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Continuous precipitation loss induced more pronounced compositional and diversity changes in the lotic phytobenthos than one-off drought events

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ABSTRACT

Changing precipitation dynamics is one of the most important mechanisms that, by affecting the water regime, modifies the physical and chemical environment of aquatic assemblages. Thus, hydrological extremes can be considered as key drivers that shape algal assemblages and lead to diversity changes even in large rivers. Here, we investigated the long-term changes in the benthic diatom composition of the Rába River (River Raab), the watershed of which experienced continuous loss of precipitation in the last five years. We aim to answer the main question: Do one-off drought events and trend-like (continuous) precipitation decrease result in similar changes within diatom assemblages of this perennial river? Because, it has been already demonstrated that resilience and resistance of assemblages may vary depending on whether the drought occurs regularly or only occasionally. Our results demonstrated that one-off dry events hardly affected either assemblages' composition or biodiversity. In contrast, continuously decreasing precipitation (drying period) had a pronounced effect on taxa and trait distribution and resulted in a significant decrease in taxonomic diversity and in functional richness. It is important to stress that the observed deteriorating diversity anticipates that a lasting drought period is likely to upset the ecological balance of the ecosystem and lead to remarkable natural damage. Since the climate scenarios project extremes in water regime in the near future, including longer periods of low precipitation, any knowledge that predicts changes in microflora can help to develop action plans by authorities to save lotic ecosystems.

1. Introduction

Average temperature on Earth increased by about 1 °C since the beginning of industrialization, mainly as a result of greenhouse gas emission. By the end of the 21st century, a further 2–5 °C increase in temperature is predicted (IPCC, 2018). In parallel with increasing temperature, precipitation conditions are also projected to change with consequences like diminution of rainy days leading to severe drought or an increase in the frequency of intense, heavy rainfalls (IPCC, 2018; Pendergrass and Knutti, 2018).

These extreme climatic events affect aquatic ecosystems in several ways. Alterations in community structure (Viitasalo and Bonsdorff, 2022), appearance of invasive species (Anufriieva and Shadrin, 2018) and/or disappearance of vulnerable native ones (Manes et al., 2021), reduced biodiversity (Prakash, 2021) are just some of the phenomena that can be expected in the near future. These events are not limited to a

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given water body, but occur on the whole catchment scale, threatening the healthy ecosystem functioning in large regions (Vörösmarty et al., 2010; Hering et al., 2015).

Changing precipitation dynamics is an important climatic response, which through the alteration of water regime can modify the physical and chemical environment of aquatic assemblages. A very recent study highlighted that 51–60% of lotic habitats, mainly but not exclusively lower order streams, are affected by periodical flow cessations worldwide (Messager et al., 2021). Therefore, it is no exaggeration to say that extremes in water regime can be considered as key drivers shaping algal assemblages and lead to diversity changes both in the case of phytoplankton (Thompson et al., 2015; Bussi et al., 2016) and phytobenthos (B-Béres et al., 2019; Tornés et al., 2021).

Extremes in water discharge such as flooding or drastically low water levels can also be observed in perennial rivers worldwide (Messager et al., 2021). Although, drying itself is not typical for these waters, the low water level and the partially dry riverbed may even indicate similar changes in the community composition, as can be observed in intermittent water bodies during pool formation (B-Béres et al., 2014). However, it should be emphasized that while planktic algae of larger rivers are known to experience the adverse effects of changing environment (Larroudé et al., 2013; Hardenbicker et al., 2014; Abonyi et al., 2018), studies on the relationship between climatic extremes and benthic algae mostly focus on assemblages living in small streams (Sabater et al., 2016, 2017; B-Béres et al., 2019; Stubbington et al., 2019; Novais et al., 2020). Those studies that do deal with compositional changes in phytobenthos of large rivers caused by extreme water level fluctuations, are short-term examinations (e.g. B-Béres et al., 2014; Tornés et al., 2015). Therefore, our knowledge of the long-term effects of climatic extremes and ongoing climate change induced precipitation loss on benthic algal communities in large rivers is still incomplete.

Benthic algae are the most important and profuse microscopic elements of biofilms, usually with the pivotal dominance of diatoms. As basic components of food webs (Kireta et al., 2012) and providers of 20% of the global primary production (Smetacek, 1999), the huge ecological importance of benthic diatoms is unquestionable (B-Béres et al., 2022a). Their cosmopolite feature makes them reliable bioindicators of a wide range of environmental changes. Consequently, they are strong and accurate predictors of extreme climatic events like alteration of water discharge (see more in Novais et al., 2020) even in large perennial rivers (B-Béres et al., 2014). These hydrological modifications may lead to changes in the functional composition of assemblages pushing it towards traits that allow it to survive harsh conditions (Lukács et al., 2021): appearance of mucous tube-forming taxa, as well as increasing dominance of halophilic and halotolerant ones tipically belonging to the larger size range is expected in parallel with the increasing risk of drying (Porter-Goff et al., 2013) or drastic decrease in water level (Kókai et al., 2015). Furthermore, small-sized motile or ruderal taxa also tend to become more abundant (Kókai et al., 2015; Žuna Pfeiffer et al., 2015). Therefore, potential appearance of extremity-tolerant species during low water level period of perennial streams may lead to an increase in taxa richness (Kókai et al., 2015). However, prolonged decrease in flow may ultimately lead to diversity loss (Tornés and Ruhí, 2013; B-Béres et al., 2019; Falasco et al., 2021; Tornés et al., 2021) and the disappearance of sensitive species lacking traits suitable for survival in unfavorable habitats (Falasco et al., 2016a; Sabater et al., 2016, 2017; Várbíró et al., 2020). Therefore, diatom functional approaches enable to predict future compositional responses to global environmental changes (Soininen et al., 2016) like decreasing water discharge and current velocity.

In this study, we investigated the benthic diatom assemblages of a large lotic perennial ecosystem, the Rába River, over the last 15 years. The entire Hungarian section of the Rába was involved in the study, since it is the fourth largest river in Hungary and the most significant tributary of the Hungarian section of the Danube (Hungarian Water Authority, 2009). In the last decades, its water level fluctuated drastically (North-Transdanubian Water Directorate, 2022; Supplementary Table 1). In the last century, the number of rainy days decreased in the Carpathian Basin (Bartholy and Pongrácz, 2005), furthermore the grouping of drier and wetter periods was typical, i.e. consecutive years showed a similar distribution of precipitation (Bihari et al., 2018; Szabó et al., 2018). In contrast, from the 21st century, one-off extreme events in precipitation like one-off drought (extreme precipitation deficit) events have become typical (Bihari et al., 2018; Szabó et al., 2018). In addition, a continuous decrease in precipitation can be observed in the last five years. This decrease is referred to as a trend-like phenomenon, since it has definitely started, but the end is not yet in sight.

Analysing a long term benthic diatom data for the perennial Rába River, we aim to answer the main question: Do one-off drought events and trend-like precipitation decrease result in similar changes within diatom assemblages? Because, it has been already demonstrated that resilience and resistance of assemblages may vary depending on whether the drought occurs regularly or only occasionally (Acuña et al., 2014).

Accordingly, we set up the following hypotheses:

(H1) One-off drought events – During these events, characteristic taxa and functional traits can be identified, as well as higher diversity loss and generally lower ecological status are expected than under average rainfall conditions.

(H2) Trend-like changes – Continuous decrease in annual precipitation will result in more pronounced compositional and diversity changes within the assemblages compared to the fluctuating environment, since the latter enable structural recover in average years. This trend will be accompanied by a deterioration in diatom-based ecological status of the Rába River.

2. Material and methods

2.1. Sampling setup and measurements

The Rába River springs from the Austrian Alps and flows into the Mosoni-Duna (a tributary of the Danube) in the city of Győr (Hungary). The total length of this river is 283 km, the catchment area is 10,113 km^2, and the mean water discharge is 27 m^3 s^{-1} at Győr (Hungarian Water Authority, 2009). From the Hungarian-Austrian border to the confluence with the Danube, the Rába is a hilly river with coarse, calcareous bed material with large (1000–10,000 km^2) and very large (>10,000 km^2) catchment size (sampling points No. 1–4). After the confluence with the Marcal, it becomes a lowland river with calcareous, medium-fine bed material with very large (>10,000 km^2) catchment size (sampling points No. 5–6) (Supplementary Table 2; Hungarian Water Authority, 2022). Altogether 105 diatom samples were collected at the six sampling sites (Supplementary Table 2; Fig. 1) between 2007 and 2021. The frequency of sampling events varied for each point, however, sampling was generally done twice a year, in spring and autumn. Substrates were cobbles in all cases. Sampling points on the Rába were determined in accordance with the objectives and ordinance of the Water Framework Directive (EC, 2000). The selection of the sampling sites was based on not only hydromorphology (hilly/lowland), but also on other aspects, such as the inflowing smaller watercourses, which can affect the physical and chemical parameters of the recipient water, and can also affect freshwater organisms (Hungarian Water Authority, 2022).

Altogether 13 environmental factors were measured at each sampling event. Water temperature (T – °C), pH, conductivity (COND – μS cm^{-1}) and dissolved oxygen (DO – %) were directly measured in the field with a portable multiparameter digital meter (Multi 3630 IDS SET F, Germany). Water samples were also collected for further laboratory analyses. The following chemical parameters were measured in the environmental laboratory of the Győr-Moson-Sopron County

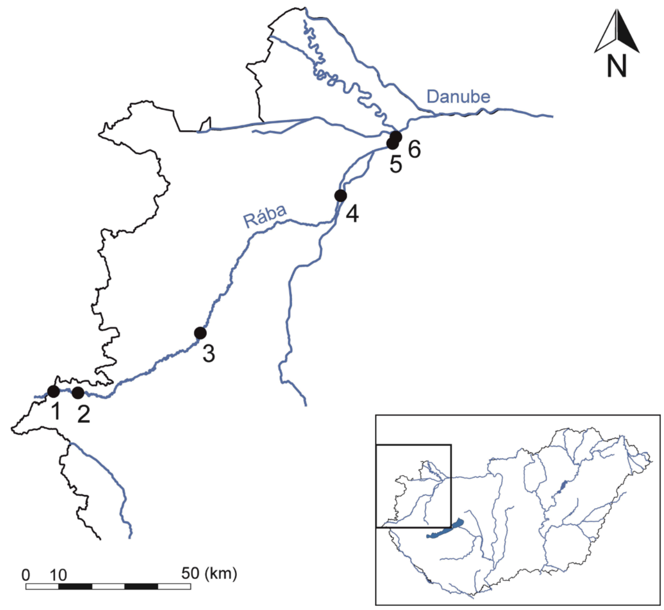

Fig. 1. Location and order of sampling sites along the Hungarian section of Rába River. 1 – Szentgotthárd; 2 – Csörötnek; 3 – Rum; 4 – Árpás; 5 – Rábapatona; 6 – Győr. The distance between sampling points is 10.8 km (between 1st and 2nd), 91.91 km (2nd-3rd), 88.09 km (3rd-4th), 15.03 km (4th-5th), 12.18 km (5th-6th), respectively.

Government Office according to national or international standards: biological oxygen demand (BOD_5 – mg L^{-1}, iodometry, MSZ EN 1899-1, 2000), chloride ion (Cl^- – mg L^{-1}, argentometry, MSZ 1484-15, 2009), chemical oxygen demand (COD_{Cr} – mg L^{-1}, chromatometry, MSZ 12750-21, 1971), ammonium ion (NH_4^+ – mg L^{-1}, spectrophotometric analysis, MSZ ISO 7150-1, 1992), nitrite ion (NO_2^- – mg L^{-1}, spectrophotometric analysis, MSZ 1484-13, 2009), nitrate ion (NO_3^- – mg L^{-1}, spectrophotometric analysis, MSZ 1484-13, 2009), total amount of N-forms (TN – mg L^{-1}, chemiluminescense based detection, MSZ EN 12260, 2004), phosphate ion (PO_4^{3-} – μg L^{-1}, spectrophotometric analysis, MSZ 12750-17, 1974), total amount of P-forms (TP – μg L^{-1}, spectrophotometric analysis, MSZ EN ISO 6878, 2004). Precipitation data measured at Szombathely meteorological station (Hungary) was provided by the Hungarian Meteorological Service (data provision on personal request).

Sampling and preservation of diatom samples were done according to international standard (EN 13946, 2014). After preparing diatom frustules by hot hydrogen-peroxide method, Naphrax® mounting medium was used for embedding. At least 400 valves were counted in each sample according to EN 14407 (2014) standard. Identification of diatom taxa was performed according to Krammer and Lange-Bertalot (1997a, 1997b, 2004a, 2004b) and Bey and Ector (2013) by using 1000–1600-fold magnification (Nikon ECLIPSE E600).

2.2. *Data processing and analyses*

To answer the study questions and test the hypotheses, the data involved in the analyses were classified according to two groupings based on precipitation data between 2007 and 2021 (Supplementary Table 3).

(i) To test the trend-like effects of continuously decreasing precipitation on the benthic diatom assemblages, a period-based grouping of data was applied (hereafter, **PeBG**): the 15-year-long sampling period could be sharply separated by the pattern of precipitation, having a fluctuating period between 2007 and 2016 (hereafter, FuP) and another drying period between 2017 and 2021 (hereafter, DrP) with monotonously decreasing annual precipitation data (Fig. 2a and b).

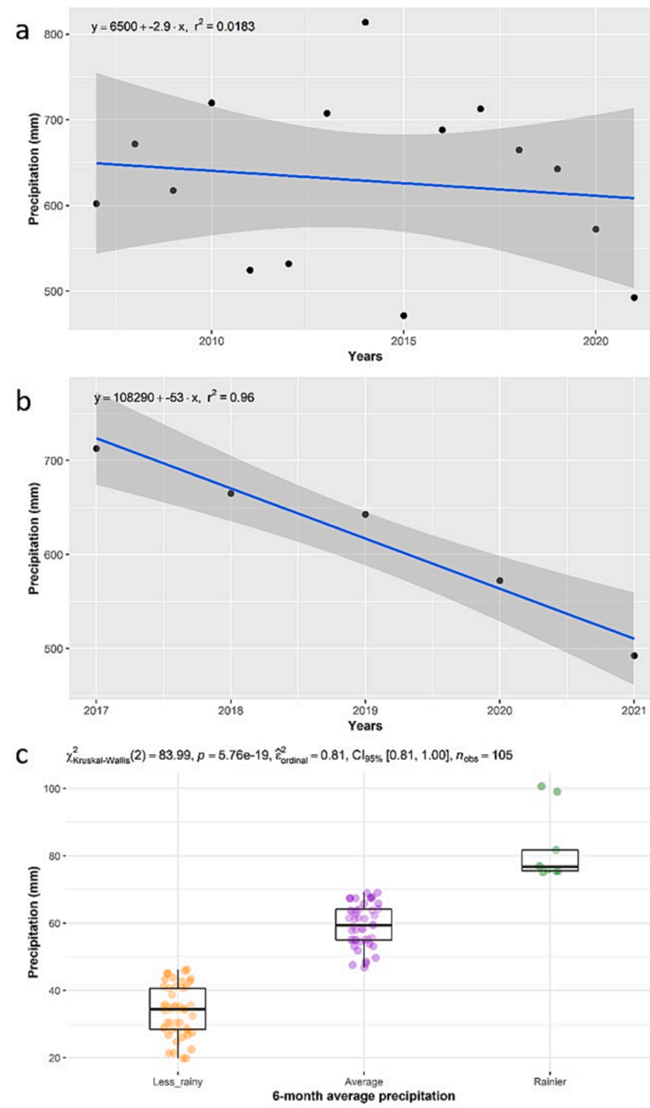

Fig. 2. (a) Annual precipitation during the whole sampling period, and (b) between 2017 and 2021, measured at Szombathely, Hungary. (c) Differences in precipitation among events of MPBG.

(ii) To test the effects of one-off droughts, the 6-month average precipitation data before biological sampling was analysed (hereafter, **MPBG**): based on the 33.3 and 66.6 percentiles of the 15-year precipitation data, three different precipitation conditions were distinguished. Nine sampling events have been included in the upper third of the data, and these were considered rainier events (hereafter, MrE). The middle third contained forty-six events that were considered average rainfall events (hereafter, ArE), while the lower third denoted less rainy events (hereafter, LrE), including the fifty driest events' data (Fig. 2c).

Diatom taxa were classified into five traits: cell size (5 categories) according to Berthon et al. (2011), guild (4 categories), life-form (3 categories) and pioneer character according to Rimet and Bouchez (2012) and length–width (L/W) ratio (6 categories) according to Stenger-Kovács et al. (2018; Supplementary Table 4).

To express ecological status of each sampling site, river tipology specific diatom based IPSITI index (Hungarian phytobenthos metric) was used suggested by the Hungarian guide for implementing EU Water Framework Directive (Várbíró et al., 2012). It was calculated according to the following equation (Várbíró et al., 2012):

$$IPSITI = (IPS + SI + TI)/3$$

IPS: Specific Pollution Sensitivity Index (Coste, 1982).
SI: Austrian Saprobic Index (Rott et al., 1997).
TI: Austrian Trophic Index (Rott et al., 1999).

IPS, SI and TI indices were calculated using OMNIDIA software package (version 5.2; Lecointe et al., 1993) based on the weighted average equation of Zelinka and Marvan (1961) modified by Coste (1982).

To assess the impact of the two hydrologically different periods (i.e. PeBG and MPBG) on the taxonomic and functional composition of assemblages, non-metric multidimensional scaling (NMDS; Canoco 5.0; ter Braak and Šmilauer, 2002) was applied using taxa abundance and trait community weighted mean (CWM) matrices. To create the CWM matrix, average values of traits in the assemblages were weighted by the relative abundances of the taxa. Permutational multivariate analysis of variance (PERMANOVA) was performed on the community matrix after NMDS analyses to test for statistically significant differences in terms of composition (Anderson, 2001) The percentage breakdown of average dissimilarity between the groups was determined by similarity percentage (SIMPER) analysis using the Bray-Curtis dissimilarity index (Clarke, 1993). The PERMANOVA and SIMPER analyses were performed using Past 4.03 (Hammer et al., 2001).

Number of taxa was expressed by taxa richness (Taxa_S). Effective Shannon's H (exponential of Shannon's H; Jost, 2006) was calculated to compare the 'true diversities' of assemblages (Beck and Schwanghart, 2010; Stuart-Smith et al., 2013; Morris et al., 2014). Taxa richness and effective Shannon's H were calculated using Past software (version 4.03; Hammer et al., 2001).

Regarding functional diversity metrics, functional richness (FRich), functional evenness (FEve) and functional divergence (FDiv) were calculated according to Villéger et al. (2008), while functional dispersion (FDis) was estimated following the description of Laliberté and Legendre (2010). The calculation of these functional diversity metrics was conducted in R environment (Laliberté and Legendre, 2010; version 3.5.2; R Core Team, 2019).

In case of normal distribution, unpaired T-test or one-way ANOVA and in case of non-normal distribution, Mann-Whitney or Kruskal-Wallis was used to compare the environmental background, diversity characteristics and ecological status between groupings (R Core Team, 2019). In order to use the correct method, the distribution (normal or non-normal) of our data was analyzed with Shapiro-Wilk test. The fixed factors were the categories of the period-based grouping (PeBG; trend-like changes) and of the one-off drought events (MPBG), while the dependent variables were the 13 environmental variables, Taxa_S, effective Shannon's H, functional richness (FRich), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and IPSITI.

3. Results

3.1. Environmental background

Although significant changes in the annual precipitation (mm) could not be detected in the whole sampling period (2007–2021; $p > 0.05$; Fig. 2a and b), according to the period-based grouping (PeBG), precipitation distribution was remarkably different between fluctuating- (FuP) and drying periods (DrP). While annual precipitation values showed stochastic yearly fluctuations in FuP, there was a significant decrease in rainfall in DrP ($p = 0.004$; Fig. 2b). As far as MRBG, i.e. grouping based on the 6-month average precipitation data before biological sampling, is concerned, the highest mean value of rainfall was detected in November 2014 (100.6 mm) and the lowest one in April 2008 (19.8 mm). This latter value was 60% less than the 6-month average in the studied 15 years (49.1 mm). Distribution of precipitation data in the three groups distinguished in the MPBG is shown on Fig. 2c.

In PeBG, water temperature, biological oxygen demand, dissolved oxygen and ammonium showed significant alterations ($p < 0.05$; Table 1). While water temperature and ammonium were higher in DrP, biological oxygen demand and dissolved oxygen were measured in lower concentrations in that period. In MPBG, water temperature and chloride were the lowest during the rainier events, while phosphate was the lowest during the less rainy events. In addition, the pH, conductivity and total phosphorus were significantly lower during the average events than in the other two conditions ($p < 0.05$; Table 1). All values of the measured environmental parameters were listed in the Supplementary Table 5.

3.2. Taxonomic composition

A total of 216 diatom taxa were identified: 202 at species and 14 at genus level. 44 taxa proved to be dominant (relative abundance ≥ 5%) in the whole sampling period and 12 of them were considered characteristic elements of benthic diatom assemblages (occurence ≥ 10% of total number of samples; Supplementary Table 6). Altogether 199 taxa were identified in the 68 samples in the fluctuating period (FuP). Afterthat, in the drying period (DrP), a total of 144 taxa were found in the 37 samples. While in the 96 samples of the rainier events (MrE) altogether 96 taxa occured, a total of 173 taxa were present in the 50 samples of the less rainy events (LrE) and altogether 183 taxa were found in the average rainfall events (ArP; 46 samples). Taxa that were recorded exclusively in one period of a grouping occurred only in few samples in every cases.

The NMDS explained 76.65% of the variance in the taxonomic composition of benthic diatom assemblages for the first two canonical axes. The eigenvalues of the first and second axes were 0.4685 and 0.2980, respectively (Fig. 3). The PERMANOVA analysis revealed significant differences ($p = 0.02$) between the fluctuating and drying periods in PeBG. The drying period was characterized by only a few species such as *Amphora pediculus* (APED), *Eolimna minima* (EOMI), *Nitzschia inconspicua* (NINC) and *Reimeria sinuta* (RSIN). In contrast, *Gomphonema*, *Navicula* and *Nitzschia* spp. were characteristics in the FuP (Fig. 3a). The quantitative contribution of species to the differences between drying and fluctuating periods is shown in Supplementary Table 7a. The PERMANOVA analysis did not reveal significant

Table 1
Results of unpaired T-test (T) or one-way ANOVA (OA) in case of normal distribution and Mann-Whitney (MW) or Kruskal-Wallis (KW) analyses in case of non-normal distribution. Dependent variables were the environmental parameters, the fixed factors were the samples according to the two groupings: PeBG – period-based grouping, MPBG – "6-month average" based events. Bold letters represent significant correlations ($p < 0.05$). T – water temperature (°C); BOD_5 – biological oxygen demand (mg L^{-1}); DO – dissolved oxygen (%); COND – conductivity (μS cm^{-1}); Cl^- – chloride (mg L^{-1}); NH_4^+ – ammonium (mg L^{-1}); NO_2^- – nitrite (mg L^{-1}); NO_3^- – nitrate (mg L^{-1}); PO_4^{3-} – phosphate (μg L^{-1}); TP – total amount of P-forms (μg L^{-1}); TN – total amount of N-forms (mg L^{-1}); COD_{Cr} – chemical oxygen demand (mg L^{-1}).

	PeBG			MPBG		
	p-value	F-value	test	p-value	F-value	test
T	**0.0111**	–	T	**0.0074**	5.152	OA
BOD_5	**0.0065**	–	MW	0.0857	–	KW
DO	**0.0009**	–	T	0.0601	2.892	OA
pH	0.6067	–	MW	**0.0347**	–	KW
COND	0.9009	–	MW	**0.0435**	–	KW
Cl^-	0.6111	–	MW	**0.0265**	–	KW
NH_4^+	**0.0012**	–	MW	0.2722	–	KW
NO_2^-	0.7873	–	MW	0.1703	–	KW
NO_3^-	0.2884	–	MW	0.2736	–	KW
PO_4^{3-}	0.1694	–	MW	**0.0016**	–	KW
TP	0.5796	–	MW	**0.0138**	–	KW
TN	0.3058	–	MW	0.2074	–	KW
COD_{Cr}	0.9358	–	MW	0.4637	–	KW

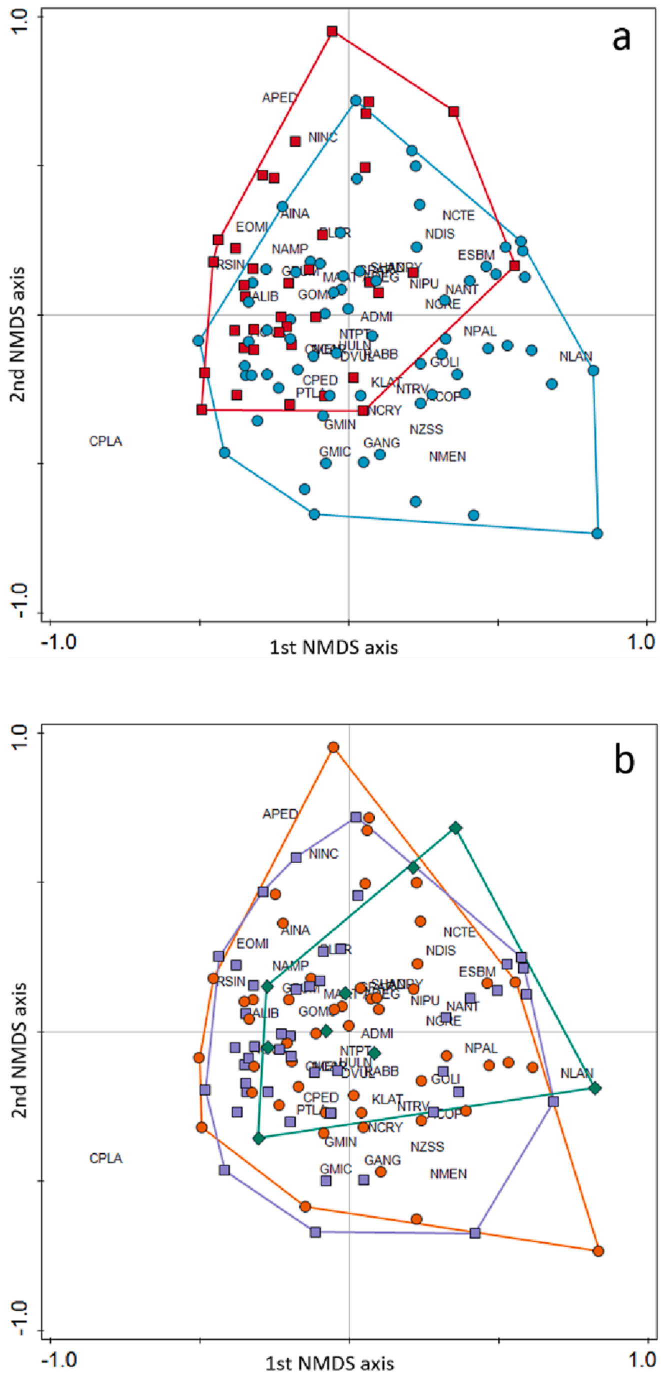

Fig. 3. Taxonomic composition according to (a) PeBG – blue circles repesent samples of FuP, red squares represent samples of DrP; and (b) MPBG – green diamonds represent samples of MrE, purple squares represent samples of ArE, orange circles represent samples of LrE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dissimilarity ($p = 0.28$) among the three different precipitation conditions of MPBG. Almost a complete overlap was observable among the rainier (MrE), less rainy (LrE) and average rainy events (ArE) (Fig. 3b). The quantitative contribution of species to the differences between less rainy and average rainfall events, less rainy and rainier events and rainier and average rainfall events is shown in Supplementary Table 7b-d.

3.3. Trait composition

The NMDS explained 82.20% of the variance in the functional composition of benthic diatom assemblages for the first two canonical axes. The eigenvalues of the first and second axes were 0.5688 and 0.2532, respectively (Fig. 4). While the PREMANOVA analysis revealed significant dissimilarity ($p = 0.001$) between the fluctuating (FuP) and drying (DrP) periods, trait compositions of the less rainy, rainier and average rainfall events (LrE, MrE and ArE) were very similar ($p > 0.05$).

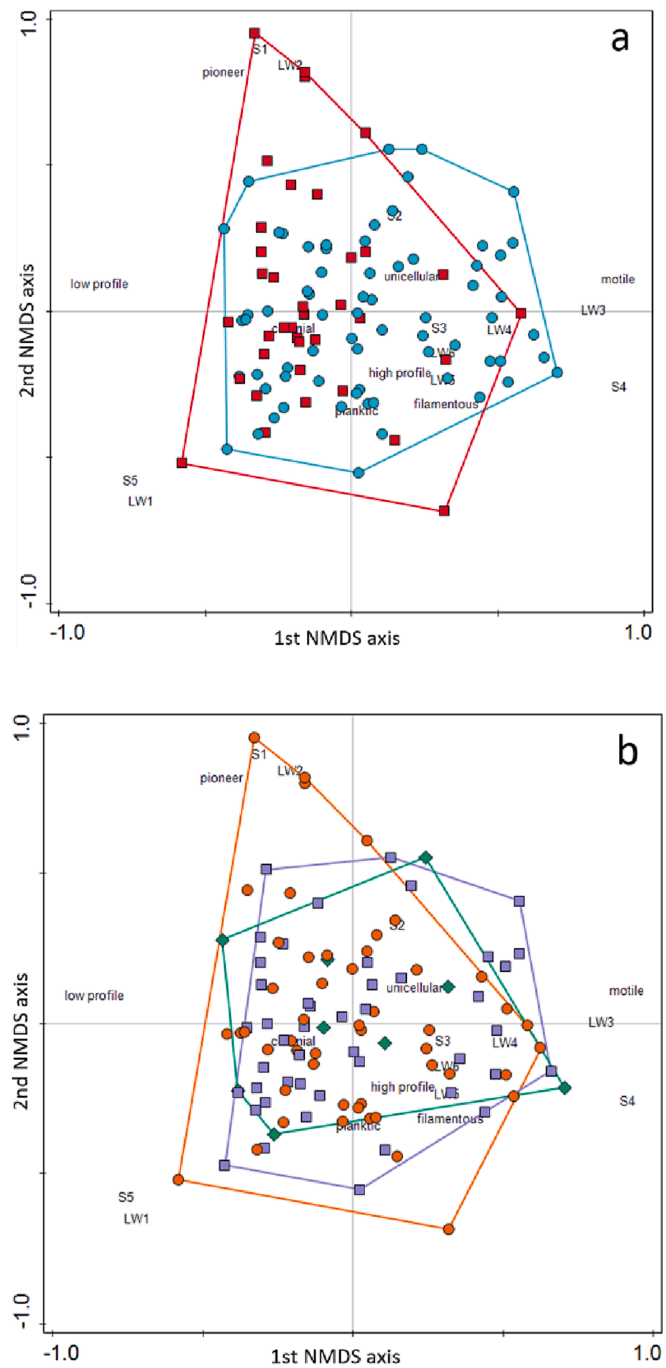

Fig. 4. Functional composition according to (a) PeBG – blue circles repesent samples of FuP, red squares represent samples of DrP; and (b) MPBG – green diamonds represent samples of MrE, purple squares represent samples of ArE, orange circles represent samples of LrE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The drying period was characterised by small (S1), quite round-shaped (LW2), pioneer taxa (Fig. 4a). Motile and LW3 trait categories, however, seemed to characterize the fluctuating period (FuP; Fig. 4a). The quantitative contribution of traits to the differences between drying and fluctuating periods as well as less rainy, rainier and average rainfall events is shown in Supplementary Table 8.

3.4. Diversity and ecological status

No significant differences were detected either in taxa richness ($p > 0.05$; Supplementary Fig. 1b) or in effective Shannon_H ($p > 0.05$; Supplementary Fig. 2b) among MrE, ArE and LrE. In contrast, both taxa number ($p < 0.002$; Supplementary Fig. 1a) and taxon diversity ($p < 0.001$; Supplementary Fig. 2a) were significantly lower in DrP than in FuP of PeBG (Table 2). One of the four calculated functional diversity metrics (FRic) revealed significant ($p \leq 0.05$) difference between drying (DrP) and fluctuating (FuP) periods (Supplementary Fig. 3; Table 2). Moreover, functional dispersion (FDis) was remarkably higher in LrE compared to ArE and MrE ($p = 0.05$) (Supplementary Fig. 4; Table 2).

Surprisingly, no significant differences in IPSITI ($p > 0.05$; Table 2, Supplementary Fig. 5) were detected either in PeBG or in MPBG.

4. Discussion

4.1. Environmental background

To the best of our knowledge, neither drastic nutrient load nor any diffuse or point source pollution affected the Rába River during the study period. However, climatic events such as one-off drought events, as well as the continuously decreasing amount of precipitation during the last five years, significantly influenced the physical and chemical conditions of the river. The single extreme events had a significant effect on T, pH and PO_4^{3-} concentration. The higher than average precipitation was presumably associated with lower daily temperatures and less intense light transmission, therefore, water temperature was significantly lower during this period. Changes in nutrient content are influenced by several abiotic and biotic processes closely related to each other (Magand et al., 2020). In the less rainy period, the high phosphate content may indicate the reduced activity of primary producers. However, the pH, which is closely related to the photosynthetic activity, was the lowest in the average rainfall period. In addition, dissolved oxygen also referring to algal activity showed no significant difference between the three precipitation conditions. Therefore, it may simply be that lower precipitation resulted in the concentration of phosphate in the less rainy period. Decreases in chloride (in rainier events), conductivity and TP (in average events) are also not surprising, as high or even normal amount of rainfall prevents salts and nutrients from becoming highly concentrated in the water.

Table 2
Results of unpaired T-test (T) or one-way ANOVA (OA) in case of normal distribution and Mann-Whitney (MW) or Kruskal-Wallis (KW) analyses in case of non-normal distribution. Dependent variables were the taxa number, the taxonomic (Effective Shannon_H) and functional diversity metrics (FRic, FEve, FDiv, FDis), and the IPSITI diatom index, the fixed factors were the two groupings. Bold letters represent significant ($p < 0.05$), italic letters represent marginally significant correlations.

	Period-based grouping (PeBG)			"6-month average" based events (MPBG)		
	p-values	F-values	test	p-values	F-values	test
Taxa number	**<0.002**	–	MW	0.76	–	KW
Effective Shannon_H	**<0.001**	–	MW	0.55	–	KW
Functional richness (FRic)	**0.01**	–	T	0.94	0.037	OA
Functional evenness (FEve)	0.62	–	MW	0.71	–	KW
Functional divergence (FDiv)	0.85	–	MW	0.78	–	KW
Functional dispersion (FDis)	0.49	–	MW	*0.05*	–	KW
IPSITI	0.10	–	MW	0.70	–	KW

The continuous decrease in precipitation observed in the past five years has already induced significant changes in the physical and chemical variables of the Rába, which may eventually lead to drastic deterioration in the river's ecological condition. Due to the decreasing water level, higher water temperature characterized the drying period inducing reduced concentration of dissolved oxygen. These results supported the well-known phenomenon that dissolvation of oxygen is less effective in such circumstances, i.e. high water temperature (Padisák, 2005). At the same time, decreasing oxygen may even predict reduced photosynthetic activity, however, the pH has not yet changed significantly in our study. In addition, the ammonium value significantly increased in the drying period, which highlights the importance of nutrient enrichment directly triggered by significantly decreasing precipitation and low water level.

4.2. Compositional changes

Our main question was whether the trend-like changes, i.e. continuous decrease in annual precipitation and the coinciding hydrological regime shift have a more pronounced selective pressure on both taxonomic and trait compositions than one-off dry events. The results revealed that continously decreasing precipitation changed significantly the structure of diatom assemblages (supporting H2), while one-off dry events did not (rejecting H1).

The small-sized (S1), pioneer and low profile *Amphora pediculus* previously identified as a characteristic species of drying habitats (Stubbington et al., 2019), reached considerably higher mean abundance in the drying period (DrP: continuous decrease in annual precipitation). As former studies pointed out, drying processes and rewetting periods have a disturbing effect on community composition in intermittent streams, leading to increasing dominance of small, pioneer species (Tornés and Ruhí, 2013; Novais et al., 2014, 2020; Piano et al., 2017; Várbíró et al., 2020). In larger rivers, these small size generalists usually dominate the benthic algal assemblages under extremely fluctuating water level conditions (B-Béres et al., 2014; Riato et al., 2017).

Other taxa, such as *Eolimna minima* (S1, motile), *Nitzschia inconspicua* (S1, LW2, motile) and *Reimeria sinuata* (low profile, unicellular) also proved to be characteristic elements of phytobenthos and showed increasing mean abundance in drying period (2017–2021). However, of the three species, only *R. sinuata* was found to be dominant (with 6% mean abundance) in this period. In previous studies, *E. minima* was usually detected in environments with higher nutrient supply and higher conductivity (Gevrey et al., 2004; Wojtal and Sobczyk, 2012; Kókai et al., 2015). *N. inconspicua* has wide tolerance spectrum in terms of salinity and nutrient enrichment (Van Dam et al., 1994). *R. sinuata* was also found to be tolerant to high levels of eutrophication (Kelly and Whitton, 1995; Gosselain et al., 2005) as well as to be a characteristic species of intermittent phase in temporary streams (B-Béres et al., 2022b). Although drying up and decrease in water level in dry periods can result in higher concentration of ions dissolved in water (see more in Magand et al., 2020), our hydrochemical results did not show this tendency. Thus, increased nutrient concentration should not be the reason for the presence of the above mentioned taxa. However, motile species (*Navicula* and *Nitzschia sensu lato*) or unicellular taxa attached to substrate with long stalk (e.g. *Reimeria* sp.) are recently recognized to tolerate drying up (Sabater et al., 2016, 2017). As for *Reimeria sinuata*, its mucilage stalk, *inter alia*, may have key role in water retention (Sabater et al., 2017) and may support the dominance of this species in drying period in our study. In contrast, drying-up characteristics of motile taxa are hard to identify at first, because motility allows species to choose favourable habitats in order to avoid disturbance such as altered water regime (Johnson et al., 1997). However, recent studies pointed out that motile guild indicates drying and siltation during the decrease of water level (Falasco et al., 2016b; Novais et al., 2020; B-Béres et al., 2022b), because motile taxa are able to penetrate to the upper layer of the sediment and thus, survive the unpleasant conditions (McKew et al., 2011). That could be the reason of some motile taxa were found to be characteristic in drying period in our study. However, we must emphasize that motile guild itself characterized the fluctuating period. In addition, in the same period, some high profile *Gomphonema* species were characteristic beside the members of motile guild. These stalk-forming high profile species can profit from the favourable nutrient- and light conditions of the upper layers of biofilm, even if they are exposed to relatively high flow disturbance here (Passy, 2007). These results are in high accordance with the findings of Novais et al. (2020) as high profile guild was found to be more abundant in flowing period than during drying.

As we mentioned above, the Rába River is the most significant tributary of the Danube in Hungary (Hungarian Water Authority, 2009). Recent studies have pointed to significant compositional and structural changes in phytoplankton assemblages of the Danube in the past decades: Abonyi et al. (2018) revealed an increase in relative abundance of benthic diatoms within the phytoplankton. This phenonemon may be closely related to the water discharge alteration of the Danube, as low water level condition is one of the key factors that even promotes the dominance of benthic diatoms in the phytoplankton assemblages. We assume that any compositional changes in the benthic algal assemblages in the tributaries of the Danube may affect the structural characteristics of its algal flora.

It is known that drying process incurring habitat loss and environmental changes as an important environmental filter plays pivotal role in forming aquatic communities' composition and basically determines their functionality. Temporary streams facing with drying have strong filtering effect on traits leading to clear dominance of small, pioneer, drought-tolerant species in the Pannonian Ecoregion (Várbíró et al., 2020). Here, indication of drying process and flow cessation should be based on species, which clearly and effectively tolerate these negative tendencies. It was noted by Várbíró et al. (2020) that limiting similarity promoting trait divergence was considered the main force in shaping community structure in Hungarian intermittent watercourses. Based on our results, it seems that this assembly rule may also play key role in functional rearrangement of large perennial rivers experiencing significant loss of precipitation.

4.3. Diversity

We hypothesized higher diversity loss in the years when the 6-month average precipitation data before biological sampling was below the 15-year average than in the years not affected by strong drought (H1). In addition, it was also assumed that continuously decreasing precipitation would result more pronounced decrease in biodiversity than fluctuating environment (H2). The results confirmed our assumptions only partially. Neither taxonomic nor functional diversity-loss were detected during events with less precipitation (rejecting H1). In contrast, continuous precipitation loss resulted in a significantly decreasing trend in taxa number, effective Shannon_H and functional richness (supporting H2). It means that diatom community was characterized by species loss and a higher dominance of some taxa and traits. Therefore, the observed taxonomic changes already have a negative effect on the functional diversity meaning that the Rába River experiences significantly reduced functional richness due to the trend-like decrease of precipitation. Since the other functional diversity metrics do not reflect this trend, the Rába's diatom assemblages are supposed to have capacity to remain their functionality even in these changing conditions, at least for the time being (Valdivia et al., 2017). However, remarkably higher functional dispersion of the less rainy events highlights that precipitation loss is very capable of driving diatom traits towards extremes such as small size and rounded shape (supporting H1).

4.4. Ecological status

Decreasing water discharge caused by reducing precipitation leads to increasing water residence time (Vörösmarty and Sahagian, 2000) that usually associated with deteriorating ecological status (Hutchins et al., 2016). Persistent droughts can significantly change and reduce biodiversity (Klamt et al., 2020) shifting the community composition towards extremes (e.g. small size, halophilic feature – Kókai et al., 2015; aerophilic feature – Tornés et al., 2021). Accordingly, lower diatom index values were expected both in years affected by one-off dry events (less rainy events) and in drying period characterized by continuous decrease in annual precipitation. These hypotheses have not been confirmed by the results (rejecting the 'ecological status part' of H1 and H2), as neither the one-off dry events nor the decreasing precipitation lead to the decline in water quality.

The question of how the drought and drying affect ecological status of waters and which metrics, i.e. diatom-based indices, can be used to show this impact on ecological conditions is intensively studied nowadays (Falasco et al., 2016b; Novais et al., 2020; B-Béres et al., 2022b). Based on the results existing so far, it seems that diatom indices (SI – Rott et al., 1997; TI – Rott et al., 1999; etc.), primarily developed for the detection of nutrient loads, are powerful tools for assessing the influence of drying or drought events in lotic ecosystems.

In our study, the lack of differences in ecological status could be explained by the very similar nutrient supply in drought-affected and non-affected periods (i.e. no significant differences in these parameters, or values of some of them even increase in drying conditions). The compositional changes within the biofilm caused by the prolonged drought can also explain this phenomenon, since in the drying period, mainly one small, low profile, pioneer species (*Amphora pediculus*) dominated the assemblages. Opinions and findings on the nutrient preference of this taxon are controversial, as it was found to indicate high quality waters (Torrisi et al., 2010; Chen et al., 2016) and nutrient-rich environment (Kelly, 1998; Gottschalk and Kahlert, 2012) as well. This species was also identified by Stubbington et al. (2019) as one of the six dry-phase indicator diatom taxa in the ecological status assessment of intermittent rivers and ephemeral streams (IRES). Besse-Lototskaya et al. (2011) already highlighted that monitoring databases contain many unreliable taxa (*inter alia* small pioneer, low profile species), mainly because of their uncertain taxonomy, which contributes the uncertainty about their trophic preference. Our results also confirm this opinion, since here *A. pediculus* indicated the effects of drought-induced disturbances on water regime, rather than simply the good water quality. Therefore, revising and, if it is necessary, modifying the indicator values of certain taxa is highly recommended in order to determine the environmental conditions being responsible for the appearance and increasing abundance of these species.

5. Conclusions

Here, we examined the influence of drought on benthic diatom assemblages in the Rába River, one of the main tributary of the Danube, over the last 15 years. In addition, trend-like changes in phytobenthos caused by the continuous decrease in annual precipitation over the last 5 years were also studied. While the results revealed trend-like differences in taxa- and trait composition of diatom assmeblages in response to the drying trend, one-off droughts did not result in compositional changes in phytobenthos. Surprisingly, drought itself had less effect on diversity metrics. The continuous decrease in annual precipitation, however, resulted in a significant decrease in taxa number and effective Shannon_H, and led to reduced functional richness. In this study, we first analysed the differences between the influence of one-off dry events and trend-like changes in precipitation on benthic diatom assemblages of a perennial large river. Our results clearly highlighted that the continuous decrease in annual precipitation results in stronger compositional and biodiversity changes within the biofilm than a single dry year. Since the climate scenarios project extremes in water regime in the near future, including longer periods of low precipitations, any knowledge, which predicts the changes in microflora, can help to develop action plans by authorities to preserve the functional and structural characteristics of lotic ecosystems, and thereby to maintain ecosystem services provided by benthic diatoms.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Author contributions

ZsNK wrote the manuscript. ZsNK, ÁL and VBB carried out the statistical analyses. KK, RM, ZN, ÁGR, JJ and KÉ provided data. KK and VBB raised the topic. GB and VBB helped in writing of the manuscript. All authors gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110051.

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