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EPIPHYTIC BRYOPHYTES OF AN URBAN FOREST: DIVERSITY, ECOLOGY, AND HOST TREE PREFERENCE IN MAKSIMIR FOREST PARK, ZAGREB

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Epiphytic bryophytes of Maksimir Forest Park were investigated during the winter of 2023 and the spring of 2024. Sampling included five tree species: sessile oak, common hornbeam, European beech, black locust, and European spruce, each represented by five individuals. 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 black locust and spruce were species-poor and had low bryophyte cover. The most frequent and abundant bryophyte was *Hypnum cupressiforme*, followed by *Metzgeria furcata*, *Platygyrium repens*, *Frullania dilatata* and *Radula complanata*. 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, which provides more photosynthetic surface and is thus advantageous in shaded forest habitats, while the most common life strategy was stress-tolerant perennial, indicating that most of the sampled environment is stable with minor stressors. The ANOSIM test revealed that bryophyte assemblages on different tree species differed significantly, however, with considerable overlap, with those on black locusts being the most distinct, with *Dicranoweissa cirrata* being characteristic of this tree species. The DCA analysis with host tree parameters (bark roughness, tree trunk circumference, total/dominant bryophyte coverage) and Ellenberg indicator values passively projected as vectors revealed no discrete separation of tree species based on epiphytic bryophyte composition; however, some patterns were evident. Black locusts and certain species-poor oak trees formed a loose group associated with rougher bark and pleurocarpous species such as *Hypnum cupressiforme* and *Platygyrium repens*. Beech and hornbeam, grouped on the opposite side of the ordination, shared similar bryophyte assemblages associated with smoother bark and higher ecological indicator values for light, nitrogen, and substrate reaction, with beech additionally harbouring bryophytes indicative of higher moisture. This was true for species-rich oak individuals as well.

Key words: moss, phorophyte, life form, life strategy, Ellenberg indicator values, tree trunk circumference, bark roughness

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Epifitske mahovine istraživane su u Park šumi Maksimir tijekom zime 2023. i proljeća 2024. godine. Uzorkovanje je obuhvatilo pet vrsta drveća: hrast kitnjak, obični grab, europsku bukvu, bagrem i običnu smreku, pri čemu je za svaku vrstu odabrano po pet jedinki. Ukupno je zabilježeno 35 svojti mahovina, od čega 31 prava mahovina i 4 jetrenjarke. Najveća raznolikost mahovina zabilježena je na bukvi, dok je najniža raznolikost i pokrovnost epifita bila na bagremu i smreki. Najčešća i najzastupljenija vrsta bila je *Hypnum cupressiforme*, zatim *Metzgeria furcata*, *Platygyrium repens*, *Frullania dilatata* i *Radula complanata*. Tijekom istraživanja, pronađena je ciljna NATURA 2000 vrsta *Dicranum viride* na bukvi i hrastu. Prevladavajući životni oblik na svim vrstama drveća bio je "smooth mat", koji osigurava veću fotosintetsku površinu te je pogodan za sjenovita šumska staništa, dok je najčešća životna strategija bila stres-tolerantna trajnica, što ukazuje na to da su istraživani okoliši uglavnom stabilni s manjim stresnim čimbenicima. ANOSIM test pokazao je da se sastavi mahovina na različitim vrstama drveća statistički značajno razlikuju, iako s određenim preklapanjem, pri čemu su se zajednice na bagremu najbolje odvojile, a vrsta *Dicranoweisia cirrata* bila je karakteristična za ovu vrstu drveća. DCA analiza, sa značajkama stabala (hrapavost kore, opseg stabla, pokrovnost mahovina – ukupna i dominantne vrste) i Ellenbergovim indikatorskim vrijednostima projiciranim kao vektori, nije otkrila jasnu razdvojenost vrsta drveća prema sastavu epifitskih mahovina, ali su određeni obrasci bili uočljivi. Bagrem i pojedini hrastovi siromašni vrstama činili su skupinu povezanu s hrapavijom korom i pleurokarpnim vrstama poput *Hypnum cupressiforme* i *Platygyrium repens*. S druge strane, bukva i grab odlikovali su se sličnim sastavom mahovina povezanim s glađom korom i višim ekološkim indikatorskim vrijednostima za svjetlo, dušik i reakciju supstrata, dok su mahovine na bukvi dodatno ukazivale na višu vlagu staništa, isto kao i one na mahovinskim vrstama bogatijim hrastovima.

Ključne riječi: prave mahovine, stabla domaćini, životna forma, životna strategija, Ellenbergove indikatorske vrijednosti, opseg stabla, hrapavost kore

INTRODUCTION

Epiphytic bryophytes inhabit the bark of trees and shrubs, maintaining a non-parasitic association, relying on the host as a structural substrate and source of different microhabitats. They can be classified as obligate, meaning that they exclusively grow on bark, or facultative, indicating their ability to colonise various substrate types (Smith, 1982). Previous studies have demonstrated that most epiphytic bryophytes exhibit a preference for certain tree species, occurring more abundantly on some trees than others, and in some cases, not occurring at all on particular species, thus displaying host specificity (Szövényi *et al.*, 2004; Mežaka *et al.*, 2012). The abundance of a particular bryophyte on a specific phorophyte is strongly determined by the overall moisture within the habitat, as well as that in the microhabitat provided by the phorophyte (Tng *et al.*, 2009; Peck *et al.*, 1995; Gosselin *et al.*, 2017; Bartels *et al.*, 2018). Futhermore, it is well known that the composition and abundance of epiphytic bryophytes are influenced by various other factors determined by the phorophyte – the pH of the tree's bark, the diameter of the tree (which directly corresponds with the area and time available for colonisation), the presence and depth of bark crevices, the tree's age, tree inclination, water availability and the extent of exposure to the sun (Mežaka *et al.*, 2012). The pH of bark varies among tree species, as it depends on the chemical composition of the bark. In general, higher pH seems to promote the richness of bryophyte species, while lower pH favours the richness of lichen species. The amount and depth of bark crevices depend on the species of tree, as well as on its age, and tree age is in correlation with the tree diameter. Thus, older and larger trees generally support a more diverse epiphytic bryophyte flora than younger and smaller trees (Mežaka *et al.*, 2012). Ranius *et al.* (2008), however, found that barks with deeper crevices harbour fewer epiphytic bryophytes, which could be explained by the fact that the chemical composition of bark changes with its age.

Forest integrity refers to the overall health of a forest, encompassing its capacity to maintain biodiversity and store carbon. The criteria used for the assessment of forest integrity, such as species composition, ecological organisation, disturbance regime or continuity, are often hard or expensive to measure, especially because focusing on only one could provide misleading conclusions. Therefore, there is a need for surrogate indicators, which will provide insight into the condition of multiple criteria simultaneously (Ferrettii, 1997; Caro & O'doherty, 1998; Glenn *et al.*, 1998; Lindenmayer, 1999; DellaSalla *et al.*, 2025). Bryophytes, especially liverworts, represent a promising surrogate as they exhibit greater sensitivity to forest management activities than vascular plants (Frego, 2007). Consequently, further research into their diversity and ecological roles is essential, and such studies are currently completely lacking in Croatia. Despite significant advances in bryophyte research over the past decade (e.g. Alegro *et al.*, 2019; Papp *et al.*, 2016; Sabovljević *et al.*, 2018; Rimac *et al.*, 2019a,b; 2021; Šegota *et al.* 2021; 2023a,b), frequent reporting on species new for the Croatian bryoflora suggests the inadequacy of current knowledge on the topic. Furthermore, only a limited number of studies focused on the bryophyte vegetation and ecology in specific habitats has been done, such as freshwater habitats (Rimac *et al.*, 2022a,b) and peatlands (Alegro & Šegota, 2010). With respect to forest ecosystems, only a single ecological study of bryophyte communities in temperate forests of eastern Croatia has been published (Alegro *et al.*, 2023).

Bryological research into Maksimir Forest Park, situated in the urban area of Zagreb, has been limited as well, with only 24 bryophyte species known from three historical sources: Heinz (1888), Horvat (1932) and Pavletić (1955). Only a few of the species recorded are epiphytes, including *Dicranum viride* (Horvat, 1932). This is a NATURA 2000 target species (European Commission, 1992) that has recently been confirmed for Maksimir after ninety years in the only recently published record from the Maksimir Forest Park (Rimac *et al.*, 2023).

Since epiphytic bryophytes represent such an important component of forest ecosystems and changes in their composition reflect changes in the quality of the environment, understanding their diversity and ecology is essential for comprehending the dynamics of forest ecosystems, as well as for the monitoring of these ecosystems. Given the limited research on the bryoflora of Zagreb, the objective of this study was to explore this particular ecological component within one of the city's largest forest parks. We aimed to investigate:

1. the diversity and composition of epiphytic bryophytes on five common tree species,
2. the ecology of epiphytic bryophyte assemblages on different tree species based on host tree parameters and ecological indicator values of bryophytes,
3. life form and life strategy spectra of bryophyte communities found on different tree species.

MATERIALS AND METHODS

Study area

Maksimir Forest Park was selected as study area due to its status as one of the largest and least anthropogenically impacted parks in Zagreb. Furthermore, it has the status of protected cultural heritage in Croatia because of its long history and notable park architecture (Web Registar kulturnih dobara RH, 2024) and is thus protected under the Nature Protection Act as a monument of park architecture. The park is situated in the southeastern part of the Maksimir city district within the city of Zagreb and is surrounded by an urban area (Fig. 1). The total area of the park covers 316 ha, its elevation ranging from 120 to 167 m above sea level (Priroda Grada Zagreba, 2024). The area falls within the temperate climate zone, and according to the Köppen climate classification, it has a moderately warm humid climate with warm summers (Šegota

& Filipčić, 2003). In addition to the forested areas, Maksimir Park also encompasses grassland and swamp vegetation. The park contains several springs as well as several artificial lakes that were created in the 18th century as part of the park's landscaping design. These lakes are an important ecological component, supporting aquatic plants and wildlife, and contributing to the park's scenic beauty. Additionally, a zoo is situated in the southernmost part of the park.

The forest vegetation of Maksimir is predominantly characterised by oak forests, which are typical of the planar and colline zones in the continental region of Croatia. *Quercus robur* is found in the lower and more waterlogged areas, closer to the lakes. It is mostly accompanied by *Carpinus betulus* but also species of alluvial forests of the planar zone, such as *Alnus glutinosa*, *Salix alba*, *Fraxinus excelsior*, *Populus alba*, and *Tilia cordata*, particularly near the lakes. *Quercus petraea*, on the other hand, occupies higher elevated parts, in association with *C. betulus* and *Fagus sylvatica*, *Castanea sativa*, *Prunus padus* and *Corylus avellana* (Priroda Grada Zagreba, 2024). The invasive alien species *Robinia pseudoacacia* (Boršić *et al.*, 2008) is present in these forest stands as well. In some parts of Maksimir, *R. pseudoacacia* is particularly abundant, posing challenges to the biodiversity of the area. At the time of its establishment, more than 300 non-native species were introduced to Maksimir Forest Park. However, most of them have been lost over time. Among the planted species were various gymnosperms, including *Picea abies*, *Pinus sylvestris* and *Pinus nigra*, which are indigenous in Croatia, but not a part of the naturally occurring vegetation of the investigated area. However, these planted species remain an important component of the park's vegetation today (Priroda Grada Zagreba, 2024).

FIELD RESEARCH

Epiphytic bryophytes were sampled in Maksimir Forest Park during the winter of 2023 and the spring of 2024. Sampling included five tree species: *Quercus petraea* (sessile oak), *Carpinus betulus* (common hornbeam), *Fagus sylvatica* (European *beech*), *Robinia pseudoacacia* (black locust) and *Picea abies* (European spruce), each represented by five individuals. This set of species included the dominant species of the indigenous forest vegetation (sessile oak, common hornbeam and European beech), the most common foreign invasive species (black locust) and one of the species most commonly planted in the area (European spruce). In all, 25 trees were sampled (Fig. 1). Trees were selected in the field using a constrained random sampling approach. Researchers walked through the area and chose suitable individuals of each species that met predefined conditions—avoiding edge effects and anthropogenic influences such as trails or forest edges, while trying to maintain similar environmental conditions (e.g., light, moisture, and distance from disturbances) to minimise confounding variables. Selection was done without prior knowledge of moss presence, ensuring randomness within ecological constraints.

The trees were sampled up to a height of approximately 2 m. All bryophytes were collected for further identification in the laboratory. For each sampled tree, the coordinates were recorded, the trunk circumference at the height of 1.3 m was measured, and the total coverage of epiphytic bryophytes, the coverage of dominant or codominant species and bark roughness were estimated. Bryophyte cover was visually estimated as a percentage of the total observed surface area - specifically, the tree bark up to approximately 2 meters in height. If two species had the same coverage on investigated

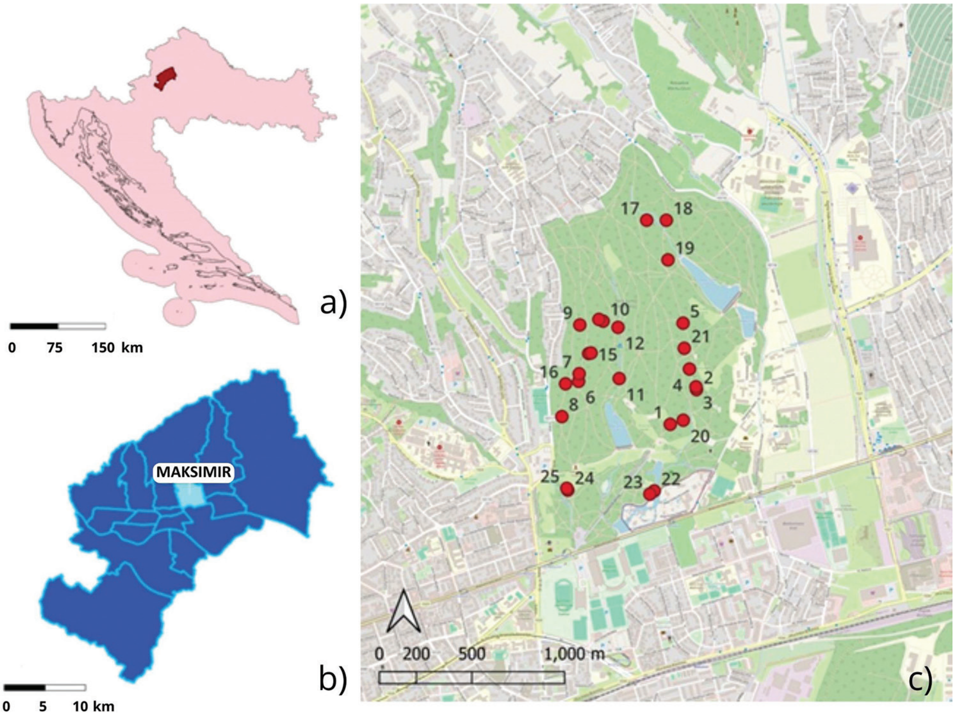

Fig. 1. Study area: a) geographical location of Zagreb (highlighted in red) within Croatia, b) position of Maksimir city district within Zagreb, c) sampling localities on open street map of the Maksimir Forest Park with the surrounding urban area. Maps were created using QGIS software.

trees, they were considered codominant. The bark roughness was estimated using a 3-degree scale (1–smooth, 2–relatively rough, 3–rough) (Tie *et al.*, 2023).

The collected bryophytes were identified using a stereomicroscope and light microscope, and the following identification keys for bryophytes: Caparrós *et al.* (2016), Frey *et al.* (2006), Hallingbäck *et al.* (2008), Lara *et al.* (2009), Lüth (2019) and Smith (2004). The bryophyte material is stored at the Herbarium Croaticum (ZA), and all records have been added to the Flora Croatica Database (Alegro & Šegota, 2024). Bryophyte nomenclature follows Hodgetts *et al.* (2020), while the nomenclature for vascular plants is based on the Euro+Med Plant Base (2006–present).

Data analysis

Data on growth forms and life strategies were obtained from BET data set (van Zuijlen *et al.*, 2023), while the data on life forms and Ellenberg indicator values were sourced from BRYOATT data set (Hill *et al.*, 2017).

Alpha diversity indices (taxa richness and Shannon-Wiener index) of bryophytes were calculated for each tree species investigated. Significant differences among tree species were tested for both indices with the nonparametric Mann–Whitney pairwise test. Furthermore, a one-way ANOSIM test, a non-parametric test of significant difference among groups, was performed to investigate the differences in bryophyte assemblages among the five tree species. Here, the Jaccard index was used as a measure of similarity. 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).

Furthermore, a detrended correspondence analysis (DCA), an indirect ordination analysis, of vegetation presence/absence data was performed in Canoco 5 (ter Braak & Šmilauer, 2012; Šmilauer & Lepš, 2014). Detrending in Canoco was carried out by segment-wise detrending, where the primary axis was divided into segments to remove systematic curvature along the second axis. Additionally, axes were rescaled in standard deviation units of species turnover, providing ecologically interpretable gradient lengths. In DCA, means of Ellenberg indicator values for light, moisture, nitrogen and pH reaction for each locality, i.e. sampled tree, as well as parameters measured and estimated during the field study (bark roughness, tree trunk circumference, total bryophyte coverage, dominant bryophyte species coverage) were passively projected onto the ordination as vectors to assess the potential ecological gradients.

Taxa identified to the genus level (*Bryum* sp., *Cynodontium* sp. and *Orthotrichum* sp.) have been excluded from the life strategy analysis, as well as from ecological analysis where Ellenberg indicator values were used, since no values could have been assigned to the genera. *Dicranum viride* and *Orthotrichum patens* were also excluded from these analyses because they didn't have assigned values in the literature used.

RESULTS

Bryophyte diversity and life history analysis

In all, 35 bryophyte taxa belonging to 17 families were recorded (Tab. 1). Of these 35 taxa, 31 were mosses and only 4 were liverworts. Thirty-two taxa were identified at the species level, while the remaining three were identified only at the genus level due to the absence of sporophytes, which are essential for precise identification. Thirteen of the mosses were pleurocarpous and fifteen were acrocarpous, while three of the liverworts were foliose and one was thallose. Acrocarpous mosses were more prevalent than pleurocarpous mosses on the majority of tree species investigated, leading to a predominance of acrocarpous mosses overall. However, pleurocarpous outnumbered acrocarpous mosses on sessile oaks (Tab. 2).

The most represented family in the study was Orthotrichaceae, which included ten different species, each with relatively low frequency. This was followed by Hypnaceae, represented solely by *Hypnum cupressiforme*, the most frequent and abundant bryophyte species in the study. Other notably frequent species were *Metzgeria furcata*, *Platygyrium repens*, *Frullania dilatata* and *Radula complanata* (Tab. 3). Noteworthily, *Dicranum viride*, a small acrocarpous moss, was found on two beech trees and one oak tree (Tab. 1). This species is a NATURA 2000 target species, listed in Annex II of the Habitats Directive, which identifies species that require the designation of protected areas and monitoring (European Commission, 1992).

Hypnum cupressiforme was the most frequently occurring dominant species (Tab. 1). It was the dominant species on all investigated black locust and spruce trees and the majority of sessile oak trees, except for a single oak tree on which *H. cupressiforme* was codominant along with the thallose liverwort *Metzgeria furcata*. These two species

Tab. 1. The list of recorded bryophyte species on sampled trees, grouped by tree species, with dominant (D) and codominant (C) species regarding the coverage indicated.

	SESSILE OAK					COMMON HORNBEAM					BLACK LOCUST					BEECH					SPRUCE				
SPECIES/LOCALITY	**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**
MARCHANTIOPHYTA																									
Frullaniaceae																									
1. *Frullania dilatata* (L.) Dumort.		+				D	+	+	+	+	+					+	+	+	+	+		+			
Metzgeriaceae																									
2. *Metzgeria furcata* (L.) Corda	+	C	+	+		+	D	C	C				+	+		D	D	+	+	D	+	+	+		
Porellaceae																									
3. *Porella platyphylla* (L.) Pfeiff.	+	+														+				+					
Radulaceae																									
4. *Radula complanate* (L.) Dumort.	+	+				+	+	+	+	+		+					+	+	+	+		+			
BRYOPHYTA																									
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.					+												+	+							

	SESSILE OAK					**COMMON HORNBEAM**					**BLACK LOCUST**					**BEECH**					**SPRUCE**				
SPECIES/LOCALITY	**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**
Hypnaceae																									
16. *Hypnum cupressiforme* Hedw.	D	C	D	D	D		+	C	C	D	D	D	D	D	D	+	+	D	D	+	D	D	D	D	D
Lembophyllaceae																									
17. *Isothecium 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. *Pulvigera 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.					+							+	+	+	+							+		+	

Tab. 2. Number of taxa, average and median number of bryophyte species, mosses and liverworts and their growth forms recorded on each tree species and in total.

TREE SPECIES	oak	hornbeam	beech	black locust	spruce	TOTAL
NUMBER OF TAXA	25	19	26	10	19	35
AVERAGE NUMBER OF SPECIES	9	8.4	11.6	4.6	6.6	8
MEDIAN NUMBER OF SPECIES	7	7	12	5	5	7
MOSSES	21	16	22	7	16	31
PLEUROCARPOUS	12	7	10	2	7	13
ACROCARPOUS	9	9	12	5	9	19
LIVERWORTS	4	3	4	3	3	4
FOLIOSE	3	2	3	2	2	3
THALLOSE	1	1	1	1	1	1

were codominant on two hornbeam trees as well, while other hornbeam trees were dominated by three different species: *H. cupressiforme*, *M. furcata* and leafy liverwort *Frullania dilatata*. Finally, *M. furcata* was dominant on three beech trees, while the remaining beech trees were dominated by *H. cupressiforme*.

Tab. 3. The most represented bryophyte families and species on each tree species and in total.

TREE SPECIES	oak	hornbeam	beech	black locust	spruce	total
Most represented bryophyte families	Brachytheciaceae (11.11%), Hypnaceae (11.11%), Pylaisiadelphaceae (11.11%), Orthotrichaceae (11.11%), Metzgeriaceae (8.89%), Rhabdoweisiaceae (8.89%)	Orthotrichaceae (19.05%), Frullaniaceae (11.90%), Radulaceae (11.90%), Hypnaceae (9.52%), Metzgeriaceae (9.52%), Pottiaceae (9.52%)	Orthotrichaceae (18.97%), Frullaniaceae (8.62%), Hypnaceae (8.62%), Metzgeriaceae (8.62%), Neckeraceae (8.62%)	Rhabdoweisiaceae (27.27%), Hypnaceae (22.73%), Pylaisiadelphaceae (22.73%)	Orthotrichaceae (18.18%), Hypnaceae (15.15%), Pottiaceae (15.15%)	Orthotrichaceae (15.42%), Hypnaceae (11.94%), Metzgeriaceae (8.96%), Pylaisiadelphaceae (8.46%), Brachytheciaceae (7.46%)
Most represented bryophyte species	*Hypnum cupressiforme* (5), *Platygyrium repens* (5), *Metzgeria furcata* (4), *Zygodon rupestris* (3)	*Frullania dilatata* (5), *Radula complanata* (5), *Hypnum cupressiforme* (4), *Metzgeria furcata* (4), *Syntrichia papillosa* (4)	*Frullania dilatata* (5), *Hypnum cupressiforme* (5), *Metzgeria furcata* (5), *Radula complanata* (4), *Syntrichia papillosa* (4)	*Hypnum cupressiforme* (5), *Platygyrium repens* (5), *Dicranoweisia cirrata* (4)	*Hypnum cupressiforme* (5), *Syntrichia papillosa* (4), *Metzgeria furcata* (3), *Ptychostomum moravicum* (3)	*Hypnum cupressiforme* (24), *Metzgeria furcata* (18), *Platygyrium repens* (17), *Frullania dilatata* (13), *Radula complanata* (13)

Considering the number of taxa, beech trees were the richest within the study, with 7 to 16 taxa recorded per tree and an average of 11.6, closely matching the median of 12. Oak trees show more variability in taxa richness, ranging from only 4 taxa up to 16 taxa, with an average of 9 and a median of 7. The hornbeam has a somewhat narrower range, from 6 to 11 taxa, with an average of 8.4 and a median of 7. Black locust and spruce exhibited lower bryophyte taxa richness, with black locust ranging from 3 to 6 taxa (average 4.6, median 5) and spruce from 2 to 15 taxa (average 6.6, median 5), due to one spruce tree being inconsistently rich in bryophyte species (Tab. 2). The Shannon-Wiener Index showed similar patterns of diversity across the investigated tree species (Fig. 2). However, the Mann–Whitney test revealed a statistically significant difference in alpha diversity – both taxa richness and Shannon-Wiener index – only between black locust and beech, and between black locust and hornbeam (Appendix 2).

The predominant life form in the study was the smooth mat, comprising 35.3% of recorded bryophytes. This life form was the most represented across all investigated tree species (oak-31.1%, hornbeam-38.1%, black locust-52.2%, beech-32.8%, spruce-30.3%) (Fig. 3). The second most represented life form in the study was the cushion with 17.4%. This life form was the second most frequent on hornbeam (19.0%), black locust (26.1%) and spruce (21.2%) as well. The second most represented life form on oak and beech was the rough mat, amounting to 20.0% on oak and 17.2% on beech, while it was completely lacking on black locust. Thalloid mat, turf and tuft were found on all trees sampled, while the fan was recorded only on oak, hornbeam and beech trees, and dendroid life form only on oak and beech trees, but in very small proportions.

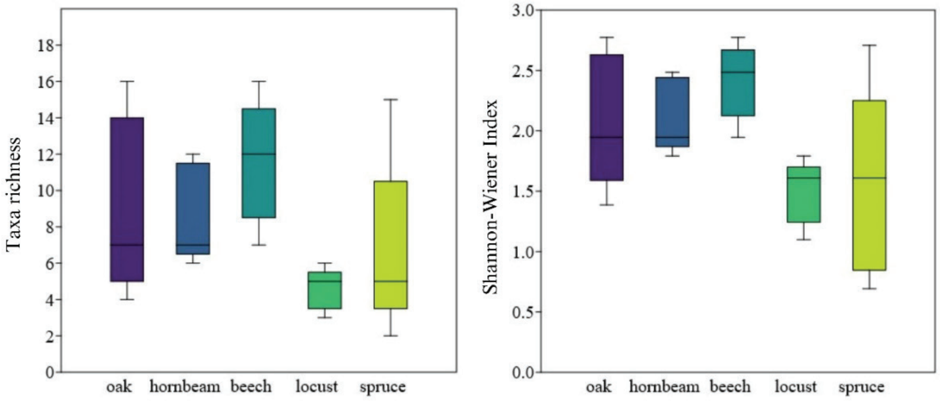

Fig. 2. Taxon richness and Shannon-Wiener diversity index of bryophytes across investigated tree species. Whiskers show minimum and maximum values, boxes represent interquartile range, and horizontal lines denote the median.

Overall, the most dominant life strategy was stress-tolerant perennial (27.1%), followed by perennial (22.9%) and colonist (21.9%) (Fig. 4). Oak was dominated by stress-tolerant perennials (34.1%) and perennials (26.8%), while hornbeam was colonised mostly by colonists (25.0%), long-lived shuttles (25.0%), perennials (20.0%) and stress-tolerant perennials (17.50%). Black locust was dominated by stress-tolerant perennials (47.6%), followed by pioneer colonists (19.1%). Notably, short-lived shuttle

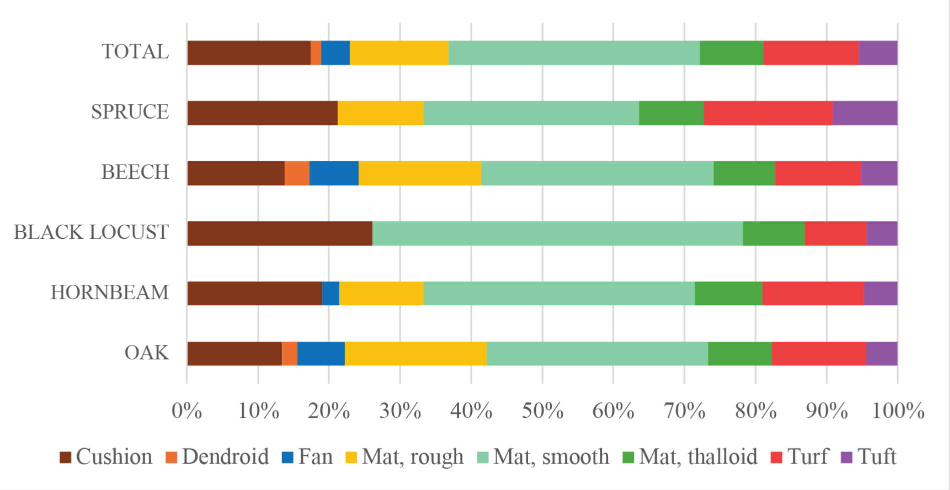

Fig. 3. Life form spectra of epiphytic bryophytes for the investigated tree species and overall within the study.

species were absent from this species. Beech, like hornbeam, was largely colonised by perennials (28.1%), stress-tolerant perennials (24.6%), colonists (19.3%) and long-lived shuttle species (15.8%). Short-lived shuttle species were observed on oak, hornbeam and beech trees in small proportions, as well as competitive perennials on oak, black locust and beech trees. On the other hand, spruce trees were highly dominated by colonists (42.4%), followed by perennials and stress-tolerant perennials in equal amounts (21.2%), while no short-lived shuttle species were observed on this tree species, as in black locust.

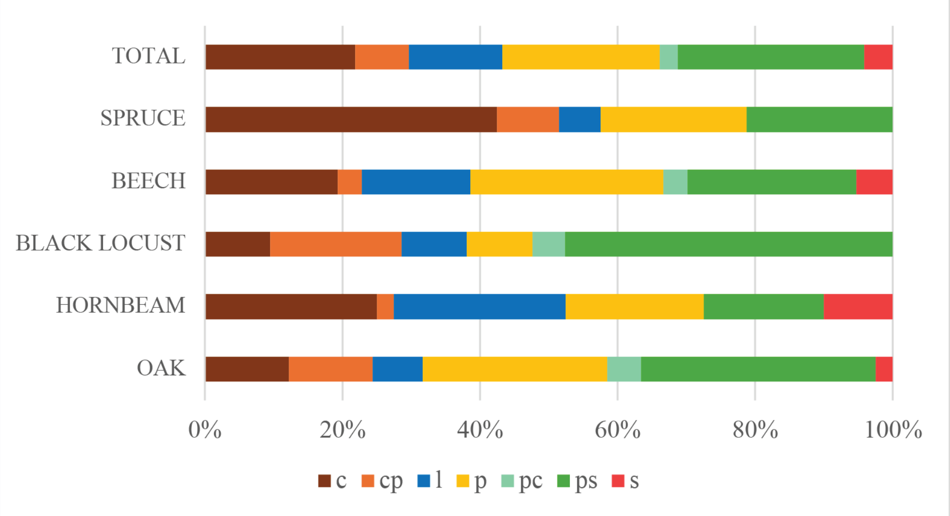

Fig. 4. Life strategy spectra of epiphytic bryophytes for the investigated tree species and overall within the study. Abbreviations: c–colonist, cp–pioneer colonist, l–long-lived shuttle, p–perennial, pc–competitive perennial, ps–stress-tolerant perennial, s–short-lived shuttle.

Ecological analysis

The ANOSIM test showed a statistically significant difference among epiphytic bryophyte assemblages across different tree species, although a noticeable overlap was observed (global R statistics=0.39, p=0.0001). The pairwise ANOSIM test further demonstrated that bryophyte assemblages from black locust were very different from those on hornbeam and beech, and different but with a considerable overlap in species composition from those in spruce. Bryophyte assemblages on spruce were distinct from those on hornbeam and beech as well, however, there was some overlap in species composition, given the relatively low R statistics (Tab. 4). Additionally, bryophyte composition on oak significantly differed from that on hornbeam, again with some overlap.

Tab. 4. Pairwise analyses of similarity (ANOSIM) of bryophyte assemblages from different tree species (Global R = 0.39, p=0.0001). Statistically significant values (p<0.05) are marked with an asterisk (*). Abbreviations: O–oak, H–hornbeam, B–beech, L–black locust, S–spruce.

	***R* values**				
	O	**H**	**B**	**L**	**S**
O		0.43*	0.35	0.11	0.22
H	0.43*		0.09	0.86*	0.34*
B	0.35	0.09		0.90*	0.30*
L	0.11	0.79*	0.90*		0.35*
S	0.22	0.34*	0.30*	0.35*	

Indicator Species Analysis revealed three species characteristic of hornbeam trees (leafy liverworts *Frullania dilatata* and *Radula complanata* and the acrocarpous moss *Lewinskya speciosa*), which preferred this tree species under the experimental conditions of Maksimir Forest Park. Three bryophyte species preferred beech (*Frullania dilatata*, pleurocarpous *Pseudanomodon attenuatus* and acrocarpous *Pulvigera lyellii*) and one preferred black locust (the minute acrocarpous species *Dicranoweisia cirrata*) (Tab. 5).

Tab. 5. Results of Indicator Species Analysis. Abbreviations: O–oak, H–hornbeam, B–beech, L–black locust, S–spruce.

INDICATOR SPECIES	TREE SPECIES	p	IndVal (%)
Lewinskya speciosa	hornbeam	0.017	45.00
Frullania dilatata	hornbeam	0.025	38.46
Radula complanata	hornbeam	0.025	38.46
Pseudanomodon attenuatus	beech	0.015	45.00
Pulvigera lyellii	beech	0.038	40.00
Frullania dilatata	beech	0.024	38.46
Dicranoweisia cirrata	black locust	0.002	45.71

In the detrended correspondence analysis (DCA), the eigenvalue for axis 1 was 0.36, while that of axis 2 was 0.20. The lengths of axes 1 and 2 were 2.58 and 2.4 SD, respectively. The DCA analysis did not reveal discrete groups of tree species based on their epiphytic bryophyte composition along the first two axes. However, a grouping of black locust trees, characterised by a rougher bark texture, along with several species-poor oak trees, was observed on the right side of the ordination diagram (Fig. 5). These trees were characterised by species such as *Hypnum cupressiforme*, the most frequent dominant species, as well as another common pleurocarpous bryophyte *Platygyrium repens* and acrocarpous species *Dicranoweisia cirrata* and *Dicranum tauricum*. Oak trees were scattered along the first axis, with two individuals hosting bryophyte assemblages of higher diversity (Appendix 1), which showed greater similarity to those found on beech trees and three with lower bryophyte diversity, whose bryophyte species composition was more similar to that found on black locust (Fig. 5). Oak trees were, in general, characterised by higher coverage of epiphytic bryophytes, as well as higher coverage of dominant species (Appendix 3). On the other hand, a grouping of hornbeam and beech trees on the left side of the diagram indicated their similarity in species composition. These tree species were characterised by smoother bark and a higher proportion of bryophytes with higher indicator values for light, nitrogen and substrate reaction than black locust trees. Beech trees were furthermore characterised by species with higher indicator values for moisture, similar to species-rich oak individuals. Considering the total bryophyte coverage, both hornbeam and beech exhibited considerable ranges, 10–40% for hornbeam and 7–60% for beech (Appendix 3). Spruce trees were scattered along both ordination axes, with spruce from locality 25 differing from other investigated trees the most (Tab. 1, Fig. 5). This tree was characterised by a low number of species (5), with two found only on this tree. Additionally, spruce was characterised by medium bark roughness and the lowest values of total (range 1–25%, average 7.4%) and dominant bryophyte coverage (range 1–20%, average 6.2%) (Appendix 3).

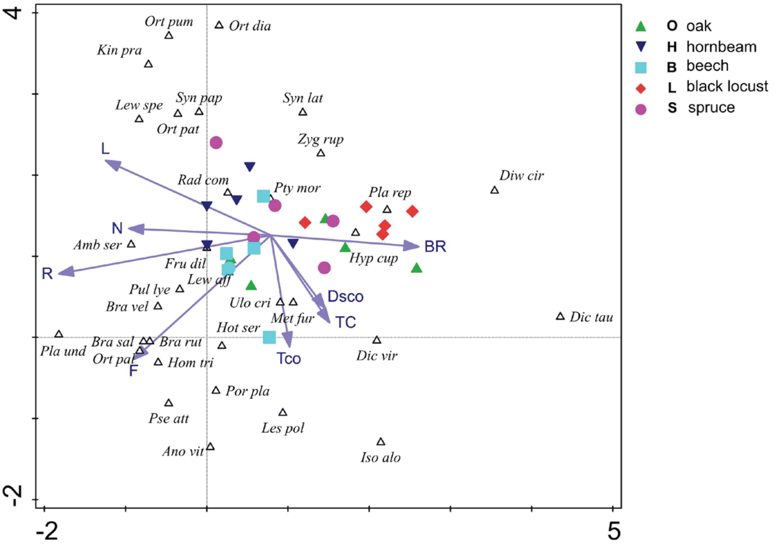

Fig. 5. DCA analysis of samples (trees) and bryophyte species with Ellenberg ecological indicator values and measured or estimated ecological parameters passively projected as vectors. Abbreviations: Ellenberg indicator values – L–light, N–nitrogen, R-pH reaction, F–moisture; TC–tree trunk circumference; Tco–total bryophyte coverage; Dsco–dominant species coverage; BR–bark roughness. Bryophyte species are abbreviated using the first three letters of both their genus and species names.

DISCUSSION

Out of 35 recorded bryophyte taxa, 31 were mosses, while only four belonged to the liverworts. This pattern can be attributed to the generally lower number of liverwort representatives and their preference for habitats characterised by constant and high moisture levels (Vanderpoorten & Goffinet, 2009), which is not the case for microhabitats on tree trunks in the urban temperate forest of Maksimir Park. The most frequent dominant species on all sampled tree species was *Hypnum cupressiforme*, with the exception of beech. On beech, the most frequent dominant species was *Metzgeria furcata*. This species, along with *H. cupressiforme* is among the most commonly recorded species in Croatia (Alegro & Šegota, 2024). Notably, hornbeam and beech trees exhibited a relatively high frequency of *Frullania dilatata*, *M. furcata* and *Radula complanat*a, which are all liverworts. Both hornbeam and beech trees have a smooth bark, which *F. dilatata* and *R. complanata* appear to prefer. Furthermore, *H. cupressiforme* was in this study highly associated with rough bark, suggesting that on smooth bark, where *H. cupressiforme* does not thrive, other species may establish dominance. The findings of this study are comparable to those of Ódor *et al.* (2013), who identified *H. cupcressiforme*, *Platygyrium repens*, *Isothecium alopecuroides*, *R. complanata*, and *F. dilatata* as the most common epiphytic bryophyte species in a temperate managed forest in Hungary. Similarly, *H. cupressiforme*, *P. repens*, *R. complanata* and *F. dilatata* were among the most frequent species in Maksimir Forest Park. However, while in our research *F. dilatata* was characteristic of hornbeam and beech, and *R. complanata* of hornbeam, Ódor *et al.* (2013) reported these species as being more closely associated with oak. This could be explained by the fact that the trees in their study had a smaller diameter at breast height, meaning they were younger and had smoother bark. In contrast, the oak trees sampled in Maksimir had an average diameter at breast height greater than 225 cm, indicating they were older and had rougher bark. As a result, species that prefer smooth bark were more likely to inhabit beech and hornbeam. 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, while *Lewinskia speciosa* and *Pulvigera lyellii* preferred hornbeam and beech, respectively.

Among the oak trees sampled in Maksimir Forest, two were rich in epiphytic bryophytes, whereas the remaining three were comparatively species-poor. No clear pattern that could explain this difference was identified in the measured and observed host tree parameters, although it is also possible that the observed variation is partly due to pure stochasticity and natural variability in species composition, especially given the relatively small sample size. However, a considerable number of the bryophytes recorded exclusively on the more bryophyte-rich oak trees, such as *Amblystegium serpens*, *Anomodon viticulosus*, *Brachytheciastrum velutinum*, *Brachythecium rutabulum*, *Brachythecium salebrosum* and *Pseudanomodon attenuatus*, have higher Ellenberg indicator values for moisture. This suggests that these particular oak trees offered microhabitats with greater moisture availability. Most of these species are considered facultative epiphytes, typically growing at the base of tree trunks near the moist forest floor - areas that retain more humidity than the drier upper trunk and branch zones. Furthermore, in the DCA analysis, two bryophyte-rich oak trees were grouped with beech trees rich in epiphytic bryophytes, some of which had higher ecological indicator values for moisture as well. That indicates that the sampled beech trees may have provided similarly humid microhabitats despite their smoother bark texture. This can be influenced by several factors, such as surrounding tree species density and canopy cover, 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 the present study. In Maksimir Forest, beech exhibited the highest overall diversity of epiphytic bryophytes, followed by oak and hornbeam. This finding is different from what was observed in temperate forests in Hungary, where oak supported the richest bryophyte assemblages, followed by beech and hornbeam, which were comparable in species diversity (Ódor *et al.*, 2013). Epiphyte diversity is influenced not only by the bark roughness, with rougher bark promoting higher diversity, but also by the tree height and diameter, which are good proxies for tree age (Király *et al.*, 2013). Older trees typically provide a larger surface area, higher microhabitat heterogeneity and longer colonisation time available, all of which promote higher epiphytic bryophyte diversity (Fritz *et al.*, 2008; Király *et al.*, 2013). Beech trees sampled in Maksimir Forest had quite a large diameter at breast height, compared to hornbeam, which may explain the higher diversity observed in beech. If all sampled trees had a similar diameter at breast height, it is possible that some of the variability in species richness would be reduced, allowing underlying ecological patterns—such as the influence of bark texture or microclimatic conditions—to emerge more clearly. Regarding the tree size, results from Hungarian temperate forests show that tree size has a limited effect on bryophyte assemblage composition, probably due to intensive management with short rotation cycles and the absence of old, large trees, resulting in a narrow tree diameter and age range sampled (Odor *et al.*, 2013). Additionally, due to the long history of timber-oriented forest management, it is likely that dispersal-limited species dependent on long-lived substrates have already disappeared from the region (Hauck *et al.*, 2013). To support the potential recolonisation of these sensitive epiphytic species, increasing the density of old trees through set-aside areas, retention forestry, and the preservation of veteran trees is thus essential.

Furthermore, the high epiphytic bryophyte diversity observed on beech trees in Makismir could be attributed to the competitive dynamics among bryophyte species. As previously discussed, *H. cupressiforme* thrives on rough bark but is less dominant on the smooth bark of beech. The reduced prevalence of *H. cupressiforme* may have allowed other bryophyte species to establish and proliferate, thereby increasing overall species richness.

Although black locust exhibited low species richness, it was the only tree species that distinctly differed from other tree species in terms of its epiphytic bryophyte assemblages, with *Dicranoweisia cirrata* being the most characteristic species associated with this tree species. This epiphyte was associated with black locust in other studies dealing with urban epiphytes as well (Stingl, 1995; Fudali & Szymanowski, 2019). Despite having a rough bark, it supported the lowest bryophyte diversity. The composition and diversity of epiphytic bryophytes and their communities are strongly influenced by the physical and chemical properties of bark, such as pH, nutrient content and water capacity (Jagodziński *et al.*, 2018). These factors were not measured in the present study, but may have a crucial role in explaining the low diversity observed in black locusts. Regarding the Ellenberg indicator values for nitrogen and pH reaction, bryophyte species on black locust indicated lower values of these factors. However, several studies have reported a relatively rich, though compositionally distinct, bryophyte flora on black locust trees in secondary woodlands (Jagodziński *et al.*, 2018) and urban environments (Fudali & Szymanowski, 2019). Notably, the latter study involved a much more extensive field effort, where only a small percentage of black locust trees hosted bryophytes, yet those trees supported a relatively high overall diversity. In contrast, the low diversity recorded in our study may be attributed to the limited number of trees sampled and the small research area compared to the aforementioned study.

Low bryophyte species richness observed in spruce may be attributed to the bark and canopy characteristics. That is, the bark peels off in pieces, creating unstable conditions which hinder the establishment and growth of epiphytes. Furthermore, the bark is very acidic (Kuusinen, 1996), which is unfavourable for most bryophytes and and is abundant in tannins and resins that inhibit the growth of bryophytes (Goia *et al.*, 2015), while the canopy is such that it limits the amount of rainwater reaching the trunk, creating very dry conditions, unsuitable for bryophytes (Barkman, 1958). In general, deciduous trees typically support greater species richness than conifers, and their presence within conifer-dominated stands is known to play a crucial role in enhancing epiphyte diversity (Gustafsson & Eriksson, 1995; Kuusinen & Penttinen, 1999; Cleavitt *et al.*, 2009; Király *et al.*, 2013; Fudali & Szymanowski, 2019). However, one sampled spruce tree had an inconsistently high number and coverage of epiphytic bryophyte species within our study. Given that the total number of sampled spruce trees was limited to five, this single outlier does not provide sufficient data to draw broader ecological conclusions.

Dicranum viride, a small acrocarpous moss, was recorded on two beech trees and one oak tree. This species is mostly associated with beech trees but can be found on *Ulmus*, *Tilia*, *Quercus*, *Carpinus* and, rarely, *Betula* species. It is most commonly found on the tree trunks of middle age, where suitable microhabitat conditions support its growth (Dierssen, 2001; Baisheva *et al.*, 2013; Mežaka *et al.*, 2023; Wysocki *et al.*, 2023). One of the main threats to this species is unsuitable forest management that disrupts habitat continuity, while tree cutting and removal directly reduce the amount of suitable substrates and microhabitats within the forest. Additionally, this increases light penetration to the trunks, which negatively affects moisture retention and creates less favourable conditions for epiphytic bryophytes (Baisheva *et al.*, 2013; Wierzcholska *et al.*, 2020; Gréaume *et al.*, 2023; Percel *et al.*, 2024). Air pollution represents another significant threat to *D. viride* because it affects the pH of the environment. The presence of this species in Maksimir Forest Park may indicate that forest management practices and air quality in the area are relatively good. However, due to a lack of data on its population size and condition, it is not possible to determine whether these conditions are truly optimal. Therefore, it is recommended to assess and monitor the *D. viride* population in the park and to restrict tree removal to cases of absolute necessity to preserve suitable habitat conditions.

The predominance of the smooth mat life form in this study, followed by the rough mat on oak and beech, is consistent with the climatic and microclimatic conditions characteristic of temperate forests, such as those found in Maksimir Forest Park. The light intensity in the forest habitat is low, and there is no possibility of damage to the photosynthetic apparatus of bryophytes. Additionally, relatively stable humidity levels prevent excessive desiccation, allowing species to expose a greater surface area for photosynthesis, gas exchange and evaporation. Thus, the mat life form, which maximises photosynthetic surface area, is particularly advantageous in shaded forest environments. This life form, however, lacks adaptations for reducing water loss or protection against intense solar radiation, which are characteristic of the species of dry and open habitats (Bates, 1998). In contrast, in some tree species, such as hornbeam, black locust and spruce, the second most common life form in our study was the cushion, which employs an opposite survival strategy to mats. Cushions are highly adapted to dry and insolated habitats or microhabitats, where they can thrive under conditions of increased sun exposure and reduced moisture availability (Bates, 1998). Life form spectra observed in our study suggest that each tree can provide several different microhabitats, with vertical zonation of the species and different growth and life forms already well documented in the literature (Fritz, 2009; McCune, 1993). This is governed mainly by microclimatic factors such as light availability and air and substrate humidity (Hosokawa & Odani, 1957; Peck *et al.*, 1995). Pleurocarpous species which grow as mats are confined to more humid tree bases, and these are usually facultative epiphytes growing on forest soil as well. On the other hand, acrocarpous cushion-forming species are better adapted to dryer conditions and more frequently found on the higher tree sections more exposed to sunlight.

The predominant life strategy within this study was the stress-tolerant perennial, followed by perennial and colonist strategies. Since trees have been sampled from bases up to 2 m in height, it is not surprising that the majority of species were perennials, as tree bases provide quite a stable environment. In contrast, colonists tend to occupy newer or less stable environments, such as young trees or the bark of spruce trees (During, 1979). Indeed, when individual tree species were considered, the dominant life strategy of bryophytes on spruce by far was the colonist strategy, reflecting the transient nature of its bark as a substrate. Perennial bryophytes were predominant on oak and beech trees, followed by the stress-tolerant perennials, reflecting the rather stable conditions these trees provide for their epiphytes. Black locust, however, was notably dominated by stress-tolerant perennials, suggesting the presence of a continuous stress factor which epiphytic bryophytes inhabiting this species can tolerate. On the other hand, on hornbeam, colonists and species with long-lived shuttle life strategy exhibited an equal prevalence, which may indicate the presence of a significant but periodic stressor affecting epiphytic bryophyte communities (During, 1979). However, expanding the study with a larger sample size might offer a clearer picture of how bryophyte life strategies are distributed across different tree species, as such an approach could reveal subtler ecological patterns and allow for more robust statistical analyses.

CONCLUSION

In Maksimir Forest Park, a total of 35 epiphytic bryophyte taxa were recorded, the majority of which were mosses – a pattern consistent with the microclimatic conditions typically found on tree trunks in urban temperate forests. Beech trees exhibited the highest bryophyte species richness, probably due to more suitable microclimatic conditions and the reduced dominance of *Hypnum cupressiform*e, which allowed for greater species coexistence. In contrast, black locust and spruce supported lower bryophyte diversity, probably due to unfavourable bark characteristics such as acidity, instability, and chemical composition. Black locust was the only tree species with a clearly distinct bryophyte assemblage, with *Dicranoweisia cirrata* identified as a characteristic species. Oak trees displayed variability in species richness, which may be attributed to differences in surrounding microhabitat conditions. Two bryophyte-rich oak trees grouped in ordination analysis closely with species-rich beech trees, suggesting the presence of more humid microenvironments favourable for bryophyte diversity, while others aligned more closely with black locust in terms of lower diversity. Overall, bryophyte communities were largely dominated by smooth mat life forms, indicating an adaptation to humid and stable forest conditions, while cushions and rough mats were more selectively distributed among tree species. In terms of life strategies, stress-tolerant perennials prevailed on most trees, whereas colonists were primarily associated with less stable or temporary substrates, such as spruce, reflecting the influence of microhabitat stability on bryophyte strategy. Importantly, the presence of *Dicranum viride*, a species of conservation concern under the EU Habitats Directive, points to relatively favourable habitat quality and forest management practices in Maksimir. However, monitoring and protection of old, structurally diverse trees remain crucial for maintaining and enhancing epiphytic bryophyte diversity. These findings underscore the importance of preserving habitat heterogeneity and ecological continuity in urban forests. Nevertheless, to understand the dynamics and long-term trends of epiphytic bryophyte communities in this area fully, further research with broader spatial and temporal coverage is needed.

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Appendix 1. Investigated localities (tree individuals) with coordinates, tree species, tree trunk circumference at 1.3 m (TC), total bryophyte coverage (Tco), dominant species coverage (Dsco), bark roughness (BR), taxa richness (TR) and Shannon-Wiener diversity index (Shan.). If two species had identical maximum coverage values, they were indicated as codominant and were both considered with their respective coverages indicated in parenthesis under Dsco.

LOCALITY	COORDINATES (WGS84)	Tree species	TC (cm)	Tco (%)	Dsco (%)	BR (1-3)	TR	Shan.
1	y45.825660, x16.022151	sessile oak	280	40	25	3	12	2.49
2	y45.827340, x16.023972	sessile oak	140	60	40 (20+20)	3	16	2.77
3	y45.827477, x16.023935	common hornbeam	85	20	15	1	6	1.79
4	y45.828335, x16.023483	beech	205	60	35	1	7	1.95
5	y45.830557, x16.023040	common hornbeam	107	35	15	1	12	2.49
6	y45.827740, x16.015782	black locust	128	20	20	3	4	1.39
7	y45.828107, x16.015819	black locust	180	40	30	3	5	1.61
8	y45.826035, x16.014621	sessile oak	300	40	30	3	4	1.39
9	y45.830469, x16.015867	sessile oak	175	60	50	3	6	1.79
10	y45.830653, x16.017484	sessile oak	230	50	30	3	7	1.95
11	y45.827876, x16.018603	common hornbeam	128	40	20 (10+10)	2	7	1.95
12	y45.830352, x16.018520	common hornbeam	58	10	8 (4+4)	1	7	1.95
13	y45.830739, x16.017190	black locust	110	30	15	3	5	1.61
14	y45.829087, x16.016480	black locust	192	35	20	3	6	1.79
15	y45.829112, x16.016647	black locust	80	10	5	3	3	1.10
16	y45.827622, x16.014874	common hornbeam	143	10	6	1	11	2.40
17	y45.835538, x16.020512	beech	160	30	10	1	16	2.77
18	y45.835536, x16.021878	spruce	156	3	2	2	5	1.61
19	y45.833618, x16.021991	beech	156	30	15	1	12	2.49
20	y45.825858, x16.023053	beech	177	7	4	1	13	2.57
21	y45.829342, x16.023123	beech	162	30	10	2	10	2.30
22	y45.822438, x16.021036	spruce	184	25	20	2	15	2.71
23	y45.822284, x16.020734	spruce	184	1	1	2	2	0.69
24	y45.822473, x16.015030	spruce	160	5	5	2	6	1.79
25	y45.822565, x16.014961	spruce	156	3	3	2	5	1.61

Appendix 2. Results of Mann–Whitney pairwise post hoc tests; significant differences in diversity indices between tree species pairs are marked with an asterisk (* p < 0.05).

Taxa richness					
	beech	black locust	common hornbeam	sessile oak	spruce
beech		0.01*	0.17	0.34	0.09
black locust	0.01*		0.02*	0.09	0.59
common hornbeam	0.17	0.02*		1,00	0.17
sessile oak	0.34	0.09	1,00		0.34
spruce	0.09	0.59	0.17	0.34	
Shannon-Wiener					
	beech	black locust	common hornbeam	sessile oak	spruce
beech		0.01*	0.17	0.34	0.09
black locust	0.02*		0.02*	0.09	0.92
common hornbeam	0.17	0.02*		1,00	0.17
sessile oak	0.34	0.09	1,00		0.25
spruce	0.09	0.91	0.17	0.25	

Appendix 3. Minimal, maximal and average values for bark roughness, dominant species coverage, total coverage and tree circumference for every tree species.

		oak	hornbeam	beech	locust	spruce
BARK ROUGHNESS (1–3)	min	3	1	1	3	2
	max	3	2	2	3	2
	average	3	1.2	1.2	3	2
DOMINANT SPECIES COVERAGE (%)	min	15	6	4	5	1
	max	50	20	35	30	20
	average	28	12.8	14.8	18	6.2
TOTAL COVERAGE (%)	min	40	10	7	10	1
	max	60	40	60	40	25
	average	50	23	31.4	27	7.4
TREE TRUNK CIRCUMFERENCE (cm)	min	140	58	156	80	156
	max	300	143	205	192	184
	average	225	104.2	172	138	168