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Functional properties of planktic microalgae determine their habitat selection

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Abstract In this study, we aim to investigate how the functional properties of microalgae help to delineate the major groups of aquatic habitats. Using functional trait-based and Reynolds' functional group-based approaches similarities of the microalgal flora of all aquatic habitats occurring in Hungary were compared. The habitats covered the whole size spectrum of standing waters (10^{-2}–10^{8} m^2) and water currents (watershed: 10^2–10^{11} m^2), , limnological and chemical properties. Both functional trait-based and functional group-based habitat classifications overrode the hydromorphology-based typology, however, functional group-based clusters showed closer resemblance to limnological-hydromorphological types than clusters created by trait-based approaches both for qualitative and quantitative data. Most of the aquatic habitats that have similar limnological characteristics showed resemblance in the functional properties of their microflora. Rivers and river-related habitats were the most diverse functionally. These were followed by standing waters with extended macrophyte coverage. The small, unique habitats displayed the lowest functional richness. The occurrence of several functional groups in some extreme habitats implies two alternative explanations: first, the habitat template of the groups is wider than defined in the original description; second, detailed information on the autecology of species assigned to a functional group necessitates the creation of new groups specific for the unique habitats.

Keywords Phytoplankton · Trait composition · Habitat selection

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Introduction

Phytoplankton plays a key role in freshwater ecosystems and has great ecological importance by providing the base of the aquatic food web and taking place in natural purification processes of freshwaters (Falkowski et al., 2008; Naselli-Flores & Padisák, 2022). Due to its prominent ecological role, phytoplankton is considered a key target in several monitoring programmes (Batten et al., 2019). Water quality assessment of rivers, lakes and the majority of the scientific investigations focus on large water bodies, therefore their limnological and biological characteristics are well-described in the literature. However, microalgae can occur anywhere, where the conditions are suitable for them, from the small telmata through the cave waters to the marshlands. It has been demonstrated that small and medium-sized water bodies (area:10^4–10^5 m^2) are characterized by a considerable amount of variation in terms of their environmental parameters (Zawal et al., 2013; Várbíró et al., 2017). This enables the small water bodies to maintain higher species diversity than the large ones (Hawksworth, 1996; Turner & Corlett, 1996; Gibb & Hochuli, 2002; Honnay et al., 1999; Williams et al., 2004). Their importance also lies in the fact that they can host ecologically valuable or floristically unique species (Kiss & Ács, 2002; Kristensen & Globevnik, 2014; Kuczyńska-Kippen, 2020). Currently, fewer data are available regarding the distribution of freshwater algae, and even less of those precious taxa that inhabit specific, sometimes endangered waterbodies.

The hydromorphological properties of freshwaters have a pronounced influence on the formation of habitat types at a given area (Kofoid, 1903; Murray & Pullar, 1904; Huitfeldt-Kaas, 1906), and on the composition of the occurring assemblages. The recognition that waters with similar physical properties are also similar in their biological characteristics led to the description of the first stagnant- and flowing water types (such as shallow and deep lakes, rhithral and potamal rivers, etc.) (Borics et al., 2016). The first comprehensive typologies for the Hungarian waters appeared in the sixties (Sebestyén, 1963) and in the seventies (Dévai, 1976). After the introduction of the Water Framework Directive (EC, 2000) in Hungary, a more complex typology (based on five variables: altitude, size, depth, bed material and the type of water transport) had to be defined. Using this typology, stagnant surface waters were categorized into 17 water types, while the flowing waters were grouped into 25 types (GD, 2004; GD, 2010) in Hungary. These hydromorphological classifications follow a "top-down logic" (Zenker & Baier, 2009), during which the typological classification starts from the geographical, physical, chemical and hydromorphological properties of water. Water bodies can be also classified by the examination of the common features of the biological elements (phytoplankton, benthic diatoms, macrophytes, benthic invertebrates, fish) (Borics et al., 2014a). In contrast to the hydromorphological typology, biological typology is a bottom-up classification, in which similarities in the community composition of assemblages are considered in grouping of waters (Davy-Bowker et al., 2006). In the case of phytoplankton, several metrics can be applied (diversity metrics, taxon ratios, etc.) to separate or merge the biological water types. However, aquatic ecosystems can be evaluated not only at the level of species but also at a higher organizational level, i.e., based on associations or functional groups (Borics et al., 2007). This seems to be a promising approach because it has been demonstrated that functional diversity may be a stronger determinant of ecosystem processes than species diversity (Huston, 1997; Hooper & Vitousek, 1997; Tilman et al., 1997; Wardle, 1999). The functional approaches in phytoplankton research received a large impetus from the work of Reynolds et al. (2002), who assigned phytoplankton species into so-called functional groups. This system shows a close resemblance to the associations in the phytocoenological system of Braun-Blanquet (1951). Most of the species in Reynolds's functional groups have similar morphological and physiological characteristics, but it is not an obligation. The most important is that the species of this group show similar responses to the constraints of the environment, thus they have to be considered as response groups (Violle et al., 2007). This approach has been developed for lakes and ponds, but the applicability of the concept has not been studied for small, unique water types, in which besides the planktic habitats, benthic and metaphytic habitats also occur.

In order to explore the habitat selection of the different phytoplankton functional groups, we reviewed the published literature on microalgal research in Hungary over the last 140 years and created a species-by-site matrix containing a wide range of species and localities. In the matrix, each species has been classified into one functional group and each locality was grouped into one hydromorphological type. Our goal was to produce a phytoplankton-based bottom-up typology and compare that with the hydromorphological water types. We assume that this approach helps to better understand the background of species occurrences and reveal those characteristics of the environment that help the microalgal species to survive in their habitats. The main questions were the following:

- Which algae (functional traits/functional groups) characterize the various habitat types?
- Are there any differences between the functional trait-based and functional group-based typologies?
- Do the similarities in limnological characteristics of the habitat types coincide with the similarities in their microflora?
- Which are the functionally most diverse habitats?

Materials and methods

Data sources of species inventory

We prepared a microalgal database for Hungary. Literature data were collected from various algal handbooks (Felföldy, 1972, 1981, 1985; Németh, 1997; Schmidt & Fehér, 1998, 1999, 2001; Grigorszky et al., 1999; Uherkovich et al., 1995), from the recent literature, including published results of floristic studies and data derived from the grey literature (e.g., unpublished Ph.D. theses, governmental reports). This literature contained not only the descriptions of species but also the localities of occurrences. Finally, we further expanded the database by the inclusion of phytoplankton monitoring data of Water Management Directorates, covering the region of Hungary. The species-by-site matrix contains mostly planktic and metaphytic species, benthic diatoms were not recorded in this database.

Habitat types

Based on the limnological characteristics of the localities, we assigned them into habitat types by applying the following type descriptor variables: water categories (surface and subsurface waters; water currents and standing waters), chemical composition (organic, high alkalinity, moderate alkalinity), origin (artificial or natural), water balance (stationary or temporary), size ($>10 km^2$), depth (deep: mean depth >4 m). The habitat typology is summarized in Supplementary Table 1. These types covered all aquatic habitats in the region from the various small, water-filled, ephemeral holes (phyto- lito- and dendrotelmata) to the large lakes and rivers.

Classification of species

During the functional classification of species, we applied functional trait-based and functional group-based approaches.

Functional trait (hereinafter FT) has been defined as a morphological, physiological, or behavioural feature that is measurable at the individual level. Phytoplankton species were characterized by 12 FT according to Litchman & Klausmeier (2008): flagellated, filamentous, single-celled, colonial, large flagellated, larger than 40 µm, nitrogen-fixing, mixotrophic, vacuolated, silicious and pennate. All these were defined as binary traits (0 = lacking; 1 = having the trait).

Functional group (hereinafter FG) has been defined as the group of taxa that shows similar responses to a wide range of environmental factors of their habitats. Phytoplankton species were assigned to 31 FGs using the criteria of Reynolds et al. (2002) and Padisák et al. (2009). Each group was named by letter codes and each species was classified into one FG.

Comparison of the FT and FG across water types

In order to compare the different water types at FT and FG levels, we created qualitative matrices, in which we marked with 1, if the FT/FG occurred and we marked with 0, if the FT/FG lacked from the habitat type.

Calculation of trait frequency value

Having only floristic data in the literature, the frequency cannot be given explicitly at the site level. However, as a proximate measure of FT/FG frequency, we can calculate the frequency of the FT/FG in the given habitat type using the number of sites where the FT or FG occurred and the overall number of sites in the given habitat type. The resulting values fall between 0 and 1 and can be considered as the frequency values of FTs and FGs (Eq. 1) in the habitats.

$$\mathrm{Fij} = \frac{\mathrm{NLij}}{\mathrm{TNLj}} \tag{1}$$

F_{ij}: FT/FG frequency value of ith FT/FG in the jth water type.

NL_{ij}: number of localities where the ith FT/FG occurred in the jth water type.

TNL_j: total number of localities in the jth water type.

Statistical analyses

In order to study the similarities between habitat types we used agglomerative hierarchical clustering methods. Data analyses were carried out on both the qualitative and the quantitative data. We used Jaccard dissimilarity (Eq. 2) (Jaccard, 1901) for the binary and Bray–Curtis dissimilarity (Eq. 3) (Bray & Curtis, 1957) for the quantitative data to express similarity (Legendre & Legendre, 1983). The hierarchical clustering has been based on Ward's algorithm.

$$\mathrm{J(FT/FG, Hj)} = \frac{|\, FT/FG \cap Hj \,|}{|\, FT/FG \cup Hj \,|} \tag{2}$$

J (FT/FG, Hj): Jaccard dissimilarity.

FT/FG∩Hj: the number of common elementsof FT/ FG in the jth habitat type.

FT/FG∪Hj: the number of unique elements of FT/ FG in the jth habitat type

$$BC_{jk} = \frac{\sum_i \left| x_{ij} - x_{ik} \right|}{\sum_i \left(x_{ij} - x_{ik} \right)} \tag{3}$$

BC_{jk}: Bray–Curtis dissimilarity.

x_{ij}: the total number of FT/FG counted on site i and j.

x_{jk}: the total number of FT/FG counted on site i and k.

To identify the relationships between the FT-based versus FG-based, and the qualitative versus quantitative approaches a Mantel test was applied (Mantel, 1967). All analyses were performed in R 4.1.0 and RStudio Build 446 (R Core Team, 2021), using package vegan version 2.6–4 (Oksanen et al., 2020).

To reveal differences in the functional richness of the habitats, we calculated cumulative frequency values of FTs and FGs (Σ F_{ij}) and displayed them in ranked order distribution.

Results

Description of the species-by-site matrix

The presence/absence matrix contains 2489 taxa in rows, representing 12 phyla (Bacillariophyta, Bigyra, Charophyta, Chlorophyta, Cryptophyta, Cryptista, Cyanobacteria, Euglenozoa, Haptophyta, Miozoa, Ochrophyta, Rhodophyta) and includes 1145 localities in columns, representing wide range in size and hydrology, from tiny telmata to the large rivers (e.g., Danube) and lakes (e.g., Lake Fertő and Balaton) of Hungary.

FT and FG-based classification of the habitat types using qualitative data

Using qualitative (binary) data at FT level, the habitat types could be classified into 5 groups (Fig. 1). Cryobiotopes, cave waters, soil surfaces, ricelands and telmata have been separated from the majority of water types at the first and second node of the dendrogram. In these types, only a few traits were represented. In case of the other large and less unique habitats, the binary data revealed the presence only of two large clusters, with a seemingly arbitrary grouping of hydromorphologically and limnologically different habitats (Fig. 1).

The clustering using the qualitative dataset and the FG has given a more detailed grouping of the habitats (Fig. 2). The habitats are divided at the first node into 2 clusters. Those, usually small habitats that share only a few common FGs with other habitats, are located in one branch of the cluster. Except for ponds (< 1 ha) and large saline lakes, all habitats of the cluster have a temporary character. The other branch of the cluster included all perennial waters. Many of these habitats formed limnologically similar subgroups, however, there were several strange clusters (marked with red boxes in Fig. 2) which were very

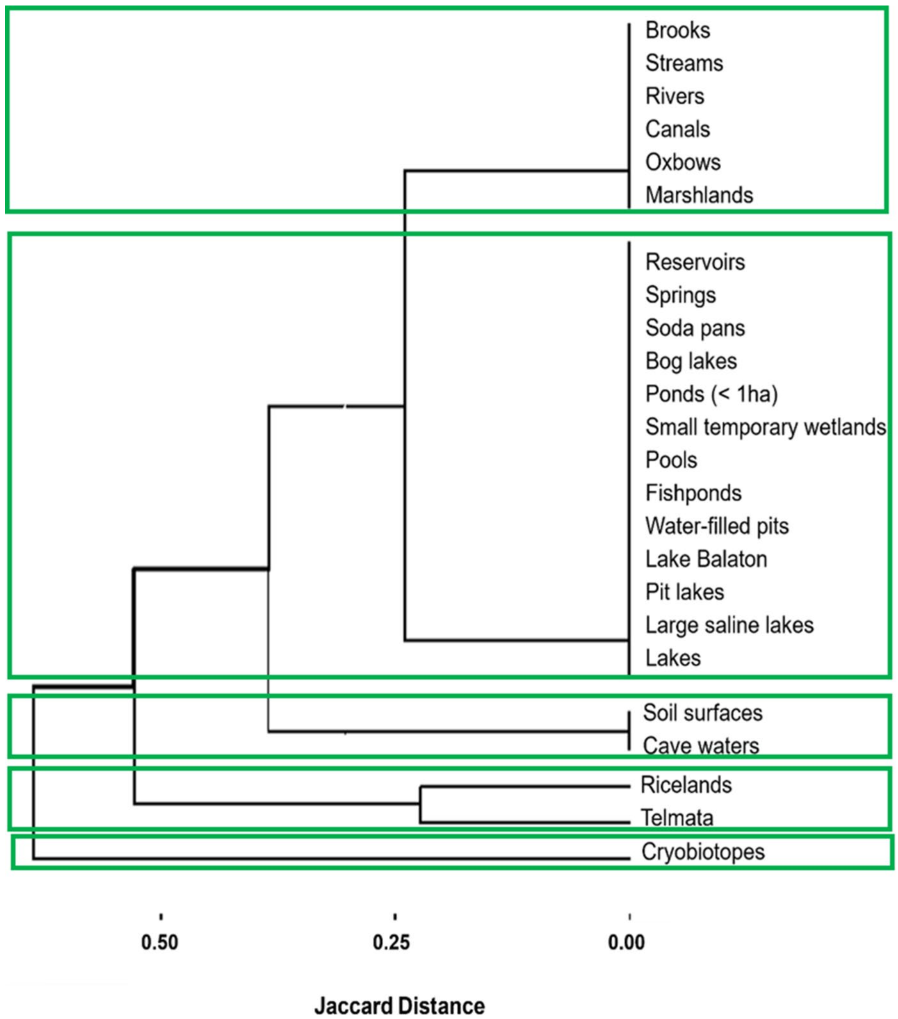

Fig. 1 FT-based classification of the habitat types using qualitative data (Jaccard-distance)

different in their limnological/hydromorphological characteristics, like the cluster of Lake Balaton with streams.

FT and FG-based classification of the habitat types using quantitative data

FT-based typology using quantitative data provided more detailed habitat grouping than the qualitative approach. Applying trait frequency values at FT level, we found several well-explainable clusters (indicated by green boxes in Fig. 3) on the dendrogram: (1) rivers and river-related habitats; (2) very small aquatic and semiaquatic habitats; (3) shallow large and medium-sized lakes; (4) small benthic habitats; (5) macrophyte-dominated habitats; (6) medium-sized deep lakes with no or negligible presence of macrophytes. The habitat types, falling into these clusters show close resemblance in their limnological/hydromorphological characteristics. Moreover, cryobiotopes formed a separate branch in the dendrogram. This approach, however, also resulted in strange clusters, like bog lakes and soda pans, which have considerable differences in their pH and ionic composition.

Based on the frequency values of FGs the analysis provided two well-explained clusters (Fig. 4). In the first cluster three subgroups can be identified. The (1) cryobiotopes, being one of the most extreme habitats, have been separated at the second node. The other two large clusters in this branch of the dendrogram were the (2) very small aquatic and semiaquatic habitats and (3) the shallow, medium-sized, macrophyte-dominated standing waters. In the other branch of the dendrogram (4)

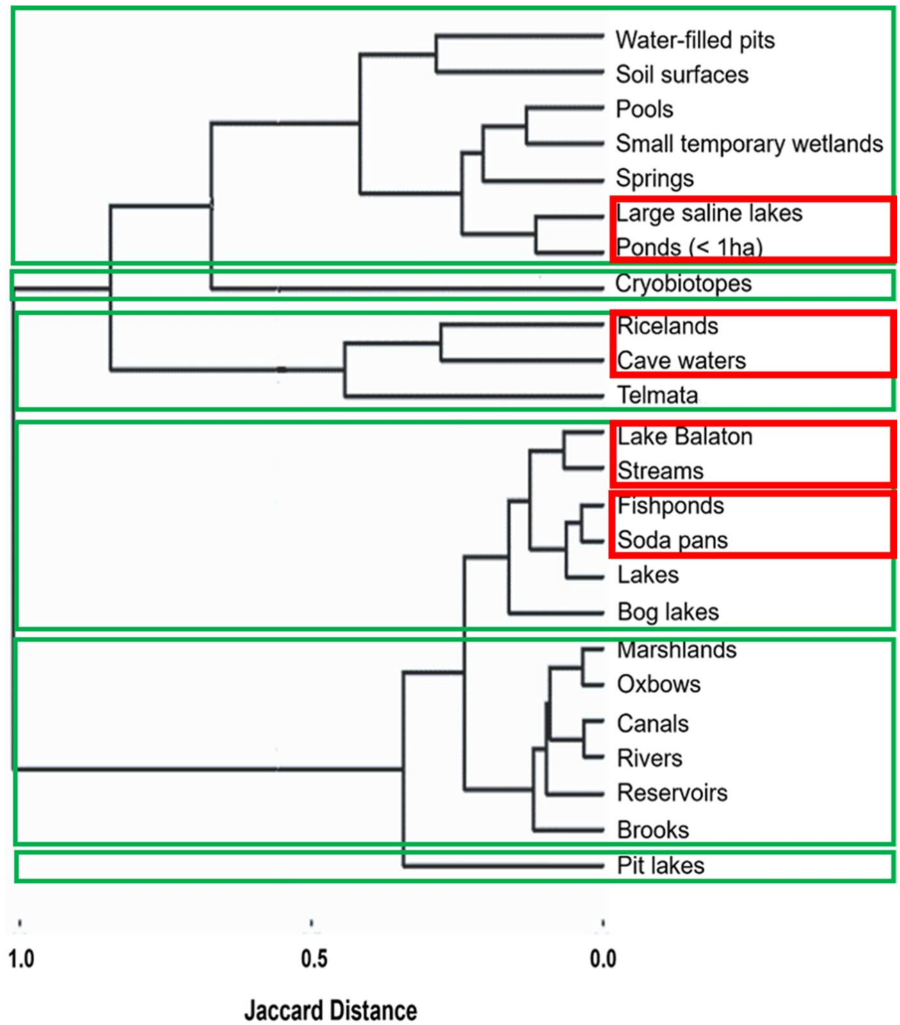

Fig. 2 FG-based classification of the habitat types using qualitative data (Jaccard-distance). Reliable groups are marked with green boxes. Strange clusters -which are very different in their limnological/hydro morphological characteristics- are marked with red boxes

medium-sized lakes with no or negligible presence of macrophytes, moreover (5) rivers and river-fed habitats made two large clusters. Within the large clusters, there were several separable groups at the branch ends, which show close resemblance in their limnological and hydromorphological characteristics. These were the pools and small temporary wetlands; ponds (< 1 ha) and soda pans; ricelands and bog lakes; brooks and canals; oxbows, streams and reservoirs. Two habitats appeared at unexpected positions in this cluster. Lake Balaton was placed in the subgroup of the shallow, medium-sized, macrophyte-dominated standing waters, while the large saline lakes were positioned in the group of rivers and river-fed habitats.

Relationships between the applied approaches

We applied the Mantel test to evaluate the strength of the correlation between the results of the functional (FT/FG-based) and qualitative/quantitative approaches. The test yielded the values in Table 1. Dissimilarity matrices showed significant correlations in all four comparisons. The weakest correlations were found when the qualitative and quantitative matrices' results were compared both in the case of FT- and FG-based approaches. The correlations were stronger when the FT and FG-based approaches were compared using the same type of data matrices (i.e., qualitative and quantitative). The strongest correlation was found when

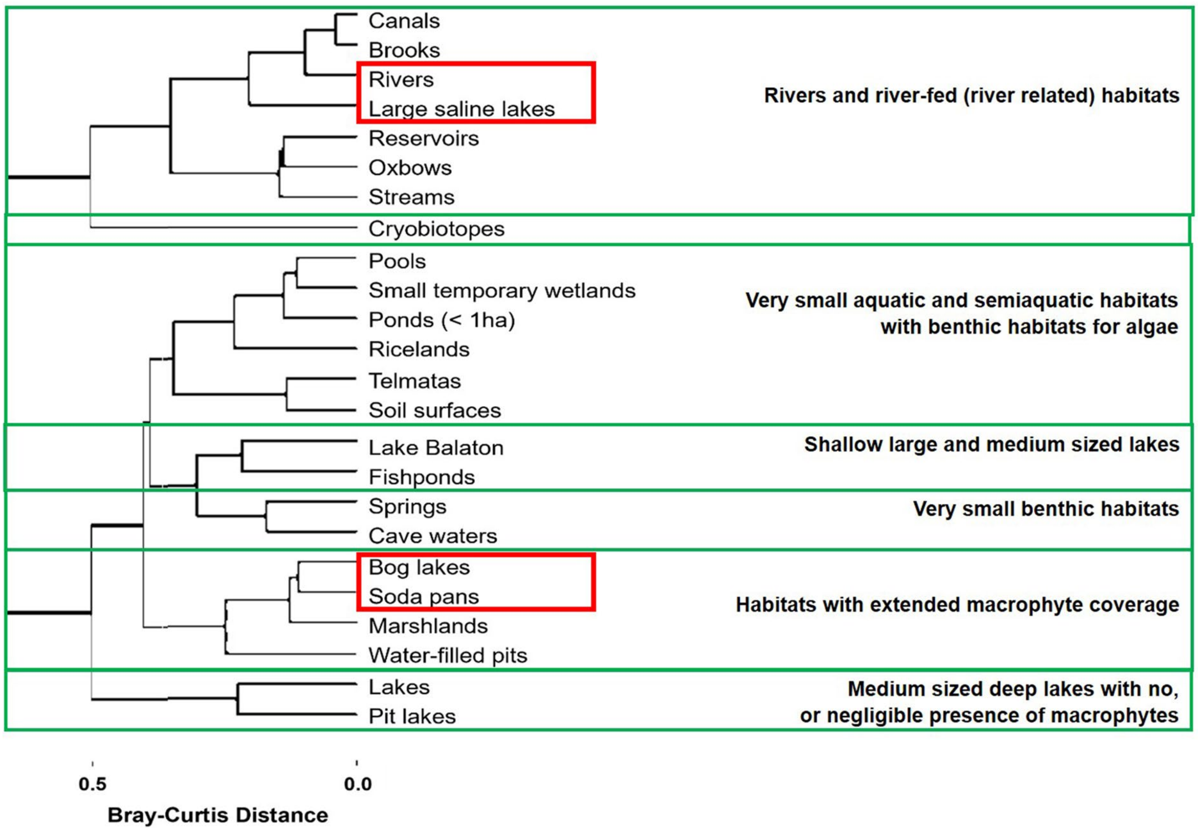

Fig. 3 FT-based classification of the habitat types using quantitative data (Bray–Curtis distance). Reliable groups are marked with green boxes, strange groups are marked with red boxes. Next to the groups, we have indicated the common properties of those water types that belong to the same group

the quantitative matrices of the FT- and FG-based approaches were contrasted.

Functional richness of the habitats

Functional richness of the habitats has been expressed as the cumulative frequency distribution of FTs (Fig. 5a) and FGs (Fig. 5b). The data showed considerable differences among the habitats. The largest values were characteristic of the water currents and for other river-related habitats in the case of both FTs and FGs. Large- and middle-sized standing waters are positioned in the middle range of the ranked occupancy distributions. The very small unique habitats (cave waters, soil surfaces, springs and telmata) had the lowest values. The order of the habitats was quite similar in the case of both approaches. Larger differences between the positions of habitats in the ranked occupancy distribution appeared in the case of Lake Balaton and springs.

FTs and FGs characteristic for the habitats

Among the eleven FTs there were several ones (flagellated, single-celled, > 40 µm, colonial, mixotrophic) that occurred in the majority (> 20%) of the sites in each habitat type (Table 2), excluding cryobiotopes as very special habitats. Except for very small, unique habitats, although in lower frequency, each trait was present in each habitat type. Thus, the differences among the habitats appeared rather in the lack or low-frequency occurrence of the trait than in their dominance.

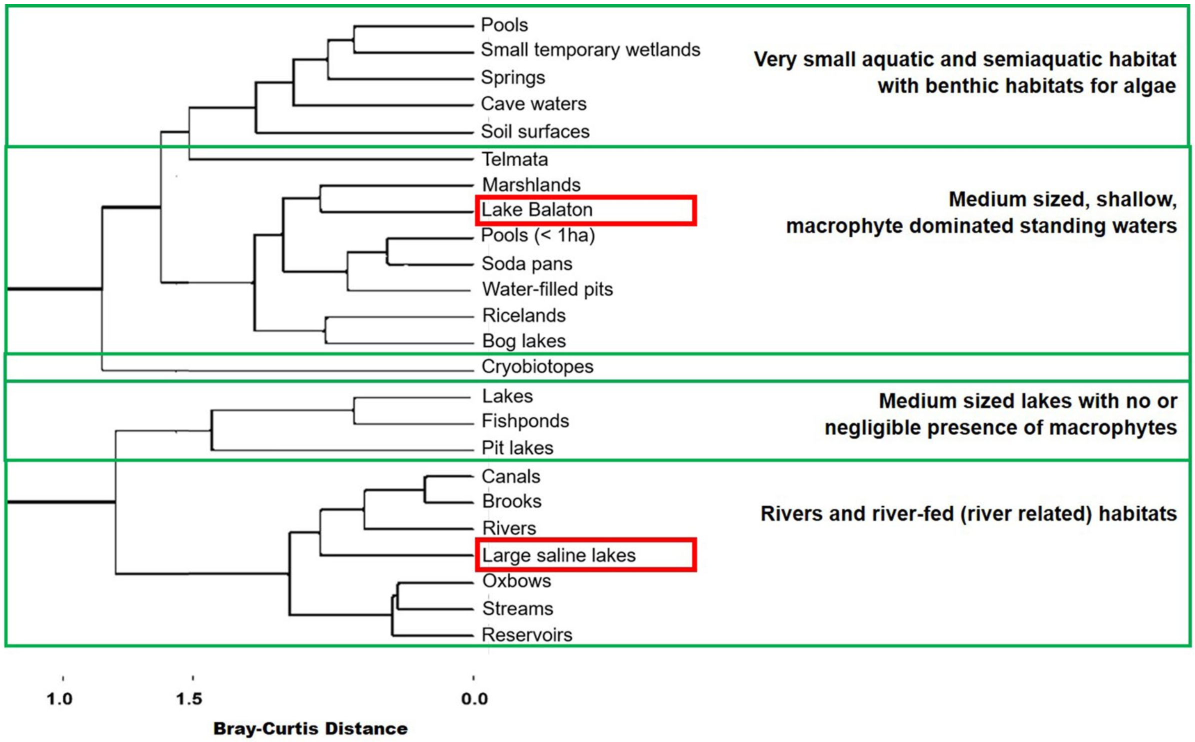

Fig. 4 FG-based classification of the habitat types using quantitative data (Bray–Curtis dissimilarity). Reliable groups are marked with green boxes, strange groups are marked with red boxes. Next to the groups, we have indicated the common properties of those water types belonging to the same group

Table 1 Mantel statistic based on Pearson's product-moment correlation; number of permutations: 999

Comparision	R	P-value
$FT_{bray} \times FT_{jaccard}$	0.5218	0.003
$FG_{bray} \times FG_{jaccard}$	0.6891	0.001
$FG_{bray} \times FT_{bray}$	0.8962	0.001
$FG_{jaccard} \times FT_{jaccard}$	0.8308	0.001

FGbray/ FTbray dissimilarity matrix based on Bray–Curtis distance, FGjaccard/ FTjaccard dissimilarity matrix based on Jaccard-distance (FG-Functional groups; FT- Functional traits)

As to the FGs, the types showed more conspicuous differences (Table 3). Although there were many FGs (especially X1, F, J) that occurred in almost every habitat in high frequency (> 20%) (Table 4), several of them (e.g., A, B, H2, M, S1, S2, Y_{Ph}, Z) occurred only in low-frequency or were absent in some habitats. It was especially true for the small, unique habitats, like cryobiotopes or telmata in which only 10 FGs were present.

Discussion

In this study, we applied functional-based approaches to categorize all types of aquatic habitats, where algae occurred in Hungary. Similar approaches were applied during the implementation of the Water Framework Directive (WFD, 2000), when hydromorphological river- and lake types had to be validated biologically (Borics et al., 2014b; Bolgovics et al., 2017a). There are two basic differences between the present clustering of water types and the WFD-compliant typologies. The first is that the WFD types are constrained types because standing waters and water currents have to be treated and classified separately. While during the validation of the WFD-compliant typologies separation of lakes and rivers was an obligation, in this study, similarities in the composition of algal assemblages of all aquatic habitats were analyzed, independently of their size, hydrology or chemical character. The other difference is that in the WFD-compliant typologies compositional differences

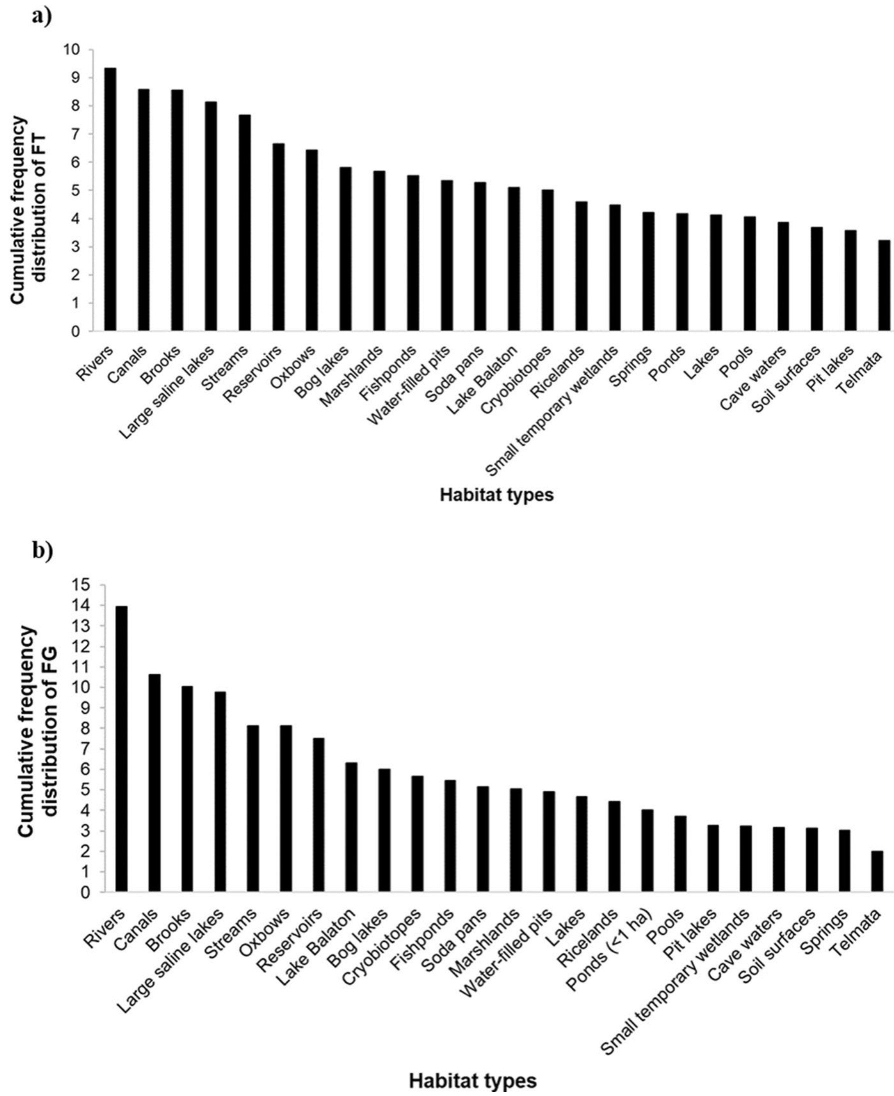

Fig. 5 Cumulative frequency distribution of FTs (**a**) and FGs (**b**) across habitat types

are much less pronounced than differences in their biomass. In contrast, the present types reflect compositional and functional similarities among limnologically different environments, regardless of their a priori categorization. Reynolds et al. (1994) drew attention to the similarities of phytoplankton in rivers and shallow lakes and explained the background of this pattern. However, here we revealed some surprising similarities of otherwise apparently different systems, for example, cave waters—springs that were located in the same cluster branch in the FT-based classification (Fig. 3), or the Lake Balaton—marshlands group in the FG-based clustering (Fig. 4). These results imply that several a priori different habitats might share some common, but less obvious characteristics that override the basic differences and enable the development of functionally similar algal assemblages.

The bottom-up grouping of habitats had various outcomes because of differences in the applied statistical and functional classification approaches.

Experiences of habitat clustering using qualitative data

Using qualitative data, we found only a few FT- and FG-based habitat clusters that show close resemblances in their limnological/hydromorphological

Table 2 Percentage distribution of each trait found in the different habitat types. Percentage distributions: < 5%, 5–10%, 11–20%, > 20%. Percentages refer to the ratio of occupied localities within the type

Main groups	Habitat types	< 5%	5–10%	11–20%	> 20%
Rivers and river-fed (river related) habitats	Brooks	9			1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Rivers			9	1, 2, 3, 4, 5, 6, 7, 8, 10, 11
	Canals	9			1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Oxbows	9			1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Reservoirs				1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Large saline lakes				1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Streams		9	11	1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
Cryobiotopes	Cryobiotopes				2, 3, 4, 6, 7, 10
Very small aquatic and semiaquatic habitat with benthic habitats for algae	Pools		11,12	7, 10	1, 2, 3, 4, 5, 6, 8
	Ponds (< 1 ha)		11,12	7, 10	1, 2, 3, 4, 5, 6, 8
	Small temporary wetlands		11,12	7, 10	1, 2, 3, 4, 5, 6, 8
	Ricelands			11, 12	1, 2, 3, 4, 5, 6, 8
	Soil surfaces		10	2, 7	1, 3, 4, 5, 6, 8
	Telmata			2	1, 3, 4, 5, 6, 8
Shallow large and medium sized lakes	Lake Balaton			7, 10, 11, 12	1, 2, 3, 4, 5, 6, 8
	Fishponds				1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
Very small benthic habitats	Springs	12			1, 2, 3, 4, 5, 6, 7, 8, 10
	Cave waters			10	1, 2, 3, 4, 5, 6, 7, 8
Habitats with extended macrophyte coverage	Soda pans			7, 10, 12	1, 2, 3, 4, 5, 6, 8, 11
	Marshlands				1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Bog lakes			12	1, 2, 3, 4, 5, 6, 7, 8, 10, 11
	Water-filled pits		11,12	2, 7, 10	1, 3, 4, 5, 6, 8
Medium sized lakes with no or negligible presence of macrophytes	Lakes			5, 7, 10, 12	1, 2, 3, 4, 6, 8, 11
	Pit lakes		7, 10, 12	4, 5	1, 2, 3, 6, 8, 11

Functional traits: 1- Flagellated; 2- Filamentous; 3-Single-celled; 4-Colonial; 5-Large flagellated; 6-Larger than 40 µm; 7-Nitrogen-fixing; 8-Mixotrophic; 9-Heterotrophic; 10-Vacuolated; 11-Silicious; 12-Pennate

characteristics. The reason lies in the applied statistical method. The Jaccard index is a simple and intuitive measure of dissimilarity between data samples (Verma & Aggarwa, 2020). However, since it uses qualitative data, it is sensitive to the number of common traits between the habitat types. Because phytoplankton species are very good dispersers (Padisák et al., 2016), aquatic habitats are under continuous propagule pressure. This means that species, which otherwise have little chance to survive and build stable populations in a given habitat, can be almost continuously present there even in low numbers. In very small habitats, because of the large sample volume/habitat volume ratios, the species detectability is high (Buckland et al., 2011; Bolgovics et al., 2019), therefore, accidentally occurring, low abundance species can be readily observed. This could be a reason why using the incidence-based approach the biologically based habitat groups contained hydromorphologically highly different water types.

Experiences of habitat clustering using quantitative data

For quantitative data, we applied the Bray–Curtis dissimilarity index. Using this approach biologically based groups could be easily reconciled with those, based on hydromorphological properties. Most of the groups created in this way were well-explainable, especially those, that are based on the FGs.

The river-related habitats and those, that provide habitat for planktic diatoms and contain several benthic algae have been clustered into clearly separable groups at both FT and FG levels (Figs. 3 and 4).

Table 3 Percentage distribution of each functional group found in the different habitat types

Main groups	Habitat types	< 5%	5–10%	11–20%	> 20%
Rivers and river-fed (river related) habitats	Brooks	B, M, T, Z	K, LM, S2, W2	G, SN	C, D, E, F, H1, J, Lo, P, S1, TIC, W1, X1, X2, X3, Y, YpH
	Rivers	H2, WS	S2, T, Z	A, LM, W2	B, C, D, E, F, G, H1, J, K, Lo, M, N, P, S1, SN, TIC, W1, X1, X2, X3, Y, YpH
	Canals	A, T, WS	LM, M, N, W2	B, K, S2, SN, Z	C, D, E, F, G, H1, J, Lo, P, S1, TIC, W1, X1, X2, X3, Y, YpH
	Oxbows	A, H2, LM,	M, S2, Z	G, K, S1, SN, T, W2, YpH	B, C, D, E, F, H1, J, Lo, N, P, TIC, W1, X1, X2, X3, Y
	Reservoirs	K, LM, M, S2, Z	A, E, W2,	G, N, S1, SN, TIC, YpH	B, C, D, F, H1, J, Lo, P, W1, X1, X2, X3, Y
	Streams	A, H2, K, Q, Z	M, S2, SN, T, W2	B, G, N, TIC, YpH	C, D, E, F, H1, J, Lo, P, S1, W1, X1, X2, X3, Y
	Large saline lakes	–	–	B, H2, T, W2, X3, Z	C, D, F, G, H1, J, K, Lo, M, N, P, S1, S2, SN, TIC, W1, X1, X2, Y
Medium sized lakes with no or negligible presence of macrophytes	Lakes	E, S1, T, YpH	G, K, S2, SN, W2, X3, Y, Z	A, H1, Lo, N, TIC, W1, X2	B, C, D, F, J, P, X1
	Pit lakes	W2, X3, YpH, Z	E, F, G, H1, J, K, Lo, TIC, X1, X2, Y	P, W1	A, B, C, D
	Fishponds	E, K, W2	A, G, S2, T, X3, YpH	M, N, S1, SN, TIC, X2, Y	B, C, D, F, H1, J, Lo, P, W1, X1
Cryobiotopes	Cryobiotopes	–	–	–	H1, J, K, Lo, M, S2, T, TIC, X1, Z
Medium sized, shallow, macrophyte dominated standing waters	Ponds (< 1 ha)	C, S1, SN	D, K, M, S2, T, Y	G, H1, Lo, TIC, W2, X3	F, J, N, P, W1, X1, X2
	Lake Balaton	–	A, B, C, D, K, M, N, Q, SN, W2, YpH, Z	G, H1, Lo, P, S2, TIC, X3, Y	F, J, S1, T, W1, X1, X2
	Marshlands	B, G, H2, LM, S1, S2	K, SN, T, W2, YpH, Z	D, E, M, N, X3, Y	C, F, H1, J, Lo, P, TIC, W1, X1, X2
	Soda pans	A, E, M, YpH, Z	B, K, S1, S2, SN, T,	G, H1, Lo, TIC, X3, Y	C, D, F, J, N, P, W1, W2, X1, X2
	Water-filled pits	–	H1, H2, K, Lo, S1, S2, X3	M, TIC	F, G, J, N, P, W1, W2, X1, X2, YpH
	Ricelands	–	X3, YpH	D, G, Lo, T, TIC,	F, J, N, P, W1, W2, X1, X2
	Bog lakes	B, M, Q, S1, S2, SN, WS, YpH	C, K	D, E, H1, X3	F, G, J, Lo, N, P, T, TIC, W1, W2, X1, X2, Y

Table 3 (continued)

Main groups	Habitat types	< 5%	5–10%	11–20%	> 20%
Very small aquatic and semiaquatic habitat with benthic habitats for algae	Springs	B, C, H1, H2, S2, Z	D, M	G, K, Lo, T, W1, W2	F, J, N, P, TIC, X1, X2
	Small temporary wetlands	C, S1	H1, M, S2, X3, Z	G, K, N, P, T, TIC, W2	F, J, Lo, W1, X1, X2
	Pools	–	D, H1, H2, T, Z	G, Lo, M, N, S1, W2, X1, X3,	F, J, K, P, S2, TIC, W1,X1
	Cave waters	–	Lo, S2, W2, YpH	G, N, P	F, J, K, T, TIC, W1, X1, X2
	Soil surfaces	–	G, H1, S1, S2, Z	Lo, TIC, W2, X2	F, J, K, W1, X1, X3
	Telmata	–	–	N, T, W2, X1, X3	F, J, P, W1, X2

Percentage distributions: < 5%, 5–10%, 11–20%, > 20%

These habitats show close resemblance in several of their limnological and hydromorphological characteristics. Very small aquatic and semiaquatic sites are rich in benthic elements, while in habitats with extended macrophytes stands, metaphytic elements like desmids or euglenophytes occur in large numbers (Görgényi et al., 2019). The very small aquatic and semiaquatic habitats constituted a separate group. The common feature of these habitats is that they provide well-illuminated solid substrates for benthic algae.

Using both FT- and FG-based approaches, only the cryobiotopes show no similarity with any other types of habitats. This habitat type provides conditions only for a narrow set of species (Kol, 1968).

The FG-based approach appeared to be the best in creating reliable groups of habitats. The five clusters we identified, represent limnologically different subgroups of habitats.

In the cluster of “Rivers and river-fed habitats” besides the water currents, standing waters (oxbows and reservoirs) can also be found. These waters are continuously or occasionally flushed by the nearby rivers, which shapes their biotic assemblages (Stević et al., 2013; Bortolini et al., 2017), resulting in diverse microflora and dominant occurrence of B, C, D, functional groups (Table 3). The appearance of “Large saline lakes” in this cluster can also be explained by the large relative abundance of benthic and meroplanktic algae that frequently occur in both habitats (Padisák & Dokulil, 1994). Several benthic diatoms that constitute an important part of the microflora of these waters (*Navicula salinarum* Grunow, *Nitzschia liebethruthii* Rabenh. or *Halamphora* spp.) are euryhaline taxa with wide salinity tolerance (Van Dam et al., 1994).

The lakes, pit lakes and fishponds constituted the habitat cluster of “Medium-sized lakes with no or negligible presence of macrophytes”. Partly because of the presence of high fish stock and partly because of the steep lake basin walls (Schultze et al., 2022), the littoral macrophyte coverage in these lakes is considerably smaller than in the unaffected, natural habitats. As it was previously demonstrated, in these water bodies, due to the relatively small diversity of phytoplankton (Görgényi et al., 2022) and the enhanced mixing of water (caused by the fish stock or the large fetch; Borics et al., 2015), planktic diatoms from the A, B, C functional groups—that are

Table 4 The most frequent FG-s of each habitat type

Habitat types	Most frequent FG	Frequency occurrence of FG's (%)
Cave waters	X1	18
	X2	11
Springs	N	13
	P	9
Streams	C	9
	MP	8
Brooks	C	9
	J	8
Rivers	X1	7
	F	6
Canals	X1	8
	C	7
Oxbows	X1	8
	J	7
Reservoirs	C	11
	X1	7
Soda pans	X1	11
	F	10
Soil surfaces	X1	20
	F	11
Bog lakes	P	9
	N	8
Ponds (< 1 ha)	X1	14
	F	13
Small temporary wetlands	X1	14
	W1	10
Telmata	W1	22
	X2	17
Pools	X1, J, F	9
	TC	7
Fishponds	C, X1	9
	F	8
Water-filled pits	F, J, W1, X1	10
	X2	8
Lake Balaton	F, J, X1	10
	T, X2	6
Ricelands	N, P	16
	J	11
Cryobiotopes	H1, K, Lo, S2, TC, X1	12
	J, M, MP, T, Z	6
Marshlands	W1	13
	J	10
Pit lakes	C	25
	B, D	17
Large saline lakes	W1	10
	F, J, Lo, X1, X2	6

Table 4 (continued)

Habitat types	Most frequent FG	Frequency occurrence of FG's (%)
Lakes	C	13
	D	10

sensitive to sinking—can be characteristic for these habitats.

The "Medium-sized, shallow, macrophyte-dominated waters" also created a characteristic group. These waters have extended littoral zones, or as in the case of the bog lakes and marshlands the entire basin belongs to this realm. The littoral macrophytes provide ideal habitats for many benthic and metaphytic species (Lukács et al., 2023, in this volume), considered the most diverse compartment of the lake ecosystems (Vadeboncoeur et al., 2011). Several planktic species from the F and J functional groups and flagellates from the W1, W2 and X2 groups prefer these habitats. Only Lake Balaton could be considered as an unexpected habitat in this cluster. Because of the enormous differences in size and limnological characteristics, their close relationship is really surprising. However, the river Zala, which feeds Lake Balaton, crosses a huge marshland (Kis-Balaton) before entering the lake. This marshland connection provides many marsh-dweller species to the flora of Lake Balaton.

The "Very small, aquatic and semiaquatic habitats" constitute a unique habitat cluster, too. Because of their small size, planktic diatoms, planktic species from the F, J and X group, and small flagellates from the X2 functional group are missing from these waters. In contrast, tichoplanktic elements (TIC) are the most characteristic of this cluster.

Finally, "Cryobiotopes" constitute a single cluster. Species inhabiting this special environment must adapt to extreme environmental conditions in terms of temperature, light and nutrient availability (Kawecka 1986). Although species from ten FGs occurred in this habitat type, we note here, that these species were so-called cryoxene elements that accidentally occurred on ice or snow surfaces. Cryobiont and cryophyilic algae (Kol, 1968) were not found in the microflora.

Ranked FT and FG occupancy of the habitats

Despite the theoretical differences between the FT and FG-based approaches, the order of the habitats in the ranked FT and FG occupancy distributions appeared to be quite similar. Both approaches positioned river-related habitats in the first quarter of the distributions. This is surprising considering that rivers are highly selective environments allowing only a few groups to dominate (Rojo et al., 1994). However, rivers are continuously, or at least periodically connected to the wide array of aquatic habitats in their watershed. Elements of the microflora of these habitats enhance the diversity of both large potamal (Borics et al., 2014a) and small rhithral rivers (Bolgovics et al., 2017b).

Relationships between the applied approaches

Habitat clusters of the quantitative FT and FG-based approaches showed considerable resemblance (Figs. 3 and 4), which was corroborated by the high correlation value ($R = 0.896$; $P = 0.001$) yielded by the Mantel test. Classification of the habitats provided by the two approaches resulted in hidromorphologically and limnologically well-identifiable habitat groups, but the simplest, FG-based approach provided the most interpretable classification. In phytoplankton ecology, FTs are based on those morphological, physiological and behavioural features of algae (Weithoff, 2003; Litchman & Klausmeier, 2008) that affect their fitness (Violle et al., 2007) and basically influence their functioning and ecological roles in the planktic assemblages. Trait-based analyses have been used to show that phytoplankton functional composition responds to changes in mixing regimes (Becker et al., 2009; Wang et al., 2011), anthropogenic stresses (Abonyi et al., 2012), and hydrological changes in rivers (Stanković et al., 2012; Abonyi et al., 2014). In contrast, FGs have rather been developed for describing characteristic functional community compositions in the specific set of environment conditions. FGs can be considered as kinds of response groups, containing species that respond similarly to the particular environmental conditions (species with the same habitat template (niche)). These functional groups separate species on the basis of their habitats and not on the similarity of their features. As this approach is associated with very detailed environmental templates, it is generally acknowledged, that it is the most optimal classification approach for the aquatic ecology research and aquatic environment evaluation (Salmaso et al., 2015). The FG-based approach is very relevant, as it plays a significant role in studies aimed at assessing ecological status of waters required by the Water Framework Directive (EC Parliament & Council, 2000). Moreover, this approach has also been used to describe the seasonal dynamics of phytoplankton (Padisák et al., 2003; Salmaso and Padisák, 2007; Wang et al, 2018), to explore the biomass (productivity)—diversity relationship in algae (Borics et al., 2012, 2014a; Skácelová and Lepš, 2014; Török et al., 2016), and to better understand the response of algal assemblages to climate change (Domis et al., 2007).

Theoretical differences between the FT-based and FG-based approaches

As it was shown above, results of habitat grouping using FT-based and FG-based approaches showed some differences that can be traced back to the differences between the organizational levels and inherent components of the two terms (Violle et al., 2007). FTs are acting at the level of individuals and can be defined as measurable morphological, physiological or phenological characteristics that directly impact the growth, reproduction and survival of the individuals. In contrast, the FGs appear at the level of communities and include those species that are associated with similar combinations of environmental factors (Gitay & Noble, 1997). Reynolds's FGs show a close resemblance to Braun-Blanquet's macrophyte associations (Braun-Blanquet, 1932) since the groups have a well-defined niche or habitat template. These differences in the functional approaches resulted in differences in the grouping of habitat types.

Reynolds's FG approach was developed to help understand the recruitment and functioning of lakes' phytoplankton (Reynolds et al., 2002). Later it was extended and applied to rivers (Borics et al., 2007; Várbíró et al., 2007) and some new coda were also proposed (Padisák et al., 2009). In recent years, some studies have been published explicitly focusing on how the habitat templates of Reynolds' FGs fit or diverge from the original description. Nagy-László et al. (2020) showed that the niche position and niche breadth of several FGs in riverine environments differed from that established for lakes. Investigating phytoplankton of tropical drinking water reservoirs, Amorim & Moura (2022) re-created the habitat templates of some Reynolds' FGs. They described both wider and narrower ranges of the relevant components of the FGs' habitat templates.

We experienced that the extreme habitats, like cryobiotopes, cave waters, macrophyte-dominated bog lakes, small pools and telmata have been separated well by the FG approach. This result implies that the FG approach can be applied for habitat classification even in those cases when the habitats are different from those that were used for the development of the original FG concept (Reynolds, 2002).

However, the functional approaches have some shortcomings. Grouping of species into a single FG is acceptable in the case of those genera, which have only a few species in freshwaters (*Phacotus, Uroglena, Gonyostomum,* etc.). The approximately 500 *Chlamydomonas* species that have been described from various aquatic habitats, like large lakes and rivers, small ponds or pools of a couple of square meters, from among *Sphagnum* tussocks (Ettl, 1983) have now been assigned to the X2 codon (Padisák et al., 2009). Moreover, centric diatoms have also widespread distribution, yet they have been assigned only to three codas (A, B and C). This, at the level of our present knowledge, is understandable, but no doubt, it is a rough simplification of reality.

Unique microflora of the special habitats

Reviewing the microflora of extreme habitats, Padisák & Naselli-Flores (2021) provided an extensive outline of the microalgae of unique habitats like high salinity or low pH lakes and ponds, or those that have extremities in light availability, mixing regime or temperature. In this study, several unique habitats were included of which extremities lie in their very small size (telmata), in their low temperature (cryobiotopes) or in the lack of light (cave waters).

Telmata are distinct aquatic microhabitats characterized by small size (10^{-2} m^2) and ephemerality. These can be considered as hidden freshwater habitats supporting unique microflora and microfauna (Mogi, 2004). Not surprisingly, only a little is known about the algal diversity and the compositions of the microalgae communities of the telmata. Most of the studies focused on bromeliad phytotelmata. Recent taxonomic studies showed that the main microalgal groups reported from bromeliad phytotelmata were mostly unicellular (X1) and colonial (F, J) species of chlorophytes (Ramos et al., 2018a), zygnematophytes (N) (Sophia, 1999; Ramos et al., 2017a, 2018b), diatoms (benthic forms, TIB) (Lyra, 1971), cyanobacteria (TIC) (Ramos et al., 2018b, 2019), dinoflagellates (Lo) (Ramos et al., 2016) and euglenophytes (W1) (Ramos et al., 2017b). However, apart from these studies, there are no or very few specific studies aimed at exploring the microflora of other types of telmata. In addition to phytotelmata the database used for this study contains data also for litotelmata and anthropogenic telmata. Compared to the literature data these telmata provided a much larger set of FGs, such as F, J, P, N, T, W1, W2, X1, X2, X3.

The cryobiotopes, i.e., snow or ice surfaces, can be characterized by low temperature and high light intensity. Kol (1968) devoted a complete book presenting the unique microflora of these habitats. Besides many benthic forms, she described several flagellated (X2) and colonial (F) chlorophytes, dinoflagellates (Lo), desmids (N, P), euglenophytes (W1), chrysophytes (E) and cyanobacteria (TIC, K, Lo) from these biotopes. Later findings (Vincent & Vincent, 1982; Izaguirre et al., 2021) also confirmed that besides cyanobacteria, flagellated species of chrysophytes and chlorophytes are also characteristic of this biotope. In our database, both flagellated chlorophytes (*Carteria, Chlamydomonas* spp.—X2) and colonial (*Chroococcus* spp.—Lo, *Aphanocapsa* spp.—K) or filamentous (*Oscillatoria, Phormidium* spp.—TIC) cyanobacteria were present in high frequency.

Cave waters also can be considered as unique habitats. Although cave waters are characterized by the lack of light, several groups might occasionally occur in these habitats. The most trivial ones are those cyanobacteria and green algae that form thin crusts on rock surfaces (Palik, 1960a, b; Hajdu, 1966; Scott, 1909; Sánches et al., 2002; Popkova & Mazina, 2019). The majority of these taxa occur at those places in caves, where anthropogenic illumination makes it possible (Pasic & Mulaomerovic, 2014). However, species that lack photosynthesis have an alternative way of nutrition (using organic materials) may also occur in cave waters (Hajdu, 1966). The investigated cave waters in Hungary contain similar taxa from the above-mentioned phyla, including *Chroococcus* spp. -Lo, *Chlamydomonas* spp. -X2, *Volvox, Pandorina* spp. -G and *Chlorella* spp. -X1 species. We note here that the structure of limestone enables surface water to infiltrate, and thus obligate autotrophic elements might occur in cave waters.

Conservation outlook

The use of functional approaches in ecology (both FT- and FG-based ones) reduces system complexity and helps to identify the key mechanisms that govern the operation of the systems. However, there are several cases when the fine taxonomic resolution cannot be set aside. While in the case of environmental quality assessment, much emphasis has been given to the functioning of the systems, and thus, the response of major algal groups to environmental loads has been quantified (Carvalho et al., 2013), in the case of nature conservation, diversity and presence of unique or rare species has great importance (Görgényi et al., 2022), as they increase the resilience of ecosystems against disturbances. Nevertheless, it does not mean that functional approaches have no relevance in nature conservation issues. Similarities in the functional composition of the systems make possible the replacement of functionally equivalent species between them. Replacement of the natural elements of the habitats by functionally equivalent invaders means a real danger for the natural flora (Szabó et al., 2019; Živković et al., 2019) and fauna (Russell, 2014; Kaldre et al., 2017). Similar processes have also been recorded for microalgae. The serious bloom-forming *Raphidiopsis raciborskii* (Wołoszyńska) Aguilera et al. appeared first in canals and rivers in Hungary (Bancsi et al., 1978) but because of its functional equivalence with other filamentous cyanobacteria, the species became a serious invader in other aquatic habitats like shallow lakes and ponds that show a close resemblance to rivers in several limnological characteristics (Padisák et al., 1997; Borics et al., 2000).

Conclusion

The present study revealed the functional similarities and differences among the whole range of aquatic habitats in Hungary from the point of view of microalgae. Quantitative approaches have given more reliable habitat clusters than qualitative ones. Habitats in these clusters showed close resemblance in their limnological characteristics. Rivers and river-related habitats appeared to be the functionally most diverse, while the small aquatic (and semiaquatic) habitats showed the smallest functional richness. Official monitoring of microalgal assemblages (both planktic and benthic ones) focuses on the large (> 50 ha—standing waters; catchment area > 10km^2—watercourses) waterbodies, but as the present study revealed smaller habitats also possess remarkable functional richness. This functional richness gives them resilience to disturbances and may help them to preserve their unique species pool.

Author contributions JG and GB: drafted the key issues of this paper and wrote the manuscript. JG, ET, ZK, ÁL, VB, ÉA, KKT and BT: carried out the collecting and processing the data of the database. GV: carried out the statistical analyses. All authors reviewed and approved the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Research involving human and animals rights No human participants and animals were involved in the research.

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