



Lake morphology as an important constraint for benthic diatoms in temperate, humic forest ponds

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ABSTRACT

Small lakes are among the most threatened ecosystems in the world. Their protection is of crucial importance since they support an unusually high biodiversity relative to their size. The present study aimed at selecting the main drivers, especially the role of the morphological variables, shaping benthic diatom communities in unique, but rarely investigated forest pond ecosystems in the temperate region, using traditional (species-based methods and diversity indices) and novel approaches (trait-based methods and functional diversity indices) of diatom ecology. Therefore, we analyzed the effects of the environmental (temperature, conductivity, colour, shading, pH, nutrient forms, anions) and morphological (surface area, depth) variables of 70 temperate, forest ponds located in two regions of Hungary on the composition (species- and trait-based) and diversity (traditional and functional) of their benthic diatom communities. Based on the multivariate analyses, no regional differences in the environmental and morphological variables were observed among the ponds. Our results showed that both environmental variables and lake morphology had significant effects on the benthic diatom communities, but they contributed to their variation with different proportions. Environmental variables such as nutrient content ($r_{\text{soluble reactive phosphate}} = 0.72$) and conductivity ($r = 0.65$) affected mostly the species composition, and the traditional diversity metrics ($r_{\text{total phosphate}} = -0.42$, $r_{\text{conductivity}} = -0.54$). In contrast, morphological features of the ponds were the most important drivers of diatom trait composition. This functional response of diatoms manifested in the selection of species according to their size, shape and lifeforms, moreover, in changing of functional diversity. Overall, this study revealed the complex interplay between environmental variables and lake morphology in shaping the composition of benthic diatom communities. Furthermore, it highlights the necessity to apply different methods to understand the ecology and functioning of these special aquatic ecosystems.

1. Introduction

Small lakes are the most prevalent freshwater ecosystems on Earth. They offer favorable conditions for various aquatic organisms either microscopic or macroscopic (Bolgovics et al., 2019) thus providing an unusually high biodiversity relative to their size (Biggs et al., 2017; Fehlinger et al., 2022). Moreover, they contribute substantially to aquatic-terrestrial coupling of matter- and energy transport by providing breeding sites for amphibians and drinking water for terrestrial birds

and mammals. These lakes cover approximately 1% of the land areas (Dudgeon et al., 2006), and they are among the most threatened ecosystems worldwide (Eliasz-Kowalska and Wojtal, 2020) due to nutrient enrichment, forestry practices, agricultural pressure and climate change. However, their ecological status is affected not only by anthropogenic factors (e.g. climate change; Morandín-Ahuerma et al., 2019; Ognjanova-Rumenova et al., 2019) but also by the morphology of the lake (Huang et al., 2014). Morphometric characteristics (e.g., surface area, depth, submersed and emergent vegetation cover) of ponds differ

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significantly from bigger lakes (Richardson et al., 2022), which can directly change limnological and metabolic processes (Staeher et al., 2012) and indirectly their biotic associations both compositionally and functionally (Moses et al., 2011). Therefore, separating and analyzing ponds independently from lakes and wetlands is important from both ecological and management perspectives (Richardson et al., 2022). Nevertheless, our ecological knowledge about these unique aquatic ecosystems has been obviously limited compared to bigger, permanent lakes. Although, there is a number of studies about forest lakes from the boreal regions already from 1980's, especially from Finland and Russia focusing mainly on their chemical properties (e.g. Vuorenmaa et al., 2006), fish (e.g. Olin et al., 2012), phytoplankton (e.g. Arvola, 1986) and macroinvertebrate (e.g. Flenner and Sahlén, 2008) communities, studies from the temperate region or the tropics - where forest ponds are characteristic elements of mountainous areas with their shallow water depth, small surface area and brownish color - are definitely scarce (from Polish forest lakes: Celewicz-Goldyn et al., 2017; Spyra, 2017; Bohemian forest lakes: Vrba et al., 2016; Nedbalová et al., 2006; Danish forest lakes: Sand-Jensen and Staeher, 2009; Martinsen et al., 2020; rainforest lakes of Chile and Canada: Douglas et al., 2022). However, their protection and preservation based on relevant ecological information would be crucial and more and more urgent, especially because of their sensitive hydrological balance in the context of climate change (Korytowski and Szafranski, 2008).

These small lake ecosystems, like ponds, have a high potential for development of benthic algae (Wetzel, 1983; 2001), which among diatoms can dominate and play an important role as primary producers and food sources for higher trophic levels (Kireta et al., 2012, Celewicz-Goodyn and Kuczyńska-Kippen, 2018). Because of their short generation time (Cattaneo et al., 2004), they can be used as excellent bioindicators of environmental changes (Blanco et al., 2008; Tan et al., 2017; Kock et al., 2019), such as acidity (Korhola et al., 1999), nutrient load (Winter and Duthie, 2000) or climatic factors (e.g., temperature, precipitation, and water intermittence; Rühland et al., 2015; Pajunen et al., 2017, B-Béres et al., 2022). Classification of diatom taxa into guilds (Passy, 2007, Rimet and Bouchez, 2012) has revolutionized the diatom ecological studies in discovering the relationship between diatoms and environmental factors (e.g., Berthon et al., 2011, Rimet and Bouchez, 2012; Stenger-Kovács et al., 2013). Moreover, not only the guilds but also easily measurable traits of diatoms (like e.g. cell size) are related to changing environmental factors (e.g., nutrition availability, organic contamination, shear stress, conductivity, Berthon et al., 2011; Lange et al., 2016; Soininen et al., 2016; Tapolczai et al., 2017; Stenger-Kovács et al., 2018; B-Béres et al., 2017). The combination of guilds and traits as eco-morphological groups (B-Béres et al., 2016) proved to be a useful method in functional analyses (Stenger-Kovács et al., 2018, 2020a) to follow and understand the ecological and evolutionary processes. Use of functional diversity metrics (He et al., 2015) provides a further potential tool to discover ecosystem responses to environmental changes (Péru and Dolédec, 2010; Stenger-Kovács et al., 2020b) or to predict ecological stability of the ecosystems (Schneider et al., 2017). However, functional diversity indices based on guild and traits have been rarely applied predictors of environmental variables in aquatic ecosystems (Ding et al., 2017), especially in case of primary producers (Kale and Karthick, 2015; Letáková et al., 2018) like benthic algal communities (Török et al., 2016; Stenger-Kovács et al., 2020b).

Therefore, this study was aimed at the separate analyses of temperate, humic forest ponds to investigate their environmental (physical and chemical variables of the water) and morphological (water depth and surface area) variables as well as their diatom assemblages in two different regions of Hungary. Our main question was whether morphological variables are relevant factors beside the environmental variables, moreover, if they can have a key role in the structure and function of the diatom communities of small ponds. Therefore, we have targeted to reveal the main constraints that significantly affect diatom species-, guild-, and trait composition, furthermore, traditional and

functional diversity indices and finally to determine the pure and shared effects of the environmental and morphological variables on diatom communities.

2. Material and methods

2.1. Study area

Hungary is located in Central Europe with an area of 93,030 km². It measures about 250 km in the north-south and 524 km in the east-west. The climate of Hungary is continental, warm to hot in summer and cold in winter. Because of climate change, the number of hot days increased especially in the central and southern regions (Uzzoli et al., 2018), furthermore, the number of frost days decreased in the country (Mike and Lakatos, 2009). Summer air temperatures range from 27 to 35 °C, and winter temperatures from 0 to -15 °C. The annual rainfall average is approximately 600 mm (Kovács and Jakab, 2021). Brownish, forest lakes can be found mainly in two parts of the country: the Transdanubia Central Highlands (TD) and the Northern Highlands (NH). These closed-basin, forest ponds are very shallow (their mean depth is ~ 30 cm), they have a small surface area (mean: 690 m²) and most of them dry up during summers regularly. Their brownish colour is due to their high humic acid content originating from allochthon sources (high amount leaf litter from the surrounding deciduous forests).

2.2. Physical and chemical variables of the ponds

Between 2014 and 2018 a total of 70 small lakes were investigated in two regions (TD and NH) of Hungary (Fig. 1). Water and phyto-benthos samples were collected in the spring (March-April) and autumn (October-November). Water temperature, pH and conductivity were measured in situ using a Hach Lange HQD4 portable multimeter in addition to shading. In parallel, water samples were collected for physical and chemical analysis at each sampling site. Nutrient forms (NO₃⁻, NO₂⁻, NH₄⁺, TP, and SRP), anions (Cl⁻, SO₄²⁻ and HCO₃⁻), COD (chemical oxygen demand), and Pt colour were determined by titrimetric and spectrophotometric methods according to international standards (APHA, 1998; Wetzel and Likens, 2000). Morphological variables like surface area and depth of the lakes were also measured in the field.

2.3. Diatom sampling, preparation, and analyses

Diatom samples were collected by toothbrush from the characteristic substrates (macrophytes or mud) of the lakes following the recommendations of King et al. (2006). The sampling frequency depended on the water supply of the ponds. Diatom samples were preserved in ethanol until their oxidation treatment with the hot hydrogen-peroxide (CEN, 2003). Diatom valves were identified to species level under light microscopy (Zeiss, Axio A1) at 1000× magnification using immersion oil (Zeiss, 518 N) and applying international taxonomic guides (Krammer and Lange-Bertalot, 1991; Lange-Bertalot et al., 2017; Stenger-Kovács and Lengyel, 2015; Lange-Bertalot and Metzeltin, 1996a, 1996b; Bey and Ector, 2013). At least 400 valves were counted on each slide, and the relative abundance of the species was determined. Species were categorized into different ecological groups like guilds and traits categories: i) four diatom guilds (L – low profile, H – high profile, M – motile, and P – planktic guilds, Passy, 2007; Rimet and Bouchez, 2012); (ii) six groups of the length/width ratio (LW, Tapolczai et al., 2017); (iii) five categories of the biovolume (BV, Berthon et al., 2011); and (iv) the combination (35) of these traits as ecomorphological groups (B-Béres et al., 2016; Table 1).

Traditional diversity indices like species number and Shannon diversity (Shannon & Weaver, 1949) were calculated, furthermore, based on the ecological groups, components of functional diversity indices were also calculated: “FDiv” functional divergence, “FEve” functional

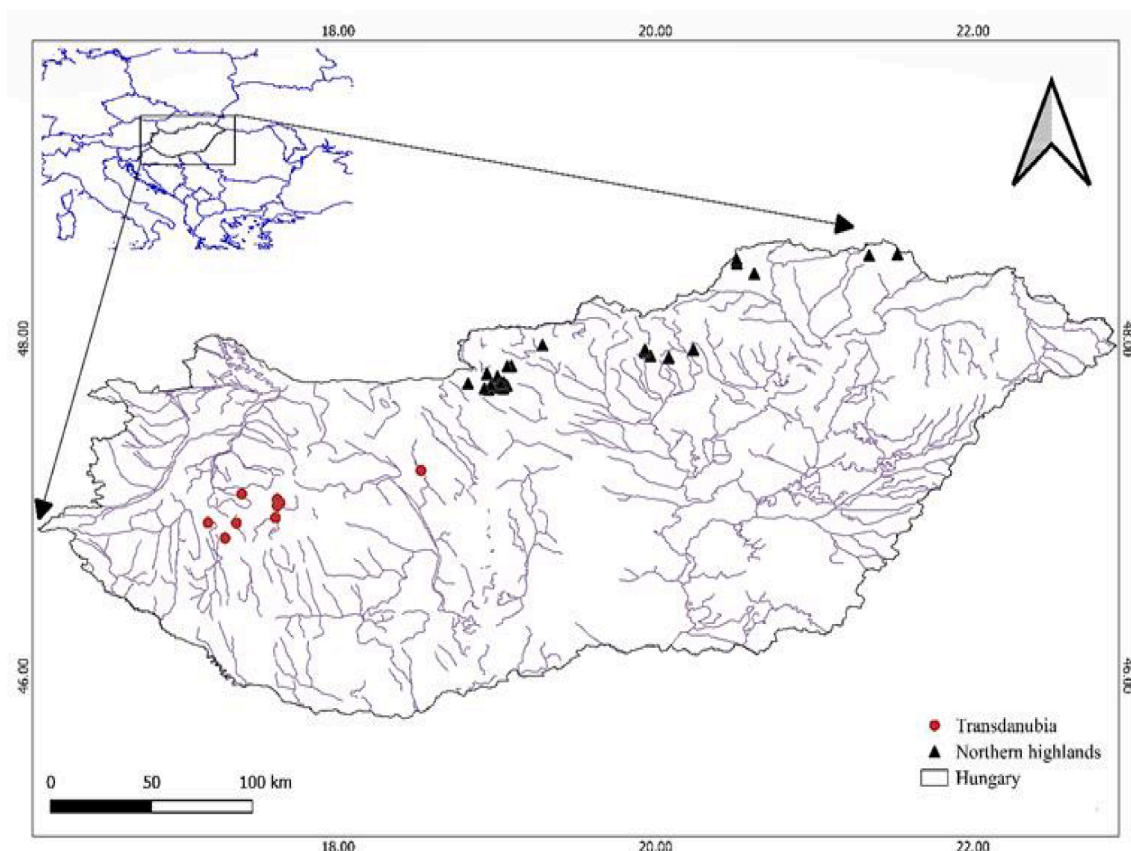


Fig. 1. Map of the study area and the location of sampling used for analysis.

Table 1
The applied guilds and traits.

Guilds	Biovolume	Length-width ratio	Combined ecomorphological groups
High profile (H)	$BV1 < 100 \mu\text{m}^3$	$LW1 < 2$	HBV1, HBV2, HBV3, HBV4, HBV5
Motile (M)	$100 \mu\text{m}^3 \leq BV2 < 300 \mu\text{m}^3$	$2 \leq LW2 < 4$	HLW2, HLW3, HLW4, HLW5, HLW6
Low profile (L)	$300 \mu\text{m}^3 \leq BV3 < 600 \mu\text{m}^3$	$4 \leq LW3 < 6$	LBV1, LBV2, LBV3, LBV4, LBV5
Planktic (P)	$600 \mu\text{m}^3 \leq BV4 < 1500 \mu\text{m}^3$	$6 \leq LW3 < 12$	LLW1, LLW2, LLW3, LLW4
	$BV5 \leq 1500 \mu\text{m}^3$	$12 \leq LW4 < 20$	MBV1, MBV2, MBV3, MBV4, MBV5
		$LW6 \leq 20$	MLW1, MLW2, MLW3, MLW4, MLW5
			PBV3, PBV4, PBV5
			PLW1, PLW2, PLW6

evenness, “Fric” functional richness, “FGR” functional group richness and “RaoQ” Rao’s quadratic entropy’s using the “FD” package (Laliberté and Legendre, 2010) of the R software. For further analyses the species and trait abundances as well as the traditional and functional diversity indices were Hellinger transformed.

2.4. Statistical analyses

All of the statistical analyses and graphical displays were conducted with R software (version 4.1.2, R Core Team, 2021) under the “vegan” package (Oksanen et al., 2019). Normal distribution of the physical and chemical variables was checked by Shapiro–Wilk test. Log-transformation ($\log(x + 1)$) was applied for SRP, depth, conductivity, and shading while square root transformation for NO_2^- , Cl^- , and TP. No

transformation was used for shading and temperature (Table 2). NO_3^- and NH_4^+ were excluded from the statistical analyses, because they were under the analytical detection limit in most of the samples. The regional differences in the individual environmental and morphological variables of the ponds were tested using Welch test.

Non-metric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity and permutation ($n = 999$) was applied to study regional differences (TD and NH) among the samples based on the environmental and morphological variables collectively, species and trait (individual and combined traits) compositions, traditional and functional diversity indices. NMDS analyses were run with the “metaMDS” (McCune and Grace, 2002) package in R software. We applied a PERMANOVA test (Anderson, 2001) to check the significance of the NMDS models (number of permutations = 999).

We used redundancy analysis (RDA) to reveal the relationship between the environmental and morphological properties of the ponds and the species- and trait (individual and combined traits) composition, traditional and functional diversity indices. Forward selection procedure devised by Blanchet et al. (2008) was used to select the master variables. “Ordistep” test (Blanchet et al., 2008) was applied to check the significance of the RDA models (number of permutations = 999).

Variance partitioning analyses were performed using the function “varpart” (Legendre and Legendre, 2012) to evaluate the pure and shared effect of the environmental and the morphological variables of the ponds on the diatom communities (species and trait composition, traditional and functional diversity indices). The adjusted R^2 was computed to provide unbiased estimates of the explained fractions of variance. The significance levels of the variance partitioning analyses were tested by ANOVA (number of permutations = 999).

Table 2

Mean and ranges of the environmental and morphological variables of the brownish, forest ponds in the two, studied regions of Hungary and their differences according to Welch test (bold = significant difference, DL – under detection limit).

Environmental and morphological variables	Unit	Transformation	Transdanubian Central Highlands (TD) (n = 17)		Northern highlands (NH) (n = 53)		Welch test p-value
			Min - Max	Mean	Min - Max	Mean	
			Surface area	m ²	Y = ln(X + 1)	16–3533	
Depth	cm	Y = ln(X + 1)	10–60	21.0	8.0–60	32	0.02
Shading	%	–	10–100	70	100	29	0.001
Temperature	°C	–	8.3–22.6	15.2	9.2–24.5	16.0	0.53
pH	–	–	5.5–7.8	6.8	5.8–8.1	6.8	0.65
Conductivity	µS cm ⁻¹	Y = ln(X + 1)	76–1027	189	5–1653	187	0.07
Cl⁻	mg L ⁻¹	Y = (X) ^{0.5}	DL – 95	8.0	DL- 499.8	22.8	0.13
HCO₃⁻	mg L ⁻¹	“boxcox” function	21.4–374.5	107.8	9.2–563.6	100	<0.001
COD	mg L ⁻¹ O ₂	Y = (X) ^{0.5}	11.3–60.8	30	4.3–81.6	29.7	0.66
TP	µg L ⁻¹	Y = (X) ^{0.5}	59.3–840.0	421.6	58.9–1441.2	451.1	0.81
SRP	µg L ⁻¹	Y = ln(X + 1)	20.8–526.9	194.3	DL-862.3	174.0	0.55
NO₂⁻	µg L ⁻¹	Y = (X) ^{0.5}	0.01–6.1	3.1	DL – 53.5	7.2	0.02
SO₄²⁻	mg L ⁻¹	Y = (X) ^{0.5}	0.6–18.6	10.5	0.5–119.8	25.3	<0.001
Pt colour	mg L ⁻¹ Pt	Y = (X) ^{0.5}	74.5–338.8	207.3	36.7–762.5	204.2	0.52

3. Results

3.1. Environmental and morphological variables of the ponds in the two regions

When we compared the morphological variables of the ponds individually, we found significantly higher ($p = 0.01$) surface area (mean: 748 m²) and depth ($p = 0.02$; mean: 32 cm) in the NH region than in the TD region (surface area: 479 m²; mean: 21 cm). The mean shading was the highest in the TD region (70%), while it was only 29% in the NH region. Based on the Welch test, this difference was also significant ($p = 0.001$). The mean water temperature was generally recorded ≤ 16 °C, and Pt color was also similar (mean: 204 in NH and 207 mg L⁻¹ in TD) in the two regions. The conductivity observed in the regions was very similar (mean: 189 µS cm⁻¹ in TD and 187 µS cm⁻¹ in NH region). The major anion concentration showed a general trend of HCO₃⁻ > SO₄²⁻ > Cl⁻. The average concentration of HCO₃⁻ and SO₄²⁻ were higher (107.8 and 10.5 mg L⁻¹, respectively) in the TD region. The differences in the HCO₃⁻ and SO₄²⁻ concentrations were statistically significant ($p < 0.001$) between the two regions. The mean concentration of Cl⁻ was almost three times higher in the NH region (22.8 mg L⁻¹) than in the TD region (8.0 mg L⁻¹). In case of the nutrients (NO₂⁻, TP and SRP), the mean NO₂⁻ (7.2 µg L⁻¹) and the mean TP (451.1 µg L⁻¹) was also highest in the NH region, while the mean SRP (194.3 µg L⁻¹) was higher in the TD region (Table 2). However, only the differences in the NO₂⁻ concentrations were statistically significant ($p = 0.02$) between the two regions.

3.2. Diatom communities of the ponds

A total of 174 diatom taxa were identified in the 70 phytoenthos samples. The most frequent species were the members of the genera *Nitzschia* (e.g., *Nitzschia palea* (Kützing) W.Smith), *Navicula* (e.g., *Navicula cryptocephala* Kützing), *Eunotia* (e.g., *Eunotia bilunaris* (Ehrenberg) Schaarschmidt), *Pinnularia* (e.g., *Pinnularia obscura* Krasske) and *Gomphonema* (e.g., *Gomphonema exilissimum* (Grunow) Lange-Bertalot & E. Reichardt). Of these, 101 species belonged to the motile guild, 50 to the high-, 17 to the low profile and six to the planktic guild. In terms of the biovolume, 45 species were sorted into BV5, 39 species into BV4, 38 species into BV2, 35 species into BV3 and 17 species into BV1 categories. Furthermore, diatom species were categorized according to the length/width ratio: 62 species into LW3, 53 species into LW4, 40 species into LW2, seven-seven species into LW1 and LW6 and five species into LW5 category. The means of the Shannon diversity and species number were

2.01 ± 0.37 and 17.7 ± 4.75, respectively.

Based on the environmental and morphological factors, species abundances, guilds, traits, ecomorphological groups, and diversity indices, the NMDS analyses demonstrated that there were no regional differences between the lakes (Fig. 2A, B, C, D, E) depending on a PERMANOVA test ($p > 0.1$). The dimensionality of the data was determined with a stress factor < 0.2 (Fig. 2).

3.3. Environmental and morphological constraints on diatoms

In the RDA analyses of the species composition and environmental variables, the explained variance was low (12.3%) for the first two axes (8.2% for the first axis and 4.1 % for the second axis, Fig. 3A) showing that the abundance of species was primarily affected by the environmental variables (Cl⁻, conductivity and TP). Conductivity, Cl⁻ ($r = 0.83$ and $r = 0.65$, respectively) as well as nutrients (TP and NO₂⁻), ($r = -0.47$, $r = -0.41$, respectively) were mainly related to the first axis, while depth and temperature ($r = -0.52$, $r = -0.3$, respectively) to the second axis. The high Cl⁻ content was indicated by *Meridion circulare* (Gréville) C.Agardh [MCIR] and *Gomphonema micropus* Kützing [GMIC], while high conductivity by *Nitzschia alpina* Hustedt [NAZL] On the other hand, *Pinnularia sinistra* Krammer [PSIN], *Gomphonema exilissimum* (Grunow) Lange-Bertalot & E.Reichardt [GEXL], *Eunotia implicata* Nörpel, Alles & Lange-Bertalot [EIMP], and *Pinnularia marchica* I.Schönfelder [PMAR] were related to higher nutrient concentration (TP, NO₂⁻, and SRP). The deeper water depth was correlated positively with the abundance of *Nitzschia palea* (Kützing) W.Smith [NPAL] and negatively with *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot [PTLA] (Fig. 3A).

The RDA analysis of the 15 different individual guilds and traits demonstrated that these ecological groups were mostly affected by the surface area of the ponds (Fig. 3B). Surface area, shading, and temperature ($r = -0.58$, $r = 0.35$, $r = 0.31$, respectively) were the most important variables along the first axis (explained variance 4.3%), while the surface area, NO₂⁻ and depth ($r = -0.49$, $r = -0.41$, $r = -0.36$, respectively) along the second axis (explained variance of 3.4%) The explained variance of the first two axes was low (7.7%). High- and low-profile guilds, large length/width ratio and bigger biovolume (H, L, LW6 and BV5) were positively associated with the surface area and NO₂⁻, while the biovolume BV5 and the planktic guild were correlated negatively to Cl⁻ (Fig. 3B). Small biovolume, larger length/width ratio and the planktic guild (BV1, LW4, P) were positively correlated to water depth, temperature and conductivity. The motile guild and middle

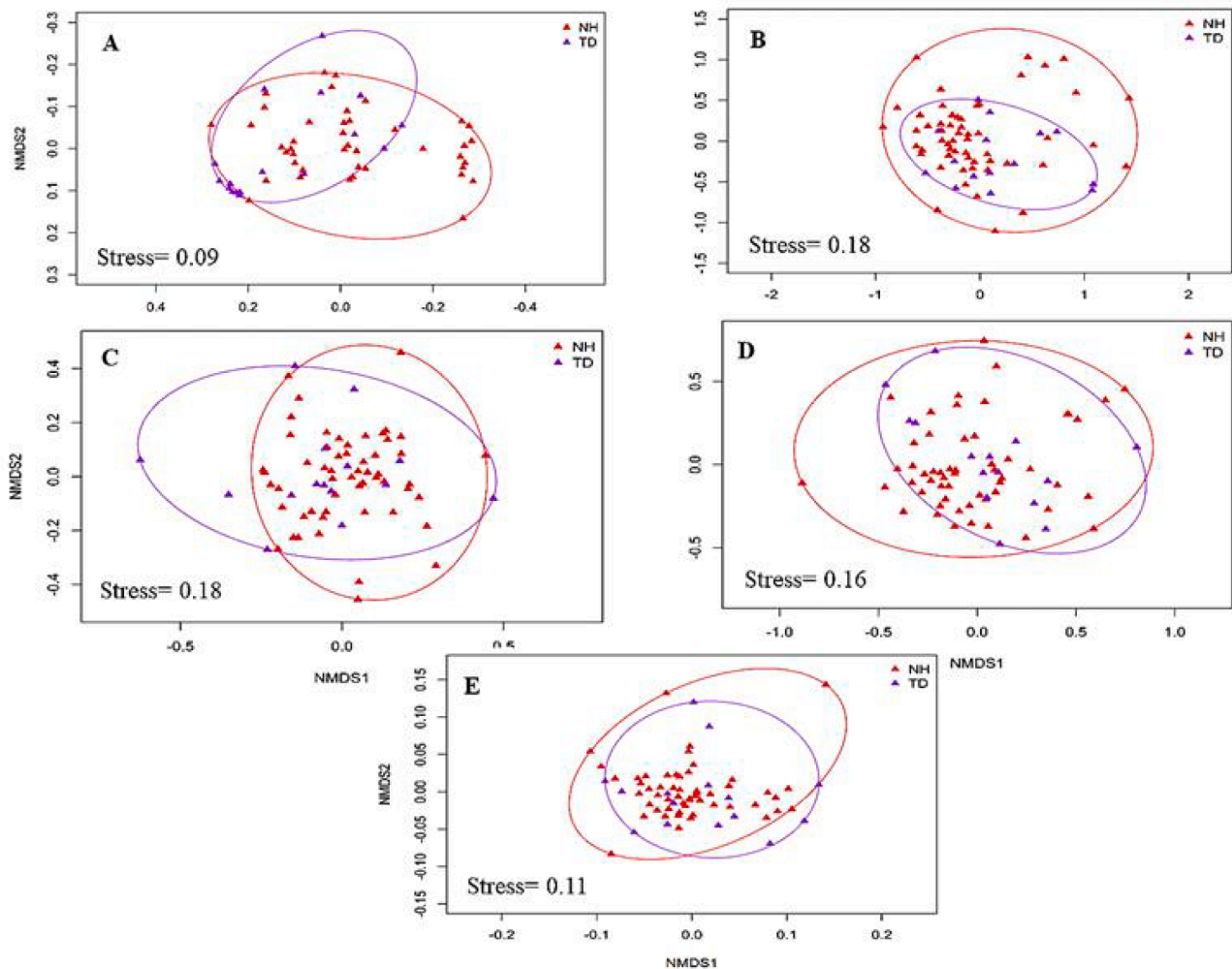


Fig. 2. Non-metric multidimensional scaling (NMDS) plots of the studied ponds based on the (A) environmental and morphological variables, (B) relative abundance of the diatom species (C) relative abundance of the individual diatom guilds and traits, (D) relative abundance of the combined ecological groups and (E) functional diversity indices in both regions (NH: Northern Highlands; TD: Transdanubian Central Highlands).

biovolumes (M and BV3, BV4) indicated the higher shading. Smaller biovolume (BV2) and middle length/width ratio (LW3) correlated positively with P forms.

Based on the combined ecological groups (35 groups) (Fig. 3C), composition along the first axis (explained variance was 7.4%) was strongly determined by conductivity, NO_2^- , TP, and Cl^- ($r = 0.8$, $r = -0.38$, $r = 0.37$, $r = -0.37$, respectively). Along the axis 2 (explained variance was 3%) shading, surface area, and conductivity ($r = 0.45$, $r = 0.45$, $r = 0.31$, respectively) were the most important constraints on the combined groups. HBV2 and MBV3 were correlated positively with conductivity and chloride. HLW3 and MLW4 were positively related to nutrients (TP, SRP, and NO_2^-) and LLW2, MLW3 and LBV5 were positively associated with the temperature. On the other, the higher surface area and shading were indicated by HLW4 (Fig. 3C).

Functional diversity indices were affected both by environmental variables and morphological factors (Fig. 3D). The variance explained by the first two axes was low (6.6%). Functional diversity indices were mostly determined by Cl^- , temperature and NO_2^- ($r = 0.42$, $r = -0.41$, and $r = 0.37$, respectively), along axis 2 (explained variance was 3.4%) by conductivity, Cl^- , surface area and temperature ($r = 0.73$, $r = 0.53$, $r = 0.34$ and $r = 0.32$ respectively). Fig. 3D demonstrated that the FEve showed a negative correlation with all of the measured variables, while FRic, RaoQ, and FDis were positively related to temperature and surface area and negatively to depth, shading, and SRP. FGR was positively related to NO_2^- and TP (Fig. 3D).

Traditional diversity metrics (Shannon index and species number) (Fig. 3E) were mainly affected by surface area and environmental variables like shading, P forms and conductivity. Along axis 1 (explained variance was 11.7%), these diversity metrics were strongly determined by SRP and shading ($r = 0.72$ and $r = 0.52$, respectively). Along axis 2 (explained variance was 0.05%), they were affected by surface area, conductivity, TP and shading ($r = 0.64$, $r = -0.54$, $r = 0.49$, and $r = -0.42$, respectively). The Shannon diversity increased with the enhancing nutrients, Cl^- and shading. The species number was positively affected by temperature, depth and surface area.

3.4. Pure and shared effects of the environmental and morphological variables of ponds on diatoms

Based on the VarPart analyses, we found that the pure effects of the environmental variables on species composition (0.05) and on the traditional diversity metrics (species number and Shannon diversity) (0.08) were higher than the pure effects of the morphological factors (0.01 and 0.02) (Fig. 4A, E). On the other hand, morphological factors (0.06 and 0.07 each) had a greater pure effect on the individual traits and guilds (0.06) and combined ecological groups (0.07) than environmental variables (0.02 and 0.04) (Fig. 4B, C). In case of the functional diversity indices, the environmental variables and morphological factors had a similar pure effect (0.02) (Fig. 4D). The shared effect of the environmental and morphological variables was very low (0.1) or none.

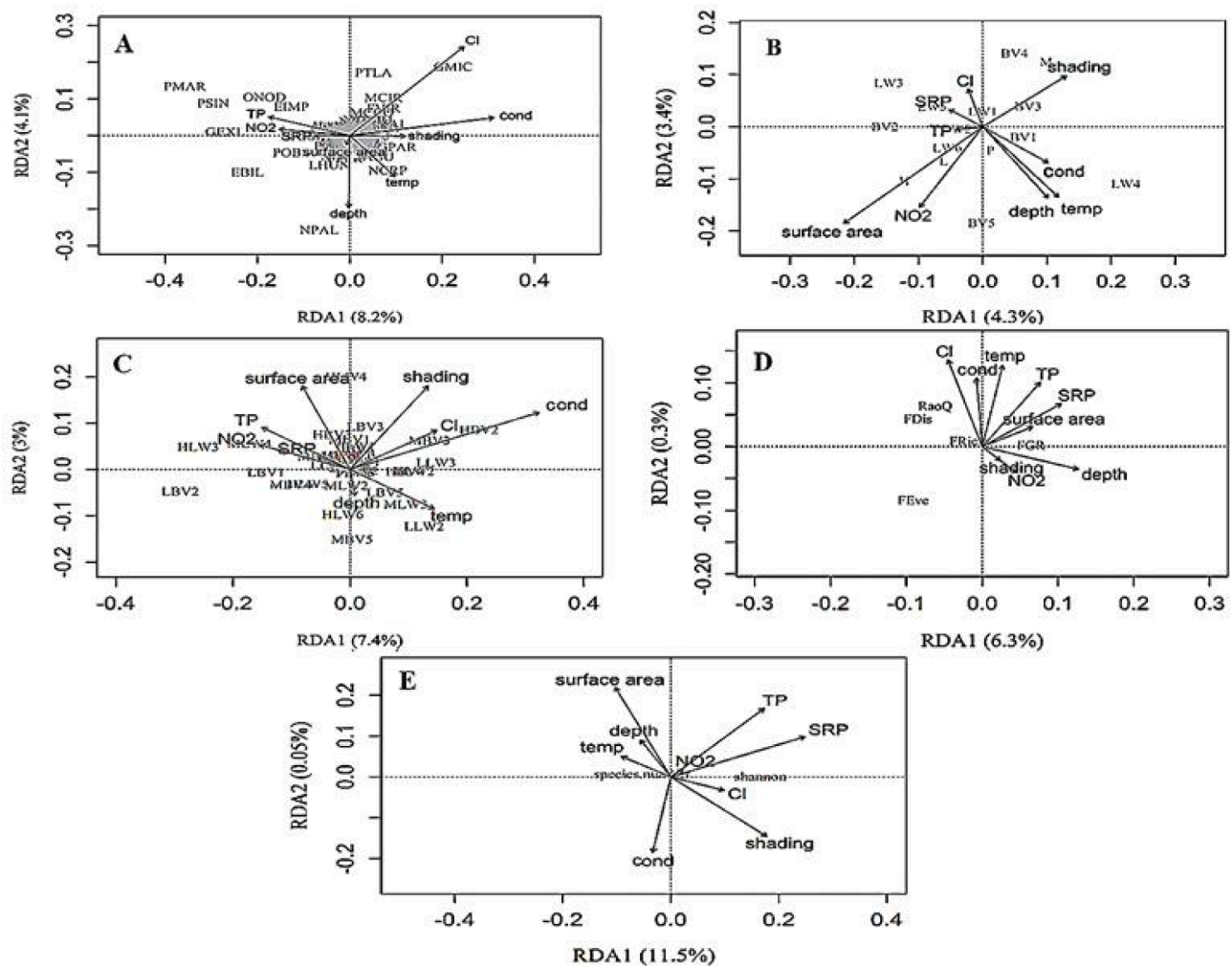


Fig. 3. RDA analysis of the environmental variables and (A) the diatom species composition, (B) the individual traits of diatoms, (C) their combined trait composition (D), functional and (E) traditional diversity metrics in brownish lakes of Hungary.

4. Discussion

Forest lakes of boreal and temperate regions can be generally characterized with a relatively wide range of water depth (1–40 m, Martinsen et al., 2020; Nedbalová et al., 2006), surface area (1–900 ha, Rask and Hiisiuuri, 1985; Hongve et al., 2004) and low nutrient content (e.g., TP: 1.6–12.3 $\mu\text{g l}^{-1}$ in Nedbalová et al., 2006). However, Hungarian closed-basin ponds as important elements of the forest in the Carpathian Basin with seasonal or constant water masses are prominently different in these features. Their maximal surface area is only 0.6 ha, and their maximal water depth is 0.6 m, which is similar to that of the Danish Forest lakes (Sand-Jensen and Staehr, 2009; Martinsen et al., 2020). However, TP concentrations are similarly high in both countries (58.9–1441 $\mu\text{g l}^{-1}$, present study; 128–331 $\mu\text{g l}^{-1}$ in Martinsen et al., 2020) due to the mixed sediment and the considerable leaf litter load (Hubai et al., 2009). The Pt colour of these temperate forest ponds in Hungary (762.5 mg L^{-1}) can exceed the previously published maximal values from the Finish, boreal forest lakes (557 mg L^{-1} , Olin et al., 2010). The pH of the forest lakes is characteristically acidic (e.g. Thies, 1991; Johansson, 1983) with sometimes extreme values (pH < 2, Von Einem and Granéli, 2010), but can move forward to the neutral and alkaline range (e.g., Holopainen et al., 2008) as it was experienced in the studied temperate ponds.

4.1. Regional differences

In general, the increasing distance between lakes can result in pronounced difference in water chemistry (e.g., Kling et al., 2000) and morphological features. Despite the two regions are quite distinct in view of their relief, structure and rock formations (Halmos et al., 2005), only some regional differences were detected when the individual environmental and morphological variables were compared separately. Ponds in the TD region are smaller both in size and in depth, which features can play an important role in the annual hydrological cycle. Smaller water bodies are characterized by fewer hydrological phases than bigger ones, which influences the chemical and physical properties and the biota of the lakes, as was observed in soda pans of the Carpathian Basin (Lengyel et al., 2019).

Furthermore, the ponds located in the TD region are more shaded by the surrounding forests similar to a subtropical reservoir, where the direct effect of macrophytic (*Pistia stratiotes*) cover on the periphytic diatom communities was shown (de Faria et al., 2013). The available light regime determined by shading and water depth is a key environmental factor controlling ecophysiological processes (Falkowski and LaRoche, 1991; Kirk, 1994; MacIntyre et al., 2002) and it can have influence on many environmental factors such as pH, O_2 and nutrient availability (Mallin and Paerl, 1992; Wetzel, 2001; Coops et al., 2003; Cardoso et al., 2017). For example, a forested catchment reduces light input and provides easily accessible dissolved nutrients to species in

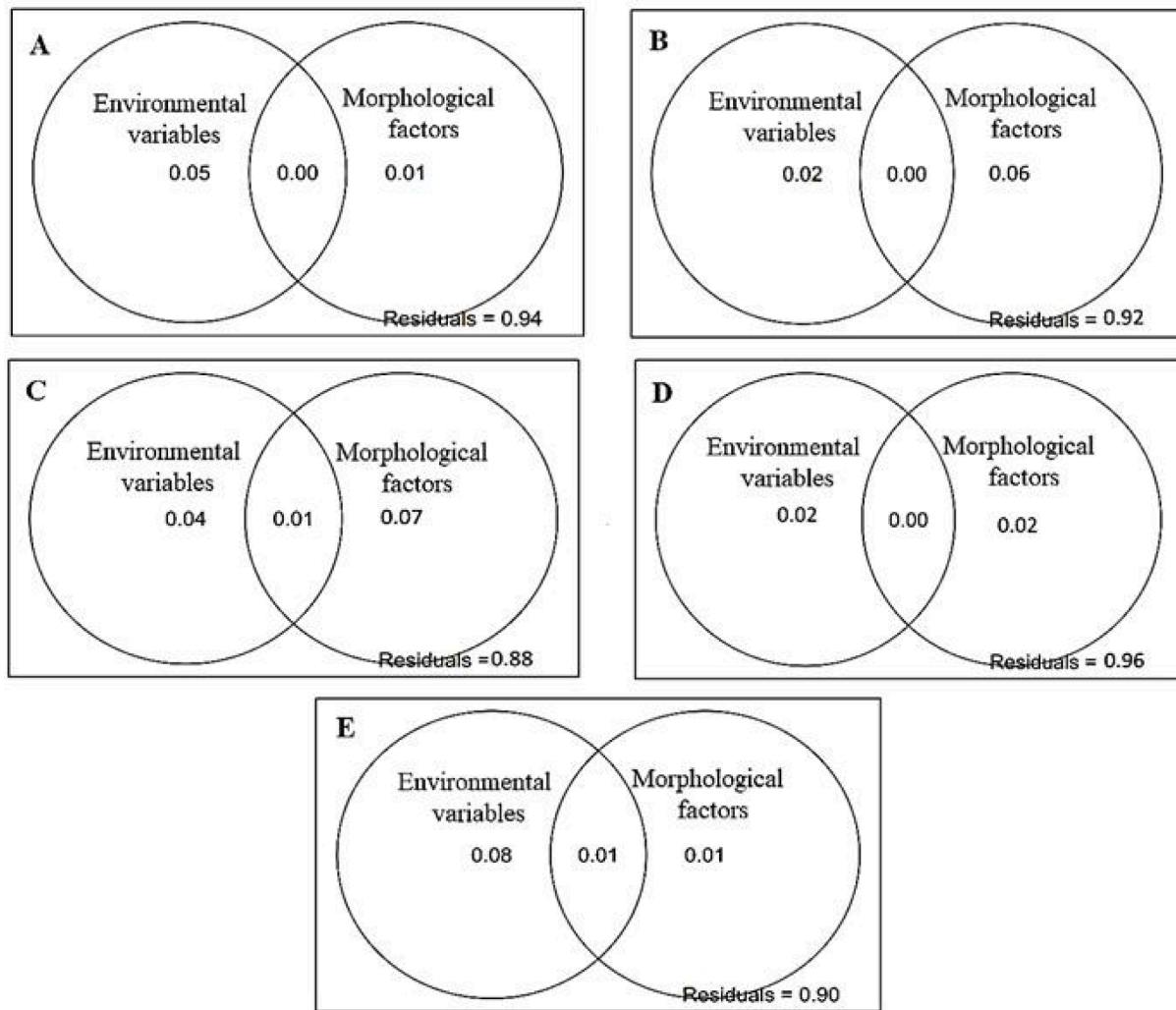


Fig. 4. Partitioning of variation in case of (A) diatom species composition, (B) their individual traits composition (C), their combined trait composition, (D) functional and (E) traditional diversity metrics between the two groups of the explanatory variables.

small lentic ecosystems (Sand-Jensen and Staehr, 2009).

The dominance of HCO_3^- was characteristic for both regions, but its concentration was significantly higher in the TD region, because of their depression in basalt bedrock with limestone windows (Lengyel et al., 2015). The anion concentration in term of SO_4^{2-} was low in both regions (mean: $\leq 25.3 \text{ mg L}^{-1}$), however, it was substantially higher in NH regions, where more gypsum-anhydrite deposits can be found (Hahn et al., 1998), which may explain the higher sulphate content of the lakes found here. In these forest ponds NO_2^- was the dominant N form and it was generally low in both regions (mean: $\leq 7.2 \mu\text{g L}^{-1}$) but was significantly lower in TD regions. The other nitrogen forms were under detection limit in most cases, because nitrification can require high dissolved oxygen content, thus it can contribute to the anoxic condition resulted in the accumulation of NO_2^- as intermediate product (Wetzel, 2001).

Nevertheless, when all parameters were analyzed together, regional differences disappeared in case of environmental and morphological variables as well as the community structural characteristics of the ponds. Despite some apparent environmental and morphological differences between the regions, the characteristics and the diatom compositions of the ponds in the DT region were embedded among the lakes of the NH region.

4.2. Lake morphological constraints on diatoms

Morphological features of lakes, like the size (surface area), have a significant influence on the diatom composition and diversity (Rimet et al., 2015; Bolgovics et al., 2019). Several studies (Bolgovics et al., 2019; Várbró et al., 2017) found that species richness of phytoplankton and benthic diatoms increases with the size of the water body, similarly to macroinvertebrate communities (Zenker and Baier, 2009) along this gradient. In forest ponds of this study, benthic diatom diversity was positively associated with surface area supporting the earlier observation on a wide range of lake sizes ($10^{-2} - 10^7 \text{ m}^2$; Bolgovics et al., 2019; Várbró et al., 2017). Our study also revealed that the water depth of the forest ponds has a significant effect on diatom species composition similar to South European shallow lakes (Rodríguez-Alcalá et al., 2020). Accordingly, deeper water resulted mainly in a higher abundance of *Nitzschia palea*, and a loss of *Planothidium lanceolatum*. The former observation is at issue in the literature, since *Nitzschia palea* is often found as the dominant taxon in rather shallow ecosystems (e.g., Riato and Leira, 2020; Stenger-Kovács and Lengyel, 2015). These opposing observations require further ecophysiological research. However, the correlation of *Planothidium lanceolatum* with depth was already known from paleolimnological studies (e.g., Sterken et al., 2012).

The single trait and guild composition, as well as combined traits were significantly affected by the surface area and water depth of ponds.

Small biovolume, a larger length/width ratio and the planktic guild (BV1, LW4, P) were positively correlated with water depth. In contrast, high- and low-profile guilds with medium size and medium length/width ratio (e.g. HLW3, LVB3) were shown to be negatively associated with depth. With the increasing lake depth decreasing light availability is typical in lakes (Coops et al., 2003; Cardoso et al., 2017). Under such circumstances small-sized taxa are favored. They can survive in reduced light environments (Stenger-Kovács et al., 2013; B-Béres et al., 2016; Lukács et al., 2018) because they are able to use light more efficiently (Kirk, 1994). The elongated cells (higher length/width ratio) can serve as light trap similar to observations in inorganically turbid environments (Stenger-Kovács et al., 2020a). The dominance of planktic species in the benthic community indicates well the larger water body, where their life form is more pronounced (Wang et al., 2018). With the decreasing of the water depth, a size- and shape modification of the taxa can be observed in the community. The medium cell size and the less elongated shape can be a response to the increased light. The reduced functional diversity can also indicate higher water depth (Longhi and Beisner, 2010), responding to the less favorable light and life conditions, where only the well-adapted species with well-selected traits, as ecological uniqueness (Coops et al., 2003) can survive.

A number of traits (H, L, LW6, BV5, HLW3, HBV3, LVB3) and functional diversity were found to be positively associated with the surface area which trend was also found in phytoplankton of Canadian lakes (Longhi and Beisner, 2010). Bigger lakes can offer more heterogeneous, complex habitats, and more possibilities to develop a diverse diatom community in their appearance as it was noticed also in the species number (Bolgovics et al., 2019), which results in co-occurrence of environmentally different species due to the better resource partitioning (e.g., Schoener, 1974; Bradford and Kastendick, 2010).

These results unequivocally highlight that water depth and lake size have important effects on the ecology and functioning of the ecosystems (Coops et al., 2003), even in very small ponds within a small scale of water depth (8–60 cm) and surface area (16–6359 m²).

4.3. Environmental constraints on diatoms

Environmental filtering is the most important structuring process (Jovanovska et al., 2022), which influences diatom composition on local, regional (Wang et al., 2022) or even global scale (Soininen et al., 2016; Rodríguez-Alcalá et al., 2020). In forest ponds, species composition and species diversity were especially explained by conductivity and nutrients, which variables are well-known constraints on diatoms of bigger freshwater lakes (e.g., Kovács et al., 2006; Ognjanova-Rumenova et al., 2009; Dell' uomo and Torrisi, 2011). At a European scale, Rodríguez-Alcalá et al. (2020) found that nutrient content is the main driver in the northern, while conductivity in southern lakes. In our forest ponds *Pinnularia marchica* (PMAR) and *Eunotia implicata* (EIMP) were characteristic preferring the low conductivity, slightly acidic water with low nutrient concentration (Luís et al., 2011; Şahin and Baranova, 2022).

Regarding the single as well as combined traits and guilds, shading, temperature and nutrients were generally the most determinant environmental parameters in forest ponds. Especially, the high-profile guild was negatively related to shading, since this guild by its position in the benthic layer prefers higher light intensity (Passy, 2007). In more shaded ponds dominance of small-size cells (BV1) and motile guild (M) were dominant similarly as in saline ponds (Ács et al., 2019) and freshwater streams (Lange et al., 2016). Their motility makes it possible to select the most suitable habitat and to avoid stress conditions set by the shaded environment (Ács et al., 2019). On the other hand, the medium length/width ratio of high-profile and motile taxa (HLW3, MLW4) was related positively to nutrients. This is supported the earlier observations highlighting the strong correlation of the motile guild with the elevated nutrient concentrations (Passy, 2007; Berthon et al., 2011). On the other hand, the temperature had an impact on all the three diatom ecological guilds, with the motile group being particularly affected

negatively by cold water temperatures (Stenger-Kovács et al., 2013), which supported our results. There seems to be some indication that diatom cells may increase in size when exposed to colder temperatures, but it is unclear whether this applies universally across all species (Soininen and Teittinen, 2019; Svensson et al., 2014).

All of the functional diversity indices were strongly correlated with several environmental variables of the forest ponds, such as with conductivity, temperature and Cl⁻. Functional diversity indices have already been considered as especially sensitive to conductivity and temperature in soda pans (Stenger-Kovács et al., 2019) and in rock pools (Aarnio and Soininen, 2021). Functional diversity indices are successful in revealing complex environmental interactions in communities due to their robustness and ability to identify interspecific environmental adaptations (Cadotte et al., 2011). However, some indices like FEve had no relationship with the local environment in similarly to different kinds of other types of aquatic ecosystems (e.g. saline ponds, Stenger-Kovács et al., 2020; in tropical headwater streams, Taniwaki et al., 2019), which points out that their selection and application must be carried out with care.

4.4. Variation partitioning of diatoms

Environment variables had the strongest pure effect on species composition and traditional diversity metrics (Shannon index and species number) similarly to European lakes where local abiotic factors override spatial effects (Rodríguez-Alcalá et al., 2020) and thus are considered as main controllers of diatom composition (Rimet et al., 2019). The great role of the environmental variables on functional diversity metrics has already been highlighted since these trait-based indices can provide more relevant information regarding environmental variables than the species-based taxonomical indices (e.g., Wang et al., 2022; Wu et al., 2019; Soininen et al., 2016; Teittinen et al., 2018; Stenger-Kovács et al., 2020b). However, in our study, the variance in functional diversity indices is explained by both environmental variables and morphological features of the forest ponds at the same extent. This means that lake morphology can be an as important factor as the water chemical features of lakes, or that either the individual and combined trait composition of benthic diatoms provide a clear functional response to the lake morphology.

5. Conclusion

In temperate forest ponds species-based community response is more pronounced to the environmental variables (mostly to conductivity and nutrients) than the morphological ones, while lake morphology clearly triggers a functional response even on a small scale. Namely, benthic diatom communities and functional diversity change along the gradient of water depth and surface area by the selection of well-adapted species in size, shape and lifeforms due to the changing light regime and habitat heterogeneity. Our study underscores the fact that different methodologies cannot substitute each other, since both approaches provide distinct, unique insights and valuable information from ecological, conservation and management perspectives. Therefore, using a combination of these approaches can be crucial in maintaining these special aquatic habitats.

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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

The authors do not have permission to share data.

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