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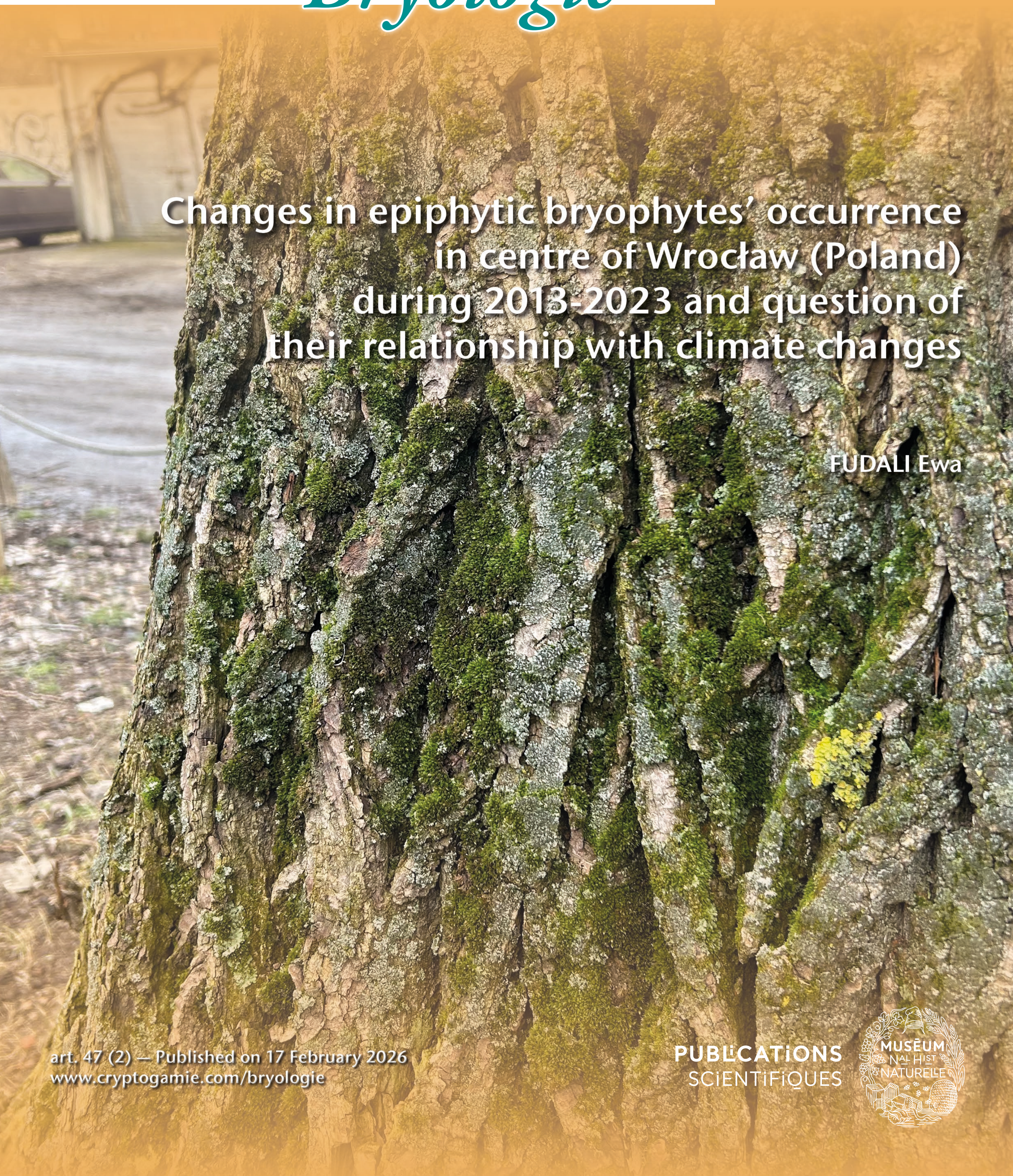

Changes in epiphytic bryophytes' occurrence in centre of Wrocław (Poland) during 2013-2023 and question of their relationship with climate changes

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Changes in epiphytic bryophytes' occurrence in centre of Wrocław (Poland) during 2013-2023 and question of their relationship with climate changes

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ABSTRACT
Last decade is considered as warmer than previous ones. Epiphytic bryophytes are known as quickly reacting on microclimate changes. The question whether occurrence and spread of epiphytic bryophytes in cities is presently facilitated or limited due to warming was studied through a comparison of species diversity, frequency and abundance in 2013 and 2023 in 109 research plots situated in central part of the Wrocław city. In result an increase in the total number of inhabited trees and the total area covered with epiphytes was evidenced, especially on built-up areas and streets. Fourteen species have shown an upward trend while six – the opposite tendency. An increase in the richness of obligatory epiphytes was found (five, including three new for Wrocław) but no new thermophilic species appeared. Two of newly found epiphytes are considered as sensitive to the air pollution. So bryofloristical changes seem to result from the improvement of the air purity not warming. Improving air purity could caused, with high probability, also the expansion of resistant to pollution epiphytes: *Hypnum cupressiforme* Hedw., *Dicranoweisia cirrata* (Hedw.) Lindb. ex Milde and *Orthotrichum diaphanum* Schrad. ex Brid. But the potential effect of the increased temperatures and frost-free winter months, observed in Wrocław since 2019, on spread in the city of two thermophytic species, *Orthotrichum pumilum* Sw. ex anon and *O. diaphanum*, should be considered when explain these phenomena. The mixed impact of both processes seem to be probable. Parks and built-up areas differed in the intensity of species exchange of epiphytic bryophytes.

KEY WORDS
Urban bryophytes,
bryophytes' dynamic tendencies,
urban areas,
warming effects,
effects of the reduced air pollution level.

RÉSUMÉ
Évolution dans la présence de bryophytes épiphytes dans le centre de Wrocław (Pologne) au cours de la période 2013-2023 et questionnement sur leurs rapports avec les changements climatiques.
La dernière décennie est considérée comme plus chaude que les précédentes. Les bryophytes épiphytes sont connus comme réagissant rapidement aux changements de microclimat. La question de savoir si l'apparition et la propagation des bryophytes épiphytes dans les villes sont actuellement favorisées ou limitées par le réchauffement climatique a été étudiée en comparant la diversité, la fréquence et l'abondance des espèces en 2013 et 2023 sur 109 parcelles de recherche situées dans le centre de la ville de Wrocław. En conséquence, une augmentation du nombre total d'arbres habités et de la superficie totale couverte d'épiphytes ont été mises en évidence, en particulier dans les zones et les rues bâties. Quatorze espèces ont montré une tendance à la hausse tandis que six ont connu la tendance inverse. Une augmentation dans la richesse des épiphytes obligatoires a été observée (cinq, dont trois nouvelles pour Wrocław), mais aucune nouvelle espèce thermophile n'est apparue. Deux épiphytes nouvellement trouvés sont considérés comme sensibles à la pollution atmosphérique. Les changements bryofloristiques semblent donc résulter de l'amélioration de la pureté de l'air et non du réchauffement climatique. L'amélioration de la pureté de l'air pourrait provoquer, avec une forte probabilité, l'expansion d'épiphytes résistants à la pollution : *Hypnum cupressiforme* Hedw., *Dicranoweisia cirrata* (Hedw.) Lindb. ex Milde et *Orthotrichum diaphanum* Schrad. ex Brid. Mais l'effet potentiel de l'augmentation des températures et des mois d'hiver sans gel, observés à Wrocław depuis 2019, sur la propagation dans la ville de deux espèces thermophytiques, *Orthotrichum pumilum* Sw. ex anon et *O. diaphanum*, doit être pris en compte lors de l'explication de ces phénomènes. L'impact mixte des deux processus semble être probable. Les parcs et les zones bâties diffèrent dans l'intensité des échanges d'espèces de bryophytes épiphytes.

MOTS CLÉS
Bryophytes urbaines, tendances dynamiques des bryophytes, zones urbaines, effets du réchauffement climatique, effets de la réduction du niveau de pollution de l'air.

INTRODUCTION

In general opinion bryophytes, especially those growing on tree trunks, are plants sensitive to changes in the environment condition. For many years they have been used as reaction indicators in assessing the change of level of such airborne pollutants as nitrogen and sulphur (Davies *et al.* 2006; Zechmeister *et al.* 2007; Plášek *et al.* 2014; Hutsemékers *et al.* 2023) or the general urban air quality (Dymytrova 2009; Sérgio *et al.* 2016). According to some authors they are also highly susceptible to climate change (Gignac 2001; Song *et al.* 2012), what is manifested in quick modification of their distribution range (Frahm & Klaus 2001) or reduced rates of growth (Song *et al.* 2012).

This sensitivity of epiphytic bryophytes results from their structure and the specific water management. They are poikilohydric plants lacking roots and an outer waxy cuticle what makes them able for direct uptake of moisture from the atmosphere but without homeostatic regulation of their water status. Thus, they are susceptible to ambient wetting-drying cycles (Green *et al.* 2011). That is why water availability is thought to be the overriding environmental factor determining the distribution of poikilohydric epiphytes (Barkman 1958; Bates *et al.* 2004). Dry periods are particularly critical for juvenile mosses and germination of spores; these stages are also sensitive to frost. Described biological features make many of the species also sensitive to the air pollutants, gaseous and dusty, which can penetrate every cell of the bryophytes body and damage their structures. These pollutants act on epiphytic bryophytes also indirectly throught changing tree trunk chemistry, including its reaction (pH), what can disturb growth and distribution of the species with narrow ecological amplitudes which are observed among epiphytes (Barkman 1958; Greven 1992; Dierssen 2001).

Urban built-up areas create difficult conditions for epiphytic bryophytes, including constraints such as dry air and pollution from fuel combustion, and limited availability of substrate (tree trunks). However, in the last two decades, a process of recolonization by epiphytic mosses has been reported in some European cities. It was emphasized the improvement of air quality in these cities, especially decrease in SO_2 content, as the main reason for these changes (Sérgio *et al.* 2016; Stebel & Fojcik 2016). But during that time also another environmental change acted. The world has been continuously getting warmer. In cities, due to greater heat capacity of concrete and other materials covering most of the ground compared to bare or vegetated soil, the temperature increase may be locally more intense, deepening the UHI-induced decrease in the air humidity (Munzi *et al.* 2014). The question whether occurrence and spread of epiphytic bryophytes in cities with the reduced air pollution level is presently facilitated or limited due to warming has arisen. Is the current epiphytic bryoflora distinguished by the presence of species preferring warm air as it has been evidenced in 2010 for epiphytic lichens in two German cities (Kirschbaum *et al.* 2012)? There are no papers reporting studies on that problem. The last years were considered as the warmest from the time of regular temperature measures. According to the opinion of Plášek *et al.* (2014), even in a relatively short time epiphytic bryophytes can gain considerable changes in richness and diversity as a result of the environmental changes.

In the southern part of Belgium, Hutsemékers *et al.* (2023) studied relationships between the temporal change of the epiphytic bryophytes' species composition, climatic conditions and air pollution loads. These research showed that if we consider the whole interval of the last 40 years the main factor contributing to the changes in the species composition was really the improvement of air quality, and climate change itself had a minor effect. At the same time, these authors believe that the current changes in the epiphytic flora can be better explained by the spatial variability of climatic conditions than by existing pollution. Similar opinion in relation to drivers of current epiphytic lichens diversity in cities was formulated by Munzi *et al.* (2014). Experts expect an increase in days with extremely high temperatures in summer and a reduction in frosty days in winter due to warming in central and eastern Europe. The second expected effect is an increase in the intensity, frequency and regularity of heavy rains, even in winters, what would influence relative humidity in the air (EEA Report No 1. 2024). Frahm & Klaus (2001) believed that bryophytes have their main growth period in temperate latitudes just in the wintertime, from December to March. Thus, theoretically, frost-free winters with high air humidity could favor the vegetation of bryophytes, especially the processes of spore germination and the formation and growth of gametophores.

Wrocław seemed to be a good place to study whether the occurrence of the city's epiphytic bryophytes have changed during the last 10 years in a way indicating a significant impact of warming. The epiphytic bryoflora of the whole city was examined in 2013-2015 using the method of randomly selected tree-planted research plots described by geographic coordinates (Fudali & Szymanowski 2019) what made easy to find them again. After, it was described and published (Fudali 2019; Fudali & Żołnierz 2019) what gave data for comparison. Since 2018, the city council has been implementing the program of the furnace replacement, what resulted in a significant decrease in emissions of SO_2 and CO (Ostrycharz *et al.* 2024). Therefore, in 2023, 109 research plots located in the city center, previously investigated in 2013, were re-examined for the presence of epiphytes and their abundance using similar methods.

The paper presents comparative analysis of collected data focused on answering the question whether the species composition, frequency within the city center and abundance of epiphytic bryophytes has recently undergone changes that would clearly indicate the influence of warming. It has been assumed possible difference in these reactions between parks and built-up areas with streets, as these urban-use complexes differ significantly in terms of microclimate, tree arrangement, tree-trunks availability for the colonization by epiphytes as well as the diversity and richness of epiphytic bryophytes (Fudali 2019).

MATERIAL AND METHODS

Study area

Wrocław, situated in the south-western part of the country, is one of the biggest and oldest towns in Poland, occupying an area circa 293 km^2 and inhabited by about 674 000 permanent residents (GUS 2022) and since 2022 by over 200 000 immigrants. The city is located in a flat area formed by the Odra River and its five tributaries which connect with the river in the city. A compactly built-up centrum, comprising old downtown, factories, large housing estates built mostly in the period of 1960s-1990s, and strongly developed network of streets, covers about 30% of the city area. About 17% of the centrum surface is occupied by urban greenery (four large parks and few smaller ones, tree-lined walking routes – Lewicki 2014). Typical for the city center are tree-covered lawns between buildings.

The climate is transitional, between oceanic and continental with short and mild winters. The average annual temperature is about 10°C, and the annual temperature amplitude is 20.5°C. Within the centre of Wrocław, an urban heat island is detected, raising the annual mean temperature by 1°C, and in windless and cloudless night, even exceeding 9°C (Szymanowski & Kryza 2009). The average annual relative air humidity in the city centre is about 6% lower than outside it, and on clear nights in summer it is even 40% lower. In the years 2013-2023 the average annual temperature in Wrocław showed fluctuations, ranging between 8.92°C and 11.5°C but did not appear a clear upward trend. However, such trend was visible in winter and autumn months: January, February, March, September and October. Since 2019 average months temperature between December and March was in Wrocław never below 0°C. In these months, the days with precipitation accounted for 40-51% (Szokalska 2018-2023).

In the period 2019-2023, the level of SO_2 and CO in the air within Wrocław did not exceed the lower thresholds of the assessment (respectively: 50 µg/m^3: 5 µg/m^3), while for NO_2 the permissible level for average annual concentrations (32 µg m^3) was exceeded and 1-hour concentrations were in the range of 140-100 µg/m^3. A large load of air pollution is suspended dust, PM10, PM 2.5, for which the daily permissible level was observed to be exceeded; average annual concentration of PM2.5 dust was above 17 µg/m^3 (Ostrycharz *et al.* 2024).

Sampling design and field surveys

The concept of the described research was based on the re-examination of 109 research plots previously studied in 2013. Then an initial network of 100 × 100-m plots (squares) was established over the whole area of Wrocław. Next, based on a 1-m surface digital terrain model (LIDAR–originated) determining the canopy of trees, all the squares where trees existed were selected. From that set, 500 research plots were randomly drawn using computer program (Fudali & Szymanowski 2019). For the current research, the location of the plots was limited to the city center, because this area seemed to be the most affected by environmental changes related to the increase in temperature, both as a result of global warming and the urban heat island. To test the working hypothesis, 37 locations in the city center parks (P), 33 – from those situated within housing estates with tree-covered lawns (B), 29 – from those covering housing estates mixed with streets (the latter

TABLE 1. — Comparison of the numbers of the research plots and trees on which epiphytic bryophytes were found in 2013 and 2023 as well as the total cover area occupied by them in relation to the type of urban-use complexes. Key: symbols of urban-use complexes: **B**, built up areas with green squares; **B-U**, built up areas with green squares together with streets (the latter covering 10-40% of the plot area); **P**, parks; **U**, streets with tree-lines.

	Number of plots with				Total number of trees with				Total cover area [dm²] of			
	Bryophytes on trunks		Obligatory epiphytes		Bryophytes on trunks		Obligatory epiphytes		Bryophytes on trunks		Obligatory epiphytes	
Type of urban-use complex	2013	2023	2013	2023	2013	2023	2013	2023	2013	2023	2013	2023
P	34	34	31	32	228	341	145	218	405.9	1328	136.7	305
B	27	28	14	22	134	218	37	91	198.2	549.8	5.1	27.4
B-U	19	25	14	17	75	130	27	48	111.3	351.6	4.8	19.1
U	6	8	4	7	19	34	8	15	49.4	103.9	2.8	12.5
In total	86	95	63	78	456	723	217	372	764.8	2334	149.4	364

occupied 10-40% of the plot area – B-U) and 10 – from those covered mostly with streets (U) were chosen from the remaining plots located in the city center which had a mixed nature of the land use. In every research plot all trees with a girth of more than 30 cm were studied at the height range of 0.8-1.2 m above ground level to find presence of bryophyes and, then, to record a phytosociological releves, each covering 30 × 40 cm. The area occupied by the individual species was noted in % coverage and later, during analyses, converted into the size of the area covered with the species in [dm²]. Species than could not readily be identified in the field were sampled for determination in the laboratory. The moss and liverworts nomenclature follows Hodgetts *et al.* (2020).

Since the bryophytes occurring on tree trunks have varying colonization abilities to other substrates (e.g., soil, rocks, rotten wood) two types of epiphytes are usually distinguished in the contex of bryophyte ecology: obligatory (inhabiting only tree trunks) and facultative (colonizing tree trunks and other substrates). Classifying a species as an obligatory or facultative epiphyte always relates to regional conditions (Barkman 1958). In the presented study the group of the facultative species was additionally divided on epiphytic-epilithical that colononize tree trunks and rocklike habitats (e.g., walls and concrete) and multisubstrate ones. The species affiliations to one of these groups were based on bryological data published for Wrocław and its vicinity to date (Fudali & Żołnierz 2019 and literature quoted therein). During field surveys the presence of 11 species which usually occur in other habitats and appear incidentally on the trees was noted, but they were omitted in further analyses which concerned typical epiphytes.

STATISTICAL ANALYSES

The aim of the analysis was to assess the changes in the number of trees inhabited by epiphytes and in the area occupied by these epiphytes on tree trunks in the research years 2013 and 2023 in the urban areas of Wrocław. The study aimed to identify whether the changes that occurred are statistically significant in different spatial groups classified according to the urban-use complex variable. In the analysis, the nonparametric Kruskal-Wallis test was used, which allows for the comparison of the median between more than two groups in the case of data that do not meet the assumptions of normality. The analysis was performed using the SciPy© library, in the Python v10 environment.

RESULTS AND DISCUSSION

ASSESMENT OF CHANGES IN THE EPIPHYTIC BRYOPHYTES OCCURRENCE

In the general assessment, the number of research plots in which bryophytes were recorded on tree trunks (in the tree segment studied) as well as the number of inhabited trees and the size of the area occupied by the bryophytes increased visibly (Table 1). This upward trend refers also to all the types of land use but there were quantitative differences among them.

The largest percentage increase in the number of trees with bryophytes was calculated for U (79%) and B-U (73%) while the smallest for P (50%). But when only obligatory epiphytes were considered – the largest percentage increase appeared in B (146%). However, in P the number of trees covered with bryophytes (both in the entire diversity of species and when only the obligatory epiphytes are considered) remained the largest. The Kruskal-Wallis test showed that statistically significant changes in this parameter were observed only for two urban-use complexes: B and P (Table 2). In relations to the area of tree trunk covered by epiphytes, the largest percentage increase was observed for P (227%) and B-U (216%) and only for these types was statistically important (Table 2). But when only obligatory epiphytes were considered – the largest percentage increase appeared in B (437%) and U (346%).

It is worthy to point out, that in both years of research the percentage share of obligatory epiphytes in the total area of the bryophytic cover on tree trunks was similar, reaching: 19.6%: 9.8% respectively (Table 1).

DYNAMIC TRENDS IN THE SPECIES OCCURRENCE

Not all species recorded on tree trunks showed an upward trend in the number of the research plots and inhabited trees (Table 3). This trend is visible among most of the obligatory epiphytes (64%) and most of facultative epiphytes with epiphytic-epilithic preferrences (67%) and in a case of *Hypnum cupressiforme* Hedw. which represent the facultative multisubstrates epiphytes. But the majority of the latter showed opposite tendency or lack of changes.

Table 2. — P-value in Kruskal-Wallis test showing statistical importance of changes observed in number of trees inhabiting by epiphytic bryophytes and their total cover area on research plots in relations to the urban-use complexes analysed. Abbreviation: *p˂0.05 statistically significant difference.

Type of urban-use complex	p_value_trees number	p_value_cover area
P	0.0002*	0.0000000002*
BS	0.0059*	0.667
BS + U	0.4651	0.001*
U	0.0599	0.097

Table 3. — Comparision of the total number of plots and trees colonized by the individual species in the years studied. Key: symbols of dynamic tendencies: **E**, clear expansion; **Es**, weak expansion; **En**, species recorded for the first time in Wrocław; **R**, spatial regression; **Rd**, disappearance; **S**, stagnation.

Name of species	Total number of plots		Total number of trees colonised		Dynamic tendency
	2013	2023	2013	2023	
Obligatory epiphytes					
Orthotrichum pumilum Sw. ex anon.	47	69	136	246	E
Dicranoweisia cirrata (Hedw.) Lindb.	21	40	86	115	E
Platygyrium repens (Brid.) Schimp.	15	21	40	79	E
Lewinskya affinis (Schrad. ex Brid.) F.Lara, Garilleti & Goffinet	11	4	20	13	R
Dicranum tauricum Sapjegin	4	4	5	7	S
Jochenia pallescens (Hedw.) Hedenäs, Schlesak & D.Quandt	2	3	9	3	R
Leskea polycarpa Hedw.	3	3	3	3	S
Radula complanata (L.) Dumort.	2	2	2	4	Es
Syntrichia papillosa (Wilson) Jur.	1	1	1	1	S
Pseudanomodon attenuatus (Hedw.) Ignatov & Fedosov	0	1	0	2	Es
Lewinskya speciosa (Nees) F.Lara, Garilleti & Goffinet	0	1	0	2	Es
Pterygynandrum filiforme Hedw.	0	1	0	2	En
Ulota bruchii Hornsch. ex Brid.	0	1	0	1	En
Plagiothecium laetum Schimp.	1	0	1	0	Rd
Total number of records	**107**	**151**	**303**	**478**	**–**
Facultative epiphytes: epiphytic-epilithical					
Orthotrichum diaphanum Brid.	55	76	234	373	E
Syntrichia virescens (De Not.) Ochyra	18	20	22	27	Es
Ptychostomum moravicum (Podp.) Ros & Mazimpaka	8	12	22	17	R
Pylaisiapolyantha (Hedw.) Schimp.	4	6	5	7	Es
Leucodon sciuroides (Hedw.) Schwägr.	0	1	0	1	En
Orthotrichum pallens Bruch ex Brid.	14	0	20	0	Rd
Total number of records	**99**	**115**	**303**	**425**	**–**
Facultative epiphytes: multisubstrates					
Hypnum cupressiforme Hedw.	64	75	258	429	E
Amblystegium serpens (Hedw.) Schimp.	60	42	149	96	R
Dicranum scoparium Hedw.	4	4	3	4	S
Lophocolea heterophylla (Schrad.) Dumort.	2	2	2	2	S
Total number of records	**130**	**123**	**412**	**531**	**–**

Comparison of the total number of research plots in which individual species were recorded and number of colonized trees in the analysed years (Table 3) exhibits three dynamic trends among epiphytes (both obligatory and facultative): 1) spatial expansion (increase in the number of plots and trees) found for 13 species (including eight obligatory epiphytes), but strongly marked only in a case of five taxa (three obligatory and two facultative epiphytes); 2) spatial regression (decrease in the number of plots and trees up to no occurrence in 2023) – six species (three obligatory epiphytes); and 3) stagnation (no changes in the number of plots and trees) – five (three obligatory epiphytes). Group of species classified as appearing expansion tendency comprises five taxa not recorded in the plots studied in 2013, including three species (obligatory epiphytes: *Pteryginandrum filiforme* Hedw., *Ulota bruchii* Hornsch. ex Brid. and facultative *Leucodon sciuroides* (Hedw.) Schwägr.) not reported from Wrocław so far (Fudali 1998, 2005, 2019; Fudali & Żołnierz 2019). The epiphytic bryoflora was therefore subject to dynamic species shift in the period studied. This is also evident when comparing on which plots species showing tendency of stagnation occurred in 2013 and 2023. Only in the case of *Dicranum tauricum* Sapjegin these were the same plots. Similar mobility among epiphytic bryophytes and tends to temporal shifts in species composition was found in the studies from southern Belgium (Hutseméker*s et al.* 2023).

A slightly different picture of the dynamic trends of some epiphytic bryophytes emerges from the comparative analysis of the changes in the area of the trunks covered by the individual species and its percentage share in the overall epiphyte's cover (Table 4). 17 species showed increase in cover

Table 4. — Comparison of the overall area covered by the individual species in a given year and its percentage share in the total bryophyte cover. Key: symbols of the trends of changes: **D**, decrease; **I**, increase; **N**, without changes; **s**, weakly expressed. Symbols of the cathegory of epiphytes: ******, obligatory epiphytes, *****, facultative epiphytic-epilithical; **lack of symbol**, facultative multisubstrates epiphytes.

Name of species	Cover area [dm²]		Trend of changes	% share in the total bryophyte cover area		Trend of changes
	2013	2023		2013	2023	
***Orthotrichum pumilum* Sw. ex anon.	15.65	171.5	I	2	7.3	I
***Dicranoweisia cirrata* (Hedw.) Lindb.	89.5	160.7	I	11.7	6.9	D
***Platygyrium repens* (Brid.) Schimp.	37.3	123.7	I	4.9	5.3	I
***Lewinskya affinis* (Schrad. ex Brid.) F.Lara, Garilleti & Goffinet	2.5	3.1	Is	0.3	0.1	D
***Dicranum tauricum* Sapjegin	2.1	1.3	D	0.3	0.06	D
***Jochenia pallescens* (Hedw.) Hedenäs, Schlesak & D.Quandt	1.7	0.7	D	0.2	0.03	D
***Leskea polycarpa* Hedw.	1.5	0.7	D	0.2	0.03	D
***Radula complanata* (L.) Dumort.	0.006	0.12	Is	0.008	0.005	N
***Syntrichia papillosa* (Wilson) Jur.	0.01	0.1	Is	0.001	0.004	Is
***Pseudanomodon attenuatus* (Hedw.) Ignatov & Fedosov	0	0.4	Is	–	0.02	I
***Lewinskya speciosa* (Nees) F.Lara, Garilleti & Goffinet	0	0.4	Is	–	0.02	I
***Pterygynandrum filiforme* Hedw.	0	0.2	Is	–	0.008	I
***Ulota bruchii* Hornsch. ex Brid.	0	0.03	Is	–	0.001	I
***Plagiothecium laetum* Schimp.	0.06	0	D	0.008	–	D
**Orthotrichum diaphanum* Bruch ex Brid.	334.4	820.7	I	43.7	35.2	D
**Syntrichia virescens* (De Not.) Ochyra	4	5.9	Is	0.5	0.3	D
**Ptychostomum moravicum* (Podp.) Ros & Mazimpaka	7.7	17.5	I	1	0.7	D
**Pylaisia polyantha* (Hedw.) Schimp.	1.6	4.3	Is	0.2	0.2	N
**Leucodon sciuroides* (Hedw.) Schwägr.	0	0.2	Is	–	0.008	I
**Orthotrichum pallens* Bruch ex Brid.	4.3	0	D	0.6	–	D
Hypnum cupressiforme Hedw.	179.3	860.7	I	23.4	36.9	I
Amblystegium serpens (Hedw.) Schimp.	44.6	104.5	I	5.8	4.5	D
Dicranum scoparium Hedw.	0.14	0.06	D	0.02	0.003	D
Lophocolea heterophylla (Schrad.) Dumort.	0.29	0.02	D	0.04	0.001	D

Table 5. — Detailed comparison of the changes in the epiphytic species diversity found in the particular urban-use complexes between 2013 and 2023. Key: symbols of the ecological groups: **FD**, facultative epiphytes, epiphytic-epilithic; **FM**, facultative epiphytes multisubstrates; **OB**, obligatory epiphytes. Symbols of changes: (**–**), loss; (**+**), increase. Symbols of urban-use complexes as in Table 1.

Type of urban-use complex	Changes in the species number	Not recorded in 2023			New in 2023			Present in both periods		
		Epiphytes			Epiphytes			Epiphytes		
		OB	FD	FM	OB	FD	FM	OB	FD	FM
In total	3+	1	1	0	4	1	0	9	4	5
P	0	2	1	0	3	0	0	8	4	5
B	1+	1	1	0	1	2	0	4	3	3
B-U	2+	1	1	0	4	0	0	2	4	4
U	3–	2	1	2	1	0	0	1	1	3

area but only nine of them also increase in % of share. It is striking that among remaining ones there are such species as obligatory *Dicranoweisia cirrata* (Hedw.) Lindb. and facultative *Orthotrichum diaphanum* Sw. ex anon., because these species exhibited visible increase in a number of plots and inhabited trees.

Based on the analyses presented so far, it can be accepted that quantitative changes in the occurrence of epiphytic bryophytes were caused by strong expansion of several species which were: obligatory epiphytes – *Orthotrichum pumilum* Sw. ex anon, *Dicranoweisia cirrata*, *Platygyrium repens* (Brid.) Schimp. and facultative ones – *Hypnum cupressiforme* and *Orthotrichum diaphanum*. The two latter showed the greatest increase in the number of inhabited trees and the total cover area. It should be noted that most of the other obligatory epiphytes have also shown an upward trend but weakly expressed.

Regarding changes in species diversity, an upward trend in the total number of obligatory epiphytes appeared, from 10 to 13. The number of facultative species has not changed.

Assessment of changes in the species diversity in relation to urban-use complexes

Previous analyses (Table 1) showed some differences in the intensity of the quantitative changes in the epiphytic bryophytes occurrence in various urban-use complexes concerning the number of plots, inhabited trees and the cover area, what agrees with the preliminary assumption. These differences are also evident when comparing the number of epiphytic species and their diversity (Table 5).

The number of epiphytes was the highest in P and did not changed, amounting 19. A slight increase, one species, was recorded in B and B-U and amounted 12: 13 respectively, but in U a decrease from nine to five was noted. The highest

Table 6. — Changes in the number of inhabited trees and the bryophyte cover area in the particular urban-use complexes calculated for the most expansive species and these with strong regression. Key: ×, not recorded in the years of studies; (–), loss; (+), increase. Symbols of urban-use complexes as in Table 1. Symbols of the cathegory of epiphytes as in Table 4.

Name of species	Change in the number of trees occupied				Change in the cover area [dm²]			
	P	B	B-U	U	P	B	B-U	U
The most expansive species								
***Orthotrichum pumilum* Sw. ex anon.	69+	39+	1+	2+	26.7+	9.7+	10.6+	9.9+
***Dicranoweisia cirrata* (Hedw.) Lindb.	19+	9+	2+	1–	63.6+	9.3+	1.3+	1.5–
***Platygyrium repens* (Brid.) Schimp.	38+	1–	3+	1–	81.6+	3.1+	1.9+	0.2–
**Orthotrichum diaphanum* Bruch ex Brid.	12+	78+	25+	22+	21.8+	245.8+	163.5+	55.2+
Hypnum cupressiforme Hedw.	136+	17+	19+	1–	534.3+	76.3+	67.6+	2.2+
Species with clear regression								
***Lewinskya affinis* (Schrad. ex Brid.) F.Lara, Garilleti & Goffinet	9–	1+	2–	3+	1.2–	0.4+	0.1–	1.5+
***Dicranum tauricum* Sapjegin	2+	×	×	×	0.8–	×	×	×
***Jochenia pallescens* (Hedw.) Hedenäs, Schlesak & D.Quandt	7–	×	1+	×	1.1–	×	0.1+	×
***Leskea polycarpa* Hedw.	1+	1–	×	×	0.6–	0.2–	×	×
**Orthotrichum pallens* Bruch ex Brid.	5–	13–	1–	1–	0.8–	3.2–	0.1–	0.2–
Amblystegium serpens (Hedw.) Schimp.	3–	32–	14–	4–	83.2+	6.5–	1.6–	0.4–

percentage of permanent species was in P (74%) and the lowest in U (45%), while in B and B-U remained on similar levels, 67%: 63% respectively. These differences show that the intensity of epiphytic species exchange depended on the type of urban-use complex.

Among the species classified as the most expansive some differences in the intensity of changes between parks and built-up areas were found (Table 6).

In parks visibly stronger expansion than in other urban-use complexes exhibited *Hypnum cupressiforme*, *Dicranoweisia cirrata* and *Platygyrium repens*, while *Orthotrichum diaphanum* expanded most intensively in the built-up area. *Orthotrichum pumilum* seems to spread without such pronounced preferences to one of the urban-use complexes. Among the species showing the regression in 2023 two facultative epiphytes, *Orthotrichum pallens* Bruch ex Brid. and *Amblystegium serpens* (Hedw.) Schimp. showed the greatest decrease in records in built-up area and streets, but obligatory epiphytes: *Lewinskya affinis* (Schrad. ex Brid.) F.Lara, Garilleti & Goffinet, *Jochenia pallescens* (Hedw.) Hedenäs, Schlesak & D.Quandt and *Dicranum tauricum* Sapjegin lost most records in parks.

Analysis of possible causes of observed changes in species composition

Regarding some authors' opinion that distribution of epiphytic bryophytes in cities is greatly depending on air humidity, temperature and level of air pollution (*i.e.*, Stapper & Kricke 2004; Larsen *et al.* 2007; Żołnierz *et al.* 2022) the ecological characteristics (Dierssen 2001) of the species showing different dynamic tendencies (newly found, not re-found, showing clear regression and strongly expansive) were compared to find the possible reasons of the revealed changes in the epiphytic bryophytes diversity during the last 10 years (Table 7). The use of the species' general ecological indicators in such analysis undoubtedly limits its accuracy but allows for the indication of trends.

Among newly found epiphytes there was no thermophytic species althought *Pterygynandrum filiforme,* new for Wrocław, is characterized by Dierssen (2001) as species able to survive in a range of temperatures from moderate to high. Thermal requirements of not re-found species and these with clear regression also do not indicate that increase in temperatures had a direct impact on their dynamics. In the group of strongly expanding species there are similar numbers of mesothermic and thermophytic species. The latter, *Orthotrichum diaphanum* and *O. pumilum*, had already occurred in Wrocław before 2000 (Fudali 1998, 2001). Thus, last warming itself does not seem to be the driving factor causing the changes in the species diversity. However, the fact that two highly expansive species are thermophilous should not be neglected.

Most of the newly found epiphytes are able to live in a wide range of air humidity, from moderately wet to dry, similarly as many of these in regression and not re-found. The groups of expanding species and these showing regression consist on species with different requirements for air humidity which does not allow to indicate this factor as decisive for the observed bryofloristical changes.

In relation to light intensity factor, a dominant share of photophytes is visible in the group of newly found species and these in expansion, while among the epiphytes appearing regression there are both sciophytic and eurytopic epiphytes, similar to the group of the species not recorded in 2023. Thus, a possible increase in the availability of the light, for example as a result of trees removal (observed in 32 research plots – 29% of all) could facilitate the expansion or colonization of some photophytic species.

Regarding ecological requirements in relations to bark pH all the dynamic groups exhibit a clear diversity. Species with opposite requirements and eurytopic ones have similar shares in there. The only exception was the group of expanding species in which there were not acidophytes. Is the latter a reaction on a possible decrease in acidification of the urban environment due to reducing SO_2 emissions? Among the newly found

TABLE 7. — Comparision of the ecological characteristics (taken from Dierssen 2001) of the species showing different dynamic tendencies during 2012-2023. Key: symbols of the species ecological requirements: **c**, considerable; **cryo**, able to live in cold areas; **h**, highly; **m**, moderate. Symbols of the cathegory of epiphytes as in Table 4.

		Groups of different dynamics			
Ecological factor	**Range of the ecological requirements**	**New (5)**	**Vanished (2)**	**In regression (5)**	**Expansive (5)**
Temperature	cryo-mesotermic:	1**	1**	–	–
	mesotermic:	1**	–	2**	2**
	termophytic:	–	–	–	1**;1*
	mesotermic-termophytic:	1**	–	1**	–
	cryo-termophytic:	–	1*		–
	termoindifferent:	–	–	–	1▪
	undetermined	1**;1*	–	1**; 1▪	–
Air humidity	m hygrophytic:	–	–	1**	1**
	hygrophytic-mesophytic:	–	–	1**	–
	mesophytic:	1**	1**	–	–
	m-h xerophytic:	–	–	–	1**;1*
	mesophytic - m xerophytic:	3**	–	2**	1▪
	mesophytic- c xerophytic:	1*	–	–	1**
	m hygrophytic - m xerophytic	–	1*	1▪	–
Light intensity	c-m sciophytic:	1**	1**	2**	–
	m photophytic:	2**	–	–	2**
	c photophytic:	1*	–	–	1**;1*
	m sciophytic-m photophytic:	.	1*	1**;1▪	1▪
	m sciophytic-c photophytic:	1**	–	1**	–
Substratum reaction	c-m acidophytic:	1**	1**	2**	–
	subneutrophytic:	1**	1*	1**	–
	subneutro-basophytic:	1**	–	–	1**;1*
	acidophytic-subneutrophytic:	–	–	1**;1▪	2**;1▪
	acidophytic-basophytic:	1**;1*	–	–	–
Reaction to the air pollution	tolerant:	–	–	1**	1**;1▪
	sensitive:	2**;1*	–	2**	1*

species there are three classified as sensitive to the air pollution (obligatory *Lewinskya speciosa* (Nees) F.Lara, Garilleti & Goffinet, *Pterygинandrum filiforme* and facultative *Leucodon sciuroides*) and there is no species described as resistant, what can be interpreted as an indicator of the air purity improvement. Expansive spread within built-up areas of subneutral *Orthotrichum diaphanum*, which before 2000 was noted in Wrocław mostly on walls not on tree trunks (Fudali 2001) could also be a reaction to the decrease in acidification of trees bark. The presented data have agreed with observation by Hutsemékers *et al.* (2023), who reported that the first group reacting on air purity improvement were the resistant epiphytes and they expanded their range. The inflow of new species, sensitive to the air pollution, occurred in the later stages.

Summarizing this analysis, it seems highly probable that last changes evidenced in the species composition were affected mostly by an improvement of the air purity. Changes in the species diversity during the studied period seem to be weakly related to warming. Similar to analyses of Hutsemékers *et al.* (2023) who also did not show a significant impact of warming on changes in the species composition of epiphytic bryophytes in southern Belgium in 1980-2020. The air pollution decrease, with high probability, might have caused a clear expansion of resistant to pollution epiphytes such as: *Hypnum cupressiforme*, *Dicranoweisia cirrata* and *Orthotrichum diaphanum*, which were previously present in that area.

But, in my opinion, the possible impact of increased temperatures and frost–free winter months, observed in Wrocław since 2019, on expansion of *Orthotrichum pumilum* and *O. diaphanum*, classified as thermophilous species, should be also considered. In the past these species were recorded in Wrocław on tree trunks rather rarely and the visible increase in their frequency and abundance definitely occurred only after 2011 (Fudali 2012, 2018). A high percentage of days with precipitation during warmer winters may have additionally favored their growth. Unfortunatelly, the impact of climate change on the physiology of epiphytes is very poorly researched. One of the few available studies is an experiment by Song *et al.* (2012) that brought different conclusions. To determine how climate change in subtropical mountain forests in China would affect the growth and health of epiphytic bryophytes researchers transplanted species from higher elevations to lower elevations, simulating in that way predicted for that region future thermal and humidity conditions. After two years they noted remarkably reduced rates of growth and detrimental effects on the health.

Looking for other reason of the observed changes in the epiphytic bryophyte's diversity and occurrence, a possible impact of the removal of old trees and pruning of tree crowns should not be ignored. These treatments lead to increase the amount of light reaching the trunks. Half of the new species and almost all of the expansive ones were photophytic.

CONCLUSION

The most spectacular change in the occurrence of epiphytic bryophytes in the center of Wrocław in the period 2013-2023 was a significant increase in their area covering tree trunks and a clear increase in the number of inhabited trees. Such visible spatial expansion was demonstrated mostly by five species. But also most of other epiphytes have shown upward trend however it was weakly expressed. These reactions may result both from improved air purity and warmer winters with frequent precipitation as well.

In relation to the species diversity, an increase in the richness of obligatory epiphytes was found, although these new species occurred on one-two trees with negligible cover area which indicates the initial stage of their colonization. No new thermophilic species appeared. But two of newly recorded in Wrocław species are considered as sensitive to the air pollution. Thus, floristical changes seem to result from the improvement of the air purity.

The intensity of the species exchange depends on the type of land use, similar to changes in the frequency and abundance. Parks still have the richest epiphytic bryoflora and are distinguished by the largest number of inhabited trees and the largest bryophyte's cover area. However, the largest percentage of changes was recorded in built-up areas.

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