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TRAIT-BASED APPROACHES IN FRESHWATER BENTHIC MICROALGAE COMMUNITIES

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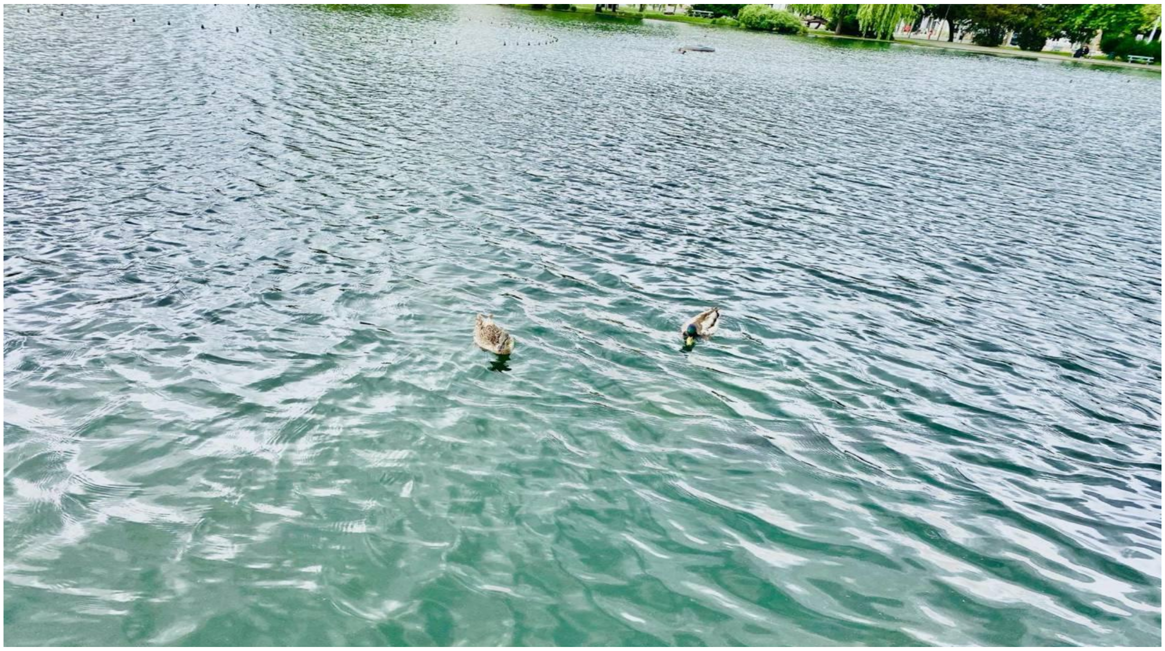

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TRAIT-BASED APPROACHES IN FRESHWATER BENTHIC MICROALGAE COMMUNITIES

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List of abbreviations and terms

Chl a	Chlorophyll a content
Cl^-	Chloride
COD	Chemical oxygen demand
F_V/F_M	The maximum quantum yield
HCO_3^-	Bicarbonate
NH	Northern highlands
NMDS	Non-metric multidimensional scaling
NO_2^-	Nitrite
Pt colour	Intensity of the brown colour in platinum unit
RDA	Redundancy Analysis
SO_4^{2-}	Sulphates
SRP	Soluble Reactive Phosphorous
SSPs	Shared Socioeconomic Pathways
TD	Transdanubian Central Highlands
Temp	Water Temperature
TP	Total Phosphorus

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Abstract

Global surface waters are threatened by anthropogenic activities and climate change. These, in turn, have a major effect on their phytobenthos communities dominated in shallow aquatic ecosystems. To discover the effect of the rising water temperature, as well as increasing salinity in surface waters on the benthic algal communities is a key task. However, not only the environmental factors, but also the natural, morphological features of lakes can have a significant effect on these organisms but how, is a crucial question of ecology. Therefore, I examined the effects of environmental (temperature, conductivity, Pt color, shading, pH, nutrient forms, anions) and morphological (surface area, depth) variables on the composition (species- and trait-based) and diversity (traditional and functional) of benthic diatom communities in temperate forest ponds in two regions of Hungary. I found that environmental factors (nutrient content and conductivity) mostly affected the species composition and traditional diversity metrics. However, diatom trait composition was mostly driven by pond morphology. Diatoms' functional response was to select species by size, shape, and lifeforms that led to change in functional diversity (**Chapter I.**)

An outdoor mesocosm system was used to study the impact of two climate change scenarios (SSP2-4.5 and SSP5-8.5, intermediate and high emission scenarios) on the structure and function of the phytobenthos communities using species- and trait-based approaches. I found that the predicted 3°C temperature increase will have a significant impact on benthic algal communities by altering species and trait composition, decreasing Shannon diversity, and increasing community variability. An even higher temperature (+5 ˚C) predicted by more pessimistic scenarios will lead to drastical changes in freshwater phytobenthos, including: (1) significant compositional alterations at the phylum level (dominance of Cyanobacteria and Chlorophyta exclusions of Bacillariophyta); (2) a shift in trait composition (benefits for smaller cell volume, filamentous life-forms, non-motile and weakly attached taxa); and (3) further reduction in phylum diversity. In

conclusion, the intermediate emission scenario has considerable biodiversity risks, whereas the high emission scenario poses severe consequences on benthic algae, threatening ecosystem function (**Chapter II**.).

To understand the salinity-induced morphological alterations of diatoms, I gathered the existing knowledge. Salinization is one of the major environmental concerns of the Anthropocene that affects aquatic habitats. Studies highlight that salt stress may considerably impact on the morphological features of diatoms. Abnormal forms show the intense and complex effects of salinity and collateral variables. (**Chapter III.**).

الخلاصة

تتعرض المياه السطحية العالمية للتهديد بسبب الأنشطة البشرية وتغير المناخ. وهذه بدورها تؤثر تأثيراً كبيراً على المجتمعات النباتية القاعية التي تهيمن عليها النظم الإيكولوجية المائية الضحلة. ومن المهام الرئيسية في هذا الصدد اكتشاف أثر ارتفاع درجة حرارة المياه، فضلاً عن زيادة الملوحة في المياه السطحية على المجتمعات الطحالب القاعية. ولكن ليس فقط العوامل البيئية، بل أيضا الخصائص الطبيعية والمورفولوجية للبحيرات يمكن أن يكون لها تأثير كبير على هذه الكائنات الحية ، بل أيضا كيف ، انها مسألة حيوية تتعلق بالبيئة. ولذلك، قمت بفحص تأثيرات المتغيرات البيئية (درجة الحرارة، والموصلية، اللون، التظليل، درجة الحموضة، أشكال المغذية، والأيونات) بالإضافة إلى التغيرات المورفولوجية (المساحة السطحية، والعمق) على التركيب (على أساس الأنواع و السمات) والتنوع (التقليدي والوظيفي) لمجتمعات الدياتوم القاعية في برك الغابات المعتدلة في منطقتين من هنغاريا. ووجدت أن العوامل البيئية (محتوى المغذيات الغذائية و موصليتها) أثرت في الغالب على تكوين الأنواع ومقاييس التنوع التقليدية. ومع ذلك، فإن تركيبة خصائص الدياتوم كانت في الغالب مدفوعة بمورفولوجيا البركة. وكانت الاستجابة الوظيفية لهذه الكائنات اختيار الأنواع حسب الحجم والشكل وأشكال الحياة وتغيير التنوع الوظيفي (الفصل الأول).

تم استخدام نظام لتمثيل المتوسط الخارجي(mesocosm) لدراسة تأثير سيناريوهين لتغير المناخ ((SSP2-4.5 and 8.5-5SSP, سيناريوهات الانبعاثات الوسيطة والعالية) على هيكل ووظائف مجتمعات النباتات القاعية باستخدام الأساليب القائمة على الأنواع والسمات. وجدت أن الزيادة المتوقعة في درجة حرارة 3 درجات مئوية سيكون لها تأثير كبير على مجتمعات الطحالب القاعية من خلال تغيير الأنواع وتكوين الصفات، وتناقص تنوع شانون(Shannon diversity)، وزيادة التنوع المجتمعي. وأن ارتفاع درجة الحرارة المتوقع بسيناريوهات (5 درجات مئوية) أكثر تشاؤماً أن يؤدي إلى تغيرات جذرية في نباتات المياه العذبة، بما في ذلك ما يلي: (1) التغيرات الكبيرة في التركيب على مستوى الشعبة (هيمنة البكتيريا الزرقاء والكلوروفيتا باستثناء البكتيريا العصوية); (2) تحول في تكوين السمات (فوائد لصغر حجم الخلية، وأشكال الحياة الخيطية، والأصناف غير المتحركة والضعيفة الارتباط); و(3) زيادة الانخفاض في تنوع الشعبة. وفي الختام، ينطوي سيناريو الانبعاثات الوسيطة على مخاطر كبيرة على التنوع البيولوجي، في حين أن سيناريو الانبعاثات العالية يفرض عواقب وخيمة على الطحالب القاعية، مما يهدد وظيفة النظام البيئي. (الفصل الثاني).

لفهم التغيرات المورفولوجية الناجمة عن الملوحة في الدياتومات، قمت بجمع المعرفة الموجودة. يعد التملح أحد الاهتمامات البيئية الرئيسية الذي يؤثر على الموائل المائية. تسلط الدراسات الضوء على أن الإجهاد الملحي قد يؤثر بشكل كبير

على السمات المورفولوجية للدياتومات. تظهر الأشكال غير الطبيعية التأثيرات الشديدة والمعقدة للملوحة والمتغيرات الجانبية. (الفصل الثالث).

Absztrakt

Felszíni vizeinket az antropogén tevékenységek és az éghajlatváltozás is veszélyeztetik, mely folyamatok jelentős hatással vannak a sekély vízi ökoszisztémákban domináló fitobentosz közösségekre. A felszíni vizek emelkedő víz hőmérséklete és sótartalma által a bentikus alga közösségekre gyakorolt hatás feltárása kulcsfontosságú feladat. Azonban nemcsak a környezeti tényezők, hanem a tavak természetes, morfológiai jellemzői is jelentős hatást gyakorolhatnak ezekre az élőlényekre, de hogy hogyan, ez egy kulcskérdés az ökológiában. E kérdések megválaszolására vizsgáltam a környezeti tényezők (hőmérséklet, vezetőképesség, Pt szín, árnyékolás, pH, tápanyagformák, anionok) és a morfometriai (felszín, mélység) jellemzők hatását a bentikus kovaalga közösségek összetételére (faj- és tulajdonság-alapú) és diverzitására (hagyományos és funkcionális) Magyarország két régiójának erdei, kis tavaiban. Megállapítottam, hogy a környezeti tényezők (tápanyagtartalom és vezetőképesség) leginkább a fajösszetételre és a hagyományos diverzitás mérőszámokra voltak hatással. A kovaalgák jelleg-alapú összetételét azonban leginkább a tó morfológiája határozta meg. A diatómák funkcionális válasza a fajok méret, alak és életforma szerinti szelekciója és a funkcionális diverzitás változása volt (I. fejezet.).

Egy szabadtéri mezokozmosz rendszerben vizsgáltam két klímaváltozási forgatókönyv (SSP2-4.5 és SSP5-8.5, közepes és magas kibocsátási forgatókönyvek) hatását a fitobentosz-közösségek szerkezetére és működésére faj- és jelleg-alapú megközelítéssel. Megállapítottam, hogy az előre jelzett 3°C-os hőmérséklet emelkedés jelentős hatással lesz a bentikus alga-közösségekre, mivel megváltoztatja a közösség faj- és jelleg összetételét, csökkenti a Shannon-diverzitást és növeli a közösség variabilitását. A pesszimistább forgatókönyv szerint még magasabb hőmérséklet emelkedés (+5 ◦C) drasztikus változásokat fog eredményezni az édesvízi fitobentoszban, beleértve a következőket: (1) jelentős összetételbeli változások törzs szinten (a

Cyanobacteria és a Chlorophyta algák dominanciája a Bacillariophyták rovására); (2) a jellegösszetételben bekövetkező változás (előnybe kerülnek a kisebb sejttérfogatú, fonalas életformák, valamint a nem mozgó és lazán kötődő taxonok); és (3) a törzsdiverzitás további csökkenése. Összefoglalva, már a közepesen pesszimista éghajlatváltozási forgatókönyv is jelentős biodiverzitási kockázatot jelent a bentikus algaközösségre nézve, míg a még pesszimistább forgatókönyv megvalósulása súlyos következményekkel járna a bentikus algákra nézve, veszélyeztetve az ökoszisztéma működését (II. fejezet).

Disszertációm III. fejezetében összefoglaló tanulmányt készítettem a diatómák sótartalom okozta morfológiai változásainak feltérképezéséhez. A szalinizáció az Antropocén egyik legnagyobb környezeti problémája, amely a vizes élőhelyeket is érinti. A tanulmányok rávilágítanak arra, hogy a sóstressz jelentősen módosítja a kovaalgák morfológiai tulajdonságait. A teratogén formák a sótartalom és más környezeti változók intenzív és összetett hatásait mutatják

General introduction

Freshwater ecosystems have played a significant role in human history since ancient times (Porter et al., 2012). The world's waters involve a wide variety of ecosystems, such as freshwater ponds, lakes, and rivers, in addition to estuaries, salt marshes, mangroves, coastlines, continental shelves, deep seas, marginal seas, and the open ocean. Lakes are areas of high biodiversity (Ognjanova-Rumenova et al., 2019; Morandín-Ahuerma et al., 2019) and are considerably susceptible to environmental changes. Moreover, due to the multitude of ecosystem services they offer, lakes can be regarded as one of the most sensitive environments on Earth (Strayer and Findlay, 2010) requiring close monitoring for necessary alterations (Eliasz-Kowalska and Wojtal, 2020). Lakes are threatened due to both direct factors, such as nutrient enrichment, forestry practices, and agricultural pressure, furthermore, indirect factors such as climate change (Ognjanova-Rumenova et al., 2019). Interdisciplinary research has uncovered that climate change is exerting a growing influence on the chemical and physical characteristic of the lake water, leading to a remarkable decline in biodiversity (Krztoń et al., 2019; Ognjanova-Rumenova et al., 2019). Consequently, it is crucial to preserve them or, at the very least, use them wisely, not only for ecological reasons but also for economic ones.

The ways that these systems are managed have to be adapted to each system and typically follow three basic rules. In the first approach, the goal is to protect the environment and improve the health or ability of freshwater habitats (as described by the WFD; European Parliament and Council, 2000). The second concept of ecosystem services shows how important it is to use ecosystems in a way that doesn't harm them (Daily et al., 1997). The third approach comes from rules at both the national and foreign levels and is meant to protect nature. There are clear lists in the rules of the individual organisms, ecosystems, and land area that need to be protected. Because of this, the idea of nature conservation includes things that happen both locally and globally (Act of Nature Conservation, 1996; Ministerial Order, 2001). There are a lot of links between these three strategies. They all try to improve and keep a healthy environment, but their objectives are not always the same. The concept of ecosystem services encourages the long-term use of water resources from the social, environmental, and economic points of view (Daily et al., 1997). The WFD-based method, on the other hand, focuses on lowering the damage that people do to environments (Moss, 2008).

Recently, diatoms have become part of standard bioassessment tools (Charles et al., 2021) for monitoring of water bodies in accordance with the United States Clean Water Act (1972) or the European Water Framework Directive (WFD: European Parliament and Council, 2000). These organisms are considered as essential for assessing the ecological condition of watercourses and have been utilized for over ten years in several European countries, including Austria, Switzerland, Germany, Belgium, France, Poland, Finland, Luxembourg, the United Kingdom, Spain, Portugal, and Italy (Maraslioglu and Soylu, 2017). The investigation of both natural and anthropogenic effects in aquatic environments is achieved through the application of these organisms (Hofmann et al., 2011; Marra et al., 2018). Diatoms are highly importance, as they serve as a primary source of oxygen and form the foundation of food chains in aquatic environments, like other divisions of algae, form the basis of food chains in aquatic environments. These silica-walled algae can become the main food source and primary producers in the aquatic food web (Wetzel, 1996). To accurately predict the future pattern of biodiversity in ecosystems, it is crucial to have a thorough comprehension of how climate warming impacts their structural and functional diversity. These specific characteristics of communities also have a role in determining the ability of the ecosystem to recover from disturbances (McLean et al. 2019). While there is ample evidence of functional diversity responses to environmental changes in temperate rivers (Schmera et al.,2017), our understanding of how these changes impact ecosystem features in lakes remains limited. Recent findings indicate that ecological characteristics can be attributed to genetic units in a manner comparable to morphological taxa.

Diatoms are a diverse and abundant kind of unicellular algae mostly used as indicators of environmental change and are essential in aquatic ecosystems (Saros and Anderson, 2015). Fast reactions of diatoms to environmental change make them important indicators of historical and present climatic conditions (Rühland et al., 2015). Understanding the complex interplay between environmental variables and diatom communities can help predict the consequences of climate change and other human impacts on aquatic ecosystems (Saros & Anderson, 2015; Falasco et al., 2009; Rühland et al., 2015).

While the use of ecophysiological traits, such as a species' ability to utilize a resource or withstand a specific stressor, has been common in diatom monitoring, the utilization of morphological traits is relatively new compared to other groups of organisms The study conducted by Rimet and Bouchez (2012) examines the characteristics of diatoms, with a specific emphasis on the size and growth forms of different diatom species. Cell size is an important characteristic that affects several ecophysiological traits, such as nutrient and light utilization, as well as resistance to grazers (Litchman and Klausmeier, 2008). Cell size is strongly connected to these characteristics, making it an essential trait that controls the ecological habitats of microorganisms (Litchman et al., 2007). Instead of focusing on morphological species-based indicators, another approach is to assess the efficacy of trait-based diatom indices (Kahlert et al., 2021). Employing readily quantifiable morphological characteristics, like size, may address the difficulties associated with diatom identification. Moreover, a trait-based index has the potential to be applied to a broader geographic area compared to a species-based index. Numerous studies have emphasized the value of phytoplankton functional groups, for example, in evaluating ecological conditions (Krasznai et al., 2010) or detecting alterations in community composition due to human-induced pollution (Bácsi et al., 2016). The combined use of different characteristics to explain changes in ecological processes and define specific habitat types has been demonstrated as crucial in phytoplankton research (Reynolds et al., 2002). The study of traits for benthic algal and cyanobacterial assemblages has just begun. These analyses include the simultaneous interpretation of several traits, as described by Lange et al. (2016). A promising strategy involves integrating guilds with cell sizes via the creation of combined eco-morphological groups (B-Béres et al., 2016). The use of combined eco-morphological groups has been shown to be an effective and reliable approach for detecting both quantitative and qualitative variations in diatom assemblages (Tapolczai et al., 2016). Trait-based indices could use over a wider geographical area, overcoming differences in taxa composition and environmental factors that usually species-specific indices' intercalibration. (Soininen et al., 2016; Tapolczai et al., 2017). Additionally, characteristics can offer ecological insights into how these organisms adapt to environmental limitations (Statzner and Bêche, 2010).

Main objectives

The use of morphological and trait-based approaches in diatom research improves aquatic ecosystem monitoring and understanding. Combining diatoms' sensitivity to environmental changes with traditional and new approaches allows for a better analysis of ecological forces. Comprehensive diatom morphological traits will be necessary for environmental monitoring and management, given the impact of climate change and other anthropogenic causes on freshwater systems. The aims of the research in this dissertation were to study the impact of environmental variables and morphological factors, raised temperatures, as well as the effect of salinization on benthic diatoms. The first chapter seeks to address the following research questions:

1. Do pond morphological features, in addition to environmental variables, play a significant role in shaping the structure and function of diatom communities in temperate humic forest ponds?
2. What are the primary variables that have a substantial impact on the composition of diatom species, guilds, and traits in these ponds and how do diatoms respond to these circumstances?
3. Whether the shared or pure effect of environmental and lakes' morphological factors are more important for diatom communities?

The second chapter aimed to address three main inquiries:

1. What structural changes that can be expected in freshwater phytobenthos under various climate model scenarios?
2. What are the effects of increased water temperatures on phytobenthos biodiversity?
3. How do different degrees of temperature increases affect the functional characteristics of phytobenthos in relation to ecosystem services?

In the third chapter, I provided a review of how diatoms can morphologically adapt to salinization.

My main question was: What are the possible effects of salinity on diatoms at cellular level?

Chapter I.

Lake morphology as an important constraint for benthic diatoms in temperate, humic forest ponds[1*]

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Photo: Lake Büdös, Photo by Edina Lengyel

[1*] This chapter was published in the following paper:

Al-Imari, T.J.K., Lengyel, E., Korponai, J., Padisák, J. and Stenger-Kovács, C., 2023. Lake morphology as an important constraint for benthic diatoms in temperate, humic forest ponds. Ecological Indicators, 155, 110939. https://doi.org/10.1016/j.ecolind.2023.110939

Due to their appropriateness for aquatic life, small lakes—1% of Earth's freshwater—have a high biodiversity. nutrient enrichment, agricultural pressure, and climate change all have an impact on their biota. Beside human activity natural features of the lake, like lake morphology can have significant impact on lentic organisms (Adeogun and Chukwuka, 2024). Research on boreal and tropical forest lakes is uncommon but vital to their protection. Diatoms, as a characteristic group alga, can be most abundant in the phytobenthos, covering different surfaces in the waterbody- and indicate environmental changes. Functional analysis and functional diversity assessments of benthic diatoms can help reveal ecological and evolutionary processes in these environments.

I.1. Introduction

The majority of Earth's freshwater habitats are small lakes. They have an exceptionally high biodiversity in relation to their size because they provide suitable conditions for a wide variety of aquatic creatures (Biggs et al., 2017; Fehlinger et al., 2022), both microscopic and macroscopic (Bolgovics et al., 2019). In addition to supporting communities of amphibians and providing water for land-dwelling birds and mammals, these bodies of water play an important role in the coupling of matter and energy movement between the aquatic and terrestrial domains. Nutrient enrichment, harvesting, agricultural pressure, and climate change are posing serious threats to these lakes (Eliasz-Kowalska and Wojtal, 2020), which represent around 1% of the land area (Dudgeon et al., 2006). But the lake's morphology (Huang et al., 2014) and human activities (e.g., climate change; Morand et al., 2019; Ognjanova-Rumenova et al., 2019) also impact their biological status. Ponds and bigger lakes differ significantly in morphometric characteristics, such as surface area, depth, submerged and emergent vegetation cover, etc. (Richardson et al., 2022). This variation can affect limnological and metabolic processes (Staehr et al., 2012), as well as the composition and function of biotic associations (Moses et al., 2011). Both management and biological considerations require the isolation of ponds from other bodies of water (Richardson et al., 2022). However, in contrast to larger, more permanent lakes, our ecological understanding of these distinct aquatic habitats is noticeably lacking. Although there is a number of studies about forest lakes from the boreal region already from 1980's, especially from Finland and Russia focusing mainly on their chemical properties (Vuorenmaa et al., 2006), fish (Olin et al., 2012), phytoplankton (Arvola et al., 1986) and macroinvertebrate (Flenner et al., 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-Gołdyn and Kuczyńska-Kippen, 2017; Spyra, 2017; Bohemian forest lakes: Vrba et al., 2016; Nedbalová et al., 2006; Danish forest lakes: Sand-Jensen and Staehr, 2009; Martinsen et al., 2020; rainforest lakes). Nevertheless, given the delicate hydrological balance they face in the face of climate change, it is of the utmost significance and growing urgency to protect and maintain them using appropriate ecological data (Korytowski and Szafrański, 2008). There is a high probability of benthic algae development in these pond-like small lake ecosystems, where benthic algae, of which most of them are diatoms, can dominate and serve as a food source for higher trophic levels (Wetzel, 1983; 2001; Kireta et al., 2012; Celewicz-Goødyn and Kuczyńska-Kippen, 2017). 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- B´eres et al., 2022). The guild classification of diatom taxa (Passy, 2007; Rimet and Bouchez, 2012), and this led to the identification of the correlation between diatoms and environmental factors (such as Berthon et al., 2011; Stenger-Kovács et al., 2013), has greatly improved the ecological studies of diatoms. Moreover, not only the guilds but also easily measurable traits of diatoms (like e.g. cell size) are related to changing environmental factors (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). Functional analyses have shown that combining guilds and traits as eco-morphological groups is a useful way to follow and understand ecological and evolutionary processes (B-Béres et al., 2016; Stenger-Kovács et al., 2018, 2020a). Using functional diversity metrics (He et al., 2015) is another potential tool to find out how ecosystems react to changes in their environment (Péru and Dolédec, 2010; Stenger-Kovács et al., 2020b) or to forecast ecological stability (Schneider et al., 2017). While functional diversity indices based on guild and traits have been used to predict environmental variables in aquatic ecosystems, they have not been widely applied (Ding et al., 2017). This is particularly true for primary producers (Kale and Karthick, 2015; Letáková et al., 2018), such as benthic algal communities (Török et al., 2016; Stenger-Kovács et al., 2020b).

The aims of this study were to examine the diatom communities as well as the physical and chemical characteristics and morphological factors (water depth and surface area) of temperate and humic forest ponds in two distinct regions of Hungary. I was primarily concerned with determining if morphological characteristics, in addition to environmental influences, play a significant role in shaping the composition and functioning of diatom communities in these ponds. The objective was to evaluate the shared and pure effects of environmental and morphological factors on diatom communities. To achieve this, I investigated the primary factors that have a significant impact on the composition of diatom communities in terms of species-, guilds-, and traits-, as well as the diversity indices related to both traditional and functional aspects.

I.2. Material and Methods

I.2.1. Study area

With an area of 93,030 km^2, Hungary is situated in Central Europe. From north to south, it extends around 250 km, and from east to west, it stretches 524 km. Hungary has a continental climate, which means that summers can be hot and humid and winters can be cold. Hot days have become more common due to climate change, particularly in the south and central areas (Uzzoli et al., 2018). On the other hand, frost days have become less common across the nation (Mike and Lakatos, 2009). Temperatures in the winter can drop to -15 °C, while those in the summer can reach 27 to 35 °C. Approximately 600 mm of rain falls each year on average (Kovács and Jakab, 2021). The Transdanubia Central Highlands (TD) and the Northern Highlands (NH) are the primary locations for brownish, forested lakes across the nation. These forest ponds with closed basins are often quite shallow, with an average depth of about 30 cm. They also have a relatively limited surface area, measuring 690 m^2, and a majority of them dry up on a regular basis during the summer. Their high humic acid content, which comes from allochthon sources (a lot of leaf litter from the nearby deciduous forests), is what gives them their brownish colour.

I.2.2. Physical and chemical parameters

Figure 1 shows 70 small lakes that were studied in two regions of Hungary, TD and NH, between 2014 and 2018. Water samples and phytobenthos samples were taken in spring (March and April) and in winter (October and November). A Hach Lange HQD4 handheld multimeter was used to measure the water's temperature, pH, and conductivity. Shading was also measured in situ. At each site, water samples were taken for chemical and physical analyses. Titrimetric and spectrophotometric procedures were used to determine nutrient forms (NO_3^-, NO_2^-, NH_4^+, TP, and SRP), anions (Cl^-, SO_4^{-2} and HCO_3^-), COD (chemical oxygen demand), and Pt color in accordance with international standards (APHA, 1998; Wetzel and Likens, 2000). Morphological factors of ponds were also measured in the field.

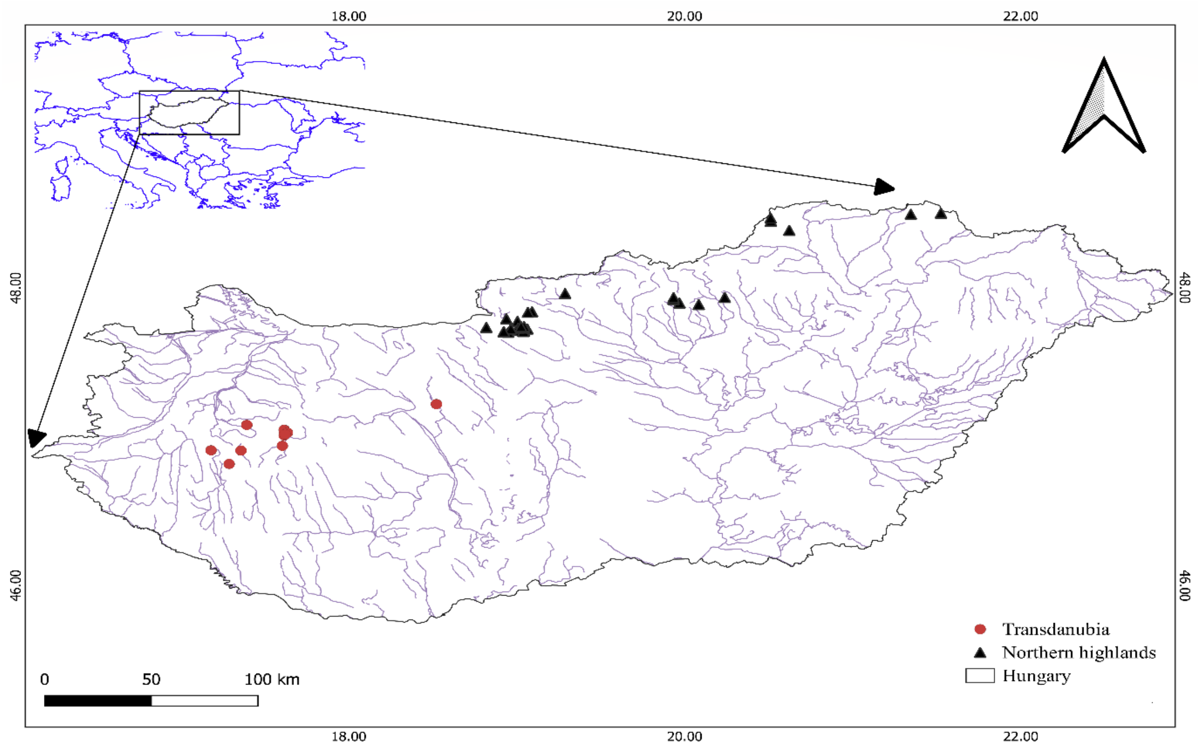

Figure 1. Map of the study area and the location of sampling used for analysis.

I.2.3. Diatom sampling, preparation, and analyses

In accordance with the guidelines made by King et al. (2006), diatom samples were obtained using a toothbrush from the distinctive substrates (macrophytes or mud) from the lakes. The water supply of the ponds determined the frequency of the samplings. In order to preserve the diatom samples until their oxidation treatment with the hot hydrogen peroxide, the samples were stored in ethanol (CEN, 2003). Diatom valves were identified to species level under light microscopy (Zeiss, Axio A1) at 1000x 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). A minimum of 400 valves were counted on each slide and the relative abundance of species was calculated. Species were classified into a variety of ecological groups, such as guilds and attribute categories, including the following: 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-to-width ratio (LW, Tapolczai et al., 2017); (iii) five categories of the biovolume (BV, Berthon et al., 2011); and (iv) the combination of these characteristics as ecomorphological groups (B-Béres et al., 2016; Table 1).

Table 1: The applied guilds and traits.

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

The study used traditional diversity indices such as species number and Shannon diversity (Shannon and Weaver, 1949). Additionally, functional diversity indices were calculated based on ecological groups, including "FDiv" for functional divergence, "FEve" for functional evenness, "FRic" for functional richness, "FGR" for functional group richness, and "RaoQ" for Rao's quadratic entropy. These calculations were performed using the "FD" package (Laliberté and Legendre, 2010) in the RStudio. For further analysis, the species and trait abundances, as well as the traditional and functional diversity indices, underwent Hellinger transformation.

I.2.4. Statistical analyses

The statistical analyses and graphical displays were performed using the "vegan" package (Oksanen et al., 2019) in the RStudio (R Core Team, 2021; version 4.1.2). The physical and chemical variables were tested for normal distribution using the Shapiro-Wilk test. For SRP, depth, conductivity, and shading, the log-transformation (log(x+1)) was used, but the square root transformation was used for NO_2^-, Cl^- and TP. Shade and temperature was not modified (Table 2). Because they were below the analytical detection limit in the majority of the samples, NO_3^- and NH_4^+ were not included in the statistical analysis. The Welch test was used to examine the variations in the morphological and environmental characteristics of the ponds across different regions.

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 for a PERMANOVA test (Anderson, 2001) to check the significance of the NMDS models (number of permutations = 999).

We used Redundancy Analysis (RDA) to explore the species-and trait (individual and trait combined traits) composition, as well as the traditional and functional diversity indexes and the link between the ponds' morphology and their environment. For the purpose of selecting the master variables, Blanchet et al. (2008) developed a forward selection process. To verify that the RDA models were statistically significant, we used the "Ordistep" test (Blanchet et al., 2008) with 999 possible permutations.

To find out how morphological and environmental factors in a pond affect diatom communities both individually and combined, we used variance partitioning analyses with the "varpart" function (Legendre and Legendre, 2012) of the *vegan* package to find out the pure and shared effect of both environmental and morphological variables on the species and trait composition, and traditional and functional diversity indices. Unbiased estimates of the explained fractions of variance were obtained by computing the adjusted r-squared. Using the analysis of variance (999 permutations), we tested the significance levels of the variance partitioning analyses.

I.3. Results

I.3.1. Environmental and morphological parameters.

When we analyzed the morphological features of the ponds separately (p = 0.01), the NH region had larger surface areas (mean: 748 m^2 ; p =0.01) and were deeper (p =0.02; mean: 32 cm) compared to the TD region (mean surface area: 479 m^2; mean depth: 21 cm). In the TD region, the mean shading was 70%, on the other hand, in the NH region was just 29%. This disparity was likewise statistically significant (p = 0.001), based on the results of the Welch test. In both localities, the average water temperature was often reported as being 16°C or below, and the Pt color was similarly low (204 mg L^{-1} in NH and 207 mg L^{-1} in TD). In both regions, the conductivity was almost identical, with a mean of 189 µS cm^{-1} in the TD region and 187 µS cm^{-1} in the NH region. In general, HCO_3^- > SO_4^{-2} > Cl^- were the order of most anion concentrations. The average concentration of HCO_3^- was 107.8 mg L^{-1}, whereas the average concentration of SO_4^{-2} was 10.5 mg L^{-1} in the TD region. The concentrations of HCO_3^- and SO_4^{-2} differed significantly (p <0.001) between the two areas. In comparison to the TD region's Cl^- mean concentration of 8.0 mg L-1, the NH region was almost three times higher at 22.8 mg L^{-1}. The average levels of NO_2^- and TP were both greatest in the NH region at 7.2 µg L^{-1} and 451.1 µg L^{-1}, respectively, when considering the nutrients. On the other hand, the average level of SRP was greater in the TD region at 194.3 µg L^{-1}, as shown in Table 2. The only variation between the two regions that was statistically significant ($p = 0.02$) was the concentration of NO_2^-.

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 based on the results of the 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**
			Min - Max	Mean	Min - Max	Mean	*p*-value
Surface area	m^2	Y= ln(X+1)	16- 3533	479	40 - 6359	748	**0.01**
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
C^{l-}	mg L^{-1}	$Y= (X)^{0.5}$	DL - 95	8.0	DL- 499.8	22.8	0.13
HCO_3^-	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
NO_2^-	µg L^{-1}	$Y= (X)^{0.5}$	0.01- 6.1	3.1	DL - 53.5	7.2	**0.02**
SO_4^{2-}	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

I.3.2. Diatom communities of the ponds

Through the scientific study of the 70 phytobenthos samples, a total of 174 diatom taxa were discovered (Table 3). The species that were found the most frequently were those belonging to the genera *Nitzschia* (e.g., *Nitzschia palea* (Kutzing) W.Smith), *Navicula* (for example, *Navicula cryptocephala* Kutzing), *Eunotia* (for example, *Eunotia bilunaris* (Ehrenberg) Schaarschmidt), *Pinnularia* (for example,

Table3: Most abundant traits of humic, forest lakes.

Guilds	**Number of species**	**Biovolume**	**Number of species**	**Length-to-width ratio**	**Nomber of species**
Motile- profile	101	BV2	38	LW2	40
High- profile	50	BV3	35	LW3	62
Low-profile	17	BV4	39	LW4	53
		BV5	45		

Pinnularia obscura Krasske), and *Gomphonema* (for example, *Gomphonema exilissimum* (Grunow) Lange-Bertalot & E.Reichardt).The NMDS analysis, including environmental and

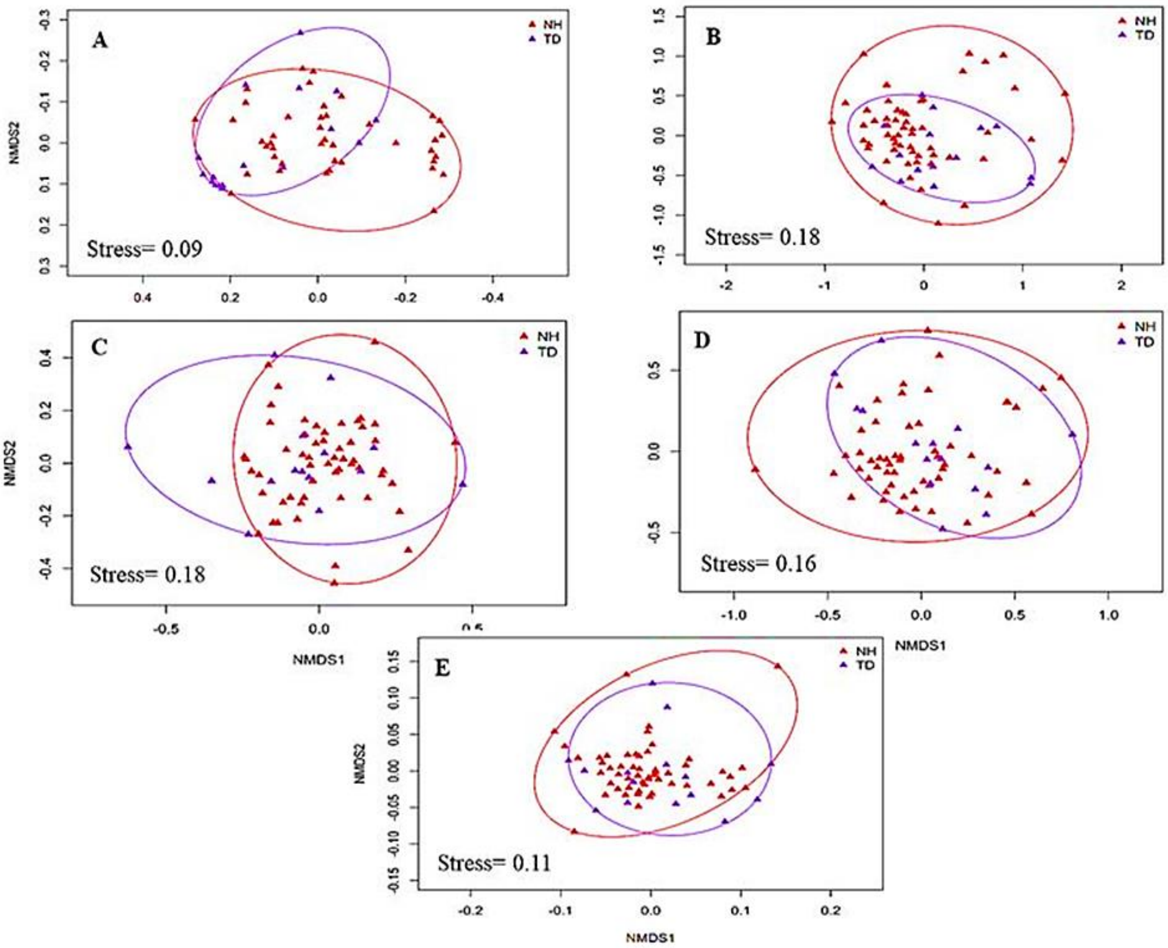

Figure 2. Non-metric multidimensional scaling (NMDS) plots of the studied ponds based on the **A** environmental and morphological variables, **B** relative abundance of the diatom species **C** relative abundance of the individual diatom guilds and traits, **D** relative abundance of the combined ecological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

morphological parameters, species abundances, guilds, traits, ecomorphological groups, and diversity indices, indicated that there were no regional variations across the lakes (Fig. 2A, B, C, D, E), as confirmed by a PERMANOVA test ($p > 0.1$). The dimensionality of data was estimated using a stress factor below 0.2 (Fig. 2).

I.3.3. Limitations imposed by the environment and morphology 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 environ- mental variables (Cl^-, conductivity and TP). The first axis was primarily associated with conductivity, Cl^- (r = 0.83 and r = 0.65, respectively), as well as nutrients TP and NO_2^- (r = -0.47, r = -0.41, respectively). On the other hand, the second axis was significantly influenced by depth and temperature (with correlation coefficients of -0.52 and -0.3, respectively). The presence of a high concentration of chloride ions was identified by the presence of *Meridion circulare* (Gréville) C.Agardh [MCIR] and *Gomphonema micropus* Kützing [GMIC], while the high level of electrical conductivity was indicated by the presence of *Nitzschia alpina* Hustedt [NAZL]. However, *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] showed a correlation with increased levels of nutrients such as total phosphorus (TP), nitrite (NO_2^-), and soluble reactive phosphorus (SRP). The deeper water was associated highly with the abundance of *Nitzschia palea* (Kützing) W.Smith [NPAL] and lowerly with *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot [PTLA] (Fig. 3A).

The RDA analysis of the 15 distinct guilds and attributes revealed that the surface area of the ponds had the greatest impact on these individual groups (Fig. 3B). The variables that had the most significant impact on the first axis, which accounted for 4.3% of the explained variance, were surface area, shading, and temperature, with correlation coefficients of -0.58, 0.35, and 0.31, respectively. On the second axis, which explained 3.4% of the variance, the variables that had the most influence were surface area, NO_2^-, and water depth, with correlation coefficients of -0.49, -0.41, and -0.36, respectively. The explained variation of the first two axes was minimal, amounting to only 7.7%. The study found a positive correlation between high- and low-profile guilds, large length/width ratio, and larger biovolume (H, L, LW6, and BV5) with surface area and NO_2^-. On the other hand, there was a negative correlation between biovolume BV5 and the planktic guild with chloride (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 presence of motile guild and the medium biovolume (M and BV3, BV4) suggested a greater level of shading. There was a positive correlation between smaller biovolume (BV2) and medium length/width ratio (LW3) with P planktic guild forms.

The composition of the combined groups (35 groups) (Fig. 3C) was highly influenced by conductivity, NO_2^-, TP, and Cl^- along the first axis, which contributed to 7.4% of the explained variation ($r = 0.8$, $r = -0.38$, $r = 0.37$, $r = -0.37$, respectively). The primary factors influencing the combined groups were shading, surface area of the ponds, and conductivity (correlation coefficients of 0.45, 0.45, and 0.31, respectively) along axis 2, which represented 3% of the explained variation. There was a favorable correlation between HBV2 and MBV3 with conductivity and chloride. HLW3 and MLW4 exhibited a positive correlation with nutrients such as TP, SRP, and NO_2^-, whereas LLW2, MLW3, and LBV5 had a positive association with temperature. Conversely, HLW4 (Fig. 3C) correlated positively with surface area of the ponds and shading.

The functional diversity indices were influenced by both environmental variables and morphological features, as shown in Figure 3D. The proportion of variation that was explained by the first two axes was rather small, at 6.6%. The functional diversity indices were most influenced by the levels of Cl^-, temperature, and NO_2^- ($r = 0.42$, $r = -0.41$, and $r = 0.37$, respectively). Along axis 2, which represented 3.4% of the explained variation, conductivity, Cl^-, surface area, and temperature had the strongest correlations (0.73, 0.53, 0.34, and 0.32, respectively). Figure 3D showed that the FEve exhibited a negative correlation with all of the observed variables, while FRic, RaoQ, and FDis had a positive relationship with temperature and surface area, and a negative relationship with depth, shading, and SRP. The correlation between FGR with NO_2^- and TP was found to be positive, as shown in Figure 3D.

The traditional diversity metrics, namely the Shannon index and species number, shown in Figure 3E, were primarily influenced by factors such as surface area and environmental variables including shade, forms of phosphorus (P), and conductivity. When considering axis 1, which contributed to 11.7% of the explained variation, the diversity metrics were significantly influenced by SRP and shade, with correlation coefficients of 0.72 and 0.52, respectively. On axis 2, which represented 0.05% of the explained variation, the variables that had an impact were surface area, conductivity, TP, and shading. The correlation coefficients for these variables were 0.64, -0.54, 0.49, and -0.42, respectively. The Shannon diversity exhibited an increase in response to the nutrients, Cl^- ions, and shading. The species number was favorably influenced by temperature, depth, and surface area.

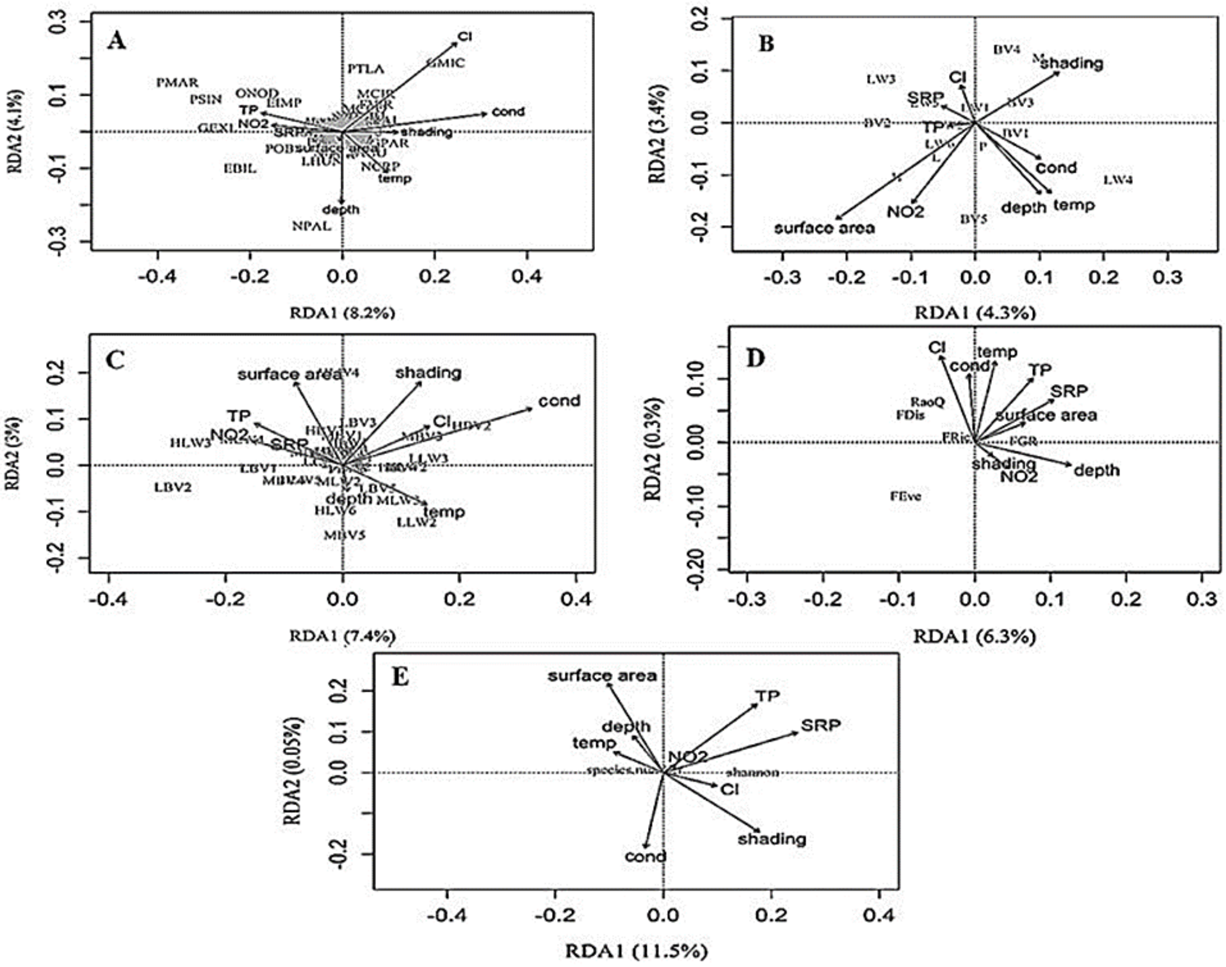

Figure 3 RDA analysis of the environmental variables and **A** the diatom species composition, **B** the individual traits of diatoms, **C** their combined trait composition **D**, functional and **E** traditional diversity metrics in brownish lakes of Hungary.

I.3.4. The impact of environmental and morphological factors on diatoms in ponds

According to the VarPart analyses, we observed that the direct influence of the environmental variables on species composition (0.05) and on traditional diversity metrics such as species number and Shannon diversity (0.08) was greater compared to the direct influence of morphological factors (0.01 and 0.02) (Fig. 4A, E). In contrast, morphological characteristics of ponds (0.06 and 0.07 each) had a more significant direct impact on the individual traits and guilds

(0.06) and combined ecological groups (0.07) compared to environmental variables (0.02 and 0.04) (Fig. 4B, C). The functional diversity indices showed that both the environmental variables and morphological parameters had a comparable pure impact of 0.02, as seen in Figure 4 D. The overall effect of the environmental and morphological factors was minimal (0.01) or nonexistent.

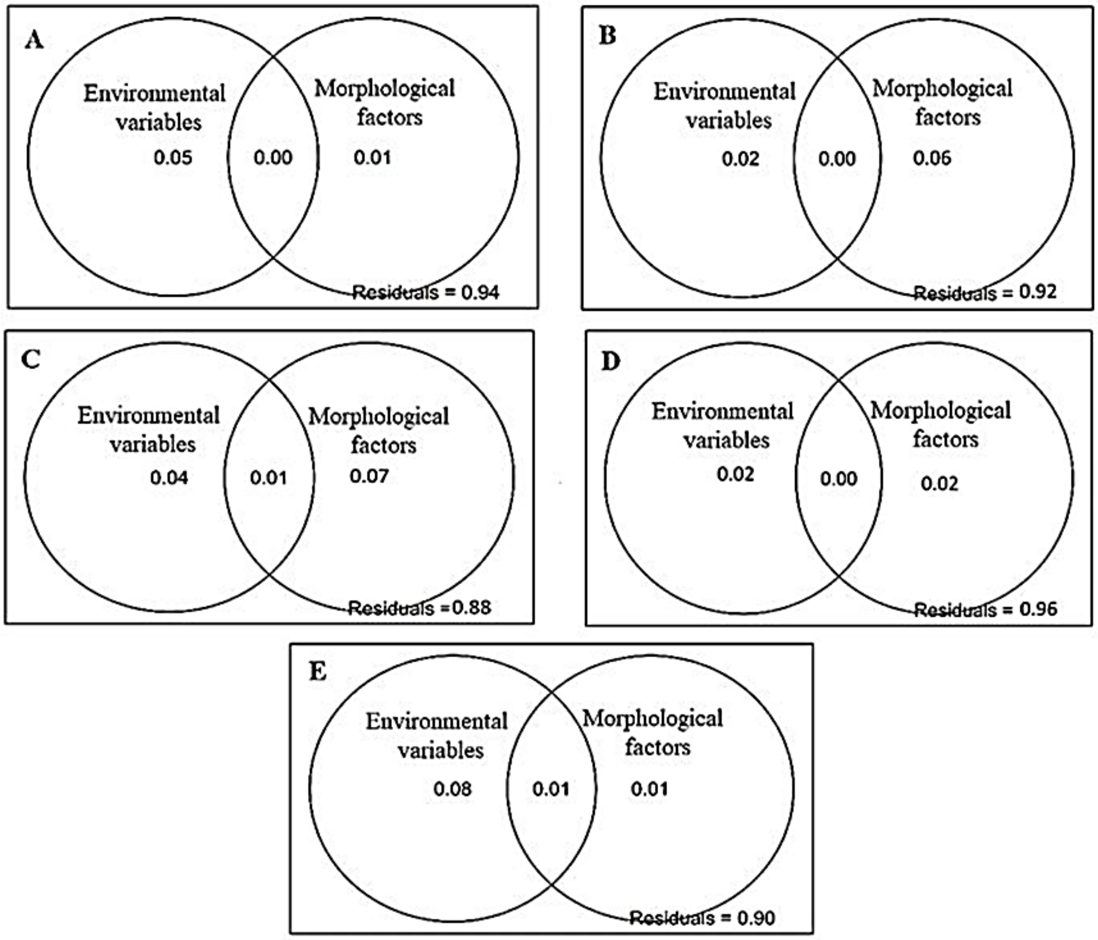

Figure 4 Partitioning of variation in case of **A** diatom species composition, **B** their individual traits composition, **C** their combined trait composition, **D** functional and **E** traditional diversity metrics between the two groups of the explanatory variables.

I.4. Discussion

In general, forest lakes in temperate and boreal regions can be described by their water depth (ranging from 1 - 40 m, Martinsen et al., 2020 and Nedbalová et al., 2006), surface area (ranging from 1 to 900 ha, Rask and Hiisivuori, 1985 and Hongve et al., 2004), and low nutrient content (e.g., TP: 1.6-12.3 µg L^{-1} in Nedbalová et al., 2006). On the other hand, these characteristics are noticeably different from Hungarian closed-basin ponds, which are significant forest components in the Carpathian Basin and either have water permanently or seasonally. Like the lakes in the Danish Forest, their maximum surface area is only approximately 0.6 ha and their maximum depth is around 0.6 m (Sand-Jensen and Staehr, 2009; Martinsen et al., 2020). The high TP content in both countries (58.9-1441 µg L^{-1} in the current research and 128-331 µg L^{-1} in Martinsen et al., 2020) might be attributed to the presence of mixed sediment and a significant amount of leaf litter (Hubai et al., 2009). These Hungarian temperate forest ponds have a Pt color of 762.5 mg L^{-1}, which is higher than the maximum values reported for boreal forest lakes in Finland (557 mg L^{-1}, Olin et al., 2010). Forest lakes often have an acidic pH (e.g., Thies, 1991; Johansson, 1983), which may reach severe levels (pH<2, Von Einem and Granéli, 2010). However, they can also show trend towards neutral or even alkaline, as shown in the temperate ponds analyzed (e.g., Holopainen et al., 2008).

I.4.1. Variations between different regions

Typically, as the distance between lakes increases, there may be significant variations in water chemistry (e.g., Kling et al., 2000) and morphological features. Although the two areas vary significantly in terms of their relief, structure, and rock formations (Halmos et al., 2005), only a few regional differences were found when comparing the different environmental and pond morphological factors independently. Ponds in the TD region are characterized by both smaller surface area and water depth, which may significantly influence the yearly hydrological cycle. Smaller water bodies have a reduced number of hydrological phases compared to larger ones, which impacts the chemical and physical characteristics as well as the organisms that inhabit the lakes. This phenomenon was discovered in the soda pans of the Carpathian Basin (Lengyel et al., 2019).

In addition, the ponds in the TD area are subjected to greater shading from the nearby woods, the same way as subtropical reservoirs. This is comparable to a study by de Faria et al. (2013) which demonstrated the direct impact of macrophyte (*Pistia stratiotes*) cover on the periphytic diatom species in such reservoirs. The relationship between shading and water depth determines the light regime, which is a crucial environmental factor that regulates ecophysiological processes (Falkowski and LaRoche, 1991; Kirk, 1994; MacIntyre et al., 2002). This light regime has a significant impact on various environmental factors, including pH, oxygen levels, and nutrient availability (Mallin and Paerl, 1992; Wetzel, 2001; Coops et al., 2003; Cardoso et al., 2017). For example, a catchment area covered by trees reduces the amount of light entering the water and provides readily available dissolved nutrients to organisms in small standing waters (Sand-Jensen and Staehr, 2009).

Both areas exhibited a prevalence of HCO_3^-, however its concentration was notably greater in the TD region due to the presence of basalt bedrock with limestone windows, as described by Lengyel et al. (2015). The concentration of the anion SO_4^{-2} was found to be quite low in both regions, with a mean value of < 25.3 mg L^{-1}. Nevertheless, it was much greater in the NH regions, where there are more deposits of gypsum-anhydrite (Hahn et al., 1998). This may be the reason for the increased sulphate content in the lakes observed in these regions. In the forest ponds, the primary type of nitrogen was NO_2^-, and its concentration was usually low in both areas (with a mean of < 7.2 µg L^{-1}). However, it was much lower in the TD regions. Under most instances, the other forms of nitrogen were not detectable due to their low concentration. This is because nitrification, which is the process of converting ammonia to nitrate, requires a high level of dissolved oxygen. However, under anoxic conditions when oxygen is limited, the buildup of nitrite (NO_2^-) may occur as an 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 com- positions of the ponds in the DT region were embedded among the lakes of the NH region.

I.4.2. The impact of lake morphology on diatoms

The size (surface area) of lakes has a notable impact on the composition and variety of diatoms (Rimet et al., 2015; Bolgovics et al., 2019). Multiple studies (Bolgovics et al., 2019; Várbíró et al., 2017) have shown that the number of different species of phytoplankton and benthic diatoms tends to rise as the size of the water body increases. This pattern is also seen in macroinvertebrate communities (Zenker and Baier, 2009) along the same gradient. The research found that there was a significant correlation between the richness of benthic diatoms and the surface area of forest ponds. This supports previous observations made on lakes of various sizes (ranging from 10^{-2} to 107 m^2) by Bolgovics et al. (2019) and Várbíró et al. (2017). Our research also found that the water depth in the forest ponds has a notable impact on the composition of diatom species, comparable to shallow lakes in Southern Europe (Rodríguez-Alcalá et al., 2020). As a result, an increase in water depth tended to increase the abundance of *Nitzschia palea* and decrease the abundance of *Planothidium lanceolatum*. The previous finding is a subject of debate in the literature, since *Nitzschia palea* is often identified as the prevailing taxon in relatively shallow environments (e.g., Riato and Leira, 2020; Stenger-Kovács and Lengyel, 2015).

Additional ecophysiological studies are needed to investigate these contradictory data. However, paleolimnological research, such as that carried out by Sterken et al. in 2012, have previously demonstrated the relationship between *Planothidium lanceolatum* and water depth. The size of the surface and the water depth of ponds had a substantial impact on both the individual characteristics and guild composition, as well as on the combined traits. The medium size and less elongated shape of cells may be the result of increased light exposure. On the other hand, guilds that have a moderate size and a moderate length/width ratio, such as HLW3 and LBV3, were shown to have a negative correlation with water depth. A common phenomenon in lakes is the reduction in light availability as the lake depth increases (Coops et al., 2003; Cardoso et al., 2017).

In such conditions, smaller taxa are preferred. These organisms are capable of thriving in environments with little light (Stenger-Kovács et al., 2013; B-Béres et al., 2016; Lukács et al., 2018) due to their enhanced ability to use light effectively (Kirk, 1994). The elongated cells, which have a larger length-to-width ratio, may function as light traps, as seen in settings with inorganic turbidity (Stenger-Kovács et al., 2020a). The prevalence of planktic species in the benthic community is a strong indicator of a bigger water body, where their lifestyle is more prominent (Wang et al., 2018). As the water depth decreases, there is an observable change in the size and morphology of the organisms in the community. The medium size and less elongated shape of cells may be the result of increased light exposure. Decreased functional variety may also suggest greater water depth (Longhi and Beisner, 2010) as a response to less favorable light and living conditions. In such environments, where only the appropriate species with well-selected traits, as ecological uniqueness can survive (Coops et al., 2003).

The study conducted by Longhi and Beisner (2010) revealed a positive correlation between surface area and many individual and combined traits groups (H, L, LW6, BV5, HLW3, HBV3, LBV3) as well as functional diversity in Canadian lake phytoplankton. Larger lakes provide a greater variety of habitats and, therefore, have the potential to support a more diverse community of diatoms. This is supported by research that has observed a higher number of diatom species in larger lakes (Bolgovics et al., 2019). The presence of environmentally distinct species in these lakes can be attributed to their ability to effectively utilize available resources, as explained by the concept of resource partitioning (e.g., Schoener, 1974; Bradford and Kastendick, 2010). The findings clearly demonstrate that water depth and lake size significantly impact the ecology and functioning of ecosystems (Coops et al., 2003), even in tiny ponds with a narrow range of water depth (8–60 cm) and surface area (16–6359 m^2).

I.4.3. The impact of environmental variable on diatoms

Environmental filtration is the primary mechanism (Jovanovska et al., 2022) that shapes the composition of diatoms communities at many scales, including local, regional (Wang et al., 2022), and global (Soininen et al., 2016; Rodríguez–Alcalá et al., 2020). The species composition and diversity in forest ponds were mostly influenced by conductivity and nutrients, which are recognized as important factors affecting diatoms in larger freshwater lakes (Kovács et al., 2006; Ognjanova-Rumenova et al., 2009; Dell'uomo and Torrisi, 2011). According to Rodríguez–Alcalá et al. (2020), nutrient content is the primary factor influencing lakes in the northern region of Europe, whereas conductivity is the dominant factor in the southern region. *Pinnularia marchica* (PMAR) and *Eunotia implicata* (EIMP) were shown to be typical species in our forest ponds, showing a preference for water with low conductivity, somewhat acidic conditions, and low nutrient content (Luís et al., 2011; Şahin and Barınova, 2022).

Shading, temperature, and nutrient levels were the primary environmental factors that influenced forest ponds, both individually and in combination, with regards to individual and combined traits groups. The high-profile guild, because of its location in the benthic layer, has a negative correlation with shading as it favors greater light intensity (Passy, 2007). In shady ponds, the dominance of small-sized cells (BV1) and the motile guild (M) was comparable to that seen in salty ponds (Ács et al., 2019) and freshwater streams (Lange et al., 2016). Their ability to move allows them to choose the most appropriate habitat and escape stressful circumstances caused by the darkened environment (Ács et al., 2019). Conversely, there was a positive correlation between the mean length/width ratio of high-profile and motile taxa (HLW3, MLW4) and nutrient levels. This is consistent with previous findings that have shown a substantial link between the motile group and high nutrient levels (Passy, 2007; Berthon et al., 2011). Conversely, the temperature had a significant influence on all three diatom ecological guilds. Specifically, the motile group was notably adversely impacted by low water temperatures, as shown in the study of Stenger-Kovács et al. (2013), which aligns with our findings. There is evidence suggesting that diatom cells may undergo an increase in size when subjected to cooler temperatures. However, it remains uncertain if this phenomenon is applicable to all species generally (Soininen and Teittinen, 2019; Svensson, et.al, 2014).

The functional diversity indices exhibited significant correlations with many environmental factors of the forest ponds, including conductivity, temperature, and Cl^-. Previous studies have shown that functional diversity indices are particularly responsive to changes in conductivity and temperature in soda pans (Stenger-Kovács et al., 2020b) and 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). Nevertheless, certain indices such as FEve exhibited no correlation with the local environment, similar to various other types of aquatic ecosystems (e.g., saline ponds, Stenger-Kovács et al., 2018; tropical headwater streams, Taniwaki et al., 2019). This highlights the need for careful selection and application of these indices.

I.4.4. variance partitioning of diatoms

The effect of environmental variables on species composition and diversity metrics (such as the Shannon index and species number) was found to be the most significant. This effect was observed in European lakes, where local abiotic factors were found to have a greater influence (Rimet et al., 2019) than spatial effects (Rodríguez-Alcalá et al., 2020). As a result, these factors are considered to be the primary regulators of diatom composition. The significant impact of environmental variables on functional diversity metrics has been emphasized, as these indices based on traits are more relevant in terms of environmental variables compared to indices based on species taxonomy (e.g., Wang et al., 2022; Soininen et al., 2016; Teittinen et al., 2018; Stenger-Kovács et al., 2020b). Nevertheless, our investigation reveals that the variance in functional diversity indices may be attributed equally to both environmental factors and morphological characteristics of the forest ponds. This implies that the shape and structure of a lake may have a significant impact on its characteristics, like the chemical properties of the water. Additionally, the composition of benthic diatoms and their specific traits may also show a clear functional response to lake morphology.

Chapter II

Impacts of global warming on freshwater lake phytobenthos and their functions[2**]

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Cover photo by Balaton Limnological Research Institute

[2**] Part of this chapter was published in the following paper:

Lengyel, E., Stenger-Kovács, C., Boros, G., Al-Imari, T.J.K., Novák, Z. and Bernát, G., 2023. Anticipated impacts of climate change on the structure and function of phytobenthos in freshwater lakes. Environmental Research, 238, 117283. https://doi.org/10.1016/j.envres.2023.117283.

Human activity has rapidly warmed the atmosphere, ocean, and land surface, causing sea level rise, ice loss, and permafrost melting. It also has considerable impact on aquatic ecosystems modifying biogeochemical cycles and causng harmful algal blooms. Water temperature can control algal growth, photosynthesis, and nutrient availability in these ecosystems. Current meteorological alterations influence shallow lakes more, and understanding climate change's impact on aquatic environments is critical for biodiversity and human wellbeing.

II.1. Introduction

There is no doubt that people have been producing substantial alterations in the Earth's climate at an unprecedented pace in recent millennia. This has resulted in a widespread and rapid increase in temperature in the atmosphere, ocean, and land surface (IPCC, 2021). Several anthropogenic environmental changes, such as alterations in the ocean's physical and chemical properties, the removal of ice sheets, the melting of permafrost and the rise in global sea levels, will persist for hundreds to millennia in an irreversible manner (IPCC, 2021). According to the IPCC (2021), as global warming continues, there will be a rise in various factors that contribute to climate change in all parts of the world. The study looks at five climate model scenarios called Shared Socioeconomic Pathways (SSPs) to see how the climate changes in response to different levels of greenhouse gas emissions, land use patterns, and air pollutants. The analysis also considers solar activity and the influence of volcanic activity (IPCC, 2021). Nevertheless, it is highly likely that both the global warming limits of 1.5 $^{\circ}$C and 2.0 $^{\circ}$C will be surpassed in the 21st century unless significant reductions in CO_2 and other greenhouse gas emissions are achieved (IPCC, 2021). Aquatic ecosystems are clearly influenced by atmospheric conditions and are therefore vulnerable to climate change, which can result in substantial alterations within them (Dokulil, 2013; Dokulil et al., 2010; George, 2010).

It is very important to be able to predict how ecosystems will change because they provide many important services to the environment, like preventing harmful algal blooms and adjusting biogeochemical cycles and primary production. This has been emphasized by various studies (Zedler and Kercher, 2005; Markensten et al., 2010; Dutkiewicz et al., 2013; Laufkötter et al., 2016; Zhou et al., 2017; Townhill et al., 2018). The temperature of water plays a crucial role in aquatic ecosystems, affecting various aspects such as the growth rates of organisms, the efficiency of photosynthesis, and biochemical processes at the cellular level, additionally, its indirectly influences nutrient availability and the stability of the water column in lakes, which in turn affects the organisms living in these ecosystems. (Dokulil, 2013; Bhateria and Jain, 2016). The intricate and temporally variable impacts of temperature (e.g., Hao et al., 2020; Pacheco et al., 2022) provide challenges for its study, particularly in the absence of experimental intervention (e.g., Denicola, 1996; Piggott et al., 2015). Lakes, as a type of aquatic environment, often experience heat waves and significant temperature variations. It has been observed that the average water temperature of lakes is rising worldwide (O'Reilly et al., 2015). Shallow lakes exhibit heightened hydrological sensitivity because of their significant surface-to-volume ratio and lack of persistent summer stratification. Consequently, they are more responsive to current meteorological conditions, including occasional extreme events, compared to deeper lakes. Even a slight fluctuation in temperature can lead to substantial alterations in the limnological and ecological characteristics of these systems (e.g., Hammer, 1990; Mooij et al., 2005). The worldwide degradation and loss of shallow aquatic habitats have already been documented (e.g., Williams, 2002; Mitsch, 2013). Algae play a crucial role in aquatic ecosystems and offer various advantages to humans. These include supporting functions such as primary production, biogeochemical cycling, and habitat creation, as well as regulate aspects like climate and biological control.

Additionally, they provide provisioning services through biotechnology and cultural services like inspiration and education. For more detailed information, refer to recent reviews by (B-Béres et al., 2023; Lengyel et al., 2023; Naselli-Flores and Padisák, 2023). Hence, a comprehensive and profound understanding of their reaction to climate change is imperative for the preservation of biodiversity and the welfare of humanity. The effects of temperature on phytoplankton have been extensively studied using laboratory experiments, field observations, and ecological models. These studies have predicted significant changes in phytoplankton. Examples of such studies include Dutkiewicz et al. (2013), Barton et al. (2016), Townhill et al. (2018), Filiz et al. (2020), Pálffy et al. (2021), and Yuan et al. (2023). Nevertheless, benthic algae have greater significance as primary producers in shallow environments (Stevenson et al., 1996) since they surpass planktonic output. According to Vadeboncoeur and Steinman (2002) and Wu (2016), oligotrophication or even eutrophication may enhance and intensify their significant impact. While research on phytobenthos is growing, studies on lotic communities are more prevalent than those on lakes (Zhao et al., 2023). Lakes are primarily associated with eutrophication (e.g., de Oliveira Carneiro and Ferragut, 2023) and trophic interactions (e.g., Ersoy et al., 2020; Cheng et al., 2023). Although global warming may have varying impacts on biota, such as those studied by Woolway et al. (2020), there have been limited investigations into the effects of elevated water temperatures on the benthic algal community. As a result, our understanding of this crucial aspect of vulnerable, shallow ecosystems remains incomplete. Phytobenthos research primarily focuses on diatom features rather than the overall community, despite advice to the contrary (Stoermer and Smol, 2001; Zhao et al., 2023; EC European Communities, 2000; Kelly, 2013). The existing research on the entire phytobenthos has primarily employed conventional community analyses based on taxonomy (e.g., Mahdy et al., 2015; Hao et al., 2018, 2020; Bondar-Kunze et al., 2021).

However, there is a notable scarcity of studies utilizing functional, trait-based approaches (Larras et al., 2013; Piggott et al., 2015), despite the urgent need for their implementation (Zhao et al., 2023). Although classification methods for functional categories have been established and utilized for phytoplankton, the organization of phytobenthos has only just commenced, as evidenced by the works of Berthon et al. (2011), B-Béres et al. (2016), Lange et al. (2016), and Lukács et al. (2018). Functional, trait-based approaches offer various benefits in comparison to species-based methods. These analyses do not necessitate extensive taxonomic knowledge but yield broad insights (e.g., Flynn et al., 2011) and more precise forecasts of ecosystem transformations (e.g., Abonyi et al., 2018; Stenger-Kovács et al., 2020a). As a result, we still don't fully understand how the expected rise in temperatures caused by climate change will affect all the plants and animals in lentic ecosystems.

Consequently, our understanding of the impact of increased temperatures caused by climate change on the entire phytobenthos in lentic ecosystems remains incomplete. Our primary objective was to empirically investigate the potential impacts of elevated temperatures projected by different climate scenarios (SPP2-4.5 and SPP5-8.5) on the lentic phytobenthos using both conventional and functional methods in the study.

II.2. Methodology

II.2.1. Experimental setup

The experiment was conducted in an outdoor mesocosm system located at the HUN-REN Balaton Limnological Research Institute in Tihany, Hungary (Pálffy et al., 2021). The system comprises 12 identical cylindrical plastic tanks, each with a diameter of 2 meters and a depth of 1.5 meters. As shown in Figure 5A, an insulated wall encloses these tanks. Every tank was furnished with a collection of sensors to record significant environmental factors directly at the location (such as temperature, irradiance, pH, redox potential, dissolved oxygen concentration, oxygen saturation, conductivity, TDS, salinity). Prior to the experiment, the tanks underwent a meticulous cleaning process and were sterilized by repeatedly flushing them with hot water at a temperature above 90 °C under high pressure. For the colonization and development of phytobenthos, we utilized clean limestone (travertine) slabs and cubes as a substratum. The slabs measured 5 × 5 × 1 cm, while the cubes measured 1 × 1 × 1 cm. Before filling the tanks, a total of 48 slabs were set in a circular pattern around the center of each tank base (Fig. 5 B). Furthermore, a total of 8 little cubes were positioned on flat, plastic supports and thereafter submerged to the depths of the tanks.

The water level in each tank was precisely maintained at a depth of 0.8 meters. The unprocessed freshwater was extracted from Lake Balaton by pumping it from a location around 100 meters away from the beach. Twenty-four bigger limestone bricks, each with a top surface of 10 × 10 cm, were submerged in the littoral zone of Lake Balaton at a depth of 20–30 cm. This was done two months before the experiment with the intention of allowing a mature biofilm to develop on the bricks. Subsequently, all the biofilms were meticulously rinsed into a compact plastic receptacle using a toothbrush, ensuring the exclusion of macroinvertebrates, particularly snails and their eggs. This concentrated and uniform sample of organisms that live at the bottom of a body of water was split into 50 mL portions that were used to add benthic algae, which are common in Lake Balaton, to each mesocosm tank.

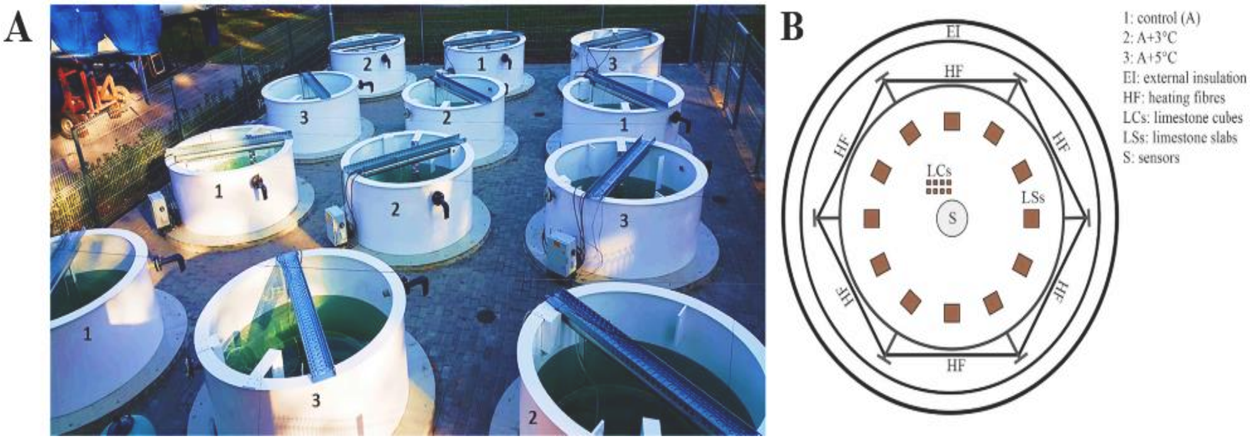

Figure 5 The mesocosm system **A** used in the present study from bird's eye view and **B** the schematic arrangement of the applied slabs on the bottom of the tanks.

II.2.2. Description of the experiment

In order to forecast the impacts of various climate change scenarios on benthic algae, the experiment was conducted concurrently with three temperature treatments (Fig.6). Each treatment was applied to four randomly chosen mesocosm tanks:

- Treatment 1: The temperature remains unheated and follows the natural fluctuations of the ambient temperature (A);
- Treatment 2: The temperature is constantly increased by 3 ˚C compared to the unheated control, simulating the SSP2-4.5 emissions scenario of IPPC (A+3);
- Treatment 3: The temperature is constantly increased by 5 ˚C compared to the unheated control, simulating the SSP5-8.5 emissions scenario of IPPC (A+5).

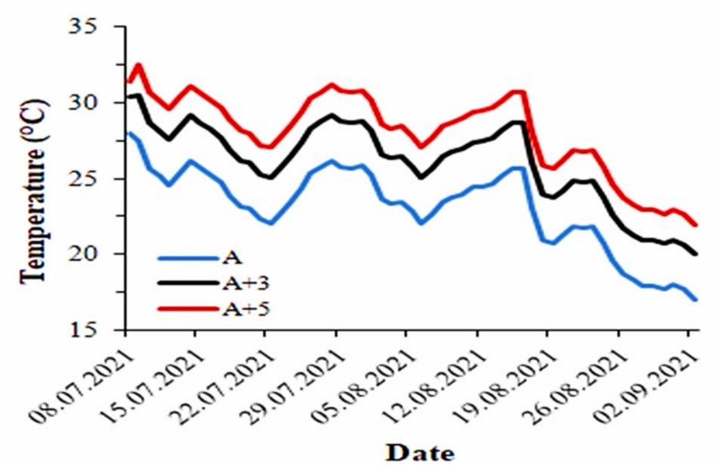

Figure 6 Temperature regimes in the mesocosms during the experiment based on the daily means.

The experiment was conducted over the summer of 2021, spanning 8 weeks from July 8th to September 2nd. Throughout the investigation, samples were collected on a weekly basis from each mesocosm tank in the following manner:

I. Six substrates of random selection, each measuring 5 × 5 × 1 cm, were extracted from each tank. The biofilm on the substrates was removed using a toothbrush and then mixed with 100 mL of filtered water. The water was filtered using a glass microfiber filter with a pore size of 0.7 μm, specifically the Whatman Grade GF/F filter. The filtered water was obtained from the same mesocosm. Portions of this standardized sample were utilized to analyze the taxonomic composition, chlorophyll a (Chl a) concentration, and photosynthetic efficiency of the phytobenthos (see section 4.2.3.).

II. Furthermore, a single substrate (measuring 1 × 1 × 1 cm) was randomly extracted from each tank in order to measure the biofilm's thickness.

II.2.3. Benthic algal samples analysis

Following each sampling session, the Chl a content of the samples was promptly measured by spectrophotometry after a methanolic extraction with hot methanol (Tett et al., 1975). The subsamples utilized for determining the composition of benthic algae were conserved in Lugol's solution until microscopic examination. The taxonomic identification of algal species was conducted using the standard Utermöhl (1958) approach. A total of 400 cells were observed and classified at the species and/or genus level using a light microscope (magnification of 400x, Zeiss Axiovert 100) with the assistance of taxonomic guides (von Berg et al., 2004; Komárek and Anagnostidis, 2007; Komárek, 2013; Moestrup and Calado, 2018; Coesel and Meesters, 2014; Buczkó, 2002). The assignment of each species to specific trait categories, such as cell volume, motility, life-forms, and kind of attachment, was determined based on the research conducted by Berthon et al. (2011), Lange et al. (2016), and Lukács et al. (2018). These categories are described in Table 4. The statistical studies utilized combinations of these traits rather than individual traits, as the former exhibit more sensitivity to environmental changes (e.g. Lukács et al., 2018; B-Béres et al., 2016). The biofilm thickness of the phytobenthos was determined promptly after sample using a Leica SP8 confocal microscope (Leica, Wetzlar, Germany) equipped with an HC PL APO CS 40×/0.85 dry objective and a TD 488/552/638 main beam splitter. Following a brief immersion in liquid agar to immobilize mobile cells, the substrates were inverted and placed onto a Greiner Bio-One 62861 CELLview Cell Culture Dish (Greiner AG, Kremsmünster, Austria). The diatom species described in this chapter are included in Appendix 1 including number of species and their traits.

Table 4: The applied traits and their categories

Cell size	Motility	Life forms	Attachment
<100 µm3 (S1)	Slow Movement (SM)	Unicellar (U)	Weak attachment (Wa)
100 – 299 µm3 (S2)	Fast Movement (FM)	Colonial (C)	Moderate attachment (Ma)
300 – 599 µm3 (S3)	Non-Motile (NM)	Filamentous (F)	Strong attachment (Sa)
600 – 1499 µm3 (S4)			
<1500 µm3 (S5)			

Subsequently, five random locations of interest were chosen on each substrate. The dimensions of these sections were 384 × 192 μm and 1024 × 512, with a pixel resolution of 188 nm/pixel. The 488 nm laser was used to stimulate both Chl a and phycobilisome autofluorescence, whereas the 638 nm laser was used exclusively for phycobilisome autofluorescence. The resulting fluorescence was monitored using PMT detectors within the spectral windows of 690–800 nm and 650–680 nm. Multiple photos were captured at various z-planes, each 5 μm apart, within the biofilm, spanning from the inner (limestone surface) to the outer layer. The biofilm thickness was estimated by measuring the distance between these two layers.

II.2.4. Statistical analyses

Statistical analyses were performed in the R statistical software (version 4.2.1., R Core Team, 2021) using the ‘vegan’ (Oksanen et al., 2022), ‘cluster’ (Maechler et al., 2022), ‘indicspecies’ (De Cáceres et al., 2022), ‘nlme’ (Pinheiro et al., 2022), and ‘FD’ (Laliberté et al., 2022) packages.

Dissimilarity indices in species composition were calculated between all sample pairs using (i) Bray-Curtis (based on abundance data) and (ii) Jaccard indices (based on presence-absence data). Linear regression models were developed to evaluate changes in the dissimilarity of the communities along the time scale. One-way ANOVA and Tukey’s post hoc test were used to examine whether the dissimilarity indices differed significantly among treatments. After Hellinger transformation of the species abundance data, Nonmetric Multidimensional Scaling (NMDS) was applied to analyze the benthic algae composition (species, algal groups, combined traits) of the three treatments. ADONIS2 analyses were performed to test whether the applied treatments resulted in significantly different compositions using 999 permutations. In case of significant difference, pairwise ADONIS tests were run to compare the treatments with each other.

SIMPER test was used to identify the species, algal groups, and combined traits which contribute the most to the differences among the treatments. After the identification of the optimal number of clusters by Mantel test, functional diversity index (RaoQ) was calculated based on the combined traits using the ‘dbFD’ function of the ‘FD’ package. In order to determine the most associated phytobenthos species with the different treatments, indicator species analysis (IndVal) was performed. In this analysis, components ‘A’ and ‘B’ refer to the specificity (the probability that the species belongs to the target treatment) and fidelity (the probability of finding the species in the given treatment), respectively.

Welch’s tests were conducted to examine whether the phytobenthos grown under the three temperature treatments had different species richness, Shannon- and functional diversity, Chl a content, biofilm thickness, and maximum quantum yield. Mixed-effects linear models were developed to clarify the interrelationship between these community parameters and the temperature treatments using hierarchical random factors (sampling time nested in treatments). In order to determine the most important parameters affecting the photosynthetic performance of the phytobenthos, a multivariate linear model was constructed using all possible parameters after their transformation to the same scale. This full model was reduced by a manual backward selection procedure based on the p-values. The similarity of the strength of the reduced and the full model was checked by F-test. Finally, partial coefficients were calculated for the comparison of the individual effect of each parameter in the reduced model.

II.3. Results

II.3.1. Structure of the phytobenthos

II.3.1.1. Classification at the phylum level

A total of 70 species were classified into several phyla, including Chlorophyta (34), Bacillariophyta (13), Cyanobacteria (13), Cryptista (3), Chrysophyta (3), Euglenozoa (3), and Rhodophyta (1). The NMDS analysis revealed that the temperature treatments had a substantial impact on the composition of benthic algae at the phylum level (ADONIS2 $R^2 = 0.17$, $p = 0.001$, Fig. 7 A, B). In terms of the pairwise statistical tests, there was no significant difference between treatments A and A+3. However, treatment A+5 showed a significant difference compared to both treatments A and A+3 (pairwise ADONIS, $p < 0.05$). The taxa Bacillariophyta, Chlorophyta, and Cyanobacteria were the primary contributors to the differentiation of these treatments. The presence of Bacillariophyta was mostly observed in treatments A and A+3, whereas Chlorophyta and Cyanobacteria were specifically related to treatment A+5.

II.3.1.2. Classification at the species level

NMDS analysis also showed significant differences in species compositions between all treatments (ADONIS2 $R^2 = 0.11$ and $p = 0.001$, Fig. 7 C, D). The pairwise values are as follows: A and A+3: $R^2 = 0.04$, $p = 0.048$; A and A+5: $R^2 = 0.12$, $p = 0.003$; A+3 and A+5: $R^2 = 0.08$, $p = 0.003$. Altogether, the species were determined to be indicator species through IndVal analyses (Table 5).

Specifically, one species (*Diatoma* sp.) was identified as an indicator for treatment A, two species (*Cyclotella* sp., *Navicula* sp.) were indicators for treatments A and A+3.

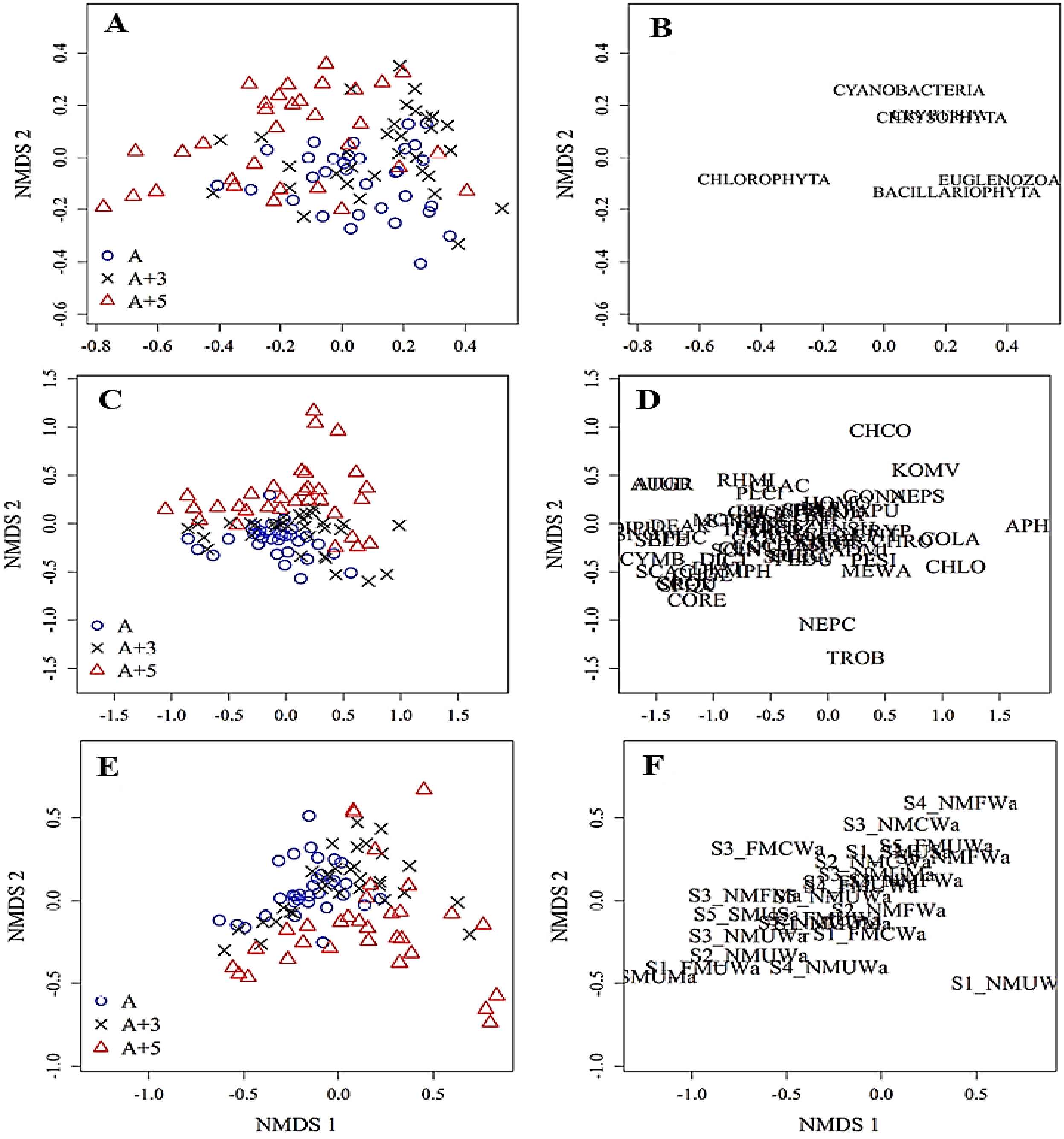

Figure 7. NMDS plots of phytobenthos samples based on the abundance data of algal phyla (A, B; stress: 0.12), species (C, D; stress: 0.15), and traits (E, F; stress: 0.17). The symbols in panels A and C represent the sampling events (n = 32 for each treatment), while panel B and D display their community composition (abbreviations, see Table 4).

The Bray-Curtis dissimilarity index, which measures the difference in species composition, varied between 0.24 and 0.50 (Fig. 8A) among the three treatments. In treatment A, there was no significant change over time, unlike the other two treatments which showed substantial positive associations ($R^2_{A+3} = 0.65$ and $p = 0.015$, $R^2_{A+5} = 0.58$ and $p = 0.028$). Both one-way ANOVA and Tukey's analysis revealed a significant difference only between treatments A and A+5 ($p = 0.002$). Like the Bray-Curtis dissimilarity index, the Jaccard dissimilarity index varied between 0.32 and 0.56 (Fig. 8 B). Nevertheless, the latter index remained somewhat stable over time in all the treatment. On the other hand, the Jaccard indices in treatment A+5 exhibited significantly higher values compared to treatments A ($p = 0.004$) and A+3 ($p = 0.039$).

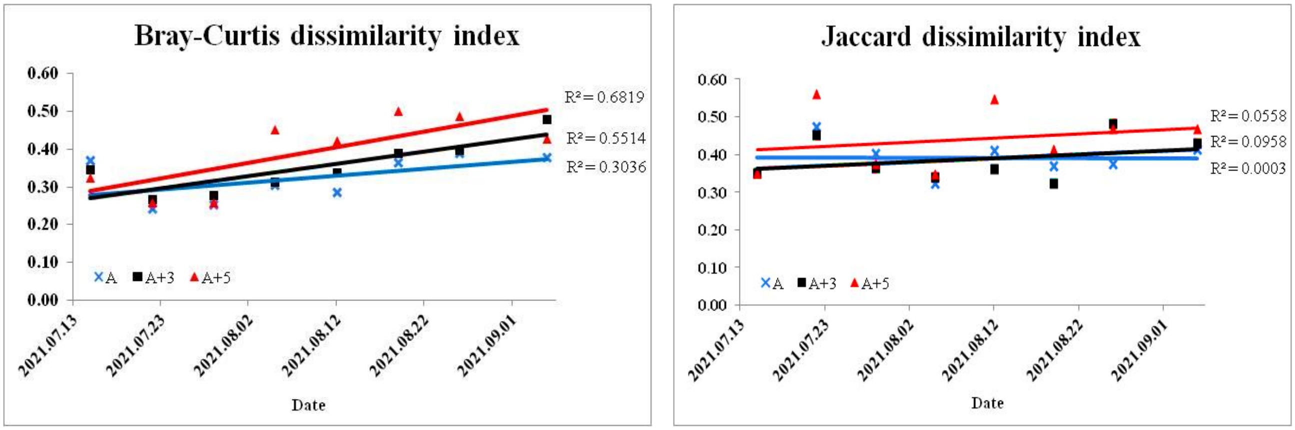

Figure 8. Temporal changes of the mean dissimilarity indices (n = 6, **A**: Bray-Curtis, **B**: Jaccard) along the three treatments.

Table 5: List of the most characteristic species and traits for each treatment, and the significance level between them (***$p < 0.001$, **$0.001 < p < 0.01$, *$0.01 < p < 0.05$), on the basis of the NMDS and SIMPER analysis, as well as the indicator values (Ind A: specificity, Ind B: fidelity) of indicator species based on the IndVal analysis.

Phylum	**Code**	**Full name**	**A**	**A+3**	**A+5**	**p (A - A+3)**	**p (A - A+5)**	**p (A+3 - A+5)**	**IndA**	**Ind B**	**treatments**
Bacillariophyceae	AUGR	*Aulacoseira granulata* (Ehrenberg) Simonsen			x		***	***			
	COCC	*Cocconeis* sp.	x			*					
	CENT	*Cyclotell*a sp.	x			**			0.92	0.48	A, A+3
	CYMB	*Cymbella* sp.	x			***	***				
	DIAT	*Diatoma* sp.	x			***	***		1.00	0.19	A
	EPIT	*Epithemia* sp.		x				*			
	GOMP	*Gomphonema* sp.	x				***				
	NAVI	*Navicula* sp.	x				***		0.93	0.91	A, A+3
Chlorophyta	AJUD	*Ankyra judayi* (G.M.Smith) Fott			x		***	***			
	CHGL	*Chlamydomonas globosa* J.W.Snow	x			*					
	CHCO	*Choricystis coccoides* (Rodhe & Skuja) Fott			x		***	***	0.91	0.90	A+5
	CLAC	*Closterium acutum* Brebisson			x		***	***			
	COMI	*Coelastrum microporum* Nageli		x		***		***			
	COLA	*Cosmarium laeve* Rabenhorst			x			**	0.90	0.16	A+5
	CRQU	*Crucigenia quadrata* Morren		x		***		***			
	SCQU	*Desmodesmus communis* (E.Hegewald) E. Hegewald		x		***		***			
	DICT	*Dictyosphaerium* sp.	x			***	***				
	GONA	*Gonatozygon* sp.			x		**				

	CORE	*Hariotina reticulata* P.A.Dangeard	x			***	***				
	KLEB	*Klebsormidium* sp.	x			***	***				
	MOCO	*Monoraphidium contortum* (Thuret) Komarkova-Legnerova			x		**	**			
	NEPC	*Nephrochlamys* sp.	x			***	***				
	NEPS	*Nephroselmis* sp.			x		***	***			
	PEDU	*Pediastrum duplex*	x			***	***				
	SCIN	*Schroederia indica*	x			**			0.96	0.28	A, A+3
	SPEX	*Spermatozopsis exsultans* Korshikov		x		***		***			
	SPHA	*Sphaerocystis* sp.			x		**	*			
	SPIR	*Spirogyra* sp.	x			***	***				
	TEOB	*Tetradesmus obliquus* (Turpin) M.J.Wynne	x			***	***				
Cyanobacteria	APHT	*Aphanothece* sp.		x		***		***	0.93	0.36	A+3, A+5
	CHRO	*Chroococcus* sp.		x				**			
	KOMV	*Komvophoron* sp.			x		*				
	LEPT	*Leptolyngbya* sp.			x		*	**			
	PLCI	*Limnolyngbya circumcreta* (G.S.West) X.Li & R. Li.			x			*			
Cryptista	CRYP	*Cryptomonas* sp.		x		*		*	0.90	0.44	A, A+3
	GYMN	*Gymnodinium* sp.	x			**					
	PAPU	*Parvodinium pusillum*		x				**			
Euglenozoa	ENSU	*Entosiphon sulcatus* (Dujardin) F.Stein		x		*					
	TROB	*Trachelomonas oblonga* Lemmermann	x			***	***				

II.3.1.3. Level of functionality

The temperature treatments were distinctly differentiated based on 16 features (ADONIS2 $R^2 = 0.13$, $p = 0.001$, Fig. 7 E, F; Table 6). Treatment A exhibited statistically significant distinctions compared to A+3 ($R^2 = 0.05$, $p = 0.03$), with the involvement of six traits. Treatment A+5 demonstrated significant differences compared to both A+3 ($R^2 = 0.08$, $p = 0.003$) and A ($R^2 = 0.15$, $p = 0.003$) based on seven and 11 traits, respectively. Based on the relative abundances, treatment A was mainly associated to higher biovolumes (≥S3), unicellular (U) and colonial (C) life-forms, stronger attachment (Ma or Sa), and the ability for movement (SM or FM). The relative abundance of species with a cell volume of S2 reduced in treatment A+3. Treatment A+5 exhibited small biovolumes (S2≤), a higher proportion of filamentous life-forms (F), weak attachment (Wa), and lack of motility (NM).

Table 6: List of the most characteristic traits for each treatment, and the significance level between them (***$p < 0.001$, **$0.001 < p < 0.01$, *$0.01 < p < 0.05$) on the basis of the NMDS and SIMPER analysis, as well as the indicator values (Ind A: specificity, Ind B: fidelity) of indicator species based on the IndVal analysis.

Code	**Full description**	**A**	**A+3**	**A+5**	**p (A - A+3)**	**p (A - A+5)**	**p (A+3 - A+5)**	**Ind A**	**Ind B**	**Treatments**
S1_FMUWa	<100 μm^3, fast movement, unicellar, weak attachment		x		***		***			
S1_FMCWa	<100 μm^3, fast movement, colonial, weak attachment			x		*	**			
S1_NMUWa	<100 μm^3, non-motile, unicellar, weak attachment			x		***	***			
S1_NMCWa	<100 μm^3, non-motile, colonial, weak attachment			x		*				
S2_NMUWa	100–299 μm^3, non-motile, unicellar, weak attachment		x		*					
S2_NMCWa	100–299 μm^3, non-motile, colonial, weak attachment		x				**			

S2_NMFWa	100–299 μm^3, non-motile, filamentous, weak attachment			x		***	*			
S3_FMUWa	300–599 μm^3, fast movement, unicellar, weak attachment	x				***				
S3_SMUMa	300–599 μm^3, slow movement, unicellar, moderate attachment	x			***	***				
S3_NMUWa	300–599 μm^3, non-motile, unicellar, weak attachment	x			**			0.92	0.48	A, A+3
S3_NMUMa	300–599 μm^3, non-motile, unicellar, moderate attachment	x				**				
S3_NMFMa	300–599 μm^3, non-motile, filamentous, moderate attachment	x			***	***				
S4_NMUWa	600–1499 μm^3, non-motile, unicellar, weak attachment			x		***	***			
S5_FMUWa	>1500 μm^3, fast movement, unicellar, weak attachment		x				**			
S5_SMUSa	>1500 μm^3, slow movement, unicellar, strong attachment	x			***					
S5_NMUWa	>1500 μm^3, non-motile, unicellar, weak attachment	x				*				
S5_NMFWa	>1500 μm^3, non-motile, filamentous, weak attachment		x			**				

*II.*3.2. *Phytobenthos Diversity*

II.3.2.1. Shannon and richness of the species

The species richness ranged from 7 to 29, with an average of 18 ± 4. In terms of treatments, the A+5 treatment showed a significantly reduced number of different species compared to both the A+3 treatment ($p = 0.01$) and the A treatment ($p < 0.001$) (Fig. 9A). An analysis using a mixed-effects linear model revealed a substantial decline in species richness as temperature increased ($p = 0.0015$), with a slope of 0.55/◦C (Fig. 9A).

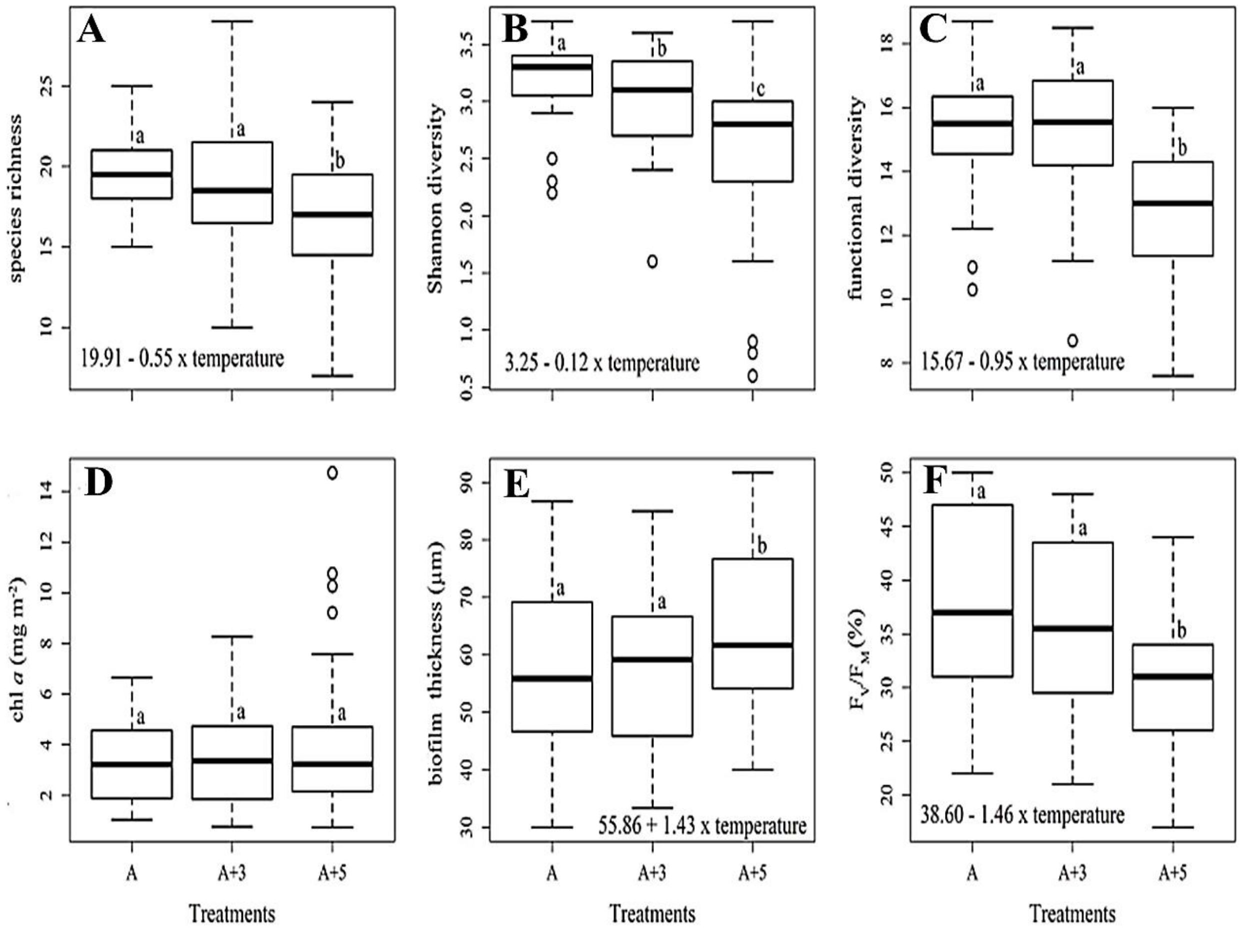

Figure 9. Boxplots of species richness **A**, Shannon **B,** and functional diversity **C**, Chl a content of the benthos **D**, biofilm thickness **E**, and the maximum quantum yield of PSII (F_V/F_M, **F**) in different treatments. Letters above the boxplots mark significant differences obtained by Welch's tests (groups marked with the same letters are not different, whereas groups with different letters differ significantly). Equations represent regression fits.

The Shannon diversity index varied between 0.6 and 3.7, with an average of 2.9 ± 0.7. Welch's tests indicated statistically significant variations in this index for each combination of treatments: A and A+3 ($p = 0.04$), A+3 and A+5 ($p = 0.003$), and A and A+5 ($p < 0.001$). Once again, a strong negative connection was observed with temperature ($p < 0.001$). The quantity dropped with a slope of 0.12 units/°C, as shown in Figure 9B.

II.3.2.2. Diversity in terms of functionality

The range of functional diversity (RaoQ) was between 7.6 and 18.7, with an average of 14.4 ± 2.5. Regarding the number of different species, there was no significant difference between treatment A and A+3 (Fig. 9C). However, the functional diversity was considerably reduced in treatment A+5 compared to both A+3 ($p < 0.001$) and A ($p < 0.001$). Similarly to the aforementioned two indices, a mixed-effects linear model demonstrated a statistically significant negative correlation between temperature and RaoQ ($p < 0.001$), with a slope of -0.95/°C.

II.3.3. Functional response of the phytobenthos associated with ecosystem services

II.3.3.1. Quantification of chlorophyll a

The chlorophyll a content of the phytobenthos varied between 0.7 and 14.7 mg m^{-2}, with an average of 3.7 ± 2.3 mg m^{-2}. According to Welch's tests, there was no statistically significant difference observed among the treatments. The mixed-effects linear regression analysis did not reveal any significant link with the temperature, as shown in Figure 9D.

II.3.3.2. The thickness of a biofilm.

The thickness of the biofilm revealed considerable variation, ranging from 30 to 91.7 µm (mean: 59.7 ± 14.3 µm). Furthermore, there were substantial differences in biofilm thickness observed across the different treatments, as depicted in Figure 9 E. Welch's tests detected statistically significant differences between treatments A and A+5 ($p = 0.02$), as well as between A+3 and A+5 ($p = 0.04$). The thickness of the biofilm exhibited a positive association with temperature ($p = 0.016$). This relationship was determined by a mixed-effects linear regression analysis, which revealed that the biofilm thickness increased at a rate of 1.4 µm /°C. Based on multivariate linear regression model using backward selection procedure, four parameters significantly affected the biofilm thickness. The abundance of Bacillariophytes, species richness and functional diversity had a negative correlation with this property of the phytobenthos, whilst the abundance of filamentous species positively affected it. (Table 7).

Table 7: Reduced multivariate linear models (*p* = 0.001) with partial correlation coefficients (r) and significance level (p) built among the biofilm thickness.

Biofilm thickness	**r**	***p***
Species richness	-2.10	0.01
Filamentous species abundance	0.51	0.01
Functional diversity	-2.64	0.02
Bacillariophyta abundance	-0.26	0.03

II.4. Discussion

Benthic algal composition is mostly determined by water temperature, a crucial environmental factor (Piggott et al., 2015). Significantly, it also influences/affects other abiotic parameters (e.g., sediment type, nutrient status, season) which, indirectly, can alter its main effects and may result in contentious mesocosm study findings (see, for example, Mahdy et al., 2015; Piggott et al., 2012, 2015; Hao et al., 2020; Pacheco et al., 2022). As such, experimental modification is necessary to clarify the effects of temperature (Piggott et al., 2015). Our study, which aimed to clarify the effects of global warming on benthic algae—a poorly researched field with contradicting findings up to this point—showed that the higher water temperature had a major impact on the structure and function of benthic algal communities.

II.4.1. Impact of global warming on the composition of phytobenthic communities

In the study of Hao et al. (2018) discovered that periphyton was less affected by a significant rise in global temperature (4.5 ˚C) compared to phytoplankton. In this investigation, as predicted by our theory, even a moderate (3.0 ˚C) emission scenario led to significant changes in the composition of the community at the species level and alterations in their dominance relationships. For example, there has been a decrease in the community of many diatoms, such as *Cymbella* sp.*, Navicula* sp.*, Nitzschia* sp.*, and Rhoicosphenia* sp. The benthic algal community revealed significant variability in this scenario, similar to that found in phytoplankton (Pálffy et al., 2021). Furthermore, the utilization of four characteristics (cell volume, motility, attachment, life-form) in this investigation proved to be strong, responsive, and reliable in detecting statistically significant distinctions among the treatments. Due to a rise in temperature, the benthic algae exhibited a drop in cell volume, an increase in filamentous forms, and a decrease in colonial life-forms. Decreasing in size is a commonly used approach in warmer environments for various aquatic organisms, including phytoplankton (Winder et al., 2009; Lewandowska and Sommer, 2010), periphyton (Larras et al., 2013; Piggott et al., 2015), snails (Sheridan and Bickford, 2011), and fishes (Gyllström et al., 2005; Meerhoff et al., 2007). Changes in the structure of algae, both colonial and filamentous, have been observed in the phytoplankton (Trochine et al., 2011; Rasconi et al., 2017). These changes are influenced by physical disturbances and the way they use resources, as indicated by previous studies (Trochine et al., 2011; Rasconi et al., 2017; Litchman et al., 2010).

The expected increase in water temperature, as indicated by the extremely high emissions scenario (5.0 ˚C), caused significant taxonomic changes that were evident even at a higher taxonomic level. Consistent with prior research, increased temperature clearly caused a transition in benthic algal communities, shifting them from being dominated by diatoms to being dominated by green algae and cyanobacteria (e.g., Piggott et al., 2015; Rasconi et al., 2017; Hao et al., 2018; Bondar-Kunze et al., 2021). Diatoms typically show a preference for lower temperatures (van der Grinten et al., 2005), with an optimum temperature for growth below 20 ˚C (Patrick et al., 1969; Cairns, 1956). While some diatoms can tolerate elevated temperatures, they are unable to outcompete Cyanobacteria due to their superior utilization of resources and, in certain instances, the creation of allelochemicals (van der Grinten et al., 2005). The increase in temperature also leads to variability in the benthic algal community. This variability is not limited to changes in dominance relationships, but also includes qualitative alterations. Based on the abundance data, both climate scenarios exhibited a consistent rise in variability over time, resulting in more unpredictable and stochastic effects. In relation to characteristics, the decrease in cell size will persist due to the anticipated rise in temperature resulting from the extremely high emissions scenario. small cell size offers several advantages, such as increased growth rates, rapid and efficient metabolism resulting from a thin diffusion boundary layer and a high surface-to-volume ratio, and improved resource utilization (e.g., more effective utilization of light; Litchman and Klausmeier, 2008; Litchman et al., 2010).

There is a limited amount of data available on how variations in temperature affect the life-forms of phytobenthos. Most of the available data focuses on streams, and the conclusions gained so far are conflicting. In lotic phytobenthos, increasing temperature has been found to have a positive effect on motility, as indicated by studies conducted by Piggott et al. (2015) and Lukács et al. (2018). Most studies on aquatic plant and algae communities agree that there is evidence indicating that temperature is negatively correlated with the abundance of species that can move (Piggott et al., 2015), and positively correlated with the quantity of species that cannot move

(Lukács et al., 2018). The study by Lukács et al. (2018) provided evidence supporting the detrimental impact of temperature on moderate attachment. The diversity of growth forms and sizes in the local algal species pool is crucial as it directly influences grazing and plant-animal interactions. Algal physiognomy, which varies among different growth forms, plays a significant role in determining their susceptibility to herbivory. Several studies (e.g., Tuchman and Stevenson, 1991; McCollum et al., 1998; Hillebrand et al., 2000) have highlighted the importance of these factors.

II.4.2. Impact of global warming on phytobenthos diversity

Even moderate levels of warming can lead to reduced species diversity and richness, as commonly observed in periphyton or periphytic diatoms (Piggott et al., 2015; da Silva et al., 2019; Hao et al., 2020), as well as in phytoplankton (Pálffy et al., 2021). Field data indicates that increased temperature had a detrimental impact on the diversity of various aquatic organisms, including zooplankton (Tavşanoğlu et al., 2017), macroinvertebrates (Li et al., 2013), and fish (Barbarossa et al., 2021).

According to our findings, if the temperature increases further, this process will become more severe, resulting in the loss of at least two species from the phytobenthos due to the most negative climate scenario. Species loss is a significant ecological phenomenon that has become a major problem in the 21st century. It has significant effects on ecosystem services, including primary productivity, nutrient cycling, and invasion resistance (e.g., Díaz et al., 2006). Moreover, a varied system likely shows enhanced ecosystem stability and resilience against many disruptions (Tilman et al., 2014). On the other hand, trait-based functional diversity dropped significantly (0.95/°C, Fig. 9 C) only when the temperature rose by 5 °C, which is what was expected in a high emissions scenario (SSP5-8.5), which supports our hypothesis. The negative change has significant ecological implications as it might threaten the ecological function of the ecosystem. This function can still be maintained even if there is a loss or decline of dominant species, due to the presence of less abundant but functionally similar species (Chillo et al., 2011).

II.4.3. The impact of global warming on the functioning of phytobenthos and its implications for ecosystem services

The climate change estimates had already shown substantial alterations in the functioning of the lotic benthic diatom community, resulting in a reduction in the thickness of the biofilm. The fundamental alterations in structure might threaten the formation of biofilm, its stability, primary production, and the higher trophic level (as discussed by Stenger-Kovács and B-Béres, Submitted). The present study, which focuses on the entire phytobenthos, does not support the projected structural alterations. Our study indicates that only the most pessimistic scenario of global warming has a notable impact on biofilm thickness, increasing it by approximately 1.5 µm/°C. This increase is accompanied by significant changes in the structure of the biofilm, as well as a reduction in species richness and functional diversity. The declining ratio of diatoms poses a direct risk to the stability of biofilms due to their secretion of EPSs, which play a crucial role in this process (e.g., Underwood and Paterson, 2003). The augmentation in the thickness of the biofilm, along with such alterations in its structure, may potentially lead to many significant ecological consequences. Therefore, the increased temperature predicted by the high emission scenario can lead to a decrease in the overall production of freshwater phytobenthos, as observed in other studies (Scharfenberger et al., 2019; McKee et al., 2003; O’Connor et al., 2009; Cao et al., 2014). Thicker biofilm plays a crucial function in nutrient recycling by removing dissolved nitrogen (N) and phosphorus (P) from the water column. It also helps sequence the entry of nutrients into the waterbody, occurring before phytoplankton. This process contributes to the promotion of a clear water condition, as discussed in the review by Vadeboncoeur et al. (2021).

Global warming can have an impact on the structure and dynamics of trophic systems, as demonstrated by Jeppesen et al. (2010). One example is the fish-snail-phytobenthos benthic trophic route, which plays a significant role in the food web of shallow aquatic ecosystems (Jeppesen et al., 2000). For example, when there are no fish present, global warming can intensify the influence of snails on periphyton through top-down control (Hansson et al., 2013; Cao et al., 2014; Cheng et al., 2023). According to our findings, none of the climate change scenarios resulted in notable alterations in the chlorophyll a content, which could potentially have adverse ecological implications.

Chapter III

An examination of the phenotypic response of diatoms to salinization[3***]

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Cover photo: by Tiba Jassam Kaison

[3***] Part of this chapter was published in the following paper:

Stenger-Kovács, C., Béres, V.B., Buczkó, K., Al-Imari, J.T., Lázár, D., Padisák, J. and Lengyel, E., 2023. Review of phenotypic response of diatoms to salinization with biotechnological relevance. Hydrobiologia, 1-24. https://doi.org/10.1007/s10750-023-05194-7.

Natural and human-induced salinization of aquatic environments is a global concern. Salt endangers aquatic life and ecosystems, which remains poorly understood despite increased scientific attention. Although recommendations for salinity thresholds are missing, salt changes may induce osmotic shock in aquatic organisms. Diatoms, as a major aquatic algal group, can response to salinization in many ways.

III.1. Introduction

Ancient civilizations recognized the salinization of aquatic habitats (Jacobsen and Adams, 1958), but it wasn't until the end of the twentieth century (e.g., Kirst, 1989) that it gained recognition as a local environmental issue. However, in recent years, it has escalated into a worldwide issue. Primary salinization, which refers to the formation of saline inland surface waters through natural processes, can occur (Rengasamy, 2006; Herbert et al., 2015). Additionally, anthropogenic activities such as mining, the use of fertilizers, the discharge of agricultural and industrial wastewaters, and the effects of climate change significantly contribute to the increased salinity of freshwaters, known as secondary salinization (Bąk et al., 2020; Liu et al., 2020). Salinity to the prevalence of glycophytes in many organisms, such as those studied by Sudhir and Murthy (2004) and Gupta and Huang (2014), salinity has become a significant evolutionary force (Latta et al., 2012). Salinity is one of the most critical environmental limitations, posing a threat to aquatic biota and, consequently, to the ecosystem services they provide (Cunillera-Montcus et al., 2022).

Although there has been an increase in scientific attention towards salinization (Fig. 10), there are still several areas of information that remain unclear (Cunillera-Montcusí et al., 2022). These gaps in understanding are crucial for comprehending and predicting the impacts of salinization on aquatic ecosystems, society, and the economy. Aquatic organisms can experience osmotic shock in several ways due to changes in salt quality and quantity. As a result, these substances can vary in their level of toxicity to living organisms. However, regulating and setting limits for salinity in water typically only establishes thresholds for irrigation and drinking. Unfortunately, there are currently no specific standards that address thresholds that can be lethal to aquatic organisms (Kunz et al., 2013; Caedo-Argüelles et al., 2016), and the existing standards may not provide adequate protection for these organisms (Hintz et al., 2022). Organisms strive to survive, regulate, and maintain their physiological integrity in adverse conditions. The presence of salt stress, which includes both osmotic and ionic stress, affects various physiological processes (Sudhir and Murthy, 2004; Parida and Das, 2005; Gupta and Huang, 2014). Phenotypic shifts, which incur significant costs for species (Coldsnow et al., 2017), are the underlying cause of the changes observed at the community and higher levels. Biota have the ability to tolerate a specific range of fluctuations in salinity. However, different organisms have unique mechanisms to cope with the stress of salt (Erdmann and Hagemann, 2001; Ma et al., 2010). The physiological adaptation of aquatic organisms to salt has been a topic of significant interest since the second decade of the twentieth century. During this time, various organisms such as higher plants (Karsten, 2012; Kumar et al., 2014), animals (Kinne, 1966; Larsen et al., 2014; Pourmozaffar et al., 2020), bacteria (da Costa et al., 1998; Ma et al., 2010), algae (Kirst, 1989), and cyanobacteria (Erdmann and Hagemann, 2001) have been the focus of several reviews on this topic.

However, none of these sources exclusively focused on diatoms. They mostly briefly referenced diatoms or discussed them in combination with other types of algae without providing detailed information (Kirst, 1989; Bisson and Kirst, 1995; Hagemann, 2016). Nevertheless, this taxonomically distinct group of algae is considered one of the most successful organisms in terms of both ecology and evolution. The clear differences in their silica cell wall and cell functions compared to other eukaryotic algae account for their unusual phenotypic responses to salinization

(Wilhelm et al., 2006). Studies by Schobert in 1974 and Liu and Hellebust in 1976 demonstrate that researchers have been studying the impact of osmotic stress on diatoms since the 1970s. The study efforts were intermittent and limited to a select few species.

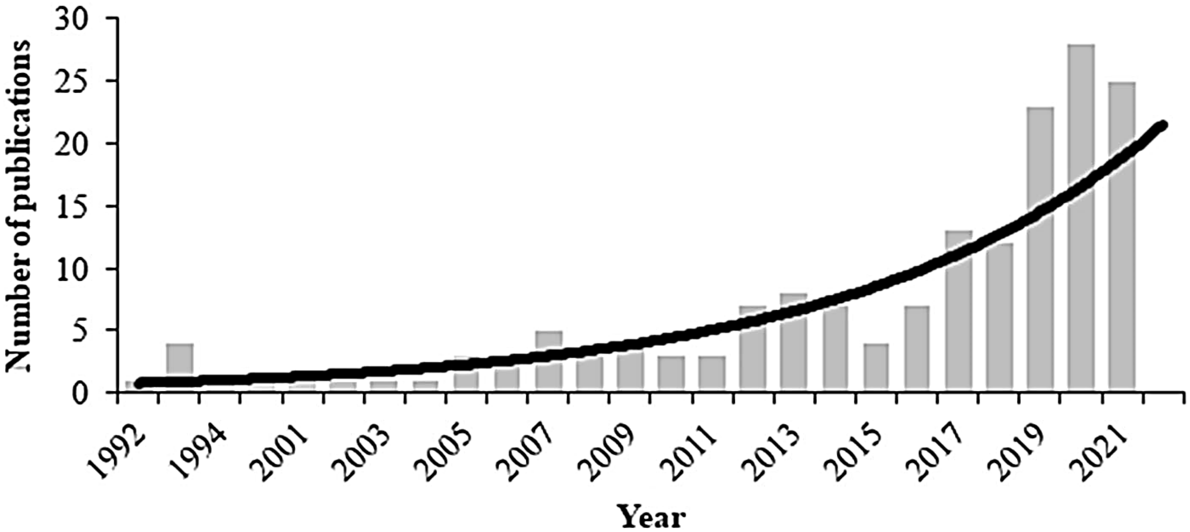

Figure 10. Number of publications focusing on salinization of aquatic ecosystems on the basis of Web of Science database (searching for "salinization in aquatic ecosystems" on June 13, 2022) and its trend (black line).

However, there isn't a lot of research on diatoms' physiological processes and how they adapt to their new environments, even though they play a big part in global primary production and the biogeochemical and nutrient cycles (Malviya et al., 2016; Struyf et al., 2009; Seckbach and Gordon, 2019). Furthermore, diatoms' salt-acclimation properties are noteworthy for other purposes. By employing their salt resistance strategy, diatoms can potentially offer opportunities for valuable and effective biotechnological applications (Seckbach and Gordon, 2019). As a result, this review aims to gather and synthesize the current ecophysiological understanding of diatoms, focusing on the impact of salinity on diatoms at cellular levels, their adaptive responses to osmotic pressure and their capacity to withstand varying ion concentrations. Appendix 2 includes the diatom species described in this review, along with their authors and currently recognized names.

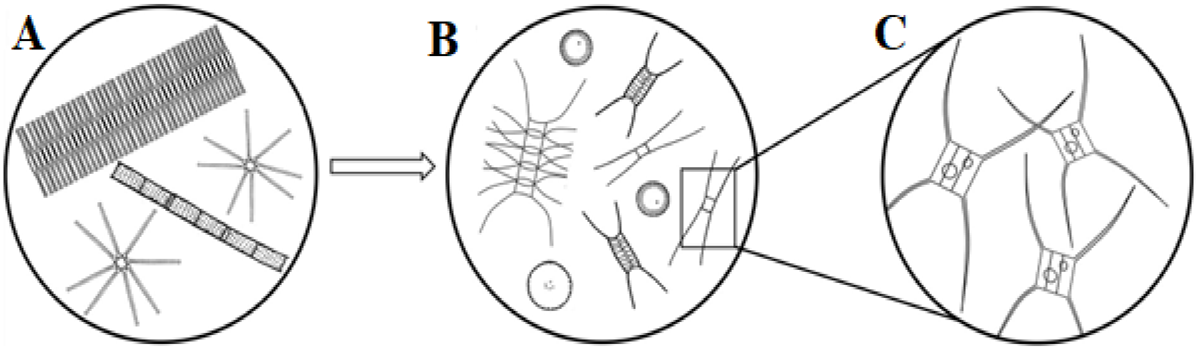

Figure 11 Shape resistance of diatoms to changing salinity in the phytoplankton: **A** common form of planktic diatoms in freshwaters. Diatom cells **B** with spines, chains, and **C** lipid materials in saline waters.

III.2. Diatom morphological reaction

Diatom species are very good at adapting to different environmental constraints, like salinity (Leterme et al., 2010), which causes many changes that can be seen in their physical features. Richter (1909) first revealed the relationship between salinity and morphological characteristics for *Nitzschia putrida* in the early twentieth century. Light microscopy easily observes the phenotypic alterations of diatoms, or only detects them at the nanoscale level. Diatoms may either retain their typical shape or undergo a full alteration in certain instances. The diversity of the gene pool determines this morphological plasticity (Cox, 2006). This adaptability can account for their ability to succeed in various, occasionally challenging habitats (Leterme et al., 2013). Conversely, these modified morphological characteristics can serve as indicators of shifts in environmental factors (Trobajo et al., 2004).

III.2.1. Shape resistance

The specific density of silica cell walls is 2.4 g cm-3, which is more than double the specific gravity of the protoplasm. Hence, diatoms have a heavy weight that prevents them from remaining suspended in a waterbody without easily adaptable processes. We can employ several evolutionary strategies, such as reducing size, decreasing specific gravity, and increasing resistance to form, to reduce the loss of species due to sedimentation (Naselli-Flores et al., 2021). The existence of *Chaetoceros*, a predominantly marine genus with only a few species adapted to live in continental saline waters, is particularly interesting in terms of shape resistance. The species utilizes a wide range of evolutionary processes to stay synchronized in the euphotic layers. The cells of diatoms are characterized by their tiny size, low level of silicification, and the presence of lipids as storage materials (Miller et al., 2014) (Fig. 11). These features contribute to the comparatively low weight of diatom cells compared to other types of cells. Also, cells on the valve often arrange themselves in chains and/or long structures, which makes it more resistant to deformation (Padisák et al., 2003) (Fig. 11).

These characteristics are predominantly common among *Thalassiosira* and *Acanthocera* species. Oceans, due to their large size and consistent conditions, serve as areas with high levels of biodiversity for diatoms (Potapova, 2011). Therefore, we can deduce that the diatoms mentioned above did not adapt to the increased salinization of freshwaters, but rather, they were unsuitable for it. They underwent evolutionary changes in response to typical marine conditions and gradually colonized areas with lower salt content, ultimately adapting to freshwater environments. This necessitated not only adaptation to relatively low salinity but also to the distinct ionic compositions of various environments. What is the reason for the limited presence of marine organisms in continental saline lakes? Waters with moderate salt concentrations are irregular and separated in both space and time. As a result, they act as barriers to migration in both directions (Potapova, 2011), which is the answer to the question. The divergence of freshwater and marine diatoms probably resulted from differences in their physiological thresholds (Potapova, 2011). Investigating this phenomenon requires conducting laboratory studies and utilizing Ecophysiological methods.

III.2.2. Dimorphism

Certain diatoms, such as *Cyclotella cryptica, C. meneghiniana, Anomoeoneis sphaerophora, Surirella peisonis,* and *Navicula cuspidata,* exhibit salinity-dependent dimorphism as a distinguishing feature. Low salinities (Fig. 12A) reveal the conventional valve structure, while high salinities (Schultz, 1971; Schmid, 1979) reveal post-auxospores. In some species, dimorphism is characterized by the presence of "*craticula*" and "*heribaudii*" structures. The normal vegetative cells produce these structures, which consist of four inner valves (two *craticulae* and two *heribaudii*). They develop as a protective response to high salt concentration or desiccation during the formation of resting spores (Schmid, 1979, 2009; web1). Only a few species of the *Craticula* genus (Levkov et al., 2016) have observed this phenomenon (Fig. 12B). Putting an organic covering on cells (*Thalassiosira weissflogii, Achnanthidium minutissimum, Navicula minima*; Vrieling et al., 2007) does the same thing and protects the cell from osmotic pressure (Gélabert et al., 2004).

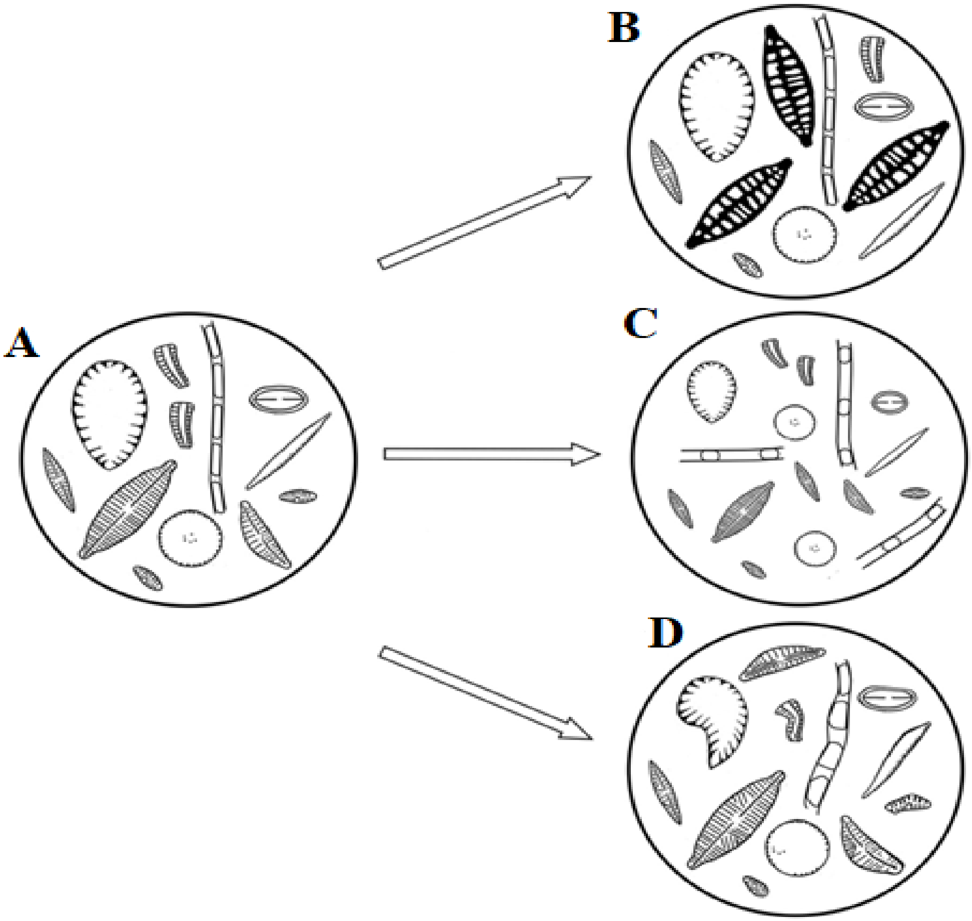

Figure 12 Morphological response of diatoms to increasing salinity: **A** the initial, normal forms of diatom species at lower salt concentration. The appearance of **B** “craticula” forms, **C** cell size reductions and altered chain morphologies, and **D** teratological forms with increasing salinity.

III.2.3. Polymorphism

The osmotic pressure that salinity generates can also influence the morphology of diatoms. It is possible for the distance between *Skeletonema subsalsum* and S. *potamos* Hasle cells (Fig. 12C) and the average number of cells in a chain to get bigger when the salinity (*S. subsalsum*) goes up. Under conditions of high salinity (35 psu), diatom species have the ability to increase the size of their individual cells, leading to shorter chains (Fig. 12C); furthermore, these cells may also experience an increase in the number of chloroplasts. This phenomenon has been observed in studies conducted by Hasle and Evensen (1975), Paasche et al. (1975), Sarno et al. (2007), Torgan et al. (2009), Balzano et al. (2011), and Falasco et al. (2021). Salinity can directly impact cell morphogenesis (Roubeix and Lancelot, 2008) by influencing the thickness of the silica wall. Specifically, the presence of external ionic strength influences the absorption of silicic acid and other ions, and the relative proportions of these ions regulate the process of silica polymerization. At high salinities, the clustering of small silica particles within the silica deposition vesicle is less pronounced, leading to the formation of thicker but more hydrated biosilica (Vrieling et al., 2007). For example, in the case of *Cyclotella meneghiniana* and *Thalassiosira pseudonana* (Olsen and Paasche, 1986), it was noted that these organisms had thin valves with underdeveloped spines and costae, and sometimes there were missing silica granules along the valve mantle in *Cyclotella meneghiniana* (Tuchman et al., 1984).

Thalassiosira pseudonana and *T. weissflogii* exhibit cell size reduction, as depicted in Figure 12C, while *Cyclotella meneghiniana* only experiences a decrease in the valve's height. These changes are observed at greater salinity levels, as reported by Hildebrand et al. (2006) and García et al. (2012). The decrease in height is caused by the turgor pressure that occurs during the interphase preceding cell division. Under conditions of high salinity, freshwater diatoms may struggle to achieve the same turgor pressure as they do under low salinity levels (Roubeix and Lancelot, 2008) due to their inability to produce a sufficiently high intracellular osmolarity. This leads to alterations in their size. In addition, an important characteristic observed at higher levels of heavy metal concentration is the reduced cell size of *Stephanodiscus minutulus, Brachysira vitrea, Asterionella formosa, Achnanthes minutissima,* and *Tabellaria flocculosa* (Lynn et al., 2000; Cattaneo et al., 2004; Su et al., 2018). The specific surface area and pore size of *Thalassiosira punctigera, Thalassiosira weissflogii, Cocconeis placentula,* and *Skeletonema* *subsalsum* increase when the salinity increases (Paasche et al., 1975; Vrieling et al., 2007; Leterme et al., 2010, 2013). The exchange of nutrients and other substances occurs through the nanoscale characteristics of the cell membrane through pores, which selectively filter molecules and nanoparticles based on their size (Fritz et al., 2010; Su et al., 2018). The species can maintain a consistent diffusive flux towards the cell by compensating for the size of the pores (Leterme et al., 2010). However, there are conflicting findings: Cocconeis pinnata exhibited a larger pore size but decreased surface area in conditions of elevated salinity, as observed by Leterme et al. (2013). There are additional instances where salinity has varying effects on the physical characteristics of diatom valves, such as changes in length, width, fibula, and stria density. This applies to both pennate and centric diatoms, including species such as *Nitzschia pusilla, N. frustulum, N. palea, N. filiformis var. conferta, Craticula subminuscula, Eolimna subminuscula, Gomphonema augur, Nitzschia palea var. debilis*, and *Stephanodiscus hantzschii*. These findings have been documented by various researchers (Geissler, 1968, 1970a, 1970b; Schultz, 1971; Jahn, 1986; Trobajo et al., 2011; Geissler, 1986). The inconsistent findings indicate that the alterations in morphology caused by salinity may vary depending on the taxonomic group or even the specific genetic clone (Trobajo et al., 2004).

III.2.4. Diatom teratological forms

Salinity can cause more pronounced, significant modifications in the valve structure, resulting in unusual forms (Noune et al., 2023) (Fig. 12D). Teratological forms are these noticeable changes and distorted shapes that can affect the physiological systems and cell mobility of diatoms (Falasco et al., 2009a). Salinity can cause notable changes in valve structure, such as changes in the number and location of the fultoportule (*Thalassiosira weissflogii*, Bussard et al., 2017; *Cyclotella meneghiniana*, Håkansson and Chepurnov, 1999), as well as the presence of irregular or missing areolae (*Synedra acus*, Basharina et al., 2012; *Thalassiosira eccentrica*, Schmid, 1984). In very salty environment, osmotic stress can change the shape of diatoms in many ways, including moving central nodules, breaking up raphae, changing the stria pattern (*Anomoeoneis costata, Anomoeoneis sphaerophora f. costata, Cyclotella meneghiniana*, Håkansson and Chepurnov, 1999; *Cyclotella cryptica*, Noune et al., 2023), and giving them strange valve shapes (*Navicula cryptocephala*, Aleem, 1950; *Navicula gregaria*, Cox, 1995; *Cyclotella cryptica*, Noune et al., 2023). These changes can make the identification of diatoms considerably difficult or even impossible (Castillo et al., 1995). In mining effluents, besides the high salinity, radioactive nuclides and high concentration of heavy metals further burden the aquatic ecosystems (Tipping et al., 2009), and besides the already mentioned teratological forms, further abnormal features can be detected as altered linear and central area in *Fragilaria capucina var. capitellata* (Falasco et al., 2009b), raphe modulations in *Cymbella excisa, Encyonema minutum* (Falasco et al., 2009b), Eunotia subarcuatoides (Furey et al., 2009), *Cocconeis sawensis* (Al-Handal et al., 2014), and Humidophila perpusilla (Millan et al., 2020), raphe canal adjustments in *Nitzschia* genus (Adshead-Simonsen et al., 1981), unusual colony forms in *Tabellaria flocculosa* with cells attached as straight chain colonies instead of the common zigzag form (Adshead-Simonsen et al., 1981), and mixed, substantially uncommon outline of the valves in *Fragilaria vaucheriae*, *Synedra vaucheriae, Encyonema sp., Planothidium frequentissimum,* and *Navicula tripunctata* (Falasco et al., 2009b). The recently published review on diatom teratology primarily focuses on deformities caused by salinity as a component of "multiple" impacts (Falasco et al., 2021) under extreme environmental conditions (Padisák and Naselli-Flores, 2021). Some of these conditions are high levels of sulfate and carbonate salts (*Cocconeis sawensis*, Al-Handal et al., 2014), natural radioactivity (*Crenotia angustior, Humidophila perpusilla, Planothidium frequentissimum,* Millan et al., 2020), low flow and high temperature, high UV radiation, geothermal flux, nutrient supply (*Cocconeis placentula*, *Nitzschia liebethruthii*, *Surirella chilensis*, Cabrol et al., 2007), and pollution from factories.

The genus *Tabularia* is mentioned as an example of collateral stress factor (Falasco et al., 2021) resulting in teratological forms of diatoms (Fig. 12D). While the external morphological changes are believed to be a result of intracellular changes in response to salinity, there is a lack of research on the connection between intracellular processes and cell wall morphogenesis, as evident from the limited information provided above, similarly, there is a scarcity of explanations regarding the regulation of valve morphology at the genetic level, as mentioned by Bussard et al. (2016). However, sulfhydryl (-SH) groups on the cell's outer surface (Lewin, 1954) control the process of silica absorption, which could potentially cause alterations in the organism's morphology due to their strong attraction to heavy metals and other toxic compounds (Cattaneo et al., 2004; Vrieling et al., 2007). The increasing amount of -SH binders decrease the absorption of silica and hinders the ATPs from functioning as active sites for the -SH groups (De La Rocha et al., 2000). Another possible reason is that elevated salt levels lead to the down-regulation of cytoskeletal genes. This, in turn, causes changes in gene expressions, leading to the repositioning of the silica deposition vesicle and subsequent changes in valve morphology (Bussard et al., 2016). In order to gain a deeper understanding of these morphological alterations, it is vital to expand our knowledge of molecular, physiological processes, and cell cycle regulation (Leterme et al., 2013). Acquiring this knowledge would enable us to comprehend the role of both plasticity and genetics in salinity tolerance, as well as the potential evolutionary response over time as salinity levels rise (Castillo et al., 2018).

Conclusion

Small lakes are crucial ecosystems for aquatic life and biodiversity. However, a lack of research on the impact of human-induces climate change and salinization on aquatic communities has limited our understanding of the risks these system face. Understanding the functions and response of these diatoms could be helpful in formulating affective conservation strategies. To address these difficulties, it is necessary to have a thorough understanding of the effects of these activities on aquatic ecosystems, which play a crucial role in regulating biogeochemical cycles and sustaining biodiversity. Studying boreal and tropical lakes is crucial from the perspective of their conservation and preservation.

Environmental parameters, such as nutrients and conductivity, more so than morphological reasons, influence the response of species-based communities in temperate forest ponds, even though the formation of lakes clearly triggers a functional response at a small scale. More precisely, variations in water depth and surface area lead to the emergence of a variety of species that are well-suited in terms of their size, shape, and lifeforms. Along this gradient, diatom communities' composition and functional diversity change. Our study demonstrates that multiple techniques are not interchangeable, as they provide distinct but complementary insights and data from an ecological, conservation, and management standpoint. To ensure the preservation of these distinct aquatic environments, it may be imperative to use a blend of these strategies.

The rise in water temperature, particularly under the intermediate emissions scenario (SSP2-4.5), might lead to substantial biological problems in freshwater ecosystems, contributing to the loss of biodiversity on our planet. Conversely, in the most pessimistic and highly emitting scenario, SSP5-8.5, we expect the freshwater benthic algal population to undergo significant and unforeseen environmental stress. The phytobenthos may experience significant alterations in both structure and function, leading to a wide range of ecological issues. Some of these factors are less net primary production, changes in water quality because macrophytes are being slowed down, more harmful algal blooms (HABs) because cyanobacteria are growing better, and changes to food webs because species and trait composition is changing. If there are very large emissions, the freshwater environment in question will likely see a drop in ecosystem services due to a decline in phytobenthos function.

Diatoms adapted a number of ways to salt, therefore they can even survive in high salinity environments. Environmental factors, such as salinity, influence the morphological plasticity of diatoms, which in turn influences the diversity of their gene pool. Salinity and heavy metals have the potential to modify the morphology of diatoms, thus affecting their physiological functions and cellular motility. Osmotic stress can lead to morphological changes, like alterations in surface area and pore size, thereby influencing nutrient and water exchange.

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On the field, the sampling of forest lakes was carried out with the assistance of many colleagues, including Dr. Edina Lengyel, Zsombor Sárkány, Katalin Hubai, Dávid Németh, Tamás Pálmai, Beáta Szabó, Géza Selmeczy, and János Korponai. The chemical laboratory analyses of all the samples of the forest lakes were performed through the collective efforts of the limnology department, involving many students, colleagues, and technicians.

For the mesocosm study, Edit Király who expertly identified the species involved. Máté Burányi provided essential support with sampling and other technical aspects, while Zoltán Novák's assistance with confocal microscopic analysis was invaluable. Gábor Bernát contributed significantly by aiding in the measurement of photosynthesis performance, and a key role in the experimental setup was carried out by Gergely Boros. The statistical analysis, writing, and functional analysis of the mesocosm study were carried out with the expert assistance of Dr. Edina Lengyel and Dr. Csilla Stenger-Kovács.

The preparation of diatom samples from the forest lakes (ponds) and as well as the identification of diatom species required detailed electron microscopic analysis were my own work. I performed all the statistical analyses of the forest lakes, with some help from Dr. János Korponai. I wrote the manuscript with a lot of assistance from Dr. Csilla Stenger-Kovács and Dr. Edina Lengyel. I participated in the diatom collection, as well as the sampling and preparation of the mesocosm research. I actively participated in the Balaton Lake sampling process and contributed to the laboratory analysis of the collected water samples. Additionally, I assisted in identifying diatoms in several other samples. I collected all of the studies related to the impact of salt on diatoms and prepared the section specifically addressing the teratology aspect of the salinization study.

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Significant results in thesis points

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

The findings of this research, even though small lakes have a small-scale functional response, environmental characteristics such as nutrients and conductivity have a greater impact on species-based communities in temperate forest ponds than morphology. Variations in water depth and surface area cause the formation of species with suitable size, shape, and lifeforms. Diatom communities' composition and functional diversity shift along this gradient. Our study shows that diverse methods give different but complementary ecological, conservation, and management insights and data. We may need to combine these methods to preserve these aquatic habitats.

II. *exImpacts of global warming on freshwater lake phytobenthos and their functions*

To summarize, the intermediate emission scenario predictably induces a high risk in terms of biodiversity concerns, while the high emission scenario will bring about significant consequences on the benthic algae, putting even the function of the ecosystem in threat.

III. *An examination of the phenotypic reaction of diatoms to salinization*

Research on salinity tolerances in diatoms is limited, with little understanding of key processes and energy costs. Long-term investigations are needed to detect diatom salinization adaptation and control ecological and economic effects. Morphological changes, such as shape resistance and species-specific variations, can be explained by increasing salinity. Diatoms have various phenotypic responses to salinity, but knowledge about their molecular background and long-term adaptation is missing.

List of academic activities during the doctoral training

1. *Papers related to the thesis.*

Al-Imari, T.J.K., Lengyel, E., Korponai, J., Padisák, J. and Stenger-Kovács, C., 2023. Lake morphology as an important constraint for benthic diatoms in temperate, humic forest ponds. Ecological Indicators, 155, 110939. ***IF: 6.9, SJR: Q1.***

Lengyel, E., Stenger-Kovács, C., Boros, G., **Al-Imari, T.J.K.,** Novák, Z. and Bernát, G., 2023. Anticipated impacts of climate change on the structure and function of phytobenthos in freshwater lakes. Environmental Research, 238, 117283. ***IF: 8.3, SJR: Q1.***

Stenger-Kovács, C., Béres, V.B., Buczkó, K., **Al-Imari, T.J.,** Lázár, D., Padisák, J. and Lengyel, E., 2023. Review of phenotypic response of diatoms to salinization with biotechnological relevance. Hydrobiologia, 1-24. ***IF: 2.6, SJR: Q1.***

2. *Congress attendances related to the thesis.*

Tiba Jassam Kaison Al-Imari, Andrea Losteiner, Edina Lengyel and Csilla Stenger-Kovács. Limnological features of small, intermittent lakes in Hungary. 12th Symposium for European Freshwater Science (SEFS 12), online conference. 25-30 Jul 2021. ***Poster presentation***.

Al-Imari Tiba Jassam Kaison, Lengyel Edina, Csilla Stenger-Kovács. Diatoms community and environmental variables of shallow, brownish forest lakes in Hungary. A Magyar Hidrológiai Társaság, Tihany, Hungary, 6th -8th October 2021. ***Oral presentation***.

Tiba Jassam Kaison Al-Imari, Edina Lengyel and Csilla Stenger-Kovács. Functional analyses of benthic diatoms in brownish forest lakes, Hungary. 8th Conference of the Czech Society for Ecology, Czech Republic 2022, szeptember 7-9. ***Poster presentation***.

Edina Lengyel, Csilla Stenger-Kovács, Gergely Boros, Zoltán Novák, Tiba Jassam Kaison Al-Imari, Gábor. Bernat. A klímaváltozás bentikus algaközösségre való hatásának előrejelzése. LXIII. Hidrobiológus Napok, Tihany, Hungary, 2022. October 5-7. ***Oral presentation***.

Lengyel Edina, Stenger-Kovács Csilla, Boros Gergely, Novák Zoltán, **Al-Imari Tiba Jassam Kaison**, Bernát Gábor. A klímaváltozás hatása a fitobentoszra. XV. Algológiai Találkozó és Továbbképzés, Debrecen, Hungary, 8-9 November 2023. ***Oral presentation***.

3. *Other oral presentation attendance*

The 13th European Diatom Meeting (formerly Central European Diatom Meeting) hosted online by Amgueddfa Cymru – National Museum Wales, 2 - 3 March, 2021.

Appendixes

Appendix1: List of trait and combined traits used in Chapter II according to the applied traits in Table 4 (n.e: not existing traits).

Biovolume	Motility	Lifeform	Attachment	Number of species
S1	SM	U	Wa	0
S1	SM	U	Sa	2
S1	SM	U	Ma	0
S1	SM	F	Wa	n.e.
S1	SM	F	Sa	n.e.
S1	SM	F	Ma	n.e.
S1	SM	C	Wa	0
S1	SM	C	Sa	n.e.
S1	SM	C	Ma	0
S1	FM	U	Wa	1
S1	FM	U	Sa	n.e.
S1	FM	U	Ma	n.e.
S1	FM	F	Wa	n.e.
S1	FM	F	Sa	n.e.
S1	FM	F	Ma	n.e.
S1	FM	C	Wa	1
S1	FM	C	Sa	n.e.
S1	FM	C	Ma	n.e.
S1	NM	U	Wa	4
S1	NM	U	Sa	0
S1	NM	U	Ma	1
S1	NM	F	Wa	0
S1	NM	F	Sa	n.e.
S1	NM	F	Ma	0
S1	NM	C	Wa	10
S1	NM	C	Sa	n.e.
S1	NM	C	Ma	0
S2	SM	U	Wa	0
S2	SM	U	Sa	1
S2	SM	U	Ma	0
S2	SM	F	Wa	n.e.
S2	SM	F	Sa	n.e.
S2	SM	F	Ma	n.e.
S2	SM	C	Wa	0
S2	SM	C	Sa	n.e.
S2	SM	C	Ma	0

S2	FM	U	Wa	2
S2	FM	U	Sa	n.e.
S2	FM	U	Ma	n.e.
S2	FM	F	Wa	n.e.
S2	FM	F	Sa	n.e.
S2	FM	F	Ma	n.e.
S2	FM	C	Wa	0
S2	FM	C	Sa	n.e.
S2	FM	C	Ma	n.e.
S2	NM	U	Wa	2
S2	NM	U	Sa	0
S2	NM	U	Ma	0
S2	NM	F	Wa	3
S2	NM	F	Sa	n.e.
S2	NM	F	Ma	0
S2	NM	C	Wa	8
S2	NM	C	Sa	n.e.
S2	NM	C	Ma	0
S3	SM	U	Wa	0
S3	SM	U	Sa	0
S3	SM	U	Ma	1
S3	SM	F	Wa	n.e.
S3	SM	F	Sa	n.e.
S3	SM	F	Ma	n.e.
S3	SM	C	Wa	0
S3	SM	C	Sa	n.e.
S3	SM	C	Ma	0
S3	FM	U	Wa	6
S3	FM	U	Sa	n.e.
S3	FM	U	Ma	n.e.
S3	FM	F	Wa	n.e.
S3	FM	F	Sa	n.e.
S3	FM	F	Ma	n.e.
S3	FM	C	Wa	2
S3	FM	C	Sa	n.e.
S3	FM	C	Ma	n.e.
S3	NM	U	Wa	1
S3	NM	U	Sa	0
S3	NM	U	Ma	2
S3	NM	F	Wa	1
S3	NM	F	Sa	n.e.
S3	NM	F	Ma	2
S3	NM	C	Wa	2

S3	NM	C	Sa	n.e.
S3	NM	C	Ma	0
S4	SM	U	Wa	0
S4	SM	U	Sa	0
S4	SM	U	Ma	0
S4	SM	F	Wa	n.e.
S4	SM	F	Sa	n.e.
S4	SM	F	Ma	n.e.
S4	SM	C	Wa	0
S4	SM	C	Sa	n.e.
S4	SM	C	Ma	0
S4	FM	U	Wa	5
S4	FM	U	Sa	n.e.
S4	FM	U	Ma	n.e.
S4	FM	F	Wa	n.e.
S4	FM	F	Sa	n.e.
S4	FM	F	Ma	n.e.
S4	FM	C	Wa	0
S4	FM	C	Sa	n.e.
S4	FM	C	Ma	n.e.
S4	NM	U	Wa	1
S4	NM	U	Sa	0
S4	NM	U	Ma	0
S4	NM	F	Wa	2
S4	NM	F	Sa	n.e.
S4	NM	F	Ma	0
S4	NM	C	Wa	0
S4	NM	C	Sa	n.e.
S4	NM	C	Ma	0
S5	SM	U	Wa	0
S5	SM	U	Sa	1
S5	SM	U	Ma	0
S5	SM	F	Wa	n.e.
S5	SM	F	Sa	n.e.
S5	SM	F	Ma	n.e.
S5	SM	C	Wa	0
S5	SM	C	Sa	n.e.
S5	SM	C	Ma	0
S5	FM	U	Wa	3
S5	FM	U	Sa	n.e.
S5	FM	U	Ma	n.e.
S5	FM	F	Wa	n.e.
S5	FM	F	Sa	n.e.

S5	FM	F	Ma	n.e.
S5	FM	C	Wa	0
S5	FM	C	Sa	n.e.
S5	FM	C	Ma	n.e.
S5	NM	U	Wa	3
S5	NM	U	Sa	0
S5	NM	U	Ma	0
S5	NM	F	Wa	3
S5	NM	F	Sa	n.e.
S5	NM	F	Ma	0
S5	NM	C	Wa	0
S5	NM	C	Sa	n.e.
S5	NM	C	Ma	0

Appendix 2: Diatom species with their authors and currently accepted names that are mentioned in Chapter III.

Published name	**Authors**	**Recently accepted names**	**Authors**
Achnanthes coarctata	(Brébisson ex W.Smith) Grunow	-	-
Achnanthes delicatula subsp. hauckiana	(Grunow) Lange-Bertalot & Ruppel	*Planothidium hauckianum*	(Grunow) Bukhtiyarova
Achnanthes minutissima	Kützing	*Achnanthidium minutissimum*	(Kützing) Czarnecki
Amphora angusta	W.Gregory	-	-
Amphora coffeaeformis	(C.Agardh) Kützing	*Halamphora coffeiformis*	(C.Agardh) Mereschkowsky
Anomoeoneis sphaerophora	Pfitzer	-	-
Anomoeoneis sphaerophora f. costata	(Kützing) A.-M.Schmid	*Anomoeoneis costata*	(Kützing) Hustedt
Asterionella formosa	Hassall	-	-
Brachysira vitrea	(Grunow) R.Ross	-	-
Chaetoceros muelleri	Lemmermann	-	-
Chaetoceros cf. wighamii	Brightwell	-	-
Cocconeis pinnata	(Hustedt) A.Cleve	*Achnanthes conspicua*	Ant.Mayer
Cocconeis placentula	Ehrenberg	-	-
Cocconeis sawensis	A.Y.Al-Handal & C.Riaux-Gobin	-	-
Crenotia angustior	(Grunow) Wojtal	-	-
Cyclotella cryptica	Reimann, J.C.Lewin & Guillard	*Stephanocyclus cryptica*	Reimann, Levin & Guillard) Kulikovskiy, Genkal & Kociolek
Cyclotella meneghiniana	Kützing	*Stephanocyclus meneghinianus*	(Kützing) Kulikovskiy, Genkal & Kociolek
Cylindrotheca closterium	(Ehrenberg) Reimann & J.C.Lewin	-	-
Cylindrotheca fusiformis	Reimann & J.C.Lewin	-	-
Cymbella excisa	Kützing	-	-
Cymbella pusilla	Grunow	*Navicymbula pusilla*	Krammer
Detonula confervacea	(Cleve) Gran	-	-
Ditylum brightwellii	(T.West) Grunow	-	-
Encyonema minutum	(Hilse) D.G.Mann	-	-
Eolimna subminuscula	(Manguin) Gerd Moser, Lange-Bertalot & Metzeltin	*Craticula subminuscula*	(Manguin) C.E.Wetzel & Ector
Eunotia subarcuatoides	Alles, Nörpel & Lange-Bertalot	-	-
Fragilaria capucina var. capitellata	(Grunow) Lange-Bertalot	-	-
Fragilaria crotonensis	Kitton	-	-
Fragilariopsis cylindrus	(Grunow ex Cleve) Helmcke & Krieger	-	-
Fragilariopsis nana	(Steemann Nielsen) Paasche	*Fragilariopsis pseudonana*	(Hasle) Hasle
Gomphonema augur	Ehrenberg		
Humidophila perpusilla	(Grunow) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	-	-
Navicula cryptocephala	Kützing	-	-
Navicula cuspidata	(Kutzing) Kutzing	*Craticula cuspidata*	(Kutzing) D.G.Mann

Navicula gregaria	Donkin	-	-
Navicula minima	Grunow	-	-
Navicula phyllepta	Kützing	-	-
Navicula tripunctata	(O.F.Müller) Bory	-	-
Neidiomorpha binodis	(Ehrenberg) M.Cantonati, Lange-Bertalot & N.Angeli	-	-
Nitzschia americana	Hasle	*Pseudo-nitzschia americana*	(Hasle) Fryxell
Nitzschia aurariae	Cholnoky	-	-
Nitzschia constricta	(Kützing) Ralfs	*Tryblionella apiculata*	W. Gregory
Nitzschia filiformis var. conferta	(P.G.Richter) Lange-Bertalot	-	-
Nitzschia frustulum	(Kützing) Grunow	-	-
Nitzschia laevis	Hustedt	*Nitzschia amibilis*	H. Suzuki
Nitzschia liebetruthii	Rabenhorst	-	-
Nitzschia ovalis	H.J.Arnott	-	-
Nitzschia palea	(Kützing) W.Smith	-	-
Nitzschia palea var. debilis	(Kützing) Grunow	-	-
Nitzschia pusilla	Grunow	-	-
Nitzschia putrida	(Cohn) Benecke	-	-
Nitzschia reskoi	Ács, Duleba, Wetzel & Ector	-	-
Nitzschia supralitorea	Lange-Bertalot	-	-
Phaeodactylum tricornutum	Bohlin	-	-
Planothidium frequentissimum	(Lange-Bertalot) Lange-Bertalot	-	-
Pseudo-nitzschia australis	Frenguelli	-	-
Pseudo-nitzschia multiseries	(Hasle) Hasle	-	-
Pseudo-nitzschia pseudodelicatissima	(Hasle) Hasle	-	-
Pseudo-nitzschia pungens	(Grunow ex Cleve) Hasle	-	-
Skeletonema potamos	(C.I.Weber) Hasle	-	-
Skeletonema subsalsum	(A.Cleve) Bethge	-	-
Stephanodiscus hantzschii	Grunow	-	-
Stephanodiscus minutulus	(Kützing) Cleve & Möller	-	-
Surirella chilensis	C.Janisch	-	-
Surirella peisonis	Pantocsek	-	-
Synedra acus	Kützing	*Ulnaria acus*	(Kützing) Aboal
Synedra vaucheriae	(Kützing) Kützing	Fragilaria vaucheriae	(Kützing) J.B.Petersen
Tabellaria flocculosa	(Roth) Kützing	-	-
Thalassiosira eccentrica	(Ehrenberg) Cleve	-	-
Thalassiosira oceanica	Hasle	-	-
Thalassiosira rotula	Meunier	*Thalassiosira gravida*	Cleve
Thalassiosira pseudonana	Hasle & Heimdal	-	-
Thalassiosira punctigera	(Castracane) Hasle	-	-
Thalassiosira weissflogii	(Grunow) G.A.Fryxell & Hasle	Conticribra weissflogii	(Grunow) Stachura-Suchoples & D.M.Williams