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Anticipated impacts of climate change on the structure and function of phytobenthos in freshwater lakes

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ABSTRACT

Climate change threatens surface waters worldwide, especially shallow lakes where one of the expected consequences is a sharp increase in their water temperatures. Phytobenthos is an essential, but still less studied component of aquatic ecosystems, and it would be important to learn more about how global warming will affect this community in shallow lakes. In this research, the effects of different climate change scenarios (SSP2-4.5 and SSP5-8.5, as intermediate and high emission scenarios) on the structure and function of the entire phytobenthos community using species- and trait-based approaches were experimentally investigated in an outdoor mesocosm system. Our results show that the forecasted 3 °C increase in temperature will already exert significant impacts on the benthic algal community by (1) altering its species and (2) trait composition (smaller cell size, lower abundance of colonial and higher of filamentous forms); (3) decreasing Shannon diversity; and (4) enhancing the variability of the community. Higher increase in the temperature (+5 °C) will imply more drastic alterations in freshwater phytobenthos by (1) inducing very high variability in species composition and compositional changes even in phylum level (towards higher abundance of Cyanobacteria and Chlorophyta at the expense of Bacillariophyta); (2) continuing shift in trait composition (benefits for smaller cell volume, filamentous life-forms, non-motile and weakly attached taxa); (3) further reducing the functional diversity; (4) increasing biofilm thickness (1.4 μm/°C) and (5) decreasing maximum quantum yield of photosystem II. In conclusion, already the intermediate emission scenario will predictably induce high risk in biodiversity issues, the high emission scenario will imply drastic impacts on the benthic algae endangering even the function of the ecosystem.

1. Introduction

It is unequivocal that humans have been causing significant changes in Earth's climate at a rate that is unprecedented in recent millennia, leading to a widespread and rapid warming of the atmosphere, ocean and land surface (IPPC, 2021). Many anthropogenic environmental changes will remain irreversible until centuries to millennia, such as changes in the ocean's physical and chemical parameters, ice sheet disappearance and melting of permafrost, and rising of the global sea level (IPPC, 2021). With further global warming, concurrent and multiple changes in climatic impact-drivers are projected to increase in all geographical regions (IPPC, 2021). A set of five climate model scenarios (SSPs, Shared Socioeconomic Pathways) is considered to explore these

climate responses to a broad range of greenhouse gas (GHG), land use and air pollutants, accounting for solar activity and background forcing from volcanoes (IPPC, 2021). However, both global warming thresholds of 1.5 °C and 2.0 °C will presumably be exceeded during the 21st century without deep reductions in CO₂ and other greenhouse gas emissions (IPPC, 2021).

Evidently, aquatic ecosystems are apparently not independent from the atmospheric conditions, thus they are also threatened by climate change which may cause significant changes in them (Dokulil, 2013; Dokulil et al., 2010; George, 2010). Since aquatic habitats provide several important ecosystem services (e.g. Zedler and Kercher, 2005), predicting ecological changes (e.g. formation of harmful algal blooms, alteration in primary production and in biogeochemical cycles) in these

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ecosystems is of great importance (e.g. Markensten et al., 2010; Dutkiewicz et al., 2013; Laufkötter et al., 2016; Zhou et al., 2017; Townhill et al., 2018). Water temperature is a key environmental driver in aquatic ecosystems having several direct (e.g. changes in individual growth rates, photosynthetic efficiencies, and cellular biochemistry) as well as indirect impacts (e.g. changes in nutrient availability and water column stability of lakes) on their biota (e.g. Dokulil, 2013; Bhateria and Jain, 2016). The complex and seasonally different effects of temperature (e.g. Hao et al., 2020; Pacheco et al., 2022) makes its investigation difficult especially without experimental manipulation (e.g. Denicola, 1996; Piggott et al., 2015). Among aquatic ecosystems, lakes are frequently exposed to heat waves and large temperature fluctuations (see e.g. Rasconi et al., 2017), their average water temperatures are increasing globally (e.g. O'Reilly et al., 2015). Shallow lakes especially have high hydrological sensitivity due to their large surface-to-volume ratio and absence of stable summer stratification, therefore, they respond more directly to actual (sometimes extreme) weather conditions than deeper ones. Sometimes even a small variation of temperature can cause significant limnological and ecological changes in them (e.g. Hammer, 1990; Mooij et al., 2005). The degradation and loss of shallow aquatic ecosystems have already raised worldwide (e.g. Williams, 2002; Mitsch, 2013).

Algae are key components of all aquatic ecosystems and provide multiple benefits for humans, including supporting (e.g. primary production, biogeochemical cycle, habitat provisioning), regulating (e.g. climate regulation, biological control), provisioning (e.g. biotechnology), and cultural services (e.g. inspiration, education; for current reviews see B-Béres et al., 2023; Lengyel et al., 2023; Naselli-Flores and Padišák, 2023). Therefore, detailed and in-depth knowledge of their response to climate change is essential for both nature conservation and human well-being. Most of the laboratory experiments, field observations and ecological models have been developed to study the effects of temperature on phytoplankton predicting significant changes in them (e.g. Dutkiewicz et al., 2013; Barton et al., 2016; Townhill et al., 2018; Filiz et al., 2020; Pálffy et al., 2021; Yuan et al., 2023). However, benthic algae play more important role as primary producers in shallow ecosystems (e.g. Stevenson et al., 1996), since they exceed planktonic production. Their great role is assumed to be favoured and become more pronounced by oligotrophication (Vadeboncoeur and Steinman, 2002) or even eutrophication (Wu, 2016).

Though there is an increasing trend in research of phytobenthos, but lotic communities are more studied than those of lakes (Zhao et al., 2023), which are rather referred to the eutrophication (e.g. de Oliveira Carneiro and Ferragut, 2023) and the trophic interactions (e.g. Ersoy et al., 2020; Cheng et al., 2023). Despite the fact that global warming could differently affect biota (e.g. Woolway et al., 2020), only very few studies examined the effects of increased water temperature on the benthic algal community leading to incomplete knowledge about a key component of particularly endangered shallow ecosystems.

As further problems, phytobenthos researches are concentrated mainly on diatom aspects instead of the entire community (Stoermer and Smol, 2001; Zhao et al., 2023) despite the recommendations (EC European Communities, 2000; Kelly, 2013). The limited studies focusing on the whole phytobenthos used traditional, taxonomy-based community analyses (e.g. Mahdy et al., 2015; Hao et al., 2018, 2020; Bondar-Kunze et al., 2021), while functional, trait-based approaches are very scarce (Larras et al., 2013; Piggott et al., 2015) despite the emphasis on their urgent use (Zhao et al., 2023). Whilst classification systems of functional groups have already been developed and used for phytoplankton (e.g. Reynolds et al., 2002), attempts to organising phytobenthos have only recently begun (Berthon et al., 2011; B-Béres et al., 2016; Lange et al., 2016; Lukács et al., 2018). These functional, trait-based approaches have several advantages compared to species-based methods; these analyses do not require high taxonomic expertise, but provides general information (e.g. Flynn et al., 2011) and more accurate prediction of ecosystem changes (e.g. Abonyi et al., 2018;

Stenger-Kovács et al., 2020).

Therefore, the overall effects of elevated temperatures projected by climate change on the whole phytobenthos in lentic ecosystem are not yet fully understood. Regarding these scientific gaps, the main goal of our work was to experimentally determine the possible effects of the increased temperatures predicted by different climate scenarios (SPP2-4.5 and SPP5-8.5) on the lentic phytobenthos using traditional and functional approaches. The research sought to answer the following main questions and formulate the next hypotheses:

- (1) *What kind of changes can be expected in the structure of freshwater phytobenthos under different climate model scenarios?*

As a result of the intermediate climate scenario, only slight changes in the phytobenthos are assumed, mostly limited to the variation in its species and phylum composition, whilst modification of trait composition was expected only in case of the high emission scenario.

- (2) *How can increased water temperature affect the diversity of phytobenthos?*

Decrease in species diversity was anticipated even with a slight increase in temperature, whilst decline in functional diversity was supposed to occur only with a significant increase in temperature.

- (3) *How can different degrees of temperature rise affect the functional properties of the phytobenthos related to ecosystem services?*

Slight increase in temperature was expected to have no or positive effects on the functional properties of the phytobenthos, whilst a very high climate scenario is presumed to induce radical negative changes in it.

2. Material and methods

2.1. The mesocosm system

The experiment was carried out in an outdoor mesocosm system at the Balaton Limnological Research Institute (Tihany, Hungary) (Pálffy et al., 2021). This system consists of 12 uniform cylindrical plastic tanks, each with a diameter of 2 m and a depth of 1.5 m, surrounded by an insulated wall (Fig. 1a). Each tank was equipped with a set of sensors for *in situ* recording of major environmental parameters (such as temperature, pH, irradiance, etc.). One day before the experiment, all the tanks were thoroughly cleaned and sterilised by multiple flushing with high-pressure hot (>90 °C) water.

For the colonisation and development of phytobenthos, clean limestone (travertine) slabs and cubes (sizes: 5 × 5 × 1 cm and 1 × 1 × 1 cm, respectively) were used as substratum. Prior to filling the tanks, altogether 48 slabs were arranged circularly around the centre of each tank base (Fig. 1b). In addition, 8 small cubes per tank were placed onto flat, plastic holders, which were also lowered to the bottom of the tanks.

Each tank was filled with freshwater up to a depth of 0.8 m. The unfiltered freshwater originated from Lake Balaton by pumping from a distance of ~100 m off the shoreline. Two months prior to the experiment, 24 larger limestone bricks with a top surface of 10 × 10 cm were placed into the littoral zone (depth 20–30 cm) of Lake Balaton in order to grow a mature biofilm on them. After this period, all the biofilms were carefully washed into a small plastic container with a toothbrush, without the entry of macroinvertebrates (especially snails and their eggs). From this dense and homogenised benthic sample, 50 mL of aliquots were taken to inoculate each mesocosm tank with benthic algae typical for Lake Balaton.

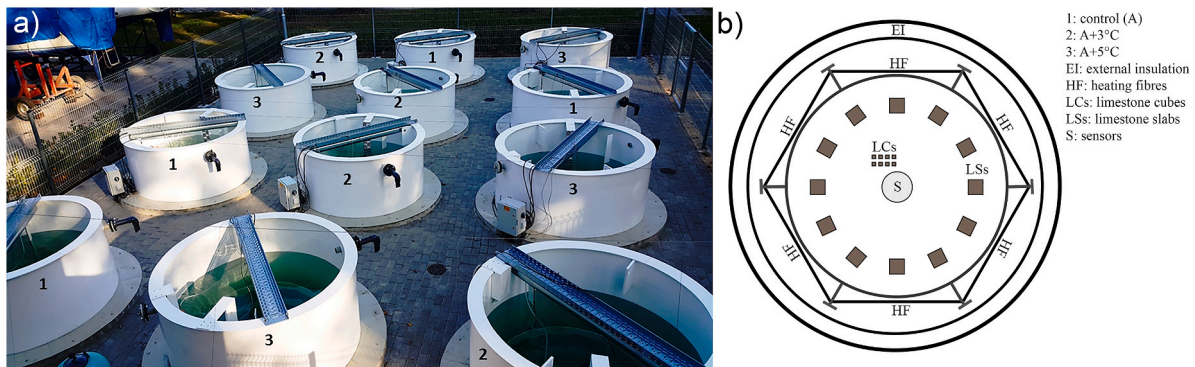


Fig. 1. The mesocosm system (a) used in the present study from bird's eye view and (b) the schematic arrangement of the applied slabs on the bottom of the tanks.

2.2. Description of the experiment

To be able to predict the effects of different climate change scenarios on benthic algae, the experiment was simultaneously performed using three temperature treatments (Fig. 2; each of them in four randomly selected mesocosm tanks):

- treatment 1: unheated/control, following the fluctuations of the ambient temperature (A);
- treatment 2: increased constantly by 3 °C compared to control simulating the SSP2-4.5 emissions scenario of IPCC (A+3);
- treatment 3: increased constantly by 5 °C compared to control simulating the SSP5-8.5 emissions scenario of IPCC (A+5).

The experiment was performed in the summer season of 2021, for 8 weeks from 8th of July to 2nd of August. During the study, samplings were taken weekly from each mesocosm tank as follows:

- Six random substrates (5 × 5 × 1 cm) were removed from each tank, their biofilm was removed with a toothbrush and suspended in 100 mL of filtered water (using a 0.7 μm pore size glass microfiber filter, Whatman Grade GF/F) taken from the same mesocosm. Subsamples of this homogenised sample were used for determining the taxonomic composition, chlorophyll *a* (Chl *a*)

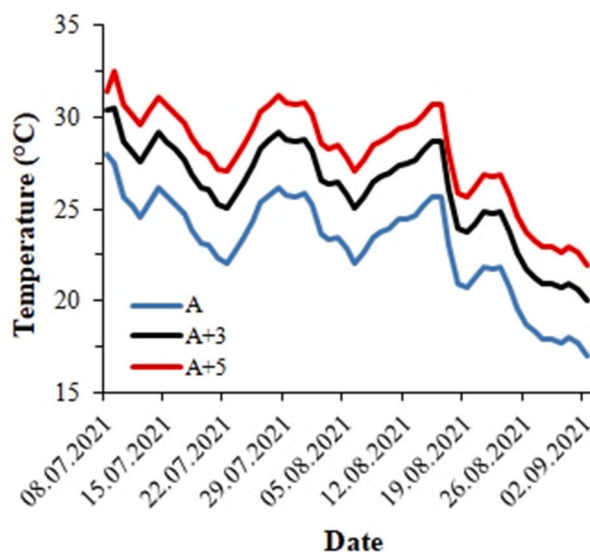


Fig. 2. Temperature regimes in the mesocosms during the experiment based on the daily means.

content, and photosynthetic performance of the phyto-benthos (see section 2.3.).

- In addition, one randomly selected substrate (1 × 1 × 1 cm) was removed from each tank for determining the thickness of the biofilm.

2.3. Analysis of the benthic algal samples

Immediately after each sampling event, the Chl *a* content of the samples were determined spectrophotometrically after a methanolic extraction using hot methanol (Tett et al., 1975).

The subsamples used for determining the benthic algae composition were preserved in Lugol's solution until microscopic analysis. Algal species were taxonomically determined with the classical Utermöhl (1958) method. Altogether, 400 cells were identified at species and/or genus level under light microscope (400 × magnifications, Zeiss Axiovert 100) using taxonomic guides (e.g. von Berg et al., 2004; Komárek and Anagnostidis, 2007). Each species was assigned to different trait categories (cell volume, motility, life-forms, type of the attachment; summarised in Table 1) based on the works of Berthon et al. (2011), Lange et al. (2016), and Lukács et al. (2018). The combinations of these traits were used in the statistical analyses (instead of single traits), due to their higher sensitivity to environmental changes (e.g. Lukács et al., 2018; B-Béres et al., 2016).

The photosynthetic performance of the phyto-benthos was assessed using an AquaPen AP 110-C portable fluorimeter (Photon System Instruments, Drásov, Czech Republic). The maximum quantum yield of photosystem II (PSII), F_V/F_M , was determined after 2 min of dark adaptation in four repetitions.

Finally, the biofilm thickness of the phyto-benthos was measured immediately after the sampling using a Leica SP8 confocal microscope (Leica, Wetzlar, Germany) equipped with a HC PL APO CS 40×/0.85 dry objective and a TD 488/552/638 main beam splitter. After a short immersion in liquid agar to immobilise motile cells, the substrates were placed upside-down onto a Greiner Bio-One 62861 CELLview Cell Culture Dish (Greiner AG, Kremsmünster, Austria) and five regions of interest were randomly selected on each substrate. The size of these

Table 1
The applied traits and their categories.

cell size	motility	life forms	attachment
<100 μm ³ (S1)	slow movement (SM)	unicellular (U)	weak attachment (Wa)
100–299 μm ³ (S2)	fast movement (FM)	colonial (C)	moderate attachment (Ma)
300–599 μm ³ (S3)	non motile (NM)	filamentous (F)	strong attachment (Sa)
600–1499 μm ³ (S4)			
1500 μm ³ < (S5)			

regions was $384 \times 192 \mu\text{m}$ and 1024×512 with a pixel resolution of 188 nm/pixel. Both Chl *a* and phycobilisome autofluorescence were excited using the 488 and 638 nm lasers, respectively, and were detected over the 690–800 nm and 650–680 nm spectral windows with PMT detectors. A series of images taken at different z-planes separated by 5 μm were recorded between the inner (limestone surface) and outer layer of the biofilm. The thickness of the biofilm was determined as a distance between these two layers.

2.4. Statistical analyses

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

Dissimilarity indices in species composition were calculated between all sample pairs using (i) Bray-Curtis (based on abundance data) and (ii) Jaccard indices (based on presence-absence data). Linear regression models were developed to evaluate changes in the dissimilarity of the communities along the time scale. One-way ANOVA and Tukey’s post hoc test were used to examine whether the dissimilarity indices differed significantly among treatments.

After Hellinger transformation of the species abundance data, Non-Metric Multidimensional Scaling (NMDS) was applied to analyse the benthic algae composition (species, algal groups, combined traits) of the three treatments. ADONIS2 analyses were performed to test whether the applied treatments resulted in significantly different compositions using 999 permutations. In case of significant difference, pairwise ADONIS tests were run to compare the treatments with each other. SIMPER test was used to identify the species, algal groups, and combined traits which contribute the most to the differences among the treatments. After the identification of the optimal number of clusters by Mantel test, functional diversity index (RaoQ) was calculated based on the combined traits using the ‘dbFD’ function of the ‘FD’ package.

In order to determine the most associated phytobenthos species with the different treatments, indicator species analysis (IndVal) was performed. In this analysis, components ‘A’ and ‘B’ refer to the specificity (the probability that the species belongs to the target treatment) and fidelity (the probability of finding the species in the given treatment), respectively.

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

3. Results

3.1. Structure of the phytobenthos

3.1.1. Phylum level

Altogether, 70 species were identified belonging to the phylum of Chlorophyta (34), Bacillariophyta (13), Cyanobacteria (13), Cryptista (3), Chrysophyta (3), Euglenozoa (3), and Rhodophyta (1). According to the NMDS analysis, the applied temperature treatments significantly

affected the benthic algae composition at phylum level (ADONIS2 $R^2 = 0.17$, $p = 0.001$, Fig. 3 a,b). Regarding the pairwise statistical tests, treatments A and A+3 did not differ significantly, whilst treatment A+5 differed significantly from both of them (pairwise ADONIS, $p < 0.05$). Bacillariophyta, Chlorophyta and Cyanobacteria contributed the most to the separation of these treatments. Bacillariophyta was mainly associated with treatments A and A+3, in contrast to Chlorophyta and Cyanobacteria which were characteristic for treatment A+5.

3.1.2. Species level

Beside the phylum level, NMDS analyses revealed also significantly different species compositions between all treatments (ADONIS2 $R^2 = 0.11$ and $p = 0.001$, Fig. 3 c,d). Pairwise values were: A and A+3: $R^2 = 0.04$, $p = 0.048$; A and A+5: $R^2 = 0.12$, $p = 0.003$; A+3 and A+5: $R^2 = 0.08$, $p = 0.003$. Altogether, 39 species (56% of the species pool) contributed to this separation, including 8 Bacillariophyta, 21 Chlorophyta, 5 Cyanobacteria, 2 Chrysophyta, 1 Cryptista and 2 Euglenozoa species (Table 2). From these, 17 species (e.g. *Cymbella* sp., *Hariotina reticulata*, *Tetrademus obliquus*, *Trachelomonas oblonga*) were characteristics for treatment A. Ten species, such as *Crucigenia quadrata*, *Desmodesmus communis*, *Spermatozopsis exsultans*, and *Aphanothece* sp. were dominant in treatment A+3, while further 12 species, e.g. *Aulacoseira granulata*, *Ankyra judayi*, *Closterium acutum*, and *Nephroselmis* sp. were associated with treatment A+5. Altogether, eight of these 39 species were identified as indicator species by IndVal analyses (Table 2): one species for treatment A (*Diatoma* sp.), four for treatments A and A+3 (*Cyclotella* sp., *Navicula* sp., *Schroederia indica*, *Gymnodinium* sp.), two for treatment A+5 (*Choricystis coccoides*, *Cosmarium laeve*), and one for treatments A+3 and A+5 (*Chroococcus* sp.).

Regarding the dissimilarity of the species composition, the Bray-Curtis dissimilarity index ranged from 0.24 to 0.50 (Fig. 4 a) in the three treatments. It did not significantly change with time in treatment A, unlike the other two treatments, which resulted in significant positive relationships ($R_{A+3}^2 = 0.65$ and $p = 0.015$, $R_{A+5}^2 = 0.58$ and $p = 0.028$). Both one-way ANOVA and Tukey’s analysis showed a significant difference only between treatments A and A+5 ($p = 0.002$). Similarly to the Bray-Curtis dissimilarity index, the Jaccard dissimilarity index ranged from 0.32 to 0.56 (Fig. 4 b). However, this latter index did not change significantly with time in any of the treatments. Regarding the treatments themselves, the Jaccard indices in treatment A+5 were significantly higher than those in treatments A ($p = 0.004$) and A+3 ($p = 0.039$).

3.1.3. Functional level

The temperature treatments were also clearly separated on the basis of 16 traits (ADONIS2 $R^2 = 0.13$, $p = 0.001$, Fig. 3 e,f, Table 3). Treatment A showed significant differences from A+3 ($R^2 = 0.05$, $p = 0.03$), with the contribution of six traits. Treatment A+5 proved to be different from both A+3 ($R^2 = 0.08$, $p = 0.003$) and A ($R^2 = 0.15$, $p = 0.003$) based on seven and 11 traits, respectively. On the basis of the relative abundances, in general, treatment A was mainly associated with higher biovolumes ($\geq S3$), unicellular (U) and colonial (C) life-form, stronger attachment (Ma or Sa) and ability of movement (SM or FM). In treatment A+3, the relative abundance of species with cell volume of S2 decreased. Treatment A+5 was characterised by small biovolumes ($S2 \leq$), more filamentous life-forms (F), weak attachment (Wa), and non-motility (NM).

3.2. Diversity of the phytobenthos

3.2.1. Species richness and shannon diversity

The species richness varied from 7 to 29 with a mean of 18 ± 4 . Regarding treatments, A+5 had significantly lower species richness compared to both A+3 ($p = 0.01$) and A ($p < 0.001$) (Fig. 5a). A mixed-effects linear model showed that the species richness decreased significantly with the increasing temperature ($p = 0.0015$) with a slope of

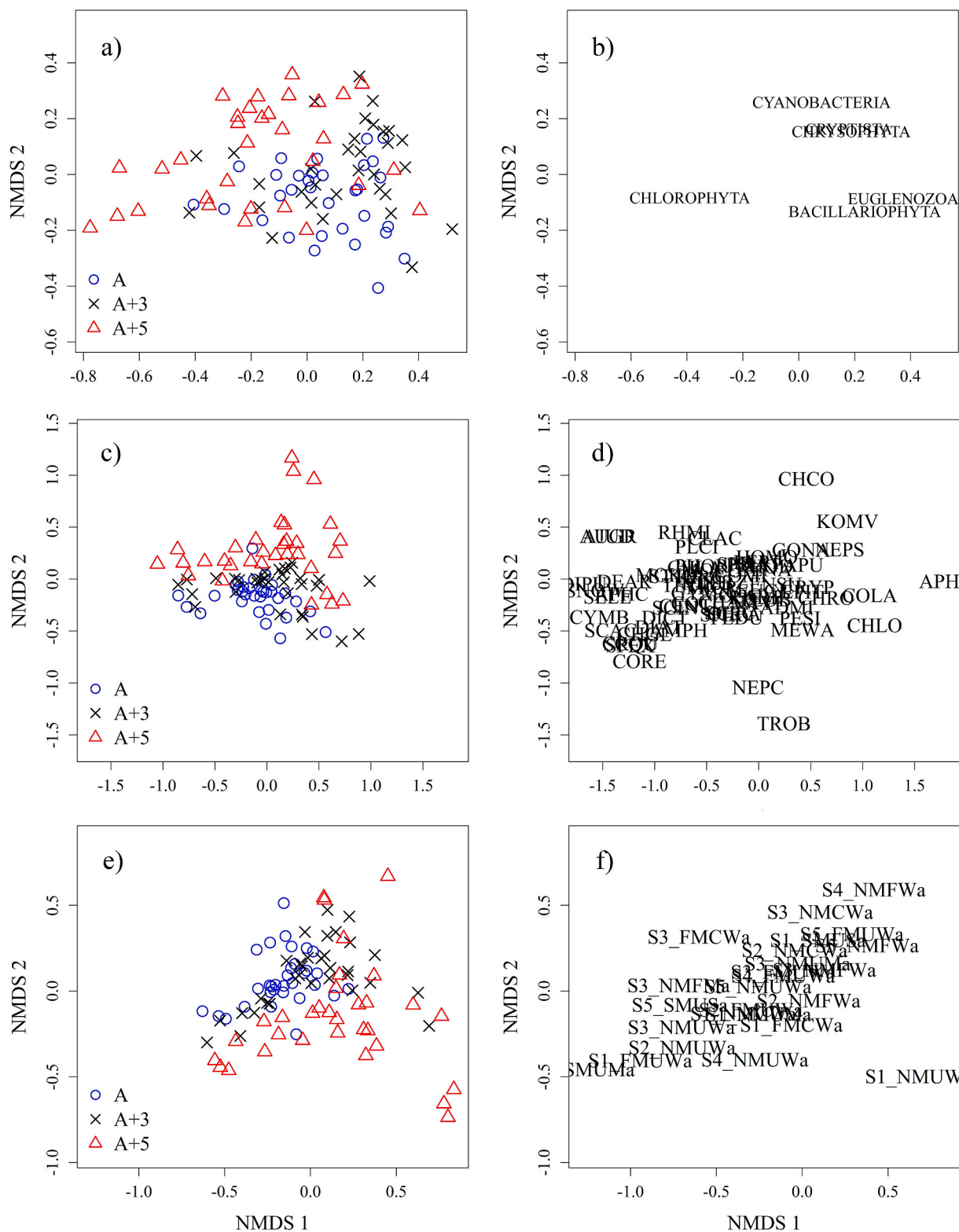


Fig. 3. NMDS plots of phytobenthos samples based on the abundance data of algal phyla (a,b; stress: 0.12), species (c,d; stress: 0.15), and traits (e,f; stress: 0.17). The symbols in panels a, c and e represent the sampling events (n = 32 for each treatment), while panel b, d and f display their community composition (For their abbreviations, see Table 2).

0.55/°C (Fig. 5a).

The Shannon diversity index ranged from 0.6 to 3.7, with a mean of 2.9 ± 0.7 . Welch's tests revealed significant differences in this index between each pair of treatments: A and A+3 ($p = 0.04$), A+3 and A+5 ($p = 0.003$), A and A+5 ($p < 0.001$). Here again, significant negative

correlation was found with temperature ($p < 0.001$). Quantitatively, it decreased with a slope of 0.12 unit/°C (Fig. 5b).

3.2.2. Functional diversity

The functional diversity (RaoQ) ranged from 7.6 to 18.7, with an

Table 2

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

Phylum	Code	Full name	A	A+3	A+5	p (A - A+3)	p (A - A+5)	p (A+3 - A+5)	Ind A	Ind B	treatments	
Bacillariophyceae	AUGR	<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen			x		***	***				
	COCC	<i>Cocconeis</i> sp.	x			*						
	CENT	<i>Cyclotella</i> sp.	x			**			0.92	0.48	A, A+3	
	CYMB	<i>Cymbella</i> sp.	x			***	***					
	DIAT	<i>Diatoma</i> sp.	x			***	***		1.00	0.19	A	
	EPIT	<i>Epithemia</i> sp.		x				*				
	GOMP	<i>Gomphonema</i> sp.	x				***					
	NAVI	<i>Navicula</i> sp.	x				***		0.93	0.91	A, A+3	
	Chlorophyta	AJUD	<i>Ankyra judayi</i> (G.M.Smith) Fott			x		***	***			
		CHGL	<i>Chlamydomonas globosa</i> J.W.Snow	x			*					
CHCO		<i>Choricystis coccoides</i> (Rodhe & Skuja) Fott			x		***	***	0.91	0.90	A+5	
CLAC		<i>Closterium acutum</i> Brébisson			x		***	***				
COMI		<i>Coelastrum microporum</i> Nägeli		x		***	***					
COLA		<i>Cosmarium laeve</i> Rabenhorst			x		**		0.90	0.16	A+5	
CRQU		<i>Crucigenia quadrata</i> Morren		x		***	***					
SCQU		<i>Desmodesmus communis</i> (E.Hegewald) E. Hegewald		x		***	***					
DICT		<i>Dictyosphaerium</i> sp.	x			***	***					
GONA		<i>Gonatozygon</i> sp.			x		**					
CORE		<i>Hariotina reticulata</i> P.A.Dangeard	x			***	***					
KLEB		<i>Klebsormidium</i> sp.	x			***	***					
MOCO		<i>Monoraphidium contortum</i> (Thuret) Komárková-Legnerová			x		**	**				
NEPC		<i>Nephrochlamys</i> sp.	x			***	***					
NEPS		<i>Nephroselmis</i> sp.			x		***	***				
PEDU		<i>Pediastrum duplex</i>	x			***	***					
SCIN		<i>Schroederia indica</i>	x			**			0.96	0.28	A, A+3	
SPEX		<i>Spermatozopsis exsultans</i> Korshikov		x		***	***					
SPHA		<i>Sphaerocystis</i> sp.			x		**	*				
SPIR		<i>Spirogyra</i> sp.	x			***	***					
TEOB	<i>Tetradesmus obliquus</i> (Turpin) M.J.Wynne	x			***	***						
Cyanobacteria	APHT	<i>Aphanothece</i> sp.		x		***	***					
	CHRO	<i>Chroococcus</i> sp.		x			**	**	0.93	0.36	A+3, A+5	
	KOMV	<i>Komvophoron</i> sp.			x		*					
	LEPT	<i>Leptolyngbya</i> sp.			x		*	**				
	PLCI	<i>Limnolyngbya circumcreta</i> (G.S.West) X.Li & R. Li.			x		*	*				
	Cryptista	CRYP	<i>Cryptomonas</i> sp.		x		*	*				
GYMN		<i>Gymnodinium</i> sp.	x			**			0.90	0.44	A, A+3	
PAPU		<i>Parvodinium pusillum</i>		x			**					
Euglenozoa	ENSU	<i>Entosiphon sulcatus</i> (Dujardin) F.Stein		x		*						
	TROB	<i>Trachelomonas oblonga</i> Lemmermann	x			***	***					

average of 14.4 ± 2.5 . Similarly to the species richness, no significant difference was found between treatment A and A+3 (Fig. 5c), while the functional diversity was significantly lower in treatment A+5 compared to both A+3 ($p < 0.001$) and A ($p < 0.001$). Similarly to the above-mentioned two indices, a mixed-effects linear model showed a significant negative relationship between temperature and RaoQ ($p < 0.001$) with a slope of $-0.95/^\circ\text{C}$.

3.3. Functional properties of the phytobenthos related to ecosystem services

3.3.1. Chlorophyll a content

The Chl a content of the phytobenthos ranged from 0.7 to 14.7 mg m^{-2} with an average of 3.7 ± 2.3 mg m^{-2} . Based on Welch's tests, there was no significant difference between the treatments. According to the mixed-effects linear regression, no significant correlation was found with the temperature (Fig. 5d).

3.3.2. Biofilm thickness

The biofilm thickness varied over a broad range from 30 to 91.7 μm (mean: 59.7 ± 14.3 μm), and differed significantly among the treatments (Fig. 5e). Welch's tests revealed significant differences between treatments A and A+5 ($p = 0.02$), as well as between A+3 and A+5 ($p = 0.04$). The biofilm thickness showed positive correlation with

temperature ($p = 0.016$): based on a mixed-effects linear regression, it increased with a slope of 1.4 $\mu\text{m}/^\circ\text{C}$. Based on multivariate linear regression model using backward selection procedure, four parameters significantly affected the biofilm thickness. The abundance of Bacillariophytes, species richness and functional diversity had a negative correlation with this property of the phytobenthos, whilst the abundance of filamentous species positively affected it.

3.3.3. Photosynthetic performance

The maximum quantum yield, F_V/F_M , of PSII ranged from 0.17 to 0.50 with an average of 0.35 ± 0.08 (Fig. 5f). Pairwise comparisons of the treatments showed significant differences between A and A+5 ($p < 0.001$) as well as between A+3 and A+5 ($p = 0.001$). F_V/F_M showed negative correlation with temperature ($p < 0.001$) on the basis of a mixed-effects linear regression, by decreasing with a slope of $0.015/^\circ\text{C}$. According to the multivariate linear regression model, five parameters significantly affected the maximum quantum yield of PSII (Table 4). The maximum quantum yield of PSII had positive correlation only with the abundance of Bacillariophytes, while the higher abundance of Cyanobacteria, filamentous life-forms, a greater proportion of prokaryote and smaller cell volume negatively affected it.

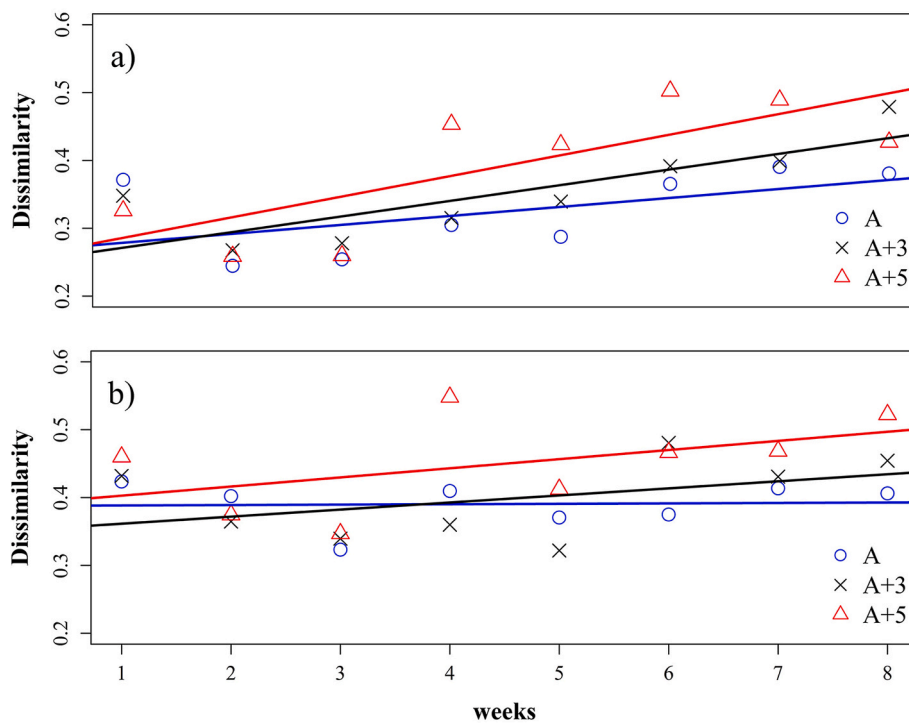


Fig. 4. Temporal changes of the mean dissimilarity indices (n = 6, a: Bray-Curtis, b: Jaccard) along the three treatments.

Table 3

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

Code	Full description	A	A+3	A+5	p (A - A+3)	p (A - A+5)	p (A+3 - A+5)	Ind A	Ind B	Treatments
S1_FMUWa	<100 μm ³ , fast movement, unicellular, weak attachment		x		***		***			
S1_FMCWa	<100 μm ³ , fast movement, colonial, weak attachment			x		*	**			
S1_NMUWa	<100 μm ³ , non-motile, unicellular, weak attachment			x		***	***			
S1_NMCWa	<100 μm ³ , non-motile, colonial, weak attachment			x		*				
S2_NMUWa	100–299 μm ³ , non-motile, unicellular, weak attachment		x		*					
S2_NMCWa	100–299 μm ³ , non-motile, colonial, weak attachment		x				**			
S2_NMFWa	100–299 μm ³ , non-motile, filamentous, weak attachment			x		***	*			
S3_FMUWa	300–599 μm ³ , fast movement, unicellular, weak attachment	x			***	***				
S3_SMUMa	300–599 μm ³ , slow movement, unicellular, moderate attachment	x			***	***				
S3_NMUWa	300–599 μm ³ , non-motile, unicellular, weak attachment	x			**			0.92	0.48	A, A+3
S3_NMUMa	300–599 μm ³ , non-motile, unicellular, moderate attachment	x				**				
S3_NMFMa	300–599 μm ³ , non-motile, filamentous, moderate attachment	x			***	***				
S4_NMUWa	600–1499 μm ³ , non-motile, unicellular, weak attachment			x		***	***			
S5_FMUWa	>1500 μm ³ , fast movement, unicellular, weak attachment		x				**			
S5_SMUSa	>1500 μm ³ , slow movement, unicellular, strong attachment	x			*					
S5_NMUWa	>1500 μm ³ , non-motile, unicellular, weak attachment	x				*				
S5_NMFWa	>1500 μm ³ , non-motile, filamentous, weak attachment			x		**				

4. Discussion

Water temperature, as a key environmental parameter, largely determines the composition of benthic algae (Piggott et al., 2015). Importantly, it also affects/affected by other abiotic parameters (e.g. sediment type, nutrient status, season) which, indirectly, can modify its primary effects and may lead to controversial results of mesocosm studies (see e.g. Mahdy et al., 2015; Piggott et al., 2012, 2015; Hao et al., 2020; Pacheco et al., 2022). Thus the clarification of the effects of temperature requires experimental manipulation (Piggott et al., 2015). The results of our pilot study, aiming to improve our understanding on the impact of global warming on benthic algae, a thus far poorly studied research area with contradictory results, showed that the enhanced water temperature had significant effects on benthic algal communities both in terms of their structure and function.

4.1. Effects of global warming on the structure of the phytoenthos

Hao et al. (2018) found that even a greater increase in global temperature (4.5 °C) had only a lower impact on periphyton compared to phytoplankton. In the present study in accordance with our hypothesis, even an intermediate (3.0 °C) emission scenario resulted in major shifts in community composition at species level and changes in their dominance relations. For instance, the abundance of most diatoms (e.g. *Cymbella* sp., *Navicula* sp., *Nitzschia* sp., *Rhoicosphenia* sp.) has started to decline. High variability of the benthic algal community was also observed in case of this scenario, similarly to those of phytoplankton (Sommer et al., 2007; Pálffy et al., 2021). Moreover, the combination of four traits (cell volume, motility, attachment, life-form) used in the present study were strong, sensitive and reliable enough to highlight statistically significant differences between the treatments. As a result of

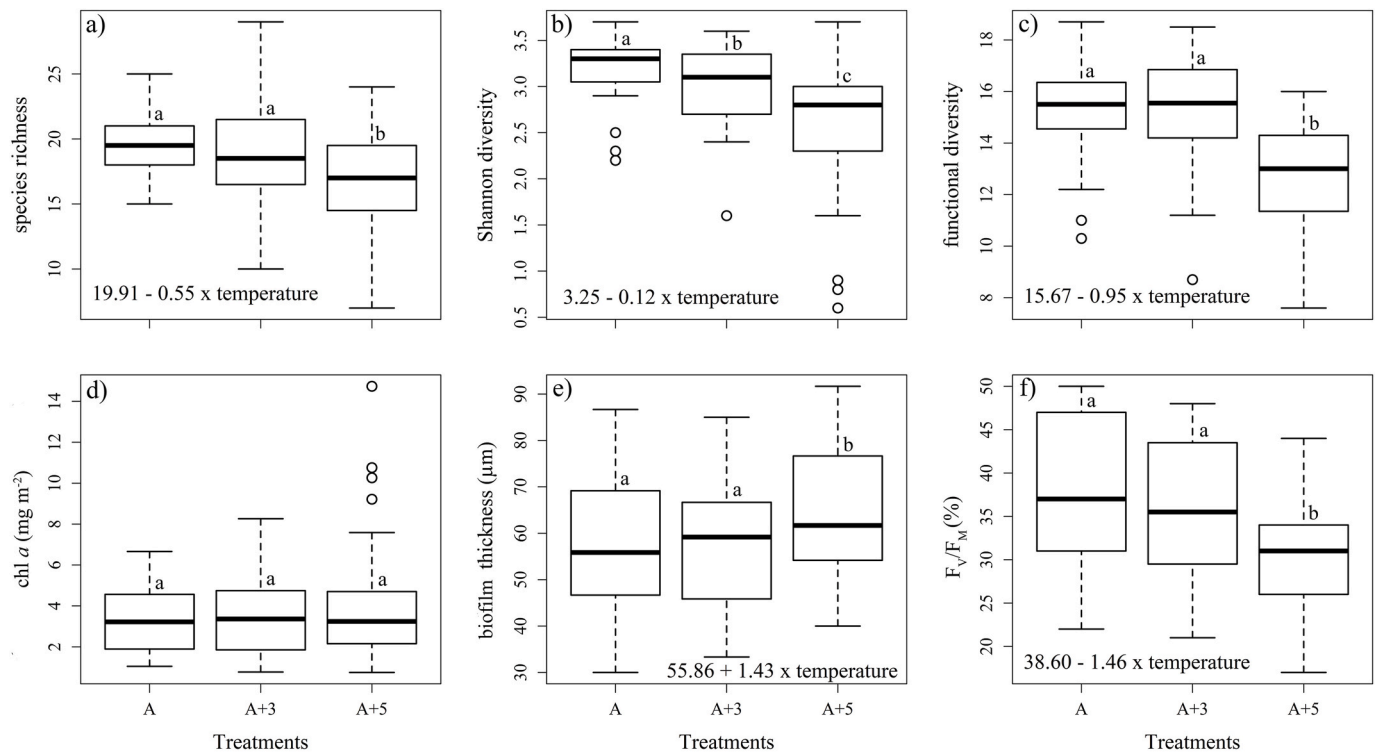


Fig. 5. Boxplots of species richness (a), Shannon- (b) and functional diversity (c), Chl *a* content of the benthos (d), biofilm thickness (e), and the maximum quantum yield of PSII (F_v/F_m , f) in different treatments. Letters above the boxplots mark significant differences obtained by Welch's tests (groups marked with the same letters are not different, whereas groups with different letters differ significantly). Equations represent regression fits.

Table 4

Reduced multivariate linear models ($p = 0.001$) with partial correlation coefficients (r) and significance level (p) built among the biofilm thickness as well as the maximum quantum yield of PSII (F_v/F_m) and community properties.

	r	p
Biofilm thickness		
Species richness	-2.10	0.01
Filamentous species abundance	0.51	0.01
Functional diversity	-2.64	0.02
Bacillariophyta abundance	-0.26	0.03
F_v/F_m		
Bacillariophyta abundance	0.80	<0.001
Size (small:big ratio)	-2.65	<0.001
Lifeforms (fil:U + C ratio)	-0.48	0.004
Pro- to eukaryotes ratio	-0.76	0.02
Cyanobacteria abundance	-1.12	0.05

an increase of 3 °C in temperature, the benthic algae started to reduce their cell volume, increase filamentous and decrease colonial life-forms. Reduction in size is a well-known strategies in warmer environment in regard of many aquatic organisms, such as phytoplankton (Winder et al., 2009; Lewandowska and Sommer, 2010), periphyton (Larras et al., 2013; Piggott et al., 2015), snails (Sheridan and Bickford, 2011), fishes (Gyllström et al., 2005; Meerhoff et al., 2007). Shifts in colonial and filamentous forms of algae were already also reported in the phytoplankton (Trochine et al., 2011; Rasconi et al., 2017), where physical disturbance and resource utilisation basically determine their life-forms (Litchman et al., 2010).

Further increase in water temperature such as projected by the very high emissions scenario (5.0 °C) induced such drastic taxonomic changes which were reflected even at a higher taxonomic level, such as phylum level. Similar to many previous studies, enhanced temperature unequivocally shifted the benthic algal communities from diatom-dominated ones to green algae and cyanobacteria-dominated

communities (e.g. Piggott et al., 2015; Rasconi et al., 2017; Hao et al., 2018; Bondar-Kunze et al., 2021). Diatoms usually prefer lower temperatures (van der Grinten et al., 2005) having an optimum growth temperature below 20 °C (Patrick et al., 1969; Cairns, 1956). Although some diatoms are able to grow even at higher temperatures, they cannot compete with Cyanobacteria, due to their better resource utilisation and, in some cases, production of allelochemicals (van der Grinten et al., 2005). Whilst Chlorophyta usually shows better performance at warmer temperatures having optima between 15 and 25 °C, Cyanobacteria can even grow above 30 °C (Patrick et al., 1969; Cairns, 1956; Seaburg et al., 1981; van der Grinten et al., 2005). Their co-occurrence may be allowed by their different niche preferences (Litchman et al., 2010). Beside the changes in phylum, during such a rise in temperature, the variability of benthic algal community is not restricted only to the changes in the dominance relations, but it also manifested as qualitative changes. However, on the basis of abundance data, both climate scenarios resulted in a continuous increase in variability over time leading to its more unpredictable/stochastic impacts. Regarding the traits, the reduction in cell size will continue as a result of further increase in the temperature projected by the very high emissions scenario. Small cell size has many benefits, including high growth rates, fast and efficient metabolism due to a small diffusion boundary layer and high surface-to-area ratio, and better resource availability (e.g. more efficiently light utilisation; Litchman and Klausmeier, 2008; Litchman et al., 2010). Available, corresponding data referring to changes in life-forms of phyto-benthos with increasing temperature are scarce, focused mainly on streams and the obtained results are quite contradictory. Our results are in accordance with those of Piggott et al. (2015) suggesting that filamentous species (e.g. *Leptolyngbya* sp., *Planktolyngbya circumcreta*) become more prevalent with increasing temperature. In lotic phyto-benthos, the relationship between temperature and motility is the opposite (Piggott et al., 2015; Lukács et al., 2018) than in phytoplankton (Litchman and Klausmeier, 2008), where enhancing temperature benefited sinking velocity (e.g. Bach et al., 2012). Our results related to

lentic phytobenthos, concur that findings suggesting that temperature has negative correlation with the abundance of motile species (e.g. *Gymnodinium* sp., *Trachelomonas oblonga*) (Piggott et al., 2015), and positive relationship with that of non-motile taxa (Lukács et al., 2018). Regarding the type of attachment, the negative effect of temperature on moderate attachment was supported (Lukács et al., 2018). The available growth forms and sizes in the local algal species pool are very important, because they basically determine the grazing and the plant-animal interaction through algal physiognomy, which have different susceptibilities to herbivory (e.g. Steinman, 1991; Tuchman and Stevenson, 1991; McCollum et al., 1998; Hillebrand et al., 2000). Thus the trait composition of the phytobenthos may modify the process of the top-down control and even the food web.

4.2. Effects of global warming on the diversity of the phytobenthos

Warming even at intermediate level may result in lower species diversity as well as species richness, such as it was usually observed in periphyton or periphytic diatoms (Piggott et al., 2015; da Silva et al., 2019; Hao et al., 2020), phytoplankton (Pálffy et al., 2021). Based on field data, enhanced temperature negatively affects the diversity of other aquatic organisms too, such as zooplankton (Tavşanoğlu et al., 2017), macroinvertebrate (Li et al., 2013), fish (Barbarossa et al., 2021). Based on our results, further increases in the temperature will intensify this process and at least two species will be lost from the phytobenthos as a consequence of the most pessimistic climate scenario. Species loss is a very serious ecological process; it has already been a great concern in the 21st century, since it has negative implications on ecosystem services such as primary productivity, nutrient cycling and invasion resistance (e.g. Díaz et al., 2006). Furthermore, a diverse system tends to have greater ecosystem stability and resistance against several disturbances (Tilman et al., 2014).

In contrast, trait-based functional diversity decreased significantly (0.95/°C, Fig. 5 c) only by the 5 °C projected by a very high emissions scenario (SSP5-8.5) in accordance with our hypothesis. This negative change has a great ecological importance, since it may endanger the ecological function of the ecosystem which can be maintained despite the loss or decline of dominant species by less abundant but functionally equivalent species (Chillo et al., 2011).

4.3. Effects of global warming on the function of the phytobenthos related to ecosystem services

Climate change projections had already suggested significant changes in function of the lotic benthic diatom community leading to thinner biofilm. The underlying structural changes would threaten the development of biofilm, its stability and primary production, as well as the higher trophic level (reviewed by Stenger-Kovács and B-Béres, Submitted). These predicted structural changes are not supported by present study focusing the whole phytobenthos. According to our study, only the most pessimistic scenario of global warming enhances significantly the biofilm thickness (by approximately 1.5 µm/°C, ~3%), which is accompanied by relevant structural changes such as increased abundance of filamentous life-forms, reduces in the abundance of Bacillariophyta as well as the species richness and functional diversity. The decreasing proportion of diatoms is in itself a threat to biofilm stability, since these algal groups secrete EPSs, which are very important in this process (e.g. Underwood and Paterson, 2003). Increase in thickness of the biofilm and these kinds of structural changes could also have many serious ecological consequences. Firstly, thicker biofilm can strip dissolved N and P from the water column playing key role in nutrient recycling, sequence nutrients (firstly before phytoplankton) entering to the waterbody, promote the clear water state (reviewed by Vadeboncoeur et al., 2021). For instance, in the bioremediation process, periphyton can be responsible even for 60% of the phosphorus retained in the vegetated areas of freshwaters (Dodds, 2003). In contrast, a large

proportion of biofilm could also become light limited leading to photosynthetically inactivation and less productivity (Schnurr and Allen, 2015; Villanueva et al., 2011). However higher temperature predicted by climate change generally benefits aquatic macrophytes (e.g. Landkildehus et al., 2014; Ersoy et al., 2020; Liu et al., 2021; Lind et al., 2022), high biomass of periphyton can overgrowth them due to the more efficient use of resources and shading – especially in case of filamentous algae and Cyanobacteria – (Zhang et al., 2019, 2020), and consequently can cause the decline of submerged macrophyte communities contributing to the shift from clear water phase of the ecosystem to turbid one (Phillips et al., 2016). Furthermore, benthic Filamentous Algal Blooms (FABs) can cause problem even in fishing, harbour toxins, accumulate harmful bacteria, change in food web, for instance, by selecting benthic grazers or undesirable recreation water quality (reviewed by Vadeboncoeur et al., 2021).

Regarding photosynthetic performance, only the most pessimistic scenario of global warming may result in a loss of the maximum quantum yield of PSII (~1.5%/°C) without significant alteration of the chlorophyll *a* content of the phytobenthos. According to the general phenomenon, photosynthetic activity increases with enhancing temperature (e.g. Lassen et al., 2010; Costello et al., 2018). But above the optimal temperature, high temperature could mean stress and can negatively affect photosynthesis, for instance, by causing less fluid membrane, higher respiration rate or inactivating the oxygen-evolving complex (e.g. Falkowski and Raven, 2013; Hopkins and Hüner, 2004). Thus enhanced temperature projected by the high emission scenario can result in lower net production of freshwater phytobenthos similar to other research (Scharfenberger et al., 2019; McKee et al., 2003; O'Connor et al., 2009; Cao et al., 2014). Importantly, the decreased F_V/F_M ratios reflect changes in community composition supporting Suggett et al. (2009). Due to different inherent properties of their photosynthetic apparatus Chlorophytes and diatoms have much higher F_V/F_M values than that of Cyanobacteria (Campbell et al., 1998; Koblížek et al., 2001; Suggett et al., 2003; Yentsch et al., 2004). Thus, the increasing abundance of prokaryotic primary producers (i.e. Cyanobacteria) resulted in lower F_V/F_M values, which can even result in lower productivity (Reynolds, 2006). Likewise, the observed changes in traits as the result of both climate scenarios can also contribute to a decrease in F_V/F_M for similar reasons. The shift in community towards smaller cell volume may also result in a decreased F_V/F_M , due to a relatively low F_V/F_M of small flagellated eukaryotes (Aiken et al., 2004; Cermeño et al., 2005; Moore et al., 2005; Fishwick et al., 2006; Suggett et al., 2009). The observed negative effects of increasing abundance of filamentous life-forms on F_V/F_M are presumably also related to Cyanobacteria abundance.

Warming can affect trophic structures and its dynamics (Jeppesen et al., 2010), such as the fish-snail-phytobenthos benthic trophic pathway which can contribute considerably to the aquatic food web in shallow ecosystems (Jeppesen et al., 2000). For instance, in the absence of fishes, global warming can increase the strength of the top-down control of snails on periphyton (Hansson et al., 2013; Cao et al., 2014; Cheng et al., 2023). Based on our result, none of the climate change scenarios caused significant changes in chlorophyll *a* content, which may have negative ecological consequences. If the biomass of phytobenthos did not increase at the same rate as the consumer population under warming, then fewer resources will be available which can modify the food web structure leading to loss of ecosystem function and services.

5. Conclusion

The intermediate emissions scenario (SSP2-4.5) has a moderate effect on phytobenthos and can induce significant ecological problems in freshwaters, such as contributing to the Earth's biodiversity loss. In contrast, the most pessimistic, very high emissions scenario (SSP5-8.5) will presumably cause a very strong and unpredictable environmental

pressure on the freshwater benthic algal community. It can induce more drastic structural and functional changes in the phyto-benthos causing a multitude of ecological problems, such as lower the net primary production; shifts in water quality by inhibiting macrophytes; proliferation of HABs (Harmful Algal Blooms) by favouring Cyanobacteria; changes food webs by altering their species and trait compositions. Overall, in the case of the very high emissions scenario, many functions of the phyto-benthos will likely be reduced leading to the loss of ecosystem services of the given freshwater ecosystem.

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CRediT authorship contribution statement

Edina Lengyel: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Csilla Stenger-Kovács:** Conceptualization, Methodology, Investigation, Resources, Writing – review & editing. **Gergely Boros:** Methodology, Investigation, Resources, Writing – review & editing. **Tiba Jassam Kaisan Al-Imari:** Investigation, Visualization. **Zoltán Novák:** Investigation, Visualization. **Gábor Bernát:** Methodology, Investigation, Resources, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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