STUDIA BOTANICA HUNGARICA
(Antea: Fragmenta Botanica)
Volume 56(1) 2025

Hungarian National Museum Public Collection Centre, Budapest
Hungarian Natural History Museum
Budapest, 2025

Magyar Nemzeti Múzeum
Közgyűjteményi Központ

Hungarian National Museum Public Collection Centre, Budapest
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MINISTRY OF CULTURE AND INNOVATION

Studia bot. hung. 56(1), 2025

This volume was supported by the Hungarian Academy of Sciences.

Studia botanica hungarica is indexed in Biological Abstracts, CAB Abstracts and Magyar Tudományos Művek Tára (MTMT), archived by REAL-J.

The front cover picture is a line drawing of *Iris hungarica* W. et K. 1807 published in Kitaibel's *Descriptiones et icones plantarum rariorum Hungariae* (Vol. III, tab. 226). Today it is considered as a subspecies of *Iris aphylla* L. It is a characteristic member of forest-steppes in NE Hungary (Zemplén Mts, Szendrőlád, Nyírség). It also occurs in Romania, Slovakia and Ukraine.

K. DOBOLYI

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SPECIAL VOLUME
DEDICATED FOR THE 70TH BIRTHDAY OF
PROF. DR JUDIT PADISÁK, FULL MEMBER OF THE
HUNGARIAN ACADEMY OF SCIENCES

DOI: 10.17110/StudBot.2025.56.1.5 Studia bot. hung. 56(1), pp. 5–6, 2025

PREFACE

Gábor BORICS

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This volume contains 12 studies dealing mainly with various aspects of microalgal ecology including planktic, benthic, and metaphytic assemblages of various aquatic habitats and their relations to climate change, environmental constraints, and methodological differences. What is common in these studies is that their authors are all researchers whose scientific careers were inspired by Professor Judit Padisák, one of the most influential phytoplankton ecologists, who turned 70 this year. The authors dedicated their works to Judit, whose life has always been defined by openness, scientific excellence, intellectual generosity, and an unwavering commitment to the advancement of ecology. Her scientific approach has fundamentally been shaped by the recognition that the organization and functioning of microbial assemblages of waters should not differ from those of the terrestrial systems, because the laws of ecology are universally valid regardless of size. Judit has the ability to recognize the essential elements of how the various ecosystems work and thus finds parallels between terrestrial systems and phytoplankton, although these operate at completely different scales of size and time. She boldly applied succession models of terrestrial vegetation to phytoplankton, or the Intermediate Disturbance Hypothesis to understand diversity changes of phytoplankton. She also recognized the importance of functional groups and traits of phytoplankton species in phytoplankton ecology and knew that these not only support the understanding of the functioning of these systems, but can serve as a basis for developing ecological status assessment methods that can be used to quantitatively describe water quality, which is the first step to their preservation.

Beyond her own scientific accomplishment, Judit Padisák has built international collaborations and played a central role in educating and mentoring of future ecologists in various universities on four continents. She supervised almost thirty PhD students from many countries. Her style of mentorship is characterised by encouragement and high standard. These have enabled her mentees to become professionals in their field. Many of them are now leading research groups and departments and play a key role in teaching, research, and practical hydrobiology in their countries.

Judit's public appearances can be found on numerous platforms. Each of these exudes authenticity, backed by more than forty years of research experience and numerous problems that have been experienced and solved.

This special issue of *Studia botanica hungarica* comprises a selection of scientific papers that reflect the breadth and depth of Judit Padisák's influence, from theoretical contributions to applied ecological research. This book is a tribute to a scientist whose career exemplifies the openness, power of curiosity, critical thinking, and to a mentor whose impact lives on in the work of younger generations of scientists.

The authors offer this volume with deep appreciation, for a lifetime of scientific discovery, for the countless students and colleagues Judit has inspired, and for the enduring mark she has left on our understanding of aquatic life.

DOI: 10.17110/StudBot.2025.56.1.7 *Studia bot. hung. 56(1), pp. 7–14, 2025*

ON THE TRAIL OF THE HUNGARIAN SILICA-SCALED CHRYSOPHYTES: A HISTORICAL REVIEW

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Lengyel, E. (2025): On the trail of the Hungarian silica-scaled chrysophytes: a historical review. – *Studia bot. hung.* **56**(1): 7–14.

Abstract: Silica-scaled chrysophytes form a unique group of protists and have significant contribution to ecosystem services (provisioning, supporting, regulating, and cultural services). In Hungary, scientific research on silica-scaled chrysophytes actually began in the early 1990s, since has undergone rapid development. Professor Judit Padisák, a leading figure in Hungarian hydrobiology and limnoecology, played a key role in this field. The development of Hungarian research was made possible not only by her personal scientific commitment, but also by her national and international cooperation efforts. Therefore, the present paper summarises the history of Hungarian research on silica-scaled chrysophytes in honour of Professor Judit Padisák's passion and scientific works.

Key words: chrysophyceae, history, Hungary, Judit Padisák, recent flora

INTRODUCTION

Chrysophytes belong to the superkingdom of Eukaryota, clade of Stramenopiles, phylum of Ochrophyta, and class of Chrysophyceae (Kristiansen and Škaloud 2017, Schoch *et al.* 2020) forming many genetically and morphologically distinct lineages. Within this algal group, there are many species with siliceous coverage (scale, spine, bristle) including *Chrysosphaerella*, *Lepidochromonas*, *Mallomonas*, *Neotessella*, *Paraphysomonas*, *Polylepidomonas*, *Spiniferomonas*, and *Synura* (Kapustin and Gusev 2019, Kristiansen and Preisig 2007, Kristiansen and Škaloud 2017). This ultrastructure is the basis of the well-developed taxonomic system for species differentiation, and their consistent and reliable studies (Kristiansen 2005, Škaloud *et al.* 2013*a*). The species number is continuously changing year by year due to the newly described species worldwide (Fig. 1). Currently, approximately 350 taxa of silica-scaled chrysophytes are described (Guiry and Guiry 2025), but this number certainly does not reflect their real species richness, which has been probably underestimated and far from complete.

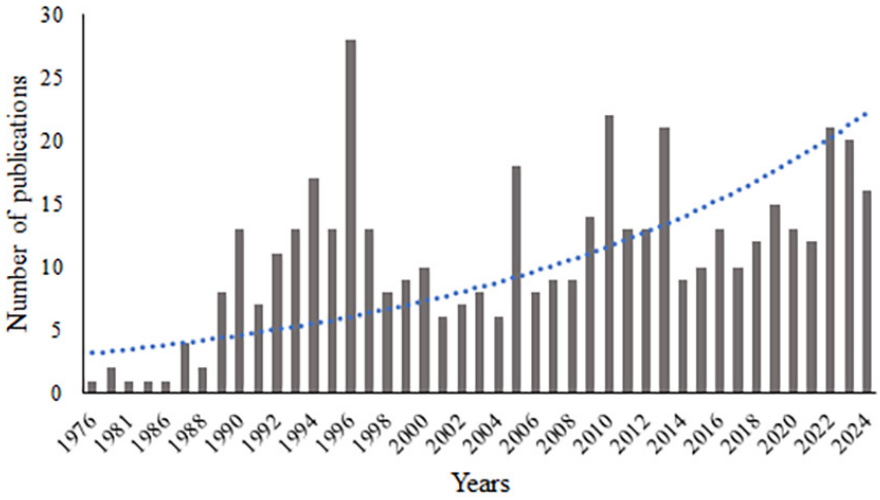

Fig. 1. The number of publications describing new taxa of silica-scaled chrysophytes – involving fossil and recent taxa – on the basis of the "Web of Science" database (searching for keywords of 'new', 'species', 'silica-scaled' at July 31, 2025) and its temporal trend (dotted line).

Despite the relatively low taxon number compared to other algal groups, silica-scaled chrysophytes are unique organisms and they have significant contribution to many ecosystem services (reviewed by LENGYEL *et al.* 2023): supporting (e.g. primary production, biogeochemical cycling), regulating (e.g. water purification), provisioning (e.g. production of biochemicals), and cultural services (e.g. inspiration source). Despite their huge importance, silica-scaled chrysophytes still represent a pretty much neglected algal group compared to others (e.g. diatoms), thus there is a need for their more detailed research in the future.

BIOGEOGRAPHICAL IMPORTANCE

Silica-scaled chrysophytes have special ecophysiological characteristics (KRISTIANSEN and ŠKALOUD 2017, SANDGREN 1988, SANDGREN *et al.* 1995). They do not have enzymes that would enable them to use hydrogen carbonate as a carbon source and absorb phosphate from alkaline waters. They are nutritionally opportunistic. Furthermore, they have flagellates enabling them to have 'wobbly' movement. On the basis of these characteristics, their distribution can be very limited and restricted to slightly acidic habitats with medium-high humic content, and low exposure to wind. With the exception of certain areas, this type of water is typically rare worldwide, occurring mostly in isolated locations.

Consequently, many species have well-defined geographic distribution types, such as bipolar, cosmopolitan, pantropic, endemic, etc. (Kristiansen 2001*a*, *b*, Kristiansen and Vigna 1996).

In Hungary, this kind of aquatic habitats (Fig. 2) is likely to be scarce for geochemical reasons, but the country is in a special biogeographical borderline situation. Nordic species appear in large numbers in early spring, whilst tropical species are typical in summer. Changes in species distributions may indicate climate change processes, therefore the research of Hungarian silica-scaled chrysophytes may be of great importance for our future.

Fig. 2. A typical habitat of silica-chrysophytes situated in Hungary (a small brownish forest lake in Mt Kab).

HUNGARIAN RESEARCH

Before 1990 – The beginnings

The earliest publication dates back to 1865 (Margó 1865), which reported the presence of the species *Synura uvella*. After that, plenty of references were published about the Hungarian flora of silica-scaled chrysophytes recording altogether 32 taxa (reviewed by Kristiansen and Padisák 1992, collected in the database "Flora et Iconographia Algarium Hungariae" (Buczkó and Rajczy 1998)). Nevertheless, all these studies are based on light microscopy (LM), thus

the real identity of the species is highly debatable. Therefore silica-scaled chrysophytes had remained virtually unknown in Hungary until the late 1980s, as their accurate and reliable identification required electron microscopy (EM), which was only available to a limited extent at that time.

Hungarian research using transmission electron microscopy was started by Lajos Hajdu (1975), who firstly recorded the presence of *Paraphysomonas vestita*. Later, the periphytic algal flora in the River Danube was studied, which also resulted in the verification of further three species of silica-scaled chrysophytes, such as *Mallomonas tonsurata*, *Synura glabra*, and *S. petersenii* (Ács and Kiss 1991, Kiss 1987).

Between 1990 and 2000 – The pioneering phase

This period was characterised by intensive researches exploring the hidden flora of silica-scaled chrysophytes using electron microscopy. Surveys were conducted in many parts of the country including approximately 100 aquatic habitats. Judit Padisák's research represented a significant milestone in these investigations. One of her major studies on this topic was published jointly with Professor Kristiansen in 1992. They recorded altogether eight taxa from the Kis-Balaton Water Protecting reservoir, including three new Hungarian occurrences (*Chrysosphaerella annulata*, *Spiniferomonas trioralis*, *Synura curtispina*). Shortly afterwards, seven taxa were found by investigating the algal flora in the River Danube, River Tisza, Eastern Main Canal, and Lake Balaton (Kiss and Kristiansen 1994). As a result of this extended survey, *Synura echinulata* was newly recorded.

From the following years, research shifted its focus from biodiversity aspects to ecological assessments, and studies began on linking species to environmental parameters (pH, conductivity, nutrient content, etc.). Judit Padisák was the centre of these researches, too, who contributed significantly to bringing Hungarian research of silica-scaled chrysophytes into line with international trends through many co-operations. Two prominent figures of these international relations were Leontin Stefan Péterfi (Babeş-Bolyai University, Romania) and Laura Momeu (Institute of Biological Research, Romania). As part of the early major collaborations, permanent and temporary lakes of Hortobágy (Péterfi *et al.* 1998*a*), as well as the bog-lake called 'Baláta-tó' located in the southeastern part of the country (Péterfi *et al.* 1998*b*) were studied. These investigations led to the discovery of 26–26 taxa, among them a total of 25 were considered new for Hungary (listed in Appendix 1). As further novelty, many of the records were new not only for the country, but also for the Carpathian Basin (e.g. *Mallomonas corymbosa*) or even for Europe (e.g. *Mallomonas scalaris*; Péterfi *et al.* 1998*a*, *b*). Additionally, a huge variability in species with different habitat preferences was also found with a special attention to

the occurrences of two tropical/subtropical species (*Mallomonas cyathellata* and *M. portae-ferreae*). Overall, a broader interest of habitat specific case-studies than local ones was concluded due to their surprisingly rich flora and their potential importance in understanding mechanisms in the field of phycogeography.

After 2000 – The broadening research

As a consequence of the previous findings, larger-scale investigations were started to explore different types of aquatic habitats. In light of this, the Kis-Balaton Reservoir was re-examined first (Barreto *et al.* 2000), which resulted in greater species richness than it was previously found (Kiss and Kristiansen 1994). Altogether 20 taxa were new for this habitat and 12 taxa for Hungary (listed in Appendix 1). Within the framework of another international cooperation, samples collected from different types of habitats (e.g. backwaters, fishponds, small lakes) in various areas of Hungary between 1995 and 1996 were reanalysed (Padisák *et al.* 2000). As a result, 20 silica-scaled taxa were recorded without any new Hungarian occurrence. Subsequently, 33 localities were studied in 1999 in order to give floristical overview about the Hungarian flora. This comprehensive research yielded

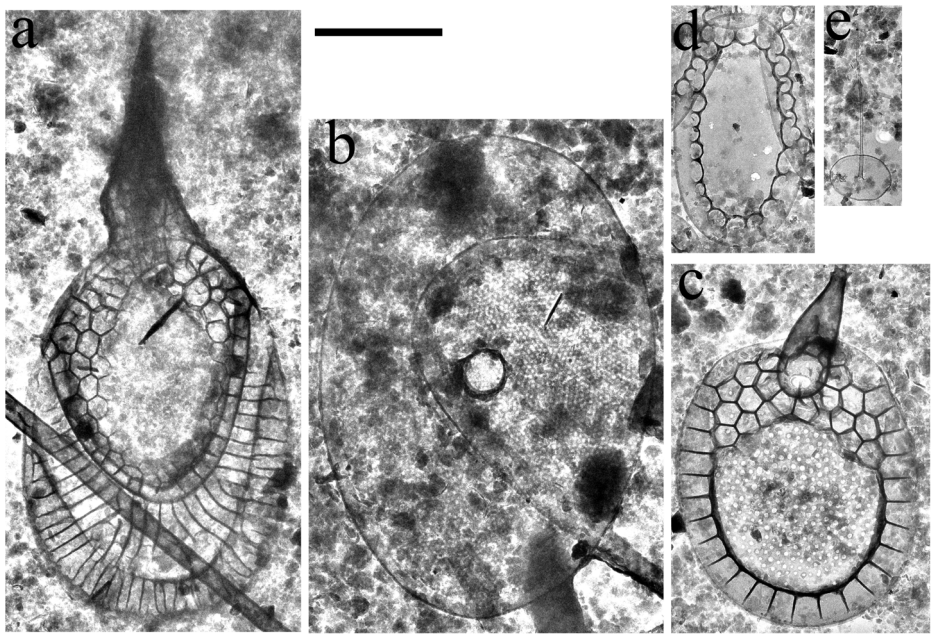

Fig. 3. Transmission electron microscope (TEM) microphotographs of some characteristic silica-scaled chrysophytes found in Hungary. Silica scale of *Mallomonas insignis* (a), *Neotessella lapponica* (b), *Synura uvella* (c), *Chrysosphaerella brevispina* (d), *Pharaphysomonas vestita* (e). Scale bar: 2 µm.

many outstanding results published in 2001 and 2005. Firstly, three new taxa on a global scale were described from the Visegrád Mts, which is unique and outstanding in terms of Hungarian research (Barreto 2001). Up to date, the distribution of *Mallomonas formosa* and *M. cucullata* is solely known from Hungary, whilst *M. tubulosa* was recorded from France and the Czech Republic too (Škaloud *et al.* 2013*b*). As another significant aspect, this study explored many different areas (e.g. Mátra, Visegrád and Pilis Mountains) and habitat types (e.g. groundwater ponds, forest ponds, quarry ponds, swamps) which had previously been unknown in terms of silica-scaled chrysophytes research (Barreto 2005). Overall, Sára Barreto's research contributed to the knowledge of Hungarian flora with 38 new findings and description of their ecological requirements. The latest research was conducted in 2013 and focused on the survey of small forest ponds located in Mt Kab in the Transdanubian Mts (Padisák *et al.* 2015). As a result, a particularly rich flora was discovered including 35 taxa with five new occurrences. Thereby, the Hungarian flora of silica-scaled chrysophytes was extended and currently consists of 98 taxa (Fig. 3, Appendix 1, electronic supplement).

Future perspectives

Research on silica-scaled chrysophyte algae is a classic example of how a new methodological paradigm (EM) emerges in the scientific life of a country. Significant progress has been made in data collection, mapping and morphotype analysis, thus we have moved from an initial taxonomic gap to an internationally comparable body of knowledge that is also recorded in a famous electronic database. The post-2010 era has been characterised internationally by the spread of molecular taxonomy based on DNA sequencing. Given the biodiversity of the Hungarian flora discovered so far, these methods could be pioneering in the future in finding more hidden species.

CONCLUSIONS

Although the species list is far from complete, the research results summarised in the present paper highlight Hungary's richness in silica-scaled chrysophyte algae. The series of national examples all prove that most of the aquatic habitats studied are particularly important in terms of biodiversity. All the anthropogenic activities (e.g. land-use), future climate change, and increasingly frequent extreme weather events can lead to dramatic loss in their biodiversity, and, consequently, in the ecosystem function and services they maintain. Furthermore, Hungarian flora may also play a prominent role in the research of biogeographical patterns and species distributions. For these reasons, further detailed research is strongly necessary.

* * *

Acknowledgements – I owe a personal debt of gratitude to Professor Dr Judit Padisák for guiding me and setting me on the path of silica-scaled chrysophyte research. I thank her for all the support she has given me so far. I am grateful to her for making it possible for me to work with Yvonne Němcová, another iconic figure in chrysophyte research. I am also particularly grateful to Yvonne Němcová (Charles University, Prague) for introducing me to methodological and taxonomical issues. TEM studies were performed at Nanolab, the electron microscopy laboratory of the University of Pannonia. I thank the National Research, Development and Innovation Office and Széchenyi Plan Plus programme for their supports.

Összefoglaló: A szilíciumpikkelyes flagelláták a protiszták egyedi csoportját alkotják, amelyek jelentős szerepet játszanak az ökoszisztéma-szolgáltatásokban (ellátó, támogató, szabályozó és kulturális). Magyarországon a szilíciumpikkelyes flagelláták tudományos kutatása csak az 1990-es évek elején kezdődött el igazán, majd gyors fejlődésen ment keresztül. Prof. Dr. Padisák Judit, a magyar hidrobiológia és limnoökológia kiemelkedő alakja kulcsszerepet játszott ebben a folyamatban. A magyar kutatások fejlődését nemcsak személyes tudományos elkötelezettsége, hanem hazai és nemzetközi kapcsolatépítései is lehetővé tették. Jelen tanulmány célja, hogy összefoglalja a szilíciumpikkelyes flagelláták magyarországi kutatásának történetét, tisztelegve Prof. Dr. Padisák Judit szenvedélyes és tudományos munkássága előtt.

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Appendix 1 – available elctronically at *http://publication.nhmus.hu/studbot/bannales.php?volume=56*

(submitted: 05.08.2025; accepted: 09.09.2025)

DOI: 10.17110/StudBot.2025.56.1.15 *Studia bot. hung. 56(1), pp. 15–24, 2025*

DISTANCE-DECAY RELATIONSHIPS IN LOTIC ENVIRONMENTS: A CASE STUDY FROM THE LAKE BALATON REGION, HUNGARY

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Selmeczy, G. B., Király, E., Lengyel, E., Zsuga-Biró, R., Stenger-Kovács, Cs. & Abbas, A. (2025): Distance-decay relationships in lotic environments: a case study from the Lake Balaton region, Hungary. – *Studia bot. hung.* **56**(1): 15–24.

Abstract: A high number of processes and parameters are responsible for shaping phytoplankton communities, among which nutrient availability and light intensity most often receive particular attention; however, the distance between communities (distance-decay relationships – DDRs) has been little studied in this context. Thus, to extend our knowledge, DDRs were studied in lotic waterbodies in the region of Lake Balaton (Hungary). Our analysis shows that the distance-decay relationship does not affect the structure of the phytoplankton community across different streams. However, when examining different locations in the same streams, we found a small but significant effect. We conclude that deterministic processes like environmental filtering and species interaction are more important mechanisms shaping the structure of communities than stochastic processes like dispersal mechanisms and random effects.

Key words: algal communities, diversity, Reynolds's functional group, tychoplankton

INTRODUCTION

Studying the various aspects of diversity plays a central role in ecological research. The Convention on Biological Diversity (CBD; article 2) defines biodiversity as the variability among living organisms from all sources, including terrestrial, marine, and other aquatic ecosystems, as well as the ecological complexes of which they are a part; this encompasses diversity within species, between species, and among ecosystems (Gaston and Spicer 2013). Thus, measuring biodiversity is quite complex and involves the analysis of genetic diversity, species types, assemblages, biotic communities, traits, functional groups, and their abundance, biomass, or other measures (DeLong 1996).

Understanding the structure and changes of phytoplankton assemblages through species alone is a major challenge. Although taxonomic information at species level can provide the most complete level of information, the defined species niches are missing in many cases. The classification of species into different traits and functional groups has greatly aided this understanding, and a few of them have become widespread: Reynolds's functional groups (RFG) (Padisák *et al.* 2009, Reynolds 1980, Reynolds *et al.* 2002), morpho-functional groups (MFG) (Salmaso and Padisák 2007), and the morphologically based functional groups (Kruk *et al.* 2010). It was a long journey to arrive at these classifications, during which algologists tried to classify the species along different ecological concepts, such as r and K selection (Margalef 1978) and CSR strategy (e.g. Reynolds 1988). Nowadays, in addition to the traditional microscopy-based identification, DNA-based methods are gaining an increasingly important role in phytoplankton research (e.g., Tapolczai *et al.* 2025). Judit Padisák played a decisive role in developing the categorization of phytoplankton species and developing the concepts. This study is a tribute to her work, as it is exciting and challenging to gain a more precise understanding of the functioning of phytoplankton assemblages, which is largely based on her work. Although the explanations are becoming more precise, there is still a lot of information missing to accurately understand the changes occurring in phytoplankton assemblages. This is obvious when a typical phytoplankton biomonitoring data set (phytoplankton and classical environmental variables data matrix) is analysed with variation partitioning: a significant part of the variance cannot be explained. In this regard, we investigate a variable that is rarely considered, namely the effect of the geographical distance between communities on their composition.

The distance–decay relationship (DDR) indicates the similarity between ecological communities decreases as geographical distance increases. Consequently, it is anticipated that communities that are geographically distant will exhibit greater dissimilarity in their structure and composition than those that are closer (Nekola and White 1999, Soininen *et al.* 2007).

According to Baas Becking (1934) "Everything is everywhere, but the environment selects.", which means that the taxa in a microbial community are determined primarily by environmental factors and not the limitation of migration. This idea is actually the forerunner of the niche theory (Hutchinson 1957). But is it truly the case that "Everything is everywhere"? To test the theory, we examined whether the composition of phytoplankton communities could be related to the distance between sampling points (both within and between streams).

Thus, in this study, we aimed to explore the diversity and the distance-decay relationships of the phytoplankton community of the main inflows of Lake Balaton. We hypothesise that there is no DDR among the sampled locations, because the effects of the local environment are the most important driving mecha-

nism of the community structure. However, in case of the same watercourses, distance should be an important variable, because of the high number of drifting cells.

MATERIALS AND METHODS

Study site and the measured variables

A total of 38 locations of 18 watercourses were included in this study (Fig. 1) All the sampled streams and rivers are located in West Hungary and flows into Lake Balaton. Eight out of 18 watercourses were sampled at one location, all the other watercourses were sampled at least at two different locations. Thus, it was possible to analyse DDR within and between watercourses. Sampling was carried out in September 2022. Physical and chemical variables (T = temperature (°C), DO = oxygen concentration (mg/L) and DO% = saturation (%), pH, Cond = conductivity (μScm^{-1}), and Turb = turbidity (FNU)) were measured with a Hach Lange HQ40d multimeter and a Hach Lange TSS portable turbidimeter at the sampling sites. Additionally, ~1.5 litres water sample was collected and carried to the laboratory to measure the following variables: total phosphorus, soluble reactive phosphorus, total nitrogen, nitrite, nitrate, ammonium, soluble reactive silica, sulphate, chloride, bicarbonate, alkalinity, and chemical oxygen demand according to APHA (2012)

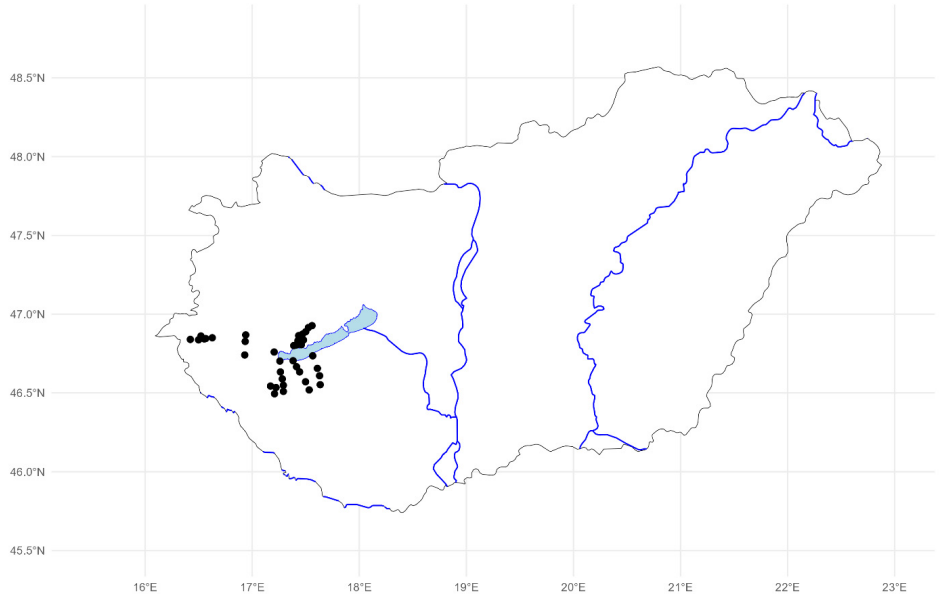

Fig. 1. Location of the sampling sites (black dots) in the Balaton region. Lake Balaton and the largest rivers (Duna and Tisza) are indicated in light blue and blue.

methods. Phytoplankton samples were collected in glass containers and Lugol's solution was added immediately. At least 400 settling units (cells, filaments, and colonies) were counted in each sample using a Zeiss Axiovert 100 (Oberkochen, Germany) inverted microscope according to the standard methods developed by Lund *et al.* (1958) and Utermöhl (1958). Phytoplankton biomass was calculated based on the most similar geometric forms according to Hillebrand *et al.* (1999) using the Opticount cell counting software (Hepperle 2008) and supposing 1 g cm^{-3} density. Phytoplankton taxa were sorted into Reynolds' functional groups according to the classification of Reynolds *et al.* (2002) updated by Padisák *et al.* (2009).

Statistical analysis

Data analysis was carried out in R 4.5.1. environment (R Core Team 2025). Principal component analysis (PCA) was used to explore the main patterns among environmental variables and the phytoplankton community. Intercorrelations of the environmental variables were checked, thus oxygen saturation and alkalinity were not used to keep $r < 0.8$. Then environmental variables were scaled and the phytoplankton dataset was Hellinger transformed. "Envfit" function in the "vegan" package (Oksanen *et al.* 2022) was used to fit the environmental variables onto the PCA ordination.

DDR analysis "Geodist" function from the geodist package (Padgham and Sumner 2025) was used to calculate the spatial distances among the sampling locations and "vegdist" function in the "vegan" package (Oksanen *et al.* 2022) was adopted to get the Bray-Curtis dissimilarity matrix of the phytoplankton communities. Linear regression was used to analyse the relationship between the spatial distances and the dissimilarity values. Analyses of the samples occurred separately within and between the watercourses in the linear regression, thus the hierarchical structure is handled properly.

Variation partitioning was used to quantify the pure and the shared effects of the spatial and environmental variables on the RFG-based community composition. First, the most important environmental and spatial variables were selected with forward selection in an RDA model using the "ordistep" function. The VIFs of the explanatory variables were limited to ten in the RDA model following Borcard *et al.* (2018). Secondly, variation partitioning was implemented with the "varpart" function and, third, the significance of the different fractions (the variation explained by a given set of variables) was tested by ANOVA with 1000 permutations. Spatial variables used in the variation partitioning were calculated as follows: First, a distance matrix was acquired based on the GPS coordinates, then spatial predictors were calculated using the PCNM (Principal Coordinates of Neighbour Matrices) method with the "pcnm" function. All functions used in the variation partitioning are available in the "vegan" package (Oksanen *et al.* 2022).

RESULTS

Description of the phytoplankton assemblages and environmental variables

Altogether, 253 taxa were found in the 38 locations (Fig. 1) belonging to 30 RFG's and 8 main taxonomic groups. Chlorophyta and Bacillariophyceae were the richest taxonomic groups with 89 and 56 taxa, respectively. The Bacillariophyceae group was dominated by tychoplanktonic elements, which is characteristic of small lotic waterbodies. Coda **X2** and $\mathbf{T}_b$ were the most frequently occurring groups, which were found in 36 and 35 sampling spots. *Rhodomonas* spp. were typical taxa in the **X2** group; additionally, *Navicula* and *Nitzschia* spp. represented mostly the $\mathbf{T}_b$ coda. In the case of biomass, **W1** and **Y** groups were the most dominant, represented primarily by *Euglena* spp. and *Cryptomonas* spp.

The first two axes of the principal component analysis explained 36.7% of the total variance of the phytoplankton community (Fig. 2). Significant relationships were visualised on the PCA ordination among the phytoplankton functional groups and environmental variables. Three variables NO_2^- ($R^2 = 0.161$, $P = 0.045$), NH_4^+ ($R^2 = 0.178$, $P = 0.029$) and T ($R^2 = 0.2$, $P = 0.019$) were correlated significantly with the community structure.

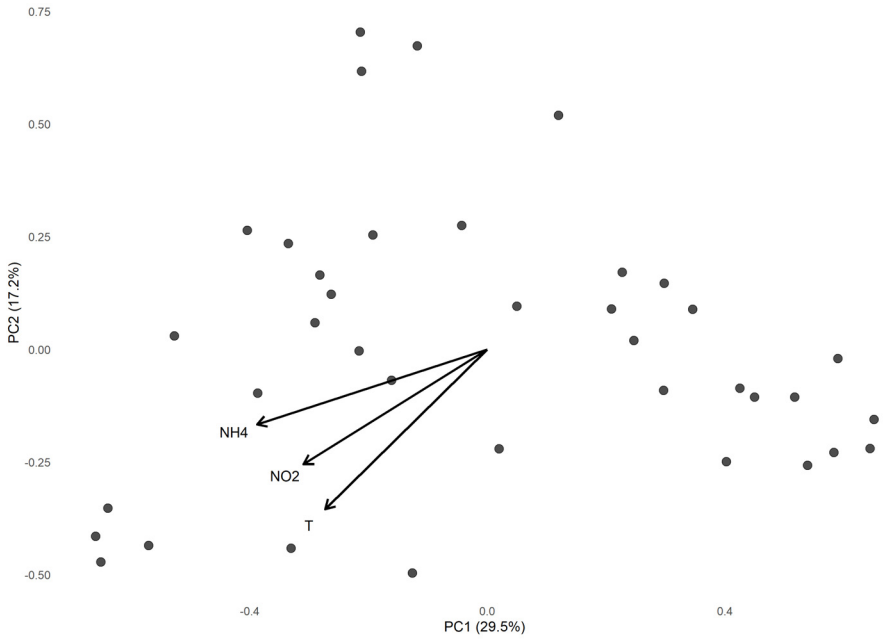

Fig. 2. PCA ordination based on the phytoplankton community and environmental variables (only significant ones are indicated).

Distance decay relationship

The distance among sampling locations varied between 1 and 100 km. Bray–Curtis dissimilarity of the phytoplankton community was not changed significantly with increasing spatial distance in the case of different streams (Fig. 3). However, if we compared the dissimilarity of the phytoplankton community in the case of given streams but at different locations, we found a small ($R^2 = 0.1053$) but significant ($p = 0.047$) effect (Table 1).

Variation partitioning revealed that the phytoplankton assemblages categorised according to RFG's were determined by the analysed environmental variables in 6.4%, additionally variance explained by spatial structure was 9.7%. The shared effect was 3.5% and quite a significant part (80.4%) remained unexplained (Fig. 4).

DISCUSSION

Our results suggest that the distance-decay relationship does not affect the structure of the phytoplankton communities across different streams. However, when examining different locations within the same stream, we found a small but significant effect. Additionally, variation partitioning has shown that both environ-

Fig. 3. Distance decay relationship based on Bray–Curtis dissimilarities of the phytoplankton assemblages. Red dots are indicated values from different streams and blue dots are indicated values comparing locations from the same waterbodies.

Table 1. Results of the linear models.

Type	Predictor	Estimate	Std. error	t value	M. R^2	p	Significance
Within stream	(Intercept)	0.6077	0.0591	10.286	0.1053	2.91×10^{-12}	***
	distance	0.0075	0.00364	2.058	0.1053	0.0469	*
Between streams	(Intercept)	0.8771	0.0105	83.406	4.43×10^{-5}	$<2 \times 10^{-16}$	***
	distance	−0.000040	0.000234	−0.171	4.43×10^{-5}	0.864	

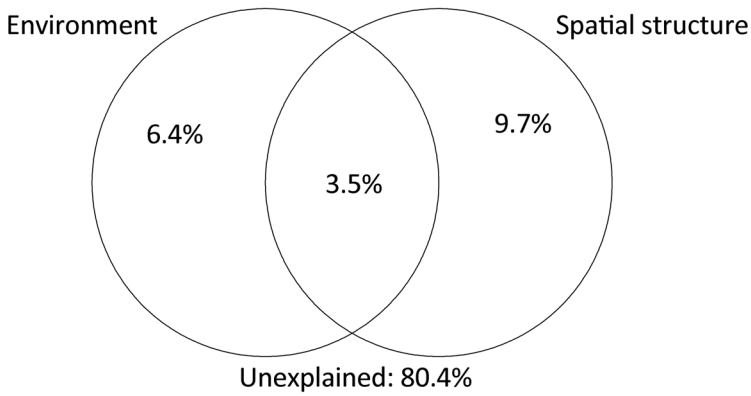

Fig. 4. Results of the variation partitioning analysis conducted on phytoplankton functional groups. Percentages indicate the proportion of variation explained by environmental and spatial variables, and the shared and unexplained components.

mental variables and spatial structure are responsible for explaining some part of the variance; moreover, spatial structure accounts for 9.7%. These results indicate that distance plays a negligible role in shaping phytoplankton communities across streams, suggesting that deterministic processes are far more important than stochastic ones. The most important deterministic processes (niche theory – HUTCHINSON (1957)) are environmental filtering and interaction among species, while neutral theory (HUBBEL 2001) assumes that stochastic processes are shaping the communities like dispersion, stochastic fluctuations in birth and death rates, and other random events/effects. Thus, in our case, dispersal processes appear unimportant for shaping a given community. Migration of species between waterbodies in the case of phytoplankton is a relatively poorly studied topic (GREEN *et al.* 2023), with a few exceptions: TESSON *et al.* (2018) studied the survival of resting cysts of dinoflagellates by migratory waterbirds, whereas MANNING *et al.* (2021) showed the survival of diatoms transported externally on waterbirds. Although CELLAMARE *et al.* (2010) suggested quite long time ago that waterbirds could be an important vector for the dispersal of phytoplankton species from Africa to Europe. However, experimental studies in this topic appeared only quite recently, during which it was discovered that

Raphidiopsis raciborskii (Sha *et al.* 2025) and many other species (Görgényi *et al.* 2023) can survive passing through a waterfowl's digestive system, as they remain viable in the faeces. This phenomenon probably contributed to the spread of some successful species, such as *Raphidiopsis raciborskii*, across continents (Padisák 1997).

In the case of within-stream analysis we found a small but significant DDR. It would be really interesting to know what the reader thinks about this result. Phytoplankton samples taken in a small stream only show a small degree of similarity as a function of distance. As stated in the hypothesis, we expected greater similarity due to the masses of cells drifting down in the watercourse. DDR can be explained by various factors, both intrinsic and extrinsic ones (Nekola and White 1999). Although different factors are important for different organisms, the dispersal ability is a determining variable in the characteristics of DDR. DDR of the phytoplankton communities was analysed in the tributaries of the Amazon River (Wetzel *et al.* 2012). Although these waterbodies are much larger than those we studied, and the distances are much longer as well, the authors found higher similarities among the locations compared to our results. The results of the authors confirmed that higher dispersal abilities cause lower distance decay rate. Unfortunately, we cannot compare how well the spatial structure explains the variance of the data. In our case, it is quite low (10%). It suggests that despite the drifting cells, other variables are so important that they largely shape the communities. Most of the studies found that environmental variables are critically important (e.g. Wojciechowski *et al.* 2017). However, only ~7% of the variance of the phytoplankton community data is explained by the measured environmental variables. The unexplained variance could be due to species interaction, microhabitat effects, or other factors that are difficult to measure and study.

Taken together, these findings highlight the complexity of phytoplankton community assembly and emphasize that our understanding of the principles governing the functioning and structure of phytoplankton communities is still far from complete.

* * *

Acknowledgements – We are thankful to the contribution of colleagues and students of the Limnology Research Group, University of Pannonia. This study was supported by the RRF-2.3.1-21-2022-00008 project and GBS was supported by the Hungarian National Research, Development and Innovation Office (NKFIH) FK 137979.

Összefoglaló: Számos tényező és különböző folyamatok felelősek a fitoplankton közösségek alakításáért, amelyek közül a tápanyagok hozzáférhetősége és a fényintenzitás kap leggyakrabban kiemelt figyelmet. A közösségek közötti távolság hatását (distance-decay relationship (DDR)) kevéssé vizsgálták ebben az összefüggésben, ezért munkánk során a DDR hatást vizsgáltuk a Balatonba befolyó víztestekben. Eredményeink alapján, a DDR nem befolyásolja a fitoplankton közösség szerkezetét a különböző vízfolyások között. Azonban, amikor ugyanazon vízfolyások különböző

helyszíneit vizsgáltuk, kicsi, de szignifikáns hatást találtunk. A kutatás eredményei arra engednek következtetni, hogy a determinisztikus folyamatok, mint például a környezeti szűrés és a fajok kölcsönhatása fontosabb mechanizmusok a közösségek szerkezetének alakításában, mint a sztochasztikus folyamatok, úgymint a diszperziós mechanizmusok és a véletlenszerű hatások.

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(submitted: 04.08.2025; accepted: 11.09.2025)

DOI: 10.17110/StudBot.2025.56.1.25 *Studia bot. hung. 56(1), pp. 25–46, 2025*

METHODOLOGICAL INSIGHTS INTO THE EFFECTS OF DIFFERENT MACROPHYTE STANDS ON THE ASSEMBLAGE STRUCTURE OF METAPHYTON IN LAKE TISZA (HUNGARY)

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Abstract: Metaphyton is one of the least studied aquatic communities, and little emphasis has been placed on its research so far. Our aim was to investigate the qualitative and quantitative characteristics of metaphytic algae in different macrophyte stands and to identify the most suitable sampling method, as no standardized approach exists. Sampling was conducted in the Sarud Basin of Lake Tisza between June and August 2022, targeting coontail (*Ceratophyllum demersum*; submerged) and water caltrop (*Trapa natans*; floating) stands. Three methods were applied: grab sample (GS), benthic diatom protocol (DP), and a modified diatom protocol (MDP). We expected significant differences in community structure, habitat preference, and diversity across methods and plant types. Our findings confirmed that both structure and diversity differed depending on the sampling method. However, no compositional or diversity differences were observed between the algal assemblages inhabiting different plant stands, suggesting that both macrophyte types serve an equally important ecological function in Lake Tisza.

Key words: metaphyton, multi-purpose artificial lake, sampling methods, taxonomic diversity

INTRODUCTION

Just as healthy, natural ecosystems depend on diversity, so too does human society. However, the very activities that sustain human life are contributing to biodiversity loss (Díaz *et al.* 2006). Our current understanding of life's diversity on Earth is uneven: ecological and conservation research has traditionally focused on macroscopic organisms or species of direct relevance to human use, while aquatic communities – particularly microorganisms such as algae – remain significantly underrepresented (MEA 2003). In the field of conservation literature, freshwater biodiversity has received comparatively little attention, despite the fact that these ecosystems harbour exceptionally high species richness and are subject to more intense anthropogenic pressures than many other habitat types (Strayer and Dudgeon 2010). At the same time, they are undergoing documented and inferred biodiversity declines on a scale and at a rate increasingly referred to as an 'invisible tragedy' unfolding beneath the water's surface (Reid *et al.* 2019, Richter *et al.* 1997). Biodiversity is being lost at a rate that outpaces our understanding of it (Tokeshi and Arakaki 2012). Long-standing and pervasive threats to freshwater biota include habitat destruction, overexploitation, and biological invasions. In addition, emerging stressors such as climate change, microplastics, and novel pollutants have recently been recognised (Dudgeon *et al.* 2006, Reid *et al.* 2019). Microorganisms are crucial for biodiversity assessment and also play an essential role in regulating and supporting ecosystem services, which are key to many provisioning services (Nee 2004). Microscopic algae are involved in approximately 20 different ecosystem services (B-Béres *et al.* 2023, Naselli-Flores and Padisák 2023). Their diversity in terms of size, morphology, primary and secondary metabolites is key to the efficiency of regulatory processes and the global stability of aquatic ecosystems (Ptacnik *et al.* 2008).

Habitat heterogeneity is a key factor in the functioning of aquatic ecosystems. It shapes species distributions and interactions and influences pivotal ecological processes (Gianuca *et al.* 2017). Empirical evidence indicates a positive relationship between habitat diversity and species richness (Bolgovics *et al.* 2019, Munguia *et al.* 2011), highlighting its importance for biodiversity conservation (Schuler *et al.* 2017). Aquatic macrophytes create a three-dimensional and structurally complex habitat in the littoral zones of lakes, contributing to a wide range of physical, chemical, and biological interactions. Submerged, free-floating, and floating plant types have been shown to exert differing influences on phytoplankton dynamics (Scheffer 2004). These effects include modifications of light conditions and nutrient availability (De Tezanos and O'Farrell 2014, Hasler and Jones 1949, Koleszár *et al.* 2022), the provision of refuge for filter-feeding zooplankton (Choi *et al.* 2014, Jeppesen *et al.* 1997, Timms and Moss 1984), and the release

of allelopathic compounds (Hilt 2006, Hilt and Gross 2008, Hootsmans and Blindow 1994, Körner and Nicklisch 2002). These physical, chemical, and biological influences generate a series of microgradients within the aquatic vegetation, thereby facilitating the development of diverse microalgal communities. The habitat enclosed by macrophytes thus represents a distinct ecological niche that supports unique microalgal assemblages, collectively referred to as metaphyton. Metaphyton is distinct from both pelagic phytoplankton and benthic, substrate-associated communities (Lukács *et al.* 2024). In freshwater ecosystems, these assemblages serve as important sources of propagules, contributing substantially to the high phytoplankton diversity observed in lakes and facilitating the dispersal of species from the littoral zone to open waters (Moss and Karim 1969). Submerged macrophytes can host rich and diverse algal communities that differ markedly from the phytoplankton found in the surrounding open water (Krasznai *et al.* 2010). The taxonomic composition of the macrophyte assemblage in a given water body strongly influences the structure and characteristics of the associated metaphytic community, including relative abundances of taxa, species richness, biomass, and overall diversity. Greater morphological complexity of macrophytes is generally associated with increased algal biomass and diversity, primarily due to enhanced niche availability (Ferreiro *et al.* 2013, Hinojosa-Garro *et al.* 2010, Levi *et al.* 2017, Pettit *et al.* 2016). However, several additional factors also influence the quality and composition of algal communities developing within macrophyte stands. These include colonization rate and duration (Casartelli and Ferragut 2018), as well as the age and structural characteristics of the macrophyte stand, such as leaf morphology (Ferreiro *et al.* 2013, Lalonde and Downing 1991, Laugaste and Reunanen 2005, Pettit *et al.* 2016, Tóth 2013).

Lake Tisza (formerly known as the Kisköre Reservoir), with its area of 127 km^2 (12,700 ha) is the largest artificial and the second largest shallow lake in the Carpathian Basin. The site features a mosaic-like structure, composed of physiognomically distinct water bodies. The lake is generally divided into four primary basins and the main course of the Tisza River. The presence of cut-off meanders, oxbow lakes, elevated floodplain areas, and islands has led to the internal compartmentalisation of the reservoir area, even though the water level generally exceeds the elevation of some of these features. A levee ridge (high bank) runs through the reservoir area and follows the course of the Tisza River, separating the river from the other water bodies of the reservoir over a considerable stretch. To ensure a continuous supply of fresh water from the Tisza, twelve inlet-outlet channels (flushing channels) were constructed by cutting through this ridge. The primary function of Lake Tisza is water storage, mainly for flood control, water regulation, and agricultural irrigation. However, it also supports various recreational activities, including tourism, leisure, water sports, and fishing (Kókai *et al.*, 2019). Finally, it is a

site of high conservation importance, designated as a UNESCO World Heritage Site (UNESCO 1999), a Ramsar site, and part of the Natura 2000 network (WEB1, WEB2). Due to its rich and protected bird fauna, the reservoir is subject to eutrophication, which promotes the development of diverse aquatic vegetation.

Although the phytoplankton of the dammed section of the Tisza River and Lake Tisza has been studied since the 1970s (e.g. HAMAR 1987), and biomonitoring including benthic diatoms is currently carried out in accordance with the Water Framework Directive (EC 2000), knowledge of the structure of metaphytic algal communities and the factors driving their dynamics remains limited.

As there is no universally applied, standardised method for metaphyton sampling, the primary objective of this study was to identify the most suitable sampling technique. To this end, samples were collected from different macrophyte stands (floating and submerged) of Lake Tisza using three different methods: (1) by taking water samples from within the vegetation, (2) following the standard phytobenthos sampling protocol, and (3) using a modified version of the latter. We hypothesised that the samples collected using the three different sampling methods would (i) differ significantly in community structure and diversity, and (ii) show significant differences in the proportion of planktic, benthic, and metaphytic taxa. Furthermore, we hypothesised (iii) that the type of vegetation (floating or submerged) would influence the structure and biodiversity of the algal community. A more structurally complex macrophyte stand was expected to support a more diverse algal assemblage.

MATERIALS AND METHODS

Study area

The Sarud Basin was selected for the investigation of the metaphyton (Fig. 1). The total area of the basin is 23.19 km^2, of which 5.02 km^2 is covered by marsh and other aquatic vegetation, and 18.17 km^2 by open water surface. At the peak of the vegetation period, the surface coverage by floating macrophytes is approximately 15%. In 2022, the most common and dominant aquatic plant species in the Sarud Basin were *Ceratophyllum demersum* (coontail), *Nymphoides peltata* (yellow floating heart), and *Phragmites australis* (common reed), with their stands reaching 25–50% coverage (abundance-dominance value = 3). The species with 5–25% coverage (abundance-dominance value = 2) included *Hydrocharis morsus-ranae* (European frogbit), *Lemna minor* (common duckweed), *Najas marina* (spiny naiad), and *Najas minor* (lesser naiad), *Potamogeton perfoliatus* (claspingleaf pondweed), *Trapa natans* (water caltrop), *Typha angustifolia* (narrowleaf cattail), and *Utricularia vulgaris* (common bladderwort) (CSÉPES *et al.* 2022).

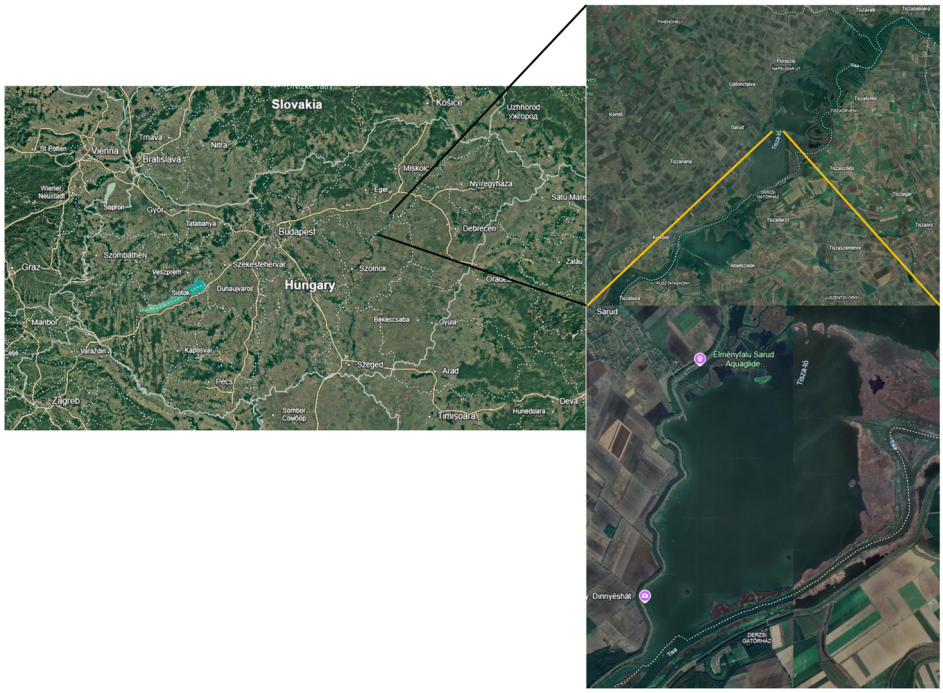

Fig. 1. Location of Lake Tisza on the map of Hungary, highlighting the Sarud Basin with the sampling areas. The red circle marks the water caltrop (*Trapa natans*), the blue one marks the coontail (*Ceratophyllum demersum*) sampling area.

Sampling setup and identification

In 2022, a total of 18 metaphyton samples were collected on three occasions: in June, July, and August. As part of the National Laboratory for Water Science and Water Safety project – which, among other objectives, examines the ecological impacts of *Trapa natans* management in the Kisköre Reservoir – metaphyton assemblages associated with stands of *T. natans* were investigated here. To address our research questions and test the hypotheses, samples were also collected from *Ceratophyllum demersum* stands. This species was one of the most abundant macrophytes in the Sarud Basin in 2022 (see above). Furthermore, the submerged growth form, leaf morphology, and structural traits of *C. demersum* differ significantly from those of *T. natans*.

As mentioned above, three sampling methods were used: grab sampling (GS), the benthic diatom sampling protocol (DP), and the modified diatom sampling protocol (MDP).

1. Grab sample (GS): Water samples were collected using a sampling jug from three different points within each stand of macrophytes. The sampling depth was approximately 20–30 cm, and the distance between sampling points depended on the extent of the *Ceratophyllum demersum* and *Trapa natans* patches, but did not exceed 2–2.5 m. The samples were then pooled in a single container to create a composite sample. An aliquot of approximately 250 ml was then retained from this composite sample for microscopic analysis.

2. Benthic diatom sampling protocol (DP): This method is based on the EN 13496 (2014) protocol and the national guide (Ács *et al.* 2020). During each sampling event, five *Trapa natans* rosettes were removed from the macrophyte stand. Five to eight leaves were collected from each rosette, taking care to exclude any that had been persistently and extensively exposed above the water surface. Only the leaf rosettes were examined; the stems and roots were excluded from the analysis. In the case of *Ceratophyllum demersum*, at least five plants were removed from each macrophyte stand. In all cases, the basal, sediment-covered sections were cut off. To eliminate loosely attached algal species, the specimens of *C. demersum* and the rosettes of *T. natans* were shaken two to four times during collection. The collected samples of each plant type were pooled into a single container and thoroughly rinsed with boiled, cooled tap water. After thorough homogenisation, a 20 ml subsample was retained for microscopic analysis.

3. Modified diatom sampling protocol (MDP): This method differed from the previous one (DP) in that the aquatic plants were not shaken after being removed from the water. The plants, which were still dripping wet, were placed directly into the storage container. This increased the likelihood of including weakly attached benthic species, as well as planktic and metaphytic algal taxa that were associated with, or occurred among, the macrophytes.

As there is no established or standardised method for investigating metaphyton, the samples were analysed using the Utermöhl method (Utermöhl 1958) for phytoplankton, in accordance with the European standard (EN 15204) and the protocol described by Ács *et al.* (2020). The samples were preserved with Lugol's solution until the samples achieved a cognac-like colour. Analysis was performed using a Leica DMIL inverted plankton-counting microscope at 600× magnification. For samples with high algal density and substantial debris content, analyses were conducted using 5×, 8×, 10× or 30× dilutions. These dilutions were prepared using a mixture of tap water and Lugol's solution. Identification was carried out at species or genus level using the following identification books: Coesel and Meesters (2007), Ettl (1983), Grigorszky *et al.* (1999), Huber-Pestalozzi (1950), Komárek (2013), Komárek and Anagnostidis (1998,

2005), Krammer and Lange-Bertalot (1997*a*, *b*, 2004*a*, *b*), Németh (1997), Schmidt and Fehér (1998–1999, 2001), Starmach (1985).

Data processing and analyses

Algal taxa were classified into three habitat groups as planktic, benthic or metaphytic according to Padisák *et al.* (2009) and the REBECCA database (Moe *et al.* 2008).

Taxa richness was used to express the number of taxa (Taxa_S). To compare the 'true diversity' of the assemblages, effective Shannon's H (effSH) was calculated following Jost (2006), as applied in previous studies (Beck and Schwanghart 2010, Morris *et al.* 2014, Stuart-Smith *et al.* 2013). Both taxa richness and effective Shannon's H were calculated using PAST software (version 4.17; Hammer *et al.* 2001). With regard to the calculation of functional diversity, Rao's quadratic entropy (RaoQ) (Rao 1982) was performed using Canoco 5.0; ter Braak and Šmilauer 2002).

To assess the influence of sampling methods and the growth forms of aquatic plant stands on the taxonomic and habitat group composition of assemblages, non-metric multidimensional scaling (NMDS; Canoco 5.0; ter Braak and Šmilauer 2002) was performed using species abundance and trait community weighted mean (CWM) matrices. The CWM matrix was created by calculating the mean values of the habitat groups in the assemblages, with the relative abundances of the taxa taken into account. All taxa were included in the NMDS analyses; however, only dominant taxa (relative abundance > 0.03) are displayed in the figures. Following the NMDS, permutational multivariate analysis of variance (PERMANOVA) was applied to test for statistically significant differences in community composition (Anderson 2001). To identify characteristic taxa and habitat groups associated with the various sampling methods and plant stands, indicator species analyses (ISA) were carried out based on taxa relative abundances and the CWM values of habitat groups (Dufrêne and Legendre 1997). Both PERMANOVA and ISA analyses were conducted using PAST software (version 4.17; Hammer *et al.* 2001).

To test differences in diversity indices, method types and plant stands were used as fixed factors, similarly to the taxonomic and habitat group analyses. The Shapiro–Wilk test was applied to assess the distribution (normal or non-normal) of the variables. For normally distributed data, Welch's test or one-way ANOVA was used, while for non-normally distributed data, the Mann–Whitney or Kruskal–Wallis test was applied to compare diversity metrics across sampling methods and plant growth forms. All analyses were performed using PAST software (version 4.17; Hammer *et al.* 2001).

RESULTS

In this study, we identified a total of 288 taxa from the two plant stands (submerged and floating) using the three sampling methods (Appendix 1, electronic supplement). Of these, 232 were identified at the species level and 56 at the genus or higher taxonomic level. The taxonomic composition of the species found was as follows: 65 Bacillariophyceae, 56 Sphaeropleales, 40 Cyanobacteria, 30 Euglenophyta, 26 Trebouxiophyceae, 25 Desmidiales, 12 Cryptophyceae, 6 Volvocales, 4 Chrysophyceae, 4 Dinophyta, 4 Mediophyceae, 3 Coscinodiscophyceae, 3 Eustigmatophyceae, 3 Xanthophyceae, 2 Ulotrichales, 2 Zygnematales, 1 Klebsormidiales, 1 Oedogoniales, and 1 Tetrasporales taxon. In 90% of the samples, a total of eight taxa were identified (at least 16 samples). These were *Aulacoseira distans* (Ehrenberg) Simonsen, *Euastrum denticulatum* F. Gay, *Nitzschia paleacea* (Grunow) Grunow, *Scenedesmus ecornis* (Ehrenberg) Chodat, *Scenedesmus quadricauda* (Turpin) Brébisson, *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal et Kociolek, *Tetradesmus lagerheimii* M. J. Wynne et Guiry, and *Tetraedron minimum* (A. Braun) Hansgirg.

Based on the habitat preference of each algae species, we have classified the taxa into three distinct categories: planktic, benthic, and metaphytic. Planktic algae constituted the largest trait, with 176 taxa, in addition 74 taxa were benthic, and 38 were metaphytic. Metaphytic group were the least represented, both in terms of taxon number and relative abundance, occurring in individual samples between 1.2% (GS_TR07) and 5.6% (MDP_TR08) of the time. In contrast, the relative abundance of planktic and benthic organisms varied widely, ranging from 13.1% (MDP_CE07) to 94.3% (GS_TR06) for planktic and from 2.5% (GS_TR06) to 84.9% (MDP_CE07) for benthic (Fig. 2).

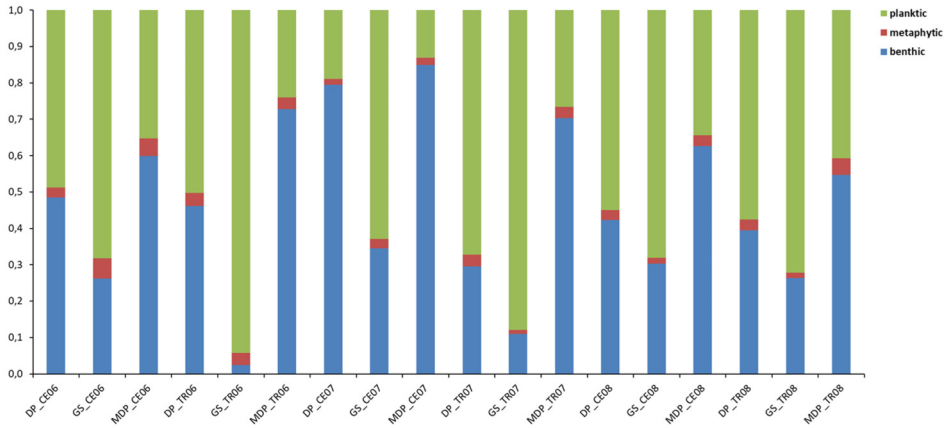

Fig. 2. The percentage relative abundance of planktic, metaphytic, and benthic taxa per sample.

Sampling methods

Of the 288 species identified, a total of 194 taxa were found in the Grab samples (GS), 206 in the Benthic diatom sampling protocol-based samples (DP), and 176 in the Modified diatom sampling protocol-based samples (MDP). A total of 104 taxa were identified across all three sampling types. In contrast, 47 taxa were found exclusively in GS, 38 taxa in DP, and 19 taxa in MDP. The number of taxa found using only two methods was the highest in the case of the DP and MDP methods (37) and the lowest in the case of the GS and MDP methods (16) (Fig. 3).

All 24 dominant taxa were found in the DP and MDP samples, while 21 dominant taxa were found in the GS samples. Taxa exhibiting relative abundance between 1 and 5% were found in similar proportions in all three methods: 69 taxa in the GS samples, 71 taxa in the DP samples, and 65 taxa in the MDP samples. Taxa with relative abundance of less than 1% accounted for approximately 50% of the taxa found, with 104 taxa in the GS samples, 111 taxa in the DP samples, and 87 taxa in the MDP samples.

With regard to the distribution of habitat groups according to the three sampling methods, it is evident that GS samples exhibited a higher proportion of planktic taxa and a lower proportion of benthic taxa. No significant differences

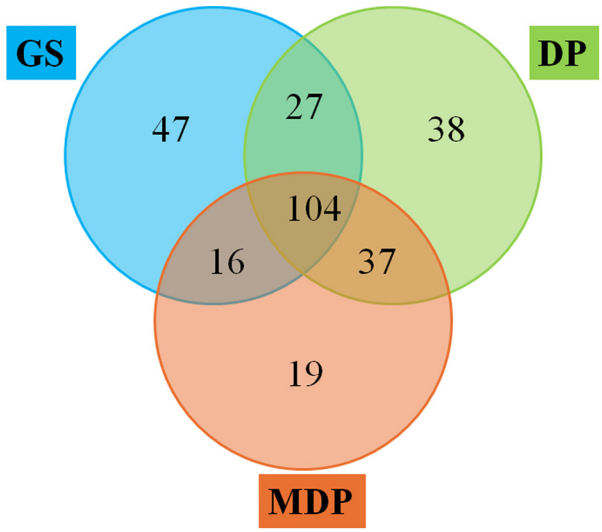

Fig. 3. Venn diagram shows the distribution of taxa identified in samples taken using the three sampling methods, according to the number of common and unique taxa. Blue = grab samples (GS); green = benthic diatom sampling protocol-based samples (DP); and brown = modified diatom sampling protocol-based samples (MDP).

were observed between the composition of DP and MDP samples, nor in the proportion of metaphytic taxa. 37 benthic (19.1%), 23 metaphyic (11.9%), and 131 planktic taxa were identified in the GS samples (69%). 59 benthic (28.7%), 25 metaphyic (12.1%), and 122 planktic (59.2%) taxa were identified in the DP samples. 54 benthic (30.7%), 19 metaphyic (10.8%), and 103 planktic (58.5%) taxa were identified in the MDP samples. However, examining the total relative abundance of habitat groups in the different sampling method categories, clear differences were revealed. While the relative abundance of planktic (P) taxa in the GS samples was 75.6%, and that of benthic (B) taxa was 21.8%, the ratio was 49.6% P: 47.6% B in the DP samples and 29% P: 67.5% B in the MDP samples. The relative abundance of metaphytic taxa was low for all three methods (GS: 2.6%, DP: 2.9%, MDP: 3.4%). Following the ISA analyses, a significant correlation was identified between the sampling method and the occurrence of 23 taxa in GS samples, 6 taxa in DP samples, and 20 taxa in MDP samples. Focusing on the dominant taxa, the analyses revealed that planktic species were the most indicative in GS samples including *Coelastrum microporum* Nägeli, *Lemmermannia tetrapedia* (Kirchner) Lemmermann, *Monoraphidium contortum* (Thuret) Komárková-Legnerová, and *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal et Kociolek. In contrast, in MDP samples, benthic species were the most indicative including *Cymbella* sp. small, *Fragilaria* sp., *Navicula capitatoradiata* H. Germain ex Gasse, *Navicula cryptotenella* Lange-Bertalot, and *Navicula* sp. Finally, no dominant indicator species were found in the DP samples.

The NMDS analyses revealed a distinct difference in taxa and habitat groups between sampling methods (Fig. 4). The PERMANOVA analysis confirmed that these differences were significant ($p = 0.0003$ and $p = 0.0002$). However, the pair-wise analysis of the taxonomic composition revealed that only the GS samples were distinct from the DP and MDP samples. In contrast, the pair-wise analyses revealed significant differences in all the three habitat groups.

No differences were found in taxonomy-based metrics (Taxa_S: $p = 0.25$; effSH: $p = 0.30$) or in habitat group-based metrics (RaoQ: $p = 0.10$) between the three sampling methods. However, a significant difference was observed in the functional diversity of the DP and GS assemblages ($p = 0.035$).

Plant stands – submerged and floating

Of the 288 species identified, 222 were found on the *Ceratophyllum demersum* and 237 on the *Trapa natans* stands, of which 51 were unique to the *C. demersum* and 66 to the *T. natans*, with 171 taxa found on both plant stands. We considered those taxa to be dominant that were present in at least one sample with a relative abundance higher than 5%. A total of 24 taxa were identified as dominant,

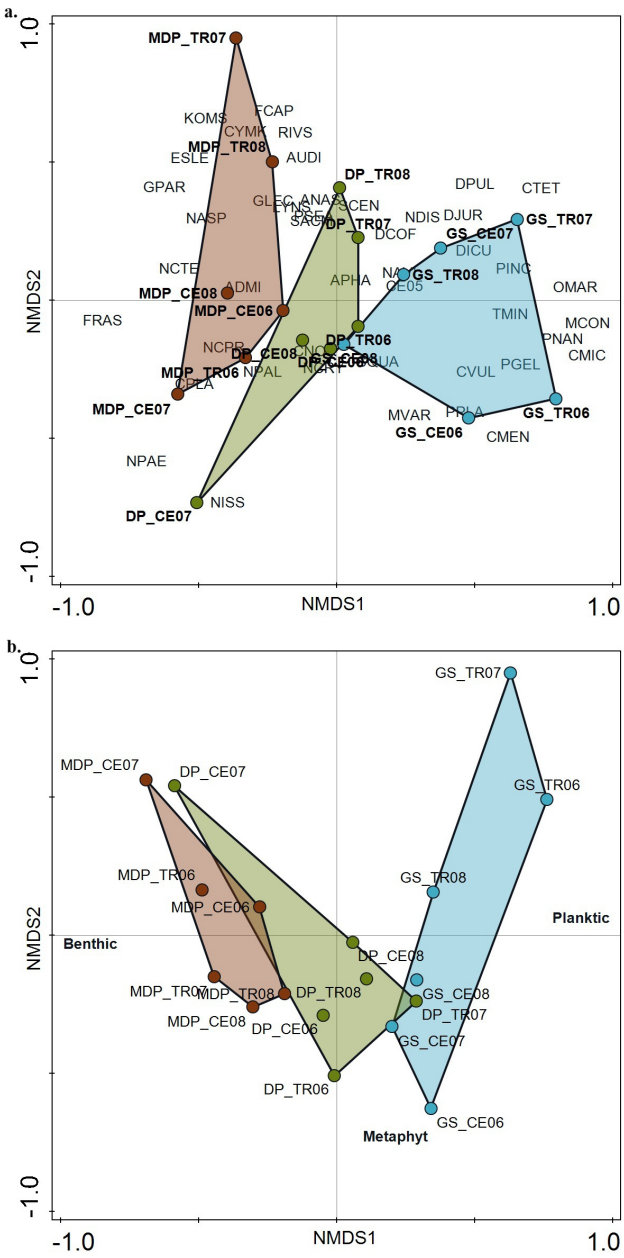

Fig. 4. The NMDS visualisation of samples taken by different sampling methods according to (a) taxonomic and (b) habitat group composition. Blue = grab samples (GS); green = benthic diatom sampling protocol-based samples (DP); and brown = modified diatom sampling protocol-based samples (MDP).

of which 22 were found in both plant stands, while 2 were unique to *T. natans* (*Fragilaria capucina* Desmazières and *Rivularia* sp.). The taxonomic composition of the dominant species was as follows: 12 Bacillariophyceae, 4 Sphaeropleales, 3 Trebouxiophyceae, 2 Coscinodiscophyceae, 2 Cyanobacteria, and 1 Mediophyceae. Concurrently, 85 taxa attained a relative abundance of between 1 and 5% on at least one occasion, of which 74 were identified in both plant stands, 3 were found exclusively on the coontrail, and 8 were present only in the *T. natans* population. Their taxonomic composition was also more diverse than that of taxa with a relative abundance higher than 5%: The following taxa were identified: 24 Sphaeropleales, 18 Bacillariophyceae, 15 Cyanobacteria, 9 Trebouxiophyceae, 8 Cryptophyceae, 3 Desmidiales, 1 Chrysophyceae, 1 Dinophyta, 1 Euglenophyta, 1 Eustigmatophyceae, 1 Mediophyceae, 1 Oedogoniales, 1 Ulotrichales, and 1 Volvocales. A significant proportion of the taxa identified, 179 in total, had a relative abundance of less than 1%. It is noteworthy that the majority of unique taxa (104 out of 117) were among these rare taxa.

A total of 222 taxa were identified from the *C. demersum* stand, with 57 classified as benthic, 28 as metaphytic, and 138 as planktic. A total of 22 taxa were dominant, while 78 taxa had a relative abundance of 1–5% and 123 taxa had a relative abundance of less than 1%. The Indicator Value analysis revealed that 8 taxa were indicative of *C. demersum*. These were: *Cryptoglena skujae* Marin et Melkonian, *Gonium pectorale* O. F. Müller, *Nitzschia acicularis* (Kützing) W. Smith, *Nitzschia palea* (Kützing) W. Smith, *Nitzschia paleacea* (Grunow) Grunow, *Nitzschia* spp. (32–64 × 4–8 μm), *Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal et Kociolek, and *Surirella librile* (Ehrenberg) Ehrenberg. Of the 8 indicator taxa, 4 were dominant, 1 had a relative abundance of 1–5%, 3 had a relative abundance of less than 1%, and 50–50% were benthic and planktic.

The *T. natans* stand was found to be slightly more species-rich than the *C. demersum* stand, with a total of 237 taxa identified, including 62 benthic, 30 metaphytic, and 145 planktic species. Our analysis identified 24 dominant taxa, 82 taxa with a relative abundance of 1–5%, and 131 taxa with a relative abundance of less than 1%. Among these 6 were identified as being indicative of *T. natans*. The following species are recognised: *Crucigenia fenestrata* (Schmidle) Schmidle, *Dictyosphaerium ehrenbergianum* Nägeli, *Lemmermannia tetrapedia* (Kirchner) Lemmermann, *Monoraphidium minutum* (Nägeli) Komárková-Legnerová, *Planktolyngbya contorta* (Lemmermann) Anagnostidis et Komárek, and *Scenedesmus ecornis* (Ehrenberg) Chodat. All 6 indicator species are planktic, of which 1 was dominant, 4 had a relative abundance of 1–5%, and 1 had a relative abundance of less than 1%.

We also examined the differences between the taxonomic and habitat group composition of plant stands using NMDS visualisation (Fig. 5). However, we found no significant differences in either composition. This was confirmed

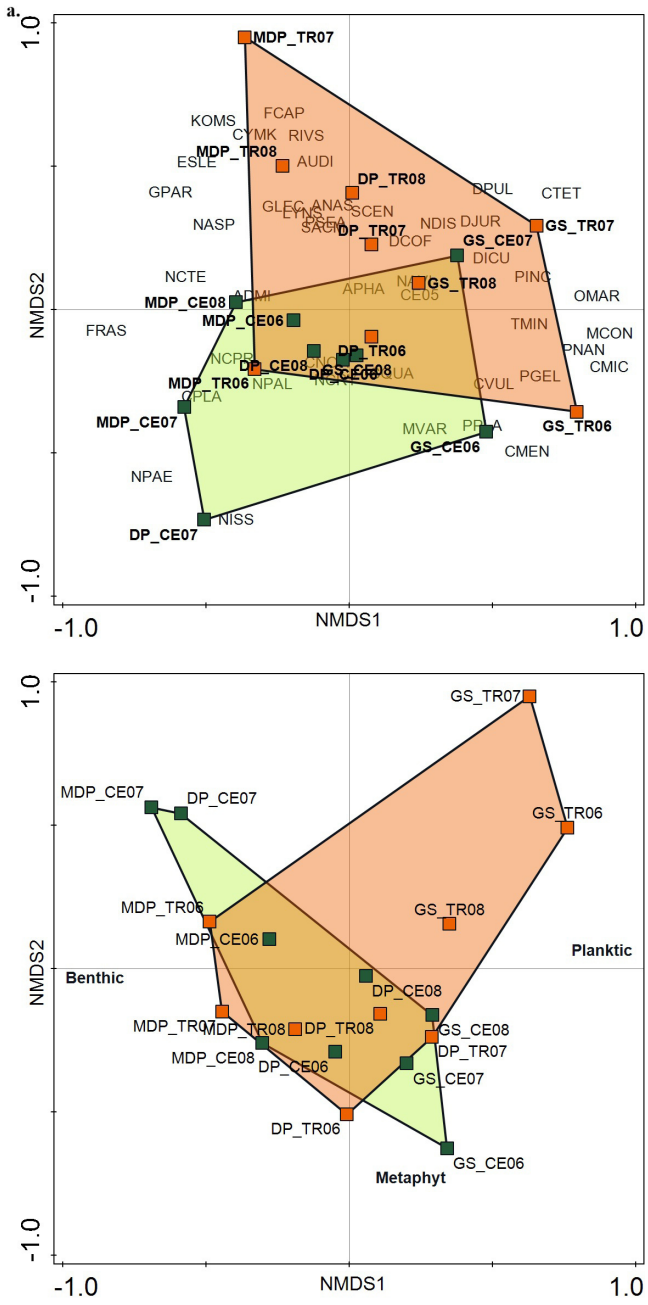

Fig. 5. The NMDS visualisation of samples taken from *Ceratophyllum demersum* (green) and *Trapa natans* (orange) stands according to (a) taxonomic and (b) habitat group composition.

by PERMANOVA analysis ($p = 0.1143$ for taxonomic composition, $p = 0.2521$ for habitat group analysis).

In terms of biodiversity, no differences were found in taxonomy-based metrics (Taxa_S: $p = 0.40$; effSH: $p = 0.14$) or in habitat group-based metrics (RaoQ: $p = 0.48$) between the two plant samples.

DISCUSSION

In contrast to phytoplankton, metaphyton provides a habitat for benthic and epiphytic algae, both in terms of quality and quantity (Krasznai *et al.* 2010). Furthermore, it serves as a potential propagule source for planktic habitats (Lukács *et al.* 2024). Therefore, recognising its ecological importance is essential for understanding the functioning of the lake ecosystem. The primary aim of this study was to identify the most effective sampling method for collecting metaphyton from submerged and floating macrophyte stands, and to assess whether the type of plant stand influences the composition and diversity of the associated algal assemblages. Using three different methods, a diverse metaphytic algal assemblage was identified in the Sarud Basin.

Sampling methods

The results of our study partially supported our first hypothesis (significant differences in the composition of assemblages but no differences in the diversity metrices), however, they rejected the second hypothesis (no difference in proportion of planktic, benthic, and metaphytic algae). Based solely on the number of taxa detected, the DP method proved to be the most effective. However, in the case of the grab sampling (GS) method, a greater number of taxa were unique to that sampling approach. More than one-third of the taxa (36.1%) were detected irrespective of the sampling method employed, while an equal proportion demonstrated sensitivity to only one particular method. Based on taxonomic composition, the DP method exhibited the highest overlap with the other two sampling methods.

The sensitivity of the sampling methods to habitat groups, based on their total relative abundances, showed significant differences: while the GS method was more sensitive to planktic elements and the MDP method to benthic ones, the DP method exhibited a similar level of sensitivity to both trait groups. Due to their low relative abundance, metaphytic taxa did not show significant differences between the sampling methods. Nevertheless, the highest sum-relative abundance of metaphytic algae was observed with the MDP method (MDP_TR08), whereas the highest number of taxa was recorded in samples collected

using the DP method (DP_TR06). A similar pattern was observed among the dominant indicator species, with planktic taxa being indicative of the GS samples, while benthic taxa were indicative of the MDP samples. It should be noted that planktic elements would have been expected to occur in higher proportions in the MDP samples. However, due to the two- to three-order magnitude difference in individual counts between planktic and benthic algae, and the extensive dilution required for sample processing, planktic taxa with low abundances were likely undetected.

Surprisingly, the DP method was found to be the most effective of the three sampling methods for collecting metaphyton, as it exhibits similar sensitivity to both planktic and benthic elements, unlike the MDP method. This method, *i.e.*, the DP, produces the highest number of taxa and appears to be the most representative for sampling both the water space among macrophytes and the organisms attached to the plant surfaces. These results appear to contradict the logical assumption that the MDP method would show greater sensitivity to both planktic and metaphytic taxa. In the MDP protocol, the vegetation used as substrate is not shaken, which should allow algal species inhabiting the water between plants, as well as taxa weakly attached to plant surfaces, to appear more abundantly in the samples. In contrast, the DP method involves shaking the plant to collect only the true benthic community. The detached plants are then rinsed with clean, boiled tap water or distilled water to remove the attached taxa. Samples obtained using either method must be diluted for microscopic analysis, which greatly reduces the likelihood of detecting rare taxa. In the case of the MDP method, however, the water between the plants is presumably very turbid and rich in debris. This often requires stronger dilution than with the DP method, which further reduces the probability of detecting rare species. This may explain why the MDP method is more strongly biased towards benthic taxa than the DP method.

It is also important to emphasise that the DP method is slightly less sensitive to planktic elements than the GS method, meaning some rare planktic taxa may be not detected. Although our study provides useful insights into the diversity and structure of the metaphyton, we cannot conclude with certainty that the combined use of the DP and GS methods reliably captures the entire metaphytic community of a habitat. A more extensive research effort involving a wider variety of lake types and stands of macrophytes would be necessary to draw such general conclusions. However, within the two stands of macrophytes investigated here, the combined application of these methods appeared to recover a large proportion of the taxa inhabiting the metaphyton, even when considering the limitations of the microscopic processing protocol (i.e., the absence of targeted species searches).

Plant stands – submerged and floating

Contrary to our hypothesis, no significant differences were found in taxonomic composition or habitat group structure between *Ceratophyllum demersum* and *Trapa natans* stands (rejecting H3). Based on the selected macrophyte stands, our results also do not support the findings of Ferreiro *et al.* (2013), which suggested that higher morphological complexity of macrophytes (i.e., presence or absence of thorns, their number and/or the importance of edges; in this case, *C. demersum*) leads to higher algal community diversity. Nemes-Kókai *et al.* (2024) also demonstrated a significant difference in the algal assemblages associated with different macrophyte stands (floating, submerged, and emergent), based on investigations carried out between 2016 and 2019. It is important to note, however, that both Ferreiro *et al.* (2013) and Nemes-Kókai *et al.* (2024) investigated a benthic diatom community, the microscopic analysis of which differs from the identification method applied in our study. However, the two plant stands differed markedly in the composition of indicator species and in the habitat preferences of those species. While only planktic species were identified as indicators for *T. natans*, the indicator species associated with *C. demersum* included both planktic and benthic taxa, with the latter being more numerous. This pattern is likely due to the tendency of planktic species to settle on the floating leaves of *T. natans*, while the submerged foliage of *C. demersum* provides a suitable microhabitat for benthic diatoms. With regard to specifically metaphytic algae, their relative abundance and diversity did not differ significantly between the two macrophyte stands. While the highest taxon richness was found in a *Trapa* sample (DP_TR06), the highest sum-relative abundance (GS_CE06) and relative abundance (*Peridinium* sp.; GS_CE06) were recorded in the *C. demersum* stand.

These findings suggest that both types of macrophyte stands play an important role in sustaining the algal assemblages of Lake Tisza. Their similar assemblage structure indicates that samples collected from different vegetation types (floating or submerged) within the same year can be compared and evaluated meaningfully. However, further research is needed to determine whether interannual variation also occurs in the metaphyton associated with different macrophyte stands, as observed in benthic diatom assemblages.

CONCLUSIONS

We investigated the metaphyton assemblage of Lake Tisza with the aim of identifying the most suitable sampling method for efficiently collecting high-quality algal samples from different types of macrophyte stands, including both submerged and floating vegetation. The results obtained partially supported our

hypothesis (H1), demonstrating that both the community structure and, to a certain extent, the diversity of samples collected by different methods varied. The findings highlighted that, considering the practical difficulties of microscopic processing, the DP method – originally developed for benthic diatom sampling – is the most suitable for collecting metaphyton samples. The different sampling methods demonstrated varying sensitivity to planktic and benthic algae; however, no significant differences were identified in the number or relative abundance of metaphytic taxa (rejecting H2). No compositional or diversity-related differences were observed between the different macrophyte stand types (rejecting H3), further supporting the conclusion that both vegetation types play an important and equally valuable ecological role within the aquatic ecosystem of Lake Tisza.

* * *

Acknowledgements – I would like to express my gratitude for Judit Padisák, who started me on my algology career, was my diploma work supervisor during my university studies, and recommended me for my current job, where I could further expand my knowledge. The research presented in the article was carried out within the framework of the Széchenyi Plan Plus program with the support of the RRF 2.3.1 212022 00008 project (GySz, ECs, MTN, ZsNK, ÁL, VBB). The project was financially also supported by the National Research, Development and Innovation Office – NKFIH FK 132 142 (VBB) and NKFIH KKP 144068 (ÁL, VBB).

Összefoglaló: A metafiton a legkevésbé vizsgált vízi életközösségek egyike, kutatására eddig kevés hangsúlyt helyeztek. Célunk az volt, hogy feltárjuk a metafitikus algák minőségi és mennyiségi jellemzőit különböző vízinövény-állományokban, valamint meghatározzuk a mintavételükre legalkalmasabb módszert, mivel szabványosított módszer jelenleg nem létezik. A mintavételekre 2022 júniusa és augusztusa között került sor a Tisza-tó Sarudi-medencéjében érdes tócsagaz (*Ceratophyllum demersum*; alámerült) és sulyom (*Trapa natans*; úszó) állományokban. Három módszert alkalmaztunk: merítéses mintavétel (GS), bentikus kovaalga-mintavételi módszer (DP), valamint annak módosított változata (MDP). Feltételeztük, hogy jelentős különbségeket tapasztalunk a közösségszerkezetben, az élőhely-preferenciában és a diverzitásban a módszerek és növénytípusok között. Eredményeink megerősítették, hogy a közösségszerkezet és a diverzitás valóban különbözik a választott mintavételi módszertől függően. Ugyanakkor az algaközösségek fajösszetételében és diverzitásában nem találtunk különbséget a különböző növényállományok között, ami arra utal, hogy mindkét vízi növény típus egyformán fontos ökológiai szerepet tölt be a Tisza-tóban.

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Appendix 1 – available elctronically at *http://publication.nhmus.hu/studbot/bannales.php?volume=56*

(submitted: 31.07.2025; accepted: 18.09.2025)

DOI: 10.17110/StudBot.2025.56.1.47 Studia bot. hung. 56(1), pp. 47–56, 2025

DIATOM COLLECTION IN THE HERBARIUM OF THE HUNGARIAN NATURAL HISTORY MUSEUM

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Abstract: The diatom collection is housed in the Department of Botany of the Hungarian Natural History Museum in Budapest and is considered one of the most important diatom collections worldwide. It is rich in type material and specimens of historical and scientific significance**.** The collection comprises approximately 30,000 items, including microscope slides, vials with wet raw samples, fossil material (diatomite), SEM stubs, and various forms of associated documentation, such as drawings and light- and electron-microscope images. Here we shortly present the Pantocsek's collection, which forms the foundation of the diatom holdings, together with the collections of Judit Padisák and László Vida, both of which were revised in 2024–2025. We provide a detailed overview of the slides prepared by Judit Padisák, on the occasion of her 70th birthday in 2025, celebrating her outstanding achievements as a renowned limno-ecologist. Notably, *Frustulia creuzburgensis* (Krasske) Hustedt represents a new record for the Hungarian diatom flora from her collection, published herein.

Key words: collection, diatoms, historic data, József Pantocsek, Judit Padisák, László Vida

INTRODUCTION

The Collection of Algae is housed in the Department of Botany of the Hungarian Natural History Museum in the Hungarian National Museum Public Collections Centre in Budapest (Index Herbariorum code BP) is considered as an important and old collection worldwide. The collection (as well as the "algae" themselves) is heterogeneous, consisting of several subunits, including herbarium sheets, vials, microscopy preparations, and materials prepared for scanning electron microscopy. The Collection of Algae is international in scope and contains marine, freshwater, and terrestrial algae as well as cyanobacteria.

The structure of the Collection of Algae comprises three main parts: (1) the herbarium section, which includes dried materials and capsules. The inventory list of this collection part is available upon request, since it is continuously

being revised and updated; (2) the collection of liquid samples, which contains preserved water samples; and (3) the diatom collection.

The most widely used and scientifically important part is the diatom collection, which has remained a focus of international interest (Buczkó 2012). The significance of diatom collections worldwide is well demonstrated, and numerous recent studies address their importance (Alers-García *et al.* 2021, B-Béres *et al.* 2023). Diatoms are among the most abundant aquatic organisms. Diatom collections are fundamental resources for studies in taxonomy, phylogeny, ecology, biogeography, applied biology, monitoring, and conservation. They provide essential material for examining morphological variation, reconstructing phylogenetic relationships, and understanding the distribution and ecology of diatom species. Containing both fossil and recent specimens from freshwater, brackish, and marine habitats, these collections form an irreplaceable archive of diatom diversity (Ljubešić *et al.* 2025).

The aim of this paper is to summarise the recent activities related to the diatom collection of the Hungarian Natural History Museum and to draw the attention of experts working in different parts of the world to this valuable resource. Museums are the institutions of preservation, conservation, and long-term safeguarding. An explicit goal is to convince colleagues that the diatom material (slides, samples, catalogues) is best preserved and most usefully applied here, where both current and future phycologists may access and utilise it.

Although diatoms are among the most suitable organisms for preparing long-lasting collections, the Department of Botany had no expert for this group for a long period of time, and the possible loss of old slides also was an additional difficulty. However, the former curators, distinguished by their outstanding expertise, achieved significant success in various fields of algological research. The following is a list of the curators associated with the collection of algae (Table 1).

MATERIAL AND METHODS

The most important parts of the collection are well organised and have already been revised, but a comprehensive revision of the diatom collection is currently underway. In 2009, we began assigning continuous catalogue numbers.

ENUMERATION

The Diatom Collection is an extensively documented main part of the Collection of Algae. The foundation of the diatom collection, the Pantocsek Collection, was completed in the 1980s (Krenner 1981).

Table 1. The staff of the Collection of Algae (including diatom collection) in the Department of Botany.

Curator	Tenure as curator (period of service)	Personal data (year of birth)	Some specialities
Gyula Csíkmádéfalvi Istvánffi (before 1886 Gyula Schaarsmith)	1889–1898	1860–1930	algal flora of Lake Balaton
Nándor Filarszky	1899–1929	1858–1941	charophyta
Márta Halász	1938–1963	1905–1971	mires, bogs, algae of river Danube
Gábor Szemes	1947–1951	1907–1993	diatoms
Erzsébet Kol	1948–1969	1897–1980	soft algae, snow and ice algae
Zsuzsanna Páricsy-Komáromy	1967–1985	1942–1985	soil algae
Lajos Hajdu	1971–1982	1946–	numeric analysis
Judit Padisák	1982–1993	1955–	limnoecology, chrysophytes
Éva Ács	1987–1995	1964–	diatoms
Krisztina Buczkó	1985–	1962–	diatoms
Luca Viktória Kardos	2025–	2003–	

BP-HNHM-ALG-D-0001 and BP-HNHM-ALG-D-1049

The first and well-known part of the diatom collection is Pantocsek's herbarium containing 1049 slides.

József Pantocsek (1846–1916) was a physician and medical director who, in addition to his primary profession, developed a strong interest in plant science, becoming a prominent botanist. He devoted much of his remaining time to the study of diatoms. Pantocsek described more than 1,300 new diatom taxa and amassed a rich diatom collection, which was purchased by the Department of Botany of the Hungarian Natural History Museum after his death in 1917. Unfortunately, the collection suffered heavy losses during the Second World War, when many of the specimens were either completely destroyed or severely damaged. Despite this, the surviving portion – now only about one-fifth of the original size – remains of international scientific interest. The remnants of the collection were restored by József Krenner (Krenner 1981). In addition to cleaning and restoring the material, Krenner identified the diatoms on the slides and provided detailed descriptions of the preparations. Thanks to his dedicated work, the surviving Pantocsek's collection retains its deserved scientific prominence.

Fortunately, associated cleaned samples are also available from 78 localities, which can be used for scanning electron microscopy. This part of the diatom col-

lection has a special designation: BP-HNHM-ALG-DC, where "DC" refers to the Diatom Cleaned material. Recently, several new slides have been prepared from Pantocsek's cleaned material, which are being used for typification and the emended description of taxa (Kociolek *et al*. 2025*a*, *b*).

BP-HNHM-ALG-D-1058 and BP-HNHM-ALG-D-1286

In chronological order, the next part of the collection consists of slides that can be connected to the scientific activity of Judit Padisák in the Botanical Department. Between 1982 and 1993, she served as the curator of the Collection of Algae. In total, we reviewed 229 of her slides, representing 120 taxa. She followed Pantocsek's noteworthy method for marking a taxon of interest. A small metal ring was attached to the slide around the specified taxon, making it easy to locate. As shown in Figure 1, this was a highly distinctive technique. The water samples from which the slides were prepared were collected primarily by other researchers. Most of them were obtained by György Dévai, who contributed 105 samples to the collection. 44 slides were prepared from samples collected by Zsuzsanna Páricsyné-Komáromy (Buczkó 1986, Szujkó-Lacza 1986). Mycologists János

Fig. 1. Diatom slides identified by Judit Padisák during her curatorial work at the Hungarian Natural History Museum (1982).

Gönczöl and Ágnes Révay (Magyar and Lőkös 2021) provided 35 samples to Judit Padisák, while László Forró (Zsuga and Korponai 2023) contributed 22 samples. Júlia Szujkóné Lacza, former head of the Botanical Department, is listed as the collector of 14 samples. László Tóth collected 6 samples, whereas only two specimens can be regarded as Judit Padisák's own collections (one from Lake Mondsee and another from tap water in Szolnok).

The collectors covered a wide range of localities and habitats. Lake Balaton (particularly Keszthely Bay), sodic pans (Hattyúszék, Szívósszék, Lake Kondor, Lake Kerek), karstic areas of the Bükk Mountains (Bükk National Park; Jávorkút, Bolhási sinkhole, Csipkéskút sinkhole, Garadna stream, Szinva brook), and Lake Kolon in Kiskunság National Park were sampled repeatedly between 1979 and 1982. As a result, these sites are especially well represented in the collection.

The taxonomic composition is dominated by the widespread freshwater taxa of Hungary. Among these, *Gyrosigma wansbeckii* (Donkin) Cleve 1894 deserves mention: although not a rare species (Guiry and Guiry 2025), records from Hungary are scarce (Szabados 1952, 1957, Szemes 1959). Judit Padisák observed it at Kerek Clearing. Another notable find is *Frustulia creuzburgensis* (Krasske) Hustedt 1957 (formerly *Navicula creuzburgensis* Krasske 1927), which appears to represent a new record for the Hungarian diatom flora (BP 1131).

BP-HNHM-ALG-D-1287 and BP-HNHM-ALG-D-2196

The next important contributor to the diatom collection was László Vida, whose slides are listed between numbers 1287 and 2196, adding 909 items to the core of the collection. Although Vida worked as an engineer, botany – first plants in general and later diatoms – remained at the centre of his interests throughout his life. He had a strong enthusiasm for diatoms, and his contributions to species identification were remarkable, ultimately proving of greater importance than his slide collection itself. After his death, his slides were donated to the Museum by his brother, Gábor Vida, the renowned botanist and geneticist, and member of the Hungarian Academy of Sciences (Web1).

The significance of this contribution is closely tied to the 'Bakony Research' project, within the framework of which (1971–1979) L. Vida conducted intensive studies of diatom assemblages (Bauer and Kenyeres 2004). He received 350 samples from Erzsébet Kol, the eminent algologist of the Botanical Department, who investigated the soft algae but left the diatoms unstudied (Kol 1968*a*, *b*). Vida filled this gap by systematically working on the diatoms. A detailed – though largely unpublished – list was handed over to the Bakony Museum and was later incorporated into the Hungarian Natural History Museum as part of his legacy. Another part of Vida's diatom collection originated from various locali-

ties across Hungary. A detailed taxonomic enumeration of this material – excluding the 'Bakony Research' project – was published by Krisztina Buczkó (1989).

From BP-HNHM-ALG-D-2197

The remainder of the diatom collection is currently under revision, which includes discarding unsuitable slides. Many of the samples and slides originated from the Szigetköz section of the Danube, Aggtelek National Park, mountain lakes, ponds, and mires of Romania. Since 2003, several core samples have been deposited in the collection; these were drilled for palaeoecological reconstruction purposes. The estimated number of diatom slides prepared between 1985 and 2025 is around 2,000, while the number of core samples is about 2,200.

In 2024 and 2025, the Collection of Algae of the Hungarian Natural History Museum received a substantial number of diatom samples from the Pest County Government Agency. Nearly 2,000 slides were transferred, the majority of which have already undergone revision. The diatom samples are in excellent condition,

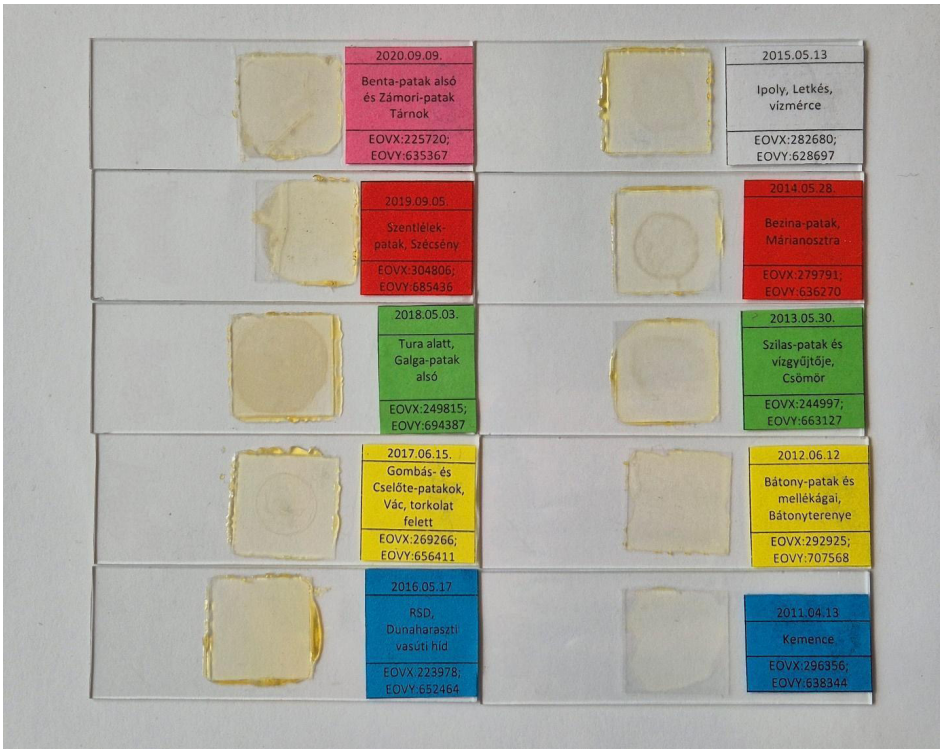

Fig. 2. Diatom slides received from the Pest County Government Agency, representing material under revision from 10 different years.

carefully organized, and accompanied by precise collection data (e.g., date, coordinates, etc.). The annual water quality surveys conducted by the Pest County Government Agency were implemented within the framework of the Water Framework Directive (WFD) (European Community, 2000) program. For this purpose, regular sampling was carried out at designated sites with precisely defined coordinates. The collected samples were prepared as microscope slides and evaluated by the Agency; however, their transfer to the Hungarian Natural History Museum has provided an exceptional opportunity for further research. In addition to the slides, the associated cleaned samples were also made available, which can be used for scanning electron microscopy. The wealth of information potentially derived from these materials, along with the broad research opportunities they offer, is of great scientific importance. Because the sampling was carried out annually at fixed locations, these materials provide a unique opportunity to study the temporal dynamics of diatom communities in Hungarian waters. Such long-term datasets are invaluable for detecting ecological changes, including the appearance of invasive species or the decline of native taxa, thereby contributing to biodiversity monitoring and conservation efforts. Altogether, the collection comprises 16 years' worth of samples from 2008 to 2024, derived from 190 sites across the country, covering 112 water bodies, and corresponding to an average of 112 slides per year.

DISCUSSION

The importance of diatom collections is becoming increasingly evident, and accordingly, they are continuously expanding both worldwide and in our region (B-Béres *et al.* 2023, De Wolf and Sterrenburg 1991, Ljubešić *et al.* 2025, WEB2).

The Collection of Algae housed in the Hungarian Natural History Museum can be regarded as consisting of three principal parts: the herbarium section (with dried materials and capsules), the collection of liquid samples (preserved water samples), and the diatom collection. The slides deposited in the diatom collection are owned by collection numbers; the first 2300 slides were given to the Pantocsek, Vida and Padisák collections. József Pantocsek's collection starts from number 1 and ends with 1049. Numbers up to 1057 had been allocated upon request primarily for type material. Samples numbered 1058 to 1286 belong to Judit Padisák's collection, followed by László Vida's collection from 1287 to 2196. These constitute the core of the diatom collection, which continues to grow in number as new material is added, and taxonomic revisions take place. The continuous numbering makes the collection size clear-cut and easily reviewable, therefore this practice will be retained. The slides, deposited after 1985 have re-

cently been marked by collecting numbers that refer to the collecting year. Even though this overview has drawn attention to some key parts of the collection, it is important to note that the Collection of Algae holds substantial significance of scientific value.

At the Hungarian Natural History Museum, we carry the responsibility of preserving knowledge of the past, protecting it for future research, and sharing it as a legacy with the generations to come. We also gladly welcome new collections, which become part of our shared heritage and enduring memory.

CONTRIBUTION OF JUDIT PADISÁK TO THE DEVELOPMENT OF COLLECTION

Judit Padisák is a highly recognized limnoecologist whose outstanding scientific achievements have been acknowledged with numerous national and international awards. Throughout her career, she has approached the study of phytoplankton with a unique perspective, applying ecological theories originally developed for terrestrial systems to aquatic microbial communities. This innovative framework has allowed her to reveal fundamental patterns in phytoplankton succession and diversity, significantly advancing our understanding of freshwater ecosystems. Beyond her scientific achievements, she has played an important role as a collection developer and provider of fundamental baseline data.

In 2025, as she celebrates her 70th birthday, we pay tribute to Judit Padisák's remarkable scientific career and her lasting contributions to limnology.

* * *

Acknowledgements – The development of the Algae Collection has involved, in addition to researchers, the contribution of numerous colleagues, preparators, assistants, and external collaborators. We would especially like to acknowledge the work of Erika (Mrs Frigyesné Lehoczky), Emike (Dr Jánosné Ackermann), Valika (Valéria Pálházi) and Zsóka (Erzsébet György) who worked as preparators at Department of Botany.

Összefoglaló: A Magyar Természettudományi Múzeum Növénytárának Algagyűjteményén belül a kovaalga-gyűjtemény a legfontosabb és leggyakrabban használt egység, amely jelenleg mintegy 30 000 tételt foglal magában. A gyűjtemény alapját a világszerte ismert Pantocsek-gyűjtemény adja, amely a második világháborús pusztítások ellenére is kiemelt nemzetközi tudományos jelentőséggel bír. Ehhez járulnak hozzá Padisák Judit és Vida László gyűjteményei. Ez a három gyűjteményrész 2300-ig folyamatos sorszámokkal ellátott, az 1980-as évektől bekerült minták évenkénti újrainduló számokon vannak nyilvántartva. A revízió során számos új vagy ritka előfordulás került megerősítésre, köztük a *Frustulia creuzburgensis*, amely Padisák Judit gyűjteményéből származik, és elsőként dokumentált előfordulást jelent a magyar kovaalga-flórában. A tanulmány célja, hogy bemutassa a gyűjtemény történeti alapjait és újabb gyarapodásait, valamint felhívja a figyelmet annak kutatási potenciáljára. A kovaalga-gyűjtemény kiemelkedő forrás a taxonómiai, ökoló-

giai, filogenetikai és biogeográfiai vizsgálatokhoz, s hozzájárul a hazai vizek biodiverzitásának nyomon követéséhez, az inváziós fajok azonosításához és az eltűnőben lévő taxonok dokumentálásához. Írásunkat a 70. születésnapját ünneplő Padisák Judit akadémikusnak ajánljuk, aki kiemelkedő szerepet játszott a gyűjtemény fejlesztésében és a limnoökológiai kutatások nemzetközi szintű előmozdításában.

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WEB1: *https://hu.wikipedia.org/wiki/Vida_G%C3%A1bor_(biol%C3%B3gus)*.

WEB2: *Diatom collection* - AWI

(submitted: 22.08.2025; accepted: 17.09.2025)

DOI: 10.17110/StudBot.2025.56.1.57 *Studia bot. hung. 56(1), pp. 57–66, 2025*

THROUGH THE STREETS OF KÖRMEND WITH MAGNIFYING GLASS IN HAND, ALWAYS STOPPING AT A PATCH OF GREENISH COLOUR

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T-Krasznai, E. (2025): Through the streets of Körmend with magnifying glass in hand, always stopping at a patch of greenish colour. – *Studia bot. hung.* **56**(1): 57–66.

Abstract: A total of 15 taxa of eukaryotic algae and cyanobacteria were identified on different surfaces in various artificial environments in the town of Körmend, W Hungary. The lowest possible taxonomic level was used to identify the organisms. The most common taxon was *Apatococcus lobatus*, which occurred in 6 out of 9 sampling sites. *Gloeocapsa novacekii*, *Gloeocapsopsis dvorakii*, and *Hassallia byssoidea*, which have rarely been mentioned in Hungary, were also common in Körmend. The green basal part of the Körmend Millennium Monument was found to be the most diverse habitat with 8 taxa. Research on terrestrial algae is important from both a scientific and a conservation standpoint, especially given the ongoing global biodiversity crisis. Contributing with new data to the knowledge on microbial diversitywould help to better understand and protect terrestrial microbial communities.

Key words: *Apatococcus,* artificial surfaces, *Gloeocapsa*, statue, terrestrial algae

INTRODUCTION

For as long as the world has existed, terrestrial algae have played an important role in fundamental geological processes such as the weathering of rocks. While they are active in the formation and transformation of soil and sediment, we see the positive side of their activities as the focus of human attention. However, when they act on rock art of artistic or historical importance, especially on buildings and monuments (Popović *et al.* 2018), we see them as obviously harmful from an aesthetic point of view. There are many examples around the world of how terrestrial algae cause aesthetic damage to cultural heritage, such as Angkor temples, Cambodia (Bartoli *et al.* 2014); Pompeii, Italy (Traversetti *et al.* 2018) or the Hieroglyphic Stairway in Copàn, Honduras (Caneva *et al.* 2005).

Various types of substrates such as stone, concrete, tree bark or soil are favourable to different microorganisms. As they grow, they can change the chemical and mineralogical composition of the original rock by altering its stability, permeability, colour, and density (Kováčik 2000).

The susceptibility of stones and rocks to organisms is referred to as bioreceptivity (Guillitte 1995). Rather than differences in rock chemistry and mineral composition, it is the high open porosity, capillary water content, surface roughness, and pH of surface erosion that promote the growth of phototrophic biofilms (Pinna 2021). In addition, many factors affect the colonisation of cyanobacteria and algae in terrestrial environments, such as water (humidity), temperature, light, pH, and UV radiation (Nowicka-Krawczyk *et al.* 2022). To survive and thrive in terrestrial environments, terrestrial algae have different cellular adaptations and life mechanisms (Nowicka-Krawczyk *et al.* 2022, Terlova *et al.* 2021). In contrast to aquatic habitats, they form biofilms (endo- and epilithic) on terrestrial surfaces, produce various protective biomolecules and extracellular matrices, and alter cell volume in response to desiccation, UV radiation, and high/low temperature fluctuations (Karsten *et al.* 2007, Levin *et al.* 2023).

There are an increasing number of articles on the extensive, colourful reproduction of subaerial algae species on monuments or other buildings of high architectural value (Liu *et al.* 2020, Purbani *et al.* 2020). The composition of the emerging biofilm communities depends on the geographical area and climatic zone, mainly consisting of cyanobacteria in warmer regions and eukaryotic microalgae in temperate regions (Karsten *et al.* 2007, Nowicka-Krawczyk *et al.* 2022). There is also an increase in the number of articles on how to control them, as they cause aesthetically unacceptable discolouration of buildings, sculptures or monuments (De Luca *et al.* 2024, Nowicka-Krawczyk *et al.* 2019). However, in order to defend against them, we must first know what there is.

Despite the appropriate climatic conditions and environmental factors, relatively few articles have been published recently on the distribution of terrestrial algae in Hungary (T-Krasznai *et al.* 2023). Therefore, our aim was to contribute to filling this gap. The study of the flora and fauna of the plains of the river Rába in the surroundings of Körmend has been ongoing since the 1990s. Several summary studies have been published on the plants (Balogh 2023, Szinetár 1994*a*, *b*) and the insect (Nagy 2021) or spider (Kovács *et al.* 2012) fauna. However, the algal flora of the terrestrial habitats has not been investigated so far. Here, we report on aerial cyanobacteria and algae flora on the surface of buildings and sculptures from different parts of Körmend.

MATERIAL AND METHODS

The samples were collected from 9 different locations in Körmend, Hungary on 24.07.2024 (Fig. 1). Samples were taken with toothbrushes from a variety of artificial environments, such as statues, walls and gates as well as various surfaces, including concrete, limestone, cement walls, plastic, and metal (see Fig. 2, Table 1).

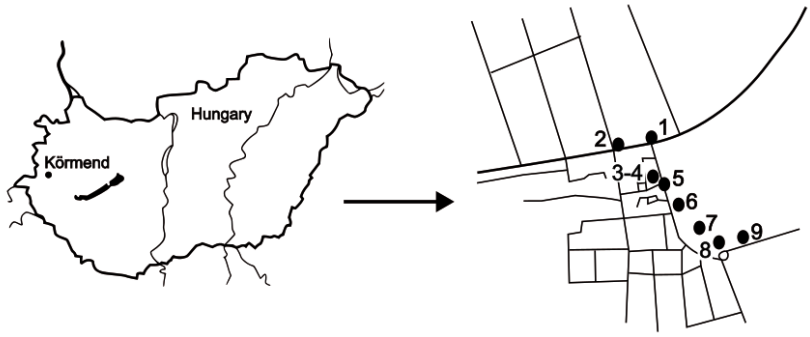

Fig. 1. The map of sampling area in Körmend, Hungary. The numbers indicate the sampling locations (see Table 1 for more details).

Fig. 2. Photos of some sampling points in Körmend. The numbers indicate the sampling locations (see Table 1 for more details).

Table 1. List of sampling sites and the nature of habitat.

No.	Place of collection	Substrata	Colour
1	Rákóczi street, cement wall in front of shop	cement wall	green
2	J. Vida street underpass edge	concrete	green
3	Körmend Millennium Monument, red part	limestone	red
4	Körmend Millennium Monument, base	limestone	green
5	Faludi Ferenc Library in Körmend, northern wall	concrete	red
6	Dr Batthyányi street, utility box	plastic	green
7	The gate of Körmend Castle	metal	green
8	Körmendi Children's Library, northern wall	cement wall	green
9	Unrestored western wall of the guardhouse of Körmend Castle	concrete	brown

Table 2. List of cyanobacteria and algae identified in the sampling points in Körmend, Hungary. The numbers indicate the sampling locations (see Table 1 for more details).

Species name	1	2	3	4	5	6	7	8	9
Cyanobacteria									
Hassallia byssoidea Hassall ex Bornet et Flahault				+	+				+
Gloeocapsa novacekii Komárek et Anagnotidis			+	+	+				+
Gloeocapsopsis cf. *dvorakii* (Novácek) Komárek et Anagnostidis ex Komárek			+	+	+				
cf. *Gloeocapsopsis* sp.	+								
Microcoleus sp.				+					
Nostoc commune Vaucher ex Bornet et Flahault									+
cf. *Nostoc* sp.				+					
Phormidium sp.				+					
Chlorophyta									
Apatococcus lobatus (Chodat) J. B. Petersen	+	+		+		+	+	+	
Stichococcus cf. *bacillaris* Nägeli	+								
cf. *Trentepohlia* sp.			+		+				
Charophyta									
Klebsormidium sp.				+					
Heterokontophyta									
Achnanthes sp.	+								
Hantzschia amphioxys (Ehrenberg) Grunow									+
cf. *Pinnularia* cf. *borealis* Ehrenberg									+
Total species number	**4**	**1**	**3**	**8**	**4**	**1**	**1**	**1**	**5**

The fresh samples were immediately studied with a Zeiss Axio Observer 7 inverted microscope at 100–630× magnification. The species observed were documented using a Canon EOS R6 digital camera. Organisms were identified at the lowest possible taxonomic level. Most recent accepted name of taxa was considered by AlgaeBase (Guiry and Guiry 2025). The morphological features of the cells, colonies and thalli were used to identify cyanobacteria and algae.

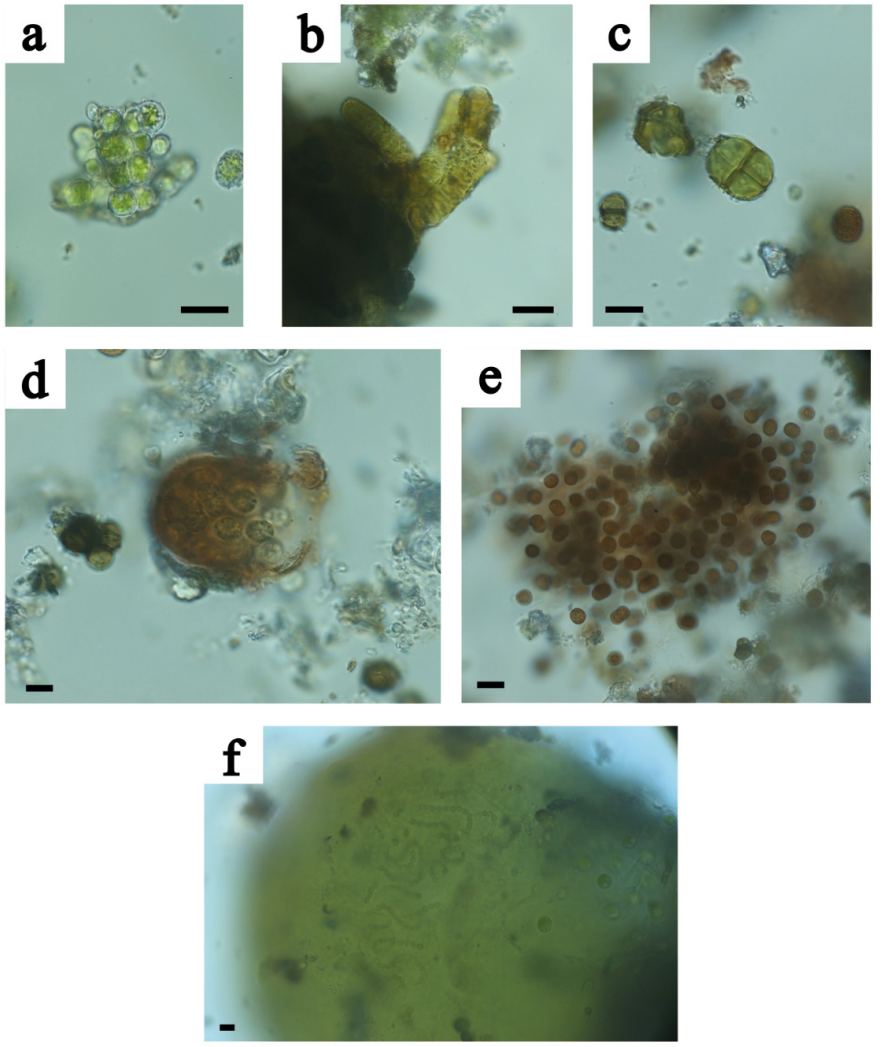

Fig. 3. Photos of the terrestrial species in Körmend – a) *Apatococcus lobatus* (Chodat) J. B. Petersen; b) *Hassallia byssoidea* Hassall ex Bornet et Flahault; c) *Gloeocapsopsis dvorakii* (Novácek) Komárek et Anagnostidis ex Komárek; d–e) *Gloeocapsa novacekii* Komárek et Anagnotidis; f) *Nostoc commune* Vaucher ex Bornet et Flahault. Scale bar 10 μm.

RESULTS

A total of 15 eukaryotic algae and cyanobacteria taxa were identified at genus or species level from the different substrata and localities (Table 2). The Cyanobacteria was the most diverse group with 8 taxa, while 3–3 taxa of Chlorophyta and Heterokontophyta were recorded, respectively. Only one taxon of Charophyta occurred in the samples.

The most abundant taxon, *Apatococcus lobatus* (Chodat) J. B. Petersen, occurred at 6 sampling sites (Fig. 3a). *Gloeocapsa novacekii* Komárek et Anagnotidis (Fig. 3d–e), *Gloeocapsopsis dvorakii* (Novácek) Komárek et Anagnostidis ex Komárek (Fig. 3c), and *Hassallia byssoidea* Hassall ex Bornet et Flahault (Fig. 3b) were also common in two different parts of Körmend (sampling sites 3–5 and 9; Fig. 1). The other species occurred only at 1–1 sampling site.

The base of the Körmend Millennium Monument was the most diverse habitat with 8 taxa. Four of the 9 sampling sites were dominated by only one species (*Apatococcus lobatus*) (Table 2).

The samples taken from the green patches of the cement wall, limestone, plastic, metal, and concrete surfaces (Fig. 2; site 1, 2, 6, 7, 8) were dominated by *Apatococcus lobatus*. The green patches at the base of the Millennium Monument in Körmend were more species-rich than the other green patches.

Species that were previously rarely mentioned in Hungary, such as *Gloeocapsa novacekii* and *Gloeocapsopsis dvorakii* as well as *Hassallia byssoidea* were common in red surface samples.

The taxa *Hantzschia amphioxys* (Ehrenberg) Grunow, *Pinnularia* cf. *borealis* Ehrenberg, and *Nostoc commune* Vaucher ex Bornet et Flahault (Fig. 3f), which were identified in samples from the brownish surface of the unrestored western wall of the guardhouse of Körmend Castle, were not found at other sites (Fig. 2, site 9).

DISCUSSION

Terrestrial algae are a special group within the algae groups that have adapted to desiccation and extreme environments (Nowicka-Krawczyk *et al.* 2022), which can be harsher than those found in aquatic habitats. They are often found in shaded micro-environments that offer some protection from the weather, such as pavements, old buildings, soil surfaces, rocks, and ancient built structures. The species composition and diversity of these habitats are mainly determined by microclimatic factors such as humidity and desiccation as well as surface properties (Macedo *et al*. 2009; Rindi and Guiry 2004).

Our results show that the algal assemblage collected in different parts of Körmend is characterised by a generally low diversity. The study identified fifteen

species of algae and cyanobacteria at the lowest possible level of identification. Those species that could not be identified are not mentioned. The taxa occurred on a variety of substrates and in various locations, forming patches of different colours.

The number of species we found (15 taxa) is considered to be average compared to the number of species published in surveys (10 taxa – Ljaljević-Grbić *et al.* 2010; 18 taxa – Popović *et al.* 2018; 17 taxa – Rindi and Guiry 2004; 25 taxa – Uher 2008). However, in larger surveys, the number of species may exceed 50–100 species (47 taxa – Samad and Adhikary 2008; 172 taxa – Macedo *et al.* 2009). In terrestrial environments, it is not unusual for a biofilm to be formed by only a few species, or even just a single species. Gartner and Stoyneva (2003) found that the green layers were formed only by *Apatococcus lobatus*. The green microalga *Apatococcus lobatus* is widely distributed in terrestrial habitats. It can be found throughout many climatic zones (Gustavs *et al.* 2016). This is supported by our results, there were sites such as surfaces of cement wall, plastic, metal, and concrete, where only *A. lobatus* was present.

Only a few taxa found by us are mentioned in the most recent database of algae and cyanobacteria in Hungary (Görgényi *et al.* 2023; Németh and Buczkó 2024; T-Krasznai *et al.* 2023). Of the species identified herein, the coccoid cyanobacteria *Gloeocapsa novacekii* was previously mentioned only from Debrecen, Hungary (T-Krasznai *et al.* 2023). Its occurrence in Körmend is not only new, but also the second distribution data for Hungary. Two records of the filamentous cyanobacterium *Hassallia byssoidea* were previously published from Hungary: one from Kiskunság (Komáromy and Padisák 1999), and one from Debrecen (T-Krasznai *et al.* 2023). Its occurrence in Körmend represents a new distribution data set for Hungary. *Gloeocapsopsis dvorakii*, a coccoid cyanobacterium, is also a rare species in Hungary. To the best of our knowledge, it is new to the Hungarian algae flora. It was described as *Gloeocapsa dvorakii* Novácek in 1929. This aerophytic species can be distinguished from other *Gloeocapsopsis* species by its rusty-red or orange-red sheaths.

In the shadow of the global biodiversity crisis and mass extinctions, the importance of biodiversity conservation is becoming increasingly apparent (Cowie *et al.* 2022). Even in aquatic environments, the biodiversity of microorganisms is still a neglected area, thus relatively little is known about the diversity and biogeography of terrestrial algae. Despite systematic research conducted by some countries on these algal groups, they are considered understudied at the global level (Hauer 2007, Hauer *et al.* 2015). However, species-level identification of terrestrial algae is often difficult because of the high morphological similarity of species (Rindi and Guiry 2004). Although genetic tests (e.g. DNA-based identification) can help to improve identification (Jusko and Johansen 2024,

Nguyen *et al*. 2017), these can be costly and adequate financial support is often lacking. A further limitation is that the coverage of databases is not yet complete, so that many sequences appear only as "barcodes" without species names. Nevertheless, there are species that can be identified even by light microscopy at genus or even species level. We believe that these types of experiments, even if incomplete, are more useful than the complete absence of data.

In conclusion, research on terrestrial algae is important both scientifically and for conservation, especially in the current biodiversity crisis. Filling the gap in our knowledge of terrestrial algae could improve our understanding of terrestrial microbial communities and help to conserve them.

* * *

Acknowledgements – This work is dedicated to Professor Judit Padisák, in celebration of her birthday and in recognition of her outstanding contribution to hydrobiology. I would like to share the story of how we met. I first met Professor Padisák exactly 20 years ago as a university student at a National Association for Student Research OTDK conference. Later, I was the only member of our group to participate in my first international conference in Smolenice. She was so kind and supportive, which I will never forget. Since then, she has always helped me in a constructive way whenever I have had any problems or questions. In today's fast-paced world, she is one of the few people who still take the time to pause and appreciate the beautiful world of algae.

Összefoglaló: Magyarország nyugati részén található Körmend városának különböző mesterséges felületeiről összesen 15 eukarióta alga és cianobaktérium taxont azonosítottunk. Az élőlények azonosítása a lehető legalacsonyabb rendszertani szinten történt. A leggyakoribb taxon az *Apatococcus lobatus* zöldalga faj volt, amely a 9 mintavételi helyből 6 helyen fordult elő. A hazánkban ritkán említett *Gloeocapsa novacekii*, *Gloeocapsopsis dvorakii*, *Hassallia byssoidea* szintén gyakoriak voltak Körmenden. A Körmendi Millenniumi Emlékmű alsó része volt a legváltozatosabb élőhely 8 taxonnal. *Gloeocapsopsis dvorakii* új adat Magyarország flórájára. A szárazföldi algák kutatása mind tudományos, mind természetvédelmi szempontból fontos, különösen a napjainkban is zajló biodiverzitás-válság miatt. A tudáshiány bárminemű csökkentése hozzájárul a szárazföldi mikrobiális közösségek jobb megértéséhez és védelméhez.

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(submitted: 30.07.2025; accepted: 02.09.2025)

DOI: 10.17110/StudBot.2025.56.1.67 Studia bot. hung. 56(1), pp. 67–92, 2025

RARE TRAITS OF DIATOMS

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Abstract: Rare species is a central topic of conservation biology. Nevertheless, we do not have enough knowledge about their characteristics which can lead to their extinction. For this purpose, this study aimed to establish a diatom trait database (morphological and lifeform traits, a total of 142) and identify rare traits. The developed database contains 13,162 records for diatom species of the Danube catchment area in Hungary and Croatia. Using Rabinowitz's original approach and applying new rarity indices published in the literature, rare diatom traits were determined in different terms. 75% of diatom traits were common features, while 25% of these were small population-sized traits. They were exclusively morphological characteristics of diatoms (four chloroplasts per cell, five different chloroplast shapes and larger size categories) exhibited predominantly by rare species. 7% of the total traits were absolute rare (small population-sized, habitat specialists and geographically restricted at the same time) traits. Namely, nine big size categories and two chloroplast shapes, which were associated with the special conditions provided by the Sava, Drava, and Odra Rivers in Croatia and the Rába in Hungary. Rare species with these unique traits are functionally distinct and vulnerable members of the communities.

Key words: diatoms, lifeforms, morphological features, rarity, traits

INTRODUCTION

To investigate or even to find rare species is a challenge even in the case of organisms visible to the naked eye, not to mention the microscopic ones. For this reason, ecological studies and consequently ecological knowledge about rarity is limited. In aquatic ecosystems, it is especially true for algae. Judit Padisák was

the first ecolimnologist who recognised the ecological importance of rare algal species already in the 1990's. She used an unusual quantity measure to identify rare phytoplankton species, the relative frequency (Padisák 1992). In her first study on rarity, she found that around half of the planktic algal species are rare, which is also characteristic in benthic diatoms, revealed by a recent study on regional scale (Stenger-Kovács *et al.* 2025). Padisák (1992) also noted that the number of the samplings fundamentally influences the detection of rare species (Padisák *et al.* 2010) beside the sampling design (Specht *et al.* 2017) and the classification method of a species into the categories of commonness and rarity (Nislow *et al.* 2011). Moreover, she highlighted that rare species cannot be neglected for understanding ecological processes (Padisák *et al.* 2010). Detailed knowledge about these silent species would be crucial, since these species in certain environmental changes can become common or even invasive, therefore, rarity, commonness, and biological invasions must be handled together (Padisák *et al.* 2010). However, the significance of rare species among algal ecologists has just been recognised and the journey Padisák began has been continued (Görgényi *et al.* 2023, Stenger-Kovács *et al.* 2025). These studies step over the traditional, conservational perspectives focusing on Red List species.

However, what Judit Padisák is internationally known for, is the establishment and development of the functional ecology of phytoplankton. In this approach, the basic theory is that species are grouped into well-defined functional or morpho-functional groups according to their ecological characteristics (Reynolds 1980, 1984) and similar morphological features (Reynolds *et al.* 2002). This approach was refined and expanded by Padisák and Reynolds (1998), and the ecological importance of functional and morphological characteristics (traits, e.g. size, shape, colonial, unicellular, flagella) of the phytoplankton species was highlighted by a number of studies published by Padisák and her co-authors (e.g. Salmaso and Padisák 2007, Vanderley *et al.* 2022, Žutinić *et al.* 2014). Following the worldwide spread of trait-based approaches in phytoplankton ecology (e.g. Kruk *et al.* 2002), several decades behind, these analyses have appeared and broadened in benthic diatom ecology (e.g. B-Béres *et al.* 2016, 2017, Soininen *et al.* 2016, Stenger-Kovács *et al.* 2018, 2020, Tapolczai *et al.* 2016, 2017).

Judit Padisák was the person who inspired this study. Thanks to her, our scientific attention has turned to the investigation of rarity, especially diatom rarity from a functional, trait-based perspective. Ecology of outliers can help to understand the effect of biodiversity loss on ecosystem function (Violle *et al.* 2017), therefore identifying functional rarity is crucial.

Accordingly, our main aim in this study was (i) to develop a diatom trait database for the rivers of the Danube catchment area in Hungary and Croatia and (ii)

to identify rare traits of diatoms from different terms following Rabinowitz's approach (1981) based on rarity indices by Maciel (2021). Furthermore, (iii) to answer whether common or rare species have rare traits?

MATERIALS AND METHODS

Collection and treatment of phytobentos samples

Phytobentos samples were collected from 99 sampling sites in River Danube's network system in Hungary (48 sites) and in Croatia (51 sites) in two seasons (spring and autumn) of 2022 (Table 1). The samples were taken from rock substrates with a toothbrush and preserved in ethanol. These samples were treated by the hot hydrogen-peroxide method (CEN 2003) to clean diatom frustules from organic materials. One drop of the purified valves was embedded in Pleurax© synthetic resin.

Table 1. Sampling sites and their GPS coordinates of the Danube catchment area.

Hungary			Croatia		
River	GPS-N	GPS-E	River	GPS-N	GPS-E
Által-ér	47.731578	18.32382	Bednja 1	46.2409738	16.1690811
Bitva	47.2921826	17.3730207	Bednja 2	46.291004	16.7383304
Cinca	47.2909945	17.1714543	Drava 2	45.7904535	17.980645
Cuhai-Bakony-ér	47.70461	17.856468	Drava 3	45.7277505	18.3197518
Csíkvándi-Bakony-ér	47.4595103	17.4466295	Drava 4	45.6673405	18.4889481
Csörnöc-Herpenyő 1	47.2232517	16.9464436	Drava 5	45.617589	18.583732
Csörnöc-Herpenyő 2	47.023333	16.7016046	Drava 6	45.572097	18.6486069
Damásdi-patak	47.831161	18.853865	Drava 7	45.5530337	18.8642468
Dobroda-patak	48.207931	19.594151	Drava 8	46.1102261	17.1525354
Danube HUN1	47.816204	18.862622	Drava 9	46.128741	17.070945
Danube HUN2	47.762361	18.540508	Drava 10	45.7831074	18.2006111
Danube HUN3	47.740468	18.161742	Drava 11	45.942418	17.46927
Danube HUN4	47.738873	17.825387	Drava 12	46.2413055	16.9382756
Danube HUN5	47.768855	17.695974	Drava 13	46.2971501	16.8791159
Fekete-víz	48.03547	19.21186	Danube_CRO1	45.83849	18.852161
Gerence-patak	47.4021181	17.4716095	Danube_CRO2	45.2306027	19.3789696
Hajagos	47.3052291	17.2925608	Karašica 1	45.7086722	18.294293
Hosszú-víz	47.2287199	16.8408572	Karašica 2	45.7283359	17.966283
Ipoly 1	48.097534	19.482762	Krapina 1	45.8347708	15.8228039
Ipoly 2	48.23556	19.605588	Krapina 2	46.104752	16.2011741
Ipoly 3	48.065698	19.107886	Kupa 1	45.4836406	16.3688803
Ipoly 4	48.031432	18.82434	Kupa 2	45.645271	15.3564433
Ipoly 5	47.846207	18.827692	Kupa 3	45.614169	15.479493

Table 1. Sampling sites and their GPS coordinates of the Danube catchment area.

Hungary			Croatia		
River	GPS-N	GPS-E	River	GPS-N	GPS-E
Kodó	47.2106331	17.159439	Mura 1	46.419121	16.6912483
Kozár-borzó	47.2070853	16.7520865	Mura 2	46.5145696	16.4405221
Lókos stream	48.04637	19.202505	Mura 3	46.325253	16.8711927
Marcal 1	47.4488467	17.383294	Odra	45.30072	16.205618
Marcal 2	47.3187165	17.2749847	Orljava 1	45.2862258	17.805124
Marcal 3	47.1800447	17.203338	Orljava 2	45.145141	17.704758
Marcal 4	47.019367	17.1780178	Plitvica 1	46.2682566	16.3809813
Marcal 5	47.609778	17.514591	Plitvica 2	46.2948749	16.7145553
Ménes-patak	48.110939	19.515189	Sava 1	45.040493	18.6959194
Mosoni-Danube	47.733882	17.755304	Sava 2	45.0601558	18.5047005
Pándzsa	47.645157	17.663524	Sava 3	45.139754	18.073944
Pápai-Bakony ér	47.3407368	17.4011407	Sava 4	45.0990681	17.7378568
Perint	47.2852455	16.591909	Sava 5	45.2688108	16.9154738
Rába 1	46.9804976	16.5266711	Sava 6	45.4014717	16.53887
Rába 2	47.1268512	16.8504796	Sava 7	45.479194	16.384163
Rába 3	47.2450628	16.9525601	Sava 8	45.788939	15.8593526
Rába 4	47.621064	17.488968	Sava 9	45.8624521	15.688058
Rába 5	47.4230911	17.1328756	Sava 10	45.44469	16.1347
Rátka-patak	47.2410121	16.7989645	Sava 10	45.74637	16.229709
Sokorói-Bakony-ér	47.561259	17.574898	Sava 11	45.1340401	17.6729085
Sorok stream	47.125671	16.7602657	Sava 12	45.6477778	16.3396059
Szávai channel	47.746114	17.683105	Sava 13	45.3622414	16.7577718
Torna stream	47.10381177	17.2611613	Sava 14	45.16701	17.25817
Únyi stream	47.67255	18.675955	Sava 15	45.8343174	15.7710688
Vörös stream	46.9700392	16.4077611	Sava 16	44.8513247	18.9595429
			Una 1	45.2615941	16.9128728
			Una 2	45.2220957	16.549762
			Una 3	45.0497854	16.3725921

Microscopic analyses of diatoms

Altogether 183 diatom slides were adequate for microscopic analyses. Diatom taxa were identified to species and variates level using the taxonomic guides of Lange-Bertalot *et al.* (2017), Bey and Ector (2013), Peeters and Ector (2018, 2019), and Ács *et al.* (2023). Around 400 diatom valves per slide were counted in a light microscope (Zeiss Axio Imager A1, Plan-apochromat DIC lens) for the calculation of the relative abundance of the species.

Development of a diatom trait database

Based on Rimet and Bouchez (2012), eight morphological traits and 19 lifeforms as diatom traits (Table 2) were determined for 409 diatom species. The missing traits of the species were collected from open databases and publications. Diatom data were looked for in Alverson *et al.* (2021), Bahls (2016), Bąk *et al.* (2014), Beauger *et al.* (2015), Bedoshvili *et al.* (2009), Bertolli *et al.* (2020), Bey and Ector (2013), Bishop (2017), Bishop and Stancheva (2017), Budzyńska and Wojtal (2011), Burgle and Edlund (2015), Cox (1997), Cox and Williams (2006), De Stefano and Romero (2005), Environmental Agency (2020), Frohn (2016), Furey (2010), Grunow (1860), Hatcher (2018), Hillebrandt (1999), Hustedt (1930), Jovanovska *et al.* (2019), Jovanovska and Winter (2021), Jüttner (2025*a*, *b*, *c*), Jüttner and Cox (2025), Jüttner and Mann (2025), Jüttner and Van de Vijver (2025), Jüttner *et al.* (2025*a*, *b*, *c*), Kelly (2025), Kezlya *et al.* (2022), Kiss *et al.* (2013), Kociolek (2011), Kociolek *et al.* (2015), Krammer (1997, 2002), Kulikovskiy *et al.* (2011, 2019, 2023), Lange-Bertalot and Fuhrmann (2016), Lange-Bertalot *et al.* (2011, 2017, 2020), Levkov *et al.* (2013), Liu *et al.* (2012), Mann (2025*a*, *b*, *c*, *d*, *e*, *f*), Mann and Jüttner (2025*a*, *b*, *c*), Mann *et al.* (2025), Mendoza (2015), Morales *et al.* (2010), Patrick and Reimer (1975), Peeters and Ector (2018, 2019), Phytoplankton guide (2012 *a*, *b*), Polaskey and Bishop (2015), Potapova (2009, 2020), Potapova *et al.* (2008), Rimet (2011), Rimet *et al.* (2024), Round *et al.* (1990), Spaulding and Edlund (2008*a*, *b*, *c*, *d*), Stancheva *et al.* (2020), Stepanek (2011), Tapolczai *et al.* (2019), Tuji and Williams (2006), Van de Vijver *et al.* (2022), Wetzel *et al.* (2019), Williams (2025), and the OMNIDIA software 6.1 (Lecointe *et al.* 1993).

Table 2. The studied morphological and lifeform traits.

Morphological traits	Lifeform traits	
chloroplast number	motile / non motile	colonial/ non colonial
chloroplast shape	pioneer / non pioneer	mucous tube colony
valve length	attached / not attached	chain colony
valve width	adnate	zig-zag colony
valve height	pedunculate	rosette colony
length/width ratio	pad	ribbon colony
cell biovolume	stalk	stellate colony
valve shape		arbuscular colony

First, the shape of the diatom valves was determined relying primarily on the work of Hillebrand *et al.* (1999), and then biovolumes were calculated using the length, width, and height data. If we could not find any information about them (mainly in the case of the valve height), we estimated it from our photo documentation or from the generalized generic data.

For each trait, the extent of the trait was determined, the distribution of the data, furthermore, where and how much jumps were found in the data. Based on this, the continuous variables were converted into categorical variables resulting in 142 different trait categories (Appendix 1). Including four morphological trait categories related to the number of chloroplasts, 15 to the shape of the chloroplasts, 37 to lengths, ten to widths, and 19 to heights. These latter morphological parameters were also used as the basis for the 27 volume and 11 length /width trait categories (Appendix 1, electronic supplement).

Rarity indices

For the 142 trait categories rarity indices were calculated like geographic range (gr), habitat specificity (hs), and population size (ps) indices based on studies by Maciel (2021) and Stenger-Kovács *et al.* (2025) guided by Rabinowitz's approach (Rabinowitz 1981). The formulae of the calculated indices are as follows:

(1) psi = 1/ p_{max}; p_{max}= maximal population size

(2) hsi = 1/ h_{max}; h_{max}= maximal number of occurrence

(3) gri = 1/{[(latitude range)*(longitude range)] + 1}

Finally, the absolute rarity index (rr) was calculated as the median of the previous three indices (psi, hsi, gri). The range of these indices varied between 0 and 1. Values close to 0 indicate more common features, and values closer to 1 indicate rarer traits. In our analysis, the trait was considered as a rare character if its index value was one. Finally, traits were classified into rarity categories based on Rabinowitz's approach (Rabinowitz 1981) (Table 3).

Table 3. Number of diatom traits in the categories of the Rabinowitz system.

Local population size	Geographic range	Habitat demand	Number of diatom traits	commonness/rarity
at least somewhere big	wide	generalist	106	frequent, common
		specialist	0	
	narrow	generalist	0	
		specialist	0	rare in certain term
always small	wide	generalist	25	
		specialist	0	
	narrow	generalist	0	
		specialist	11	absolute rare

RESULTS

Diatom trait database of the Danube catchment area

Our database contains 183 samples, a total of 409 diatom species with a combination of 142 categories of 27 traits (eight morphological and 19 life-form traits) (Appendix 1). This database is freely available at the following link: *https://zenodo.org/records/17062977*

Rarities

Small population traits

In total, 36 traits could be considered as rare in terms of population size (psi index was equal to one). One trait was concerned to chloroplast number (Chloroplast number is 4) and five traits to the chloroplast shape (X shaped, shapeless at rim, large plate, lamellar, appressed) (Fig. 1A–E). Four rare traits

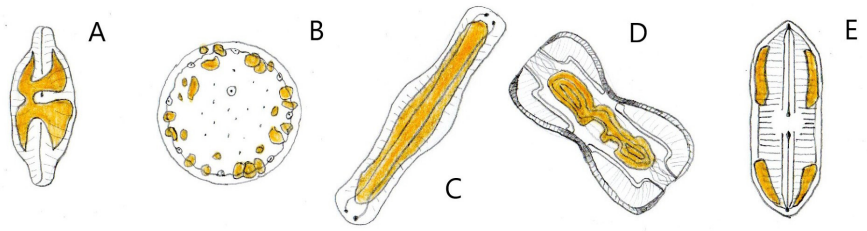

Fig. 1. Drawings of rare chloroplast shapes based on population size (illustrations not scaled, drawn by Orsolya Halmai). A = X-shaped chloroplast (*Placoneis undulata*); B = shapeless chloroplasts at rim (*Praestephanos* cf. *triporus*); C = large plate chloroplast (*Epithemia gibba*); D = lamellar chloroplast (*Entomoneis paludosa*); E = appressed chloroplasts (*Neidium cuneatiforme*).

connected to the width of the valve (width between 25–30 µm, 45–50 µm, 55–60 µm and 85–90 µm), eight for the length (e.g. 0–5 µm, 205–210 µm, 210–215 µm, 300–305 µm), five are for the height of the valve (8–9 µm, 10–11 µm, 15–16 µm, 27–28 µm, 52–53 µm). Twelve traits belong to the biovolume category (e.g. 6,500–7,500 µm^3; 228,500–229,500 µm^3), and one to the length/width category (40–50) (Fig. 2). These 36 traits were carried by 37 different diatom species. Of these, 36 are rare species in terms of population size (e.g. *Cymatopleura apiculata*, *Surirella ovalis*), among these species 16 were absolutely rare since they were also habitat specialists and even rare in terms of geographic distribution (e.g. *Amphora lange-bertalotii* var. *tenuis*, *Tryblionella gracilis*, *Ulnaria danica*, *Neidium cuneati-*

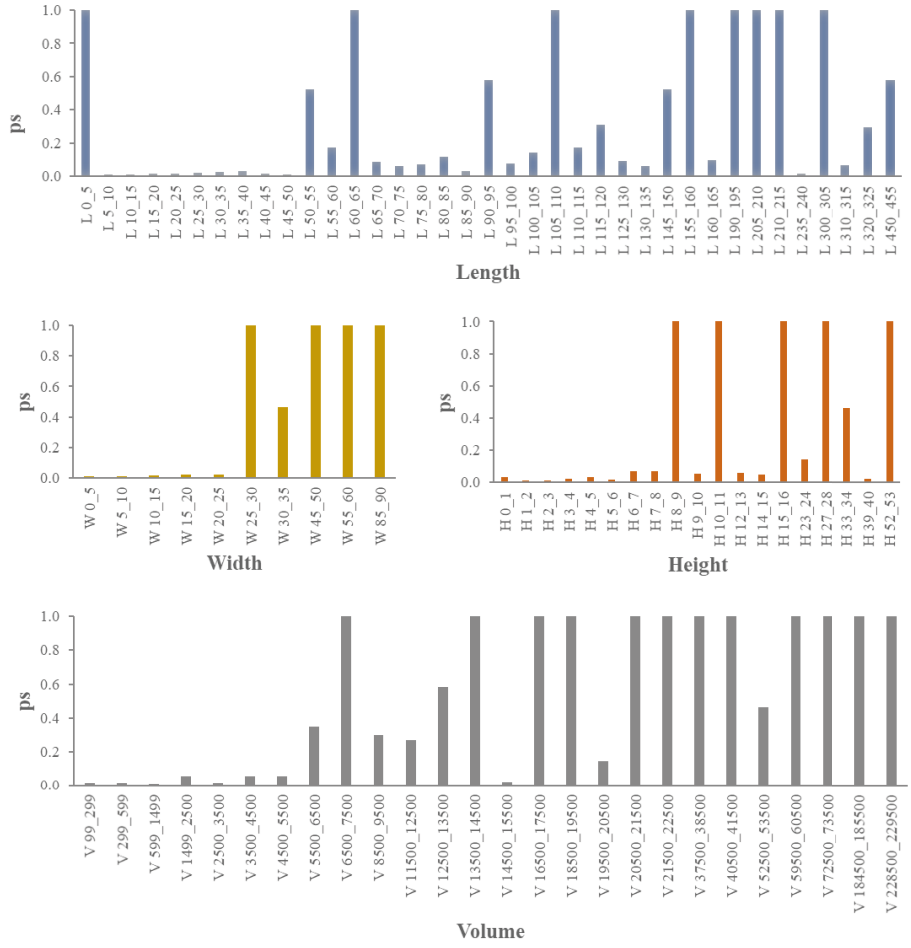

Fig. 2. The ps index values of morphological traits, such as length, width, height, and volume (size unit in μm).

forme). Only one common species (*Nitzschia gracilis*) had one rare trait (length 60–65 μm). Seventeen rare diatom species were identified that have more than one rare, small population-sized trait (Table 4), e.g. *Cymbella neolanceolata* with four rare traits. These traits created a very unique morphological feature of this species with the length of 155–160 μm, width of 25–30 μm, height 27–28 μm, and consequently, the volume of 20,500–21,500 μm^3.

Table 4. Rare diatom species and their rare traits. (A = rare in terms of small population size; B = rare in terms of geographical distribution; C = rare in terms of habitat specificity; Chp = chloroplast; D = absolute rare; H = height; L = length; V = volume; W = width)

Species	A	B	C	D	Trait	A	B	C	D
Amphipleura pellucida Kützing (Kützing)	×	×	×	×	L: 105–110 µm	×			
Amphora lange-bertalotii var. *tenuis* Levkov et Metzeltin	×	×	×	×	H: 8–9 µm	×			
Amphora lange-bertalotii Levkov et Metzeltin	×				L: 60–65 µm	×			
Aulacoseira pfaffiana (Reinsch) Krammer	×	×	×	×	L: 0–5 µm	×			
Cymatopleura apiculata W. Smith (Ralfs)	×				V: 21,500–22,500 µm^3	×			
Cymbella neocistula Krammer	×				V: 6,500–7,500 µm^3	×			
Cymbella neolanceolata W. Silva	×				L: 155–160 µm	×			
					V: 20,500–21,500 µm^3	×			
					W: 25–30 µm	×			
					H: 27–28 µm	×			
Didymosphenia geminata (Lyngbye) M. Schmidt	×				V: 21,500–22,500 µm^3	×			
Diploneis elliptica (Kützing) Cleve	×	×	×	×	H: 15–16 µm	×	×	×	×
					V: 40,500–41,500 µm^3	×	×	×	×
Ellerbeckia arenaria (Moore ex Ralfs) Crawford	×	×	×	×	V: 72,500–73,500 µm^3	×	×	×	×
					W: 85–90 µm	×	×	×	×
Encyonema leibleinii (C. Agardh) W. J. Silva, R. Jahn, T. A. Veiga Ludwig et M. Menezes	×				V: 13,500–14,500 µm^3	×			
					H: 10–11 µm	×			
Entomoneis paludosa (W. Smith) Reimer	×				Chp: shape lamellar	×			
					V: 6,500–7,500 µm^3	×			
Epithemia gibba Kützing	×				Chp: shape large-plate	×			
					V: 184,500–185,500 µm^3	×			
Fistulifera saprophila (Lange-Bertalot et Bonik) Lange-Bertalot	×				Chp: number 4	×			
Fragilaria perdelicatissima Lange-Bertalot et Van de Vijver	×				L: 60–65 µm	×			
Gyrosigma attenuatum (Kützing) Rabenhorst	×				L: 190–195 µm	×			
Iconella tenera (W. Gregory) Ruck et Nakov	×				V: 37,500–38,500 µm^3	×			
					W: 25–30 µm	×			
Lindavia balatonis (Pantocsek) Nakov, Guillory, Julius, Theriot et Alverson	×				H: 8–9 µm	×			

Table 4. (continued)

Species	A	B	C	D	Trait	A	B	C	D
Neidiomorpha binodeformis (Krammer) Cantonati, Lange-Bertalot et Angeli	×	×	×	×	Chp: shape appressed	×			
Neidiomorpha binodis (Ehrenberg) Cantonati, Lange-Bertalot et Angeli	×	×	×	×	Chp: shape appressed	×			
Neidium ampliatum (Ehrenberg) Krammer	×	×	×	×	Chp: number 4	×			
					Chp: shape appressed	×			
Neidium cuneatiforme Levkov	×	×	×	×	Chp: number 4	×			
					Chp: shape appressed	×			
Neidium dubium (Ehrenberg) Cleve	×				Chp: number 4	×			
					Chp: shape appressed	×			
Nitzschia graciliformis Lange-Bertalot et Simonsen	×				L/W: 40–50 µm	×			
Nitzschia gracilis Hantzsch					L: 60–65 µm	×			
Pinnularia viridis (Nitzsch) Ehrenberg	×				V: 16,500–17,500 µm³	×			
					L: 105–110 µm	×			
Placoneis undulata (Østrup) Lange-Bertalot	×	×	×	×	Chp: shape x	×	×	×	×
Praestephanos cf. *triporus* (Genkal et G. V. Kuzmin) Tuji et J.-S. Ki	×	×	×	×	Chp: shapeless at rim	×	×	×	×
					L: 0–5 µm	×			
Stauroneis phoenicenteron (Nitzsch) Ehrenberg	×	×	×	×	L: 210–215 µm	×	×	×	×
					V: 21,500–22,500 µm³	×			
Surirella librile (Ehrenberg) Ehrenberg	×				H: 27–28 µm	×			
					V: 59,500–60,500 µm³	×			
Surirella ovalis Brébisson	×				W: 25–30 µm	×			
Surirella undulata (Ehrenberg) Ehrenberg	×				H: 52–53 µm	×			
					V: 22,8500–22,9500 µm³	×			
					W: 55–60 µm	×			
Thalassiosira lacustris (Grunow) Hasle in Hasle et Fryxell	×	×	×	×	V: 18,500–19,500 µm³	×	×	×	×
					W: 45–50 µm	×	×	×	×
					H: 10–11 µm	×			
Tryblionella angustata W. Smith	×				L: 60–65 µm	×			
Tryblionella gracilis W. Smith	×	×	×	×	V: 6,500–7,500 µm³	×			
Ulnaria capitata (Ehrenberg) Compère	×	×	×	×	L: 300–305 µm	×	×	×	×
Ulnaria danica (Kützing) Compère et Bukhtiyarova	×	×	×	×	L: 205–210 µm	×	×	×	×
					L/W: 40–50 µm	×			

Habitat specialist, geographically restricted, and absolute rare traits

Of the 36 small population-sized traits, 11 were also considered to be rare in terms of both habitat specificity and geographic distribution. These are therefore absolute rare traits: two chloroplast forms (X-shaped, shapeless at rim) (Fig. 1A–B), two width (45–50 µm, 85–90 µm), three length (205–210 µm, 210–215 µm, 300–305 µm), one height (15–16 µm), and three biovolume (18,500–19,500 µm^3, 40,500–41,500 µm^3, 72,500–73,500 µm^3) (Fig. 3). These rare features are carried by 8 absolute rare species like *Diploneis elliptica*, *Ellerbeckia arenaria*, *Placoneis undulata*, *Praestephanos* cf. *triporus*, *Stauroneis phoenicenteron*, *Thalassiosira lacustris*,

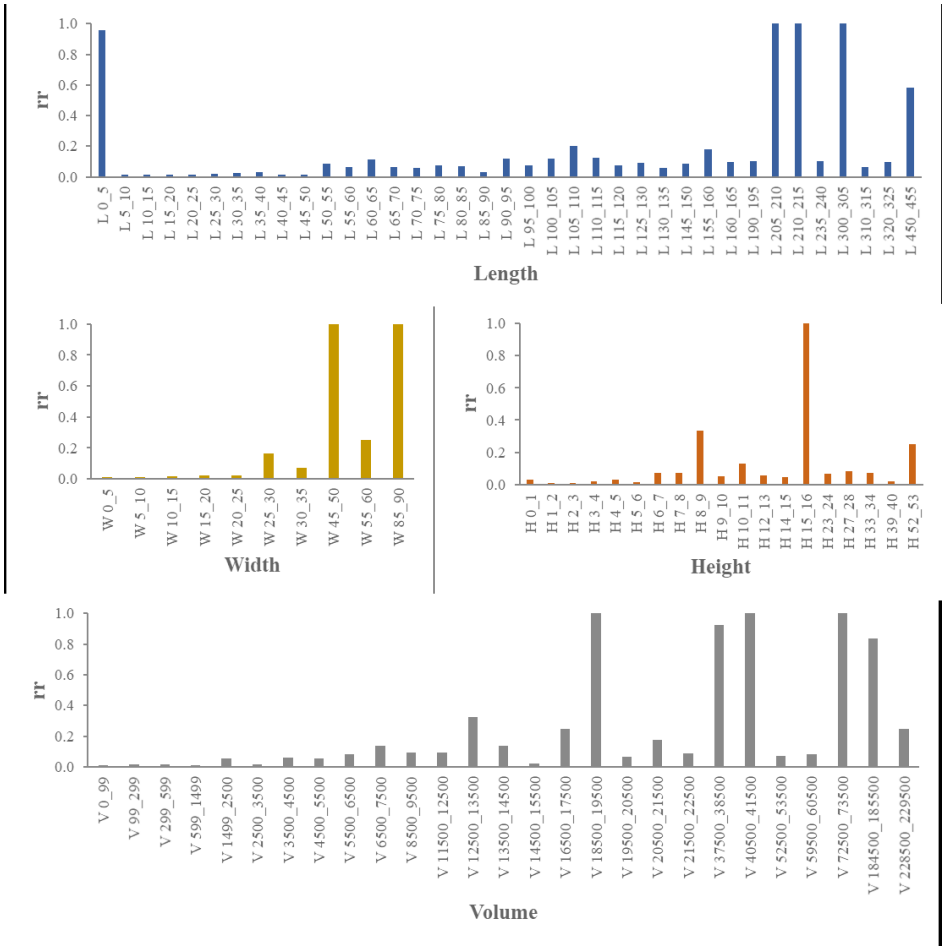

Fig. 3. The rr index values of morphological traits, such as length, width, height, and volume (size unit in µm).

Ulnaria capitata, and *Ulnaria danica*. Three of them (*Diploneis elliptica*, *Ellerbeckia arenaria*, and *Thalassiosira lacustris*) carried more than one absolutely rare trait (Fig. 4). *Diploneis elliptica* can be characterised by the height of 15–16 μm and the volume of 40,500–41,500. *Ellerbeckia arenaria* has also two absolutely rare traits like the width 85–90 μm and the volume 72,500–73,500 μm^3. *Thalassiosira lacustris* has two absolute rare traits (width 45–50 μm, volume 18,500–19,500 μm^3) and one rare trait (height 10–11 μm) in terms of population size.

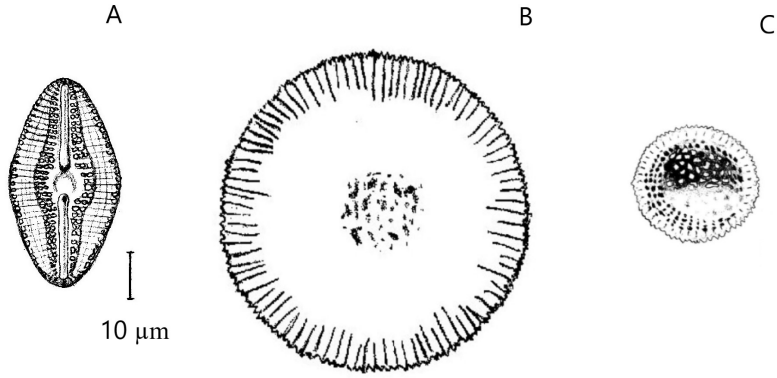

Fig. 4. Three absolute rare diatom species with more absolute rare traits (drawn by Orsolya Halmai). A = *Diploneis elliptica*, B = *Ellerbeckia arenaria*, C = *Thalassiosira lacustris*.

Nine of the 11 traits were identified in diatom species, mainly present in samples from the Sava, Drava, and Odra rivers in Croatia, and the remaining two traits being observed in the Rába River in Hungary (Table 5). In two different

Table 5. Absolute rare diatom traits with example species found in special habitats and regions.

Trait	River	Settlement	Species example
Length 300–305 μm	Drava	Legrad	*Ulnaria capitata*
X-shaped chloroplast	Drava	Petrijevci	*Placoneis undulata*
Length 205–210 μm	Odra	Sisak	*Ulnaria danica*
Length 210–215 μm	Odra	Sisak	*Stauroneis phoenicenteron*
Width 85–90 μm	Rába	Sárvár	*Ellerbeckia arenaria*
Biovolume 72,500–73,500 μm^3			
Shapeless chloroplast at rim	Sava	Topolje	*Praestephanos* cf. *triporus*
Height 15–16 μm	Sava	Lukavec	*Diploneis elliptica*
Biovolume 40,500–41,500 μm^3			
Width 45–50 μm	Sava	Županje	*Thalassiosira lacustris*
Biovolume 18,500–19,500 μm^3			

sampling sites of the Drava River, one–one trait was absolutely rare (Length 300–305 μm and X-shaped chloroplast). In the Odra River, two rare traits (Length 205–210 μm and 210–215 μm) occurred in samples taken at Sisak. In the Sava River at Topolje the shapeless chloroplast at rim, at Lukavec the height 15–16 μm and volume 40,500–41,500 μm^3 traits were found as rare. In the Sava River at Županje, the rare traits were the width 45–50 μm and volume 18,500–19,500 μm^3 were also found. Finally, in the sample of the Rába River at Sárvár, the rare traits were the width of 85–90 μm and volume of 72,500–73,500 μm^3.

System of rare traits following Rabinowitz's approach

Among 142 traits 106 were common features of the diatom species (mostly lifeform traits like attachment types, colony forms, and motility), which are generalist with high population size and wide distribution. 25 traits (chloroplast shapes: plate, large plate, and compressed; number of chloroplasts 4; length 0–5 μm, 60–65 μm, 105–110 μm, 155–160 μm, and 190–195 μm; length/width 40–50 μm; height 8–9 μm, 10–11 μm, 27–28 μm, and 52–53 μm; width 25–30 μm and 55–60 μm; biovolume 6,500–7,500 μm^3, 13,500–14,500 μm^3, 16,500–17,500 μm^3, 20,500–21,500 μm^3, 21,500–22,500 μm^3, 37,500–38,500 μm^3, 59,500–60,500 μm^3, 184,500–185,500 μm^3, and 228,500–229,500 μm^3) had small population size, but they were generalist with wide geographic distribution (Table 3). Only 11 traits (chloroplast shapes: shapeless at rim, X-shape; length 205–210 μm, 210–215 μm, and 300–305 μm; height 15–16 μm, width 45–50 μm, 85–90 μm; biovolume 18,500–19,500 μm^3, 40,500–41,500 μm^3, and 72,500–73,500 μm^3) were considered as absolute rare (Table 3). These traits were habitat specialists with small population size and geographically restricted distribution. We found any diatom trait in other categories of the Rabinowitz system (Table 3).

DISCUSSION

Database

In ecology, trait-based approaches are rapidly spreading and starting to come into general use taking advantage of this method. Among other organisms, benthic diatoms are especially suitable for trait-based studies because these organisms have well-defined, measurable, and investigable traits similar to soft algal species (Laraib *et al.* 2023). However, a coherent, trans-regional diatom trait database is missing in contrast to phytoplankton (Laraib *et al.* 2023) or plants (Sonkoly *et al.* 2023). Therefore, using the only existing and available French database of Rimet and Bouchez (2012) and completing it with data

from different sources we established an integrated (taxonomic and traits information) diatom database with 13,162 records for the Danube catchment area in Hungary and Croatia. This database provides further possibilities for functional analyses in the future and can be integrated into an extended dataset of a large biogeographic area.

Ecological significance of rare diatom traits

In the benthic diatom communities that were studied, despite the high number of lifeform traits that were considered (19 in total), exclusively morphological characteristics were among the rare diatom traits. Consequently, all lifeform traits – including those such as colony formation with specific shapes, which are generally assumed to be rare – were classified as common.

It was found that approximately 25% of the trait categories were associated with low population sizes. These include: four chloroplasts per cell, five distinct chloroplast shapes, and variation in cell wall dimensions, including width, length, height, and biovolume.

Although the membrane structures of diatom species are very similar, their chloroplast shape, number, and location in the cell are more diverse than in other groups of the Heterokonthophyta division (Mann 1996). The chloroplast morphology and number can have ecological and functional significance since these traits can considerably influence the light trapping and the photosynthesis activity (Häder *et al.* 2022), but these are rarely investigated in the case of algae (Van den Driessche 1966). In this study, chloroplast morphology and its number were among the small population size traits and also the absolute rare traits. These traits are strongly connected to different diatom evolutionary lineages with fixed number and shape (Julius and Theriot 2010) and therefore can be used for identification of diatom taxa in live samples (Cox 1996). However, environmental stress can modify the number of chloroplasts (Julius 2007). The more and smaller chloroplasts in an algal cell (e.g in centric diatoms) have a bigger total surface, furthermore, they can move more freely within the cell to access an adequate light environment (Solymosi 2012). Consequently, their efficiency of light interception is higher. On the other hand, one big chloroplast – which is very common in algae (Solymosi 2012) and characteristic for pennate diatoms – can be also optimal in a certain (e.g. less scattered light) environment (Głowacka *et al.,* 2023). Four chloroplasts as a rare trait is located between these two common chloroplast types, which may not be a "perfect" light trap and may lead to its rarity.

Certain chloroplast shapes (e.g. stellate, spiral) of algae can also enhance the inner surface of the chloroplast and as a dynamic system can adapt to differ-

ent light conditions (Solymosi 2012). However, these features are completely missing in diatom species. But the X-shaped chloroplasts found rare here can also have various benefits (Cao *et al.* 2011) like high inner surface area, better light absorbance from different directions, more efficient pigment distribution, and quick transportation of photosynthetic products. Not to mention better space filling, which can provide mechanical stability for the cell. However, despite these advantages, this trait remained rare and in the absence of studies, we could only guess its reason.

This study revealed that larger size categories are rarer in the studied diatom communities, whether in terms of width, length, height or biovolume. However, it should be noted that these four morphological traits are not independent. Our analyses showed (not published data), that the biovolume of a diatom cell is primarily influenced by the height and length of the valve, while the effect of the width on the biovolume is less expressed. Larger cell volume > 6,500 μm^3 can be considered as a rare trait in terms of small population, while >18,500 μm^3 the biovolume was absolutely rare. Rimet and Bouchez (2012) in their study distinguished 5 different biovolume categories, where the biggest one was the size class 5 (1,500 μm^3 and above). Since this study showed that biovolume can reach even 229,500 μm^3 it would be worth, to classify further size classes to understand the ecological role of the larger, rarer sizes. Namely, biovolume is an important morphological trait, which is closely related to important physiological processes, such as nutrient uptake and growth rate. Larger cells have slower nutrient uptake. Very large or very small cells grow 30 times more slowly than the others. Cells around 100 μm^3 are the fastest growing (Hillebrand *et al.* 2022). Moreover, larger cell size is associated with cells being more resistant to grazing (Pančić and Kiørboe 2018). In terms of their ecological strategy, large, slow-growing cells are K-strategists, compared to small, fast-growing r-strategists (Wentzky *et al.* 2020).

The small population sized traits were carried by 37 different diatom species. Most of them (36) were rare species (e.g. C*ymatopleura apiculata*, *Amphipleura pellucida*) and only one was a common species (*Nitzschia gracilis* with a length of 60–65 μm) (Stenger-Kovács *et al.* 2025). Furthermore, 17 rare species displayed more than one rare trait, in terms of small population sizes, creating very unique morphological features. This finding indicates that rare traits are predominantly exhibited by rare diatom species, which also confirms that the large size, as a rare trait clearly contributes to the rarity of the species that possess them.

Approximately 7% of the total traits (i.e. exactly 11) were both habitat specialists and geographically restricted, while 93% of them can be considered to be generalist and widespread. Since these rare traits were among the small popu-

lation sized traits, therefore, they can be considered as absolute traits. Nine of them were connected to the big sizes of the species through their length, width, height or biovolume and only two chloroplast shapes (X-shaped, Shapeless chloroplast at rim) were absolutely rare. These 11 absolute rare traits are possessed by eight absolutely rare species (e.g., *Thalassiosira lacustris*, *Ellerbeckia arenaria*, and *Diploneis elliptica,* Stenger-Kovács *et al.* 2025). Each of these three example species exhibited two absolute rare traits and, in addition, shared a common preference for oligotrophic environments (Lange-Bertalot *et al.* 2017). Furthermore, these absolute rare features were primarily associated with Croatian rivers (Sava, Drava, and Odra), with the exception of the Hungarian Rába river. These regions and river sites (Drava at Legrad and Petrijevci, Odra at Sisak, Rába at Sárvár, and Sava at Topolje, Lukavec, and Županje) may ensure special conditions to host rare species with rare traits. This suggests that the Sava, Drava, Odra, and Rába rivers may be particularly important for maintaining regional biodiversity due to their environmental characteristics. Based on our water chemistry measurements these sampling sites had lower conductivity (mean is 477 μS cm^{-1}), COD/chemical oxygen demand (mean = 7 mg L^{-1}), and nutrient concentrations (mean TP/total phosphorous 78 μg L^{-1}, SRP/soluble reactive phosphorous 11 μg L^{-1}, nitrite 9 mg L^{-1}) than of the other 183 sites (mean conductivity = 579 μS cm^{-1}, COD = 15 mg L^{-1}, TP = 150 μg L^{-1}, SRP = 59 μg L^{-1}, nitrite = 17 mg L^{-1}) in the studied area. The presence of diatoms with large biovolumes in surface waters that have lower nutrient concentrations seems somewhat controversial. However, this pattern can be explained by the fact that diatoms in oligotrophic environments often adopt a K-selected strategy (Finkel *et al.* 2010). Larger cell volume can support more storage vacuoles for nutrients and ensure a great surface area for uptake (Finkel *et al.* 2010). In such environments, large diatoms can survive longer in low-nutrient conditions by storing resources (Litchman *et al.* 2007) and growing at a slower rate. Furthermore, these waters often have higher transparency, allowing light to penetrate deeper (Leach *et al.* 2018). In nutrient-poor systems, competition can be lower because there are fewer fast-growing species (Litchman *et al.* 2007). Some studies also highlight that large diatoms not just occur occasionally but can thrive in environments that are nutrient-poor or have fluctuating nutrient content under specific conditions, such as deep mixing, high light availability, and low grazing pressure (Finkel *et al.* 2010, Kemp and Villareal 2018, Litchman *et al.* 2009).

In summary, the bigger sizes and special chloroplasts are unique characteristics of diatoms. Rare species carrying these rare traits become a functionally distinct and potentially vulnerable member of the local or regional community. However, these species can serve as core species (Stenger-Kovács *et al.* 2025)

and ecological memory of the communities (Padisák 1992). Quoting Judit Padisák they "will influence the present and future responses of the communities", and consequently, determine ecosystem functioning.

* * *

Acknowledgements – We acknowledge the contribution of colleagues of the Limnology Research Group, University of Pannonia and Department of Biology, University of Zagreb for their technical assistance in the field and laboratory analyses. We also thank the support of the RRF2.3.1 21 2022 00008 project (JP, CSK, BA, EL, GBS, RZSB, EK) within the framework of the Széchenyi Plan Plus programme. EL was supported by the University Research Fellowship Programme of the Ministry of Culture and Innovation (2024-2.1.1.1-EKÖP-2024-00025). The study was financed by the Hungarian National Research, Development and Innovation Office (NKFIH) K 137950.

Dedication – We offer this study on the occasion of the 70th birthday of our Professor Judit Padisák, who is one of the most famous and renowned limnoecologists. She is that person, who we all could have learned the hard work and scientific humility from and who we get never ending scientific, personal and familiar support from. Thank you Judit and we wish you health and happiness not only on your birthday but also other times of your life.

Összefoglaló: A ritka faj a természetvédelem központi témája. Ennek ellenére nem rendelkezünk elegendő ismerettel azokról a tulajdonságaikról, amelyek a kihalásukhoz vezethetnek. Éppen ezért ebben a tanulmányban egy kovaalga jelleg adatbázis (morfológiai és életforma jellegek, összesen 142 féle) létrehozását és a ritka jellemzők azonosítását tűztük ki célul. A kifejlesztett adatbázis 13 162 rekordot tartalmaz a Duna vízgyűjtőterületén Magyarországon és Horvátországban előforduló kovaalga fajokról. Rabinowitz eredeti megközelítését és a szakirodalomban közzétett új ritkasági indexeket alkalmazva a kovaalgák jellegeinek ritkaságát különböző szempontok alapján határoztuk meg. A kovaalgák jellegeinek 75%-a gyakori jelleg, míg 25%-uk kis populációjú (ritka) jelleg volt. Ezek kizárólag a kovaaalgák morfológiai jellemzői voltak (sejtenkénti négy kloroplasztisz, öt különböző kloroplasztiszforma és a nagyobb méretkategóriák), amelyek elsősorban a ritka fajok jellemző tulajdonságai voltak. Az összes vizsgált jelleg 7%-a abszolút ritka (kis populációméretű, élőhely-specialista és földrajzilag korlátozott elterjedésű) tulajdonság volt. Ezek nevezetesen kilenc nagy méretkategória és két kloroplasztiszalak volt, amelyek a különleges állapotú horvátországi Száva, Dráva és Odra folyók, valamint a magyarországi Rába folyókhoz kötődtek. Ezekkel az egyedi tulajdonságokkal rendelkező ritka fajok funkcionálisan elkülönülő és sebezhető tagjai a kovaalga közösségeknek.

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Appendix 1 – available elctronically at *http://publication.nhmus.hu/studbot/bannales.php?volume=56*

(submitted: 30.07.2025; accepted: 09.09.2025)

DOI: 10.17110/StudBot.2025.56.1.93 Studia bot. hung. 56(1), pp. 93–110, 2025

CLIMATE CHANGE-DRIVEN SHIFTS IN PHYTOBENTHOS ASSEMBLAGES OF THE PANNONIAN ECOREGION: A DECADAL OVERVIEW

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Abstract: This study synthesises research exploring how climate change-induced hydrological extremes influence the structure, species composition, and functional diversity of benthic diatom assemblages in watercourses of varying sizes (from 10 km² to approximately 10,000 km² catchment areas), across multiple temporal (1–15 years) and spatial (Pannonian and Mediterranean) scales. The focus is particularly on intermittent small streams in the Carpathian Basin, encompassing both the Great Hungarian Plain and the Transdanubian region. Rather than treating drying as a separate event, these investigations approach it as a gradual process composed of successive hydrological phases – flowing, standing, and dry – each with distinct impacts on assemblage structure and diversity. The findings contribute to a deeper understanding of how benthic diatom assemblages respond to climatic extremes, offering insight into ecosystem resilience and vulnerability under ongoing environmental change. This work is dedicated to Professor Judit Padisák – as a gesture of gratitude and a tribute to a distant yet ever-supportive mentor, whose early encouragement and continued watchful presence have been invaluable throughout this journey.

Key words: benthic algae, biodiversity, climate change, composition, intermittent streams, large rivers

PROLOGUE

Once upon a time, in a galaxy far, far away, on a planet called Earth, there lived a biologist. From the very beginning of her university studies, she fell in love with microscopic, tiny organisms – algae. So, when, according to the Earth calendar, she was offered a position as an algologist in the early 2010s, the topic was, at least in theory, not unfamiliar to her. Despite her dedication and curiosity, she was filled with fear, for unlike her previous tasks, this position required taxonomic knowledge and field experience – areas where she still felt her knowledge was lacking. Yet the girl did not back down. She saw the task as a challenge, seeking more than simply providing raw data or uncovering simple connections – she had a desire for more. Her aim was to see and understand the ecological patterns – to grasp both local and regional changes. Her first steps were supported by a small group of people who, like her, had limited knowledge about this particular group of organisms: the benthic diatoms. Yet they helped her in every possible way. Thanks to their support, the moment finally came when she completed her first professional work analysing ecological patterns based on benthic diatom data, which was submitted to an international journal. But their initial efforts did not meet the desired outcome. Still, she did not give up the fight. She revised the manuscript again and again, constantly trying to ensure that the international experts – whom she held in the highest regard – would at least consider reviewing her work. Eventually, she submitted it to a journal where she knew there was a good chance that one of the editors would be Judit Padisák, a renowned researcher known and respected both in her home country and internationally. Of course, she too knew – and feared – the researcher she called "Professor", a woman whose strictness and consistency were the stuff of legend among students, even though she had never taught the young biologist girl directly. However, it was also widely acknowledged that Professor Padisák was always willing to offer a chance to those who demonstrated a genuine desire to learn. And the biologist girl truly did. Because she loved and respected the path she had chosen – one that was no longer just a job, but a calling. Her hands were trembling as she opened the response letter; it was a major revision, accompanied by two thorough and highly professional reviews. Answering them was no easy task. The biologist girl learned a great deal through writing the response letters and revising the manuscript. But in the end – after nearly a year and a half of struggle – it happened: their paper was eventually accepted. This experience motivated the girl to continue her work, and the deep gratitude she felt toward the Professor encouraged her to keep learning. More than ten years have passed since then, but her professional dedication has remained unchanged. Over the years, her relationship with Professor Padisák has gradually deepened.

This study presents the most important results of my/our professional work over the past ten years, and at the same time serves as an expression of gratitude and a tribute to Professor Padisák, who gave me the initial push and has never let me fall since.

INTRODUCTION

Today's ecological and conservation challenges rarely allow for the kind of deep contemplation one experiences when first looking through a microscope and encountering the astonishing morphological diversity of diatoms. The decline in biodiversity has reached a point where many leading researchers no longer speak of a potential future event, but of an ongoing sixth mass extinction (Ceballos *et al.* 2015, Cowie *et al.* 2022). Global climate change is identified as one of the main drivers of the biodiversity crisis (Cowie *et al.* 2022, Reid *et al.* 2019). The situation is particularly severe in freshwater ecosystems, where ongoing changes are often referred to as a "silent tragedy" (Reid *et al.* 2019). Even experts tend to overlook the fact that research has traditionally focused on macroscopic, primarily vertebrate, emblematic or economically significant taxa, while microscopic communities (Naselli-Flores and Padisák 2022), such as benthic diatoms, are perhaps not given as much attention as they could be (MEA 2003, Caldwell *et al.* 2024). Over the past decades, diatoms have primarily appeared in scientific studies as bioindicators (for a detailed review, see Lobo *et al.* 2016), largely due to their designation as target organisms and communities under the European Union's Water Framework Directive (EC 2000) and the United States' Clean Water Act (1972). Diatoms can provide a reliable representation of the ecological and biological status of water bodies, as well as the changes occurring within them. In contrast, theoretical ecological and classical conservation-oriented research has only begun to develop significantly in the past decade (Soininen and Teittinen 2019). As a result, our knowledge on this topic could be regarded as somewhat limited in comparison to that related to phytoplankton (for a detailed review, see Naselli-Flores *et al.* 2021), despite the undeniable role of benthic diatoms in ecosystem services, including their ecological and conservation significance (B-Béres *et al.* 2023).

Due to the species-level uniqueness of their siliceous frustules, recent ecological studies have primarily focused on diatom species, species complexes, or other lower taxonomic units. However, it is important to note that the past 10–15 years have also seen a shift in this approach (for a detailed discussion, see Stenger-Kovács and B-Béres 2024). The catalyst for this shift was the diatom guild classification system introduced by Passy (2007), which opened new perspectives for functional and trait-based studies of diatoms. Initially, alongside

exploratory research, the studies were strongly application-oriented (for more details, see TAPOLCZAI *et al.* 2016), aiming to reduce uncertainties arising from species-level analyses and more reliably integrating the information content of guilds and traits into ecological status assessments. Since then, trait- and guild-based approaches have become an integral part of diatom research (STENGER-KOVÁCS and B-BÉRES 2024), playing an increasingly important role in addressing both theoretical and applied ecological questions. Studies conducted across various spatial and temporal scales offer the opportunity to interpret global environmental challenges – such as climate change, water scarcity, salinization, and eutrophication – not only in local contexts but also at regional, inter-ecoregional, and global levels (for more details, see MAIDANA *et al.* 2024). This approach provides a strong scientific foundation for well-informed and timely interventions necessary for the protection of surface waters.

In this study, we have attempted to summarise and contextualise the results of research that shed light on how climate change-related extremes affect the structure, species diversity, and functional diversity of diatom assemblages in watercourses of varying sizes (10 $km^2 \geq$ catchment area $\approx$ 10,000 km^2) across different temporal scales (1–15 years) and spatial scales (Pannonian and Mediterranean regions). Particular emphasis is placed on the structural and diversity changes occurring in diatom assemblages of intermittent small streams in the Carpathian Basin (continental region), covering both the Great Hungarian Plain and the Transdanubian region. In these studies, drying is not treated as a discrete event but rather is described and assessed as a process encompassing successive hydrological phases – flowing, standing, and dry – and their impacts on the community.

Perennial, non-intermittent rivers

Regionally, one of the most significant consequences of climate change is the alteration of precipitation patterns, including an increase in the number of dry days, changes in daily maximum precipitation, as well as in the total annual precipitation and its distribution (ITM 2020). These changes can have a significant impact on the hydrological regimes of watercourses, which in some cases may result in changes to water levels, drying events, or flash floods (ITM 2020). Extreme fluctuations in discharge are observed worldwide even in perennial rivers (MESSAGER *et al.* 2021). Although complete drying is less likely in these water bodies – at least in regions such as the Carpathian Basin – low water levels and partially dried riverbeds can induce similar community changes as those observed in intermittent water bodies during the formation of isolated pools (B-BÉRES *et al.* 2014). It is important to emphasise that while planktic algae in larger rivers are

known to respond adversely to changes in environmental conditions (Abonyi *et al.* 2018, Hardenbicker *et al.* 2014), most studies examining the relationship between climatic extremes and benthic algae focus on communities in smaller watercourses (B-Béres *et al.* 2019, Novais *et al.* 2020, Sabater *et al.* 2016, 2017, Stubbington *et al.* 2019).

Sebes-Körös River

Although our research over the past decade has primarily focused on intermittent small watercourses, in our initial study mentioned in the prologue (B-Béres *et al.* 2014), we examined the impact of drastic discharge fluctuations on diatom assemblages in a large Hungarian river, the Sebes-Körös. The study was conducted between April and November 2012. Following a prolonged spring and early summer flood, there was a drastic decrease in the discharge of the Sebes-Körös at the end of June, resulting in low-flow conditions that persisted throughout the sampling period. At the same time, it was observed that certain environmental parameters, such as total nitrogen and conductivity, increased to almost double their springtime minima by autumn, showing a close relationship with the passing of time. It is interesting to note that other parameters, such as total phosphorus, did not show a clear trend correlated with discharge or time. However, their extreme values still varied by more than a factor of two. We hypothesized that these extreme environmental changes would significantly alter assemblage structure and reduce biological diversity. Additionally, for the first time in large Hungarian rivers, we investigated changes in diatom guilds associated with discharge fluctuations, a novel approach at the time. Our results, both at the taxonomic and guild levels, clearly demonstrated a significant restructuring of the assemblage. At the same time, our findings also suggested that species within the same guild may respond differently to environmental changes. Furthermore, we demonstrated that changes in the overall relative abundance of certain guilds (e.g. motile or low-profile guilds) do not always positively correlate with changes in guild' taxon richness. With regard to biological diversity, while there was a clear decline in species richness during the study period, other diversity indices did not show a clear relationship with discharge or closely correlated environmental parameters. The drastic decrease in discharge at the end of June unequivocally resulted in reduced biological diversity, which subsequently increased until the autumnal drop in temperature.

These results provided a solid foundation for our subsequent work, which included the proposal and testing of a combination of guilds with other traits (B-Béres *et al.* 2016, Lukács *et al.* 2018).

Rába River

Studies addressing composition changes in phytobenthic assemblages of large rivers caused by water level fluctuations are mostly short-term (e.g., B-Béres *et al.* 2014, Tornés *et al.* 2015). As a result, our knowledge of the long-term effects of climatic extremes and climate change-induced precipitation deficits on benthic algal assemblages in large rivers remains very limited.

After the study presented in the previous section, a significant amount of time passed before large rivers once again became the focus of attention. However, in 2021, thanks to our colleague Krisztián Kovács, we were fortunate enough to have the opportunity to analyse a 15-year (2007–2021) diatom dataset from the River Rába (Nemes-Kókai *et al.* 2023).

During this period, daily precipitation data were available. Analysis of these data revealed that between 2007 and 2016, drier and wetter years alternated, whereas from 2017 onward, a continuous decline in annual precipitation was observed in the region. We hypothesized that this trend-like decrease in precipitation would lead to a more substantial restructuring of the assemblages than during the preceding fluctuating period, and would also result in a significant decline in diversity. We also examined the extent to which single extreme wet or dry periods affect benthic diatom assemblages compared to average years. Our

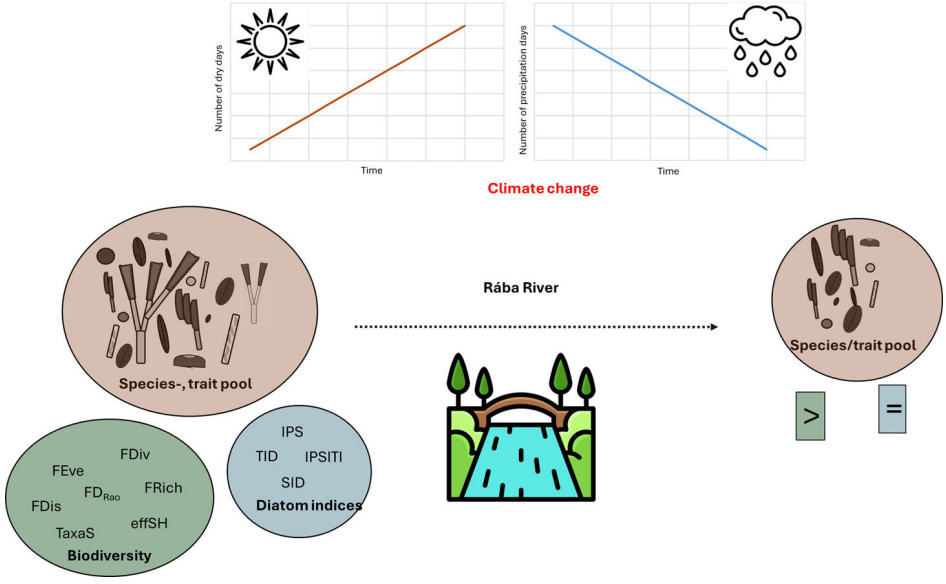

Fig. 1. The impact of climate change on the structure and biodiversity of diatom assemblages, and the ecological status of the Rába River.

results indicated that isolated extreme events had only a minor impact on the composition of benthic diatom assemblages and diversity. In contrast, the prolonged decrease in precipitation significantly reduced both taxonomic and functional diversity. During this period, small-sized species that are strongly attached to the substrate became dominant, while the proportion of larger, tree-like species declined substantially (Fig. 1). This is particularly concerning, as these algae play a key role in riverine food webs. Their absence or population decline may therefore have indirect negative effects on larger organisms inhabiting the river. According to climate model projections, there is a possibility that extreme climatic events, including prolonged periods of low precipitation, could become more frequent in the near future. This suggests that the assemblage-level changes and their impacts, as demonstrated in our study, should be anticipated and may even warrant intervention. One of the most important issues to consider is the possibility of a tipping point, which could potentially lead to long-lasting and difficult-to-reverse changes in biodiversity and community structure.

Intermittent small streams

It is worth noting that in the Carpathian Basin, there has been an increase in the number of drought days over the past century. By the 2000s, the driest period of the year had shifted from the winter months to mid-summer. As a result of these anomalies, a typological shift can be observed in small streams in the region: watercourses that were previously perennial are now drying out more frequently, transitioning into intermittent systems. In Hungary, there are approximately 10,000 watercourses, of which only about 10% are regularly monitored under the National Monitoring Program (Stubbington *et al.* 2018). This is due to the fact that only these watercourses have catchment areas exceeding the 10 km^2 threshold required by the EU Water Framework Directive (WFD). Current knowledge suggests that more than 30% of these monitored streams now fall into the intermittent category, although this classification currently only applies to small watercourses. The areas most affected by drought and drying are predominantly located in the Great Hungarian Plain (Web1). For streams with catchments smaller than 10 km^2, only sporadic data are available, but the proportion of drying watercourses in these systems is presumed to be significantly higher.

It is worth noting that the second half of the 2010s saw the launch of intensive research on stream drying. Some of these studies addressed structural changes in algal communities of such watercourses, with a particular focus on the Mediterranean region. In contrast, processes occurring in temperate regions, where drying have not historically been regular features of flow regimes, and where aquatic organisms and communities have therefore not yet had time to

adapt, are still only sporadically documented. This has led to a significant lack of baseline data and knowledge. Yet, beyond their national natural value, streams affected by desiccation also serve economically important functions such as irrigation, drainage, water storage, and energy production. It is possible that changes in the structure of aquatic communities – particularly periphytic algae – may result in shifts in water quality. These changes have not only ecological and conservation implications, but also serious economic consequences, highlighting the urgent need to develop new conservation biology and, importantly, economic strategies.

Impact of a one-summer drought on benthic diatoms in small perennial lowland streams

We began our work on the drying of small streams in 2012 (Kókai *et al.* 2015). At that time, our focus was not yet on drying itself, but rather on the impact of water scarcity on diatom assemblages in 15 lowland streams. We hypothesised that the summer drought period might possibly induce structural changes in the composition of diatom assemblages, which could result in an increase in the proportion of halophilic species within the assemblages. In addition, we also examined how the proportions and relative abundances of taxa with different cell volumes (size) changed within the assemblage. In our study, we found significant correlations between the taxonomic and morphological (cell size) composition of benthic diatom assemblages and the increased conductivity, total nitrogen (TN), and total phosphorus (TP) concentrations induced by summer drought. At the same time, our results also highlighted that among the cell volume groups, only the extremely small and extremely large categories responded clearly to environmental changes. Although the proportion of halophilic taxa increased by more than 50% in the assemblages during the drought period, it was typically the number and relative abundance of large-sized taxa that increased. We observed contrasting trends in different diversity metrics, namely species diversity and evenness: while species richness increased in the assemblages as a result of the drought, evenness declined. This may indicate, on the one hand, that certain opportunistic taxa exploited the disturbed environment and became dominant within the assemblages, and on the other hand, that generalist taxa appeared, contributing to the increase in species richness. At the same time, it may also indicate a lack of stability – that is, a transitional state – suggesting that if the unfavourable conditions persist, the decline in diversity may be reflected in species richness as well. It would seem that the results demonstrate that a small stream does not need to completely dry out for precipitation deficit to induce structural shifts and changes in the diversity of benthic algal assemblages.

Colonisation of benthic algae in a small intermittent stream

Subsequently, in 2014, we conducted a colonisation study on an intermittent lowland stream, Tócó (B-Béres *et al.* 2016, Lukács *et al.* 2018, 2021). We investigated how extreme weather events influence the colonisation of benthic algae and the development of mature periphytic assemblages. We studied this through changes in the composition of the assemblage's taxonomic, trait-based, and combined trait-based groups, as well as various diversity metrics. We showed how the Combined Morphological and Functional Grouping (CMFG) system – created by merging morphological and functional characteristics of benthic diatoms – as well as the functional groups developed by combining the traits of the entire phytobenthic assemblage (diatoms and soft algae), are capable of indicating stochastic processes such as colonisation in a lowland, semi-static stream with a resolution equivalent to that of taxonomic classification (B-Béres *et al.* 2016, Lukács *et al.* 2018). In addition, based on flow regimes (flow velocity and water depth), the colonisation period could be divided into two distinct hydrological periods – a moderately disturbed period and a highly disturbed period –, during which we examined how assemblage structure and diversity changed (Lukács *et al.* 2021). Our results revealed that the taxonomic and trait-based composition of the communities differed significantly between the two periods. The moderately disturbed period was characterised by large-sized and/or filamentous and/or weakly attached algae, whereas the highly disturbed period was dominated by small-sized and/or unicellular and/or strongly attached and/or fast-moving taxa. Furthermore, we demonstrated that the sensitivity of taxonomic and phylogenetic diversity metrics, as well as trait-based diversity metrics, differed across the periods characterised by varying levels of disturbance – that is, they changed differently between the two periods. Taxonomic and phylogenetic diversity, in accordance with the intermediate disturbance hypothesis, were significantly higher during the moderately disturbed period. In contrast, during the highly disturbed period characterised by extremes, diversity was significantly lower. In contrast, functional diversity metrics – except for functional dispersion, which was higher during the moderately disturbed period – did not differ significantly between the two periods (Fig. 2). This suggests that extreme hydrological conditions (such as drying or flash floods) did not immediately impair the functional integrity of the system. However, it is important to emphasise that in this study, we examined the processes of drying (sampling ended at the beginning of the drying), not the dry phase itself.

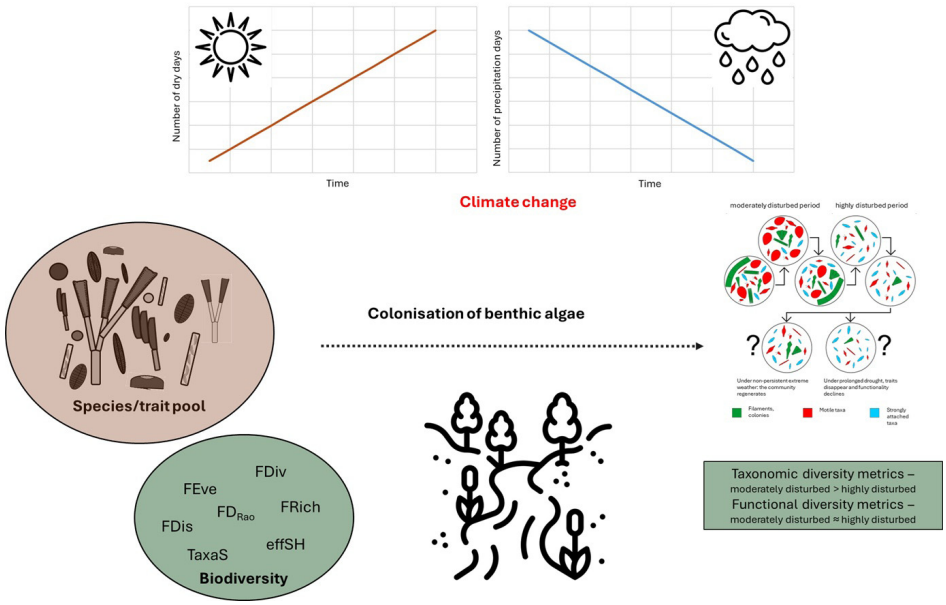

Fig. 2. The impact of climate change on the colonisation dynamics (composition and biodiversity) of benthic algal assemblages during moderately and highly disturbed periods (The figure is based on LUKÁCS (2021), with modifications. https://dea.lib.unideb.hu/items/94cb4c14-58c8-4e8b-8d59-9efecc733210).

Perennial and intermittent lowland streams in the Pannonian Ecoregion

As previously discussed, climate change has led to changes in the water supply of small streams, with many that used to be perennial becoming intermittent. We also observed this phenomenon in the 2010s in our lowland small streams. Year by year, it became increasingly common for these watercourses that were previously easy to sample and had flowing water to dry up as early as late spring or early summer. We tested how this affects the trait composition and functional diversity of diatom communities using a dataset from the period 2008–2015 (B-BÉRES *et al.* 2019). Based on the results, we have obtained that the traits characteristic of intermittent small streams have been identified, such as small size, pioneer nature, and aerophile character. In contrast, traits such as motility, high LW (length : width) ratio, or planktic lifeform were typical of perennial waters. The difference in biological diversity between the two water types was evident in functional richness (lower in drying streams) and Berger-Parker trait diversity (higher in drying streams), while functional evenness and divergence did not yet differ significantly (Fig. 3). Our results clearly highlighted that the separation between the two water types had begun, with diatom assemblages in intermittent

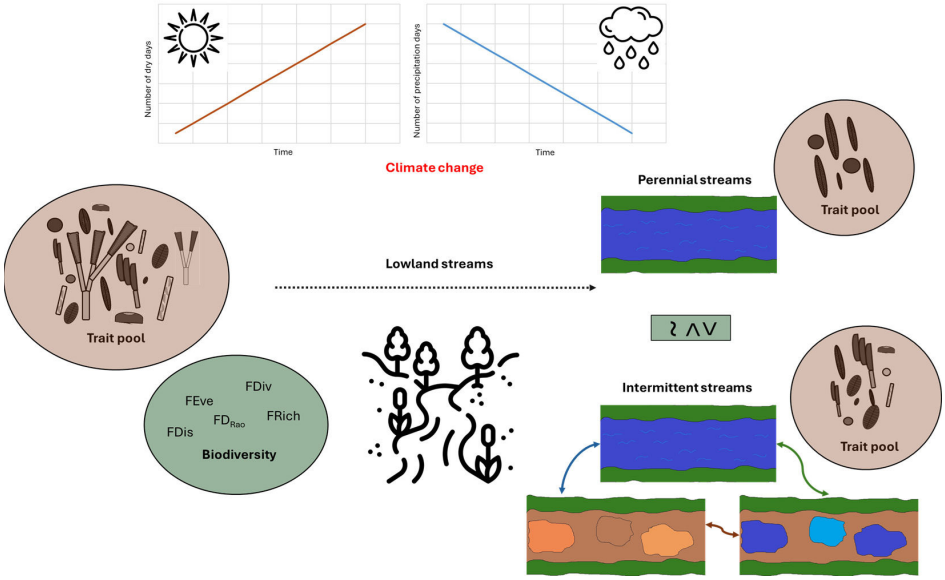

Fig. 3. The impact of climate change on the functional composition and diversity of diatom assemblages in small lowland intermittent streams.

streams potentially being more vulnerable than those in perennial streams. It is therefore important to pay particular attention to these waters, even though they do not dry out every year or for the same duration.

The impact of climate change on benthic diatoms: ecoregional differences

In a subsequent study covering multiple ecoregions (Mediterranean region – Portugal and temperate region – Hungary), we demonstrated that the duration of exposure to drying risk (recent decades *vs.* historic) leads to different structural changes in diatom assemblages in intermittent small streams (VÁRBÍRÓ *et al.* 2020). While certain diatom traits (small size, and/or pioneer, and/or low-profile guild) were clearly definable in intermittent small streams in the temperate region, such traits were not detectable in the Mediterranean region. In contrast, in both regions, colonial life form and high-profile guild were characteristic traits of diatom communities in perennial streams. Furthermore, we showed that community assembly forces (such as environmental filtering and limiting similarity) play different roles in shaping the diatom structure of the studied streams in the two ecoregions. While limiting similarity was the main community assembly force in Hungarian waters, in Portuguese streams environmental filtering played an equally important role as limiting similarity in structuring the assemblages.

Effects of hydrological phases and channel concrete lining on the benthic algal assemblages of an intermittent lowland stream

According to the currently most widely accepted classification, six hydrological states are distinguished in intermittent streams (hyper-, eu-, oligo-, a-, hyporheic, and edaphic; Gallart *et al.* 2012), which can be grouped into three main hydrological phases: flowing, standing, and dry (Gallart *et al.* 2017). Hydrological changes occurring in streams are not necessarily linear; depending on weather conditions during a given period, the process of drying out may be interrupted and may revert to a previous state. Such a reversal can occur, for example, when water becomes confined to isolated pools during a drier period (arheic state; standing water phase). However, a heavy or prolonged rainfall event can cause the system to shift back to an oligo-, eu-, or even hyperheic state (flowing phase), reversing the drying process. The species and trait composition, as well as the diversity of benthic diatom assemblages in the different hydrological phases of intermittent streams (Gallart *et al.* 2017), are strongly influenced by the duration of drought (rain-free) periods and the length of time the streambed remains dry (Acuña *et al.* 2017, Sabater *et al.* 2017, Tornés *et al.* 2021). However, lowland streams in Hungary are not only exposed to the risk of drying out, but are also subject to various other natural and anthropogenic impacts, which can cause short- or long-term changes in habitat conditions. Artificial interventions can also be observed in stream sections before and after bridges, where the channel has been fully concreted or covered with hollow concrete elements. Such channel modifications can significantly alter hydrological conditions (e.g. water velocity), potentially leading to the accumulation of silt or sand, and ultimately to changes in physical and chemical parameters (Gál *et al.* 2020), as well as a deterioration in ecological status (Wemple *et al.* 2018). To the best of our knowledge, the effects of channel concreting on diatom assemblages have not yet been studied in either perennial or intermittent streams. In our most recent work (Kiss *et al.* 2024), we therefore investigated how the drying process (flowing *vs*. standing phase) and channel modification (natural vs. concreted) influence the structure and biological diversity of the benthic diatom assemblages in a lowland stream. We found that while the community structure clearly differed between the two phases of drying, the diversity metrics examined did not show significant differences. In the flowing phase, colonial taxa belonging to the high-profile guild and/or moderately attached taxa dominated, whereas in the standing phase, unicellular and/or strongly attached species from the low-profile guild were characteristic (Fig. 4). The seemingly surprising results can be explained by a typical feature

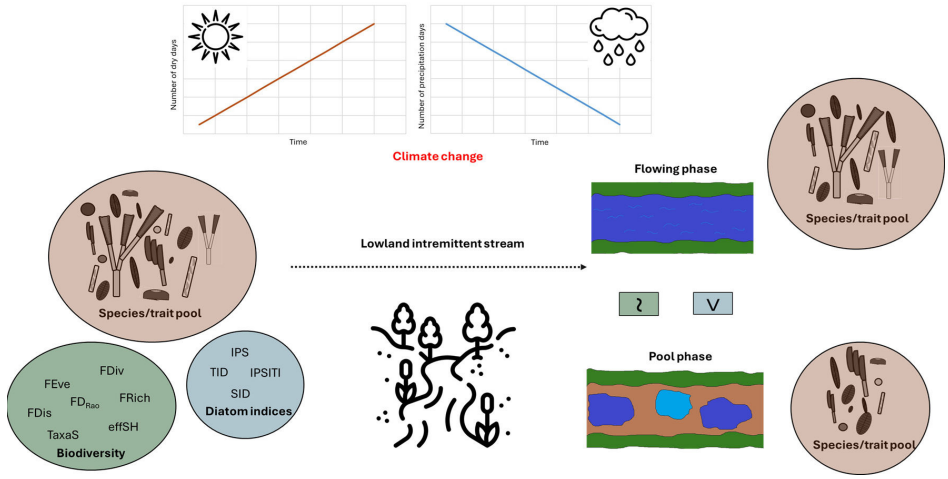

Fig. 4. The impact of climate change on the structure and biodiversity of diatom assemblages, and the ecological status in a small lowland intermittent stream.

of lowland streams: these watercourses are rich in emergent and submerged vegetation, which provide suitable habitats for chain-forming or filamentous algae even during the flowing phase (Passy 2007). As the water level decreases during the drying process (provided that the suspended sediment content is not high, as was the case in our study), the benthic communities are exposed to high levels of UV radiation. This environment favours species capable of tolerating such conditions (Kókai *et al.* 2019, Leira *et al.* 2015), or those able to escape into deeper sediment layers (McKew *et al.* 2011). Furthermore, our findings demonstrated that channel modification did not impact the taxonomic or trait-based structure of the community. However, we observed higher biological diversity in the concreted section of the stream compared to the natural section. It should be noted that this does not imply that streambeds should be concreted in order to promote biodiversity (see negative correlation: Bouska *et al.* 2010, Gál *et al.* 2020, Wellman *et al.* 2000). In this case, mass effect and/or species sorting are likely the main community assembly processes, enabling the presence of taxa even under suboptimal environmental conditions, as well as their spread to any suitable habitat (Soininen and Teittinen 2019). For obvious and understandable reasons, the artificial habitat is a direct continuation of the natural one, thus both assembly processes exert a strong influence. This is particularly evident in the context of mobile taxa, whose distribution may be more strongly affected by the mass effect (Jamoneau *et al.* 2018).

CONCLUSIONS AND OUTLOOK

The work carried out over the past more than ten years has contributed to a better understanding of the strong and often overriding pressure exerted by climate change-induced hydrological extremes (such as drastic water level changes, desiccation, and flash floods) on benthic diatom assemblages, affecting their structure and biological diversity. At the same time, our results also highlighted that while drawing global conclusions is both possible and necessary in many respects, numerous questions can only be addressed at the ecoregional level. This is particularly evident in Hungary, where the lowland regions are predominantly affected by desertification and subsequent watercourse drying. These waters are typically highly eutrophic and not phosphorus-limited, indicating that their communities are fundamentally different from those found in the low-nutrient Mediterranean or mountainous waters. Their roles in water management also differ, considering the importance of lowland waters for irrigation, water storage, and drainage. Therefore, it is crucial to understand the extent to which and the direction in which drying out will alter community structure and water quality over the long term. It must be emphasized that, in the medium to long term, the development of responsible water management plans (e.g. the need for reservoir construction, water supplementation) can only be undertaken with this knowledge. As our results have also demonstrated, climate change has an impact on both small streams and large rivers. In the near future, it is vital to ascertain the direction in which the community structure of these large rivers is changing, what this indicates, and what it means for water quality. For instance, the replenishment of smaller water bodies is contingent on the availability of larger water bodies. It is imperative that this is also given due consideration when preparing water management plans. It is evident that the problem is far from solved, and many questions remain unanswered. However, over the past 10 years, we have made significant progress in exploring a field with both scientific and practical importance. After all, our surface waters are national treasures, whose protection and preservation are matters of national interest.

* * *

Acknowledgements – I would like to express my sincere gratitude to all my colleagues, BSc and MSc students who have supported our work over the past 13 years. We also thank the following grants for their invaluable support: Open access funding provided by ELKH Centre for Ecological Research. Funding were provided by the National Research, Development and Innovation Office (Grant No. NKFIH FK 132 142 – VBB, ÁL, IB, ETK, GB, GV, KT, CsSK, SK, ZsNK), the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (Grant No. BO-00458-

20-8 – VBB), Ministry of Innovation and Technology (Grant No. ÚNKP-20-5 – VBB), Ministry of Innovation and Technology (Grant No. ÚNKP-21-5 –VBB) and Ministry of Innovation and Technology (Grant No. ÚNKP-22-5 – VBB). Above all, I am deeply grateful for Professor Padisák's encouraging presence and guidance from the very first steps.

Összefoglaló: Ebben az összefoglaló tanulmányban bemutatjuk, hogyan befolyásolják a klímaváltozás által kiváltott hidrológiai szélsőségek a bentikus kovaalga-közösségek szerkezetét, fajösszetételét és funkcionális diverzitását különböző méretű vízfolyásokban (10 km^2 ≤ vízgyűjtő terület ≈ 10 000 km^2), különböző időskálán (1–15 év), és térbeli léptékben (pannon és mediterrán régiók). Kiemelten foglalkozunk a Kárpát-medence (kontinentális régió) kiszáradó kisvízfolyásaival, mind az Alföld, mind a Dunántúl régióiban. A kiszáradást nem diszkrét eseményként kezeljük, hanem folyamatként, amely olyan egymást követő hidrológiai fázisokból – áramló, álló és száraz – áll, ahol minden fázis jól definiálható és eltérő hatással van a bentikus algaközösség szerkezetére és diverzitására. Az eredmények hozzájárulnak a bentikus kovaalga-közösségek klímaváltozással kapcsolatos szélsőséges hatásokra adott válaszának mélyebb megértéséhez, betekintést nyújtva ezen speciális ökoszisztémák ellenálló képességébe és sebezhetőségébe a folyamatos környezeti változások közepette. A tanulmányt Padisák Judit professzor asszonynak ajánlom – hálaként és tisztelgésként egy térben ugyan távoli, ám mindig támogató mentor előtt, akinek biztatása és folyamatos figyelme felbecsülhetetlen segítséget nyújtott szakmai utamon.

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web1: *www.vizeink.hu*

(submitted: 31.07.2025; accepted: 11.09.2025)

DOI: 10.17110/StudBot.2025.56.1.111 Studia bot. hung. 56(1), pp. 111–132, 2025

HOW DOES THE INVASIVE ZOOPLANKTON SPECIES AFFECT THE ZOOPLANKTON COMMUNITY IN SMALL AND SHALLOW WATERS? APPEARANCE AND DISTRIBUTION OF *SINODIAPTOMUS SARSI* (COPEPODA, CALANOIDA)

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Korponai, J., †Forró, L., Selmeczy, G. B., Vadkerti, E. & Padisák, J. (2025): How does the invasive zooplankton species affect the zooplankton community in small and shallow waters? Appearance and distribution of Sinodiaptomus sarsi (Copepoda, Calanoida). – *Studia bot. hung.* **56**(1): 111–132.

Abstract: During our study on small and shallow waters in Hungary, a new invasive species of copepod, *Sinodiaptomus sarsi* (Rylov, 1923), was found in our zooplankton samples collected in 2017. In Hungary, we found it in 17 lakes, with significant biomass in the 4th fishing lake on the outskirts of Püspökladány, Szénaréti-tó in Nyírbátor, the Fegyverneki-Holt-Tisza, and Lake Déli-tó in Gyopárosfürdő. As a result, we confirm that *Sinodiaptomus sarsi* has successfully established populations in Hungarian waters, yet we found no clear evidence that its presence has significantly altered the overall zooplankton community structure. As a selective filter feeder, it can potentially fulfil the functional role of native calanoid copepods in lentic ecosystems. However, its distribution may be restricted by its thermal requirements, which could confine its presence to specific habitats or seasons. *S. sarsi* appears to be an invasive and opportunistic member of Hungarian freshwater zooplankton, with its role and distribution likely determined by the interplay of temperature regimes, trophic state, and predator pressure. Monitoring its dispersion will be essential to detect potential shifts in population dynamics, particularly under changing climatic and eutrophication scenarios.

Key words: composition, feeding, Reynolds's functional groups, *Sinodiaptomus sarsi*, traits, zooplankton

INTRODUCTION

Humans significantly affect the environment. (Díaz *et al.* 2019). The demands of a growing human population have driven its impact on biota (Keck *et al.* 2025). Intensifying land use, resource depletion, environmental pollution, climate change, and globalisation threaten biodiversity. Globalisation not only exhausts natural resources but also increases the uniformity of biota. Diverse ecosystems are more resilient to disturbances like climate extremes, disease outbreaks, and invasive species. When biodiversity declines, ecosystems become more fragile and less able to adapt to environmental change. Human activities have extensively altered freshwater ecosystems, whose species loss rates rival those found in tropical forests (Ricciardi and Rasmussen 1999). Besides species loss, alien species are among the most important, least controlled, and least reversible of human impacts on the freshwater (Strayer 2010).

Invasive zooplankton species can restructure aquatic ecosystems, alter food webs, alter nutrient cycling, and replace native taxa in ecosystem functioning (Havel *et al.* 2015). Making their study is critical for understanding and mitigating human-induced biodiversity change. Zooplankton are crucial components of aquatic systems, transferring energy from primary producers to higher trophic levels (Lampert and Sommer 2007).

The calanoid copepod *Sinodiaptomus sarsi* (Rylov, 1923) is native to East Asia and was originally described in fishponds and reservoirs in eastern China. Since then, the species has spread to western Asia and has been found in Turkey in the 1990s (Gündüz 1998). The first European record was from Sophia in Bulgaria, where it was from a fish tank (Bledzki and Rybak 2016). However, its presence remained uncertain until 2016, when Mykitchak (2016) found it in Ukraine in the Carpathian Mountain region near the Slovakian border (Mykitchak 2018, Mykitchak and Koval 2018). Subsequently, the species was also reported from also Ukraine, from Kyiv (Svetlichny and Samchyshyna 2021), and Romania (Battes *et al.* 2020).

MATERIALS AND METHODS

Study area and the measured variables

During the study, a total of 70 lakes were sampled. Due to a lack of environmental data, only 64 were assessed in this study (Fig. 1). All the visited lakes are located in Hungary (Central Europe), and their surface areas range between 0.08 and 102 ha. The depths at the sampling sites ranged from 0.8 to 14 m. The sampling sites were approached by a belly boat, and the depth of the lakes was measured with Deeper Smart Sonar Pro+. Sampling was con-

ducted during the summer (July–August) of 2017. Zooplankton samples were taken by a 12 L volume of a Schindler-Patalas plankton trap with a 65 μm mesh from two depths. Three replicates were taken from near the surface of the water, and the other three were taken from near the bottom. Then, the samples were integrated and preserved using Lugol's solution. Subsamples were taken, and a counting chamber was used for enumerating zooplankton under a Nikon Diaphot inverted microscope (1 ml subsamples for rotifers, 5 ml subsample for microcrustaceans). At least 100 specimens were counted for each zooplankton group (microcrustaceans and rotifers). Microcrustacean biomass was calculated based on weight-length regressions (Downing and Rigler 1981), while rotifer biomass was assessed based on its biovolume. The length of the first 30 individuals of each microcrustacean species encountered in each sample was measured with an ocular micrometre. Biomass data were given in mg w.w. m^{-3} and introduced into all statistical analyses. Functional groups for zooplankton were determined based on their foraging strategies (Table 1). For the identification of zooplankton, we used Battes *et al.* (2020), Bledzki and Rybak (2016), Gulyás and Forró (1999), Podshivalina and Sheveleva (2020), Gündüz (1998), Svetlichny and Samchyshyna (2021) for microcrustaceans, and Bancsi (1986, 1988) for rotifers.

The conductivity (COND, μs cm^{-1}), pH and water temperature (TEMP, °C), and dissolved oxygen (DO, mg L^{-1}) were measured on site. Water samples were analysed for total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), dissolved inorganic nitrogen (DIN) (as sum of nitriteN (NO_2-N),

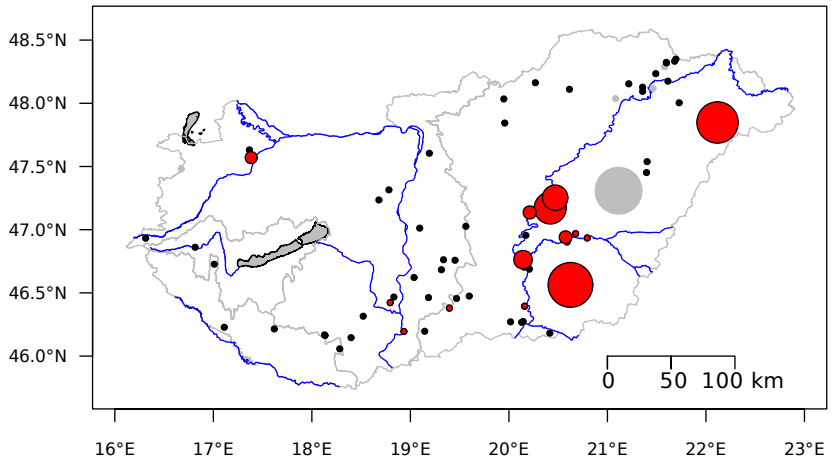

Fig. 1. Map of the sampling sites. (Dots represent the water bodies. Grey dots show those waters which are not involved in the statistical analyses. Red and black dots represent waters inhabited and uninhabited by *Sinodiaptomus sarsi*, respectively. The size of the dots refers to the biomass of *S. sarsi*).

Table 1. List of zooplankton species with functional groups.

Taxon name	Code	Traits	Groups
Bosmina coregoni	Bos_core	bacteria_feeder	Cladocera
Bosmina longirostris	Bos_long	bacteria_feeder	Cladocera
Iliocryptus acutifrons	Ili_acut	benthic_picker	Cladocera
Iliocryptus agilis	Ili_agil	benthic_picker	Cladocera
Leptodora kindtii	Lep_kind	large_predator	Cladocera
Acropterus harpae	Acr_harp	large_substratum scrapers	Cladocera
Simocephalus vetulus	Sim_vetu	littoral_large_filterers	Cladocera
Daphnia ambigua	Dap_ambi	pelagic_large_filterers	Cladocera
Daphnia cucullata	Dap_cucu	pelagic_large_filterers	Cladocera
Daphnia galeata	Dap_gale	pelagic_large_filterers	Cladocera
Daphnia magna	Dap_magn	pelagic_large_filterers	Cladocera
Daphnia parvula	Dap_parv	pelagic_large_filterers	Cladocera
Diaphanosoma brachyurum	Dia_brac	pelagic_non_daphnid_filterers	Cladocera
Moina brachiata	Moi_brac	pelagic_small_filterers	Cladocera
Moina micrura	Moi_micr	pelagic_small_filterers	Cladocera
Moina weismanni	Moi_weis	pelagic_small_filterers	Cladocera
Ceriodaphnia laticaudata	Cer_lati	small_littoral_daphnid_filterers	Cladocera
Ceriodaphnia pulchella	Cer_pulc	small_littoral_daphnid_filterers	Cladocera
Ceriodaphnia quadrangula	Cer_quad	small_littoral_daphnid_filterers	Cladocera
Ceriodaphnia reticulata	Cer_reti	small_littoral_daphnid_filterers	Cladocera
Ceriodaphnia rotunda	Cer_rotu	small_littoral_daphnid_filterers	Cladocera
Ceriodaphnia sp.	Cer_sp.	small_littoral_daphnid_filterers	Cladocera
Alona rectangula	Alo_rect	small_substratum_scrapers	Cladocera
Alonella excisa	Alo_exci	small_substratum_scrapers	Cladocera
Alonella exigua	Alo_exig	small_substratum_scrapers	Cladocera
Chydorus sphaericus	Chy_spha	small_substratum_scrapers	Cladocera
Macrothrix hirsuticornis	Mac_hirs	substratum_scrapers	Cladocera
Macrothrix laticornis	Mac_lati	substratum_scrapers	Cladocera
Pleuroxus denticulatus	Ple_dent	substratum_scrapers	Cladocera
Pleuroxus uncinatus	Ple_unci	substratum_scrapers	Cladocera
Scapholebaris mucronata	Sca_mucr	substratum_scrapers	Cladocera
Acanthocyclops robustus	Aca_robu	large_omnivore	Copepoda
Eudiaptomus gracilis	Eud_grac	selective_filterer	Copepoda
Sinodiaptomus sarsi	Sin_sars	selective_filterer	Copepoda
Nauplius calanoids	Nau_cal	small_filterer	Copepoda
Nauplius cyclopoids	Nau_cyc	small_filterer	Copepoda
Acanthocyclops robustus copepodite	Aca_cop	small_omnivore	Copepoda
Eucyclops serrulatus copepodite	Euc_serr	small_omnivore	Copepoda
Macrocyclops albidus copepodid	Mac_albi	small_omnivore	Copepoda
Mesocyclops leuckarti	Mes_leuc	small_omnivore	Copepoda
Thermocyclops crassus	The_cras	small_omnivore	Copepoda
Thermocyclops dybowski	The_dybo	small_omnivore	Copepoda

Table 1. (continued)

Taxon name	Code	Traits	Groups
Anuraeopsis fissa	Anu_fiss	micro_filterer	Rotifera
Bdelloidea spp.	Bde_spp	micro_filterer	Rotifera
Brachionus angularis	Bra_angu	micro_filterer	Rotifera
Brachionus budapestiensis	Bra_buda	micro_filterer	Rotifera
Brachionus calyciflorus	Bra_caly	micro_filterer	Rotifera
Brachionus diversicornis	Bra_dive	micro_filterer	Rotifera
Brachionus dorcas	Bra_dorc	micro_filterer	Rotifera
Brachionus elevatus	Bra_elev	micro_filterer	Rotifera
Brachionus falcatus	Bra_falc	micro_filterer	Rotifera
Brachionus fernandoi	Bra_fern	micro_filterer	Rotifera
Brachionus forficula	Bra_forf	micro_filterer	Rotifera
Brachionus leydigi	Bra_leyd	micro_filterer	Rotifera
Brachionus quadridentatus	Bra_quad	micro_filterer	Rotifera
Brachionus urceolata	Bra_urce	micro_filterer	Rotifera
Brachionus variablis	Bra_vari	micro_filterer	Rotifera
Cephalodella gibba	Cep_gibb	micro_filterer	Rotifera
Cephalodella mucronata	Cep_mucr	micro_filterer	Rotifera
Cephalodella sp.	Cep_sp	micro_filterer	Rotifera
Collotheca sp.	Col_sp	micro_filterer	Rotifera
Colurella spp.	Col_spp	micro_filterer	Rotifera
Filinia limnetica	Fil_limn	micro_filterer	Rotifera
Filinia longiseta	Fil_long	micro_filterer	Rotifera
Filinia opoliensis	Fil_opol	micro_filterer	Rotifera
Hexarta intermedia	Hex_inte	micro_filterer	Rotifera
Keratella cochlearis	Ker_coch	micro_filterer	Rotifera
Keratella cochlearis-tecta	Ker_coch	micro_filterer	Rotifera
Keratella quadrata	Ker_quad	micro_filterer	Rotifera
Keratella serrulata	Ker_serr	micro_filterer	Rotifera
Keratella tropica	Ker_trop	micro_filterer	Rotifera
Keratella valga	Ker_valg	micro_filterer	Rotifera
Lecane bulla	Lec_bull	micro_filterer	Rotifera
Lecane closterocerca	Lec_clos	micro_filterer	Rotifera
Lecane cornuta	Lec_corn	micro_filterer	Rotifera
Lecane elsa	Lec_elsa	micro_filterer	Rotifera
Lecane hamata	Lec_hama	micro_filterer	Rotifera
Lecane ludwigi	Lec_ludw	micro_filterer	Rotifera
Lecane luna	Lec_luna	micro_filterer	Rotifera
Lecane lunaris	Lec_luna	micro_filterer	Rotifera
Lepadella acuminata	Lep_acum	micro_filterer	Rotifera
Lepadella dactyloseta	Lep_dact	micro_filterer	Rotifera
Lepadella patella	Lep_pate	micro_filterer	Rotifera
Lepadella rhomboides	Lep_rhom	micro_filterer	Rotifera

Table 1. (continued)

Taxon name	Code	Traits	Groups
Lepadella sp.	Lep_sp	micro_filterer	Rotifera
Lophocharis salpina	Lop_salp	micro_filterer	Rotifera
Mytilina acanthophora	Myt_acan	micro_filterer	Rotifera
Mytilina mucronata	Myt_mucr	micro_filterer	Rotifera
Platyias patulus	Pla_patu	micro_filterer	Rotifera
Platyias quadricornis	Pla_quad	micro_filterer	Rotifera
Polyarthra dissimulans	Pol_diss	micro_filterer	Rotifera
Polyarthra dolychoptera	Pol_doly	micro_filterer	Rotifera
Polyarthra euryptera	Pol_eury	micro_filterer	Rotifera
Polyarthra vulgaris	Pol_vulg	micro_filterer	Rotifera
Pompholyx complanata	Pom_comp	micro_filterer	Rotifera
Pompholyx sulcata	Pom_sulc	micro_filterer	Rotifera
Rotaria spp.	Rot_spp	micro_filterer	Rotifera
Squatinella mutica	Squ_muti	micro_filterer	Rotifera
Synchaeta oblonga	Syn_oblo	micro_filterer	Rotifera
Synchaeta spp.	Syn_spp	micro_filterer	Rotifera
Testudinella patina	Tes_pati	micro_filterer	Rotifera
Trichocerca capucina	Tri_capu	micro_filterer	Rotifera
Trichocerca cylindrica	Tri_cyli	micro_filterer	Rotifera
Trichocerca elongata	Tri_elon	micro_filterer	Rotifera
Trichocerca pusilla	Tri_pusi	micro_filterer	Rotifera
Trichocerca rattus	Tri_ratt	micro_filterer	Rotifera
Trichocerca similis	Tri_simi	micro_filterer	Rotifera
Trichocerca spp.	Tri_spp	micro_filterer	Rotifera
Asplanchna priodonta	Asp_prio	micro_pred	Rotifera
Asplanchna sieboldi	Asp_sieb	micro_pred	Rotifera

nitrateN (NO_3-N), ammoniumN (NH_4-N)), soluble reactive silica (Si), sulphate (SO_4^{2-}), chloride (Cl^-), carbonate (CO_3^{2-}), bicarbonate (HCO_3^-), and chemical oxygen demand (COD). TP and COD were expressed in μg L^{-1}, while the others were given in mg L^{-1} (see Selmeczy *et al.* 2023). Phytoplankton biomass was determined based on cell volumes from the most similar geometric forms and was sorted into Reynolds's functional groups (RFG) (see Selmeczy *et al.* 2023).

Land use types were employed based on the Corine Land Cover (CLC) database (European Union, Copernicus Land Monitoring Service 2018, European Environment Agency). Five categories were determined: urban areas, agricultural areas, forest and seminatural areas, wetlands, and water (see Selmeczy *et al.* 2023). Geographical environmental variables were compiled from the physical (watershed area (km^2), lake surface area (km^2)) and metadata (longitude, latitude, and altitude) of the lakes.

Statistical analyses

The constrained ordination method was selected, revealing the factors that can regulate or respond to the zooplankton community. Prior to any statistical analyses, all data were transformed. The biomass data were Hellinger transformed following Legendre and Gallagher's (2001) suggestions, and their heterogeneity was checked by the decorana function of vegan. Since the gradient lengths were less than 4, the linear constrained ordination method, Redundancy Analysis (RDA), was applied. Water chemistry data were standardised to zero means and unit variances (z-transformation), while land-use cover was submitted to a square root transformation. Data analyses were carried out in the R environment 4.5.1 (R Core Team 2025) with the following packages: vegan (Oksanen *et al.* 2025), maps (Becker *et al.* 2025) and raster (Hijmans 2025). Environmental variables, which were introduced into RDA, were selected by the variance inflation factor. Variables with a VIF < 10 were submitted into RDA (Borcard *et al.* 2011), and the significant environmental and land-use variables were selected with stepwise selection in an RDA model using the "ordistep" function. The "intersetcor" function of the vegan package was used for the calculation of correlation.

Procrustes analysis was used to investigate the degree of concordance between each pair of ordinations. Procrustes analysis rotates two ordinations to maximise the similarities between them by minimising the sum of their squared distances (Gower 1971). The residuals of a Procrustes rotation reflect the extent of the changes in the position of assemblages in the ordination space. Residuals are high if the removal of *Sinodiaptomus sarsi* strongly modifies the structure of the assemblages. The Procrustes rotation was computed by means of the "procrustes" function in the vegan package (Oksanen *et al.* 2025). Prior to the Procrustes analysis, Principal Component Analyses (PCA) were run on Hellinger-transformed zooplankton data. One PCA was applied to the entire data set, while the second was run on the data set from which the *S. sarsi* was removed.

RESULTS

Altogether, 108 taxa were found in the 70 lakes belonging to three taxonomic groups and 17 foraging traits (Table 1). Rotatoria was the richest taxonomic group with 68 taxa, followed by Cladocera with 31 taxa, while Copepoda was represented by only eight taxa. Biomass of zooplankton varied in a considerable interval (Fig. 7). The lowest zooplankton population (0.34 mg d.w. L^{-1}) was found in Bánya-tó near Tarcal village. The highest zooplankton biomass (39.83 mg d.w. L^{-1}) was recorded in the Cibakházi Holt-Tisza due to the mass production of *Brachionus diversicornis* rotifera (Fig. 7).

We found *Sinodiaptomus sarsi* (Rylov, 1923) in seventeen samples during the study. This species is new to the Hungarian fauna. Most of the lakes inhabited by this species are located in the eastern part of the Danube; only two occurrences have been recorded in the western part of Hungary with low biomass (Tolnai-Duna and Fábián-tó in Bágyogszovát). Taxonomically, this species belongs to the Diaptomidae family of the Calanoida order of Crustacea. Large in size, the adults can reach 2 mm in length. Its density varied between 0.014 and 113.542 ind L^{-1}, while biomass varied between 0.001 and 3.889 mg L^{-1}. This species occurred with the highest biomass in the 4th fishing lake on the outskirts of Püspökladány. It occurred in significant biomass in three places (Déli-tó at Gyopárosfürdő, Szénaréti-tó at Nyírbátor, and Fegyverneki-Holt-Tisza, while its biomass was moderate in the rest of the lakes. This species can be easily identified by its morphological characteristics. Females carry a dorsal bulge on the 5th thoracic segment (Fig. 2). The second segment of exopodite of the fifth swimming leg (P5) of males ends in a lamellate thumb-like process (Fig. 4). Its endopodite reaches the apex of exopodite (Fig. 5). Females have spinules on both margins of the end claw of the fifth leg exopodite (Fig. 6).

Rotifer biomass varied between 0 and 22 mg d.w. L^{-1}, they took the highest part (36%) of the total zooplankton biomass. Rotifers were sorted into two foraging traits: micro filterers and micro predators. Micro filterers took a significant share of zooplankton; their biomass varied from 0 to 21 mg d.w. L^{-1} accounted for a little more than one third of the total zooplankton biomass. The most frequent micro filterers belonged to *Branchionus*, *Keratella*, *Pompholyx*, and

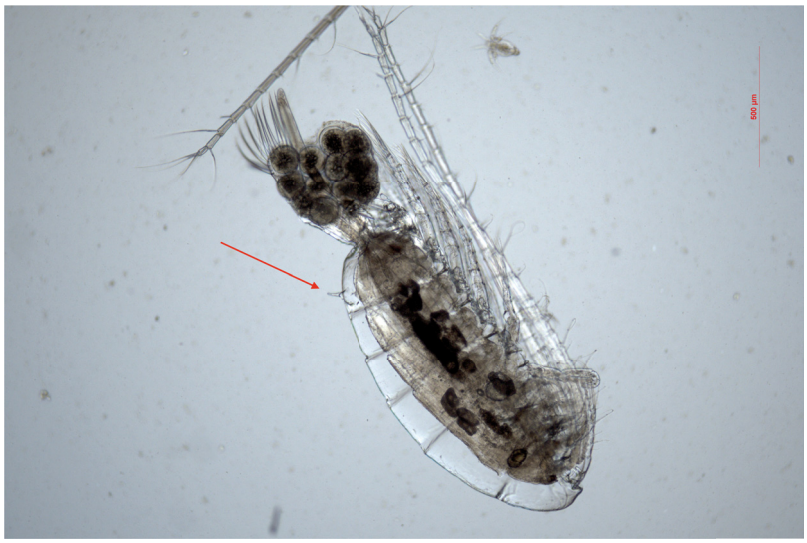

Fig. 2. General habitus of female *Sinodiaptomus sarsi* with egg sack. The red arrow points to the dorsal bulge on the 5th thoracic segment (40× magnification).

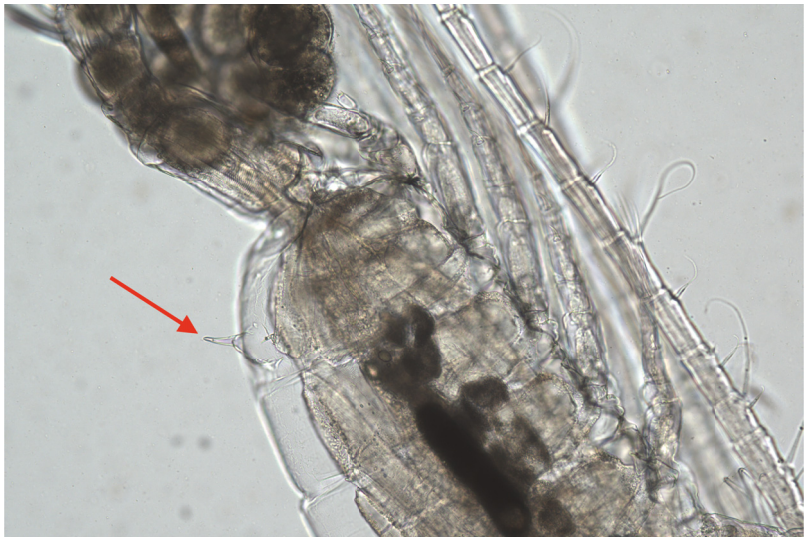

Fig. 3. Female of *Sinodiaptomus sarsi* with egg sacks with 100× magnification. The red arrow indicates the dorsal bulge on the 5th thoracic segment.

Polyarthra genera, while micro predators were *Asplanchna* species, and it took only 1% of the total zooplankton biomass (Figs 7–8).

Copepod biomass accounted for the largest part (44%) of the total zooplankton biomass. Its biomass varied between 0 and 14 mg d.w. L^{-1}. Copepod species

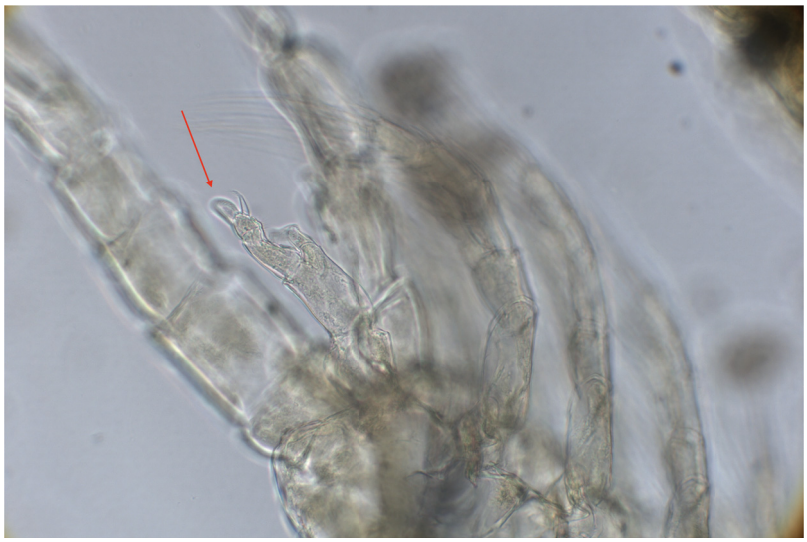

Fig. 4. The left 5th swimming leg (P5) of a male of *Sinodiaptomus sarsi*. The red arrow shows the second segment of exopodite ending in a lamellate thumb-like process (100× magnification).

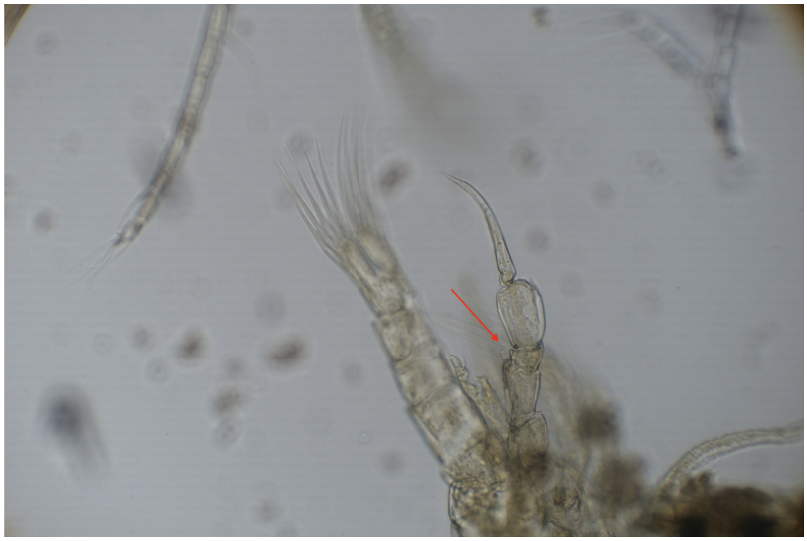

Fig. 5. The right fifth swimming leg (P5) of a male of *Sinodiaptomus sarsi*. The red arrow shows the endopodite reaching the apex of exopodite (100× magnification).

can be sorted into two large foraging groups. Only the adult *Acanthocyclops robustus* (G. O. Sars, 1863) cyclopoid gave a large omnivore trait. The adults and immature copepodites of *Eudiaptomus gracilis* (Sars, 1863) and *Sinodiaptomus sarsi* calanoids were selective filterers, sharing even 5% of total biomass. Nauplii were grouped into small filterers. It took a small part (5%) of the zooplankton biomass.

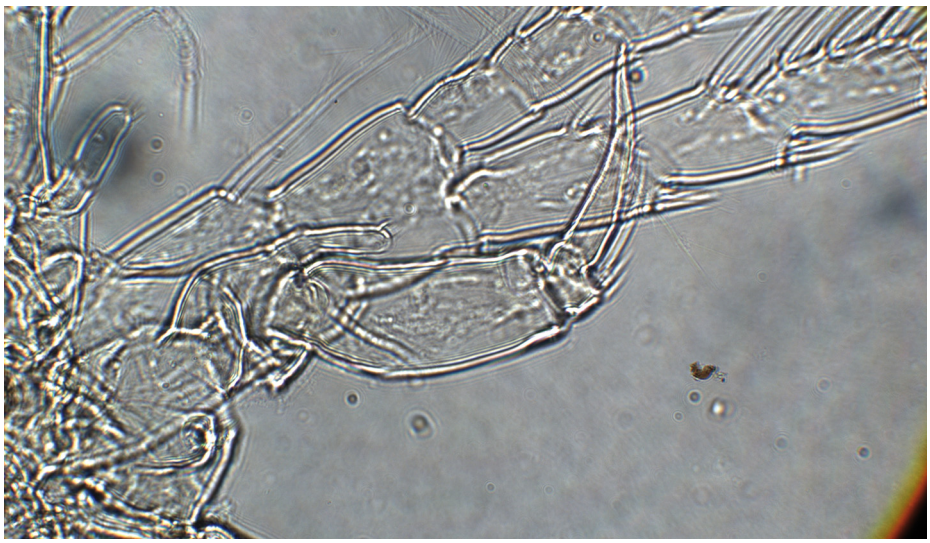

Fig. 6. The fifth swimming leg (P5) of a female of *Sinodiaptomus sarsi* (400× magnification).

Thermocyclops crassus (Fischer, 1853) and copepodite stages of all other cyclopoids belonged to the small omnivores. The biomass of this group varied between 0 and 14 mg d.w L^{-1}, and it was another group which shared one-third (33%) of the total zooplankton biomass (Figs 7–8).

Cladoceran biomass gave the lowest part (20%) of the zooplankton biomass, varying between 0 and 11 mg d.w L^{-1}. Cladocerans were classified into eleven groups based on their feeding traits (Table 1). Cladocera species, which were represented by the highest biomass, can be sorted into four foraging trait categories: bacteria feeders represented by bosminids with 11% biomass, pelagic large filterers by daphnids with 4%, pelagic non-daphnia by only *Diaphanosoma brachyurum* (Liévin, 1848) with 2%, pelagic small filterers such as moinids with 2%, and littoral daphnid filterers as *Ceriodaphnia* species with 1% sharing (Figs 7–8).

RDA analyses revealed that environmental parameters explained only a small part of the zooplankton variances of either species structure or trait aspect (Table 2). Although latitude became the uniquely significant constrained variable for the composition of the zooplankton species (RDA1: explained variance = 0.0154, F_{pseudo} = 1.9164, p = 0.014, r = 0.543), neither the land use of the surroundings nor the geographical background of the lakes seemed to affect the zooplankton. This was proven because latitude lost its constraint; therefore, no constraining factor remained in the traits-geographical RDA (Table 2). Relationships between zooplankton and water quality, or phytoplankton, were significant in both approaches (Table 2). From the water quality variables, temperatures (temp), total phosphorus (TP), and dissolved oxygen (DO) were effective factors in the composition of zooplankton since these variables were significant in both species-water quality and trait-water quality ordinations (Table 3). The first three components were significant in species-water quality RDA (RDA1: explained variance = 0.0305, F_{pseudo} = 4.1131, p = 0.001, RDA2: explained variance = 0.0221, F_{pseudo} = 2.9792, p = 0.004; RDA3: explained variance = 0.0174, F_{pseudo} = 2.3454, p = 0.016). The first redundant component of this RDA presented the highest correlation with Cl^- (r = -0.810) and TP (r = –0.779), the second component of species-water quality RDA was correlated with DO (r = –0.911), while TEMP was the variable that explained variance significantly (r = 0.846) in the third component of this RDA. Regarding the traits and water quality, the first two components were significant in their RDA (RDA1: explained variance = 0.0178, F_{pseudo} = 4.3382, p = 0.004; RDA2: explained variance = 0.0127, F_{pseudo} = 3.087, p = 0.026), and DO, TEMP, and TP also proved significant explanatory variables. The first redundant component of this RDA presented the highest correlation with DO (r = 0.804), while the second component was correlated with TEMP (r = –0.757) and TP (r = –0.700). Since the first redundancy component (RDA1) of species and the second redundancy component (RDA2) of trait RDAs showed a high correlation with TP, and the correlation between the components (Spearman's r = 0.674,

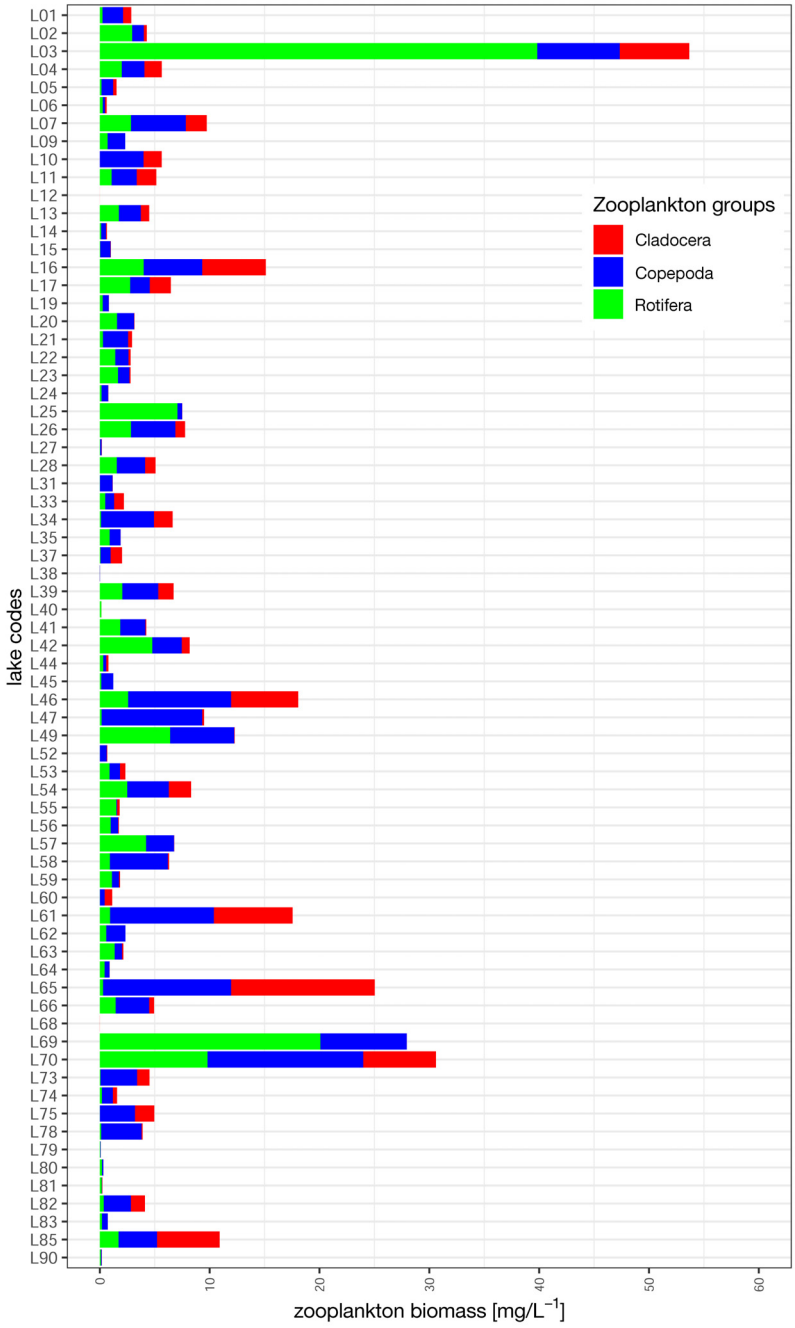

Fig. 7. Biomass of the main groups of zooplankton biomass of the studied lakes.

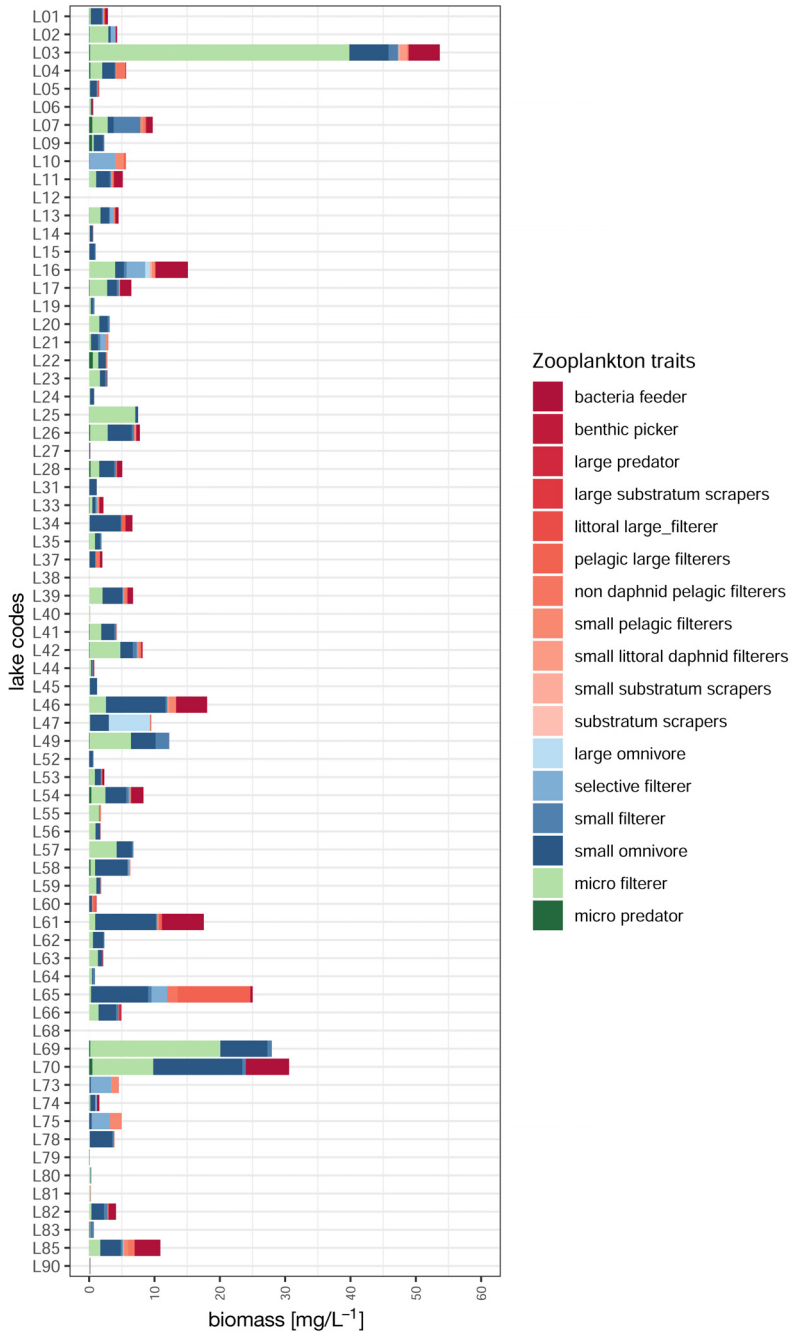

Fig. 8. Distribution of the biomass of zooplankton functional groups (feeding traits).

Table 2. Summary table of RDA results.

		Inertia	%	R^2_{adj}	F_{Pseudo}	*p*
Community						
water quality	total	0.5135	100	0.0908	2.5723	**0.001**
	constrained	0.0762	14.85			
	unconstrained	0.4372	85.15			
phytoplankton	total	0.5135	100	0.0843	2.4503	**0.001**
	constrained	0.0732	14.25			
	unconstrained	0.4403	85.75			
land use	total	0.5135	100	0	0	0
	constrained	0	0			
	unconstrained	0.5135	100			
geographical	total	0.5135	100	0.0143	1.9164	**0.014**
	constrained	0.0154	3			
		0.4981	97			
Feeding trait						
water quality	total	0.2835	100	0.0868	2.9957	**0.001**
	constrained	0.0369	13.03			
	unconstrained	0.2466	86.97			
phytoplankton	total	0.2835	100	0.108	2.9066	**0.001**
	constrained	0.0467	16.46			
	unconstrained	0.2368	83.54			
land use	total	0.2835	100	0	0	0
	constrained	0	0			
	unconstrained	0.2835	100			
geographical	total	0.2835	100	0	0	0
	constrained	0	0			
	unconstrained	0.2835	100			

S = 14228, p-value < 0.001) was high, the distribution of lakes was determined by the eutrophic gradient. Increasing component scores decreases trophic status.

The phytoplankton can also explain species and trait compositions of zooplankton since their relationship with zooplankton became significant in both species and trait RDAs (Table 2, Figs 9–10). In species-phytoplanton RDA, the first two components were significant (RDA1: explained variance = 0.0388, F_{pseudo} = 5.1966, $p = 0.001$; RDA2: explained variance = 0.0169, $F_{pseudo} = 2.2670$, $p = 0.045$). Four RFGs were proven to be effective factors in connection with zooplankton. The codons X1, SN, Y, and LM were significant with zooplankton species composition, while codons H1, X1, XPh, and T were with zooplankton trait (Table 3). The first redundant component of species RDA presented the highest correlation with codon X1 ($r = 0.728$), SN ($r = - 0.643$), and codon LM ($r = 0.560$), while the second component was correlated with codon Y ($r = –0.938$). In the traits and phytoplankton RDA, the first two redundant components were significant (RDA1: explained

variance = 0.0232, F_{pseudo} = 5.7671, p = 0.002; RDA2: explained variance = 0.0142, F_{pseudo} = 3.5293, p = 0.035), and X1 RFG kept its substantial explanatory variable status. However, the highest correlation was with the third RDA component (r = 0.720), although this component was insignificant (RDA3 = 0.0065, F_{pseudo} = 1.6303, p = 0.344). In this RDA analysis, codons H1, XPh, and T also became substantial variables. The first redundant component of this trait-phytoplankton RDA was the strongest correlation with codon XPh (r = –0.628) and codon T (r = –0.602) groups, while the second component was correlated with codon H1 (r = 0.723).

DISCUSSION

Aquatic ecosystems are threatened in Hungary (Borics *et al.* 2016). Nutrient enrichment, invasion of alien species, and water scarcity can be considered threatening factors. Hungarian aquatic fauna enriched with a new calanoid copepod species, *Sinodiaptomus sarsi* (Rylov, 1923). This species was first recorded in neighbouring Romania and Ukraine in 2020 (Battes *et al.* 2020, Podshivalina and Sheveleva 2020, Svetlichny and Samchyshyna 2021). In Europe, most

Table 3. Anova table.

		Df	Variance	F	p
Community					
water quality	Cl	1	0.024	3.223	**0.003**
	DO	1	0.022	3.004	**0.002**
	TP	1	0.016	2.147	**0.013**
	TEMP	1	0.014	1.915	**0.018**
	residual	59	0.437		
phytoplankton	X1	1	0.025	3.356	**0.001**
	SN	1	0.016	2.209	**0.004**
	Y	1	0.015	1.982	**0.01**
	LM	1	0.017		
	residual	59	0.44		
geographical	latitude	1	0.015	1.916	**0.021**
	residual	62	0.498		
Functional groups					
water quality	DO	1	0.014	3.481	**0.003**
	TEMP	1	0.013	3.14	**0.013**
	TP	1	0.01	2.365	**0.04**
	residual	60	0.247		
phytoplankton	H1	1	0.012	2.954	**0.006**
	X1	1	0.01	2.608	**0.018**
	XPh	1	0.012	3.035	**0.005**
	T	1	0.012	3.029	**0.009**
	residual	590.237			

known occurrences of *S. sarsi* are restricted to fishponds and urban lakes. All seventeen lakes in which *S. sarsi* was detected in Hungary are fishponds managed for angling. In four of the lakes – 4th-tó at Püspökladány, Szénaréti-tó at Nyírbátor, Fegyverneki Holt-Tisza at Fegyvernek, Déli-tó at Orosháza-Gyopárosfürdő – the biomass of *S. sarsi* exceeded 1 mg L^{-1}. Given that these lakes are separated by an average distance of approximately 100 km, the pattern strongly suggests that the species' spread is a byproduct of fish stocking.

Statistical analyses revealed that trophic conditions were the primary determinant of zooplankton community structure. Both taxonomic and functional approaches indicated that the lakes were arranged along the RDA1 axis.

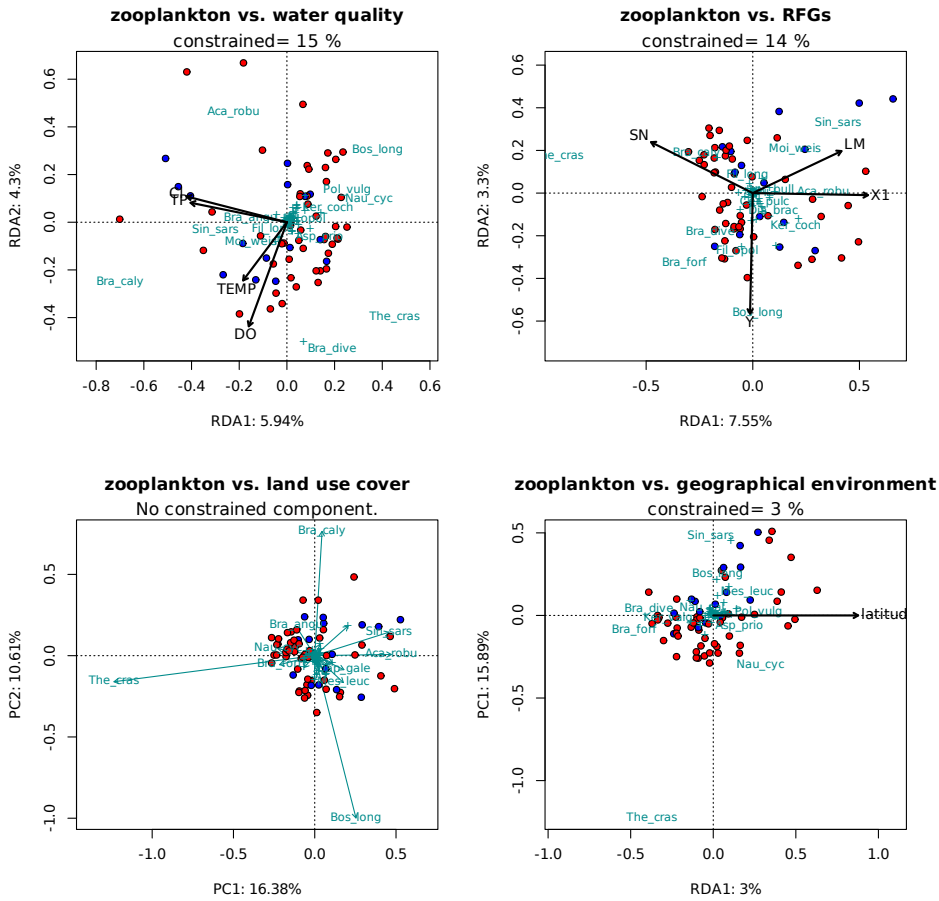

Fig. 9. Triplot of the redundancy analysis on zooplankton community with environmental variables: A = water quality; B = phytoplankton functional groups (RFG); C = the land use types; D = geographical metadata. (Red and blue dots represent sites with and without *Sinodiaptomus sarsi*, respectively).

Zooplankton community composition was mainly driven by limnological conditions (Figs 9–10). Although we assumed that land use would influence aquatic environments, no significant relationship was found between land use and zooplankton composition. However, species composition varied along a latitudinal gradient (Figs 9–10).

Zooplankton assemblages were associated with RFG codons characteristic of eutrophic to hypertrophic conditions, including X1, SN, Y, LM, XPh, and H1. Codons X1 and SN became significant variables in both taxonomic and functional analyses. The dissolved oxygen (DO), total phosphorus (TP), and temperature (TEMP) were also the significant explanatory variables.

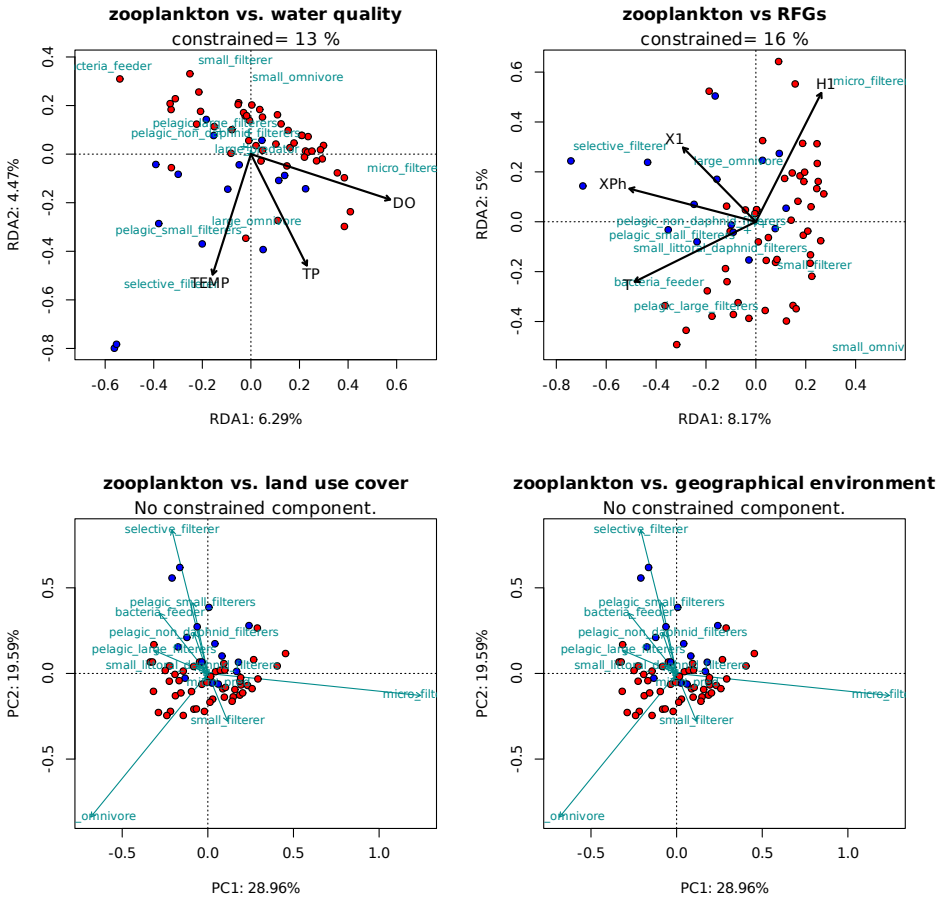

Fig. 10. Triplot of the redundancy analysis on zooplankton functional groups with environmental variables: A = water quality; B = phytoplankton functional groups (RFG); C = the land use types; D = geographical metadata. (Blue dots represent sites with *Sinodiaptomus sarsi*; red dots are sites without).

Total phosphorus acts as a primary driver of eutrophication (Vollenweider and Kerekes 1982); elevated daytime oxygen concentrations are a consequence of high primary production (Wetzel 2001), while temperature accelerates eutrophication processes (Jeppesen *et al.* 2003, 2014, Moss *et al.* 2009). Warmer environments tend to reduce organism body size (Atkinson 1995, Gibert and DeLong 2014, Korponai *et al.* 2020, Roberts *et al.* 2010), favouring the dominance of small-bodied zooplankters. Our observations confirmed this pattern: rotifers and small copepods, such as *Thermocylops crassus*, and small cladocerans, such as *Moina* spp., were dominant in the samples from warmer waters (Bledzki and Rybak 2016). This was further supported by the strong correlation of small pelagic filter feeders (*Moina* spp.) and selective filterers (calanoids) with the RDA2 component (Figs 9–10).

The thermophilic nature of *Sinodiaptomus sarsi* was also confirmed. Originally reported from subtropical regions of Asia, the species was later recorded in Central Asia (Mykitchak 2016, Podshivalina and Sheveleva 2020, Svetlichny and Samchyshyna 2021), supporting the conclusion that it is thermophilous. RDA results corroborated this, as both temperature and *S. sarsi* also presented the highest correlation with the RDA3 component.

According to OECD classification (Vollenweider and Kerekes 1982), eutrophic conditions correspond to TP concentrations of 35–100 μg L^{-1}. TP concentrations in the studied lakes exceeded the lower limit of eutrophic status, and the zooplankton communities were characteristic of highly eutrophic waters. Our analyses further indicated that *Sinodiaptomus sarsi* prefers hypertrophic conditions, as evidenced by its strong negative correlation with the RDA1 axis, similar to TP. Alongside *S. sarsi*, *Brachionus calyciflorus* Pallas, 1766, and *Thermocyclops crassus* showed the highest negative correlations with RDA1, while *Bosmina longirostris* O. F. Müller, 1776 exhibited a strong positive correlation, suggesting a preference for lower trophic states.

Higher biomass of codon X1 was associated with copepods (selective filter feeders and small omnivores). Variation in the occurrence of other codons – SN, Y, LM, XPh, T, and H1 – can be attributed to heterogeneity among the lakes. In eutrophic lakes with fish, zooplankton communities are typically dominated by rotifers, small cladocerans, and copepods due to high predation pressure (Bonecker *et al.* 2011, Christoffersen *et al.* 1993, Iglesias *et al.* 2011, Korponai *et al.* 1997). The studied lakes, being managed for angling, experience significant fish predation, which is reflected in communities dominated by rotifers, small-bodied cladocerans (*Bosmina longirostris*, *Daphnia galeata*, *Moina* spp., *Diaphanosoma brachyurum*, *Chydorus sphaericus*), and copepods (*Eudiaptomus gracilis*, *Acanthocyclops robustus* and *Thermocyclops crassus*).

Along the eutrophication gradient, the hypertrophic status was associated with codon X1 (Figs 9–10). This association can be explained by the top-down effect of

fish, as fish predation promotes the dominance of rotifers and copepods, which are comparatively less efficient filter feeders (Christoffersen *et al.* 1993, Jeppesen *et al.* 1997). The reduced grazing pressure exerted by zooplankton under these conditions facilitates the proliferation of members of codon X1. Codon SN was exclusively composed of *Raphidiopsis raciborskii* and represented the most important RFG among the phytoplankton (Selmeczy *et al.* 2023). H1 was represented by other nitrogen-fixing cyanobacteria (Padisák *et al.* 2009). Their appearance among the significant environmental factors indicated the nitrogen deficiency of the waters. The differing behaviours of the SN and H1 groups in the RDA analyses remain unclear; however, the functional approach underscores the significant role of rotifers, as micro-filter feeders, in shaping zooplankton community structure under eutrophic conditions.

In summary, our results indicate that *Sinodiaptomus sarsi* has successfully established populations in Hungarian waters, yet we found no clear evidence that its presence has no significantly altered the overall zooplankton community structure (Procrustes test: $r^2_{m12} = 0.04912$, $r = 0.9751$, $p < 0.001$, permutation = 999). As a selective filter feeder, it can potentially fulfil the functional role of native calanoid copepods in lentic ecosystems. However, its distribution may be restricted by its thermal requirements, which could confine its presence to specific habitats or seasons.

S. sarsi appears to be an invasive but opportunistic component of Hungarian freshwater zooplankton, with its long-term role likely determined by the interplay of temperature regimes, trophic state, and predator pressure. Continued monitoring will be essential to detect potential shifts in its population dynamics, particularly under changing climatic and eutrophication scenarios.

* * *

Acknowledgements – We are grateful to the current and former colleagues and students of the Center for Natural Science (former Department of Limnology) of Pannon University for their help in the field and in the laboratory. This study was financed by the National Research, Development, and Innovation Office (NKFIH 120595). It was also implemented by the National Multidisciplinary Laboratory for Climate Change (RRF-2.3.1-21-2022-00014) project, as part of Hungary's National Recovery and Resilience Plan, which is supported by the Recovery and Resilience Facility of the European Union, as well as within the framework of the Széchenyi Plan Plus program, with the support of the RRF 2.3.1 21 2022 00008 project. This paper is dedicated to Judit Padisák. The first author of the paper (JK) first met Jutka Padisák in the early 1990s, at his very first Hydrobiologist Day. Their first conversation was about a regression problem, and that exchange marked the start of a connection that has lasted ever since. Over the years, whether they've been in close contact or only touched base occasionally, he has always known he could rely on Jutka's professional wisdom and personal kindness. This study is partly the first author's (JK) way of repaying a long-standing debt, and of gratitude, and of expressing his deep respect and heartfelt thanks. This work is a memorial to co-author László Forró.

Összefoglaló: A magyarországi kis és sekély vizekről végzett kutatásunk során egy új inváziós copepoda faj, a *Sinodiaptomus sarsi* (Rylov, 1923) került elő a 2017-ben gyűjtött zooplankton mintáinkból. Magyarországon több, fontos horgászvízben is megtaláltuk jelentős biomasszával. A

S. sarsi sikeresen megtelepedett a hazai kisvizekben, azonban nem találtunk egyértelmű bizonyítékot arra, hogy jelenléte jelentősen hatott volna a zooplankton közösség szerkezetére. Mivel szelektív szűrő szervezet, potenciálisan betöltheti az őshonos calanoid copepodák funkcionális szerepét a hazai tavi ökoszisztémákban, kiszorítva őket a planktonból. A *S. sarsi* a magyar édesvízi zooplankton inváziós és opportunista tagja, szerepét és elterjedését valószínűleg a hőmérsékleti viszonyok, a trofikus állapot és a ragadozói nyomás kölcsönhatása határozza meg. Elterjedésének és populációdinamikájának figyelemmel kísérése elengedhetetlen lesz a faj ökológiájának megértéséhez. A változó éghajlati és trofikus környezet kedvez az inváziós fajok megjelenéséhez, amelyek negatívan hathatnak a lokális ökoszisztémákra, és így a közösségszerkezet megváltoztatásával a biodiverzitásra. Terjedésük nyomon követése és ökológiájuk megértése kulcsfontossággal bír az inváziós fajok negatív hatásának csökkentését igénylő cselekvések kidolgozásához.

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(submitted: 15.08.2025; accepted: 28.09.2025)

DOI: 10.17110/StudBot.2025.56.1.133 Studia bot. hung. 56(1), pp. 133–140, 2025

IS IT POSSIBLE TO AUTOMATE MICROSCOPIC PLANKTON SPECIES IDENTIFICATION USING AI?

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Hajnal, É. (2025): Is it possible to automate microscopic plankton species identification using AI? – *Studia bot. hung.* **56**(1): 133–140.

Abstract: With the development of artificial intelligence and the trend towards automation of various subtasks, there is a need to automate microscopic plankton species identification. Some solutions already exist with relatively modest capabilities. This study examines the results hitherto achieved in this area, the potential goals to be achieved and the way how current AI systems can be applied to this task.

Key words: AI, large language models, machine learning, plankton identification, taxonomy

INTRODUCTION

Ecology, as a scientific discipline, investigates supra-individual levels of biological organisation, employing statistical analyses, mathematical modelling, and hypothesis testing. Nonetheless, its foundation rests upon precise observation. In plankton ecology, species-level identification within individual water or surface samples is essential, necessitating both qualitative and quantitative analysis. The identification process is labour-intensive, requiring not only significant time investment for sample collection and preparation but also expert-level taxonomic knowledge, often acquired through extensive training. As noted by Karbstein *et al.* (2024), Kusumawardani *et al.* (2019), trained taxonomist him/herself is a rare and endangered species. This raises the critical question of whether species-level identification is indispensable (Karbstein *et al.* 2024), particularly considering the evolving nature of species concepts and the transformation of morphology-based species definitions (Karbstein *et al.* 2024).

In practice, several approaches can avoid species-level identification. Functional group classification, for instance, is notably more cost-effective and less complex (Salmaso *et al.* 2015). Alternatively, species proportions can be inferred from pigment composition using spectral analysers or through detailed individual analysis with flow cytometry (Labrighli *et al.* 2022). Genetic and genomic techniques also offer potential for automation, although integration with morphology-based taxonomy remains incomplete (Karbstein *et al.* 2024).

Despite these alternatives, traditional taxonomy remains vital for long-term and in-depth ecological studies due to its compatibility with historical datasets. Microscopic preparations, a cornerstone of this method, allow for retrospective verification and consistent species identification in line with taxonomic standards. Although taxonomic classifications evolve, referencing established taxonomic keys allows for database revisions and ensures continuity (Hajnal 2006, Hajnal and Padisák 2008). This methodological consistency has facilitated century-long studies of Lake Balaton's water quality (Hajnal and Padisák 2008), exemplifying the enduring value of precise identification.

Consequently, abandoning microscopic taxonomy entirely is not advisable. The pertinent question arises: to what extent can this process be automated, and how can artificial intelligence (AI) contribute? Although advancements in AI inspire optimism, scepticism persists among experts due to current limitations (Giering *et al.* 2022). In macrophyte studies, detection accuracy has reached 80–90% across several hundred species, yielding promising, albeit hobby-level, results (Habib *et al.* 2024). In contrast, automated plankton identification remains significantly less accurate (Table 1).

This research thus investigates the feasibility and potential of automating microscopic plankton identification using AI technologies. It does not aim to summarise existing literature – comprehensive reviews are already available (Eerola *et al.* 2024, Labrighli *et al.* 2022) – but rather to assess the challenges,

Table 1. Results in taxonomic identification of phytoplankton or diatom samples.

Year	Classification output	Estimated level	Acc	Methods	Reference
2007	22	genus	88%	Feature extraction + SVM	Sosik and Olson (2007)
2020	2	phylum	84%	Feature extraction with + machine learning (RF, SVM)	Rivas-Villar *et al.* (2021)
2020	4	species, morphotype	88%	Feature extraction + machine learning (SVM)	Rivas-Villar *et al.* (2021)
2021	2	genus	78%	VGG-16 CNN	Rachman *et al.* (2022)
2021	4	genus	79%	VGG-16 CNN	Rachman *et al.* (2022)
2021	6	genus	54%	VGG-16 CNN	Rachman *et al.* (2022)
2023	29	marine phytoplankton, ordo	95%	photo + fluoro-electrochemical features + KNN or NN	Chen *et al.* (2023)
2024	15	phylum, not only plankton	96.50%	ResNet50 CNN	Habib *et al.* (2024)
2024	4	species	85%	Faster-RCNN	Figueroa *et al.* (2024)

explore prospective methodologies, and analyse the initial outcomes of existing solutions in the context of rapid technological progress. Ultimately, such developments could enable high-resolution spatiotemporal data acquisition that integrates seamlessly with long-standing scientific records.

MATERIALS AND METHODS

This study is grounded in a comprehensive review of the current literature on AI-assisted plankton identification. Although not a systematic review, it critically evaluates existing systems. Relevant publications were identified using search terms such as "plankton/phytoplankton/diatom identification AI/ Artificial Intelligence" and "plankton/phytoplankton/diatom taxonomy AI/ Artificial Intelligence", yielding 17 pertinent sources. This paper addresses the following research questions: (1) What are the ideal requirements for an automated system? (2) What levels of accuracy are achievable? (3) What results have been documented? (4) Which AI technologies show the greatest promise?

RESULTS

Requirements

Figure 1 illustrates a methodological block scheme for taxonomic identification. Phytoplankton sampling is readily automatable, with robotic vessels and flow-cell systems (e.g., VPR, SIPPER, KRIP, FlowCytobot) enabling individual imaging (Chen *et al.* 2023, Sosa-Trejo *et al.* 2023, Sosik and Olson 2007). These devices can function in situ or in laboratory settings. While sampling from submerged substrates is technically feasible using robotic systems, such solutions

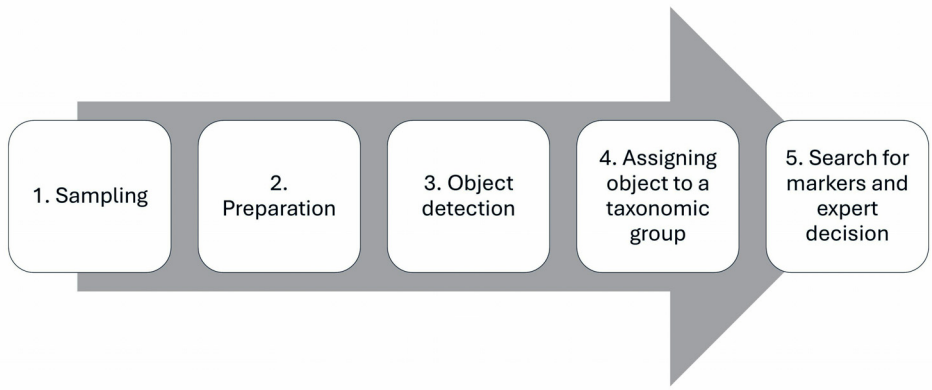

Fig. 1. Block scheme of the taxonomic identification made by human expert.

are rare and economically impractical, potentially compromising comprehensive environmental assessments.

Sample preparation remains a laboratory-intensive task that can be partially or fully automated using robotic assistance (Wolf *et al.* 2024). However, the key challenge lies in automating microscopic identification, which is in the focus of this study.

Over the past two decades, efforts to replicate expert-level taxonomic identification via automation have shaped current system requirements. The manual process involves object detection, organism delineation, taxonomic marker identification, and hierarchical classification based on observed markers (Rivas-Villar *et al.* 2021). Although replicating this exact process algorithmically is complex, scientific fidelity warrants such an approach.

The goal is to achieve human accuracy. According to experience, trained taxonomists' self-coherence is 85–95%, which is approximately the top accuracy of human work (Kelly *et al.* 2007). Its reason is that phytoplankton and diatoms are the so-called Taxonomically Complex Groups-(TCGs) (Karbstein *et al.* 2024), on the other hand, this is the psychological consequence of boring and fatigue microscopic workloads (Rivas-Villar *et al.* 2021).

An optimal system should emulate a generalist taxonomist, capable of identifying diverse species across multiple habitats. It must be self-reflective, adjusting identification resolution based on input data and its internal knowledge. Unlike conventional AI algorithms, it should recognise and abstain from classifying unfamiliar specimens.

Achieved results

Despite their importance, current automated systems fall short of these ideals. Existing models often specialise in limited taxa and lack adaptability or interpretability (Table 2). Early applications extracted manually selected image features for classification via support vector machines (SVM), random forests (RF), or k-nearest neighbours (KNN) algorithms (Rivas-Villar *et al.* 2021). Several solutions use a two-step approach, in the first step they try to separate plankton individuals from other objects, followed by the collection of features and the determination. Although the features were not stamps corresponding to the original markers, it can be stated that they were generally well interpretable and were features based on the conscious decision of the system developer.

The advent of deep learning, particularly convolutional neural networks (CNNs), such as VGG, ResNet50, and Faster-RCNN, significantly enhanced identification accuracy. However, these models continued to suffer from poor interpretability and methodological inconsistency (Eerola *et al.* 2024, Figueroa *et al.* 2024, Rachman *et al.* 2022, Sosa-Trejo *et al.* 2023).

Table 2. Multimodal Large Language Models (LLM) for combined text and image processing capabilities.

Model	Developer	Main attributes	Year
GPT-4V (Vision)	OpenAI	Combined interpretation of images and texts (*e.g.* graph reading, visual QA)	2023
Flamingo	DeepMind	Multimodal transformer, fine-tuned for image-text-based interactions	2022
BLIP / BLIP-2	Salesforce	Image-based question-answer, image description generation	2022–2023
MiniGPT-4	Open-source (Vision encoder + LLM)	Multimodal system modelled after GPT-4	2023
Kosmos-1	Microsoft	Multimodal large model: joint interpretation of text, image and OCR	2023

Macrophyte recognition, in contrast, has advanced rapidly since-2017. With competitions like Kaggle driving development and massive image datasets fuelling training, detection accuracy surpassed 90% for hundreds of plant categories (Bambil *et al.* 2020, Habib *et al.* 2024, Ibrahim *et al.* 2023, Labrighli *et al.* 2022, Xie *et al.* 2024). In contrast, plankton-focused efforts suffer from a paucity of annotated image datasets, underscoring the need for the development of large-scale image repository.

Possible current and future AI solutions

Recent AI innovations offer promising avenues for plankton identification. YOLO (You Only Look Once), a real-time object detection framework, integrates detection, classification, and post-processing into a single convolutional pass, enhancing speed and accuracy (Redmon *et al.* 2016). It generalizes well across diverse image contexts, reducing background noise and increasing adaptability.

Generative Pre-trained Transformers (GPTs), although originally language models, now include visual processing capabilities. While adept at interpreting scientific texts and simple image features, they lack the structured knowledge base and logical reasoning required for taxonomic decision-making (OpenAI *et al.* (2024).

Deep metric learning, exemplified by FaceNet, maps similar objects into proximal regions of an embedding space, distinguishing even closely related images with resilience to lighting or orientation changes (Yan *et al.* 2024). Siamese networks extend this approach, enabling interpretable comparisons between image pairs and elucidating determinant differences (Fedele *et al.* 2024).

Future improvements may arise from integrating GPT architectures with fuzzy logic systems, enabling more human-like, non-monotonic inference. Such

models could bridge the gap between linguistic processing and taxonomic logic, enhancing AI explainability and decision transparency (Novák 2011).

DISCUSSION

This review has outlined the requirements for a scientifically robust plankton identification system. While these criteria are idealized, they are essential for compatibility with existing taxonomic databases. Currently, no AI solution fully replicates the expert-driven workflow, and image feature extraction from descriptive text remains a significant limitation.

Experts agree that creating a large, well-annotated, and diverse image database is critical for both system development and validation. While multimodal LLMs, such as GPT show potential, they must be integrated with logical and model-based reasoning systems to meet scientific standards.

* * *

Acknowledgements – I extend my heartfelt gratitude to Professor Judit Padisák for the invaluable opportunity to have been her student. Her unwavering encouragement and profound influence on my research have been a source of enduring inspiration. Her methodological insights remain relevant and impactful even after two decades.

Összefoglaló: A mesterséges intelligencia és a különböző feladatok automatizálásának sikere felveti a kérdést bizonyos tudományos vizsgálatok, ez esetben a mikroszkópi alga határozás automatizálhatóságát illetően. Részeredmények már születtek ezen a területen, melyeket jelen publikáció összefoglal és értékel. Megállapítható, hogy a makrofitonok határozásában a mesterséges intelligencia alapú megoldások már jó amatőr szintre jutottak, az úgynevezett taxonómiailag komplex csoportok esetében azonban igen csekélyek az eredmények. Néhány nemzetség és néhány faj meghatározására képesek a rendszerek elfogadható biztonsággal. Fontos lépés ezen a területen a feladat specifikációja, vagyis össze kell gyűjteni egy human szakértővel egyenértékűnek tartott rendszer ismérveit. A jelenleg alkalmazott mesterséges intelligencia módszerek néhány fontos algoritmusát elemeztem ezen ismérvek alapján, külön kitértem a multimodális nagy nyelvi modellek alkalmazhatóságára. Megállapítható, hogy a manapság alkalmazott algoritmusok önmagukban nem fognak ezen a területen áttörést hozni, hanem a különböző módszerek kombinációja, amelyek a képfelismerést egy komplex tudásbázis kiépítésével egészítik ki. A végeredmény megvalósításához és teszteléséhez szükséges egy nagyméretű annotált kép gyűjtemény építése, de ez önmagában nem elegendő, hanem a taxonómiai tudás modellezésére is szükség van a sikerhez.

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(submitted: 15.07.2025; accepted: 29.09.2025)

DOI: 10.17110/StudBot.2025.56.1.141 Studia bot. hung. 56(1), pp. 141–154, 2025

PHYSIOLOGICAL AND ECOTOXICOLOGICAL EFFECTS OF GLYPHOSATE ON THE GREEN ALGAE *RAPHIDOCELIS SUBCAPITATA*

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Lengyel, E., Zsuga-Biró, R. & Hubai, K. (2025): Physiological and ecotoxicological effects of glyphosate on the green algae Raphidocelis subcapitata. – *Studia bot. hung.* **56**(1): 141–154.

Abstract: Glyphosate is the world's most widely used herbicide, yet its effects on aquatic ecosystems – especially microalgae – remain poorly understood. This study investigated the physiological responses (photosynthesis, chlorophyll-*a* and pheophytin content, nitrogen and phosphorus uptake rates, optical density, protein content, and stress enzyme activity) of *Raphidocelis subcapitata*, a standard OECD test species, to a range of glyphosate concentrations (0.45–7.2 μg L^{-1}) over 14 days. Results showed that glyphosate significantly influenced several parameters, including reductions in photosynthetic activity and nutrient uptake rates, alongside increased oxidative stress responses at higher concentrations. At low concentrations (≤ 0.9 μg L^{-1}), signs of hormesis were observed, with elevated photosynthesis and chlorophyll-*a* content. Principal component analysis revealed clear separation of treatment groups based on glyphosate levels and exposure time. The findings supported species-specific and dose-dependent effects of glyphosate on freshwater algae, and emphasised the ecological vulnerability of shallow water bodies, such as Lake Balaton, to herbicide contamination. The results highlight the necessity for a stricter monitoring system, and further research on the chronic low-level impacts of glyphosate, as well as the development of environmentally safer alternatives. Present paper was inspired by Professor Judit Padisák, who has been a committed and unwavering advocate of Lake Balaton research from the beginning of her scientific career to the present day.

Key words: glyphosate, herbicide, microalgae, physiology, toxicology

INTRODUCTION

Glyphosate (N-(phosphonomethyl)glycine) is a synthetic amino acid derivative patented by Monsanto (America) in 1971 and firstly marketed as the active ingredient of Roundup in 1974 (Tőkés 2024). Glyphosate is a non-selective total herbicide affecting nearly all green plants both monocotyledonous and dicotyle-

donous, annual and perennial weeds (Klátyik *et al.* 2023, Malik *et al.* 1989). The active ingredient glyphosate is an absorbable (systemic) agent that the plant absorbs through its green parts containing chlorophyll. Glyphosate is absorbed through leaves and stems, crossing cuticular and symplastic barriers, then moves via both phloem (mainly toward growing sinks) and to a lesser extent xylem toward roots and reproductive structures (Martinez *et al.* 2018). The symptoms of the effect appear after 1–2 weeks in the form of aging, dwarf growth, and browning of leaves and shoots. The process is irreversible, the affected plant dies (de Freitas and Silva *et al.* 2021).

By 2007, it had become one of the most widely used active ingredients in the world due to its efficiency and relative cheapness (Tőkés 2024). Approximately 72% of global pesticide usage was glyphosate and glyphosate-based herbicides; the weight of active ingredient applied globally is 800,000 tonnes/year (Klingerhöfer *et al.* 2021). According to the Hungarian Central Statistical Office, Hungarian farmers used 422 tonnes of glyphosate in 2019. This amount was applied across approximately 272,000 hectares of farmland (www1). As a result of the large-scale usage, traces of it have been widely detected in a variety of areas, such as food, rain and airborne dust, even further away from its area of use (Kisvarga *et al.* 2023). In its study, the first breakthrough result was achieved in 2009, when the toxic and endocrine-disrupting effects of glyphosate-based herbicides in human cells were demonstrated (Agro Naplo 2016). Since then, research on the negative effects of glyphosate has expanded considerably, demonstrating its toxicity to crops, soil, wildlife, livestock, and the entire ecosystem. Moreover, studies have reported serious adverse health effects even below the recommended level for agricultural use. This information led the WHO International Agency for Research on Cancer (IARC) to classify glyphosate as a probable human carcinogen in 2015 (IARC 2015), but its use is still authorised in the European Union (with the sole exception of Austria).

Most research on glyphosate focuses on higher plants and animals (Klátyik *et al.* 2023), while much less information is available on its effects on aquatic organisms and ecosystems (Klátyik *et al.* 2024*a*). Glyphosate is a water-soluble and stable compound, which makes it relatively easy to release into groundwater and surface waters. A growing number of studies have shown its presence in various water resources (Carles *et al.* 2019, Maggi *et al.* 2020, Feltracco *et al.* 2022). In most surface waters, glyphosate is found at a low level. Reported averages in rivers and lakes are often between 0.1–10 μg L^{-1} depending on season and agricultural intensity (reviewed by Klátyik *et al.* 2024*a*). Although ambient concentrations are typically lower than lethal doses, the long-term ecological consequences of chronic low-level exposure, such as species composition changes, biodiversity loss, are of concern. Small water bodies and sensitive ecosystems

where degradation is slower and biota are less tolerant are especially vulnerable. For instance, Lake Balaton is the largest shallow lake in Central Europe, whose railway network is very well developed; four railway lines provide a circular route running directly along the shoreline (with the exception of two cities, namely Tihany and Szigliget) for approximately 194 kilometres. Weed control is a part of the railway track maintenance process, which extends the entire area of Lake Balaton. Various chemical mixtures are used for this, but one of their main ingredients is glyphosate. Consequently, there is a high risk of this pesticide entering the lake (e.g. through runoff), which has already been detected in the lake with a maximum of 2.0 μg L^{-1} (Tóth *et al.* 2022). Since Lake Balaton is of particular importance from both nature conservation and an economic point of view, thus gaining a better understanding of the effects of glyphosate on ecological processes taking place in it and predicting possible future changes are extremely important for our present and future.

Overall, the effects of glyphosate on aquatic organisms are species-specific and dose-dependent, and it is therefore important to study different groups of organisms. Regarding the phytoplankton, glyphosate exerts diverse and concentration-dependent effects (reviewed by Klátyik *et al.* 2024*a*). Reported impacts range from growth inhibition, ultrastructural damage, and oxidative stress to shifts in community composition. Sensitive taxa, such as green algae and diatoms, frequently show reduced chlorophyll-*a*, carotenoids, and photosynthetic efficiency at concentrations as low as 1–10 μg L^{-1}. Other taxa, particularly some cyanobacteria and dinoflagellates, can tolerate or even utilise glyphosate as a phosphorus source under nutrient-limited conditions, in some cases, can have stimulation of growth and toxin production. This dual role means glyphosate can alter community composition rather than uniformly suppress phytoplankton. Our knowledge about glyphosate is still controversial and incomplete, which are particularly true for algae, even though their importance is very high thanks to the many ecosystem services they provide to humans (e.g. Lengyel *et al.* 2023, Naselli-Flores and Padisák 2023). Therefore, our aim is to better understand the effects of glyphosate on aquatic algae through the investigation of a green algal species. *Raphidocelis subcapitata* is well justified for standardised toxicological assessment of glyphosate, because it is a sensitive, well-established model organism representing primary producers. The OECD 201 guideline explicitly frames green algae and cyanobacteria as primary producers suitable for 72-h growth tests, and *R. subcapitata* is a common default because it grows fast, is easy to culture, and yields reproducible concentration–response curves – hence its widespread use for hazard screening and cross-study comparability.

MATERIAL AND METHODS

Algal culturing

The species *Raphidocelis subcapitata* (Korshikov) Nygaard, Komárek, J. Kristiansen et O. M. Skulberg (Fig. 1a) originated from the algal culture collection of the University of Pannonia Center of Natural Sciences (Veszprém, Hungary). The monoculture of *Raphidocelis subcapitata* was maintained in liquid medium (Fig 1b, OECD 2011). The algal culture was grown at room temperature under photosynthetic active radiation (PAR) of 50 μmol m^{-2} s^{-1} (provided by 'daylight' tubes) and a 14:10 light:dark cycle.

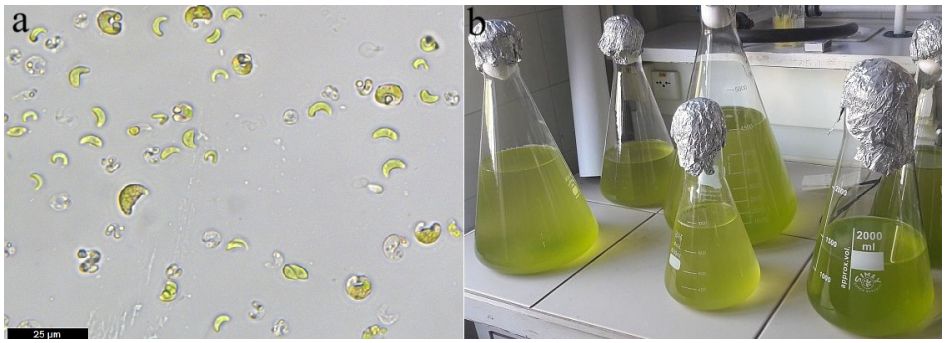

Fig. 1. Light microscopic picture (a, scale bar: 25 μm) and Batch cultures (b) of *Raphidocelis subcapitata*.

Experimental setup

All the experiments were performed under the same conditions used for culturing. Altogether five concentrations of the glyphosate were tested on the basis of its detected level in Lake Balaton (a maximum of 2.0 μg L^{-1}; Tóth *et al.* 2022): 0 (as control), 0.45, 0.9, 1.8, 3.6, 7.2 μg L^{-1}. Three parallels were used for each. The dilution series was prepared using ADAMO (360 g L^{-1}), which is a popular herbicide product available in retail stores. During the pilot study, different exposure times were applied; 130 ml of the algal culture was always taken on the zero, 1st, 3rd, 7th and 14th days for the measurements of the endpoints.

Endpoints

Altogether eight parameters were measured at each sampling event.

- The photosynthetic activity ('Ps') was determined by the oxygen yield method. Dissolved oxygen concentrations in Karlsruhe flasks were measured twice in an hour with an LDO sensor (HQ-20, Hach Lange). Net photosynthetic activity normalised to units of chl-a was calculated according to the method by Wetzel and Likens (2000).
- The optical density ('OD') was measured by a spectrophotometer (Metertech) at 750 nm.
- Immediately after the Ps and OD measurements, 20 ml of the cultures were filtered using a 1.2 μm pore size filter (Prat Dumas). The chlorophyll-*a* ('chl') and pheophytin ('pheo') content of the samples were spectrophotometrically determined after extraction with acetone (Wetzel and Likens 2000).
- For measuring peroxidase activity ('POD') and total protein content ('pro') extract was prepared. 100 ml of algae culture was filtered through a 1.2 μm pore size filter (Prat Dumas filter) and the mass was measured with analytical balance. In ice cold mortar the previously measured filters were homogenised in a phosphate buffer (50 mmol L^{-1}, pH 7) with 1 mmol L^{-1} EDTA (ethylene-diamine-tetraacetic acid) and 0.5 mmol L^{-1} PMSF (phenyl-methyl-sulfonyl fluoride). Samples were centrifuged for 20 min at 15,000× g at 4 °C and supernatants were collected. For the determination of total protein content, the Lowry method was followed with slight modifications (Peterson 1983). From extract according to Imberty *et al.* (1984) TMB (tetramethyl-benzidine) peroxidase activity was measured with a minor modification. The oxidation rate was calculated by measuring the change of absorbance at A654 nm.
- In the experimental study, nutrient uptake rates ('N rate' and 'P rate') were calculated using the SRP (Soluble Reactive Phosphorus) and NH_4^+ concentrations of the filtered samples. Concentrations of SRP and NH_4^+ were determined using spectrophotometric methods (APHA 1998).

Statistical analyses

Principal Component Analysis (PCA) was performed to examine whether the measured endpoints exhibited any patterns based on the applied glyphosate concentrations and exposure times. Two-way ANOVA tests were used to examine the effect of glyphosate concentrations, exposure time, and their interaction on the measured physiological parameters. All the statistical analyses were performed in R statistical software (4.4.3 version, R Core Team 2024) using the 'vegan' (Oksanen *et al.* 2024) package.

RESULTS

In general, the measured endpoints changed along wide ranges during the experiments (Table 1). The only exception to this was the OD, which did not show any significant changes. According to the two-way ANOVA tests (Table 1), the glyphosate concentration had significant effects on the chlorophyll-*a* and pheophytin content, the photosynthesis and the nutrient uptake rates. The exposure time had significant correlations with the measured endpoints with the exception of the optical density. Furthermore, ANOVA analysis showed statistically significant interaction between concentration and time in the case of the pheophytin content.

Table 1. Statistical parameters of the measured endpoints, and its significant relations with the glyphosate concentration, the exposure time and its interaction according to the two-way ANOVA analysis (CV = coefficient of variation, C = concentration, T = exposure time, I = interaction).

						ANOVA		
endpoints	unit	min	max	mean	CV	C	T	I
POD	nmol (min mg protein)$^{-3}$	22023.0	162299.1	51341.8	58.3		+	
protein	μg L^{-1}	20.0	49.6	32.8	23.6		+	
OD	nm	0.197	0.211	0.197	4.4			
chl-a	μg L^{-1}	0.53	1.87	1.11	30.8	+	+	
pheophytin	μg L^{-1}	0.00	0.71	0.12	159.7	+	+	+
photosythesis	mg C mg Chl-a^{-1} h^{-1})	404.3	4153.3	1441.5	75.0	+	+	
P rate		0.0	92.3	24.8	129.8	+	+	
N rate		12.6	54.5	22.5	55.7	+	+	

According to the results of the principal component analysis (PCA), the first two axes together explained 81.47% of the variance in the measured physiological parameters. The samples also showed a clear separation on the basis of the glyphosate concentration (Fig. 2a) and the exposure time (Fig. 2b). The nutrient depletion rates, chlorophyll-*a* content, and photosynthetic activity were negatively associated with glyphosate concentration and exposure time. As regards the chlorophyll-*a* content, photosynthetic activity, and nutrients uptake, increases in its amount were observed at the lower glyphosate concentrations (0.45 and 0.9 μg L^{-1}) compared to the control. In contrast, glyphosate treatment (concentration and exposure time) showed a positive correlation with POD enzyme activity and pheophytin content.

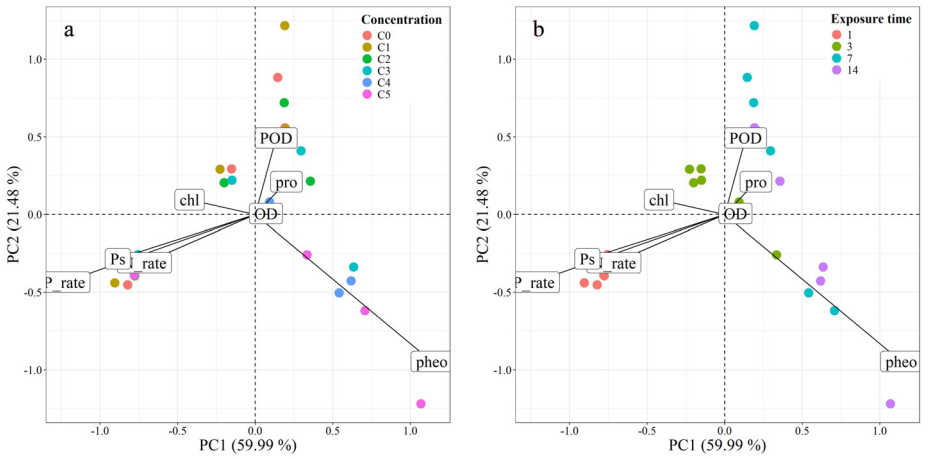

Fig. 2. The biplots of PCA (Principal Component Analysis) on the basis of the glyphosate concentrations (a) and exposure times (b) (C0 = control; C1 = 0.45 μg L^{-1}; C2 = 0.9 μg L^{-1}; C3 = 1.8 μg L^{-1}; C4 = 3.6 μg L^{-1}; C5 = 7.2 μg L^{-1}; pro = protein; Ps = photosynthesis; pheo = pheophytin; chl = chlorophyll-*a*; POD = enzyme activity; OD = optical density).

DISCUSSION

Glyphosate is the most popular herbicide used in both agriculture and households. Today, it has become the most widely used herbicide, which means that traces of it can be found in many different fields: in food, animals, rain, and different waterbodies. Although algae provide extremely important ecosystem services (e.g. Naselli-Flores and Padisák 2023), there is still limited knowledge about the effects of glyphosate on them. Furthermore, species differed in their sensitivity against this herbicide (Klátyik *et al.* 2024*b*), therefore it is in our interest to learn as much as possible about the effects of glyphosate on different algal species.

It is well known that glyphosate affects nearly all green plants (Klátyik *et al* 2023, Malik *et al.* 1989). Primary target of glyphosate is 5-enolpyruvyl-shikimate-3-phosphate synthase (EPSPS) enzyme in the Shikimate Pathway, where a key enzyme is inhibited (Duke and Powles 2008, Steinrücken and Amrhein 1980). Since the shikimate pathway is also present in microbes, glyphosate can also have significant impacts on aquatic microalgae, as it was shown in the case of the studied *Raphidocelis subcapitata*. Beside its concentration, the exposure time and their interaction were also determinant factors in many measured physiological characteristics.

Photosynthesis, chl-*a* and pheophytin content

Photosynthesis is a frequently used endpoint for testing different abiotic stresses (e.g. LÁZÁR *et al.* 2023, LENGYEL *et al.* 2015), which was also sensitive and suitable for detecting the effects of glyphosate. Similar to other microalgal species (e.g. CHOI *et al.* 2012), photosynthesis of *Raphidocelis subcapitata* was also inhibited by glyphosate (beyond 0.9 $\mu g\ L^{-1}$). This physiological process can be impacted in several direct and indirect ways: inhibition of plastoquinone biosynthesis, effect on rate of electron transport, and inhibiting the respiratory electron transport chain (reviewed by KLÁTYIK *et al.* 2024*b*). Furthermore, the reduction in chlorophyll concentration can also lead to reduced photosynthetic activity (GOMES *et al.* 2016). This was supported by the present study, since glyphosate reduced the chlorophyll-*a* content in parallel with the accumulation of pheophytin. However, stimulated photosynthesis was observed at lower glyphosate concentrations ($<0.9\ \mu g\ L^{-1}$) similar to other studies (e.g. KLÁTYIk *et al.* 2024*b*). This is a well-known biological phenomenon – called hormesis –, when a harmful parameter shows a stimulating effect at its low concentrations (MATTSON 2008). The observed hormesis phenomenon is quite reliable, since in Lake Balaton and its catchment the glyphosate concentration is under 1 $\mu g\ L^{-1}$, but sometimes it could peak around 2 $\mu g\ L^{-1}$ (TÓTH *et al.* 2022). Hormesis is not yet fully understood, but compensation can be a possible explanation; resources can be mobilised in order to achieve a favourable state (CALABRESE *et al.* 2007). However, even low concentrations caused inhibition in the long term.

Nutrient uptake

Phosphorus and nitrogen are essential macronutrients required by algae (ANDERSEN 2005). In the present study, the negative effects of glyphosate were observed on both nutrient uptakes. Rates of phosphorus and ammonium uptake were inhibited at intermediate concentration, which was in accordance with the decline of photosynthetic activity similarly to other studies (e.g. BROWN and LEAN 1995, KRIEGER *et al.* 1998). The reason for this linkage can be that the phosphorus and nitrogen uptake are energetically expensive which is supported by photosynthesis as an energy-producing process (BROWN and LEAN 1995). In the research of FENG *et al.* (2019) after glyphosate exposure oxidative stress in *Scenedesmus vacuolatus* (Shihira et Krauss) E. Kessler, M. Schäfer, C. Hümmer, A. Kloboucek et V. Huss (current accepted name: *Coelastrella vacuolata* (I. Shihira et R. W. Krauss) Hegewald et N. Hanagata) was demonstrated, which can disrupt cellular metabolism and potentially impair nutrient absorption. Similar effects of low glyphosate concentrations were presented in *Chlorella vulgar*is Beijerinck (WANG *et al.* 2022).

Pedoxidase activity, protein

Elevated ROS levels activate various antioxidant defences that help protect all molecules sensitive to oxidative radicals especially the ones with unsaturated bonds, e.g. proteins and lipids, from damage. Among these defences are increased activities of key antioxidant enzymes, including superoxide dismutase, catalase, and peroxidase (Chaufan *et al.* 2006). POD is the second defence against ROS because it can eliminate the superoxide radicals which were previously converted to hydrogen peroxide (Cho and Seo 2005).

In our study at low glyphosate concentrations (<1.8 μg L^{-1}) POD activity of *Raphidocelis subcapitata* increased until the 7th day, but at higher concentrations (3.6 μg L^{-1}<) lower activity was detected after 72 h. In the study of Tripathi *et al.* (2006) under exposure to low concentrations of toxicants (e.g. heavy metals) led to elevated *Scenedesmus* sp. ascorbate peroxidase (APX) activity after 7 days. Similarly, *Acutodesmus obliquus* (Turpin) Hegewald et Hanagata (current accepted name: *Tetradesmus obliquus* (Turpin) M. J. Wynne) exposed to 0.01–0.1 μM $Pb(NO_3)_2$ exhibited a progressive increase in POD activity over a 7-day period, with peak enzyme levels observed around day 5 and remaining elevated through day 7 (Piotrowska-Niczyporuk *et al.* 2015). Our findings are similar to Romero *et al.* (2011)'s results, such as in the case of *Chlorella kessleri* Fott et Nováková (current accepted name: *Parachlorella kessleri* (Fott et Nováková) Krienitz, E. H. Hegewald, Hepperle, V. Huss, T. Rohr et M. Wolf) also increased enzyme activities were determined over a 96 h exposure window. In the study of Wu e*t al.* (2016) during the exposure of higher glyphosate concentrations (1, 2, 5, and 10 mg L^{-1}) the peroxidase (POD) activity of *M. aeruginosa* significantly increased for 48 hours. In an experiment with *Navicula sp.* significantly increased POD activity was measured during the initial phase of exposure, potentially due to the presence of oxidative stress induced by exposure to herbicides (Zheng *et al.* 2024). Overall, these findings suggest that at sublethal concentrations, algae activate and maintain their antioxidant defence systems – particularly peroxidase-related enzymes – throughout the first week of exposure. This enzymatic upregulation appears to be a key adaptive mechanism that allows microalgae to mitigate oxidative damage induced by prolonged but mild toxicant stress. Zheng *et al.* (2022) showed stress-induced upregulation of antioxidant systems (a selenoprotein, HpMsrA) that improved tolerance to glyphosate. That supports the interpretation that upregulated antioxidant enzymes (including POD) can be protective – but protection has limits: beyond a threshold, damage accumulates.

CONCLUSIONS

Glyphosate has undoubtedly played a key role in the development of modern agriculture, particularly in increasing the efficiency of weed control and promoting soil-conserving farming practices. At the same time, the health and environmental issues associated with it require serious attention. Regarding the aquatic ecosystems, by entering surface water, glyphosate may raise concerns about even drinking water quality. As regards the ecological significance of the observed hormesis, it could improve survival and fitness of populations and help maintain biodiversity in moderately impacted ecosystems. Furthermore, it could affect ecosystem functions and promote functional redundancy, where multiple species can fulfil the same role, enhancing ecosystem stability. Nevertheless, glyphosate could have a negative effect even at very low concentrations, its repeated exposure and chronic presence may result in cumulative ecotoxicological effects. Therefore, it is the responsibility of the scientific community to clarify the real risks of glyphosate through further independent research focusing on long-term effects, different species and regularly monitor the surface waters. Furthermore, developing more sustainable alternatives for agriculture usage and more suitable management plans are highly recommended.

* * *

Acknowledgements – Professor Judit Padisák devoted her scientific career to researching Lake Balaton. From the beginning of her career, she published numerous scientific papers on the flora and fauna of Lake Balaton, with a particular focus on its phytoplankton. Up to the present time, she has continued to give numerous science vulgarizing presentations on this topic in order to bring our shared treasure, Lake Balaton, closer to everyone. Therefore, protecting the waters and wildlife of Lake Balaton is a matter close to our hearts, as Judit Padisák has taught us what a drop of Lake Balaton holds and that protecting all living things is the key to our future. Thus, the main supporter and inspirer of this article is Judit Padisák, who has enthusiastically educated the researchers of the future and the present by sharing her scientific knowledge and life experience. The study and the researchers were supported by the National Research, Development and Innovation Office through the National Laboratory for Water Science and Water Safety program (RRF-2.3.1-21-2022-00008). We are greatly thankful to Charles River Laboratories Hungary Kft. (Veszprém, Hungary) for the algal culture used in the present study.

Összefoglaló: A glifozát a világon a legszélesebb körben használt gyomirtó szer, azonban hatása a vízi ökoszisztémákra – különösen a mikroalgákra – még mindig kevéssé ismert. Jelen tanulmányban a *Raphidocelis subcapitata*, egy standard OECD tesztfaj fiziológiai reakcióit (fotoszintézis, klorofill-a és feofitin tartalom, nitrogén- és foszforfelvétel, optikai denzitás, fehérjetartalom, stresszenzimaktivitás) vizsgáltuk különböző glifozát koncentrációk (0,45–7,2 μg L^{-1}) esetén 14 napon keresztül. Az eredmények azt mutatták, hogy a glifozát jelentősen befolyásolt több paramétert is; többek között csökkentette a fotoszintetikus aktivitást és a tápanyagfelvételt, valamint magasabb koncentrációk esetén fokozta az oxidatív stresszreakciókat. Alacsony koncentrációk esetén (≤ 0,9 μg L^{-1}) a hormézis jelei voltak megfigyelhetők a fotoszintézis és a klorofill-a-tartalom tekin-

tetében. A statisztikai elemzések egyértelműen kimutatták a glifozát koncentrációjának és az expozíciós idő hatásait is. Az eredmények alátámasztották a glifozát fajspecifikus és dózisfüggő hatását az édesvízi algákra vonatkozóan, valamint hangsúlyozták a sekély víztestek, például a Balaton ökológiai sebezhetőségét a gyomirtó szerekkel való szennyeződés tekintetében. Az eredmények rávilágítanak egy szigorúbb monitoringrendszer szükségességére, a glifozát hosszú távú hatását célzó vizsgálatok szükségességére, továbbá környezetbarát alternatívák kifejlesztésére. A jelen tanulmányt Padisák Judit professzor inspirálta, aki tudományos pályafutása kezdetétől napjainkig elkötelezett és rendíthetetlen támogatója a Balaton-kutatásoknak.

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(submitted: 01.08.2025; accepted: 17.09.2025)

DOI: 10.17110/StudBot.2025.56.1.155 *Studia bot. hung. 56(1), pp. 155–168, 2025*

LEVELS OF BIODIVERSITY INSURANCE: SPECIES DISPERSAL, ESTABLISHMENT, FILTERING AND ASSEMBLY IN A CHANGING WORLD – GLIMPSES OF AN ECOLOGIST ENGAGED TO LIMNOLOGY

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Török, P. & Tóthmérész, B. (2025): Levels of biodiversity insurance: species dispersal, establishment, filtering and assembly in a changing world – glimpses of an ecologist engaged to limnology. – *Studia bot. hung.* **56**(1): 155–168.

Abstract: To address the response of ecosystems to global change it is a pivotal task to study the dynamics of communities that structure natural and semi-natural ecosystems. We highlighted new aspects of spatial insurance theory (ecosystem functionality and stability are enhanced by high biodiversity) by introducing three levels of biodiversity insurance: i) landscape-level insurance, ii) habitat-level insurance, and iii) temporal insurance. Based on the above introduced three-level-scheme of biodiversity insurance we identified and summarised several research directions and questions which could be considered in future research. For the better understanding of landscape-level insurance of biodiversity, it is important to quantify the habitat-specific species pools of several terrestrial and aquatic ecosystems, both at the local and landscape-scale. Considering the biodiversity insurance at the habitat level, it is vital to analyse the effect of abiotic and biotic filtering on species and functional diversity both in terrestrial and aquatic communities, and also to analyse how the effects of habitat level filtering processes are influenced by different levels of stress and disturbance. Finally, considering the temporal insurance of biodiversity it is important to determine how species traits interact with temporal biodiversity filters and use that knowledge to predict how species assemblages respond to a range of filter combinations.

Key words: community dynamics, ecological memory, functional trait, intermediate disturbance hypothesis, phytoplankton, spatial insurance

INTRODUCTION

One of the challenges for biodiversity research in the next decades will be to understand the complexity of ecosystem change and resilience at different spatial and temporal scales (IPBES; Díaz *et al.* 2019). To address the response of ecosystems to global change, investigating the dynamics of communities that structure

natural and semi-natural ecosystems appears as a pivotal task. However, we are still far from understanding the balance of processes that regulate species filtering and assembly dynamics at local and landscape scales. Focused research that would solve the difficult practical problems frequently occurring in ecological restoration would not only increase our understanding of community assembly and functioning but also would improve the practical implementation of restoration (Török *et al.* 2020).

In the sustainable development goals of the United Nations combatting ecosystems degradation and promoting sustainable management are listed among the highest priorities (United Nations 2019). The United Nations also dedicated the period of 2021–2030 the "Decade of Ecosystem Restoration" fostering that ecological restoration is considered as the most vital and necessary tool to counteract the degradation and to stop and/or mitigate the loss of natural habitats and the decline of biodiversity worldwide (Menz *et al.* 2013, Suding *et al.* 2015). Focused research, which fulfils the needs of both restoration theory and practice is very timely. Research that provides a strong theoretical basis to solve difficult practical problems frequently occurring in ecological restoration would not only improve the practical implementation of restoration but would increase our understanding of community assembly and functioning (Engst *et al.* 2016, Young *et al.* 2005).

Beyond the analyses of species diversity and composition, trait-based functional approaches have become increasingly involved in analysing and explaining the effects of ecosystem processes on functioning. Trait-based functional approaches can help revealing the underlying mechanisms and sustaining diversity and related ecosystem functions (Carmona *et al.* 2012, Tapolczai *et al.* 2016, Viléger *et al.* 2008). The functional approach enables (i) the comparison of ecosystems with quite different species compositions; (ii) making generalizations about dynamic changes in ecosystems caused by altered management, natural disturbance regimes or climate change; (iii) the comparison of assemblages with a high number of taxa; (iv) in the case of taxonomically problematic groups, easier classification than the taxonomic approach, and (v) it also increases the robustness of multivariate statistical analyses by decreasing the number of species axes (Grime and Pierce 2012, Salmaso *et al.* 2015). The use of the trait-based functional approach also enables to compare different ecosystem types, which comparisons might reveal dynamic and functional community attributes which otherwise remain hidden or masked by community-specific processes (Török *et al.* 2016).

With the current paper we are honouring the pioneering work of professor Judit Padisák. One of the key moments of Padisák's work is the recognition and demonstration that the rules of terrestrial community ecology also apply to phytoplankton communities (Padisák 1985). Indeed, phytoplankton assemblages, because of their rapid temporal dynamics, can provide a wealth of new information and theories regarding the rules of organization in terrestrial communities.

Moreover, we can also apply and test the classical theories born in terrestrial ecology in the case of phytoplankton assemblages (Padisák 1996). In the current paper we highlight new aspects of biodiversity insurance theory pointing out which scientific contributions Padisák made to the development of the outlined theories in forms of glimpses of a bright-minded ecologist engaged on limnology. Her creative view of ecological processes, ecological models and theories was manifested at the symposium on succession research organised in Vácrátót in 1983 and was presented in her pivotal contribution (published in Padisák 1985). Later on, the lectures of this conference were published in a book edited by Gábor Fekete (Fekete 1985).

Spatial insurance theory

Spatial dispersal, environmental filtering, biotic interactions, and spatio-temporal stochastic fluctuations caused mostly by disturbance and/or stress determine how species are assembled into local communities from regional species pools (Funk *et al.* 2021, Pärtel *et al.* 2025, Vellend *et al.* 2010). The spatial insurance theory predicts that in a heterogeneous landscape with a diverse regional species pool, local species loss is mitigated; thus, ecosystem functioning is sustained through frequent re-colonisers that replace lost species and maintain high species and functional diversity by metapopulation dynamics (Loreau *et al.* 2003, Shanafelt *et al.* 2015). Incorporating the filtering concept of species assembly (Funk *et al.* 2008, Török *et al.* 2018*a*) we identified three segments of biodiversity insurance operating at different spatial- and/or temporal scales (Fig. 1): (i) landscape-scale insurance, (ii) habitat-level insurance, and (iii) temporal insurance.

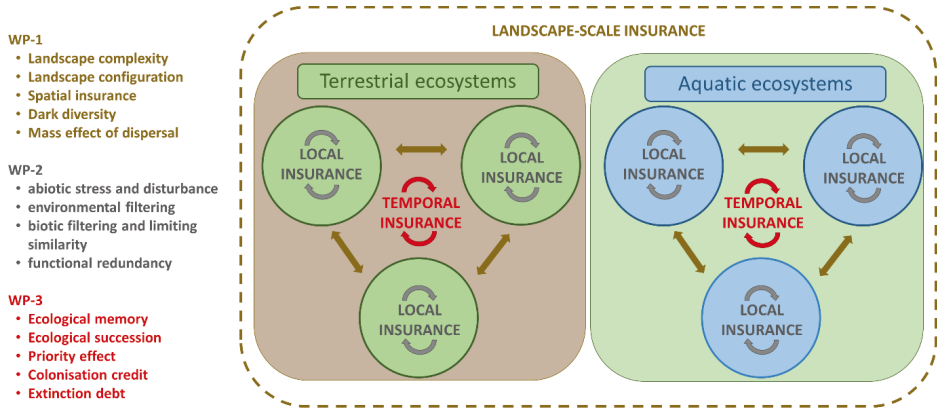

Fig. 1. Relationship between landscape-scale, local, and temporal insurance of biodiversity. Dashed line represents the embedding landscape; the circles are the patches connected to each other mostly by dispersal processes. There are pivotal similarities in the biodiversity supporting processes in terrestrial and aquatic ecosystems instead of critical differences.

Landscape-level insurance

Habitat-scale processes are strongly influenced by the complexity, either composition or configuration of the surrounding landscape in the close or wide proximity of the subjected site. Landscape composition is characterised by the diversity of landscape elements, including natural and semi-natural ecosystems, while landscape configuration focuses on the spatial arrangement of these elements (Tapolczai *et al.* 2021, Tscharntke *et al.* 2012). Focusing on a particular ecosystem, the proximity, connectivity, and abundance and patchiness of landscape elements are especially crucial.

The process of habitat fragmentation involves the subdivision of a continuous habitat patch into several small fragments, the change of spatial configuration habitats, and also an increasing edge effect (Fahrig *et al.* 2011). The increased rate of fragmentation in general decreases the chance of dispersal between identical habitat patches and one of the most important drivers of decreasing diversity (Fahrig *et al.* 2011, Tscharntke *et al.* 2012). Thus, the area of the studied habitat patch, and the quality, quantity, and spatial patterns of its surroundings are crucial to forecast the speed and direction of community change. The species inventory of a given habitat contains species characteristic to the habitat type (habitat specific species pools), but also species characteristic to other habitat types and/or problem species (derived diversity, Török and Helm 2017). The theory of mass effect of dispersal predicts that the composition and diversity of a habitat patch are strongly driven by the immigration of those species whose dispersal units are provided in great abundance in the landscape (Kiemel *et al.* 2023, Leibold *et al.* 2004). Many studies found that higher landscape complexity supports larger habitat-specific species pool, while simple landscapes with high levels of fragmentation and high proportions of man-made habitats may promote the abundance of only a limited number of rather generalist species (Marja *et al.* 2022, Tscharntke *et al.* 2012). However, the effect of landscape complexity is rarely studied in aquatic ecosystems (but see Barbosa *et al.* 1999) or involving multiple ecosystem types (either terrestrial or aquatic) and/or taxa.

Habitat-level insurance

Species establishment is generally driven by environmental filtering caused mostly by abiotic stress. This type of filtering favours species with similar functional characteristics causing trait convergence, especially in highly stressed habitats (Lhotsky *et al.* 2016). Functional redundancy, i.e., the coexistence of species with similar environmental requirements fulfilling the same ecological function in the community is an essential, but rarely validated phenomenon both in terrestrial and aquatic ecosystems (but see Tölgyesi *et al.* 2019 or Várbíró *et al.* 2017).

Increased levels of functional redundancy provide stability to the ecosystems, because species losses do not result necessarily in the loss of functions (Lukács *et al.* 2021, Török *et al.* 2024). Functional redundancy can be considered therefore as local insurance of biodiversity and community functioning. However, species that successfully pass through the environmental filter have quite similar trait combinations, and due to this similarity, they become exposed to strong biotic interactions including competition, which results in biotic filtering. In highly competitive environments, only those species can coexist which differ remarkably in some of their characteristics. Limiting similarity (two coexisting species can have only a limited overlap in their niches) thus promotes trait divergence in these communities and results in functional overdispersion (Várbíró *et al.* 2020). The strength of the environmental or the biotic filtering strongly depends on the abiotic characteristics of the habitats. This assumption is reflected by the stress dominance hypothesis, which states that species and trait-composition is shaped by environmental filtering in harsh environmental conditions (Padisák and Naselli-Flores 2021), while biotic interactions like competition play a pivotal role in the formation of assemblages in resource-rich environments (Csecserits *et al.* 2021). The effect of environmental and biotic filters and thus the trait convergence or divergence in various ecosystems are strongly masked by the disturbance regimes and other biotic interactions; for example, by the suppression of community dominants by grazing (Tóth *et al.* 2016). For the long-term sustainability of biodiversity, it is crucial to understand the small-scale stress-disturbance dynamics related to regeneration niches (Catorci *et al.* 2015). Fine-scale heterogeneity and structurally complex microhabitats may provide more regeneration niches spatially or temporally and allow species to utilize diverse methods to exploit environmental resources at the local scale (Peng *et al.* 2020).

The intermediate disturbance hypothesis (IDH) of Connell (1978) states that species diversity is the highest (maximized) when disturbance is intermediate. IDH is one of the most frequently addressed non-equilibrium models in the ecological literature for explaining the supporting mechanisms of species diversity. In the absence of disturbance competitive exclusion reduces species diversity. In case of intense disturbance only a few species could survive or establish after a disturbance event. When disturbances are intermediate there will be repeated opportunities for the re-establishment of pioneer populations which would otherwise be outcompeted, and the populations of the successful competitors could withstand the disturbance without completely taking over the community. The reason of the success is probably the generality of the IDH; on the other hand, this generality is the reason of several weakness of IDH (Reynolds *et al.* 1993).

Wilkinson (1999) summarized the history of the disturbance and diversity relationship. In terrestrial ecology the idea of disturbance relating to species

richness partly originated in the famous paper of Watt (1947). This relationship was demonstrated by a humped back model. This famous graph probably appeared first in Grime's paper (Grime 1973). Connell's paper demonstrated in a field study the usefulness of IDH explaining the influence of interspecific competition and other factors (Connell 1978).

Padisák published an excellent comparison between terrestrial and planktonic communities as a reflection on J. B. Wilson's publication (Padisák 1994). Wilson as an eminent plant ecologist focused on the development of terrestrial plant communities of New Zealand (Wilson 1990). Padisák (1994) briefly reviewed Hutchinson's plankton paradox and some of the later phytoplankton literature. She summarised the relevance of the IDH in phytoplankton dynamics, assessing its strengths and weaknesses. Finally, she pointed out that the appropriate spatial and temporal scaling of the biodiversity supporting mechanisms are the key issues in understanding community organization.

There is an asymmetry in the history of studying aquatic and terrestrial communities. It was an especially important innovation of Padisák to recognize that it is fruitful to comparatively evaluate of the ecological theories of terrestrial and aquatic ecosystems. Padisák and her co-authors emphasized in an influential paper that the IDH is too useful as a concept to reject and provides a powerful link between diversity and disturbance (Reynolds *et al.* 1993). The more robust investigations that are necessary to consolidate the tenancy of IDH need to concentrate on the separation and quantification of the stimulus- and response-components of disturbance (Reynolds *et al.* 1993).

The species richness of phytoplankton is discussed by Padisák (1993) in the context of Connell's (1978) Intermediate Disturbance Hypothesis (IDH) based on a high number of vertical phytoplankton samples obtained from four shallow central European lakes. She provided an explicit estimation of the scale of disturbance. This was especially crucial contribution providing firm data about disturbance (mixing, exceptional meteorological conditions) frequencies of phytoplankton. She demonstrated that less than 3 days can be regarded as high disturbance frequency. Approximately 3-8 days as intermediate disturbance frequency. Larger than 8–9 days means low frequency of disturbance for phytoplankton. Based on real phytoplankton dataset she concluded that her findings support the hypothesis that maximal diversity appears at intermediate disturbance frequencies.

She also demonstrated that the relative importance of intermediate frequency disturbances has its own seasonality: it is increasingly important in periods, in which competition among phytoplankton species is increasing (Padisák 1993). This observation provided an opportunity to incorporate the stochasticity-based IDH into more deterministic explanations like PEG-model of Sommer *et al.* (1986) of plankton succession. Padisák (1993) emphasised in this paper that the

main difficulty with IDH is that disturbance not only maintains species richness in an ecosystem, but it also supposes its presence. Thus, lack of early or late successional species can inactivate the mechanism of diversity maintenance.

In hydrobiology, Hutchinson's plankton paradox and the IDH are closely related, because these are explaining the mechanisms supporting biodiversity. There are species rich phytoplankton communities in a well-mixed environment, although the species compete for a small number of common limiting resources (Hutchinson 1961). In terrestrial plant ecology this paradox is less evident. In a field study Padisák and her co-authors demonstrated that species richness of non-equilibrated lakes was almost three times as high as those in equilibrium (Padisák *et al.* 2003). Surprisingly they found that environmental stress (mixing, low light, cold temperatures, high salt content, low level of nutrient) forces phytoplankton communities towards equilibrium, but no relationship between occurrence of equilibria and trophic state was found (Padisák *et al.* 2003).

Temporal insurance of biodiversity: succession and ecological memory

The relative importance of different filters and filtering processes in species assembly can vary spatially; however, there is limited understanding of mechanisms mediating the balance of deterministic and stochastic processes temporally (but see Török *et al.* 2018*b*). Analysis of patterns in ecological succession, i.e., the spatio-temporal reassembly of natural communities after natural or anthropogenic disturbances, has a long tradition in ecological research (Prach and Walker 2019). The study of temporal patterns and processes of community change has also proven fruitful for the research of dispersal mechanisms (Sullivan *et al.* 2018), the organisation of various levels of the species pools (Funk 2021), or in explaining stochastic and priority effects in species establishment (Padisák *et al.* 2016, Török *et al.* 2018*b*). Ecological processes, including ecological succession are strongly influenced by historical events. Past ecological states and experiences reflected in the form of ecological memory; thus, ecological memory can influence the present or future responses of the community, consequently shaping the dynamic patterns of community integrity and contributing to the trajectory and formation of alternative stable states of an ecosystem (Dupouey *et al.* 2002, Egan and Howell 2005).

At the beginning of her carrier Padisák studied the phytoplankton of Lake Balaton on 211 consecutive days between April and November 1980. She found 417 taxa in total during the study period. The number of planktonic species was around 300; majority of the species were extremely rare (Padisák 1992). She found that two-thirds of the 300 planktonic species were evenly distributed in time, while the others exhibited temporal peaks. It was especially remarkable that she found that half of the 200 rare species was velocity specialists, able to

grow rapidly in spatially and temporally randomly distributed, nutrient-rich microenvironment. She invented a term 'ecological memory' naming the other 100 species of the phytoplankton community, because of the capacity of past states or experiences to influence present or future responses of the community (Padisák 1992). This is an important contribution to the understanding of community functioning. The ecological memory is based on the spatial heterogeneity and/or spatial dynamics of the community. The memory of the community comprises all the species which are not completely excluded, i.e. retained in the community because of spatial and temporal heterogeneity.

Ecological memory was defined first as "the capacity of past states or experiences to influence present or future responses of the community" by studying phytoplankton assemblages (Padisák 1992). Ecological memory can be also understood as a form of biological legacy, i.e., species resembling past stages of ecosystem composition and development (Sun *et al.* 2013). In terrestrial plant communities seed banks or bud banks are located in the soil, in case of aquatic macrophytes turion banks are in the mud, or cysts or other kind of resting stage formations in many phytoplankton groups can be considered as forms of environmental legacy (e.g., nutrient loads from former disturbances) (Sun *et al.* 2013). The importance of ecological memory in temporal community change is demonstrated by former research both in terrestrial and aquatic communities (Ogle *et al.* 2015, Sun *et al.* 2013). But assessing the magnitude in which ecological memory can influence future changes in species composition and functional trait composition of ecosystems has been lacking. Analysing the relationship between successional processes and ecological memory, and the assessment of the size and diversity of ecological memory may help to explore the priority effect in species dispersal (von Gillhaussen *et al.* 2014), colonisation credit, and extinction debt theories (Bagaria *et al.* 2015, Kuussaari *et al.* 2009). It also helps to quantify the magnitude of dark- and hidden diversity in various types of ecosystems including both terrestrial and aquatic habitats (Pärtel *et al.* 2011, Stoof-Leichsenring *et al.* 2012).

Succession research was a favourite topic of botanical research during the last 150 years (Fekete 1985). Numerous theories and/or models have been developed to interpret and modelling succession processes. The concept of ecological succession is deeply rooted in the study of terrestrial plant communities (Clements 1916, Drury and Nisbet 1973, Gleason 1926). This knowledge naturally resulted in the exploration of the rules of community organization from ecological perspective, and finally in the development of ecological models and/or theories explaining community organization (Connell and Slatyer 1977). One of the most important characteristics of communities is their species richness. Thus, understanding the rules of community organization, and the mechanisms that maintain biodiversity have become a key issue to the development

and accumulation of scientific knowledge. This picture is primarily based on the history of terrestrial vegetation research (Poorter *et al.* 1973).

Ongoing climate change adds another temporal angle of complexity to sustain or restore biodiversity. Novel species pools would include species that are expected to be part of ecosystems under changed conditions (Kasari *et al.* 2016). They can be both natives but also non-natives that are expected to increase/shift their ecological range with changing climate. It may be potentially contentious to start introducing new 'suitable' species during restoration but gaining knowledge of the species and trait composition of novel species pools would allow us to foresee which species are less likely and which species are more likely to persist and contribute to a restored community in the future.

Future perspectives

Based on the above introduced scheme of biodiversity insurance we identified and summarised several research directions and questions which could be considered in future research. For the better understanding of landscape-level insurance of biodiversity it is important to quantify the habitat-specific species pools of several terrestrial and aquatic ecosystems, both at the local and landscape-scale. In particular, it is crucial to focus on answering the questions: (i) How is the local species composition influenced by the patterns, abundance, proximity, and connectivity of habitat patches? (ii) How is the local species diversity of habitats affected by landscape composition and configuration? (iii) How are species groups with different ecological strategies and trait-compositions affected by the different levels of fragmentation and different types of landscape composition? Considering the biodiversity insurance at the habitat level, it is vital to analyse the effect of abiotic and biotic filtering on species and functional diversity both in terrestrial and aquatic communities, and also to analyse how the effects of habitat level filtering processes are influenced by different levels of stress and disturbance. In particular, we can set the questions: (iv) How is the species and functional diversity related to each other in habitats characterised by various levels of stress and/or disturbance? (v) How does environmental filtering affect functional redundancy in ecosystems along a stress and disturbance gradient? (vi) In what magnitude does environmental heterogeneity contribute to the sustainment of high functional and species diversity in various ecosystems? Finally, considering the temporal insurance of biodiversity it is important to determine how species traits interact with temporal biodiversity filters and use that knowledge to predict how species assemblages will respond to a range of filter combinations. Linking the ecological memory concept with ecological succession we identified the following research questions for the future: (vii) What traits or trait combinations

favour species being incorporated into ecological memory? (viii) How diverse is the species pool accumulated in form of ecological memory in early, middle, and late stages of ecological succession? (ix) In what magnitude ecological memory contributes to the successional changes of various ecosystems?

A complex trait-based functional approach which explains biodiversity insurance has not been developed so far. It is also a novel aspect to link the functional approach with the understanding of dynamics in community composition which focuses on community functioning based both on compositional changes and ecological traits. This helps to focus practical demand-driven research on community functioning and to redefine several theories explaining colonisation, establishment and assembly with complex multi-scale analyses in terrestrial and aquatic ecosystems.

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Acknowledgements – With the current paper the authors honour the scientific work of Prof. Judit Padisák, highlighting which scientific contributions J. Padisák contributed to the development of the outlined aspects of the spatial insurance theory. The authors thank the support of the National Research, Development and Innovation Office of Hungary (grant numbers: K 137573 and KKP 144068).

Összefoglaló: Az ökoszisztémák globális változásokra adott válaszainak megértéséhez alapvető fontosságú a közösségszerveződés dinamikai folyamatainak vizsgálata. A tájléptékű biztosítás elmélete szerint az ökoszisztémák működése és stabilitása, illetve a tájléptékű biodiverzitás között szoros kapcsolat áll fenn. A közleményünkben a tájléptékű biztosítás elméletét kibontva, a biodiverzitás biztosításának három alkotóelemét ismertetjük: a (i) tájléptékű biodiverzitás-biztosítást, az (ii) élőhelyi szintű biztosítást, és az (iii) időbeli biztosítást. A biodiverzitás tájléptékű biztosításának jobb megismeréséhez ismernünk kell a szárazföldi és vízi ökoszisztémák élőhely-specifikus fajkészletét lokális és tájléptékben is. Az élőhelyi szintű biodiverzitás-biztosítás megértéséhez alapvető az abiotikus és biotikus szűrők a funkcionális diverzitásra gyakorolt hatásának elemzése, és annak értelmezése is, hogy az élőhelyi szintű szűrők működését hogyan befolyásolja a stressz és a zavarás mértéke, valamint ezek kölcsönhatása. A biodiverzitás időbeli biztosítását illetően fontos megvizsgálni, hogy a fajok egyes jellemzői milyen kölcsönhatásban vannak a biodiverzitás időbeli szűrőmechanizmusaival (például a magbankképzés). Mindezek ismerete segíthet abban, hogy előre jelezzük, hogy a közösségek hogyan reagálnak a szűrőfolyamatok minőségében és mennyiségében bekövetkező változásokra.

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(submitted: 03.08.2025; accepted: 12.09.2025)

DOI: 10.17110/StudBot.2025.56.1.169 Studia bot. hung. 56(1), pp. 169–190, 2025

FUTURE CLIMATIC SUITABILITY OF KEY AGRICULTURAL AND FOREST LAND COVER TYPES IN THE MIDDLE DANUBE BASIN UNDER SSP5-8.5

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Trájer, A. J. (2025): Future climatic suitability of key agricultural and forest land cover types in the Middle Danube Basin under SSP5-8.5. – *Studia bot. hung.* **56**(1): 169–190.

Abstract: Climate change is projected to cause substantial shifts in the distribution and climatic suitability of both natural and cultivated vegetation types across Central Europe, with the Middle Danube Basin being particularly sensitive. This study applies climate envelope modelling to assess future suitability for non-irrigated arable lands, broadleaf forests, olive groves, and Mediterranean sclerophyllous vegetation under the high-emission SSP5-8.5 scenario, using CMCC-ESM2 climate data for the period 2021–2100. Six bioclimatic variables (bio1, bio10, bio11, bio12, bio18, bio19) were used to define suitability thresholds based on Boolean logic and 5–95% percentile cuts from current conditions. The results reveal a marked decline in the climatic suitability of non-irrigated arable lands, mainly due to intensifying drought and increasing temperature variability. Broadleaf forests are expected to retreat northward, with most lowland and upland areas becoming unsuitable by the end of the century, except for some riparian gallery forests. Olive groves will likely remain climatically unstable due to persistent continental winters. However, sclerophyllous vegetation may establish in localized areas by late century as Mediterranean-like conditions emerge. These findings highlight the need for forward-looking land use and conservation strategies to support ecological resilience in this climate-sensitive region.

Key words: agriculture, bioclimatic modelling, climate change, Middle Danube, SSP5-8.5, vegetation shift

INTRODUCTION

Climate change is one of the most pressing environmental challenges of the 21st century, with sweeping implications for terrestrial ecosystems, land use patterns, and socio-economic sustainability (Foley *et al.* 2011, IPCC 2022, Legg 2021). As the global climate system warms, changes in temperature regimes, precipitation seasonality, and the frequency of extreme events are expected to reshape the ecological viability and distribution of both natural vegetation zones and cultivated landscapes (Foley *et al.* 2011; IPBES, Weltbiodiversitätsrat, 2019, Kocsis *et al.* 2024). One of the most important outcomes of these changes is the decline of forested ecosystems particularly in current subhumid regions (Allen

et al. 2010, Seidl *et al.* 2017). Particularly in Southern and Central Europe, these climatic changes may result in significant biome shifts (Giorgi and Lionello 2008, Schröter *et al.* 2005), threatening agricultural productivity, forest stability, and the ecological coherence of semi-natural landscapes (Martinez del Castillo *et al.* 2022).

In the agricultural sector, non-irrigated arable lands are especially exposed to climate variability due to their dependence on rainfall and their typically shallow root systems (Brown *et al.* 2013, Lobell *et al.* 2011, Trnka *et al.* 2014). Declining summer rainfall and increasing evapotranspiration can lead to reduced soil moisture availability, crop failure, and long-term degradation of land quality (Kis *et al.* 2023, Trnka *et al.* 2014,). Conversely, certain perennial systems, such as olive groves and Mediterranean sclerophyllous vegetation, show higher tolerance to heat and drought stress (Lo Gullo and Salleo 1988, Rico *et al.* 2024, Vicente-Serrano *et al.* 2025). However, these systems have their own bioclimatic limits and may face northward migration or regional contraction under high-emission scenarios (Kahiluoto *et al.* 2019). At the same time, climate change could undermine the persistence of olive trees in their historical Mediterranean homeland (Fraga *et al.* 2020).

Broadleaf deciduous forests, characteristic of temperate and sub-Mediterranean zones, are also at risk of climatic unsuitability. Forest types dominated by *Quercus robur*, *Fagus sylvatica*, or *Carpinus betulus* require specific temperature and humidity ranges, and are highly sensitive to drought-induced mortality, pest outbreaks, and phenological mismatches (Berényi *et al.* 2023, Hanewinkel *et al.* 2013, Zimmermann *et al.* 2009). As warming continues, these forests are expected to retreat to higher elevations or northern latitudes, while their southern edges may be replaced by more drought-adapted formations, such as sclerophyllous scrub or sparse oak-pine mosaics (Schröter *et al.* 2005).

Europe's vegetation and land-use systems are already undergoing climatic and biogeographical transitions, driven by a combination of direct climate effects and indirect socio-economic responses (Seifollahi-Aghmiuni *et al.* 2015). In Central and Southeastern Europe, this process is often framed through the Köppen-Geiger climate classification, where scenarios such as CMCC-ESM2 under SSP5-8.5 suggest a shift from humid continental (Dfb) climates toward humid subtropical (Cfa) or even semi-arid (Bsk) conditions by the end of the 21st century (Beck *et al.* 2018, Leščešen 2025). Such shifts alter the bioclimatic envelopes within which different land cover types can persist, ultimately forcing reorganization of both natural vegetation and agricultural suitability zones (Sabljic *et al.* 2023, Soares *et al.* 2025).

Research gap and aims

Despite the growing number of climate impact assessments in Europe, relatively few studies have addressed the combined climatic suitability of both cultivated and natural vegetation types within the Middle Danube Basin, a region that is particularly vulnerable due to its transitional climatic position. Previous research has mainly focused either on agricultural land or on forest ecosystems (e.g., Bayer *et al.* 2021, Chatterjee *et al.* 2018, Robertson *et al.* 2023, Xiao *et al.* 2023), but an integrated analysis across different land cover categories under consistent climatic scenarios is still lacking.

MATERIALS AND METHODS

Background

To fill the aforementioned gap, the present study applies climate envelope modelling to assess future climatic suitability of four key land cover types under the high-emission SSP5-8.5 scenario. The specific aim is to identify the direction and magnitude of suitability shifts throughout the 21st century, thereby providing a scientific basis for forward-looking land use planning and conservation strategies in this climate-sensitive region.

In a methodological sense, the potential impacts of climate change on different vegetation types in Central Europe are investigated under future climate conditions using a correlative ecological modelling approach. The applied methodology integrates high-resolution land use data, bioclimatic variables derived from Earth system model outputs, and spatial modelling techniques grounded in ecological niche theory. The key components of the methodology are described in detail below.

This research applies the Climate Envelope Modelling (CEM) approach to project changes in bioclimatic suitability for the land cover types using high-resolution climate projections (CMCC-ESM2 ssp585, 2021–2100, Lovato *et al.* 2022). CEM was chosen because, although simpler than more advanced correlative approaches (e.g., MaxEnt, Random Forest, or ensemble modelling), it offers a transparent and easily interpretable framework for identifying climatic thresholds of vegetation suitability (Ramampiandra *et al.* 2023, Warren and Seifert 2011). This clarity is advantageous when projecting land-use related suitability, where stakeholders and policymakers require unambiguous results (Kaky *et al.* 2020, Wiltshire and Tanner 2020). CEM is particularly suitable for Mediterranean and Central European vegetation types, where land use is strongly influenced by climatic extremes and management practices, allowing

for straightforward assessment of suitability shifts under future climate scenarios (Bedair *et al.* 2025, Machar *et al.* 2017).

Environmental predictors include key temperature and precipitation variables (bio1, bio10, bio11, bio12, bio18, bio19), which represent annual means, seasonal extremes, and biologically relevant thresholds for vegetation growth and phenology. The model operates on a Boolean algebra framework, incorporating percentile-based suitability thresholds (5–95% cuts from the observed environmental extremes) to define the climatic space where each vegetation type currently exists and where it may persist or shift in the future.

The outcomes of such projections are essential not only for understanding ecological vulnerability but also for informed land-use planning, biodiversity conservation, and agricultural adaptation strategies. Anticipating areas of gain or loss in climatic suitability allows stakeholders and policymakers to proactively address future challenges in land management, food security, and habitat conservation.

Logical framework of the study

This study focuses on assessing the climatic suitability of four key land cover types under projected future climate conditions: non-irrigated arable lands (CLC code 2.1.1), broadleaf forests (CLC code 3.1.1), (Mediterranean) sclerophyllous vegetation (CLC code 3.2.3), and olive groves (CLC code 2.2.3). These categories represent a spectrum from intensive agroecosystems to natural and semi-natural vegetation types, and all are integral to the ecological, cultural, and economic identity of the Mediterranean and continental regions of Europe (EEA, 2017; FAO, 2020). However, these systems are particularly sensitive to climate-driven stressors, such as prolonged droughts, heatwaves, and shifts in precipitation patterns, which may alter their spatial distribution, productivity, and long-term sustainability (Ceglar *et al.* 2017).

The logical steps of the study were as follows:

1. Selection of the study region, which is the Middle Danube Region in this study.
2. Selection of land cover categories from CLC 2018.
3. Selection of future projections.
4. Extraction of current climatic envelopes (six bioclimatic variables, 5–95% percentiles).
5. Application of Boolean algebra to define suitability masks.
6. Projection of suitability masks under future climate scenarios (CMCC-ESM2 SSP5-8.5).
7. Comparison of suitability changes across four time periods (2021–2040, 2041–2060, 2061–2080, 2081–2100).

To facilitate understanding, a workflow figure was prepared that illustrates the methodological steps. This figure reflects all four land cover types modelled independently and clarifies the sequence of analyses (Fig. 1).

Climate model and scenario selection

CMIP6 downscaled future climate projections were obtained from the WorldClim v2.1 dataset in 2.5 minutes spatial resolution (Fick and Hijmans 2017). The primary source of future climatic data used in this analysis is the CMCC-ESM2 global Earth system model, operated under the SSP5-8.5 (Shared Socioeconomic Pathway 5 – Representative Concentration Pathway 8.5) scenario, for the period 2021–2100 (including the periods of 2021–2040, 2041–2060, 2061–2080, and 2081–2100). The SSP5-8.5 pathway represents a high-emissions future characterized by continued fossil fuel use, rapid economic growth, and minimal climate mitigation policies, often referred to as a "business-as-usual" trajectory. CMCC-ESM2 was selected due to its advanced representation of coupled atmosphere–ocean dynamics and land processes, making it suitable for regional assessments of climate-driven environmental change.

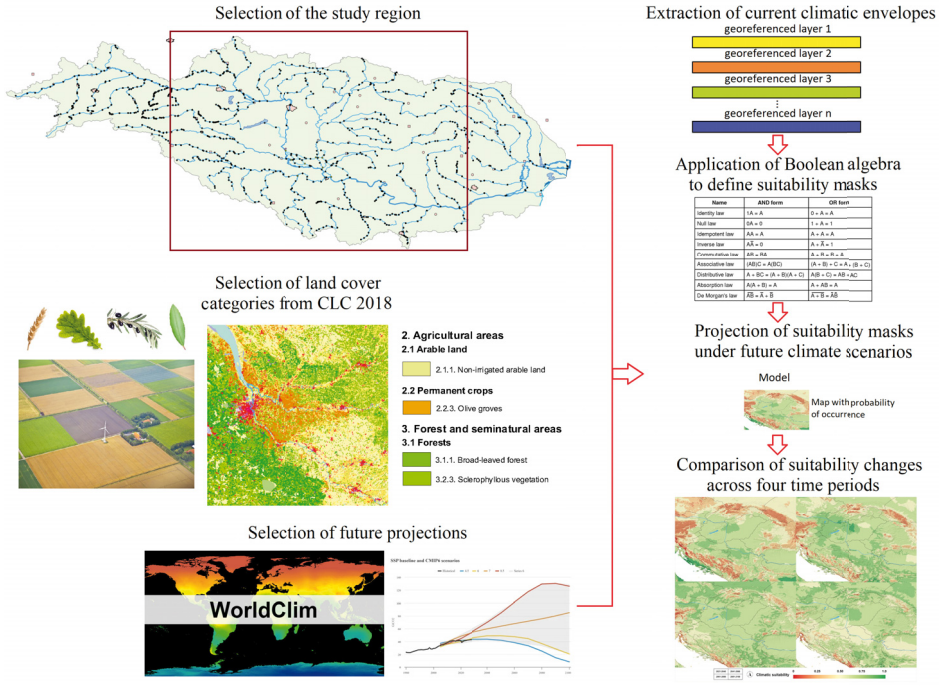

Fig. 1. Workflow of the study.

As was described, in the present study, the SSP5–8.5 (Shared Socioeconomic Pathway 5 – Representative Concentration Pathway 8.5) scenario was selected as the primary basis for modelling future climatic suitability. This high-emission scenario represents a fossil fuel-intensive development pathway, characterized by rapid economic growth, globalized markets, and a continued reliance on carbon-intensive energy sources (O'Neill *et al.* 2016). While SSP5–8.5 was initially regarded as a "worst-case" or less probable trajectory, recent analyses have shown that current global emission trends and energy policies are still largely aligned with this pathway, especially in the near- to mid-term (Hausfather and Peters 2020, Schwalm *et al.* 2020). Despite growing climate policy commitments, greenhouse gas emissions continue to rise globally, and fossil fuels remain dominant in many national energy portfolios.

Using SSP5–8.5 in ecological and land-use modelling allows researchers to assess the upper bounds of potential climatic impacts on ecosystems, agriculture, and biodiversity. This scenario provides a critical benchmark for understanding how extreme climate conditions may affect the viability of existing vegetation zones and agroecosystems if emissions remain unchecked. For climatic envelope modelling, which is sensitive to temperature and precipitation thresholds, SSP5–8.5 ensures a robust exploration of worst-case spatial shifts in habitat and land cover suitability, enabling stakeholders and policymakers to prepare for high-risk outcomes that cannot be excluded under current global trajectories (Riahi *et al.* 2017).

In addition, selecting SSP5–8.5 is particularly relevant for long-term horizon projections (e.g., 2081–2100), as many near-term mitigation effects are unlikely to fully materialize within this timeframe due to climate inertia and cumulative emissions. Therefore, applying this scenario not only enhances the precautionary dimension of the modelling framework but also contributes to the urgency of proactive adaptation strategies, especially in vulnerable regions such as the Mediterranean Basin and Central Europe, which are projected to become climate change hotspots (Giorgi and Lionello 2008).

The model outputs were used to derive a series of bioclimatic variables, which provide biologically meaningful summaries of temperature and precipitation patterns across temporal and spatial gradients. These bioclimatic indices are widely used in ecological modelling due to their direct relevance to species and land-use suitability.

Land use data

To spatially define the target habitat – non-irrigated arable lands – the CORINE Land Cover dataset was employed, which offers standardized land cover classifications across Europe. In this study, the CLC 2018 version was

used, which provides updated and harmonized coverage of the European landscape. CORINE (Coordination of Information on the Environment) provides pan-European land use data at high spatial resolution, updated regularly to reflect land cover dynamics.

The extracted polygons were classified as non-irrigated arable land (CORINE Code: 211), which include areas primarily used for crop cultivation that rely solely on natural precipitation rather than artificial irrigation. These areas represent a key agricultural resource that is particularly sensitive to climatic fluctuations, especially under future conditions of intensified drought and temperature extremes. It should be clarified that these polygons were not manually digitized or cut out from raster layers but obtained by a database query for the relevant CLC code.

As was mentioned before, in addition to non-irrigated arable lands, three further land cover categories were modelled: broadleaf forests, olive groves, and (Mediterranean) sclerophyllous vegetation. These were processed with the same CEM framework, using CLC 2018 polygons to define their current climatic ranges. Each category was treated as a distinct land cover class, with independent climatic envelopes established from the six selected bioclimatic variables. Thus, their future suitability projections were obtained separately, allowing for a comparative assessment across natural and cultivated vegetation types.

Modelling approach

To assess future climate suitability for the selected target land cover types, CEM approach was used. CEM is a correlative, rule-based method that identifies suitable climatic conditions for a given land use or species based on current bioclimatic parameters, and projects these conditions onto future climatic landscapes.

Rather than relying on species presence-absence data, CEM uses defined environmental thresholds derived from observed climatic envelopes – ranges of climatic variables within which the land cover type is currently found. This method is particularly effective for land-use suitability projections because it allows for clear and interpretable delineation of suitable versus unsuitable areas under changing climatic conditions and has been applied successfully in land-use and vegetation studies where transparent rules were necessary to guide planning decisions.

Selected bioclimatic variables

A subset of six bioclimatic variables was selected for the modelling process, chosen for their relevance to crop growth, phenological development, and water availability:

- bio1 – annual mean temperature
- bio10 – mean temperature of warmest quarter

- bio11 – mean temperature of coldest quarter
- bio12 – annual precipitation
- bio18 – precipitation of warmest quarter
- bio19 – precipitation of coldest quarter

These variables capture both annual trends and seasonal extremes in temperature and precipitation, which are critical for assessing the suitability of non-irrigated agricultural systems. The selection of these six variables follows established ecological rationale and previous studies demonstrating their strong influence on vegetation growth, phenology, and water availability (Ceglar *et al.* 2017, FAO 2020).

As these variables are partly correlated (temperature and precipitation components often show collinearity), it is important to acknowledge that CEM does not explicitly correct for multicollinearity. Since the model is rule-based and threshold-oriented, it is less sensitive to collinearity compared to regression-type models; nevertheless, the risk remains. By integrating both thermal and hydrological dimensions of the climate, this variable set provides a comprehensive basis for determining climatic thresholds.

Mathematical framework: Boolean algebra and thresholding

The suitability classification was implemented using Boolean algebra, a logical framework that allows the construction of composite suitability rules based on individual variable thresholds. Each bioclimatic variable was processed to define a binary suitability mask: suitable (1) or unsuitable (0), based on threshold ranges derived from the current climate distribution of the target land cover types.

To establish these thresholds, the 5th and 95th percentiles (i.e., 5–5% percent cuts from the extrema) of each variable were calculated within the current CORINE-defined areas corresponding to the studied land cover classes. The distribution of each variable was checked to ensure that extreme skewness would not bias the percentile-based thresholds. Although the Boolean method does not require normal distributions, trimming the outer 5% values reduces the influence of non-normal tails and ensures ecological robustness. This percentile-based trimming method reduces the influence of outliers and ensures that the derived climatic envelope reflects the core range of suitable conditions, avoiding marginal extremes that may not be ecologically robust under future scenarios.

For each V variable, an x pixel was classified as suitable if:

$$V_{5\%} \leq x \leq V_{95\%}$$

where:

$V_{5\%}$ is the 5th percentile of the variable over current target land cover types

$V_{95\%}$ is the 95th percentile of the variable over current target land cover types

All six variables were processed this way, and their suitability masks were then combined using Boolean intersection (logical AND operation). Thus, a location was considered climatically suitable under future scenarios only if it met the threshold conditions for all six variables simultaneously:

$$S(x) = V_1(x) \wedge V_{10}(x) \wedge V_{11}(x) \wedge V_{12}(x) \wedge V_{18}(x) \wedge V_{19}(x)$$

where $S(x) = 1$ indicates a suitable location, and $S(x) = 0$ indicates an unsuitable one.

In addition to the strict Boolean mask, the individual binary maps were also summed:

$$\sum x = \sum_{i=1}^{6} V_i(x)$$

This additive suitability score (ranging from 0 to 6) reflects the number of climatic variables for which a given pixel satisfies the suitability criterion. While $S(x)$ represents strict climatic suitability (all variables must meet the thresholds), $\Sigma(x)$ provides a gradient of climatic compatibility, highlighting areas that partially meet the climatic envelope. The cumulative suitability scores (0–6) were subsequently normalized to a continuous 0–1 scale to facilitate comparative spatial analysis and visualization.

The result of this modelling approach is a spatial binary raster indicating climatically suitable versus unsuitable areas for the selected target land cover types under the CMCC-ESM2 SSP5-8.5 scenario for the late 21st century. This map highlights regions that are likely to retain climatic suitability, those that are projected to lose suitability, and potentially novel areas that may emerge as suitable due to shifting climate envelopes.

This framework provides a conservative yet ecologically meaningful estimate of land use vulnerability, grounded in present-day climatic tolerances and robust percentile filtering. It allows for spatially explicit risk assessments and supports decision-making regarding agricultural adaptation, land management, and regional climate resilience planning.

Table 1 shows the climatic constraints applied in the modelling.

RESULTS

The modelling results reveal significant spatial and temporal transformations in the climatic suitability of key plantation and vegetation types in the Middle Danube region under the influence of ongoing climate change. These projected changes, derived from the CMCC-ESM2 model under the high-emis-

Table 1. The climatic constraints applied in the modelling.

Broadleaf forest (CLC 3.1.1)			
Abbreviation	Bioclimatic variable	Lower limit	Upper limit
bio1	annual mean temperature	0.54 °C	14.41 °C
bio10	mean temperature of warmest quarter	10.35 °C	22.47 °C
bio11	mean temperature of coldest quarter	7.59 °C	7.67 °C
bio12	annual precipitation	498 mm	1563 mm
bio18	precipitation of warmest quarter	76 mm	355 mm
bio19	precipitation of coldest quarter	98 mm	490 mm
Non irrigated arable land (CLC 2.1.1)			
Abbreviation	bioclimatic variable	Lower limit	Upper limit
bio1	annual mean temperature	5.99 °C	15.29 °C
bio10	mean temperature of warmest quarter	14.82 °C	23.40 °C
bio11	mean temperature of coldest quarter	−4.28 °C	7.95 °C
bio12	annual precipitation	434 mm	1008 mm
bio18	precipitation of warmest quarter	51 mm	273 mm
bio19	precipitation of coldest quarter	82 mm	289 mm
Olive grove (CLC 2.2.3)			
Abbreviation	bioclimatic variable	Lower limit	Upper limit
bio1	annual mean temperature	13.11 °C	17.47 °C
bio10	mean temperature of warmest quarter	20.72 °C	25.70 °C
bio11	mean temperature of coldest quarter	5.08 °C	10.10 °C
bio12	annual precipitation	403 mm	1451 mm
bio18	precipitation of warmest quarter	29 mm	168 mm
bio19	precipitation of coldest quarter	127 mm	632 mm
Sclerophyllous vegetation (CLC 3.2.3)			
Abbreviation	bioclimatic variable	Lower limit	Upper limit
bio1	annual mean temperature	10.45 °C	17.73 °C
bio10	mean temperature of warmest quarter	18.51 °C	25.45 °C
bio11	mean temperature of coldest quarter	2.17 °C	11.37 °C
bio12	annual precipitation	384 mm	872 mm
bio18	precipitation of warmest quarter	11 mm	134 mm
bio19	precipitation of coldest quarter	78 mm	338 mm

sions SSP5-8.5 scenario, indicate a marked reorganization of ecological conditions, with both regressive and progressive trends observed across vegetation categories. The following subsections detail the results according to modelled plantation and vegetation types.

Altering climatic suitability patterns of non-irrigated arable lands

The CEM indicates a progressive decline in the climatic suitability of non-irrigated arable lands throughout the Middle Danube region across the 21st century. This pattern becomes increasingly evident after 2050, coinciding with the intensification of aridification and the rise in mean temperatures. By the late 21st century, a significant proportion of currently suitable areas will fall outside the derived climatic envelope, particularly in the southern and central portions of the region. These areas will increasingly experience seasonal temperature extremes and precipitation deficits, especially during the warmest and coldest quarters (bio10, bio11, bio18, and bio19), exceeding the biologically sustainable thresholds for rain-fed agriculture. The retreat of suitable zones is most pronounced in lowland basins and floodplain fringes, where soil moisture deficits will become more acute. In contrast, limited areas in the northwestern margin of the region may retain marginal suitability, suggesting a potential geographic contraction rather than complete disappearance (Fig. 2).

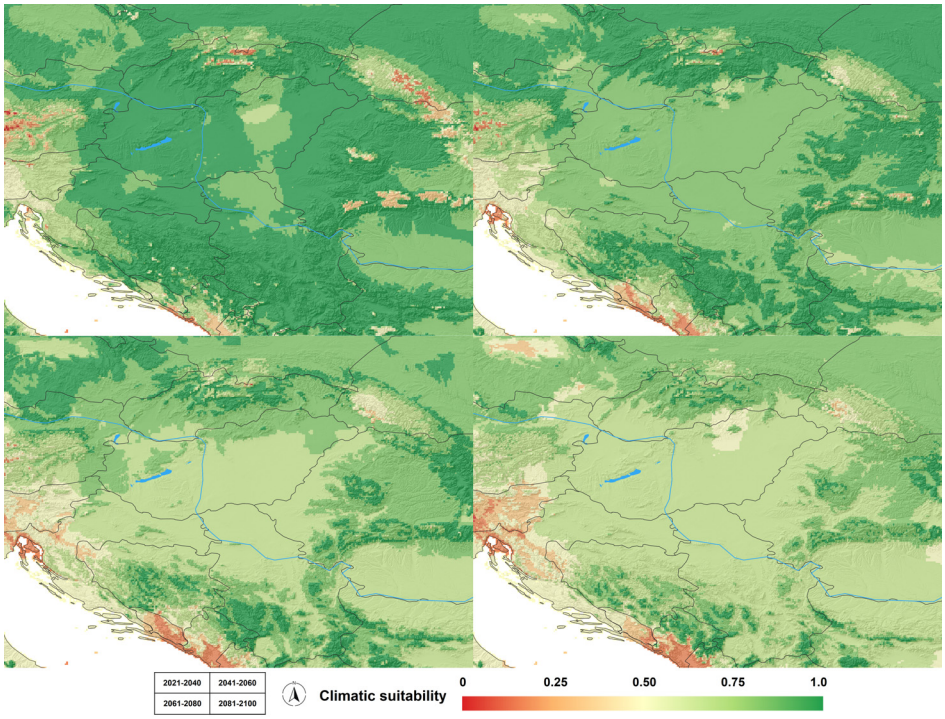

Fig. 2. Spatial distribution of projected climatic suitability for non-irrigated arable lands in the Middle Danube Region across four time slices: 2021–2040 (upper left), 2041–2060 (upper right), 2061–2080 (lower left), and 2081–2100 (lower right). Suitability values range from 0 (unsuitable, red) to 1 (highly suitable, dark green). Blue lines indicate major rivers and lakes.

Retreat of broadleaf forests due to climate change

The model projects a clear and sustained northward retreat of broadleaf forests, which currently dominate the temperate lowlands and lower hills of the Middle Danube basin. Under increasing thermal stress and declining precipitation, especially during the coldest and driest months, broadleaf forests – except for gallery forests that benefit from localized riverine microclimates – are unlikely to persist in much of their present range by the end of the century. The decline in climatic suitability is especially severe in areas where the shift from humid continental to continental steppe climate is most advanced. These areas are projected to exceed the upper thermal limits (bio1, bio10) and fall below critical precipitation thresholds (bio12, bio18) that support deciduous forest species. Consequently, vast tracts of broadleaf woodland in southern Transdanubia and along the Great Hungarian Plain may face conversion to open shrublands, steppe-like grasslands, or mixed transitional systems dominated by drought-tolerant vegetation types (Fig. 3).

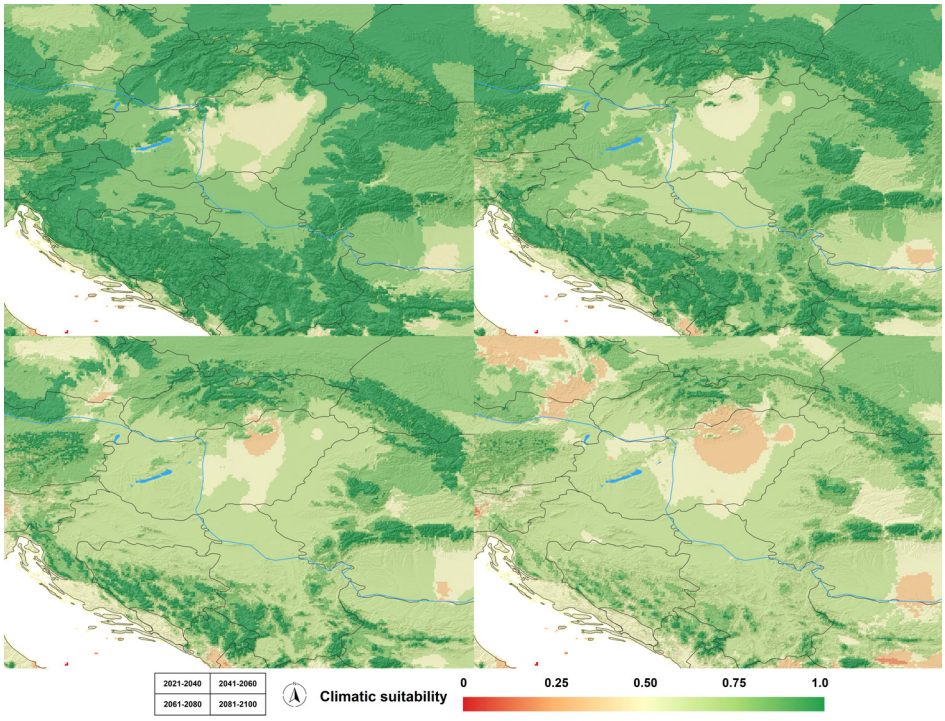

Fig. 3. Spatial distribution of projected climatic suitability for broadleaf forests in the Middle Danube Region across four time slices: 2021–2040 (upper left), 2041–2060 (upper right), 2061–2080 (lower left), and 2081–2100 (lower right). Suitability values range from 0 (unsuitable, red) to 1 (highly suitable, dark green). Blue lines indicate major rivers and lakes.

Changing climatic constraints on the plantation of olive groves

While the warming climate may suggest an expansion of thermophilic crop types, the developed model indicates that olive groves are unlikely to become climatically stable in the Middle Danube region during the 21st century. Despite moderate improvements in temperature-related variables (bio1, bio10, bio11) that fall within the olive tree's optimal range, the seasonal precipitation deficits and intra-annual variability (especially bio18 and bio19) render the region unsuitable for long-term, climate-resilient olive cultivation. The erratic precipitation and potential for winter cold extremes in early-century decades continue to constrain olive viability. Even by the late 21st century, when some southern subregions may approach the climatic limits necessary for olive grove establishment, the suitability remains spatially fragmented and climatically unstable. The persistence of frost events and unreliable summer rainfall preclude robust and sustainable plantation strategies for olives in the region (Fig. 4).

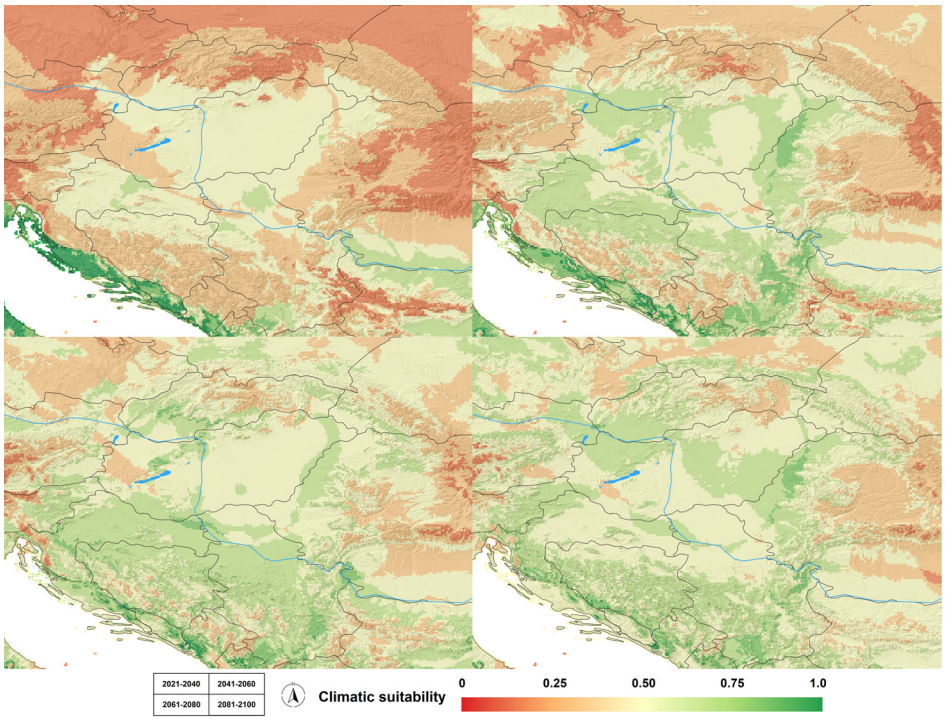

Fig. 4. Spatial distribution of projected climatic suitability for olive groves arable lands in the Middle Danube Region across four time slices: 2021–2040 (upper left), 2041–2060 (upper right), 2061–2080 (lower left), and 2081–2100 (lower right). Suitability values range from 0 (unsuitable, red) to 1 (highly suitable, dark green). Blue lines indicate major rivers and lakes.

Altering climatic suitability patterns of sclerophyllous vegetation

In contrast to the regressive trends observed for temperate ecosystems, the model reveals a gradual increase in climatic suitability for sclerophyllous vegetation, which is characteristic of the Mediterranean biome. By the second half of the 21st century, particularly after 2070, patches of the Middle Danube region begin to fall within the climatic envelope that supports evergreen, drought-tolerant vegetation types such as holm oak and Mediterranean shrubs. These areas, primarily located on south-facing slopes and dry lowland plateaus, exhibit increased alignment with the temperature and precipitation regimes (bio1, bio10, bio18) associated with sclerophyllous growth. However, this transition does not occur uniformly across the region, and the stability of these vegetation types becomes plausible only in select microclimatic niches where summer precipitation deficits are not too severe. It is projected that by the late 21st century, small but climatically stable zones could support Mediterranean-

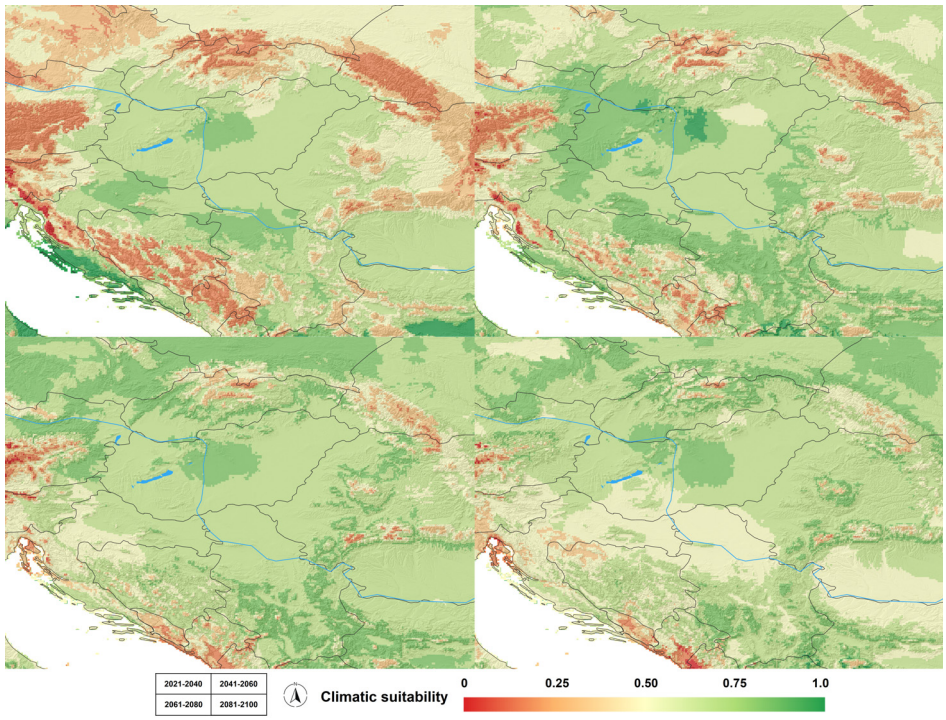

Fig. 5. Spatial distribution of projected climatic suitability for sclerophyllous vegetation in the Middle Danube Region across four time slices: 2021–2040 (upper left), 2041–2060 (upper right), 2061–2080 (lower left), and 2081–2100 (lower right). Suitability values range from 0 (unsuitable, red) to 1 (highly suitable, dark green). Blue lines indicate major rivers and lakes.

type vegetation, heralding a biome transition under prolonged warming scenarios. Nonetheless, these occurrences remain spatially constrained and highly sensitive to interannual climate variability (Fig. 5).

DISCUSSION

The results of this model experiment study align with and expand upon a growing body of literature highlighting the profound ecological consequences of climate change in Central Europe, particularly within the Middle Danube region. The gained projections, derived from the CMCC-ESM2 Earth system model under the high-emission SSP5-8.5 scenario, illustrate substantial shifts in climatic suitability for both natural and cultivated vegetation types. These findings are consistent with broader predictions of biome restructuring, land use vulnerability, and ecosystem stress across Europe in the coming decades (e.g., Beck *et al.* 2018, Thuiller *et al.* 2011).

The modelled decline in the climatic suitability of non-irrigated arable lands is in line with prior studies that have identified Central Europe as a future hotspot of agricultural stress due to increasing summer drought and higher temperatures (Trnka *et al*. 2014, Zajac *et al.* 2022). The projections suggest a retreat of suitable zones from the southern and central lowlands of the Middle Danube basin, mirroring patterns seen in climate impact models for major cereal crops, including wheat and maize, which are particularly sensitive to water deficits during reproductive phases (Zhao *et al.* 2017).

The anticipated increase in extreme weather variability, particularly during critical growing seasons, threatens the viability of rain-fed agriculture (Saleem *et al.* 2024). This is further exacerbated by the limited adaptive capacity of many traditional farming systems in this region, where irrigation infrastructure is scarce and economically unfeasible on large scales. As such, these results underscore the urgent need for adaptive agricultural strategies, including drought-resilient crop varieties, agroforestry integration, and the reconsideration of crop calendars (Wang *et al.* 2022).

The findings on the northward retreat of broadleaf forests are strongly supported by existing ecological and dendroclimatological research. Numerous studies have indicated that temperate deciduous forests across Central and Southeastern Europe are likely to suffer from increasing summer aridity and warming-induced physiological stress (e.g., Hanewinkel *et al.* 2013, Mátyás *et al.* 2010). Species such as *Q. robur*, *F. sylvatica*, and *C. betulus* have narrow tolerance ranges for drought and thermal extremes and are predicted to lose competitive dominance in favour of more xeric-adapted assemblages.

Notably, gallery forests – linear, riparian woodland ecosystems – may exhibit greater resilience due to their hydrological connection to rivers and groundwater (Dinca *et al.* 2025). These localized refugia may temporarily buffer against regional climatic stress, but even these systems are vulnerable in the long term to reduced river discharge and groundwater decline (Junk *et al.* 2013). This study confirms that while gallery forests may persist, upland and non-riparian deciduous woodlands could face widespread contraction or transformation into mixed woodland–steppe mosaics.

The projection that olive groves will remain climatically unstable in the Middle Danube region throughout the 21st century challenges common assumptions about the northward shift of Mediterranean crops. While warming trends may superficially suggest potential for olive expansion into Central Europe, the results highlight the importance of multifactorial climatic constraints, particularly winter cold events and summer drought extremes, which olive trees are highly sensitive to (e.g., Gratsea *et al.* 2022, Ponti *et al.* 2014).

Despite rising annual mean temperatures (bio1), the persistence of frost events in the coldest quarter (bio11) and inconsistent summer rainfall (bio18) are major limiting factors. Even small climatic anomalies during critical phenological periods can result in crop failure or long-term damage to perennial systems like olive plantations. This confirms the findings of regional agricultural models which suggest that the climatic envelope for olives in Europe remains largely restricted to the Mediterranean basin under current and near-future scenarios (Fraga *et al.* 2019).

Conversely, the identification of limited, climatically stable patches for Mediterranean-type sclerophyllous vegetation by the end of the century offers a compelling glimpse into the potential biome-level reorganization within the Middle Danube region. This aligns with projections from biogeographic models indicating that Mediterranean vegetation types, including evergreen oaks and shrubland species (*Quercus ilex*, *Pistacia lentiscus*), could expand into Central Europe as summer aridity and high temperatures become more common (Thuiller *et al.* 2005). In addition, under projected climate scenarios, sclerophyllous vegetation is expected to experience increasing thermal stress and reduced precipitation, potentially affecting their spatial distribution (Giorgi and Lionello 2008).

The emergence of such vegetation types in the region, however, is conditional upon not only climate suitability but also dispersal limitations, soil compatibility, land use, and disturbance regimes (Giadrossich and Scotti 2025). Fire dynamics will play a critical role in shaping the viability of sclerophyllous systems in novel environments (Roche *et al.* 2024). While the model identifies climatically favourable zones, actual vegetation transition may lag due to ecological inertia and anthropogenic landscape fragmentation.

The overall pattern revealed by the modelling framework is one of ecological reorganization marked by the decline of mesic, temperate ecosystems and the incipient rise of thermophilic and drought-tolerant assemblages. This is broadly consistent with Europe-wide climate-biodiversity projections, which point to substantial turnover in vegetation communities, with implications for biodiversity, ecosystem services, and land-based carbon storage (Legg 2021).

These transitions are not uniform but heterogeneous in space and nonlinear in time, requiring fine-scale, region-specific assessment to guide adaptation strategies. The Middle Danube region, positioned at the crossroads of temperate and Pannonian bioclimatic zones, is especially vulnerable to these changes due to its climatic marginality and historical land use intensity.

The results of this study reinforce the urgency of integrating climate adaptation into agricultural, forestry, and conservation planning, emphasizing the need for flexible land-use frameworks, the promotion of climate-resilient species and varieties, and the preservation of ecological corridors to facilitate species movement.

CONCLUSIONS

The modelling results reveal that climate change will profoundly reshape land-use and vegetation patterns in the Middle Danube region. Traditional systems such as non-irrigated arable land and broadleaf forests are projected to decline in climatic suitability, particularly after mid-century, as rising temperatures and increasing aridity push these ecosystems beyond sustainable thresholds. These highlight growing risks for agriculture and forestry that depend on temperate climatic conditions. At the same time, the projections suggest limited but notable opportunities for Mediterranean-type vegetation. Olive groves remain climatically unstable due to frost risk and erratic rainfall, but sclerophyllous vegetation shows a gradual increase in suitability, especially in microclimatic niches such as south-facing slopes and dry plateaus. These shifts point toward a potential biome transition in localized areas by the end of the century. For policymakers and land managers, the results underline the urgency of developing adaptive strategies. Declining suitability for temperate crops and forests will require forward-looking planning, while the possible emergence of drought-tolerant Mediterranean systems highlights the need to balance agricultural productivity, ecosystem resilience, and conservation priorities in a rapidly changing climate.

* * *

Acknowledgement – This study was supported by A **DA**nube **WET**lands **RES**toration (DaWet-Rest) Lighthouse project.

Összefoglaló: A klímaváltozás a 21. században alapjaiban alakíthatja át Közép-Európa növénytakaróját. A különösen érzékeny Közép-Duna-medencében már a század közepére megváltozhatnak az ökológiai feltételek, befolyásolva a mezőgazdaságot, az erdőborítottságot és a tájhasználatot. A tanulmány éghajlati burkológörbe modellezéssel vizsgálta a nem öntözött szántók, lombos erdők, olajfaültetvények és mediterrán cserjések jövőbeli klimatikus megfelelőségét a CMCC-ESM2 modell SSP5-8.5 forgatókönyve alapján (2021–2100). Az elemzés hat bioklimatikus változót és a jelenlegi európai elterjedés 5–95% percentilis határait használta. A nem öntözött szántók és lombos erdők klimatikus megfelelősége várhatóan fokozatosan csökken az aszályosodás és hőmérsékleti szélsőségek miatt, különösen az alföldi területeken. A lombos erdők a század végére főként a hegyvidékekre szorulhatnak vissza, míg sík vidéken szárazságtűrő vegetáció váltja fel őket. Az olajfaültetvények telepíthetőségének feltételei javulhatnak, de a hideg telek és nyári szárazság miatt stabil termesztés nem várható. A mediterrán cserjések számára viszont 2070 után kedvezőbbé válhat az éghajlat, és megjelenhetnek déli kitettségű lejtőkön. Az eredmények jelentős ökológiai átrendeződést jeleznek, ami hangsúlyozza a klímaadaptív tájhasználat és természetvédelem fontosságát.

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(submitted: 30.07.2025; accepted: 04.10.2025)

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Date of publication: 30th September, 2025

Responsible editor: Szilárd Csaba Demeter, president

HU-ISSN 0301-7001 (Print)
HU-ISSN 2559-8597 (Online)