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Diversification of macrophytes within aquatic nature-based solutions (NBS) developing under urban environmental conditions across European cities

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ABSTRACT

This article explores the diversification of macrophytes in aquatic nature-based solutions (NBS) under urban conditions across European cities, highlighting their role in enhancing climate resilience, biodiversity, and ecosystem quality. While aquatic NBS have been studied for engineering and social aspects, comprehensive biological analyses, particularly across geographical gradients, have been lacking. This research, part of the BiNatUr project, investigates macrophyte richness in aquatic NBS in five European cities: Belgium, Finland, Germany, Poland, and Portugal. The study involved 120 sites, with each city contributing 12 sites representing restored or constructed ponds and streams in both altered and natural states.

Surveys conducted used 10-meter quadrats to assess the abundance of macrophytes, which were identified to species level. The analysis included emergent, submerged, and floating plants, using Ellenberg indicator values (EIV) for ecological preferences related to light, temperature, continentality, moisture, pH, and nutrient levels. A total of 103 aquatic plant species were identified, with significant variability in species richness and abundance among the cities. Helsinki had the highest species richness, averaging 7.25 species per site, while Berlin had the lowest at 3.54 species per site. Macrophyte abundance was highest in Finland and Poland, with 44.8% and 35.7% coverage, respectively, and lowest in Germany at 12.2%.

Detrended Correspondence Analysis (DCA) highlighted significant differences in macrophyte community structures, with Lisbon showing a unique species composition.

The study underscores the diversity of macrophytes in urban aquatic NBS across Europe, emphasizing their value as biodiversity hotspots in urban settings. These findings provide crucial insights into macrophyte abundance, species richness, and ecological characteristics, contributing to the understanding of aquatic ecosystems under high stress in cities and informing conservation and urban planning initiatives.

1. Introduction

Urban freshwater ecosystems are a very valuable element supporting the adaptation of cities to climate change, as they constitute the basis of the natural system of cities while generating many other benefits (e.g., increase in biodiversity, recreational space for residents, limiting the impact of the urban heat island, etc.) (van der Dorst et al., 2019; Sun et al., 2024). However, pressure from urbanisation and decisions leading to their degradation have significantly reduced this role. A step to

improve the functioning of urban water areas while adapting cities to climate change is to take action to retain rainwater in ponds and seminatural (rehabilitated) streams. Additionally, retention can be increased by rehabilitating the waterbed and restoring its natural three-dimensional structure (differentiation of cross-section, longitudinal section, and meandering). This also increases the diversity of habitats, i. e., physical habitats that constitute the basis for shaping ecosystems' biological structure, strengthening their biodiversity and metabolic self-purification abilities (Krauze and Wagner, 2019; Ranta et al., 2021).

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One of the critical management means to these problems is naturebased solutions (NBS), broadly introduced as an alternative solution for engineer-based grey infrastructure approaching various environmental and social problems in cities (Kabisch et al. 2017; Sowińska-Świerkosz et al., 2021; Pinho et al., 2023). NBS implementation activities have been identified as interventions that (1) are inspired and driven by nature; (2) face social challenges or help solve these problems; (3) provide multiple services and benefits, including enhancing biodiversity; and (4) are characterised by high effectiveness and economic efficiency (Sowińska-Świerkosz and García, 2021). A good example of activities that meet these requirements are activities related to surface aquatic ecosystems, which contribute significantly to increasing biodiversity. People highly value them due to their aesthetic and recreational values, and they are called aquatic NBS (aquaNBS) (Krauze and Wagner 2019). In the case of streams, introducing small deflectors or other various channel attributes improving morphodynamical processes may benefit both the ecological conditions and the biodiversity of watercourses (Kałuża et al., 2018; Zaborowski et al., 2022; Zaborowski et al., 2023). Similarly, small water bodies in urban areas functioning as aquatic NBS, with appropriate infrastructure investment, can reach high plant biodiversity, support endangered species, provide resilience to flooding and drought, and improve the aesthetic appearance (Liquete et al., 2016; CuencaCambronero et al., 2023; Muñoz et al., 2024). Such activities are undertaken on many small watercourses, also in cities, contributing to improving residents' quality of life (Kremer et al., 2018).

There are relatively few completed studies on the diversity of macrophyte communities in aquatic NBS (e.g., Williams et al., 2020; Oertli et al., 2023; Pastor et al., 2023), and there is a notable lack of extensive research covering broader areas, such as across Europe (Hale et al., 2023). Additionally, publications focusing on urban NBS are even scarcer, and the analyses of macrophyte diversification within these studies tend to be quite general (Oertli et al., 2023).

Macrophytes play an important role in aquatic environments by providing physical structure, food and shelter (Thomaz and Cunha 2010), increasing habitat complexity and heterogeneity which, in turn, strongly affects other aquatic organisms such as benthic macroinvertebrates (Błachuta et al., 2014), fish (Meschiatti et al., 2000), zooplankton and microalgae (Kuczynska-Kippen and Joniak, 2016). Plants are sensitive indicators of the aquatic environment, able to detect eutrophication (Haury et al., 2006; Szoszkiewicz et al., 2022), and to some extent also acidification (Tremp and Kohler 1995) and morphological degradation (Haury et al., 2006). Furthermore, aquatic plants respond to various environmental factors, including light, temperature, and substrate (Bornette and Puijalon, 2011; Dengler et al., 2023).

Based on the composition of the species developing in a given habitat, its environmental quality can be determined. Assessment of a habitat based on the properties of the species growing in it is called bioindication, and various groups of organisms can be used, including macrophytes, which are considered sensitive indicators (Haury et al., 2006; Szoszkiewicz et al., 2022). Germany pioneered one of the earliest plant-based bioindication systems, introducing the Ellenberg Indicator Values (EIV). These values assess species' environmental preferences, including light availability, temperature, soil moisture, pH, and trophy based on nitrogen availability (Ellenberg, 1974). EIVs are among the most widely used methods for biological monitoring, particularly effective in bioindication through analysing the species composition of communities (Di Biase et al., 2023).

This article aims to offer valuable new insights into the diversification of macrophytes within aquatic nature-based solutions that are developing under urban environmental conditions across European cities. The study focuses on differences in species richness, abundance, and plant ecological characteristics. Specifically, it addresses the following questions: How do macrophyte communities' taxonomic diversity and ecological range vary across European cities? What environmental factors contribute to the observed differences in species richness and ecological characteristics within these urban aquatic NBS?

Additionally, the article explores whether urban aquatic NBS, despite their small size and surrounding urban modifications, can play a significant role in conserving urban biodiversity. The study underscores the importance of urban aquatic NBS in promoting and enhancing biodiversity within city environments.

2. Methods

2.1. Sampling design

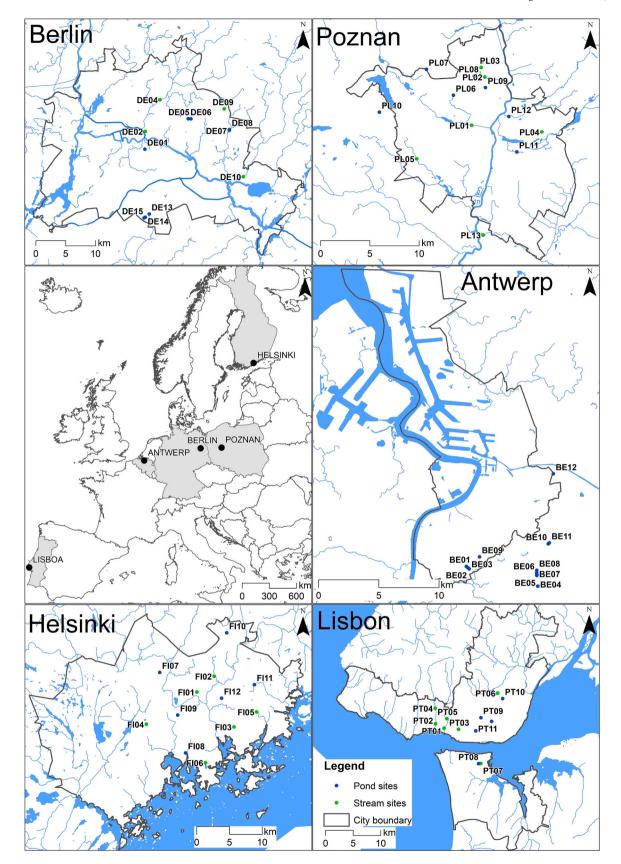
The study is conducted within the BiNatUr project under the BiodivRestore ERA-NET Cofund (GA N°101003777) from 2022 to 2025. It aims to take a comprehensive approach to examine the interactions among social, ecological, and technological factors related to aquatic NBS across five European cities: Antwerp (Belgium, abbreviation BE), Berlin (Germany, DE), Helsinki region (Finland, FI), Lisbon (Portugal, PT), and Poznań (Poland, PL) (Fig. 1). This resulted in 120 sites sampled in urban aquatic ecosystems across Europe, mostly small water bodies, with detailed parameters provided in Supplement 1. In general, the streams were narrow (median width of 2.1 m, maximum 10.6 m) and shallow (median depth of 0.3 m, maximum 0.7 m). The ponds were small in surface area (median 2,064 m², maximum 41,000 m²) and shallow (median depth of 1 m, maximum 6 m). Study sites were selected using a stratified random sampling. Site stratification was made by city (12 locations per city), type of aquatic NBS (stream and ponds), water availability throughout the year (temporary and permanent), and naturalness (most and least altered location within each NBS). The study sites were typically in urban areas – the median urban land use within a 500 m radius was 54 % and reached up to 97 % (Supplement 1).

2.2. Field sampling

Each field study location spanned 100 m and included two survey sites: a more natural section typically characterised by well-developed vegetation along the banks and a more modified section where bank vegetation has often been disturbed or even removed (Fig. 2). The survey site was based on 10-meter quadrats, which were roughly divided between the bank zone and the aquatic zone, where macrophytes were recorded. The survey encompassed emergent, submerged, and floating macrophytes. Species abundance was assessed using a 9-level cover scale (Szoszkiewicz et al., 2020), and macrophytes were identified at the species level. Field surveys were conducted during the summer season in 2023, spanning from July to early September, to include the most favourable season in each city.

2.3. Data analysis

Species richness was determined per city, considering total, submerged and floating-leaved plants, emerged helophytes and total species richness per survey transect. Moreover, several diversity metrics that incorporate relative species abundance were calculated, including Shannon diversity (Shannon and Weaver, 1949), Simpson diversity (Simpson, 1949), and evenness (Pielou, 1966). The total species richness per survey transect was plotted in boxwhiskers and tested for significant differences between cities. Macrophyte abundance per site was also calculated and compared for significant differences. The Community Weighted Mean (CWM) per site based on EIV, according to Dengler et al. (2023), was calculated considering abundance-weighted values. This calculation incorporated six EIV types: light (L), temperature (T), continentality (K), moisture (F), pH (R), and trophic conditions (N), and was then plotted and tested for significant differences between cities. Finally, the structure of macrophyte communities was analysed using Detrended Correspondence Analysis (DCA). EIVs were analyzed as supplementary variables. The results were graphically presented on separate figures for the distribution of sites and macrophyte species. Only the frequent species were analysed (four or more repetitions).



 $\textbf{Fig. 1.} \ \ \text{Distribution of the surveyed sites (n} = 60) \ \ \text{in five European cities. Helsinki region includes the city of Helsinki and Vantaa. Lisbon region includes the city of Lisbon and Almada. \\$

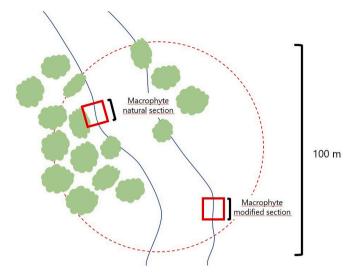


Fig. 2. The design of the field study location with two macrophyte survey 10-meter quadrats: a more natural site (typically characterized by well-developed vegetation along the banks), and a more modified site (usually disturbed or removed bank vegetation).

Statistical analyses were conducted using Statistica 14.0. Due to the absence of homogeneity in variance, the significance between cities was assessed using the non-parametric Kruskal-Wallis test. DCA was performed using Canoco for Windows 4.5.

3. Results

3.1. Species diversity and macrophyte abundance

During the survey, 103 taxa of aquatic plants were identified, consisting of 23 submerged and floating-leaved plants, along with 80 emergent helophytes (Table 1). Among these, 43 were dicotyledons, 57 were monocotyledons, and 3 were pteridophyte species. The number of identified macrophyte species in a city ranged from 29 (Lisbon) to 48 (Poznań). The complete list of identified macrophytes can be found in the Supplement 2.

On average, a few macrophytes were detected in a single survey site, with only 5.02 different taxa per site (ranging from 0 to 15) (Table 1). A complete absence of aquatic plants was found in four sites in Germany. The mean number of submerged and floating-leaved species was < 1 (only 0.76 taxa), while emerged taxa averaged 4.2 (ranging from 0 to a maximum of 5 and 13, respectively). Significant differences in macrophyte richness were observed between the cities (p < 0.01). Helsinki displayed the highest average number of taxa (7.25) and the greatest variability (SD = 4.20), while Berlin displayed the lowest, with 3.54 species per site (Fig. 3a).

Several diversity metrics incorporating relative species abundance were calculated, including Shannon, Simpson, and evenness indices. The average values of these metrics were compared between countries (Table 1). Shannon and Simpson indices, which combine relative abundance and species richness, revealed a trend similar to species richness (Fig. 3b and 2d). Significant differences were confirmed between Finland and Germany (Table 2). Additionally, the Shannon index showed an essential difference between Finland and Belgium. Regarding the evenness index, which relies solely on the relative abundance of species, the pattern was different (Fig. 3c): the most even relative abundance of detected macrophytes was found in Portugal (0.68), followed by Finland (0.64).

Substantial variations in the extent of riverbed coverage by developing macrophytes among the studied cities were detected (Table 1, Fig. 2e). The significance of differences between mean cover was confirmed by the Kruskal-Wallis test (p < 0.05, Table 2). The average coverage was 27.8 % of the surveyed transect. The lowest average macrophyte coverage was observed in Germany (12.2 %), while the highest was in Finland (44.8 %) and Poland (35.7 %).

Comparing types of aquatic ecosystems, 64 taxa were found in running waters and 90 in standing waters (Table 3). On average, a few macrophytes were detected in a single survey site, with only 5.04 different taxa per stream site (ranging from 1 to 16) and 5.15 in ponds (ranging from 0 to 13) (Table 3). Comparing diversity indices and the extent of riverbed coverage by developing macrophytes in streams and ponds across different countries, significant differences between mean cover were confirmed by the LSD test (p < 0.05) in Poland (H, D, coverage) and in Germany (D, J).

3.2. Ecological differentiation of macrophytes

The comparison of the average ecological scores (EIV) for each aquaNBS in the five European cities (Table 4, Fig. 4) proved to be significant for each EIV category (p < 0.005), except for moisture (Table 5).

Regarding the thermal indicator (Fig. 4a), the highest EIV was found in Portugal (6.67), which was significantly higher than in any of the other cities. This elevation in EIV was attributed to the exclusive presence of high EIV taxa, including *Arundo donax* (EIV = 9) and *Apium nodiflorum*, *Lythrum junceum*, *Cyperus longus*, *Azolla* sp. (all with EIV = 8). Moreover, Portugal's temperature EIV was very variable due to growing high EIV taxa (EIV = 8–9) and, on the other hand, an abundance of low-temperature species (EIV = 5) comparable to other cities. The temperature EIV between other cities was not statistically significant. Finland exhibited the lowest average temperature EIV at 5.37. The Ellenberg light indicator (Table 4, Fig. 4b) showed a similar pattern as temperature EIV to some extent. Specifically, the highest light EIV was found in Portugal (7.38), whereas the lowest values were found in Finland and Poland (7.06).

The mean habitat moisture EIV does not vary significantly between countries (Fig. 4c). This can be attributed to our consistent approach in addressing macrophyte communities with a uniform moisture perspective, irrespective of geographical gradients. Notably, in Portugal, the species with the most diverse water requirements were recorded (giving the outstanding standard deviation of the habitat moisture EIV), probably due to the seasonal nature of the rivers and water bodies in that region. The pH EIV indicator shows significant variation between

Table 1Macrophyte species diversity and abundance of aquaNBS in five surveyed cities.

Country	Species total	Submerged and floating- leaved plants	Emerged helophytes	Mean numbe Species richness	r of species per site Shannon diversity (H')	Evenness (J)	Simpson diversity (D)	Macrophyte cover %
Belgium	30	5	25	3.88	0.67	0.43	0.35	21.3
Finland	47	7	40	7.25	1.15	0.64	0.56	44.8
Germany	35	9	26	3.54	0.60	0.38	0.31	12.2
Poland	48	11	37	5.92	0.82	0.47	0.42	35.7
Portugal	29	2	27	4.46	0.97	0.68	0.50	24.4
Total	103	23	80	5.02	0.84	0.52	0.43	27.8

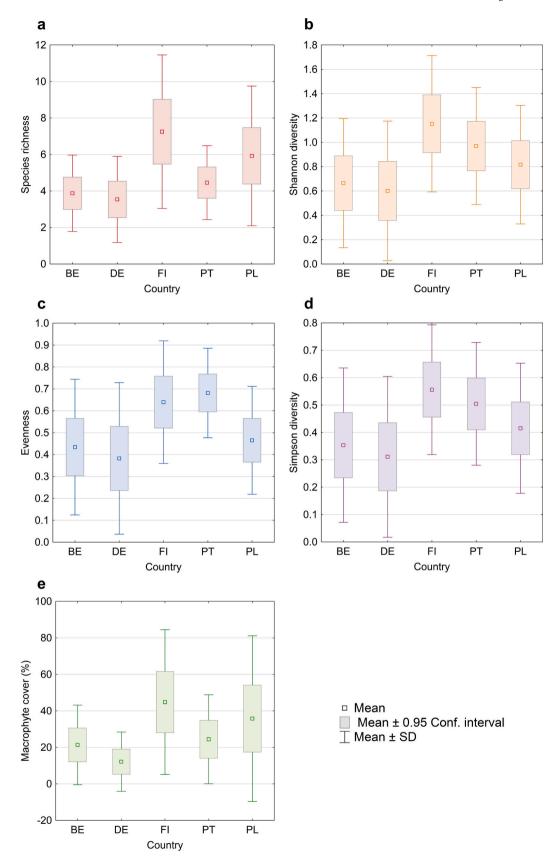


Fig. 3. A comparison of species diversity and abundance for each aquaNBS identified along the studied transect in five European cities: a – species richness, b – Shannon diversity, c – evenness, d – Simpson diversity, e – macrophyte cover (significance explained in Table 2).

Table 2Statistical verification of species diversity and abundance differentiation in aquaNBS in five European cities.

Species diversity indices and abundance	Kruskal- Wallis test	Significance (p)	Which groups are significantly different?
Species richness	13.974	0.0074	Finland from Germany
Shannon diversity (H')	14.453	0.0060	Finland from Germany and Belgium
Evenness (J)	18.731	0.0009	Portugal from Germany, Belgium and Poland
Simpson diversity (D)	13.831	0.0079	Finland from Germany
Macrophyte cover (%)	12.055	0.0169	Finland from Germany

countries (Fig. 4d). Finland stands out the most, where species preferring a pH ranging from moderately acidic to neutral (around 6.0–6.5) dominate. Species preferring the highest pH, close to neutral, were most commonly found in Germany and Poland. The Ellenberg trophic indicator shows significant variation between countries (Fig. 4e, Table 5). Similarly to the pH indicator, in Finland, species preferring significantly lower trophic conditions dominate (mean trophy EIV was 5.50). In contrast, the most eutrophic aquatic NBS were found in Berlin (6.66) followed by Antwerp (6.63).

3.3. Macrophyte communities

The results of the detrended correspondence analysis (DCA) showed that the gradient width of the first axis of DCA is 6.334 standard deviations, thus a model based on the normal distribution was used. DCA analysis based on frequent species showed the NBS macrophyte pattern across Europe. The first two axes revealed a 12.0 % cumulative variance of species data and 24.9 % cumulative variance of species-environment relation (EIVs were analyzed as supplementary variables). Fig. 5 presents the distribution of sites, and Fig. 6 displays the distribution of macrophyte species. The analysis showed that plant communities in Lisbon are markedly distinct due to the presence of unique species such as Azolla sp., Apium nodiflorum, Nasturtium officinale, Oenanthe crocata, Arundo donax, Carex flacca, Cyperus eragrostis, C. longus, C. papyrus, Typha domingensis, Lythrum junceum, Scirpoides holoschoenus. These species are primarily associated with high values of temperature EIV (T) and partly also with high solar energy EIV (L). On the other hand, communities in Finland were very different due to species typical of peat bogs and dystrophic conditions, e.g. Comarum palustre, Elatine hydropiper, Menyanthes trifoliata, Myosotis laxa, Scrophularia nodosa, Veronica scutellata, Calla palustris, Carex echinata, C. nigra, C. rostrata, C. vesicaria, Eleocharis mamillata, Juncus alpinoarticulatus, J. filiformis, Sparganium microcarpum, Potamogeton berchtoldii. These species are related with high values of habitat moisture EIV (F) and with low values of solar energy EIV (L), trophy (N) and pH (R). The acid reaction of the habitat and the scarcity of nutrients are typical features of dystrophic conditions. Moreover, several widespread taxa were found in Finland: Callitriche palustris, Lemna trisulca, and Poa palustris. The distinctiveness of the sites in Antwerp was due to the presence of Lemna minuta. Lythrum portula, Lotus pedunculatus, Rorippa palustris, Veronica catenata, Carex scoparia, Eleocharis engelmannii, Pontederia cordata and Scirpus taberneamontani. The unique species found in German sites were Acorus calamua, Callitriche sp., Potamogeton pectinatus, P. rutilus, Elodea canadensis, Carex aquatilis, C. echinata, C. elata and C. elongata. These species are related with high values of trophy EIV (N) and with low values of temperature EIV (T). Exclusive species characterised the Polish flora as Ranunculus sceleratus, Sium latifolium, Potamogeton crispus, P. gramineus, Ceratophyllum submersum, Ranunculus aquatilis, Scrophularia umbrosa, Carex riparia, Stratiotes aloides, Cardamine amara and Equisetum palustre.

4. Discussion

In this study, we examined the diversification of macrophytes within urban aquatic nature-based solutions (NBS) by performing an extensive analysis across a broad European geographical scope involving five cities in Belgium, Finland, Germany, Poland, and Portugal. While several studies have explored the diversity of macrophyte communities in aquatic NBS (e.g., Williams et al., 2020; Oertli et al., 2023; Pastor et al., 2023), extensive research spanning multiple European locations remains limited (Hale et al., 2023). Furthermore, conducting this type of botanical research in urban environments subject to significant anthropogenic pressure highlights the potential to gain fresh insights into macrophyte ecology and innovate using these plants for urban development (O'Hare et al., 2018).

Our research stands out for its high analytical value, not only because it covers a wide geographical range but also due to the extensive amount of data collected and the methodological consistency across different locations. The survey was conducted according to a unified, precise protocol in each city. The macrophyte dataset included records of emergent, submerged, and floating-leaved plants from 120 sites spanning urban ponds and streams with varying levels of hydromorphological disturbance. Moreover, permanent and temporal systems were considered. The uniform and standardised approach to sampling

Table 4Ecological differentiation of macrophytes as average ecological value (EIV) in aquaNBS in the five European cities.

Country	Temperature	Light	Moisture	pН	Trophy
Belgium	5.59	7.26	9.23	6.48	6.63
Finland	5.37	7.06	9.21	5.94	5.50
Germany	5.67	7.18	9.76	7.04	6.66
Poland	5.54	7.06	9.61	6.96	6.24
Portugal	6.67	7.38	9.18	6.58	6.25
Total	5.79	7.19	9.39	6.60	6.24

Table 3 Macrophyte species diversity and abundance in different types of aquaNBS, *significance p < 0.05 between ponds and streams in the country.

Country	Type of NBS	Species in a group	Mean values of analyzed metrics					
			Species richness (N)	Shannon diversity (H')	Simpson diversity (D)	Evenness (J)	Macrophyte cover %	
Belgium	Ponds	30	3.88	0.67	0.35	0.43	0.35	
	Streams	_	_	_	_	_	_	
Finland	Ponds	41	8.17	1.28	0.61	0.71	0.61	
	Streams	29	6.33	1.03	0.50	0.57	0.50	
Germany	Ponds	21	3.07	0.43	0.22*	0.28*	0.22	
	Streams	22	4.20	0.85	0.44*	0.52*	0.44	
Poland	Ponds	36	7.17	1.08*	0.55*	0.58	0.55*	
	Streams	29	5.42	0.65*	0.32*	0.39	0.32*	
Portugal	Ponds	18	4.30	0.98	0.50	0.70	0.50	
	Streams	12	4.57	0.96	0.51	0.67	0.51	
Total	Ponds	90	5.04	0.83	0.51	0.42	0.29	
	Streams	64	5.15	0.88	0.54	0.45	0.31	

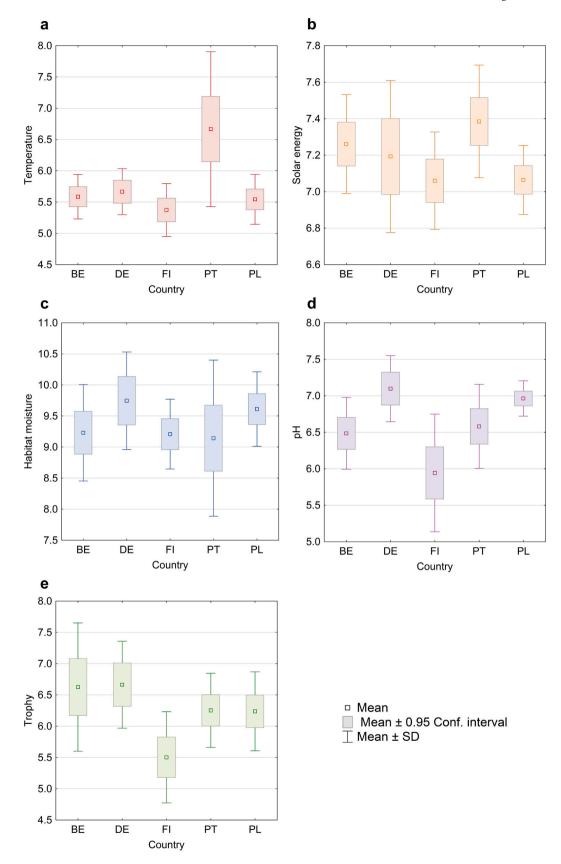


Fig. 4. A comparison of mean EIV based on macrophyte abundance in NBS of five European cities: a – temperature, b – solar energy, c – habitat moisture, d – pH, e – trophy (significance explained in Table 5).

Table 5Statistical verification of macrophyte ecological differentiation in aquaNBS in the five European cities.

Ecological scores (EIV)	Kruskal- Wallis test	Significance (p)	Which groups are significantly different?
Temperature (T)	25.136	0.0003	Portugal from other countries
Solar energy (L)	15.880	0.0032	Portugal from Finland and Poland
Moisture (F)	8.481	0.0755	_
рН (R)	42.874	<0.0001	Germany from Belgium, Finland and Portugal Belgium and Finland from Germany and Poland
Trophy (N)	26.657	0.00002	Finland from other countries

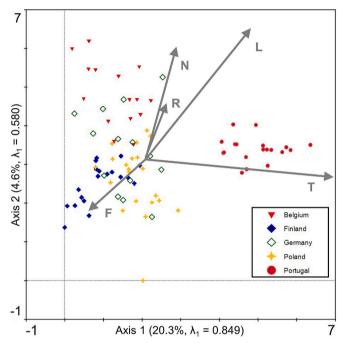


Fig. 5. A gradient of survey sites based on DCA analysis based on frequent species (more than three repetitions) and skipping species-poor sites (less than three species), EIVs were analyzed as supplementary variables: T – temperature, L – solar energy, F – habitat moisture, R – PH, N – trophy.

across these diverse settings yields a unique dataset, distinguishing our study from prior work in this field.

The macrophyte biodiversity was diversified between studied cities, and the identified number of species ranged from 30 to 47 within a single city. The average species richness within a single aquatic NBS site was also diversified across the European gradient and varied from 3.33 macrophyte species in Berlin to 7.2 in Helsinki. These numbers are notably lower compared to those recorded in numerous natural freshwater ecosystems across lowland Europe, as in the standard survey on rivers representing various quality, Szoszkiewicz et al. (2017) found species counts ranging from 15 to 18. Other modified habitats have also noted greater species richness, like ornamental ponds (Oertli et al., 2023). Conversely, more minor, modified ecosystems in England presented species richness similar to our findings, with Armitage et al. (2003) documenting 45 macrophyte species across 16 sites, and Williams et al. (2004) noting an average of 10.1 taxa in ponds, 7.3 in streams, and 6.1 in ditches within an agricultural landscape in Southern England.

Although the species diversity in the water ecosystems we analysed is relatively low compared to many other aquatic environments, as

indicated above, these systems still make a substantial contribution to local biodiversity, which is so often limited in urban settings (Magee et al., 1999; Kozlowski and Bondallaz, 2013; Oertli et al., 2018; Oertli et al., 2023). The presence of various species was proved even in urban water bodies frequently facing significant disturbances that generally diminish aquatic life. Furthermore, the plant diversity observed in our aquatic nature-based solutions (NBS) was constrained by the small size of the surveyed ponds (i.e., even 200 m²) and streams (i.e., less than 1 m wide). The smaller dimensions of the NBS necessitated a reduced sampling area, limited to 10-meter quadrats, in contrast to standard macrophyte monitoring, which typically spans 100-meter stretches in natural streams (Haury et al., 2006; Szoszkiewicz et al., 2022). Moreover, many of the ecosystems we studied were also relatively new, with plant communities still in the early stages of ecological succession, suggesting their biodiversity will likely increase over time. Furthermore, aquatic NBS are frequently designed to address urban challenges such as water regulation (buffering and infiltration of runoff), recreational use (play areas), aesthetic enhancements (planted cultivars), and urban cooling. These functions may expose the sites to more extreme conditions, including variations in water quality, water level fluctuations, frequent management, and visitor trampling. This reveals the sites to potentially more extreme conditions regarding water quality, water level fluctuations, management frequency, and human disturbance.

The analysed aquatic NBS can be regarded as vital biodiversity hotspots in cities. The research showed that among the identified 106 aquatic plants, there were various taxonomic groups, including 43 dicotyledons, 58 monocotyledons, and three pteridophyte species. Emerged helophytes (83 species) were more diversified than submerged and floating-leaved plants (23 taxa). The diversity of submerged vegetation was likely limited by the shallow depth of most ecosystems surveyed, as depth plays a critical role in submerged plants' development, as Middelboe and Markager (1997) noted. Overall, the data shows that we can achieve a substantial level of biodiversity in combination with other ecosystem services (Raquel Calapez et al., 2023).

The analysis of macrophyte abundance reveals that, on average, 28.13 % of the NBS is covered by vegetation. This is a significant percentage, primarily attributed to the shallow depth of the studied aquatic ecosystems, which allows for the growth of aquatic plants practically across the entire surveyed transects (Middelboe and Markager, 1997; Bini et al., 1999). Some variations were observed among cities, with Germany having the lowest coverage and Finland and Poland having the highest.

The differences between lotic and lentic aquatic ecosystems were not substantial when comparing diversity indices between streams and ponds. Significant differences in indices based on relative abundance (H' and D) were observed only in Poland, as well as in Germany (D and J). Additionally, in Poland, macrophyte abundance (total cover) was significantly higher in ponds than in streams. It is important to note that stream samples were not collected in Belgium (only ponds), so statistical comparisons were limited to four countries. The lack of statistical significance is due to the high variability of vegetation between individual sites, with large variance preventing statistical comparisons from reaching significance. This high variability is driven by differences in the size of urban aquaNBS and the influence of various common and acute pressures in the urban environment.

The diversity of macrophyte abundance was analysed, considering their sensitivity to various ecological parameters. We based this on six Ellenberg's indicator values expressing plant preferences for temperature, light, continentality, moisture, pH, and trophy (Dengler et al., 2023), which are widely used to investigate the importance of filtering mechanisms in shaping plant communities (Di Biase et al., 2023). Analysis shows the significant variation between the five European cities along habitat variables, especially regarding trophy and water pH. This variation underlines the large geographical scale of the study since studied sites across Europe showed diverse physicochemical attributes of the water, representing one of the main drivers of macrophyte

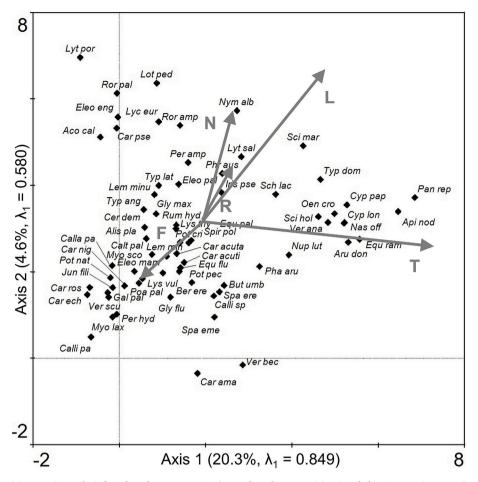


Fig. 6. Macrophyte composition - DCA analysis based on frequent species (more than three repetitions) and skipping species-poor sites (less than three species). EIVs were analyzed as supplementary variables: T – temperature, L – solar energy, F – habitat moisture, R – PH, R – PH, R – trophy. Taxa abbreviations explained in supplementary materials.

communities (Bini et al., 1999; Rameshkumar et al., 2019).

The most decisive differentiation was found for trophy EIV, which was related primarily to nitrogen, although admitting that the values better describe general nutrient availability, including the availability of phosphorus (Ellenberg et al., 1991). This gradient reflects the habitat fertility or productivity of freshwater ecosystems which can be considered a factor in eutrophication. The best quality water was found in aquatic NBS in Helsinki, where mean trophy EIV can be considered a moderately nutrient-rich habitat (Chytrý et al., 2018). This finding may be associated with limited pollution and the partially dystrophic nature of the waters in that region. On the other hand, the highest mean trophy EIV found in Antwerp indicates already nutrient-rich sites (Chytrý et al., 2018).

Ellenberg Indicator Values express plant preferences for various environmental factors. However, a deeper analysis of EIV can also be used to examine the role of filtering mechanisms in shaping plant communities according to species' ecological preferences (Di Biase et al., 2023). In our geographical gradient, vegetation is largely determined by temperature, which was exceptionally high in Portugal and lowest in Finland. The thermal factor undoubtedly had a strong impact on the observed water trophic status in these countries. High temperatures should promote the biogeochemical and physiological activity of microbes and facilitate the mineralization of organic matter in sediments increasing water trophy (Follstad Shah et al., 2017). This relationship is evident when comparing the coldest region (Finland – low trophic levels) with warmer cities (Poznań, Berlin, Antwerp – increased trophy). However, this linear relationship between temperature and habitat fertility was disrupted in Portugal, where high temperatures led

to periodic drying of the riverbed. During episodes of dry stream reaches, biogeochemical and physiological activity of microbes is lower compared to flowing sections, where microbial activity is significantly higher (Larned et al., 2010; McIntyre et al., 2009). Organic material may accumulate in dry riverbeds, but its decomposition, mineralization, and ingestion proceed slowly in the absence of water. In this way, contrary to expectations, habitat trophy as well as other gradients to some extent, did not show a linear relationship with temperature, as similar EIV-based plant community patterns have been observed in relation to other environmental gradients (Di Biase et al., 2023).

The DCA facilitated the assessment of variations in the macrophyte community structures within aquatic NBS throughout Europe. Several disparities in species composition between analysed cities were found specifically notable in Lisbon, where a range of species that were not recorded in other surveyed parts of Europe were identified. These include *Cyperus eragrostis*, *Typha domingensis*, *Lythrum junceum*, *Scirpoides holoschoenus*, and *Azolla* sp. These taxa are ecologically adapted to temperate and warmer climates, as supported by data from (POWO 2024), and their natural distribution is predominantly in the western and southern parts of Europe (GBIF.org 2024).

5. Conclusions

This article provided valuable new insights into the diversification of macrophytes in urban aquatic NBS across European cities, shedding light on the differences in species richness, abundance, and ecological characteristics. It emphasises the value of urban aquatic NBS in maintaining and enhancing biodiversity in cities.

- 1. The study shows the importance of aquatic NBS as biodiversity hotspots in urban areas. Despite their relatively small size and surrounding modifications, a large number of aquatic plants were identified, especially emerged helophytes. The study revealed significant variations in macrophyte species richness across five European cities, highlighting the diverse aquatic plant communities present in urban aquatic NBS. The number of identified macrophyte species ranged from 30 to 48 per city, with Polish sites exhibiting the highest species richness.
- 2. In a single survey site, the number of macrophytes detected ranged from 0 to 15, with Finish sites having the highest average number of taxa, at 7.25, and Berlin the lowest. These numbers are relatively low compared to natural ecosystems but are similar to those found in modified European ponds and watercourses.
- 3. Ellenberg indicator values (EIVs) of the identified macrophyte species were used to assess urban ponds and streams in terms of temperature, light, continentality, moisture, pH, and nutrient levels. Notable differences in EIVs were found between cities, illustrating the ecological variety of urban nature-based solutions throughout Europe and their influence on macrophyte community compositions. The research underscored the significance of nutrient levels in determining the structure of macrophyte communities, where Helsinki showed the most favourable water quality, featuring habitats with moderate nutrient content, and in contrast, Antwerp was at the other extreme, with its sites already exhibiting high nutrient richness.
- 4. DCA analysis revealed significant differences in species composition, particularly in Lisbon and, to some extent, Antwerp. Several species were found to be unique to these locations, underscoring the regional variation in macrophyte communities.
- 5. This research emphasises the value of urban aquatic NBS in maintaining and enhancing biodiversity in cities. The study provides a comprehensive dataset for further analysis and highlights the importance of developing the aquatic naturebased approach in urban areas.

CRediT authorship contribution statement

Krzysztof Szoszkiewicz: Methodology, Investigation. Krzysztof Achtenberg: Methodology, Investigation. Robrecht Debbaut: Resources, Methodology, Investigation, Data curation. Vladimíra Dekan Carreira: Resources. Daniel Gebler: Project administration, Methodology, Investigation, Data curation. Szymon Jusik: Writing - original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Tomasz Kałuża: Writing - original draft, Visualization, Methodology, Investigation. Krister Karttunen: Writing – review & editing, Validation, Resources, Methodology, Investigation, Data curation, Conceptualization. Niko Lehti: Investigation, Data curation. Silvia Martin Muñoz: Investigation. Mariusz Sojka: Validation, Methodology, Investigation. Ana Júlia Pereira: Writing - original draft, Investigation. Pedro Pinho: Writing review & editing, Writing - original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. Jonas Schoelynck: Writing - review & editing, Project administration, Methodology, Conceptualization. Jan Staes: Writing - review & editing, Project administration, Methodology, Conceptualization. Doerthe Tetzlaff: Writing – review & editing, Project administration. Maria Magdalena Warter: Writing - review & editing, Investigation. Kati Vierikko: Writing - review & editing, Supervision, Resources, Project administration, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at $\frac{\text{https:}}{\text{doi.}}$ org/10.1016/j.ecolind.2025.113331.

Data availability

Data will be made available on request.

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