Hydrobiologia (2024) 851:897–914
https://doi.org/10.1007/s10750-023-05405-1

MICROALGAL FUNCTIONAL TRAITS

Aquatic phases have a stronger effect on lotic benthic diatoms than human-induced microhabitat variability

Stefánia Kiss · Zsuzsanna Nemes-Kókai · Áron Lukács · István Bácsi · Enikő T-Krasznai · Kamilla Márton · Viktória B-Béres

Received: 11 March 2023 / Revised: 26 September 2023 / Accepted: 4 October 2023 / Published online: 20 November 2023

Abstract Here, we studied the influence of changes of aquatic phases (standing and flowing phases) and human-induced habitat variability (natural and artificial) on the composition and diversity of benthic diatom assemblages in a small lowland stream in the Pannonian Ecoregion. Significant differences in composition were hypothesized between phases and habitats. Lower diversity was hypothesized in the flowing phase and in the artificial habitat. In addition, worser ecological status were assumed in the artificial habitat and in the standing phase than in the others. Our results only partially supported our hypotheses. While there was no significant difference in the composition of the assemblages between the natural and concreted habitats, the alteration in flow conditions resulted in a significant change. No significant differences in diversity were found between aquatic phases. In contrast, biodiversity was higher in the artificial habitat than in the natural one. While the anthropogenic impact, i.e., concreted streambed has no significant influence on diatom-based ecological status, values of diatom indices were significantly higher in the flowing phase. Our results highlight that extreme weather events play a major role in shaping diatom assemblages even

Handling editor: Sidinei M. Thomaz

Guest editors: Viktória B-Béres, Luigi Naselli-Flores, Judit Padisák & Gábor Borics / Trait-Based Approaches in Micro-Algal Ecology

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05405-1.

S. Kiss · Z. Nemes-Kókai · Á. Lukács · E. T-Krasznai · V. B-Béres (✉)
HUN-REN Centre for Ecological Research, Institute of Aquatic Ecology, Department of Tisza Research, Functional Algology Research Group, Bem Square 18/C, Debrecen 4026, Hungary
e-mail: beres.viktoria@gmail.com

S. Kiss
e-mail: stefaniakiss007@gmail.com

Z. Nemes-Kókai
e-mail: kokai.zsuzsanna@ecolres.hu

Á. Lukács
e-mail: lukacsaron93@gmail.com

E. T-Krasznai
e-mail: ekrasznai@gmail.com

S. Kiss · Z. Nemes-Kókai · Á. Lukács
Department of Ecology, University of Debrecen, Egyetem Square 1, Debrecen 4032, Hungary

Z. Nemes-Kókai · Á. Lukács · I. Bácsi · K. Márton
HUN-REN–DE Functional and Restoration Ecology Research Group, Egyetem Sqr. 1, Debrecen 4032, Hungary
e-mail: istvan.bacsi@gmail.com

K. Márton
e-mail: kamillamarton@yahoo.com

I. Bácsi · K. Márton
Department of Hydrobiology, University of Debrecen, Egyetem Square 1, Debrecen 4032, Hungary

during a short period, which should be taken into account in water management and nature conservation measures.

Keywords Aquatic phases · Compositional and biodiversity changes · Concrete stream bed · Ecological status · Intermittent lowland stream

Introduction

Monitoring the inevitable changes in ecosystems caused by climatic extremes and actively responding to the effect of these extremes are one of the most important ecological, economic and social challenges of the century. Freshwater ecosystems are especially threatened by the consequences of climate change, such as flash floods, drastic decrease in water levels, even drying up of watercourses (Várbíró et al., 2020; Messager et al., 2021; Tornés et al., 2021). It has now been proved that intermittent watercourses, i.e., those that are dry for at least one day a year, occur on Earth as often as permanent streams (Messager et al., 2021). Worldwide, approximately 50–60% of watercourses can be considered intermittent (Messager et al., 2021), in the case of small streams, however, this value can exceed 70% (Datry et al., 2014) and their numbers are predicted to increase globally in the coming decades (Pumo et al., 2016).

Benthic diatoms play a pivotal role in the primary production of small watercourses (B-Béres et al., 2022a), which is especially true for intermittent streams in extremely low water level or drying conditions (Robson et al., 2008; Robson & Matthews, 2004). However, drying results in significant structural changes in the phytobenthic community (Tornés et al., 2021). Benthic diatom composition occurring under different hydrological conditions of intermittent streams, such as flowing, pool/standing, and drying phases (Gallart et al., 2017), is strongly dependent on the duration of drought (no precipitation) and drying (no water in the streambed) periods (Acuña et al., 2017; Sabater et al., 2017; Tornés et al., 2021). As flow and water level decrease, lentic taxa appear more and more often within the assemblages (Stubbington et al., 2017), and their abundance is controlled by the duration of low flow conditions before the actual drying (Tornés et al., 2021). In addition, changes in assemblages during the pool phase are mainly influenced by factors such as taxa composition before the drought period, the lifespan of low- or no-flow pools (Magand et al., 2020; Várbíró et al., 2020; Novais et al., 2020), grazing pressure by macroinvertebrates (Fisher & Dunbar, 2007), and the alternation of physical and chemical environments (e.g., increasing temperature and conductivity; decreasing pH and dissolved oxygen; Magand et al., 2020). In the drying phase, water scarcity is obviously the main factor in shaping of biofilm composition and results in increasing number of taxa, which are able to survive these harsh conditions (e.g., terrestrial species) (Timoner et al., 2014; Sabater et al., 2016, 2017; Stubbington et al., 2017).

The structural changes occurring during water scarcity also have a significant impact on biodiversity. However, our knowledge of the relationship between diversity and water intermittency is controversial. To resolve the contradictions, the spatial and temporal extent of diversity change must be examined. Recent studies highlight that biodiversity decreases, if the drying lasts for a long time (> 100 days; Tornés et al., 2021). The longer the dry period and the more watercourses are affected in the catchments, the more likely it is that the negative local effects will manifest at regional and then global level (Pumo et al., 2016; Acuña et al., 2017). It is also important to mention that biodiversity does not decrease linearly during drying. In the standing phase, the appearance of lentic species can even increase the diversity of the assemblages. In addition, newly immigrating aerophilic taxa can also contribute to higher diversity at the beginning of the drying phase (Sabater et al., 2016, 2017). However, recent studies point out that the longer the drying lasts, the higher the number of taxa and traits that disappear from the assemblages (Stubbington et al., 2017; Crabot et al., 2021; Tornés et al., 2021).

The diatom indices currently used to assess the diatom-based ecological status of watercourses were developed for permanent waters and are used to evaluate the quality of intermittent streams during flowing phase in many countries (e.g., EU member states) (Stubbington et al., 2019; Magand et al., 2020). Nowadays, however, there is an urgent need to decide whether these indices are also suitable for assessing the ecological status of streams during pool or dry phases. Up-to-date studies suggest that they can evaluate the effect of drying up and the accompanying environmental changes on the diatom-based ecological status of streams (Novais et al., 2020; B-Béres et al., 2022a, b).

There are a total of ~10,000 watercourses in Hungary, of which only nearly 10% are regularly examined within the framework of the National Monitoring Program (Stubbington et al., 2018; B-Béres et al., 2022b). At the same time, more than 30% of these waters already belong to the intermittent category, but currently only small streams can be classified into this type. The areas most affected by drought and drying are situated in the Great Hungarian Plain (River Basin Management Plan Report Suppl.1.1, 2022). These small streams, however, are not only threatened by drying, but are also affected by many other natural and artificial impacts that can result in short- or longer-term habitat changes. Artificial modifications can be found, for example, in streambed sections before and after bridges, which are fully concreted or covered with hollow concrete slabs. These streambed modifications can significantly affect hydrological conditions (e.g., water velocity), which can result in silt or sand deposition and ultimately changes in physical and chemical parameters (Gál et al., 2020) and the deterioration of ecological quality (Wemple et al., 2018). Our knowledge is, however, still limited of how these stream sections with partially or completely different habitats and environment contribute to the structural stability and biodiversity of aquatic biota (macroinvertebrates—Gál et al., 2020; fish—Wellman et al., 2000). As for diatom assemblages of intermittent streams, only changes caused by natural habitat differences are known so far (Witteveen et al., 2020).

The aim of our investigation was to study the structural and diversity changes in the benthic diatom assemblages of an intermittent lowland stream in the Great Hungarian Plain during different aquatic phases (flowing and standing phases) at two sampling sites, which are located very close to each other, but they differ significantly in their habitats (natural and artificial habitats). We also studied how changes in hydrological conditions and microhabitats influence the diatom-based ecological status of the stream.

We formulated the following hypotheses:

(H1) Environmental variables—Aquatic phases and anthropogenic effects strongly influence the physical and chemical characteristics of the stream.

(H2) Assemblages' composition—Significant differences in composition are hypothesized between both aquatic phases and habitats.

(H3) Biodiversity—Biodiversity is higher in standing phase than in flowing phase, while artificial habitat maintains less diversity than the natural one.

(H4) Diatom indices and diatom-based quality—Both drought and anthropogenic impact result in decreasing diatom-based quality, thus significantly lower values of indices can be expected in standing phase and artificial habitat than in the other cases.

Materials and methods

Study area, sampling setup, and environmental parameters

Altogether 24 diatom samples were collected from two sites of a small, intermittent lowland stream (Létai-ér) in the Pannonian Ecoregion (Eastern Hungary) (Fig. 1; Supplementary Fig. 1). The studied stream passes through mostly agricultural areas, pastures, and villages. Létai-ér belongs to the R04 Broad type (Solheim et al., 2019): the total length of this stream is 38.4 km, its catchment area is 157.4 km^2, the bedrock is calcareous, and the sediment size is medium to fine (River Basin Management Plan Report Suppl.1.1, 2022). The stream shape is winding, the macrovegetation cover is significant, and the characteristic taxa are mostly *Glyceria maxima* (Hartm.) Holmb. (great manna grass), *Lemna* L. spp. (duckweed*), Ceratophylum demersum* L. (hornwort), *Sparganium erectum* L. (simplestem bur-reed), *Berula erecta* (Huds.) Coville (lesser water-parsnip), *Phragmites australis* (Cav.) Trin. ex Steud. (common reed), and *Mentha* L. spp. at the studied section.

Total annual precipitation was 568.85 mm in 2020 in the region (Supplementary Table 1), which corresponds to the value for the country (500–800 mm/year; The OMSZ' General Review of the Climate of Hungary). However, there was a significant difference in the distribution of precipitation between months: While early/mid-summer (June and July) was the wettest period in 2020, April and November were the driest ones (Supplementary Table 1). But it has to be emphasized that the daily distribution of precipitation

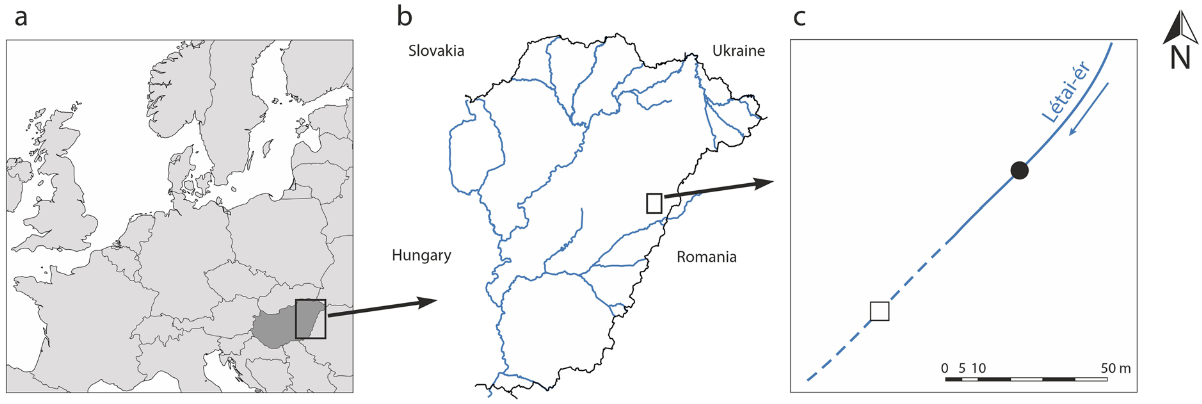


Fig. 1 The location of Hungary in Europe (**a**) and the location of study area (Létai-ér, Monostorpályi) in Eastern Hungary (**b**). The sampling sites (**c**): The solid line represents the natural part of the stream, and the black circle represents the sampling site here, while dashed line represents the artificial part of the stream and white square represents the sampling site here

was not uniform in June and in July, more than 70% of the total monthly precipitation fell on the area in 5 days in June and 3 days in July. As for the air temperature, its average daily value was the lowest in January, while the highest in August (Supplementary Table 2). Based on these data it is clear there was a strong positive correlation between air temperature and monthly precipitation in the region ($P=0.037$).

In 2020, benthic diatom and surface water samples were collected approximately every four weeks (from 06.01.2020 to 17.12.2020). Altogether 12 and 12 samples were taken from two different habitats, which are close to each other: one natural (47° 23′ 20.2″ N; 21° 46′ 23.7″ E) and one artificial (47° 23′ 19.6″ N; 21° 46′ 23.8″ E). The distance between the habitats is about 20–30 m (Fig. 1). In October, the water depth in the natural habitat was so low that surface water sample could not be taken, so the number of samples for measuring physical and chemical parameters is not equal in the two habitats (11 in natural habitat and 12 in artificial habitat). The features of the natural habitat, e.g., macrophyte cover, bedrock, sediment size, are the same as the general characteristics of the stream itself. In contrast, the artificial habitat is concreted, the sides of the streambed (littoral zone) are covered by hollow concrete slabs. The sediment is fine mud and pebbles. There are no emergent macrophytes in streambed, while duckweed and green algal filaments are common in summer.

To describe the hydrological conditions of the stream during the sampling year, we used the classification system introduced by Gallart et al. (2017). According to this system, two aquatic phases could be distinguished: flowing phase and standing/pool phase. The flowing phase is characterized by copious flow or at least scarce flow conditions, in contrast, there is no water flow in standing/pool phase (Magand et al., 2020). While 5 flowing phase and 7 standing phase events were observed in the natural habitat, the opposite was the case in artificial habitat (7 flowing phase events and 5 standing phase events) (Supplementary Table 3). It means that a total of 12 flowing phase and 12 standing phase events could be detected in 2020.

A total of 18 physical and chemical parameters were measured during samplings. Water temperature (T in °C), dissolved oxygen (O_2 in mg L^{-1}), oxygen saturation (O_2%), pH, oxidation–reduction potential (ORP in mV), conductivity (COND in µS cm^{-1}) were measured in the field with a portable multi-parameter digital meter (HQ30d, Germany). In addition, water samples were collected for further laboratory analyses. The samples were stored at 4 °C in a cooler bag during transportation to the laboratory. Total suspended solids (TSS in mg L^{-1}—MSZ 12750-6, 1971) and total dissolved solids (TDS in mg L^{-1}—Németh, 1998) were measured according to national standard and proposal. Biological oxygen demand (BOD in mg L^{-1}—MSZ EN 1899-2, 2000), chemical oxygen demand (COD_{Mn} in g m^{-3}—Felföldy, 1987), and chlorophyll-a content (Chl-a in µg L^{-1}—Felföldy, 1987) were measured according to international standard and national proposal. Nutrient, silicate, and chloride contents were determined according to international and national standards (NO_3^-–N in mg L^{-1}—MSZ 1484-13, 2009; NO_2^-–N in mg L^{-1}—MSZ 1484-13, 2009; NH_4^+–N in mg L^{-1}—MSZ ISO 7150-1, 1992; PO_4^{3-}–P in mg L^{-1}—MSZ EN ISO 6878, 2004; SO_4^{2-} in mg L^{-1}—MSZ 448-13, 1983; Si in mg L^{-1}—ASTM D859-00, 2000 and Cl^- in mg L^{-1}—MSZ 1484-15, 2009). The assessment of water quality based on physical and chemical parameters was done according to the 3rd River Basin Management Plan Report (River Basin Management Plan Report Suppl.6.3, 2022).

Diatom sample collection, preparation, and identification

Sampling and preservation of benthic diatoms were done according to international standard (EN 13946, 2014). Benthic diatom samples were collected from submerged and emergent macrophytes in the natural habitat, while pebbles and green algal filaments (in summer) were used as substrate in the artificial (concreted) habitat. At least five stems (emergent) and five entire plants (submerged) or five pebbles were sampled. Diatom samples were preserved on the field with acetate-free Lugol's solution. According to international standard (EN 13946, 2014), the hot hydrogen-peroxide method was used for digestion of organic matters and Naphrax resin was used for embedding. At least 400 valves per sample were recorded and identified at least to species level using Leica DMRB light microscope at 1000–1600× magnification (EN 14407, 2014). Literature used for the identification of taxa was Krammer and Lange-Bertalot (1997a, 1997b, 2004a, 2004b), Hofmann et al. (2006), Bey and Ector (2013), Potapova and Hamilton (2007) and Stenger-Kovács and Lengyel (2015). Names of taxa were updated using the database of AlgaeBase (Guiry & Guiry, 2023).

Data processing and analyses

Diatom taxa were classified into six traits with a total of 22 categories: length–width (L/W) ratio (6 categories) according to Stenger-Kovács et al. (2018), cell size (5 categories) according to Berthon et al. (2011), attachment types (3 categories) according to Lange et al. (2016), life forms, guilds, and pioneer character (3, 4, 1 categories, respectively) according to Rimet and Bouchez (2012) (Supplementary Table 4).

Taxa richness (Taxa_S), effective Shannon's H (effSH; Jost, 2006; Chao et al., 2014) and Rao's quadratic entropy (FD_Q; Rao, 1982) were used to measure diversity. Taxa richness and Shannon's H were calculated using Past software (version 4.12; Hammer et al., 2001). Effective Shannon's H is the exponential of Shannon's H. The functional diversity metric, Rao's quadratic entropy, is a suitable metric for multitrait analysis (Botta-Dukát, 2005). It was calculated using CANOCO 5.0 software package (Šmilauer & Lepš, 2014).

To assess the diatom-based ecological quality of the stream, four diatom indices were calculated: Specific Pollution Sensitivity index (IPS; Coste, 1982), Rott's Saprobic Index (SID; Rott et al., 1997), Rott's Trophic Index (TID; Rott et al., 1999), and the Hungarian Phytobenthos Metric (IPSITI; Várbíró et al., 2012). While diatom indices IPS, SID, and TID were calculated using the OMNIDIA software (Version 5.2; Lecointe et al., 2003), the ISPITI is the mean of the previously mentioned indices. The final value of these indices varies between 1to 20, where 1 indicates the worst and 20 represents the best quality.

Normality was tested by Shapiro–Wilk test. For testing significant differences in physical and chemical parameters between aquatic phases and habitats, unpaired t test (normal distribution data) or Mann–Whitney test (non-normal distribution data) were used. Monte Carlo permutation test (default 499 permutation) were performed to decide whether the detected pattern was significantly different from random. All these analyses were performed using Past software (version 4.12; Hammer et al., 2001).

To assess the impact of aquatic phases and habitats on the taxonomic and functional composition, nonmetric multidimensional scaling (NMDS; Canoco 5.0; Šmilauer & Lepš, 2014) was applied using the relative abundance of taxa and the 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 matrix. 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). To identify the indicative species and traits of aquatic phases and habitats, indicator value (IndVal) analyses based on the relative abundances of taxa and CWM of traits were performed (Dufrêne & Legendre, 1997) using Past software (version 4.12; Hammer et al., 2001).

To compare the values of diversity metrics and diatom indices between aquatic phases and habitats, unpaired t test was used (Past software, version 4.12; Hammer et al., 2001). The fixed factors were the phases (flowing *vs.* standing) and the habitats (natural *vs.* artificial) and the dependent variables were Taxa_S, effSH, and FD_Q as diversity metrics and IPS, SID, TID, and IPSITI as diatom indices.

Results

Environmental background

Altogether 18 environmental variables were involved in the analyses (Supplementary Table 5). Although the Létai-ér is in good condition based the annual average data of pH, conductivity, biological oxygen demand, dissolved oxygen, chloride, and inorganic nitrogen content, its phosphate concentration is very high (poor quality) (Table 1). The oxygen balance of the stream deteriorated significantly in the standing phase (mainly from mid-summer to late autumn); both dissolved oxygen and oxygen saturation were significantly lower during this phase ($P < 0.001$). Oxygen supply of the stream was strongly negatively related both to precipitation and air temperature (Supplementary Table 6). In contrast, temperature, chemical oxygen demand (COD), and phosphate-phosphorus content were significantly higher in standing phase ($P < 0.005$ and $P < 0.05$, respectively) (Table 1). Except the COD, these parameters positively correlated with air temperature and precipitation. It is important to stress again, that total amount of precipitation was high in early and mid-summer, however its distribution was clearly not uniform (Supplementary Table 1) due to the heavy rainy days in the region. As for natural and artificial, habitats, the concreting of the streambed did not result in significant differences in the physical and chemical variables (Table 1).

Taxa composition

A total of 151 diatom taxa were identified in the samples, all of them at least to species level (Supplementary Table 7). In flowing phase, altogether 123 taxa were recorded, while 117 taxa were found in standing

Table 1 Mean values of physical and chemical parameters measured in aquatic phases and in habitats

Significant differences in environmental parameters between phases or habitats are represented by *(<0.05), **($P < 0.01$), and ***($P < 0.001$). The results are based on unpaired t-test in case of normal distribution and Mann–Whitney analyses in case of non-normal distribution. Dependent variables were the environmental parameters, the fixed factors were the samples according to the phases (flowing and standing) and habitats (natural and artificial). Bold letters represent significant correlations ($P < 0.05$)

	Phases		Habitats	
	Flowing	Standing	Natural	Artificial
Dissolved oxygen (mg L^{-1})	8.2***	3.9***	5.9	6.2
Oxygen saturation (%)	79***	42***	59	64
Water temperature (°C)	12**	19**	15	16
pH	7.11	7.07	7.10	7.08
Oxidation–reduction potential (mV)	180	74	125	132
Conductivity (µS cm^{-1})	774	877	843	806
Total suspended solids (mg L^{-1})	34	121	109	45
Total dissolved solids (mg L^{-1})	4662	555	499	4713
Biological oxygen demand (mg L^{-1})	1.5	1.1	1.2	1.5
Chemical oxygen demand (g m^{-3})	11*	13*	11	12
Chloride (mg L^{-1})	39	38	39	38
Chlorophyll-a (µg L^{-1})	12	123	123	12
Ammonium-N (mg L^{-1})	0.03	0.06	0.07	0.02
Nitrite-N (mg L^{-1})	0.00	0.00	0.00	0.00
Nitrate–N (mg L^{-1})	0.46	0.57	0.48	0.53
Phosphate–P (mg L^{-1})	0.47*	0.71*	0.59	0.58
Sulfate (mg L^{-1})	35	38	34	38
Silicate (mg L^{-1})	19	46	35	28

phase. The number of diatom species that were identified in both phases were 88. As for habitats, a total of 96 and 134 taxa were found in the natural and artificial (concreted) habitats respectively, while altogether 79 taxa were found in both habitats.

According to the taxonomy-based NMDS analyses, the diatom composition showed clear separation between flowing and standing phases (Fig. 2a), while only a slight compositional separation was found between natural and artificial habitats (Fig. 2b). The PERMANOVA analyses revealed a significant difference ($P=0.0006$) in taxa composition between phases, while no compositional difference between habitats was found ($P=0.3146$). Altogether 16 diatoms, mainly *Gomphonema* Ehrenberg, *Fragilaria* Lyngbye and *Surirella* Turpin species and *Meridion circulare* (Greville) C.Agardh and *Ulnaria danica* (Kützing) Compère & Bukhtiyarova were indicative of the flowing phase (Supplementary Fig. 2a; Supplementary Table 8a). In contrast, a total of 9 diatom taxa, *Navicula* Bory and *Nitzschia* Hassall sensu lato ssp. and *Cocconeis* Ehrenberg species were significant indicators in standing phase (Supplementary Fig. 2a; Supplementary Table 8a). Although there were no significant differences in taxa composition between the natural and artificial (concreted) habitats, some species were identified as indicators of these habitats using IndVal analyses (3 and 19 species, accordingly; Supplementary Fig. 2b; Supplementary Table 8b).

Trait composition

Altogether 22 trait categories were involved in the analyses and 21 of them were found in both phases (flowing and standing) and habitats (natural and artificial). The filamentous category, however, was not present in standing phase and in natural habitat.

Similar to the taxa composition, trait-based analyses also revealed a clear separation in the flowing and standing phase composition (Fig. 3a), while there was a strong overlap between habitats (Fig. 3b). These phenomena were confirmed by PERMANOVA analyses, which showed a significant ($P=0.0013$) difference in trait structure between phases but no difference ($P=0.5893$) between habitats.

While large-sized (S4), rounded (LW2) and moderately elongated (LW4), moderately attached, colonial and high profile guild categories were indicative of flowing phase (Supplementary Fig. 3a, Supplementary Table 9a), round (LW1), slightly and greatly elongated (LW3, LW5), strongly attached, unicellular and low profile categories were characteristic in standing phase (Supplementary Fig. 3a, Supplementary Table 9a). The IndVal analyses did not reveal any indicator trait categories in natural habitat (Supplementary Fig. 3b, Supplementary Table 9b). In contrast, the most elongated category (LW6) was indicative of artificial habitat (Supplementary Fig. 3b, Supplementary Table 9b).

Biodiversity and diatom indices

Although the taxa and trait composition clearly separated due to hydrological conditions, no significant differences were detected in diversity metrics (Taxa S, effSH, FD_Q: $P>0.05$) (Fig. 4a–c). In contrast, taxa number and effective Shannon's H were clearly higher in the artificial (concreted) habitat than in the natural ones ($P=0.0098$ and $P=0.0375$, respectively). Additionally, marginally significant differences were found in FD_Q diversity metric, which was higher in artificial habitat (Fig. 4d–f).

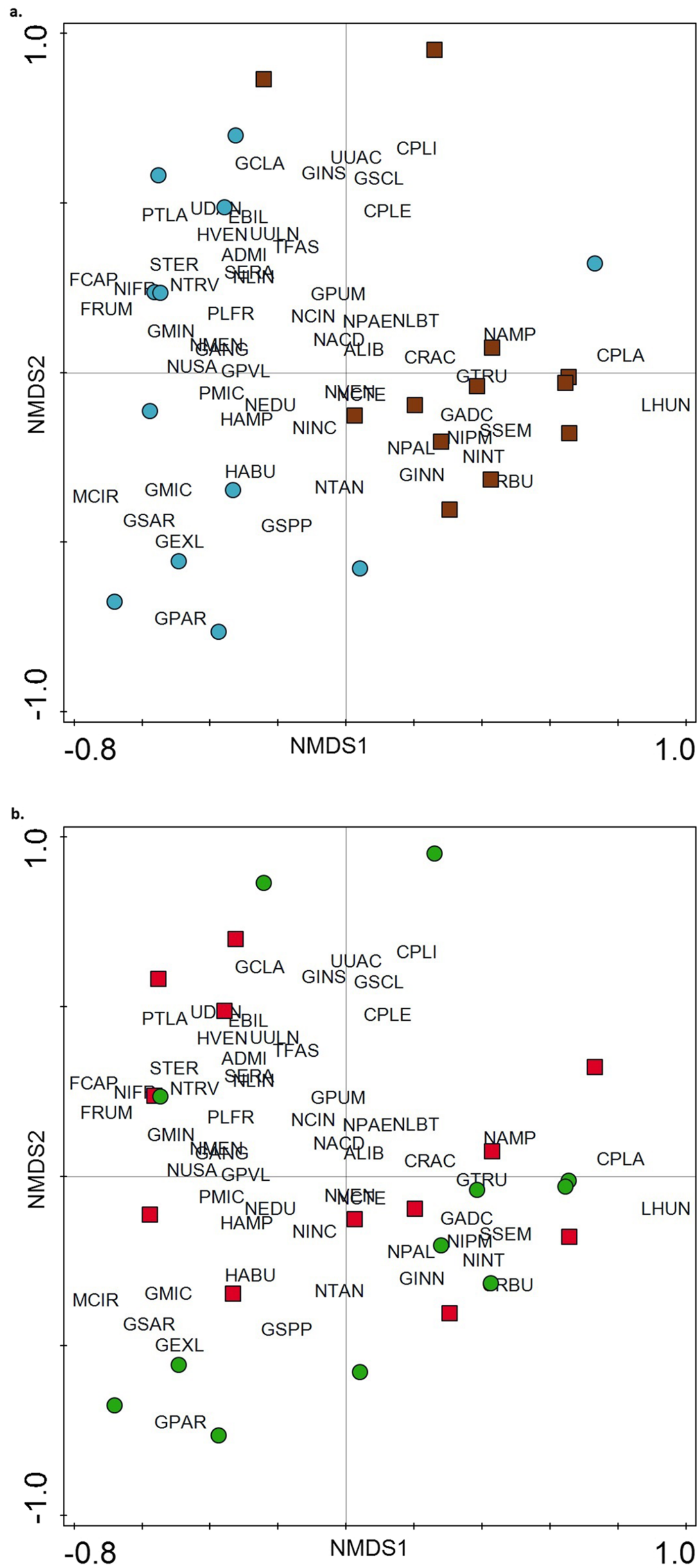
In contrast to biodiversity patterns, hydrological regime caused significant differences in the diatom index values ($P<0.01$, except of SID where $P=0.097$) (Fig. 5a–c), while none of them differed significantly in habitats ($P>0.05$) (Fig. 5d–f).

Discussion

Environmental changes

Low water level and low dilution can significantly change physical and chemical parameters in streams and rivers in drought period (extreme lack of precipitation) (Magand et al., 2020). Therefore, we hypothesized differences between flowing and standing phases in abiotic environment. Our results supported this hypothesis (H1). In our study, the water temperature, which is usually influenced by many factors (water depth, shading, TSS concentration, solar radiation, etc.—Brown & Hannah, 2008), was significantly higher in standing phase. The standing phase developed in May and lasted until December in Létai-ér. The lack of canopy cover in the sampling area, as well as the low water level (Magand et al., 2020) and the

Fig. 2 Taxonomic composition of aquatic phases (**a**) and habitats (**b**) according to NMDS. OMNIDIA codes represent dominant species (abundance ≥ 5%). **a** Blue circles—flowing phase; brown squares—standing phase; **b** green circles—natural habitat; red squares—artificial habitat



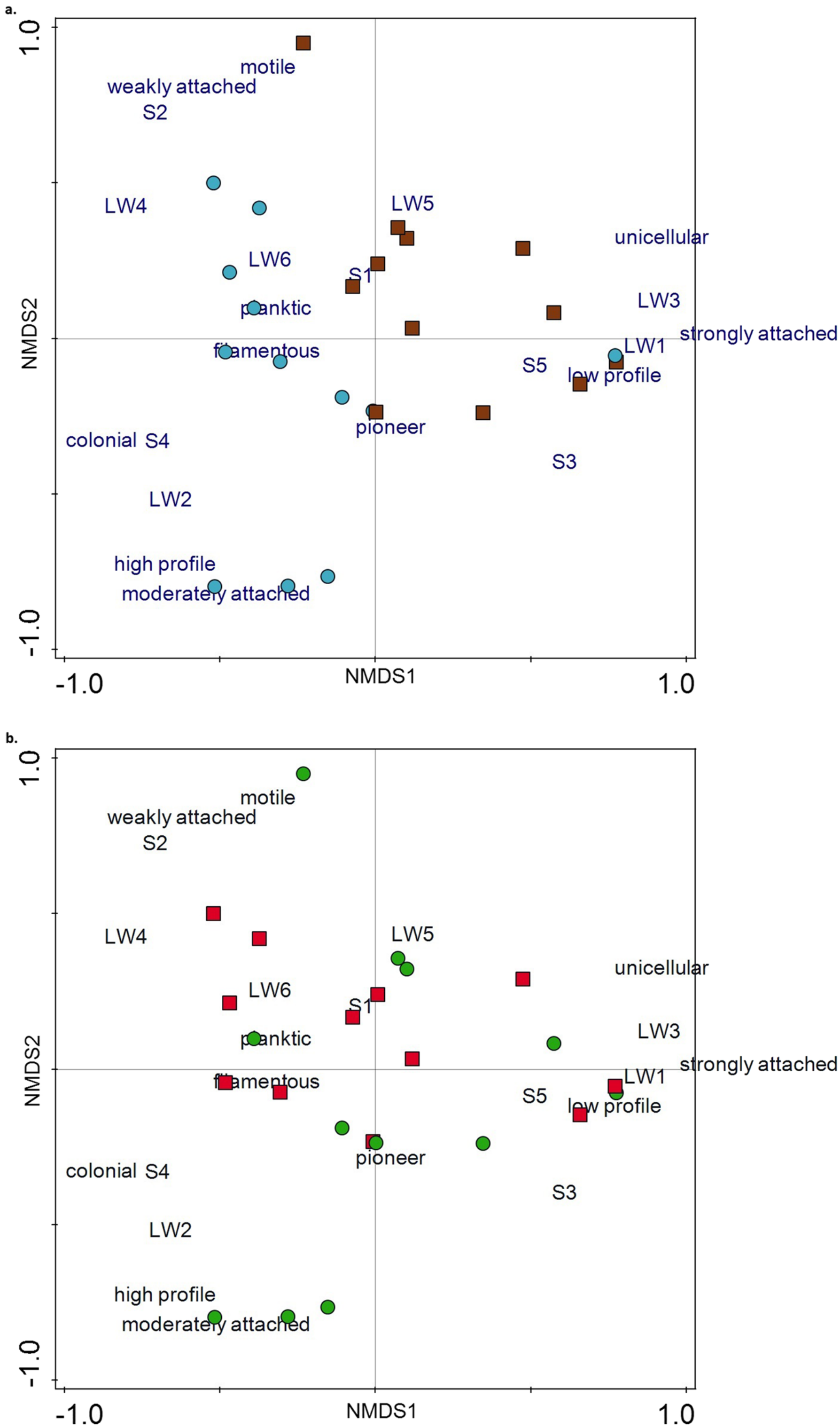


Fig. 3 Trait composition of aquatic phases (**a**) and habitats (**b**) according to NMDS. OMNIDIA codes represent dominant species (abundance ≥ 5%). **a** Blue circles—flowing phase; brown squares—standing phase; **b** green circles—natural habitat; red squares—artificial habitat

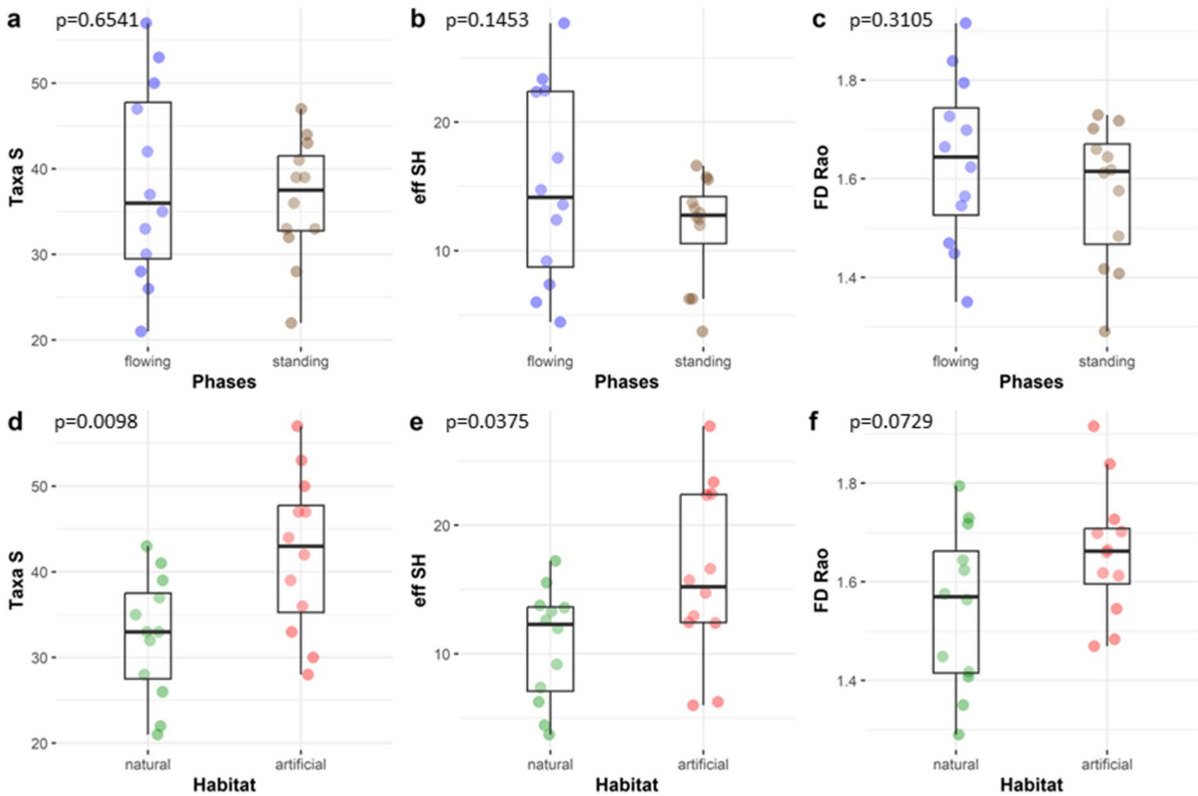


Fig. 4 Taxa richness (**a**), effective Shannon's H (**b**), and Rao's quadratic entropy (**c**) in flowing and standing phases; taxa richness (**d**), effective Shannon's H (**e**), and Rao's quadratic entropy (**f**) in natural and artificial habitats

fact that the Indian summer in 2020 was prolonged in the region (The OMSZ' Climate Data Series 1901–2020) explain the higher temperature value in standing phase. In contrast, dissolved oxygen and oxygen saturation were lower in this phase. Low flow conditions and higher water temperature reduce oxygen solubility (Padisák, 2005; Magand et al., 2020). In addition, the chemical oxygen demand (COD) was significantly higher in standing phase, which can also contribute to the lower oxygen concentration. As it was mentioned above, an extended macrophyte cover characterizes Létai-ér that results in accumulation of organic materials (OMs) in the streambed. The intense decomposition of these organic materials may be behind the increased COD level. The low or no flow conditions and low dilution capacity also provide optimal environment for the OMs' accumulation (Magand et al., 2020). Furthermore, the presence of complex polymers can be presumed, since the biological oxygen demand (BOD) did not differ significantly between the aquatic phases. These polymers are difficult to degrade biologically but at the same time are chemically accessible.

Although nutrient contents may change even extremely during drying in intermittent streams (Magand et al., 2020; Novais et al., 2020), in our study only the phosphate concentration differed significantly between the aquatic phases (higher in the standing phase). The increase of phosphate content may be the result of low water levels due to increased evaporation. Other factors, such as less intensive activity of primary producers or surface or subsurface flow inputs, can be excluded because neither chlorophyll-a concentration and BOD values nor concentrations of nitrogen-forms and conductivity differed significantly between phases. Although human activities can also increase the phosphate content of surface waters, such as sewage discharge, we did not observe any signs of this during sampling, and the nearest sewage treatment plant is ~ 8–10 km from the sampling points (River Basin Management Plan Report Suppl.3.1, 2022). That is true, however, that

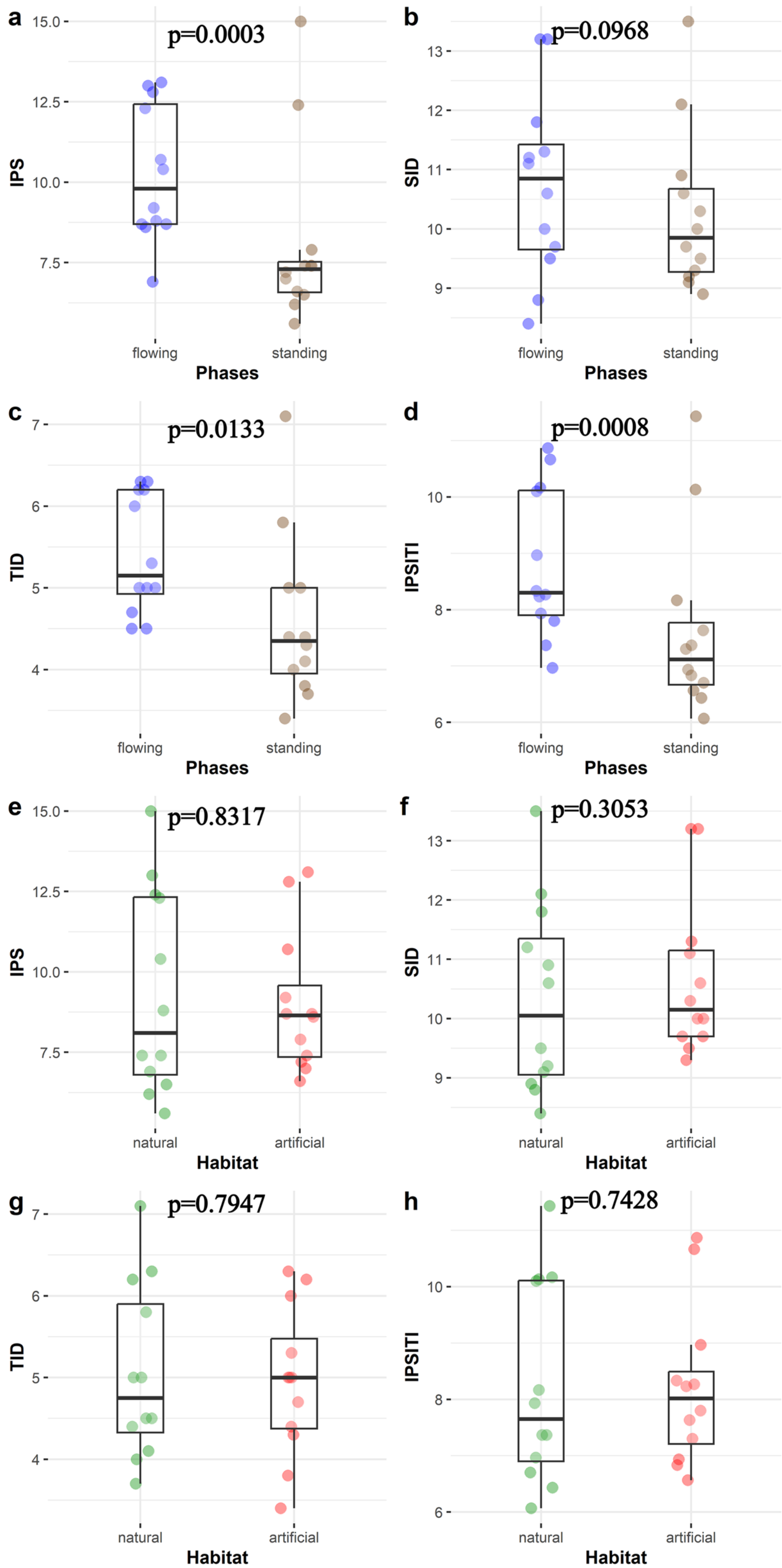


Fig. 5 Diatom indices in flowing and standing phases: IPS (**a**), SID (**b**) TID (**c**) and IPSITI (**d**); diatom indices in natural and artificial habitats: IPS (**e**), SID (**f**) TID (**g**) and IPSITI (**h**)

the stream' catchment is characterized by intensive agriculture and grazing and heavy rains in the early-, and mid-summer may wash nutrients from these areas into the stream.

Road-crossings or culverts have a significant effect on hydrological conditions of streams and greatly contribute to sediment formation. In addition, significantly less macrophyte cover can be characteristic in these artificially modified areas compared to the natural ones (Wemple et al., 2018; Gál et al., 2020). Therefore, we hypothesized a difference in the physical and chemical parameters of natural and artificial habitats. Our results, however, did not prove this assumption (rejects this part of H1). This was probably because both water phases (flowing and standing) were observed in both habitats (natural and artificial) during the study. These phases exerted more pressure on the physical and chemical parameters of the stream than the concreted streambed itself. However, no significant conclusions can be drawn from these results, due to the low sampling effort (one studied stream). In addition, the small distance (i.e., ~ 20–30 m) between the sampling sites may explain the similarity of the environmental parameters, since the flow of water from natural to artificial sites takes only ~ 25 min. (average velocity: 0.02 m s^{-1}—River Basin Management Plan Report Suppl.1.1, 2022). More data are needed to assess the impact of concreting in intermittent streams.

Compositional changes

Extremes in water regime (floods, decreasing water level, drying up—B-Béres et al., 2014; Novais et al., 2020; Tornés et al., 2021) strongly disturb the aquatic assemblages, eventually resulting in the appearance or even dominance of taxa that favor or at least tolerate these altered conditions (Timoner et al., 2014; Sabater et al., 2016, 2017). Here, we hypothesized a significant compositional difference in the diatom assemblages between the aquatic phases and our results supported this hypothesis (H2). Flowing phase was characterized by large sized (S4) and/or rounded (LW2) or moderately elongated (LW4) and/or moderately attached and/or colonial and/or high profile guild taxa. This seems to contradict our previous knowledge, because these traits and taxa bearing them usually refer to intermittent streams in standing phase (Sabater et al., 2016, 2017). It should be emphasized, however, that the studied lowland stream is rich in emergent and submerged macrophytes. These plants provide a suitable substrate for these diatoms, allowing a thick biofilm to form. In addition, the water velocity is not too high in this lowland stream (average 0.02 m s^{-1}—River Basin Management Plan Report Suppl.1.1, 2022), minimizing the physical disturbance caused by intense flow conditions. These environments (thick biofilm and low disturbance) favor colonial, elongated, and/or high profile taxa (Passy, 2007). The colonial, large sized *Meridion circulare*, which is the member of low profile guild, was also indicative in flowing phase, but was very abundant in the samples (rel. abundance > 5%) only from January to March. This species is known as a characteristic member of small streams in winter and early spring (Stenger-Kovács et al., 2013; B-Béres et al., 2022b). The elongated and planktic *Ulnaria danica* is probably settled from the water column, because the water level was not high even in this flowing phase (~ 10 cm in natural habitat; ~ 20 cm in artificial habitat).

In this study, standing phase was characterized by unicellular, slightly and greatly elongated (LW3 and LW5) taxa (motile *Nitzschia* spp. and *Navicula s.l.*), which are usually indicative for drying (McKew et al., 2011). As mentioned above, the water level was not high in the flowing phase, and it further decreased in the standing phase. Since the TSS content did not increase in standing phase (no shading effect), higher UV radiation reaching the biofilm strongly and negatively affected the resilience and resistance of the populations. Motile taxa, however, are able to migrate into the deeper sediment (McKew et al., 2011) and avoid high irradiation. Rounded (LW1), strongly attached, low profile *Cocconeis* species live in the lower layer of the biofilm (Passy, 2007). Low profile taxa are considered shade-tolerant (Liess et al., 2009; Stenger-Kovács et al., 2013; Tapolczai et al., 2016), but it seems that these species also survive in high light conditions (Leira et al., 2015; Kókai et al., 2019). At the same time, during the identification of the diatoms in the preparations, it is not possible to say whether there were living cells in the assemblages, or whether only dead diatoms were identified. Therefore, the light tolerance of large, rounded, low-profile species needs to be clarified so that these traits can be safely used to indicate aquatic phases in intermittent streams.

It is a well-known phenomenon, that habitat heterogeneity is reduced in streambed constructed by concrete (Wellman et al., 2000; Bouska et al., 2010). Significant compositional changes have already been observed in riverine macroinvertebrate (Gál et al., 2020) and fish assemblages (Wellman et al., 2000). In our study, we did not find any differences either in taxa or trait composition between the natural and artificial habitats (rejects this part of H2). Habitat change (from natural to artificial) does not seem to be as strong an environmental filter as the hydrological regime, either for taxa or for traits. This is also very surprising because different types of substrates were sampled in the two sites, i.e., macrophytes in the natural and pebbles and green algal filaments in the artificial habitats. It is known, that substrates can play an important factor controlling diatom composition (Cox, 1988; Cantonati & Spitale, 2009; Hájková et al., 2011; Cantonati et al., 2012). However, even in the same substrate type, the composition of diatoms can vary greatly depending on the current velocity and the specific location of the substrate in the streambed (Passy, 2001). But without a doubt, substrate strongly influences the structure of the assemblages and the relative abundance of taxa. Here, one possible reason could be the short distance between the sampling sites (see above). In this case, mass effect and/or species sorting may be the main organizing force allowing taxa to be present even at suboptimal environment or dispersed at any suitable sites (Soininen & Teittinen, 2019). It is especially true for motile taxa whose disperse may be more controlled by mass effect (Jamoneau et al., 2018). In this study, although no significant compositional difference was found, the IndVal analysis showed that the artificial (concreted) habitat was primarily indicated by motile taxa. Another reason for the similarity between the habitats may be the abundant macrophytes living next to the artificial site. Even though the streambed is concreted, this plant cover can play an important role, especially at higher water levels, in the formation of such similar diatom assemblages.

Biodiversity and ecological quality changes

It has been observed that lentic taxa, which appear during the formation of pools or the development of standing phase, can increase biodiversity of intermittent watercourses. Later, aerophile or even terrestrial taxa may further enhance biodiversity (Stubbington et al., 2017) up to a point (Tornés et al., 2021). Here, we found no difference in either taxonomic or in trait-based diversity metrics (rejects this part of H3). Probably because the Létai-ér was already rich in taxa and traits (e.g., colonial, high profile, moderately attached species), which are typical in mountainous or hilly streams during the fragmentation of surface water and drying up of stream (Falasco et al., 2016a).

Gál et al. (2020) found that biodiversity and the number of protected macroinvertebrate taxa decrease significantly at road crossings, while artificial streambed modification has a positive effect on the abundance of alien species. In our study, however, significantly higher species richness and effective Shannon's H and marginally significantly higher functional diversity were found in the artificial habitat (rejects H3). This is probably not because the species that appeared in the artificial habitat were not previously the members of the Létai-ér' species pool. It is more likely, that the selection pressure on the diatom assemblages in the two habitats was not strong enough to result in structural changes, but was enough to change the relative abundance of the species. During the taxonomic identification, we found such species in the artificial (concreted) habitat (increasing Taxa S) that were hidden by the high relative abundance of the dominant taxa in the natural habitat. However, the sampling effort was low in our study, thus we can not draw general conclusions that would require more data from many more sampling sites. In addition to increasing the sampling effort, however, factors such as the distance between sampling sites, vegetation cover next to the streambed, must also be taken into account.

Despite the fact that the diatom indices were primarily developed for the detection of nutrient loads, according to our knowledge so far, they are robust enough to be included in the assessment of the ecological status of intermittent streams (Barthès et al., 2015; Falasco et al., 2016b; Novais et al., 2020; B-Béres et al., 2022b). Here, we hypothesized that drought significantly negatively affects water quality. Our results support this hypothesis: the shift in the hydrological regime (flowing to standing phase) created such a harsh environment (increased phosphate concentration, lack of shading, etc.) that was enough to induce compositional changes in diatom assemblages and contribute to an increase in the relative abundance of species (mainly *Navicula* and *Nitzschia* taxa), which favor these conditions but also indicate the deterioration of the ecological status. In contrast, we surprisingly did not find any differences in diatom indices between habitats (rejects this part of H4). Although it should be noted that the habitats did not differ in either their physical or chemical parameters (see explanation above).

Conclusion

Our results highlighted that even in the absence of direct drying, changes in the hydrological regimes have a significant assemblages-forming role in a lowland intermittent stream, even within a relatively short period of time (one year), which also influence the ecological status of the stream. Prolonged drought therefore significantly increase the vulnerability of these ecosystems. At the same time, our investigation also pointed out that characteristics typical of lowland streams, such as the extensive macrophyte cover even in the flowing phase, or the rapid sedimentation of inorganic particles during the intense decrease in water level, can slightly modify the generally accepted theories of diversity change related to hydrological regimes. In addition, our results also highlighted that streambed modifications (concreting) and the covering the littoral zone with hollow concrete slabs do not necessarily result in significant compositional changes in diatom assemblages. Even an increase in diversity can be predicted if the environmental conditions (nutrient supply, light intensity, etc.) do not deteriorate. However, this definitely requires further, much more extensive research than the study presented here. After all, an incalculable number of bridges cross watercourses, including intermittent streams and rivers worldwide, whose effect on the benthic algal assemblages is not yet known. However, without this knowledge, it is difficult to propose ecological action plans for nature conservation, water management, and restoration of intermittent watercourses.

Acknowledgements The project was financially supported by the National Research, Development and Innovation Office - NKFIH FK 132 142 (VBB), by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences BO-00458-20-8 (VBB) and by the ÚNKP-20-5 (VBB), ÚNKP-21-5 (VBB) and ÚNKP-22-5 (VBB) New National Excellence Program of the Ministry for Innovation and Technology from the Source of the National Research, Development and Innovation Fund. We are thankful to Tamás Bozóki for preparation of the map (Fig. 1).

Author contributions VB-B developed the structure and drafted key issues of this paper; VB-B and SK wrote the manuscript. ZN-K proved the diatom data; IB and KM performed the physical and chemical analyses of samples in the laboratory; SK and ÁL carried out the statistical analyses; IB helped in writing of the manuscript; VB-B raised the topic; ÁL, ET-K, IB and VB-B collected samples. All authors gave final approval for publication.

Funding Open access funding provided by ELKH Centre for Ecological Research. Funding were provided by Nemzeti Kutatási Fejlesztési és Innovációs Hivatal (Grant No. NKFIH FK 132 142), the János Bolyai Research Scholarship of the Hungarian Academy of Sciences (Grant No. BO-00458-20-8), Innovációs és Technológiai Minisztérium (Grant No. ÚNKP-20-5), Innovációs és Technológiai Minisztérium (Grant No. ÚNKP-21-5) and Innovációs és Technológiai Minisztérium (Grant No. ÚNKP-22-5).

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical statement No human participants and animals were involved in the research.

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