYOATT data set regarding major biomes are the following: arctic-montane, boreo-arctic montane, wide-boreal, boreal-montane, boreo-temperate, wide-temperate, temperate, southern-temperate and mediterranean-atlantic, while the ones regarding the eastern limit are: hyperoceanic, oceanic, suboceanic, european, eurosiberian, eurasian and circumpolar. Finally, Ellenberg indicator values for light, moisture, reaction and nitrogen were used in analysis (Hill et al. 2017). Light values span from 0 to 9, from darkness to full light; moisture values span from 1 to 12, from extreme dryness to submerged; reaction values span from 1 to 9, from extreme acidity to substrata with free calcium carbonate; nitrogen values span from 1 to 7, from extremely infertile to richly fertile sites (Hill et al. 2017).

All species have been included in the life forms' analysis. I excluded *Bryum* sp., *Cynodontium* sp. and *Orthotrichum* sp. from the life strategy analysis since I couldn't assign a value to the genera. I excluded them from biogeographical elements and Ellenberg indicator values' analyses as well, for the same reason, but I also excluded *Dicranum viride* and *Orthotrichum patens* from these analyses, because they didn't have assigned values in the used literature.

I calculated alpha diversity indices (taxa richness, Shannon-Wiener and Simpson) of bryophytes for each investigated tree species in Past 4.03 software (Hammer et al. 2001).

One-way ANOSIM test, a non-parametric test of significant difference between groups, was performed to investigate the differences in bryophyte assemblages between the five tree species. Here, Jaccard index was used as a measure of similarity. Furthermore, Indicator Species Analysis was performed to single out bryophyte species characteristic of particular tree species. These analyses were performed in Past 4.03 software (Hammer et al. 2001).

Multivariate statistical methods were used to investigate the gradient and patterns in species composition across investigated tree species. Nonparametric multidimensional scaling (MDS) with 999 permutations and Bray-Curtis similarity index was performed in Primer 6 software (Clarke and Gorley 2006). Furthermore, a detrended correspondence analysis (DCA), an indirect ordination analysis, was performed in Canoco 5 (ter Braak and Šmilauer 2012; Šmilauer and Lepš 2014). In DCA, averages of Ellenberg indicator values for light, moisture, nitrogen and pH reaction for each locality, as well as parameters measured and estimated during the field study (bark roughness, tree circumference, total bryophyte coverage, dominant bryophyte species coverage) were passively projected as vectors over the ordination to assess the possible environmental gradients.

4 RESULTS

4.1 FLORISTIC ANALYSIS

The number of recorded bryophyte taxa is 35 in total, belonging to 17 families (Appendix 1). Out of 35 recorded taxa, 31 were mosses and only 4 were liverworts. 32 were identified to the species level, while the remaining three were identified only to the genus level as they lacked sporophytes which are necessary for identification. Thirteen mosses are pleurocarpous and fifteen are acrocarpous, while three liverworts are foliose and one is thallose. There is a tendency for sampled tree species to have more acrocarpous mosses present than pleurocarpous, which results with the majority of sampled mosses altogether being acrocarpous as well. However, sessile oak has more pleurocarpous mosses than acrocarpous (Table 1).

Table 1: Number of taxa, mosses and liverworts and their growth forms recorded on each tree species and in total.

TREE SPECIES	sessile oak	common hornbeam	black locust	beech	spruce	TOTAL
NUMBER OF TAXA	25	19	10	26	19	35
MOSESSES	21	16	7	22	16	31
PLEUROCARPOUS	12	7	2	10	7	13
ACROCARPOUS	9	9	5	12	9	19
LIVERWORTS	4	3	3	4	3	4
FOLIOSE	3	2	2	3	2	3
THALLOSE	1	1	1	1	1	1

The list of all recorded species in each locality is presented in Table 2. Furthermore, the dominant species at each locality are indicated and their frequency is presented in Figure 7. If two species had the same coverage on investigated trees, they were indicated as codominant and were both considered. *Hypnum cupressiforme* is the most often occurring dominant species. It was the dominant species on all investigated black locust and spruce trees and the majority of sessile oak trees, except for a single tree on which *H. cupressiforme* was codominant with thallose liverwort *Metzgeria furcata*. Similarly, these two species were codominant on two hornbeam trees, *H. cupressiforme* was dominant on one tree, *M. furcata* on one and leafy liverwort *Frullania dilatata* was dominant on one tree of this species. Finally, *M. furcata* was dominant on three beech trees and *H. cupressiforme* on two.

Table 2: The list of recorded bryophyte species on each of the sampled trees, grouped by tree species. + indicates the species' presence, while D indicates the dominant species and C indicates the co-dominant species in the particular locality.

SPECIES/ LOCALITY	SESSILE OAK					COMMON HORNBEAM					BLACK LOCUST					BEECH					SPRUCE					
	1	2	8	9	10	3	5	11	12	16	6	7	13	14	15	4	17	19	20	21	18	22	23	24	25	
<i>Amblystegium serpens</i>	+	+				+	+										+	+	+							+
<i>Anomodon viticulosus</i>	+																									
<i>Brachytheciastrum velutinum</i>		+					+										+		+			+				
<i>Brachythecium rutabulum</i>	+	+					+												+		+					
<i>Brachythecium salebrosum</i>		+																								
<i>Bryum</i> sp.		+								+																
<i>Cynodontium</i> sp.			+	+	+			+				+	+													
<i>Dicranoweisia cirrata</i>					+							+	+	+	+							+			+	
<i>Dicranum tauricum</i>					+									+												
<i>Dicranum viride</i>					+												+	+								
<i>Frullania dilatata</i>		+				D	+	+	+	+	+					+	+	+	+	+	+					
<i>Homalia trichomanoides</i>	+						+										+	+								
<i>Homalothecium sericeum</i>	+																+					+				
<i>Hypnum cupressiforme</i>	D	C	D	D	D		+	C	C	D	D	D	D	D	D	+	+	D	D	+	D	D	D	D	D	D
<i>Isoetecium alopecuroides</i>					+											+	+									
<i>Kindbergia praelonga</i>									+																	
<i>Leskea polycarpa</i>	+															+			+							+
<i>Lewinskya affinis</i>																	+					+				
<i>Lewinskya speciosa</i>		+					+		+	+																
<i>Metzgeria furcata</i>	+	C	+	+		+	D	C	C				+	+		D	D	+	+	D	+	+	+			
<i>Orthotrichum diaphanum</i>																				+		+				+
<i>Orthotrichum pallens</i>		+															+									
<i>Orthotrichum patens</i>						+				+							+					+				

The most represented families in total are Orthotrichaceae (15.42%), Hypnaceae (11.94%), Metzgeriaceae (8.96%), Pylaisiadelphaceae (8.46%) and Brachytheciaceae (7.46%) (Figure 8). The most represented families found on oak trees are Brachytheciaceae (11.11%), Hypnaceae (11.11%), Pylaisiadelphaceae (11.11%), Orthotrichaceae (11.11%), Metzgeriaceae (8.89%) and Rhabdoweisiaceae (8.89%), on hornbeam are Orthotrichaceae (19.05%), Frullaniaceae (11.90%), Radulaceae (11.90%), Hypnaceae (9.52%), Metzgeriaceae (9.52%) and Pottiaceae (9.52%), on black locust are Rhabdoweisiaceae (27.27%), Hypnaceae (22.73%) and Pylaisiadelphaceae (22.73%), on beech are Orthotrichaceae (18.97%), Frullaniaceae (8.62%), Hypnaceae (8.62%), Metzgeriaceae (8.62%), Neckeraceae (8.62%), Brachytheciaceae (6.90%), Pottiaceae (6.90%) and Radulaceae (6.90%), while the most abundant families found on spruce are Orthotrichaceae (18.18%), Hypnaceae (15.15%) and Pottiaceae (15.15%) (Figure 9).

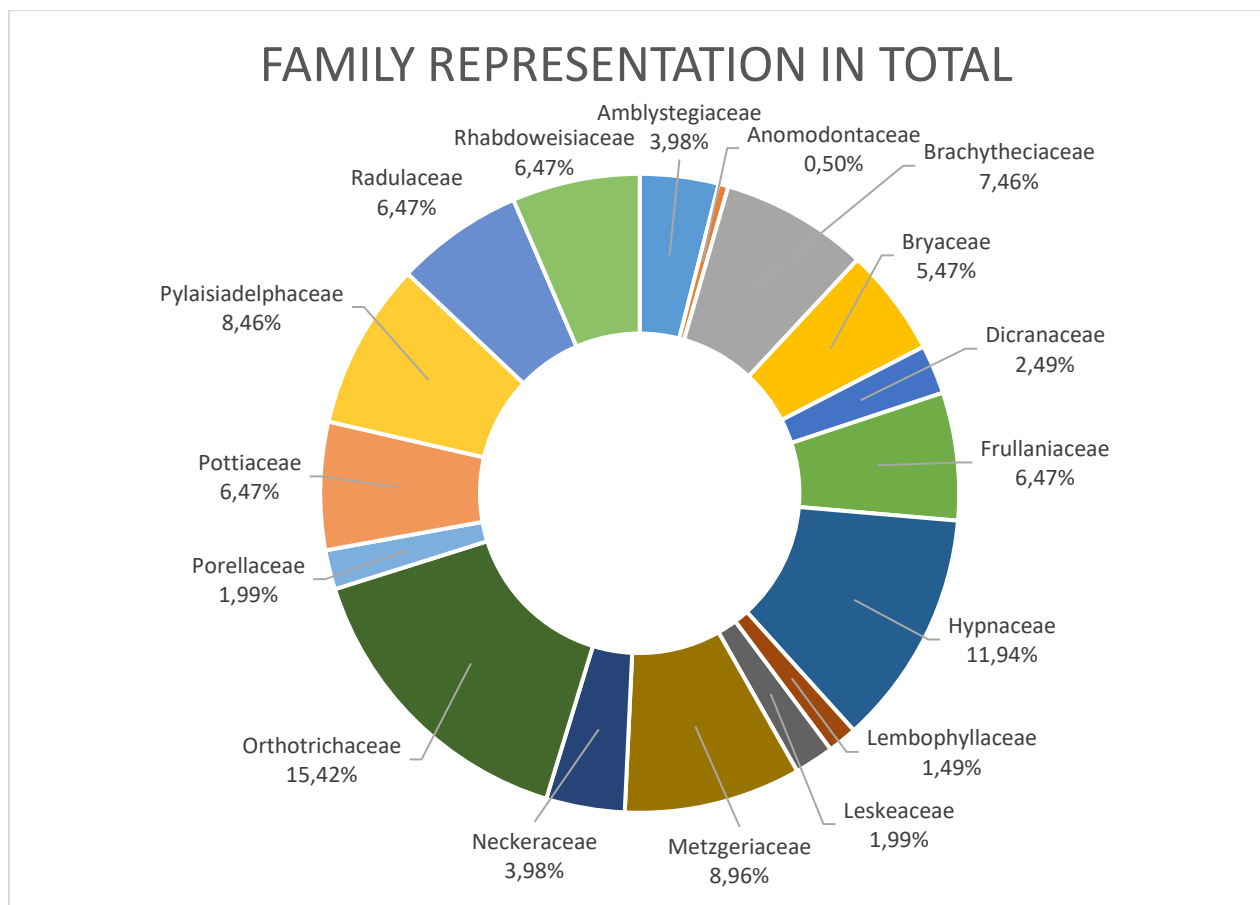


Figure 8: Representation of bryophyte families in the total sample.

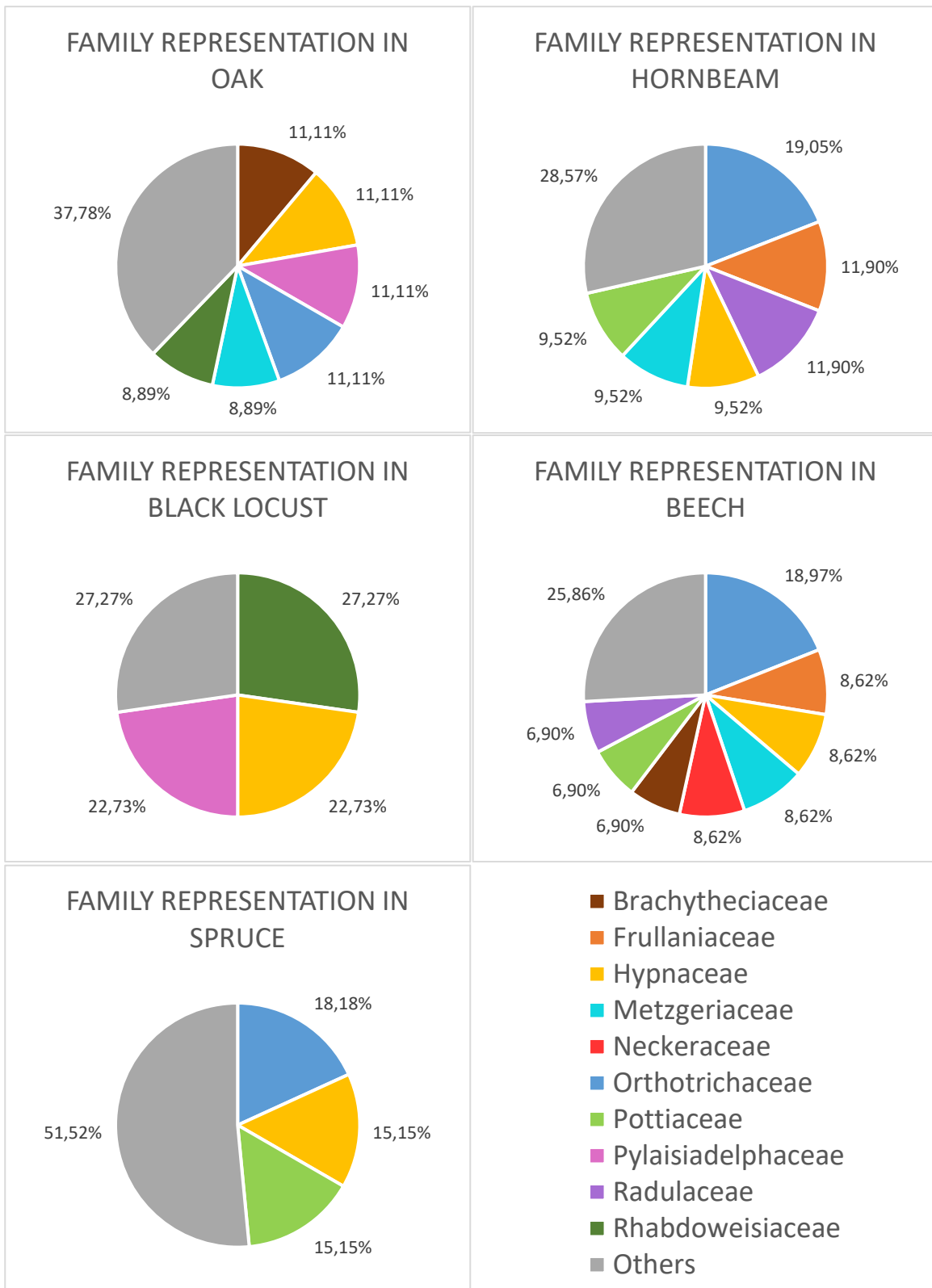


Figure 9: The most represented bryophyte families sampled from each tree species.

The most frequent species in total are *Hypnum cupressiforme* (24), *Metzgeria furcata* (18), *Platygyrium repens* (17), *Frullania dilatata* (13), *Radula complanata* (13), *Syntrichia papillosa* (12) and *Ptychostomum moravicum* (9) (Figure 10). The most frequent taxa found on oak trees are *Hypnum cupressiforme* (5), *Platygyrium repens* (5), *Metzgeria furcata* (4), *Cynodontium* sp. (3) and *Zygodon rupestris* (3), on hornbeam they are *Frullania dilatata* (5), *Radula complanata* (5), *Hypnum cupressiforme* (4), *Metzgeria furcata* (4), *Syntrichia papillosa* (4) and *Lewinskya speciosa* (3), on black locust they are *Hypnum cupressiforme* (5), *Platygyrium repens* (5) and *Dicranoweisia cirrata* (4), on beech *Frullania dilatata* (5), *Hypnum cupressiforme* (5), *Metzgeria furcata* (5), *Radula complanata* (4), *Syntrichia papillosa* (4), *Amblystegium serpens* (3), *Platygyrium repens* (3) and *Pseudanomodon attenuatus* (3), and on spruce *Hypnum cupressiforme* (5), *Syntrichia papillosa* (4), *Metzgeria furcata* (3) and *Ptychostomum moravicum* (3) (Figure 11).

Dicranum viride, small acrocarpous moss, was found on two beech trees and a single oak tree. It is a NATURA 2000 target species listed on Annex II of Habitats Directive that requires monitoring (Council Directive 92/43/EEZ).

SPECIES REPRESENTATION IN TOTAL

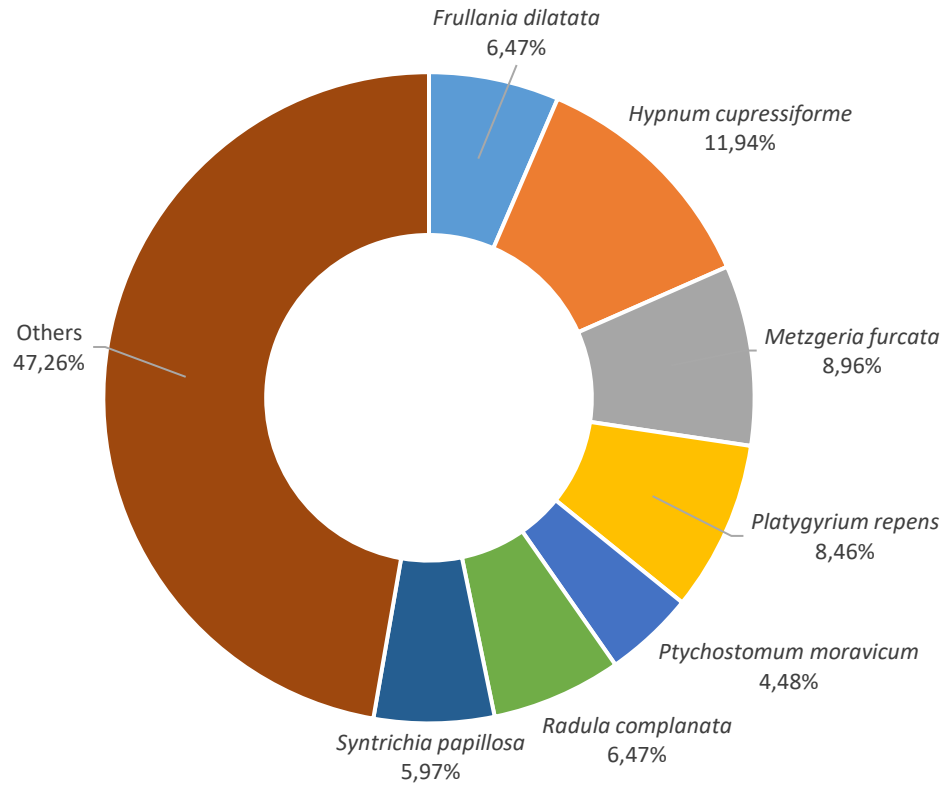


Figure 10: Representation of bryophyte taxa in a total sample.

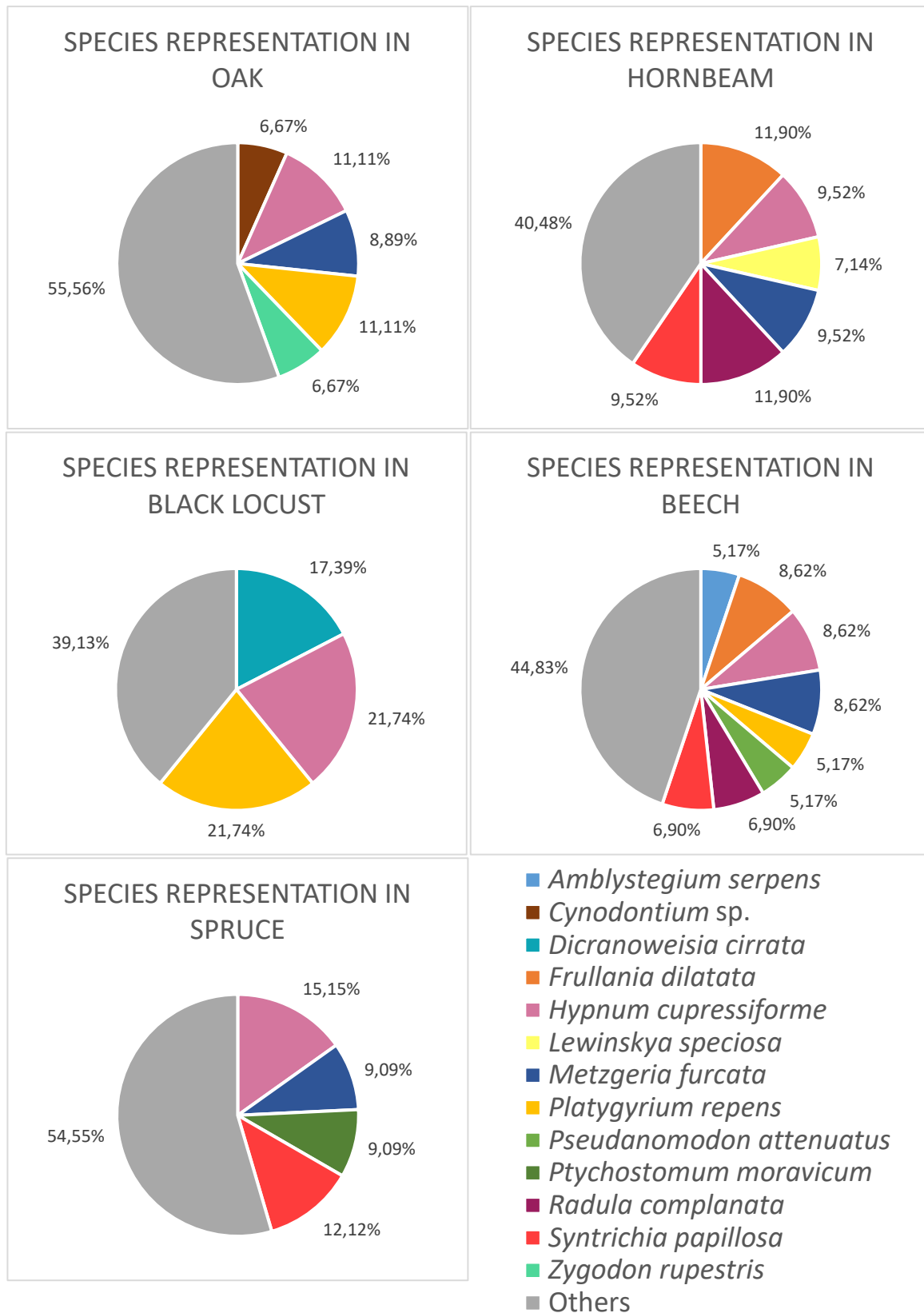


Figure 11: Representation of bryophyte taxa for each tree species.

4.2 BRYOPHYTE DIVERSITY

Considering the taxa richness (Table 3), the tree species richest in epiphytic bryophytes is beech, with relatively little variation (Figure 12). It is ranging from 7 to 16 taxa recorded on a single tree, while the average number of taxa is 11.6, which is almost the same as the mean number (12). Oak trees can be rich as well, but they vary greatly, from only 4 taxa up to 16 taxa. The average number of taxa being 9 and the mean number being 7, are lesser than that of beech. Similarly, hornbeam has a range from 6 to 11 taxa, with the average being 8.4 and the mean being 7. Bryophyte taxa richness is the lowest in black locust with the minimum amount of taxa recorded being just 3 and maximum being 6. The average number of recorded taxa on black locust is 4.6, while the mean number is 5. Spruce is in a similar position (the minimum of just 2 recorded taxa), but with one spruce tree being inconsistently rich (15 recorded taxa) (Table 2). The average is then 6.6 and the mean number of recorded taxa is 5 for spruce.

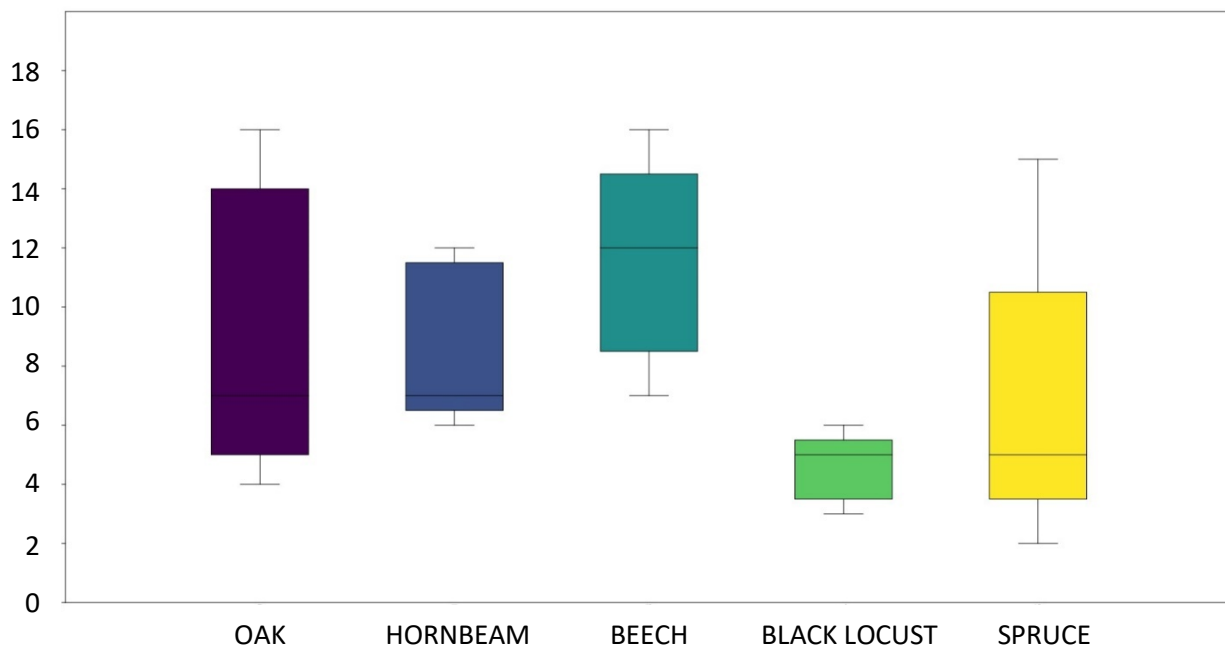


Figure 12: Number of bryophyte taxa found on each tree species.

Shannon-Wiener and Simpson Diversity Indices (Table 3) showed similar patterns across the investigated tree species (Figure 13 and Figure 14).

Table 3: Taxa richness (TR), Simpson (Simp.) and Shannon-Wiener (Shan.) Diversity Indices of bryophytes for each locality (tree individual).

LOCALITY	TR	Simp.	Shan.
1	12	0.9167	2.485
2	16	0.9375	2.773
3	6	0.8333	1.792
4	7	0.8571	1.946
5	12	0.9167	2.485
6	4	0.75	1.386
7	5	0.8	1.609
8	4	0.75	1.386
9	6	0.8333	1.792
10	7	0.8571	1.946
11	7	0.8571	1.946
12	7	0.8571	1.946
13	5	0.8	1.609
14	6	0.8333	1.792
15	3	0.6667	1.099
16	11	0.9091	2.398
17	16	0.9375	2.773
18	5	0.8	1.609
19	12	0.9167	2.485
20	13	0.9231	2.565
21	10	0.9	2.303
22	15	0.9333	2.708
23	2	0.5	0.6931
24	6	0.8333	1.792
25	5	0.8	1.609

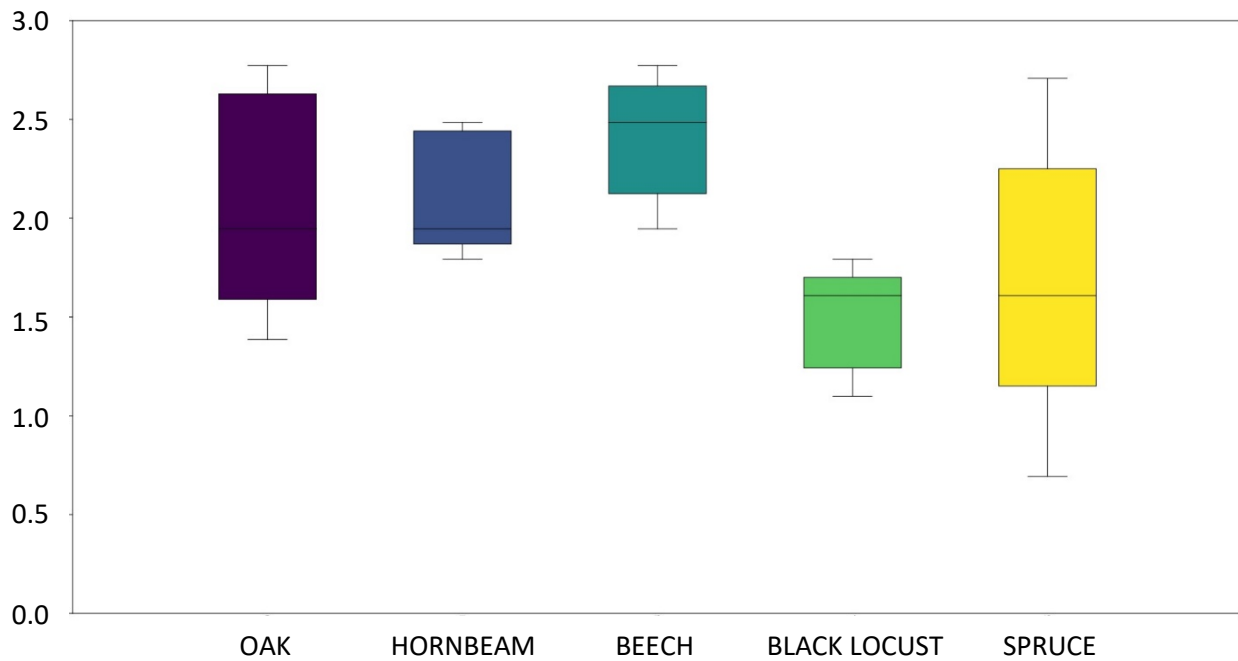


Figure 13: Shannon-Wiener Diversity Index of bryophytes for each tree species.

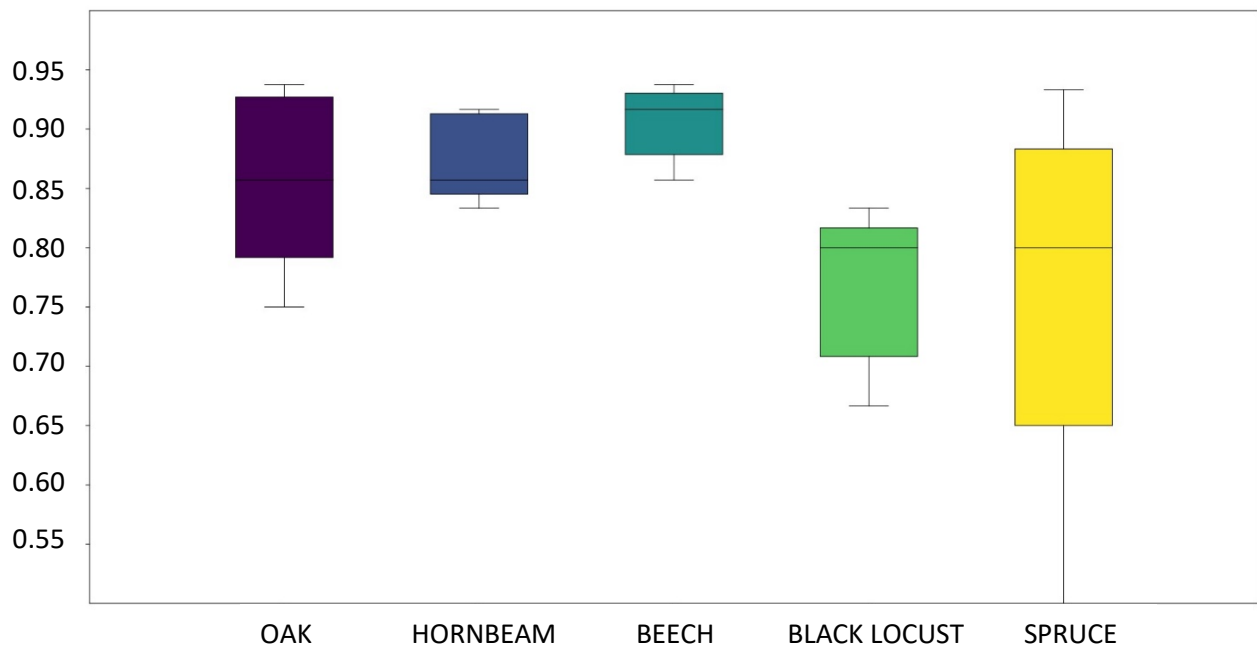


Figure 14: Simpson Diversity Index of bryophytes for each tree species.

4.3 LIFE FORM ANALYSIS

The predominant life form on all investigated tree species is a smooth mat (oak 31.11%, hornbeam 38.10%, black locust 52.17%, beech 32.76%, spruce 30.30% and total 35.32%) (Figure 15, Appendix 2). The second most common life form on oak and beech trees is a rough mat (oak 20.00%, beech 17.24%), while interestingly, it is completely lacking from black locust. The second most common life form on hornbeam, black locust, spruce and in total is cushion (hornbeam 19.05%, black locust 26.09%, spruce 21.21% and total 17.41%). On all sampled trees thalloid mat, turf and tuft can also be found, while fans can be found on oak, hornbeam and beech trees, and dendroid life forms can be found only on oak and beech trees in small percentages.

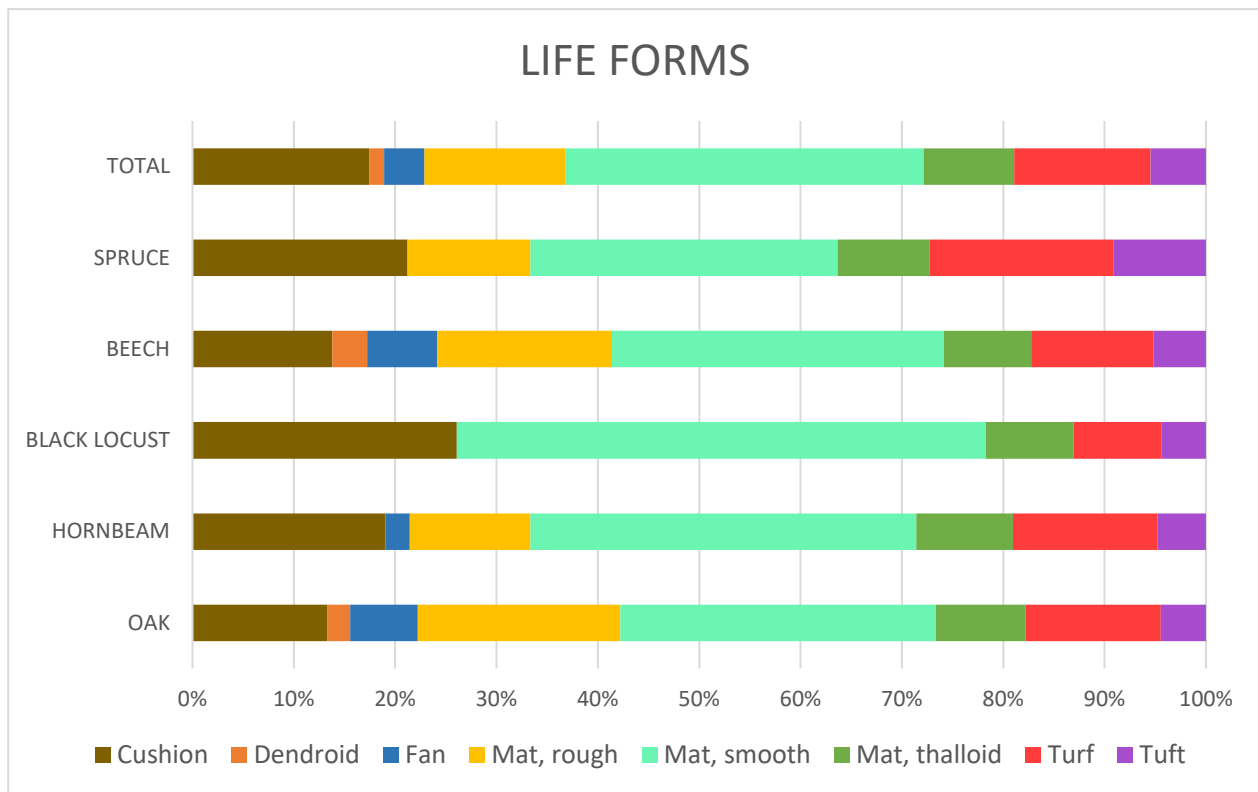


Figure 15: The share of each bryophyte life form in total and on each tree species.

4.4 LIFE STRATEGY ANALYSIS

Overall, the most dominant life strategy was stress-tolerant perennial (27.08%), followed by perennial (22.92%) and colonist (21.86%) (Figure 16, Appendix 2). Oak trees are dominated by stress-tolerant perennial (34.15%) and perennial (26.83%) life strategies. Hornbeam trees are colonised by colonists (25.00%), long-lived shuttles (25.00%), perennials (20.00%) and stress-tolerant perennials (17.50%) with relatively similar shares, while competitive perennial life strategy was not found on this tree species. Black locust is highly dominated by stress-tolerant perennials (47.62%), followed by pioneer colonists (19.05%), while there were no short-lived shuttle species found on it. Beech is, much like hornbeam, colonised in high amounts by perennials (28.07%), stress-tolerant perennials (24.56%), colonists (19.30%) and long-lived shuttle species (15.79%). Spruce trees are highly dominated by colonists (42.42%), followed by perennials and stress-tolerant perennials in equal amounts (21.21%), while short-lived shuttle species were not found on this tree species.

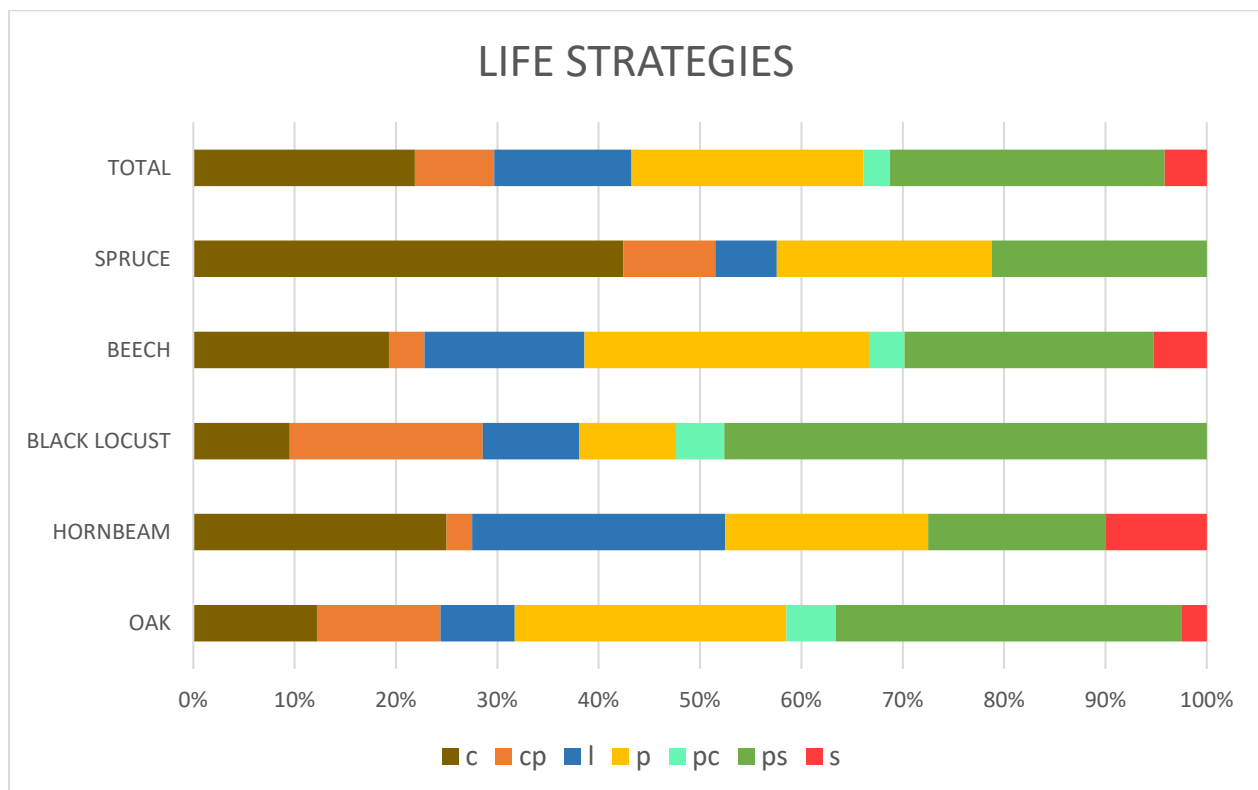


Figure 16: The share of each bryophyte life strategy in total and on each tree species. Abbreviations in the legend stand for c – colonist, cp – pioneer colonist, l – long-lived shuttle, p – perennial, pc – competitive perennial, ps – stress tolerant perennial, s – short-lived shuttle

4.5 BIOGEOGRAPHICAL ELEMENTS

All recorded species belong to one of the six major biome categories: boreo-arctic montane, boreo-temperate, temperate, wide-boreal, wide-temperate or southern-temperate. The majority of species in total belong to either the temperate (38.38%) or boreo-temperate (31.89%) element. The species found on oak, hornbeam and beech trees follow this pattern as well (temperate element on oak – 32.50%, boreo-temperate element on oak – 37.50%, temperate element on hornbeam – 34.21%, boreo-temperate element on hornbeam – 31.58%, temperate element on beech – 33.33%, boreo-temperate element on beech – 42.59%). Species collected from black locust and spruce trees mainly belong to the temperate category (black locust – 52.38%, spruce – 50.00%). Wide-temperate and southern-temperate elements are present on all tree species and in the total sample with similar percentages. Precisely, in the total sample, the share of wide-temperate element amounts to 12.97%, and that of southern-temperate to 14.05%. The exception regarding these two elements is black locust with 23.81% of recorded bryophyte species belonging to wide-temperate element, making it the second most abundant element in black locust after the temperate element. Boreo-arctic montane element was found only on oak and hornbeam, represented with a low number of species, while only one wide-boreal species was found on oak (Figure 17).

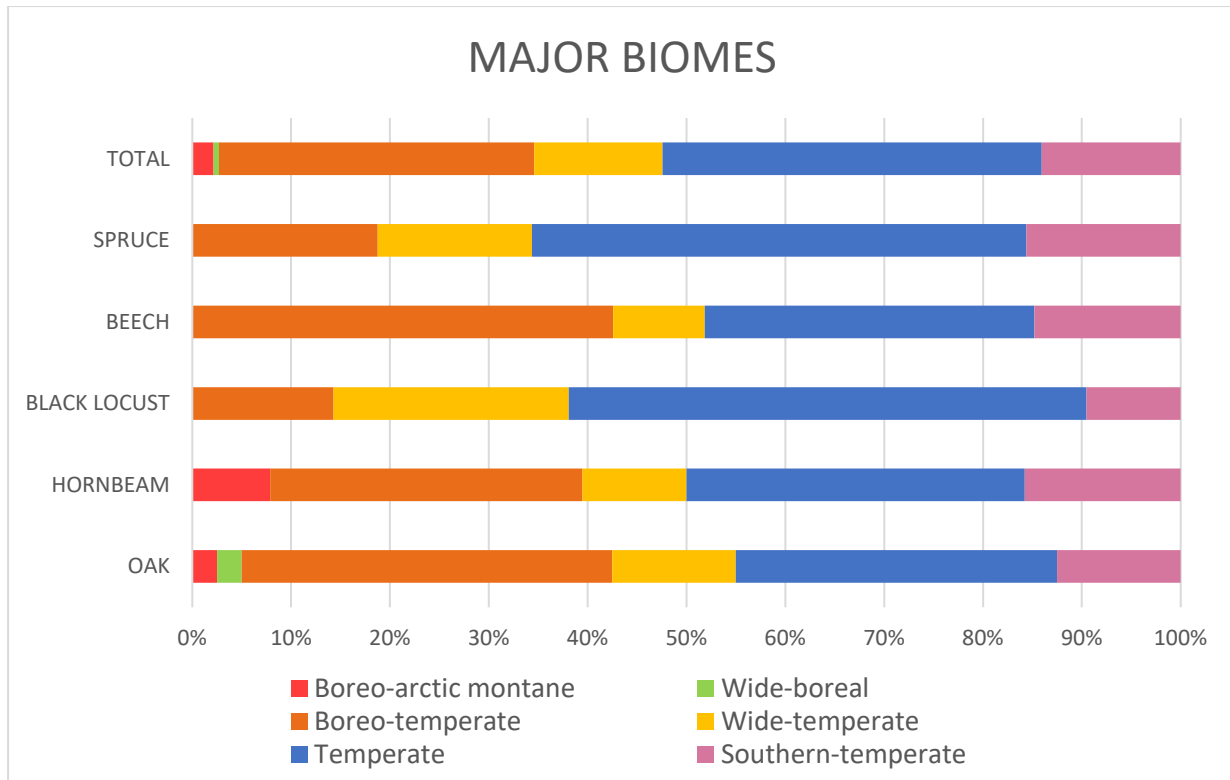


Figure 17: The share of bryophyte species belonging to different major biomes in total and on each tree species.

The following eastern limit categories were recorded: circumpolar, eurasian, eurosiberian, european or suboceanic. The share of the circumpolar element was dominant in the total sample (56.76%) and on each tree species (oak – 70.00%, hornbeam – 55.26%, black locust – 61.90%, beech – 51.85%), except spruce. On spruce, the circumpolar and european elements were equally represented with 46.88% each. In all other species, as well as in a total sample, european element is the second most represented with the following percentages: total – 32.98%, oak – 25.00%, hornbeam – 31.58%, black locust – 33.33%, beech – 33.33%. Eurasian element was recorded in all tree species, however, it was represented with quite a low number of bryophyte species. Furthermore, small shares of eurosiberian element are present on oak, beech and spruce, while the suboceanic element was limited to beech and represented with just two bryophytes (Figure 18).

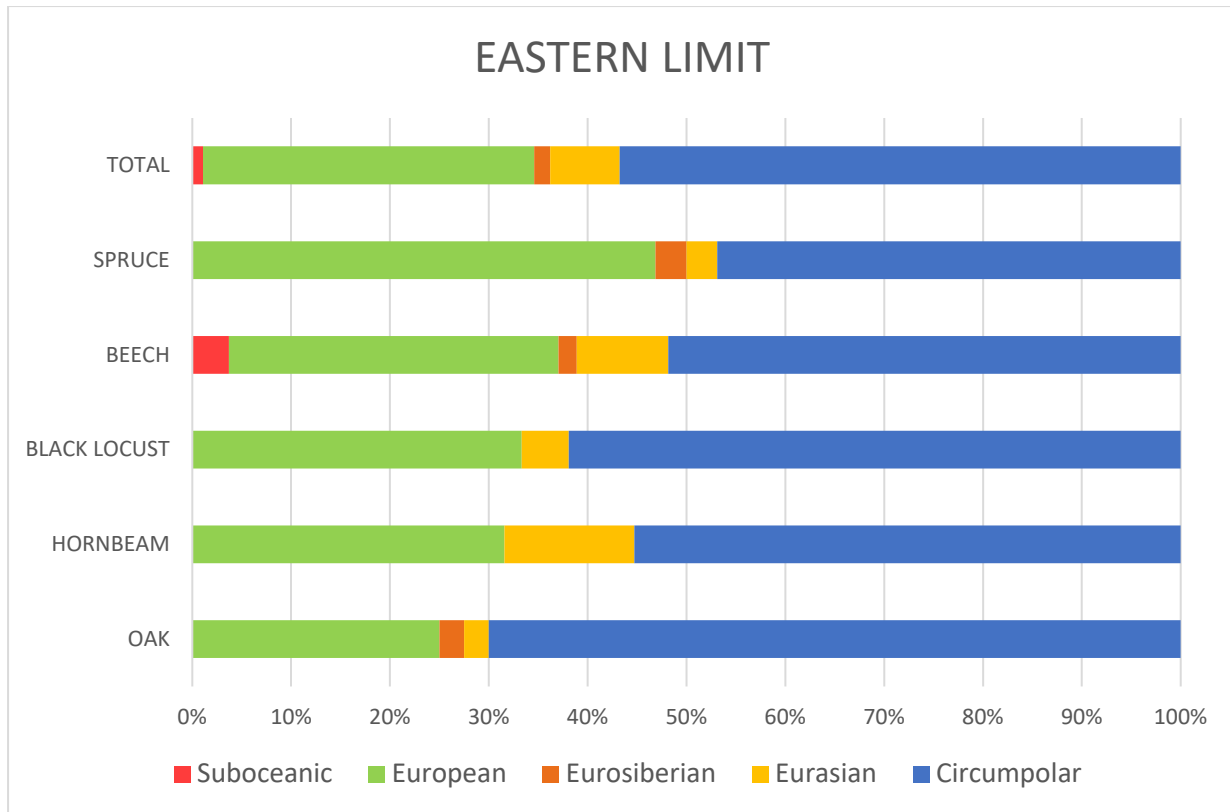


Figure 18: The share of eastern limit categories of recorded bryophyte species in total and on each tree species.

4.6 ANALYSIS OF SIMILARITIES

ANOSIM test showed that there is a statistically significant difference between the assemblages of epiphytic bryophytes on different tree species, although with some overlap (Table 4). Furthermore, the pairwise ANOSIM test showed that bryophyte assemblages from black locust are highly different from those on hornbeam and beech, and different but with a considerable overlap from those in spruce. Bryophyte assemblages recorded on spruce are different from those on hornbeam and beech as well, however, there is some overlap in species composition given the relatively low R statistics (Table 5). Bryophyte composition on oak significantly differed from that on hornbeam, again with some overlap.

Table 4: Global ANOSIM test results for all sampled tree species.

Permutation N	9999
Mean rank within	101,6
Mean rank between	160,3
R	0,3913
p (same)	0,0001

Table 5: Pairwise ANOSIM test results. Statistically significant values ($p < 0.05$) are marked in colour. The abbreviations stand for: O – oak, H – hornbeam, B – beech, L – black locust, S – spruce.

R values						p values					
	O	H	B	L	S		O	H	B	L	S
O		0,434	0,348	0,11	0,224	O		0,0403	0,054	0,1847	0,0957
H	0,434		0,09	0,786	0,342	H	0,0403		0,2592	0,0078	0,0154
B	0,348	0,09		0,9	0,304	B	0,054	0,2592		0,0087	0,0323
L	0,11	0,786	0,9		0,352	L	0,1847	0,0078	0,0087		0,0307
S	0,224	0,342	0,304	0,352		S	0,0957	0,0154	0,0323	0,0307	

4.7 INDICATOR SPECIES ANALYSIS

Indicator Species Analysis revealed three indicator species characteristic for hornbeam trees (leafy liverworts *Frullania dilatata* and *Radula complanata* and acrocarpous moss *Lewinskya speciosa*), three indicator species for beech (*Frullania dilatata*, pleurocarpous *Pseudanomodon attenuatus* and acrocarpous *Pulviger a lyellii*) and one indicator species for black locust (minute acrocarpous species *Dicranoweisia cirrata*) (Appendix 4).

4.8 MULTIVARIATE ANALYSIS

Multidimensional scaling did not reveal discrete groups of tree species based on their epiphytic bryophyte flora. However, black locust trees are situated on the right side of the ordination diagram and there is a grouping of four beech trees and four hornbeam trees on the left side of the diagram indicating their similarity in species composition. Oak trees are scattered along the first axis, with two hosting bryophyte assemblages of higher diversity (Table 3) and more similar to those found on beech trees and three with lower bryophyte diversity with bryophyte species composition more similar to that found on the black locust (Figure 19). Spruce was scattered along both axes of the ordination diagram, with individuals 23 and 25 differing from other

investigated trees the most. Spruce 23 was inhabited by only two species: *Hypnum cupressiforme* and *Metzgeria furcata*, while spruce tree 25 was characterized by a low number of species (5), with two found only on this tree.

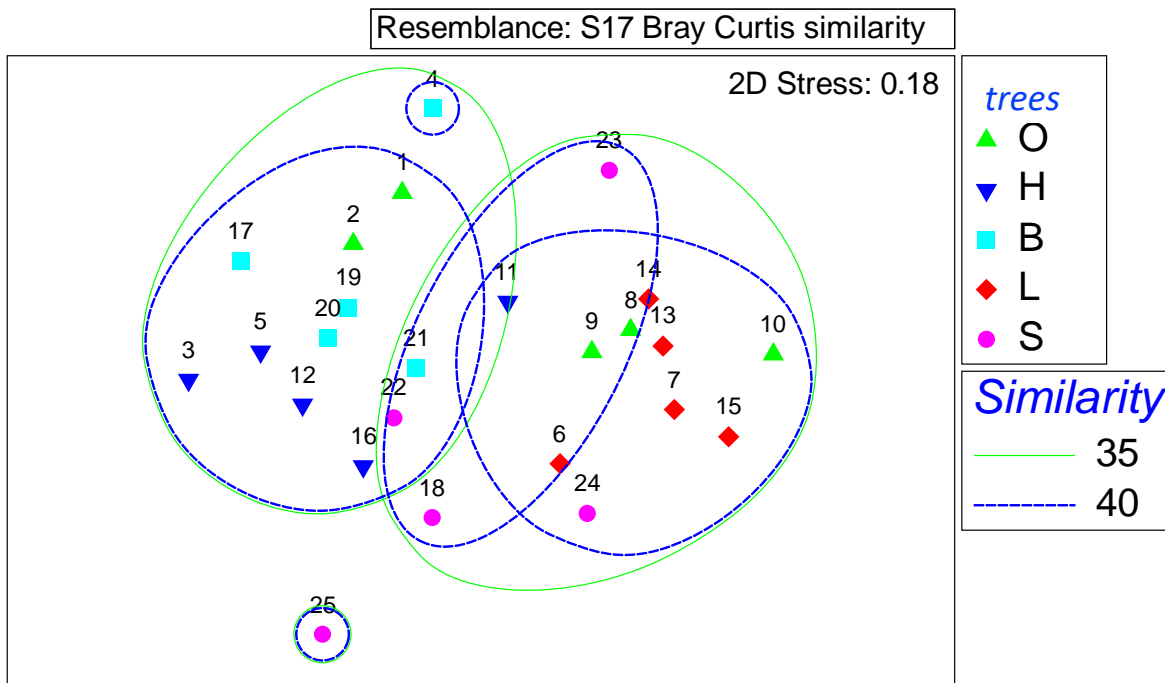


Figure 19: Ordination plot of the first two axes of multidimensional scaling (MDS) of phorophyte similarity based on epiphyte flora. The abbreviations stand for: O – oak, H – hornbeam, B – beech, L – black locust, S – spruce.

In DCA analysis, the eigenvalue of axis 1 was 0,36 and that of axis 2 was 0,20. The lengths of axes 1 and 2 were 2,58 and 2,4, respectively. DCA analysis showed similar patterns considering the bryophyte species composition on different tree species with no discrete group evident along the first two axes. However, a grouping of black locust trees, which are characterised by a rougher bark texture, along with several oak trees on the right of the ordination diagram was observed (Figure 20). These trees were characterised by species such as *Hypnum cupressiforme*, the most common dominant species as well as another common pleurocarpous bryophyte *Platygyrium repens* and acrocarpous species *Dicranoweisia cirrata* and *Dicranum tauricum*. On the other hand, hornbeam and beech trees were characterised by smoother bark and higher share of bryophytes with higher indicator values for light, nitrogen and substrate reaction when compared with black

locust trees. Beech trees were furthermore characterised by species with higher indicator values for moisture. Sampled spruce trees are in this instance, once again, rather scattered on the plot.

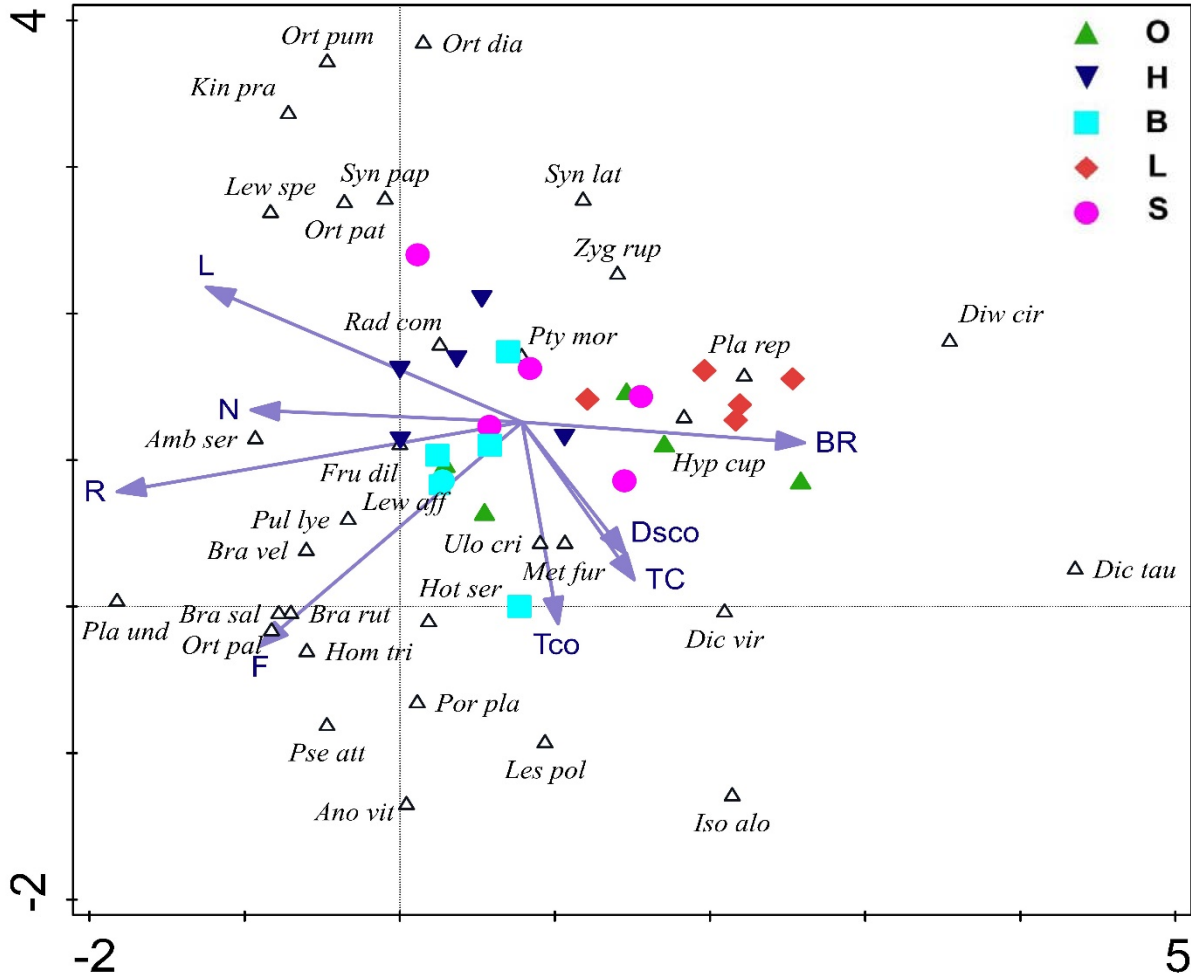


Figure 20: DCA analysis of samples (trees) and bryophyte species with ecological indicator values and measured and assessed ecological parameters passively projected as vectors. The abbreviations stand for: O – oak, H – hornbeam, B – beech, L – black locust, S – spruce, L – Ellenberg light value, N – Ellenberg nitrogen value, R – Ellenberg pH value, F – Ellenberg moisture value, Tco – total coverage, TC – tree circumference, DSCO – dominant species coverage, BR – bark roughness.

5 DISCUSSION

Out of 35 recorded taxa, 31 are mosses and only 4 are liverworts. This is due to the fact that liverworts in general have a much lower number of representatives and are associated with habitats that have constant and high moisture levels (Vanderpoorten and Goffinet 2009), which is not true for the microhabitat such as tree bark in Maksimir Forest Park. The most common dominant species on all sampled tree species, except beech, was *Hypnum cupressiforme*. On beech, the most frequently dominant species was *Metzgeria furcata*. Both *H. cupressiforme* and *M. furcata* are some of the most commonly recorded species in Croatia (Nikolić 2005 -). It is worth mentioning that hornbeam and beech trees have a relatively high frequency of *Frullania dilatata*, *M. furcata* and *Radula complanata*, which are all liverworts. Both hornbeam and beech trees have a smooth bark, which *F. dilatata* and *R. complanata* appear to prefer (Figure 20). Furthermore, *H. cupressiforme*, the most common dominant species is highly associated with rough bark, meaning that on smooth bark, where *H. cupressiforme* doesn't thrive, other species can grow dominantly as well. Ódor et al. (2013) recorded *Hypnum cupressiforme*, *Platygyrium repens*, *Isothecium alopecuroides*, *Radula complanata* and *Frullania dilatata* as the most common epiphytic species in a temperate managed forest in Hungary, which is comparable to this research considering the study area and the results. Namely, *H. cupressiforme*, *P. repens*, *R. complanata* and *F. dilatata* were among the most commonly found species in Maksimir Forest Park as well. However, while in this research *F. dilatata* was characteristic for hornbeam and beech, and *R. complanata* for hornbeam, Ódor et al. (2013) found that these species were more associated with oak. Furthermore, Ódor et al. (2013) concluded that small cushion-forming acrocarpous bryophytes were associated with these two tree species, which was the case in Maksimir as well. Namely, *Ulota crispula* and several *Orthotrichum* species were recorded predominantly on beech and hornbeam trees in Maksimir Forest, while *Lewinskia speciosa* and *Pulvigerella lyellii* were indicator species of hornbeam and beech, respectively.

Two of the sampled oak trees in Maksimir Forest are rich in epiphytic bryophytes, while the other three sampled oak trees are rather poor. There is no visible pattern in the measured parameters that would discern between the two groups, but a lot of the bryophyte species found on richer oak trees and not found on the other ones, exhibit a higher Ellenberg indicator value for moisture (*Amblystegium serpens*, *Anomodon viticulosus*, *Brachytheciastrum velutinum*, *Brachythecium*

rutabulum, *Brachythecium salebrosum*, *Pseudanomodon attenuatus*). It is known that many epiphytic bryophytes, especially mat- and weft-forming species prefer phorophytes with rough, i.e. wrinkle rich bark, such as in oak, which provides a humid microhabitat (Ódor et al. 2013). Furthermore, in DCA analysis these two oak trees grouped with beech trees rich in epiphytic species, some of which have higher ecological indicator values for moisture as well. That is to indicate that the sampled beech trees may have also been providing a more moist microhabitat, although having a smoother bark. This can be influenced by surrounding tree species, i.e. their density and canopy cover, by the density of the shrub layer and the vicinity of waterbodies, which all enhance local air humidity (Boudreault et al. 2000, Sillett et al. 2000, Cobb et al. 2001, Żołnierz et al. 2022). However, these environmental parameters were not included in this research. In Maksimir Forest, beech harboured the highest overall diversity of epiphytic bryophytes, followed by oak and hornbeam. This finding is different than what was observed in temperate forests in Hungary, where oak was the richest tree regarding the epiphytic bryoflora, followed by relatively similar beech and hornbeam. Epiphyte diversity depends not only on the bark roughness, with rougher bark promoting higher diversity, but also on the tree's height and diameter, which are good surrogates for tree age (Király et al. 2013). This promotes epiphyte diversity by providing a larger area, higher microhabitat heterogeneity and longer colonization time available in the case of older trees (Fritz et al. 2008, Király et al. 2013). Beech trees sampled in Maksimir Forest had quite a large diameter at breast height, compared with hornbeam, which may be a reason for the higher diversity observed in beech. Another possible reason for beech trees being so rich in bryophytes could be that *H. cupressiforme*, as previously mentioned, thrives on rough bark, which is very smooth in beech, so *H. cupressiforme* growing less dominantly may open up space for other species to develop.

Black locust, although poor in species number, is the only tree species that differentiated the best from other tree species based on its epiphytic bryophyte assemblages, with *Dicranoweisia cirrata* being the most characteristic of this tree species. Although it has a rough bark, it harboured the lowest bryophyte species number and overall diversity. The diversity of epiphytic bryophytes and their communities are highly influenced by the physical and chemical properties of bark, such as pH or nutrient content. These factors were not included in this research and might be important in explaining the low diversity observed in black locusts as well as the potential negative impact of allelopathic toxins which are known from this invasive tree species. Low species richness in spruce

can be explained by the fact that its bark is peeling off in pieces, which is a stressor for any epiphytic species, hindering their establishment and growth. Furthermore, the bark is very acidic, which is not preferred by most bryophytes and the canopy is such that minimizes the lead of rainwater to the trunk creating very dry and unsuitable conditions (Barkman 1958). One sampled spruce tree, however, had an inconsistently high amount of epiphytic bryophyte species, as well as coverage. Since the total amount of spruce trees sampled was only five, just one standing out doesn't provide a significant insight.

Dicranum viride, small acrocarpous moss, was found on two beech trees and a single oak tree. It is known that this species grows mostly on beech trees but can be found on *Ulmus*, *Tilia*, *Quercus* and rarely *Betula* species. It is most often found on tree trunks of middle age. The biggest threat to this species is forest management, because cutting down the trees directly reduces the amount of favourable microhabitat within the forest. Additionally, this leads to more sunlight reaching the tree trunks, which negatively affects the moisture (Oikon d.o.o. 2023). It is, hence, important for the Nature of the city of Zagreb to continue its practice of not cutting down trees unless necessary. Another threat is air pollution which changes the pH of the environment (Oikon d.o.o. 2023). Its occurrence thus indicates that the air in Maksimir Forest Park is unpolluted. Since it is a NATURA 2000 target species, its presence has to be monitored. The monitoring of the state of the species is carried out in pre-selected quadrants of 1 × 1 km. The population size estimation methodology consists of counting trunks on which the species grows and individual cushions of the species on the trunk, as well as assessing the state of the population. The state is considered good if more than 5 trunks on the plot are colonised by *D. viride*, if 1-4 trunks are colonised, the state is considered insufficient and if there is no recorded presence at all, it is considered bad. It is also necessary to assess the quality of the habitat for the species. The assessment of habitat quality is evaluated by determining the presence and intensity of logging and shading of the site (Oikon d.o.o. 2023).

The predominant life form in this research being a smooth mat, followed by a rough mat on oak and beech is consistent with Maksimir Forest Park's climate conditions and microclimatic conditions characteristic of temperate forest. The light intensity in forest habitat is low and there is no possibility that the photosynthetic apparatus of bryophytes could be damaged. Additionally, this habitat is not too dry, meaning species can afford to leave more of their surface exposed for evaporation. Mat life form provides more photosynthetic surface, which is beneficial in shaded

forest habitats, but lacks adaptations which would prevent water loss or protection from solar radiation (Bates 1998). However, in some tree species (hornbeam, black locust and spruce), the second most common life form is cushion, which employs completely opposite survival tactics than the mat (Bates 1998). That can be explained by the fact that each tree can provide several different microhabitats, with clear vertical zonation of the species and different growth and life forms (Fritz 2009, McCune 1993). This is governed mainly by microclimatic factors such as light availability and air and substrate humidity (Hosokawa and Odani 1957, Peck et al. 1995), with pleurocarpous species growing as mats being confined to more humid tree bases, while acrocarpous cushions can thrive under the dryer conditions and on parts of a tree more exposed to the sunlight.

In the total sample, the predominant life strategy is stress-tolerant perennial, followed by perennial and colonist life strategies. Since trees have been sampled from bases up to 2 m in height, it is not surprising that the majority of species are perennials as tree bases are quite stable environments. Colonists could then occupy newer or less stable environments, such as young trees or the peeling bark of spruce trees (During 1979). Indeed, if each tree species is looked at separately, the most predominant life strategy on spruce is by far the colonist. Oak and beech trees are dominated by perennials and stress-tolerant perennials, while black locust is highly dominated by stress-tolerant perennials. While oak and beech trees fit into the above-written explanation, black locust being dominated by stress-tolerant perennials indicates that its bark possesses a constant but not lethal stressor. On hornbeam, on the other hand, colonist and long-lived shuttle life strategies were found to be the most common in equal amounts, indicating a major periodical stressor (During 1979).

Regarding biogeographical elements, the temperate one was predominantly represented in the total sample, as well as on oak, hornbeam, beech and spruce trees, followed by a boreo-temperate element, which corresponds well to the climatic and biogeographic characteristics of the investigated area. Namely, the temperate element refers to the species whose main distribution is in the broadleaved deciduous forests with a moderate climate, while boreo-temperate element refers to the species which can be more or less equally found in both boreal and temperate zones (Mark et al. 1998). Similarly, the predominant major biome element found on black locust trees is also temperate, but the second most commonly found one is wide-temperate element, which also fits the climate conditions as wide-temperate element refers to species whose distribution includes boreal, temperate and mediterranean zones, albeit centered on the temperate. The majority of

recorded eastern limit elements in total and in each sampled tree species, except spruce, was circumpolar, followed by european element. In spruce, the circumpolar and european eastern limit elements are equally represented. This was expected for bryophytes since it is a group with a large number of representatives with a wide distribution.

6 CONCLUSION

1. 35 bryophyte taxa were recorded, 31 of which mosses and 4 liverworts. This is due to the fact that liverworts in general have a much lower number of representatives and are associated with habitats that have constant and high moisture levels. The most dominant bryophyte species was *Hypnum cupressiforme*.
2. The tree species most rich in bryophytes turned out to be beech. Two out of five oak trees were rich in species as well, while the other three and hornbeam trees were relatively low in species richness. Black locust and spruce were the lowest in species richness, with black locust, although poor in species number, being the only tree species that differentiated the best from other tree species based on its epiphytic bryophyte assemblages.
3. The analyses indicate that the reason for species richness of beech and oak trees could be a higher level of moisture. Furthermore, *H. cupressiforme* is highly related to a rough bark texture, meaning that it doesn't thrive on smooth bark such as in beech trees, leaving space for other species of bryophytes to develop. The reason for low species richness in black locust could be the presence of allelopathic toxins in the bark, while for spruce the reason is the bark flaking off in pieces, as well as its acidity.
4. The predominant life form found on all tree species was the smooth mat because it provides more photosynthetic surface, which is beneficial in shaded forest habitats where adaptations for preventing water loss or protection from solar radiation are not necessary. The most common life strategy found was stress-tolerant perennial indicating the majority of sampled environment is stable with minor stressors. The predominant life strategy on spruce was the colonist, due to the unstable environment, while on hornbeam, colonist and long-lived shuttle life strategies were found to be the most common in equal amounts, indicating a major periodical stressor.
5. Biogeographically, the majority of collected species belonged to the temperate major biome element and circumpolar eastern limit element, which corresponds well to the climatic and biogeographic characteristics of the investigated area.
6. NATURA 2000 target species *Dicranum viride* was found on oak and beech, which needs to be monitored according to the Oikon d.o.o. (2023) protocol.

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8 APPENDICES

- I. LIST OF ALL IDENTIFIED BRYOPHYTE TAXA AND FAMILIES THEY BELONG TO IN ALPHABETICAL ORDER
- II. RECORDED BRYOPHYTE SPECIES WITH THEIR CORRESPONDING LIFE STRATEGY, LIFE FORM, BIOGEOGRAPHICAL ELEMENTS CATEGORIES AND ELLENBERG INDICATOR VALUES
- III. INVESTIGATED LOCALITIES (TREE INDIVIDUALS) WITH THEIR COORDINATES, TREE SPECIES, TREE CIRCUMFERENCE AT 1.3 M, TOTAL BRYOPHYTE COVERAGE, DOMINANT SPECIES COVERAGE AND BARK ROUGHNESS
- IV. RESULTS OF INDICATOR SPECIES ANALYSIS

CV

I was born 6th of April 2000 in Pula, Croatia. I finished high school in 2019 at the Gymnasium in Pula and enrolled in Biology course at the Faculty of Science in Zagreb the same year. During my bachelor's studies I was rewarded the state's STEM stipend. I obtained my bachelor's degree in September of 2022 with the topic of my final paper being „Phytotoxic effect of microplastics on photosynthesis“. In October of 2022 I enrolled in Experimental biology course; module Botany, also at the Faculty of Science in Zagreb. During my studies, I've completed several internships: at the department of Molecular biology of the Faculty of Science, at public institution Nature of the city of Zagreb, at Herbarium Croaticum and at the Ministry of economy and sustainable development. I've also been working on Flora Croatica Database since March of 2023. I used to be a member of the Association of biology students (BIUS), in which I was active as a member of the section for applied botany. I have actively participated in SiSB (The Symposium of Biology Students) with a poster on Vascular flora of Jakuševac (Novi Zagreb), and I have successfully completed Bryology Summer School: From bryophyte identification to practical use 2024 in Latvia.

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Appendix 1: List of all identified bryophyte taxa and families they belong to in alphabetical order.

Liverworts:

Frullaniaceae

1. *Frullania dilatata* (L.) Dumort.

Metzgeriaceae

2. *Metzgeria furcata* (L.) Corda

Porellaceae

3. *Porella platyphylla* (L.) Pfeiff.

Radulaceae

4. *Radula complanata* (L.) Dumort.

Mosses:

Amblystegiaceae

5. *Amblystegium serpens* (Hedw.) Schimp.

Anomodontaceae

6. *Anomodon viticulosus* (Hedw.) Hook. & Taylor

Brachytheciaceae

7. *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen
8. *Brachythecium rutabulum* (Hedw.) Schimp.
9. *Brachythecium salebrosum* (Hoffm. ex F. Weber & D. Mohr) Schimp.
10. *Homalothecium sericeum* (Hedw.) Schimp.
11. *Kindbergia praelonga* (Hedw.) Ochyra

Bryaceae

12. *Bryum* sp.
13. *Ptychostomum moravicum* (Podp.) Ros & Mazimpaka

Dicranaceae

14. *Dicranum tauricum* Sapjegin
15. *Dicranum viride* (Sull. & Lesq.) Lindb.

Hypnaceae

16. *Hypnum cupressiforme* Hedw.

Lembophyllaceae

17. *Isoetecium alopecuroides* (Lam. ex Dubois) Isov.

Leskeaceae

18. *Leskea polycarpa* Hedw.

Neckeraceae

19. *Homalia trichomanoides* (Hedw.) Brid.
20. *Pseudanomodon attenuatus* (Hedw.) Ignatov & Fedosov

Orthotrichaceae

21. *Lewinskya affinis* (Schrad. ex Brid.) F. Lara, Garilleti & Goffinet
22. *Lewinskya speciosa* (Nees) F. Lara, Garilleti & Goffinet
23. *Orthotrichum diaphanum* Brid.
24. *Orthotrichum pallens* Bruch ex Brid.
25. *Orthotrichum patens* Bruch ex Brid.
26. *Orthotrichum pumilum* Sw. ex anon.
27. *Orthotrichum* sp.
28. *Pulviger a lyellii* (Hook. & Taylor) Plášek, Sawicki & Ochyra
29. *Ulota crispula* Bruch
30. *Zygodon rupestris* Schimp. ex Lorentz

Pottiaceae

31. *Syntrichia latifolia* (Bruch ex Hartm.) Huebener
32. *Syntrichia papillosa* (Wilson) Jur.

Pylaisiadelphaceae

33. *Platygyrium repens* (Brid.) Schimp

Rhabdoweisiaceae

34. *Cynodontium* sp.

35. *Dicranoweisia cirrata* (Hedw.) Lindb.

Appendix 2: Recorded bryophyte species with their corresponding life strategy (LS) (c – colonist, cp – pioneer colonist, l – long-lived shuttle, p – perennial, pc – competitive perennial, ps – stress tolerant perennial, s – short-lived shuttle), life form (LF) (Cu – cushion, De – dendroid, Fa – fan, Mr – mat, rough, Ms – mat, smooth, Mt- mat, thalloid, Tf – tuft), biogeographical elements categories (elem) and Ellenberg indicator values (L – light, F – moisture, R – reaction, N – nitrogen and HM – heavy metals tolerance). The first number in ‘elem’ column denotes belonging to a major biome (2 – boreo-arctic montane, 3 – wide-boreal, 5 – boreo-temperate, 6 – wide-temperate, 7 – temperate, 8 – southern-temperate), while the second number represents belonging to an eastern limit category (2 – suboceanic, 3 – eurosiberian, 4 – eurosiberian, 5 – Eurasian, 6 – circumpolar).

VRSTA	LS	LF	elem		L	F	R	N
<i>Amblystegium serpens</i>	p	Mr	5	6	5	6	7	6
<i>Anomodon viticulosus</i>	p	Mr	5	6	5	5	8	5
<i>Brachytheciastrum velutinum</i>	p	Mr	7	6	4	5	6	5
<i>Brachythecium rutabulum</i>	cp	Mr	7	3	6	6	6	6
<i>Brachythecium salebrosum</i>	cp	Mr	3	6	5	6	6	5
<i>Bryum</i> sp.		Tf						
<i>Cynodontium</i> sp.		Cu						
<i>Dicranoweisia cirrata</i>	cp	Cu	7	3	5	4	4	4
<i>Dicranum tauricum</i>	pc	Tf	7	3	4	4	3	3
<i>Dicranum viride</i>	pc	Tf						
<i>Frullania dilatata</i>	l	Ms	8	5	6	4	6	4
<i>Homalia trichomanoides</i>	ps	Fa	5	6	5	6	7	5
<i>Homalothecium sericeum</i>	p	Mr	8	4	7	3	7	4
<i>Hypnum cupressiforme</i>	ps	Ms	6	6	6	4	4	4
<i>Isothecium alopecuroides</i>	ps	De	5	3	4	6	6	5
<i>Kindbergia praelonga</i>	p	Mr	7	3	5	6	5	5
<i>Leskea polycarpa</i>	p	Ms	7	6	6	5	7	6
<i>Lewinskya affine</i>	c	Cu	5	3	6	4	6	5
<i>Lewinskya speciosa</i>	s	Cu	2	6	6	4	6	4
<i>Metzgeria furcata</i>	p	Mt	5	3	5	4	5	3

<i>Orthotrichum diaphanum</i>	c	Cu	8	3	7	3	7	5
<i>Orthotrichum pallens</i>	cp	Cu	5	3	6	4	6	4
<i>Orthotrichum patens</i>	c	Cu						
<i>Orthotrichum pumilum</i>	c	Cu	7	3	6	4	6	5
<i>Orthotrichum sp.</i>		Cu						
<i>Platygyrium repens</i>	ps	Ms	7	6	4	4	5	4
<i>Porella platyphylla</i>	ps	Fa	5	6	6	4	8	3
<i>Pseudanomodon attenuatus</i>	p	Mr	5	6	5	5	7	4
<i>Ptychostomum moravicum</i>	c	Tuft	7	6	5	5	6	5
<i>Pulviger a lyellii</i>	s	Tuft	7	2	6	4	6	4
<i>Radula complanata</i>	l	Ms	5	6	5	4	6	3
<i>Syntrichia latifolia</i>	c	Tf	7	3	6	6	7	6
<i>Syntrichia papillosa</i>	c	Tf	7	3	6	4	6	5
<i>Ulota crispula</i>	s	Cu	7	3	6	4	5	3
<i>Zygodon rupestris</i>	c	Tf	8	6	6	4	6	4

Appendix 3: Investigated localities (tree individuals) with their coordinates, tree species, tree circumference at 1.3 m, total bryophyte coverage, dominant species coverage and bark roughness. If two codominant species were recorded, their respective coverages are indicated in brackets along with their total coverage.

LOCALITY	COORDINATES (WGS84)	TREE SPECIES	TREE CIRCUMFERENCE (cm)	TOTAL COVERAGE (%)	DOMINANT SPECIES COVERAGE (%)	BARK ROUGHNESS (1-3)
1	y 45.825660, x16.022151	sessile oak	280	40	25	3
2	y45.827340, x16.023972	sessile oak	140	60	40 (20+20)	3
3	y45.827477, x16.023935	common hornbeam	85	20	15	1
4	y45.828335, x16.023483	beech	205	60	35	1
5	y45.830557, x16.023040	common hornbeam	107	35	15	1
6	y45.827740, x16.015782	black locust	128	20	20	3
7	y45.828107, x16.015819	black locust	180	40	30	3
8	y45.826035, x16.014621	sessile oak	300	40	30	3
9	y45.830469, x16.015867	sessile oak	175	60	50	3

10	y45.830653, x16.017484	sessile oak	230	50	30 (15+15)	3
11	y45.827876, x16.018603	common hornbeam	128	40	20	2
12	y45.830352, x16.018520	common hornbeam	58	10	8 (4+4)	1
13	y45.830739, x16.017190	black locust	110	30	15	3
14	y45.829087, x16.016480	black locust	192	35	20	3
15	y45.829112, x16.016647	black locust	80	10	5	3
16	y45.827622, x16.014874	common hornbeam	143	10	6	1
17	y45.835538, x16.020512	beech	160	30	10	1
18	y45.835536, x16.021878	spruce	156	3	2	2
19	y45.833618, x16.021991	beech	156	30	15	1
20	y45.825858, x16.023053	beech	177	7	4	1
21	y45.829342, x16.023123	beech	162	30	10	2
22	y45.822438, x16.021036	spruce	184	25	20	2
23	y45.822284, x16.020734	spruce	184	1	1	2
24	y45.822473, x16.015030	spruce	160	5	5	2
25	y45.822565, x16.014961	spruce	156	3	3	2

Appendix 4: Results of Indicator Species Analysis.

INDICATOR SPECIES	TREE SPECIES	p (raw)	IndVal (%)
<i>Dicranoweisia cirrata</i>	black locust	0.0024	45.71
<i>Frullania dilatata</i>	hornbeam	0.025	38.46
<i>Frullania dilatata</i>	beech	0.0242	38.46
<i>Lewinskya speciosa</i>	hornbeam	0.0168	45
<i>Pseudanomodon attenuatus</i>	beech	0.0154	45
<i>Pulviger a lyellii</i>	beech	0.0384	40
<i>Radula complanata</i>	hornbeam	0.0253	38.46