Original Articles

Functional dynamics of phytoplankton assemblages in hypertrophic lakes: Functional- and species diversity is highly resistant to cyanobacterial blooms

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ABSTRACT

Under increasing pressure of climatic change and anthropogenic eutrophication, water blooms, i.e. the formation of high phytoplankton biomass of a single or a few species, have become more and more frequent in lake ecosystems that is caused mostly by Cyanobacteria. The dynamics of phytoplankton under a cyanobacterial pressure may provide important information about what a competitive advantage of Cyanobacteria have over eukaryotic microalgae. The research, therefore focused on the relationship between cyanobacterial blooms and the accompanying species in hypertrophic shallow lakes where nutrients are in excess. The following hypotheses were selected for testing: i) Cyanobacterial blooms negatively affect the species richness and diversity of phytoplankton assemblages in the studied hypertrophic lakes. ii) Cyanobacterial blooms negatively affect the multi-trait functional diversity of phytoplankton assemblages in the studied hypertrophic lakes. iii) The formation of a cyanobacterial bloom causes a shift in the species and trait composition of phytoplankton assemblages. It was found that the species diversity of non-cyanobacterial assemblages was not affected negatively by increasing density of Cyanobacteria. Cyanobacterial biomass negatively affected the functional richness and functional dispersion of the assemblages, but both relationships were only marginally significant. Some temporal shift was detected in the community weighted mean values of width, colonial ability of accompanying microalgae, and also in flagellatedness and mixotrophic ability. We conclude that Cyanobacterial blooms basically alter dominance relations in the phytoplankton and reduce availability of light in waters. However, it does not necessarily coincide with the elimination of other taxa and reduction their species numbers or diversity. The formerly published data on the decrease in species richness can be likely explained by methodological deficiencies, which are responsible for reduced detectability of species. To better understand the seasonal dynamics and resilience of phytoplankton assemblages in hypertrophic water bodies the development of new methodologies by which diversity and succession of subordinate species can be evaluated is required.

1. Introduction

Importance of shallow lakes is not necessary reflected by their total area or water capacity; however, their role in sustaining freshwater biodiversity or by providing important ecosystem services including the provision of drinking water in many regions or their importance as recreational areas is increasing (Padisák et al., 2003; Reid et al., 2019; Kókai et al., 2019; B-Béres et al., 2021). Small shallow lakes are numerous (35 million shallow lakes < 0.001 km²; Meybeck, 1995) and provide highly diverse habitats (they can be e.g., small ponds with

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adjacent wetlands, pit lakes, oxbow lakes, sweet-water reservoirs). They can act as refugees and "steppingstones" for freshwater biota in heavily transformed landscapes, and they play a pivotal role in local biogeochemical cycles and water retention (Naselli-Flores and Padisák, 2022).

Under increasing pressure of climatic change and anthropogenic eutrophication, water blooms (the formation of high phytoplankton biomass of a single or a few species) have become more and more frequent in lake ecosystems that is caused mostly by Cyanobacteria (Reynolds, 2006). Cyanobacteria can occur in a wide range of environmental conditions and habitats, furthermore, some groups can become more and more dominant in the phytoplankton (Huisman et al., 2018). Some filamentous Cyanobacteria can form surface scums or produce massive planktonic biomass (Wehr et al., 2015), which can decrease the water quality for human utilisation such as recreation, drinking water supply, and also negatively affects other aquatic organisms by increasing turbidity, anoxia or toxicity (Paerl et al., 2001).

While in general high nutrient concentration is typical in hypertrophic lakes that favours the development of cyanobacterial blooms (the high-nutrient paradigm, Reynolds, 2006), cyanobacterial blooms have already been detected also from oligotrophic waters (Reinl et al., 2021). In hypertrophic lakes, it is well known that Cyanobacteria might dominate the phytoplankton assemblages in mid- or late summer periods repeatedly from year to year, in parallel with stable stratification, increasing water temperature and high availability of nutrients (Sommer et al., 1986). The diversity and dynamics of shallow, temperate waters during filamentous cyanobacterial blooms were frequently studied (Romo and Miracle, 1994; Pinckney et al., 1998; Scheffer, 2004). Most studies focused on the direct effects of Cyanobacteria on phytoplankton diversity or density in tropical (Amorim and Moura, 2021) and temperate regions (Naselli-Flores, 2003). It was found that phytoplankton blooms might cause significant changes not only in phytoplankton assemblages, but in the whole aquatic ecosystems by intensifying the water quality degradation (Paerl et al., 2001; Amorim and Moura, 2021). Thus, understanding the dynamic processes during cyanobacterial blooms in shallow lakes is very timely and crucial.

There are various characteristics of Cyanobacteria that give them a competitive advantage over eukaryotic microalgae, such as the ability of nitrogen fixing, ability of buoyancy, preference of a rather high temperature for growing, good competitive ability, and finally, their strong shading tolerance (Scheffer, 2004). The dynamics of phytoplankton under a cyanobacterial pressure may provide important information about what competitive advantage Cyanobacteria have over eukaryotic microalgae (Paerl et al., 2001) or the possibility of the bloom formation due to allelopathy (Suikkanen et al., 2004; Legrand et al., 2003). However, it is little known how the development of Cyanobacteria dominance drives non-cyanobacterial components of the phytoplankton assemblages. A reduced phytoplankton richness with increased Cyanobacteria density was observed by Bockwoldt et al. (2017) in shallow, eutrophic sites of a deep lake. Low functional and species diversity (including Cyanobacteria) was also found by Borics et al. (2012) in shallow lakes, when the dominance of bloom-forming Cyanobacteria was observed. In contrast, the dominance of Cyanobacteria resulted in low functional diversity but a relatively high number of species in microcosm experiments (Bácsi et al., 2016).

The research, therefore focused on the relationship between cyanobacterial blooms and the accompanying species in hypertrophic shallow lakes where nutrients are in excess. The following hypotheses were selected for testing: i) Cyanobacterial blooms negatively affect the species richness and diversity of phytoplankton assemblages in the studied hypertrophic lakes. ii) Cyanobacterial blooms negatively affect the multi-trait functional diversity of phytoplankton assemblages in the studied hypertrophic lakes. iii) The formation of a cyanobacterial bloom causes a shift in the species and trait composition of phytoplankton assemblages.

2. Material and methods

2.1. Study sites

Altogether sixty standing waters of different types (reservoirs, oxbows and gravel pit lakes) were sampled in Hungary from April to September 2019. All waterbodies were shallow (mean depth < 3 m), and their surface area were greater than 50 ha.

According to the OECD (1982), phosphorus and Chl-a boundaries of all sampled lakes were hypertrophic. We selected ten lakes from the sampled sixty, in which a cyanobacterial bloom was formed in the study period (Fig. 1, Table 1, Electronic Supplementary Material).

2.2. Environmental parameters and sampling

Monthly samples were collected in the May-September period from the euphotic layer of pelagial zone, which was calculated from Secchi depth ($2.5 \times$ depth of Secchi-disc, Poikane 2009). Water samples were taken by a tube sampler from a boat at the deepest part of the lakes. Conductivity (COND–μS cm^{-1}), pH, dissolved oxygen concentration (DO–mg L^{-1}), oxygen saturation (OS–%) and water temperature (T–°C) were measured in situ by a portable-multiparameter digital meter (HQ30d, Germany). For further chemical analyses, water samples were kept at 4 °C in a cooler bag during the transportation to the laboratory. Phytoplankton samples (0.5 L) were preserved in the field with Lugol's solution.

Analyses of the following chemical parameters were carried out in the laboratory according international and Hungarian national guidelines: total nitrogen (TN in mg L^{-1}, MSZ 12750-20:1972), total phosphorous (TP in mg L^{-1}, MSZ 1484-3:2006; EPA 6020A:2007), chlorophyll *a* (Chl-a in μg L^{-1}, MSZ ISO 10260:1993), biological oxygen demand (BOD in mg L^{-1}, MSZ EN 1899-1: 2000) and total suspended solids (TSS in mg L^{-1}, MSZ 12750-6:1971).

2.3. Assessment of phytoplankton

For phytoplankton analysis, samples were allowed to settle in 5 cm^3 counting chambers for at least 5 h. Although counting up to at least 400 units (cells, filaments or colonies) is the most frequently applied method in phytoplankton ecology, this method may result in the underestimation of subdominant or rare species. Therefore, we investigated 5 fields in the case of each sample independently of the number of cyanobacterial units. Investigations were done at 400-fold magnification. To assess the relative abundance of rare, large-sized taxa, we investigated the whole area of the counting chamber at 100-fold magnification.

The samples were investigated with LEICA DMIL inverted microscope. Species were documented by Canon EOS digital camera. Currently accepted names of phytoplankton species were based on the AlgaeBase (Guiry and Guiry, 2022). Phytoplankton biovolume and surface area were calculated using realistic 3D models following Borics et al. (2021).

2.4. Traits

To better understand which characteristics of microalgae are responsible for the observed patterns and processes, we used trait-level analyses. Ten phytoplankton traits were included into the analyses (detailed information on traits is summarised in Table 2). To decrease the range of scale variables, length and width scores were standardised using the method that the highest scores were considered as 1, and all others were expressed in the percentage of the highest score.

2.5. Statistical analyses

For the calculation of single trait community weighted mean values (CWMs), species richness, Shannon diversity and evenness scores and
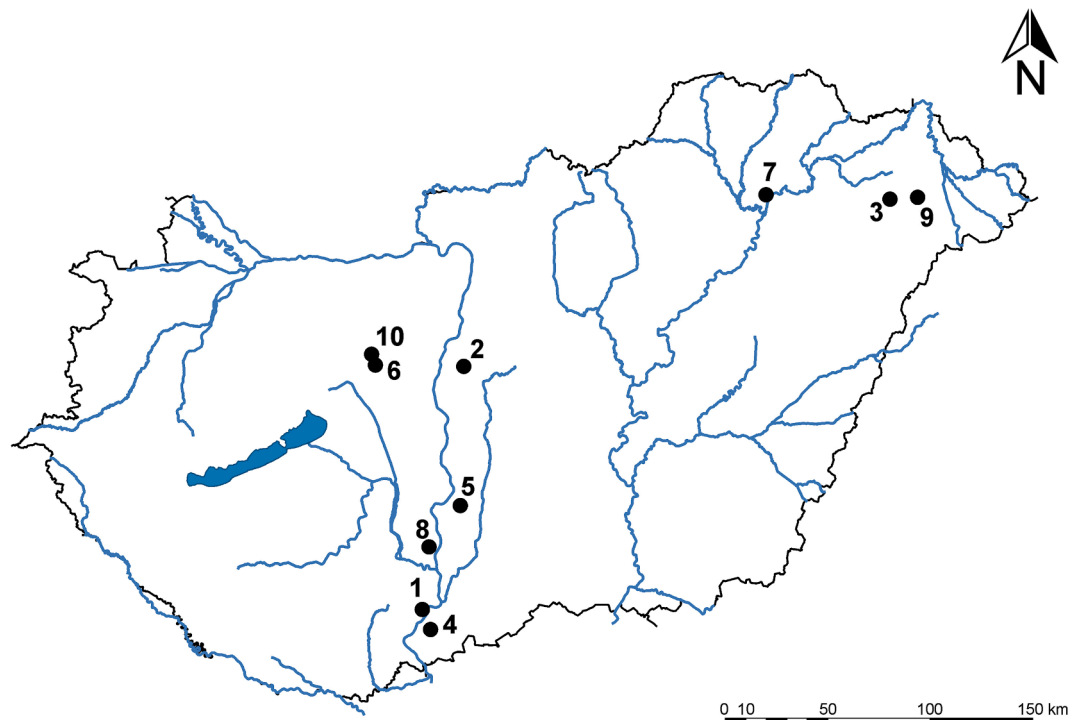
Fig. 1. Location of the selected study lakes in Hungary. Notations: 1 - Bátai-oxbow, 2 - Délegyházi lake, 3 - Leveleki reservoir, 4 - Nagybaracskai-oxbow, 5 - Szelidi lake, 6 - Pátkai reservoir, 7 - Tiszalúc-oxbow, 8 - Tolnai-Deli-Duna-oxbow, 9 - Vajai reservoir, and 10 - Zámolyi reservoir. For geocoordinates of sampled lakes see Table 1.

Table 1
General information of studied standing waters – type of water body, max. depth, surface area and trophic status.

Name	Abbreviation of lakes	Geocoordinates		Type of water body	Max. depth (cm)	Surface area (km²)	Trophy
Bátai-oxbow	BT	E18° 48′ 09,98″	N46° 09′ 28,82″	oxbow	100–410	0.66	hypertrophic
Délegyházi lake	DT	E19° 04′ 27,88″	N47° 15′ 42,96″	gravel pit lake	200–320	0.7	eu-hypertrophic
Leveleki reservoir	LT	E21° 57′ 33,49″	N47° 59′ 04,56″	reservoir	85–220	1.64	hypertrophic
Nagybaracskai-oxbow	NB	E18° 51′ 25,52″	N46° 04′ 01,34″	oxbow	120–130	0.82	hypertrophic
Szelidi lake	SZ	E19° 03′ 04,23″	N46° 37′ 47,75″	natural lake	110–290	0.52	hypertrophic
Pátkai reservoir	PT	E18° 29′ 03,99″	N47° 15′ 59,55″	reservoir	250–320	2.86	hypertrophic
Tiszalúc-oxbow	TL	E21° 07′ 18,32″	N48° 01′ 21,52″	oxbow	150–450	1.48	hypertrophic
Tolnai-Deli-Duna-oxbow	TD	E18° 50′ 44,33″	N46° 26′ 31,83″	oxbow	50–150	1.34	hypertrophic
Vajai reservoir	VT	E47° 59′ 17,73″	N22° 08′ 47,82″	reservoir	20–80	0.67	hypertrophic
Zámolyi reservoir	ZT	E18° 27′ 30,98″	N47° 18′ 55,54″	reservoir	310–330	1.69	hypertrophic

multi-trait indices, we used FDiversity programme package; in calculations, we applied for weighting Gower distances; calculations were based on counts of individuals (Casanoves et al., 2011). Amount of Cyanobacteria was used as a predictor variable. Therefore, all cyanobacterial taxa were excluded from the analyses, they were only considered in the calculation of cyanobacterial biomass. For multi-trait analyses, we computed three components of functional diversity: functional richness (FRich), functional evenness (FEve) and functional divergence (FDiv, Laliberté and Legendre, 2010) proposed by Mason et al. (2005). We also calculated functional dispersion (FDis), which measures the functional similarity amongst the characteristic species of the assemblages and therefore high dispersion reflects high levels of niche differentiation, which supports decreasing competition (Mason et al., 2005; Villéger et al., 2010).

To study the effects of environmental factors and the cyanobacterial biomass on the species composition and abundance, we calculated two separate Canonical Correspondence Analysis (CCA) using either individuum counts or species presence-absence datasets. We used CANOCO 4.5 for the analyses (Lepš and Šmilauer, 2003). To select the effective

factors for the CCA, we applied forward selection. We tested the effect of the above-mentioned environmental parameters (Secchi depth, conductivity, pH, dissolved oxygen concentration, oxygen saturation, water temperature, total nitrogen, total phosphorous, chlorophyll-a, biological oxygen demand and total suspended solids) on the composition of phytoplankton assemblages. We applied a Monte-Carlo permutation test run on a full model with 499 unrestricted permutations (the highest level of significance for this permutation setup is 0.002). Only significant factors were added to the analyses and displayed in the CCA diagrams.

A Repeated Measures Generalized Linear Model (RM-GLM) was used to evaluate temporal trends in the species diversity and functional characteristics of phytoplankton assemblages. We included sampling time as a fixed factor (expressed as months) in a repeated sampling setup. Cyanobacteria were also excluded from the analyses. To study the relationship between cyanobacterial biomass, various diversity metrics and the CWMs of traits, we applied Spearman rank-order correlation (Zar, 1999).

Table 2

Traits used in the analyses.

Trait	Type of variable	Values	Measurement unit
Flagellated	nominal	0 - absent; 1 - present	–
Mixotrophy	nominal	0 - absent; 1 - present	–
Vacuolated	nominal	0 - absent; 1 - present	–
Silicious	nominal	0 - absent; 1 - present	–
Heterotrophic	nominal	0 - absent; 1 - present	–
Colonial ability	ordinary variable	1 - single cell; 2 - colonial form; 3 - filamentous	–
Length	scale	standardised with the highest score, range: 0.02–1.00	- (µm)
Width	scale	standardised with the highest score, 0.01–1.00	- (µm)
Length/Width ratio	scale	standardised with the highest score, range: 0.20–17.50	–
Area/Volume ratio	scale	range: 0.19–9.5	- ($µm^{-1}$)

3. Results

3.1. Environmental characteristics

The water temperature ranged from 9.7 °C to 36.2 °C with a lower average of early summer (16 °C) and a higher one during summer (28 °C). Four lakes (Leveleki reservoir, Pátkai reservoir, Tolnai-Deli-Duna-oxbow, Vajai reservoir) had a lower transparency (average ranged from 17 to 50 cm) than the others' (average ranged from 36 to 135 cm) regardless to the depth of the lakes. The concentrations of the average total phosphorous (0.194 mg L^{-1}) and total nitrogen (2.5 mg L^{-1}) were high during the studied period in the studied lakes; TP ranged from 0.01 to 0.67 mg L^{-1}, while TN ranged from 0.5 to 5.8 mg L^{-1}. The chlorophyll-a content ranged from 1 to 767 µg L^{-1}, the average chlorophyll-a concentration of early summer was already high (99.8 µg L^{-1}) and in late summer it reached more elevated value (210 µg L^{-1}). The detailed physical and chemical parameters of the studied standing waters are presented in Table 3.

3.2. Changes in species richness and functional diversity

In total, 235 taxa were found from May to September in the 10 studied lakes. The most species rich taxa were Chlorophyceae (60 taxa), Cyanophyceae (51 taxa), Trebouxiophyceae (38 taxa), Bacillariophyceae (23 taxa), Euglenophyceae (19 taxa) and Zygnematopyceae (16 taxa). Phytoplankton assemblages were characterised by the dominance of *Planktolyngbya limnetica* and *Chlorella* sp. (detected in almost 60 % of all samples). Beside these species, *Raphidiopsis raciborskii, Jaaginema gracile, Pseudanabaena limnetica, Aphanocapsa delicatissima, Tetraedron minimum, Monoraphidium contortum* and *Cyanocatena planctonica* were also characteristic in the 30–40 % of all samples. (Further details on species composition in Electronic Supplementary Material).

While the cyanobacterial biomass reached its maximum in August (the amount of this varied significantly for each lake, ranged from 6.8 to 813 mg L^{-1}), it decreased considerably in September. Cyanobacterial bloom forming species were thin filamentous forms: *Aphanizomenon* sp., *Raphidiopsis raciborskii, Jaaginema gracile, Limnothrix redekei, Planktolyngbya limnetica, Pseudanabaena limnetica*, and small colonies: *Aphanocapsa delicatissima, Cyanocatena planctonica, Merismopedia tenuissima* in the studied lakes. No such temporal patterns were detected for the richness of subordinate species (Fig. 2).

The temporal changes in the species and functional diversity of non-cyanobacterial compartments of phytoplankton were tested in the studied lakes (Table 4). Neither the species diversity (species richness, Shannon diversity and evenness), nor the functional diversity was affected by time. From the community weighted means (CWM), which were calculated for each non-cyanobacterial phytoplankton assemblages, we found that there was a significant effect of time detected on the traits 'width' and 'colonial ability' (Table 4, Fig. 3).

The non-cyanobacterial species richness was not correlated with the cyanobacterial biomass in the studied lakes (Table 5). This was also supported by the CCA analyses, where the cyanobacterial biomass was not found to be a significant predictor of the composition of non-cyanobacterial species (Figs. 4 and 5).

3.3. Temporal shifts in the phytoplankton composition

We analysed the compositional changes of the phytoplankton assemblages in the 10 shallow lakes without the inclusion of cyanobacterial species with CCA (Figs. 4 and 5). In CCA based on unit counts,
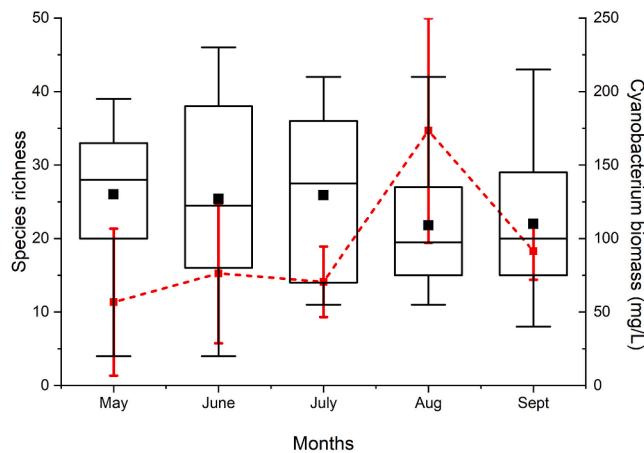
Table 3

Summary of mean data set for the chemical and physical parameters in the studied lakes: water temperature (T – °C), Secchi-depth (cm), dissolved oxygen (DO – mg L^{-1}), oxygen saturation (OS – %), Chl-a (µg L^{-1}), pH, conductivity (COND – µS cm^{-1}), biological oxygen demand (BOD_5 – mg L^{-1}), total amount of P-forms (TP – mg L^{-1}), total amount of *N*-forms (TN – mg L^{-1}) and total suspended solids (TSS – mg L^{-1}).

	T	Secchi	DO	OS	Chl-a	pH	Cond	BOD_5	TP	TN	TSS
Limit of detection			0.1	1	0.1	2	10	10	0.06	0.5	2
Bátai oxbow	22.9 ± 2.2	81.0 ± 31.8	9.5 ± 1.2	110.0 ± 16.7	222.7 ± 75.7	8.4 ± 0.3	359.2 ± 33.2	11.8 ± 3.1	0.36 ± 0.03	3.3 ± 0.9	21.6 ± 9.3
Délegyházi lake	26.4 ± 3.5	70.0 ± 10.4	9.2 ± 0.6	102.6 ± 5.4	19.2 ± 3.5	8.4 ± 0.2	1321.0 ± 33.6	5.2 ± 1.7	0.06 ± 0.02	3.8 ± 0.2	6.8 ± 2.7
Leveleki reservoir	23.4 ± 2.2	33.0 ± 7.2	7.5 ± 0.5	86.3 ± 6.0	94.9 ± 30.7	8.5 ± 0.1	427.4 ± 21.8	11.8 ± 5.1	0.11 ± 0.03	2.4 ± 0.5	16.6 ± 5.1
Nagybaracskai-oxbow	25.1 ± 1.4	63.0 ± 9.7	7.1 ± 0.4	85.7 ± 6.2	161.7 ± 97.4	7.8 ± 0.1	568.6 ± 25.4	6.6 ± 2.2	0.19 ± 0.04	1.7 ± 0.2	7.0 ± 2.7
Szelidi lake	26.6 ± 3.4	65.0 ± 8.4	10.2 ± 0.4	113.0 ± 6.0	71.7 ± 8.7	8.9 ± 0.1	2682.0 ± 54.2	9.0 ± 2.4	0.16 ± 0.05	2.4 ± 0.3	18.6 ± 5.3
Pátkai reservoir	22.6 ± 3.5	25.4 ± 4.8	9.8 ± 0.5	112.2 ± 8.6	280.2 ± 130.8	9.2 ± 0.1	1088.2 ± 20.8	16.4 ± 4.0	0.22 ± 0.02	3.7 ± 0.7	40.0 ± 8.4
Tiszalúc-oxbow	24.3 ± 2.1	82.2 ± 17.7	6.2 ± 1.2	68.7 ± 9.5	74.4 ± 16.4	8.1 ± 0.1	539.2 ± 19.6	7.0 ± 2.1	0.21 ± 0.10	2.3 ± 0.6	6.0 ± 2.5
Tolnai-Deli-Duna-oxbow	22.7 ± 2.9	31.0 ± 2.5	9.9 ± 0.8	110.8 ± 10.2	205.2 ± 51.0	9.0 ± 0.7	655.8 ± 74.2	10.0 ± 3.0	0.35 ± 0.11	1.9 ± 0.4	24.6 ± 10.4
Vajai reservoir	24.1 ± 2.4	33.0 ± 10.2	8.5 ± 0.7	98.6 ± 6.0	60.1 ± 10.9	8.4 ± 0.1	454.4 ± 32.6	9.0 ± 2.3	0.12 ± 0.03	1.6 ± 0.6	21.2 ± 12.2
Zámolyi reservoir	22.5 ± 3.4	85.0 ± 30.2	7.7 ± 0.9	88.4 ± 11.3	75.2 ± 44.8	8.7 ± 0.2	1069.4 ± 28.4	9.2 ± 2.9	0.17 ± 0.04	2.3 ± 0.5	17.4 ± 7.2

Fig. 2. Non-cyanobacterial species richness and cyanobacterial biomass in the studied lakes from May to September 2020. Boxplots show non-cyanobacterial species richness, while line diagram the change of cyanobacterial biomass (mg L^{-1}, mean $\pm$ SE) in the five study months.

Table 4
Temporal change (fixed factor 'time' expressed as months in a repeated sampling setup) of the species diversity and functional characteristics of phytoplankton assemblages in the studied lakes (characteristics were calculated with the exclusion of Cyanobacteria from the assemblages, RM-GLM, significant values are indicated with boldface, $p < 0.05$).

Characteristic	Time	
Species diversity	$F_{4,6}$	p
Species richness	0.341	0.842
Shannon diversity	0.991	0.479
Evenness	1.085	0.442
Functional diversity		
Functional richness	1.404	0.338
Functional evenness	0.663	0.640
Functional divergence	1.223	0.392
Functional dispersion	1.330	0.359
Community weighted means		
Length	2.695	0.134
Width	**4.887**	**0.043**
Length/width ratio	1.586	0.292
Flagelletedness	2.344	0.168
Colonial ability	**5.212**	**0.037**
Mixotrophic ability	2.325	0.170
Siliciousness	0.568	0.696
Area/Volume ratio	0.233	0.910

from the included factors the total phosphorous (TP, $p = 0.002$), conductivity (COND; $p = 0.004$), temperature (T; $p = 0.002$), total suspended solids (TSS; $p = 0.004$), dissolved oxygen concentration (DO; $p = 0.026$) and pH ($p = 0.0160$) were proven to be significant factors by the permutation test. Cyanobacterial biomass was not a significant factor explaining the species compositional differences in the CCA ($p = 0.1540$).

We found that in six shallow lakes (Délegyházi lake (DT; 6–10); Leveleki reservoir (LT; 11–15); Pátkai reservoir (PT; 21–25); Tiszalúc-oxbow (TL; 31–35); Tolnai-Deli-Duna-oxbow (TD; 36–40); Vajai reservoir (45–50)) there were a more or less cyclic change in the composition of subordinated species excluding Cyanobacteria – i.e. the species composition and abundance of the autumn samples became quite similar to that of in the spring. In these lakes, the same species of the same genus or functional group were characteristic in the whole sample period (DT: *Oocystis* and *Lagerheimia* genera; LT: *Fragillaria* and *Cryptomonas* genera; PT: *Monoraphidium* and *Desmodesmus* genera; TL: *Kircheriella* genus and

Lemmermannia tetrapedia (Syn.: *Crucigenia tetrapedia*); TD: *Scenedesmus* and *Tetraedron* genera).

In the other four shallow lakes (Bátai-oxbow (1–5); Nagybaracskai-oxbow (16–20); Szelidi lake (26–30); Zámolyi reservoir (41–45)), more pronounced changes were detected in the species composition and dominance. In the Bátai-oxbow (1–5), cyanobacterial bloom was still detected in September; for the whole period beside of centric diatoms and *Cryptomonas marssonni*, colonial species (*Pseudodidymocystis inconspicua*, *Desmodesmus protuberans*) and some 'spiny' species also appeared (e.g., *Golenkinia radiata*). In Nagybaracskai-oxbow (16–20), the phytoplankton assemblages were characterised by colonial species before the bloom (e.g., *Pseudodidymocystis inconspicua*, *Lemmermannia triangularis* (Syn.: *Tetrastrum triangulare*) and *Lemmermannia tetrapedia*), and they were transformed to a *Chlorella* sp. and *Cyclotella meneghiniana* characterised assemblages. Samples of Szelidi lake (26–30) arranged along an increasing conductivity and temperature. *Tetraedron minimum* characterised the assemblages in spring, replaced by *Scenedesmus* and *Chlorella* species in early summer, while after the cyanobacterial bloom, *Lemmermannia tetrapedia*, *Oocystis marssoni* and *Monoraphidium dybowskii* became characteristic. In Zámolyi reservoir (41–45), the phytoplankton assemblages were characterised by very low individual numbers of *Chlorella* sp. and *Plagioselmis nannoplanctica* in July. From this month, in parallel with the formation of cyanobacterial bloom, individual numbers of characteristic subordinated species such as *Monoraphidium tortile*, *Hyaloraphidium contortum* and various *Scenedemus* species also increased.

In case of the CCA based on presence-absence datasets (Fig. 5) from the included factors the conductivity (COND; $p = 0.002$), total phosphorous (TP; $p = 0.002$) and Secchi depth (SECCHI, $p = 0.002$) were proven as significant factors by the permutation test. Compared to the CCA based on individuum counts, the points were closely arranged. Total phosphorous showed correlation with Bátai-oxbow and Tolnai-Deli-Duna-oxbow, conductivity correlated with Szelidi lake, while Secchi depth correlated with Nagybaracskai-oxbow and Tiszalúc-oxbow.

4. Discussion

As a result of the ongoing global warming, a higher frequency and intensity, and/or longer duration of cyanobacterial blooms became common in the recent years (Huisman et al., 2018). Not only in late summer but in other periods of the year, phytoplankton assemblages are being characterised by cyanobacterial blooms especially in the nutrient enriched shallow lakes (Padisák et al., 2003; Huszár et al., 2000; Vasas et al., 2010). Primarily, Cyanobacteria have several ecophysiological adaptations such as tolerating nutrient enrichment, lack of water mixing or rising temperature that give them a competitive advantage over the other phytoplankton species. In parallel with the increasing cyanobacterial biomass, the growth rates of eukaryotic algae decrease when the water temperature rises above 20 °C (O'Neil et al., 2012). Moreover, it is known that cyanobacterial blooms may have negative effects on biodiversity, and thus ultimately on the quality of the water by changing its turbidity, salinity and alkalinity and raising its trophic status (Amorim & Moura, 2021).

Numerous studies analysed phytoplankton dynamics during cyanobacterial blooms (e.g. de Figueiredo et al., 2006; Paerl & Huisman, 2009; Naselli-Flores, 2003; Naselli-Flores & Barone, 2003). It was found that cyanobacterial blooms coincided with a decline in the number of other phytoplankton species (Skácelová & Lepš, 2014). It has been reported that a cyanobacterial bloom (caused by a monodominance of *Raphidiopsis raciborskii*) reduced diversity to zero in a hypertrophic fishpond (Borics et al., 2000). Similarly, a negative relationship between abundance of Cyanobacteria and phytoplankton diversity was found in several other lakes. Low phytoplankton richness with increased cyanobacterial biomass was observed by Padisák et al. (2003) and Naselli-Flores (2003) in small, shallow lakes, by Bockwoldt et al. (2017) in a shallow region of a deep and large mesotrophic lake, and by Escalas
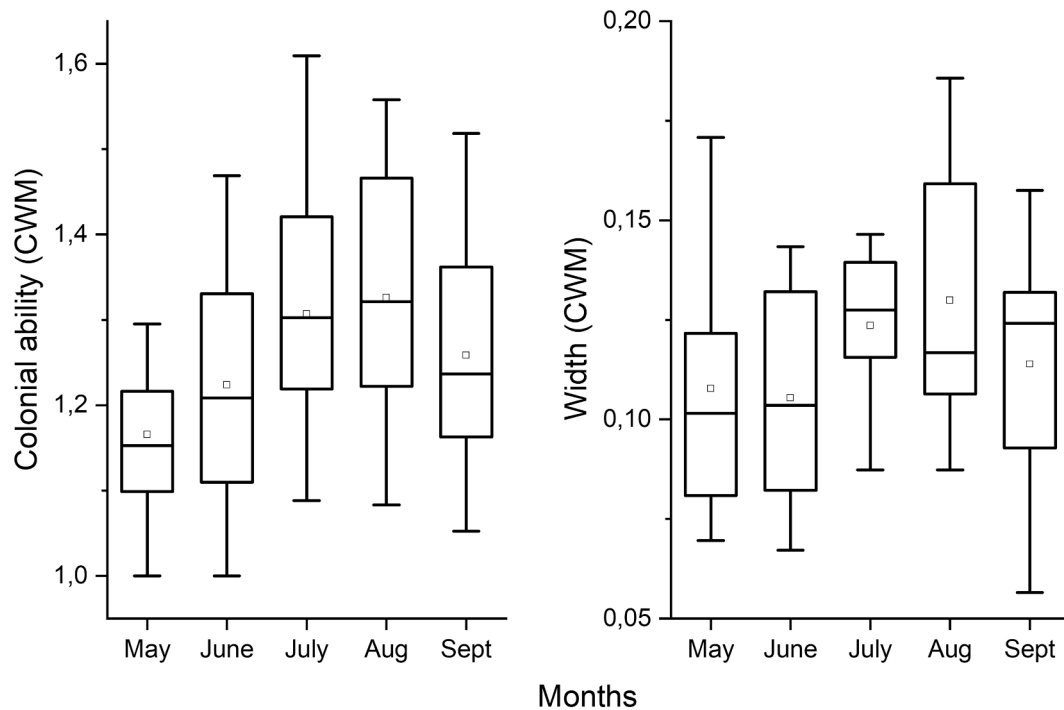
Fig. 3. Changes in CWM of traits 'colonial ability' and 'width' in the studied lakes from May to September 2020.

Table 5
Correlation of the cyanobacterial biomass and the studied diversity characteristics (Spearman rank correlation). Significant correlations (p < 0.05) were denoted by **boldface**, marginally significant correlations (p < 0.1) with *italics*.

Characteristic	*Cyanobacterial biomass*	
	R	*p*
Species diversity		
Species richness	−0.110	0.447
Shannon diversity	−0.017	0.906
Evenness	0.155	0.282
Functional diversity		
Functional richness	*−0.252*	*0.077*
Functional evenness	0.132	0.359
Functional divergence	0.160	0.267
Functional dispersion	*0.259*	*0.069*
Community weighted means		
Length	*0.249*	*0.081*
Width	0.079	0.580
Length/width ratio	*0.260*	*0.068*
Flagelletedness	**−0.397**	**0.004**
Colonial ability	−0.019	0.891
Mixotrophic ability	**−0.396**	**0.004**
Siliciousness	−0.056	0.698
Area/Volume ratio	0.112	0.436

et al. (2019) in eutrophic to hypertrophic waterbodies. Eloranta (1993) found decreasing Shannon diversity with increasing phytoplankton biomass in a eutrophic Finnish lake and similar observations were made by Bouvy et al. (2001) who demonstrated that the Shannon diversity was the lowest during a *Cylindrospermopsis raciborskii* dominated bloom period in a Brazilian reservoir.

We note here that dominance of Cyanobacteria might develop even in oligotrophic environment (Reinl et al., 2021). However, similarly to hypertrophic lakes studied in this paper, development of cyanobacterial blooms in low-productivity lakes does not coincide with the elimination of other phytoplankters. Under the dominance of Cyanobacteria many species might occur as subordinated elements of the phytoplankton. Changes in flushing rate or pulses of nutrients may quickly disrupt cyanobacterial dominance promoting fast growing r-strategist subordinated groups, e.g., diatoms, Chlorophyte or Chrysophyte (Nõges et al., 2011; Piovia-Scott et al., 2017; Stockwell et al., 2020).

In line with the mentioned findings in the previous paragraph, we hypothesised that cyanobacterial blooms negatively affect the species diversity of the non-cyanobacterial compartments of the phytoplankton assemblages in hypertrophic lakes. Surprisingly, this hypothesis was not supported by the present research. We found that the species diversity of non-cyanobacterial assemblages was not affected negatively by increasing cyanobacterial density. Although in most of the studied lakes, a cyanobacterial bloom was formed by July, diversity of subordinate species was similar in the whole study period. This was also supported by our results since the cyanobacterial biomass was not found as a significant predictor of the composition of non-cyanobacterial species.

Cyanobacterial blooms with increasing phytoplankton species richness, diversity, and evenness were found in several cases. Amorim & Moura (2021) highlighted that cyanobacterial blooms dominated by different *Microcystis* species and *Raphidiopsis raciborskii* increased phytoplankton species richness, diversity and evenness in Brazilian tropical water reservoirs. High densities of *Gloeotrichia,* which is a large filamentous Cyanobacterium, had positive effects on the biomass of small eukaryotic species (mainly Bacillariophyta and Chlorophyta) by providing them nitrogen and phosphorous in oligotrophic lakes (Carey et al., 2014). Bockwoldt et al. (2017) found that phytoplankton evenness was not related to cyanobacterial density, however, filtered samples were used in this survey, which somewhat limits the strength of this study. These examples suggest that there is a controversy regarding the role of cyanobacterial blooms in shaping diversity of subordinate species. The explanation of this controversy could be related to methodological and ecological reasons. As to the methodology, it is widely accepted that richness estimates are subject to the counting effort. To estimate species abundances with a 10 % accuracy, Lund et al. (1958) proposed to count a minimum of 400 units in the counting chambers. However, depending on the unit density in samples this number occasionally can be much higher, which may result in considerably larger
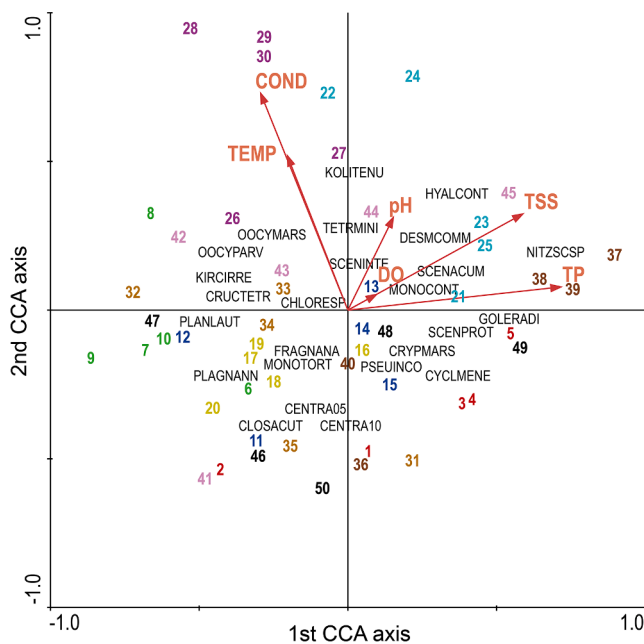
Fig. 4. The composition of phytoplankton assemblages and environmental factors displayed by a CCA. Eigenvalues for the first and second axis are 0.364 and 0.313, respectively. The species-environmental correlations are 0.923 and 0.890 for the first and second axis, respectively. The studied lakes are represented by different colours and temporal patterns are represented by the following notations: Bátai-oxbow: 1–5; Délegyházi lake: 6–10; Leveleki reservoir: 11–15; Nagybaracskai-oxbow: 16–20; Pátkai reservoir: 21–25; Szelidi lake: 26–30; Tiszalúc-oxbow: 31–35; Tolnai-Deli-Duna-oxbow: 36–40; Zámolyi reservoir: 41–45; Vajai reservoir: 46–50. The 25 most abundant species are shown, abbreviations are as follows: CHLORESP: *Chlorella* sp., CENTRA05: Centrales 3–5 μm TETRMINI: *Tetraedron minimum*, NITZSCSP: *Nitzschia* sp., MONOTORT: *Monoraphidium tortile*, HYALCONT: *Hyaloraphidium contortum*, MONOCONT: *Monoraphidium contortum*, CRUCTETR: *Crucigenia tetrapedia*, DESMCOMM: *Desmodesmus communis*, SCENPROT: *Scenedesmus protuberans*, CYCLMENE: *Cyclotella meneghiniana*, CRYPMARS: *Cryptomonas marssonii*, CENTRA: Centrales 6–10 μm, PSEUINCO: *Pseudodidymocystis inconspicua*, OOCYPARV: *Oocystis parva*, CLOSACUT: *Closterium acutum*, OOCYMARS: *Oocystis marssonii*, FRAGNANA: *Fragilaria nanana*, KIRCIRRE: *Kirchneriella irregularis*, GOLERADI: *Golenkinia radiata*, SCENINTE: *Scenedesmus intermedius*, PLAGNANN: *Plagioselmis nannoplanctica*, KOLITENU: *Koliella tenuis*, and SCENACUM: *Scenedesmus acuminatus*.

Fig. 5. Correlation between phytoplankton assemblages and environmental factors displayed by a CCA based on species presence-absence datasets. Eigenvalues for the first and second axis are 0.161 and 0.142, respectively. The species-environmental correlations are 0.891 and 0.922 for the first and second axis, respectively. The studied lakes are represented by different colours and temporal patterns are represented by the following notations: Bátai-oxbow: 1–5; Délegyházi lake: 6–10; Leveleki reservoir: 11–15; Nagybaracskai-oxbow: 16–20; Pátkai reservoir: 21–25; Szelidi lake: 26–30; Tiszalúc-oxbow: 31–35; Tolnai-Deli-Duna-oxbow: 36–40; Zámolyi reservoir: 41–45; Vajai reservoir: 46–50. The 25 most frequent species are shown, for the abbreviations of most species see Fig. 4, further species reads as: TETRCAUD: *Tetraedron caudatum*, TETRTRIA: *Tetraedron triangulare*, DACTJURI: *Dactylosphaerium jurisii*, MONOMINU: *Monoraphidium minutum*, SCENSPIN: *Scenedesmus spinosus*, and NEPHSUBS: *Nephrochlamys subsolitaria*.

species numbers. Lower estimates may occur when the investigators focus on the counting of dominant and subdominant taxa which basically determine the water quality. In this case, low-abundance species are not recorded which results in an underestimation of diversity. These differences may systematically determine the outcomes of the investigations.

Differences in the way of sampling may also be responsible for the observed differences in the diversity of subordinate taxa. Reynolds and Walsby (1975) described three scenarios of cyanobacterial distribution in the water column depending on the euphotic depth / mixing depth ratios. They demonstrated that at the onset of calm conditions Cyanobacteria may positioned in the upper layer ($Z_{eu} < Z_{mix}$), may be homogenously distributed ($Z_{eu} = Z_{mix}$), or may constitute deep layer maxima ($Z_{eu} > Z_{mix}$). These differences may be influential even if every effort is being made to precisely follow the descriptions of sampling protocols (whole water column has to be sampled in the euphotic layer).

Besides the methodological reasons, patterns of ecological processes and the characteristics of the available species pool also determine how Cyanobacteria dominance affects diversity of subordinated phytoplankters. Dominance of Cyanobacteria can be explained by their buoyancy regulation, nitrogen fixing or good light harvesting capabilities (O'Farrell et al., 2007). These behavioural and physiological traits
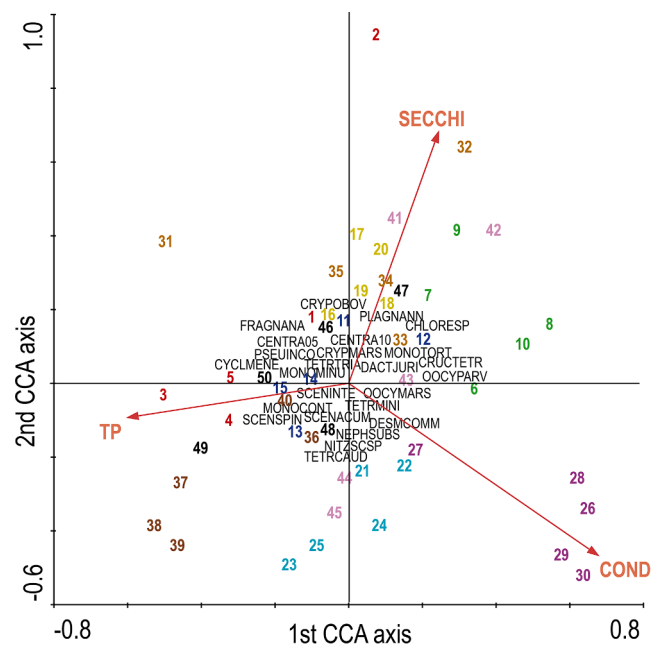
(Litchman and Clausmeier, 2008) make them possible to become dominant in calm conditions, in nitrogen- or in light deficient environment. However, these constraints can be overcome by other traits possessed by eukaryotic species. Thousands of eukaryotic taxa have flagella by which they can change their position in the water column. Many eukaryotic species have elongated shapes (*Ankistrodesmus* spp., *Koliella* spp., *Closterium* spp.), and thus similarly to filamentous blue-greens, they also work as light antennae. Diatoms can also tolerate low light conditions and increase their growth efficiency by using special physiological mechanisms (Anning et al., 2000; Fisher and Halsey, 2016; Furnas, 1990).

Although nitrogen fixation gives a competitive advantage to the heterocystous Cyanobacteria in nitrogen deficient environment, alternative nutritional strategies like mixotrophy also help eukaryotic microalgae to flourish in these environments (Pascher, 1917). The coexistence of Cyanobacteria and mixotrophic eukaryotic algae is not a simple theoretical possibility. This means that under those conditions when Cyanobacteria may possibly dominate the phytoplankton, eukaryotic competitors might also be present even attaining high abundance (Borics et al., 2021). Analysing large regional phytoplankton datasets, Reynolds et al. (2002) demonstrated the association-like coexistence of *Peridinium* and *Woronichinia* spp. in the summer epilimnia of stratified mesotrophic lakes (Lo functional group), while *Ceratium* and *Microcystis* spp. were found in eutrophic lakes (LM functional group). The presence of these associations; however, supports the so called "niche differentiation concept" (MacArthur & Levins, 1967; Pásztor et al., 2016) which states that competition for resources results in trait divergence that encourages a stable coexistence of species (Diamond, 1975).

Secondly, we hypothesised that cyanobacterial blooms negatively affected the multi-trait functional diversity of phytoplankton assemblages. This was only partially supported by the results. It was found that cyanobacterial biomass negatively affected the functional richness and functional dispersion of the assemblages, but both relationships were only marginally significant. Other multi-trait indices were not affected by biomass. In line with these findings, Borics et al. (2012) also found that functional diversity was low when cyanobacterial species dominated the phytoplankton. The likely explanation of this phenomenon is that cyanobacterial bloom was strong enough to affect trait abundances and functional trait composition of communities, but it was not strong enough to produce local or temporal decline in species richness.

Our third hypothesis was that the formation of a cyanobacterial bloom causes a shift in the species and trait composition of phytoplankton assemblages. Based on literature data, we expected that cyanobacterial blooms would affect both species and trait composition (Borics et al., 2012; Amorim and Moura, 2021; Skácelová and Lepš, 2014). We detected some temporal changes in the CWM values of width, colonial ability of subordinate microalgae (Table 4), and also in that of flagellatedness and mixotrophic ability. This temporal variation coincided with the development of large cyanobacterial biomass in late summer. In the studied standing waters, the high-biomass cyanobacterial assemblages contained strong light competitor, elongated species e.g., *Planktolyngbya limnetica*, *Raphidiopsis raciborskii*, *Jaaginema gracile*, *Pseudanabaena limnetica*. Besides these taxa, flagellated mixotrophic species (*Cryptomonas marssonii*, *Plagioselmis nannoplanctica*) were also present in a considerable amount.

By altering the surface temperature and increasing the light attenuation by absorbing more energy in the surface water layers, Cyanobacteria increase the water column stability and reduce light availability (Amorim and Moura, 2021; Rinke et al., 2010). Since Cyanobacteria can basically modify their environment, they serve as ecosystem engineers (Jones et al., 1994; Naselli-Flores and Padisák, 2022). This modified environment can favour for those groups that can tolerate stratification, low light and have high metabolic activity such as those taxa (*Cryptomonas* and *Plagioselmis*) that we observed as subordinates in our samples. Although well pronounced seasonal changes in species composition of subordinate species were found in four lakes, there were only slight changes in the species composition and the abundance of accompanying species in the case of the other six lakes. These results suggest that the species stock can be resistant to cyanobacterial bloom, i.e. although the species were outcompeted by the Cyanobacteria, they were not eliminated from the systems. This result contributes to the understanding of the high resilience of the aquatic systems (Oliver et al., 2015).

5. Conclusions

Cyanobacterial blooms basically alter dominance relations in the phytoplankton and reduce availability of light in waters. However, it does not necessarily coincide with the elimination of other species and reduction their species numbers or diversity. The published decrease in species numbers can be likely explained by methodological deficiencies, which reduce detectability of species. To better understand the seasonal dynamic and resilience of phytoplankton assemblages in hypertrophic water bodies require the development of new methodologies by which diversity and succession of subordinate species can be evaluated. This means that the currently used counting method registering up to 400–800 morphological units, which is highly biased towards the abundant species especially in the case of water blooms should also be replaced or supplemented with the assessment of standardised number of fields of counting chambers.

Authors contributions

TKE, TP and BBV conceived the ideas and designed methodology; TKE, GJ and KZs collected the data; LÁ, LV and TP analysed the data; TKE, TP and GB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CRediT authorship contribution statement

Enikő T-Krasznai: Conceptualization, Methodology, Investigation, Funding acquisition, Formal analysis, Writing – original draft, Writing – review & editing. **Péter Török:** Conceptualization, Methodology, Supervision, Funding acquisition, Visualization, Formal analysis, Writing – original draft, Writing – review & editing. **Gábor Borics:** Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review & editing. **Áron Lukács:** Data curation, Investigation, Writing – review & editing. **Zsuzsanna Kókai:** Data curation, Investigation, Writing – review & editing. **Verona Lerf:** Data curation, Writing – review & editing. **Judit Görgényi:** Data curation, Investigation, Writing – review & editing. **Viktória B-Béres:** Conceptualization, Methodology, Investigation, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

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.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109583.

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