Global Ecology and Conservation 62 (2025) e03858

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original Research Article

Structure and biodiversity of benthic diatoms shaped by water availability in streams of the Pannonian Ecoregion

Stefánia Kiss [a,b], Zsuzsanna Nemes-Kókai [a,1], István Bácsi [c,d,2], Áron Lukács [a,e,3], Kamilla Márton [c,d], Enikő T-Krasznai [a,4], Gábor Borics [a,5], Csilla Stenger-Kovács [f,g,6], Júlia Szeles [h,7], Péter Török [b,d,i,8], Viktória B-Béres [a,*,9]

[a] HUN-REN Centre for Ecological Research, Institute of Aquatic Ecology, Functional Algology Research Group, Bem square 18/c, Debrecen H-4026, Hungary
[b] Department of Ecology, University of Debrecen, Egyetem square 1, Debrecen H-4032, Hungary
[c] Department of Hydrobiology, University of Debrecen, Egyetem tér 1, Debrecen H-4032, Hungary
[d] HUN-REN–UD Functional and Restoration Ecology Research Group, Egyetem tér 1, Debrecen H-4032, Hungary
[e] University of Helsinki, Lammi Biological Station, Pääjärventie 320, Lammi 16900, Finland
[f] University of Pannonia, Center for Natural Sciences, Limnology Research Group, Egyetem street 10, Veszprém H-8200, Hungary
[g] HUN-REN-PE Limnoecology Research Group, Egyetem street 10, Veszprém H-8200, Hungary
[h] HUN-REN Centre for Ecological Research, Institute of Aquatic Ecology, Aquatic Macroinvertebrate Research Group, Bem square 18/c, Debrecen H-4026, Hungary
[i] HUN-REN Balaton Limnological Research Institute, Klebelsberg Kuno u. 3, Tihany H-8237, Hungary

A R T I C L E I N F O

Keywords:
Benthic diatoms
Hydrological phases
Pannonian Ecoregion
Red List species
Stream drying

A B S T R A C T

Intermittent streams are ecologically and economically significant but are among the most vulnerable ecosystems on Earth. Despite their increasing prevalence, our understanding of the ecological processes within these systems remains limited, particularly concerning microscopic organisms. Our study focuses on compositional and biodiversity changes in benthic diatom assemblages across two stream types (permanent vs. intermittent) and three hydrological phases (flowing, standing, and dry) in the Pannonian Ecoregion. We first assess the conservation value of these ecosystems using a diatom-specific Red List. Our results show clear structural differences in periphyton, with diversity changes observed only between stream types. These findings suggest that species loss has already begun in intermittent streams, but no functional loss was identified

* Corresponding author.
E-mail addresses: kiss.stefania@ecolres.hu (S. Kiss), nemes.kokai.zsuzsanna@gmail.com (Z. Nemes-Kókai), istvan.bacsi@gmail.com (I. Bácsi), lukacsaron93@gmail.com (Á. Lukács), kamillamarton165@gmail.com (K. Márton), ekrasznai@gmail.com (E. T-Krasznai), boricsg@gmail.com (G. Borics), stenger-kovacs.csilla@mk.uni-pannon.hu (C. Stenger-Kovács), szeles.julia@ecolres.hu (J. Szeles), molinia@gmail.com (P. Török), beres.viktoria@gmail.com (V. B-Béres).

[1] 0000–0003-0315–9343
[2] 0000–0002-3916–8623
[3] 0000–0003-3617–2843
[4] 0000–0002-0012–1422
[5] 0009–0007-3575–512X
[6] 0000–0001-6175–4904
[7] 0009–0004-9571–6200
[8] 0000–0002-4428–3327
[9] 0000–0002-9632–2703

https://doi.org/10.1016/j.gecco.2025.e03858
Received 26 March 2025; Received in revised form 1 September 2025; Accepted 12 September 2025
Available online 13 September 2025

across phases. Additionally, intermittent streams host more Red List taxa, likely due to their unique habitat (phases). Our results highlight the critical need for customized water management and conservation strategies for intermittent streams in the region, especially as these ecosystems are becoming increasingly intertwined with daily life in the Pannonian Ecoregion.

1. Introduction

Effectively managing the impacts and consequences of extreme weather events is among this century's key environmental, economic, and social challenges. These events significantly reshape ecosystems, varying primarily in the intensity and timing of their effects on specific environments (Crabot et al., 2021; Novais et al., 2020; Tornés et al., 2021; Várbíró et al. 2020). Continental freshwater ecosystems, including small watercourses, are particularly vulnerable to climate-induced phenomena such as flash floods, sudden water level drops, and partial or complete drying (B-Béres et al., 2019; Messager et al., 2021; Tornés et al., 2021; Várbíró et al. 2020). Flow fluctuations alter both the physical and chemical conditions (Gómez et al., 2017), and the habitat availability for aquatic organisms; e.g., floods expand and homogenise habitats (Death et al., 2015), while drying fragment and reduce them (Lancaster and Ledger, 2015). These structural changes in habitat ultimately affect community composition regardless of the size of the watercourse (large rivers – Sabater et al., 2016; Trábert et al., 2017; streams – B-Béres et al., 2022; Timoner et al., 2014).

Recent studies have revealed that intermittent watercourses, defined as those that cease to flow for at least one day each year, are just as common on Earth as permanent ones. Currently, approximately 50–60 % of the world's watercourses are classified as intermittent (Messager et al., 2021), however, in the case of small streams, this proportion can exceed 70 % (Datry et al., 2014). In Hungary, there are around 10,000 watercourses registered (B-Béres et al., 2022; Stubbington et al., 2018); but only approximately 10 % of them (catchment area >10 km^2) are included in the National Monitoring Program (River Basin Management Plan Report Suppl.1.1., 2021). According to the latest national survey, over 30 % of the regularly monitored watercourses are intermittent (River Basin Management Plan Report Suppl.6.4., 2021), while sporadic data emphasises (Truchy et al., 2023) the proportion is significantly higher among unmonitored streams. These up-to-date findings underscore the increased risk of water scarcity in the Pannonian Ecoregion, a large part of which is occupied by Hungary. The Great Hungarian Plain, the most vulnerable part of this ecoregion to weather extremes, has over 40 % of its monitored watercourses unable to be replenished with water, resulting in regular drying (River Basin Management Plan Report Suppl.6.4., 2021). Similar to Mediterranean and arid regions, these lowland intermittent streams are essential to agriculture (e.g., irrigation, water supply, and drainage-based flood protection), and support recreational activities like fishing. They are also vital for industry and contribute significantly to nature conservation by preserving biological diversity and providing habitats for protected species. Understanding the ecological and economic processes of these streams is therefore crucial for sustaining local well-being.

To characterize the hydrological dynamics in intermittent streams, Gallart et al. (2017) identified three distinct hydrological phases, the flowing, pool (standing) and dry phases. Although habitat variability may occur during the pool phase (e.g., due to habitat fragmentation), streambed drying ultimately results in the complete loss of aquatic habitats. The disappearance of water exerts a profound effect on the survival of certain aquatic communities (e.g. fish - Kalogianni et al., 2017; Wellman et al., 2000, phytoplankton - Douglas et al., 2023), even within short timeframes, while triggering structural shifts in others (e.g. macroscopic aquatic invertebrates - Datry, 2012; Gál et al., 2020; Sabater et al., 2017, benthic diatoms - B-Béres et al., 2022; Novais et al., 2020; Tornés et al., 2021; Várbíró et al., 2020). Research findings on the impact of drought and the drying of streambeds on biodiversity are sometimes conflicting, yet the prevailing scientific consensus is that intermittent streams support lower local diversity than permanent streams (Stubbington et al., 2017). Tornés et al. (2021) reported a significant decline in local diversity of benthic diatom assemblages in Mediterranean regions during non-flow periods lasting over 100 days. However, brief dry phase may actually enhance the community's biodiversity, for instance, by favouring lentic species during the pool (standing) phase and aerophilous taxa during the dry phase (e.g. Stubbington et al., 2017). Upon rewetting, small, fast-spreading, and well-colonising taxa may be reintroduced from the surrounding catchment area, further contributing to an increase in diversity (B-Béres et al., 2019). From a conservation perspective, a key question is the extent to which intermittent streams contribute to the preservation of protected and threatened species. As few studies have addressed this issue, the available results are often contradictory (e.g. lower contribution – Falasco et al., 2016 *vs.* higher contribution – Cantonati et al., 2020). However, it is widely accepted that intermittent streams, and especially their standing phases, can serve as refuges for Red List species (Falasco et al., 2016). Additionally, Cantonati et al. (2020) also emphasised that in regions where intermittent streams have become more prevalent than permanent ones, their role in the conservation of Red List species is significantly greater.

Regardless of the ecoregion, benthic diatoms play a vital role in understanding the environmental processes that occur during the drying of streambeds in intermittent watercourses. However, the duration of exposure to the risk of desiccation – whether over recent decades or historically – results in different community structure changes (Várbíró et al., 2020). While most targeted studies have traditionally focused on the Mediterranean and arid regions, recent interest has turned to areas with continental climates, including the Pannonian Ecoregion (B-Béres et al., 2019, 2022). Studies here have demonstrated that the structure of the benthic diatom community reflects water flow constancy (permanent and intermittent streams - B-Béres et al., 2019; Várbíró et al., 2020), the presence or absence of water in the streambed (aquatic vs. dry types – B-Béres et al., 2022), and the flow conditions (flowing vs. standing phases – Kiss et al., 2024). However, a comprehensive project covering the entire hydrological cycle (see the three phases) has not yet been conducted in the region, which would help reveal ecoregional specifics in community structure, indicator species and traits, and diversity shifts.

Therefore, our study aimed to monitor the monthly changes in the diatom community of small lowland streams in the Pannonian Ecoregion over a one-year period. Our research encompassed streams with different water supplies, including both permanent and intermittent streams. In the case of intermittent streams, the hydrological phases (flowing, standing, dry) were also examined.

The following specific research objectives were defined:

Objective 1:

The aim of the study is to compare the diatom communities of permanent and intermittent watercourses, with a focus on potential differences in species composition and diversity, and to evaluate the conservation value of intermittent streams.

Objective 2:

The aim of the study is to assess the variation in diatom community composition and biodiversity across different hydrological phases (flowing, standing, and dry), and to examine how conservation value - particularly the occurrence of threatened taxa - differs among these phases.

2. Materials and methods

2.1. Study area, climatic conditions, sampling setup and environmental parameters

A total of 99 benthic diatom samples were collected once a month for a year in 2020 from eight small watercourses in the Great Hungarian Plain (Fig. 1). In 2020, the region experienced significantly higher temperatures than the 1981–2010 average, with annual means ranging between 11 and 12°C, while precipitation patterns were variable (Lakatos et al., 2021; Supplementary Table 1). The summer was particularly warm, with multiple heatwaves and daily maxima exceeding 30 °C. According to the temperature data from the study area, January had the lowest and August the highest average daily air temperatures. Between April and the end of September, the average daily temperature remained above 10 °C (Supplementary Table 1). Precipitation was uneven in both time and space: the beginning and end of the year were drier than average, while localized thunderstorms and heavy rainfall events during the summer months led to significant precipitation. The total annual precipitation in the region for 2020 was 570.4 mm (Supplementary Table 1), aligning with the national multi-year average (500–800 mm/year; HungaroMet Climate Data Series, 2025). A marked difference was observed in the distribution of precipitation: June and July were the wettest months, accounting for nearly 40 % of the region's annual precipitation, while April and November were the driest (Supplementary Table 1). Notably, in January, April, August, and November over half of the monthly precipitation fell in a single day.

The studied watercourses belong to the R04-R05 water body category (Solheim et al., 2019). These watercourses are characterised as small to medium-sized lowland rivers with calcareous, medium-fine bed material. Their total length ranges from 10 to 70 km, and their catchment area varies between 15 and 450 km^2 (River Basin Management Plan Report Suppl.1.1., 2021). Although no specific intermittent stream category is designated in Hungary, the national database includes a note detailing which water courses are considered intermittent. Based on this database, three of the examined watercourses are classified as permanent, while five streams are classified as intermittent (Supplementary Table 2). To describe the hydrological conditions of intermittent streams, the classification system introduced by Gallart et al. (2017) was used. Based on this classification, 13 samples were collected in the flowing phase, 22 samples in the standing phase, and 28 samples in the dry phase (Supplementary Table 2). In addition, a total of 36 samples were taken from permanent streams.

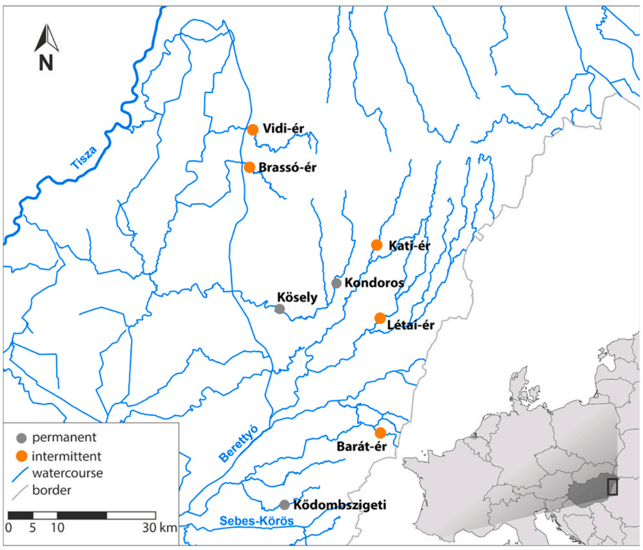

Fig. 1. The location of the study area within the Pannonian Ecoregion, in Eastern Hungary. The blue line indicates the streams, permanent streams are marked with grey circles and intermittent streams are marked with orange circles.

The examined watercourses flow predominantly through agricultural and residential areas, where aquatic vegetation is commonly found. The most notable species observed in the study area include *Phragmites australis* (common reed), *Carex* spp. (sedge), *Glyceria maxima* (great manna grass), *Typha* sp. (bulrush), *Ceratophyllum* spp. (hornworts), *Potamogeton* spp. (pondweed), *Myriophyllum* spp. (perch kelp), *Lemna* sp. (duckweed), and *Berula* sp. (water parsnips), as well as terrestrial plants during the extended dry phase.

Water samples were collected to measure environmental parameters whenever water was present in the streambed. The following parameters were directly measured in the field using a portable multi-parameter digital instrument (HQ30d, Germany): water temperature (T - °C), dissolved oxygen (DO - mg L^{-1}), oxygen saturation (O_2 - %), pH, oxidation-reduction potential (ORP - mV), and conductivity (COND - μS cm^{-1}). Additional parameters were analysed in the laboratory. The water samples were stored in a cooler bag at 4 °C until they could be transported to the laboratory. All environmental measurements were conducted in accordance with international or national standards and guidelines: chemical oxygen demand (COD_{Mn} – g m^{-3}; Felföldy, 1987), biological oxygen demand (BOD - mg L^{-1}; MSZ EN, 1899–2, 2000), chlorophyll-a (Chl-a - μg L^{-1}; Felföldy, 1987), total dissolved solids (TDS - mg L^{-1}; Németh, 1998), total suspended solids (TSS - mg L^{-1}; MSZ 12750–6, 1971), chloride-ion (Cl^- - mg L^{-1}; MSZ, 1484–15, 2009), soluble silicate (Si - mg L^{-1}; ASTM, D859–00, 2000), nitrite-nitrogen (NO_2^- –N - mg L^{-1}; MSZ, 1484–13, 2009), nitrate-nitrogen (NO_3^- –N – mg L^{-1}; MSZ, 1484–13, 2009) ammonium-nitrogen (NH_4^+–N - mg L^{-1}; MSZ ISO, 7150–1, 1992) phosphate -phosphorus (PO_4^{-3}–P - mg L^{-1}; MSZ EN ISO, 6878, 2004) and sulphate (SO_4^{-2} - mg L^{-1}; MSZ 448–13, 1983).

2.2. Diatom sample collection, preparation, and identification

In permanent watercourses, as well as in intermittent streams during both the flowing and standing phases, the sampling and preservation of benthic diatoms was carried out according to the international standard (EN 13946, 2014). At each sampling event, diatom samples were collected from the most typical aquatic macrophytes at the given time. During the dry phase, benthic diatom samples were also obtained from the most typical substrate of the given stream. Diatom samples were preserved in the field with an acetate-free Lugol's solution. The hot hydrogen peroxide method was used to digest organic matter, and Naphrax resin was used for embedding (EN 13946, 2014). A minimum of 400 valves per sample were counted and identified to at least species level using a Leica DMRB light microscope at 1000–1600 × magnification (EN 14407, 2014).Up-to-date literature was used for identification: Krammer and Lange-Bertalot (1997a, 1997b, 2004a, 2004b), Hofmann et al. (2006), Potapova and Hamilton (2007), Bey and Ector (2013), Da Silva et al. (2015) and Stenger-Kovács and Lengyel (2015). The database of AlgaeBase was used to update the nomenclature of diatom taxa (Guiry, Guiry, 2025).

2.3. Data processing and analyses

Taxa were classified into six traits with a total of 22 categories: life forms (3 categories), ecological guilds (4 categories) and pioneer characteristics according to Rimet and Bouchez (2012), attachment type (3 categories) according to Lange et al. (2016), length and width ratio (L/W1–6; 6 categories) according to Stenger-Kovács et al. (2018), and biovolume (S1–5; 5 categories) according to Berthon et al. (2011) (Supplementary Table 3).

The protected species were grouped according to the Lange-Bertalot and Steindorf' (1996) Red-list revised by Hofmann et al. (2018). Although this list was prepared for German watercourses, to the best of our knowledge it is the only Red List in Europe that specifically addresses diatoms.

We calculated taxa richness and Effective Shannon's H (Jost, 2006) using Past software (version 4.17; Hammer et al., 2001), along with Rao's quadratic entropy (RaoQ) (Rao, 1982) as an indicator of functional diversity using Canoco 5.0 (ter Braak and Smilauer, 2002).

Assessing the influence of the constancy of water supply (stream types: permanent and intermittent) and the hydrological phases (flowing, standing and dry) on taxonomic and trait composition of benthic diatom assemblages, non-metric multidimensional scaling (NMDS; Canoco 5.0; ter Braak and Smilauer, 2002) was applied using the species 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). To identify the indicative species and traits of stream types and hydrological phases, indicator value (IndVal) analyses based on the relative abundances of taxa and CWM of traits were performed (Dufrêne and Legendre, 1997). These analyses (PERMANOVA and IndVal) were conducted in Past software (version 4.17; Hammer et al., 2001).

To test differences in our variables (the 18 physical and chemical parameters, Taxa_S, Effective Shannon's H and RaoQ), we used the same groups (stream types and hydrological phases as fixed factors) as for assessing taxonomic and trait compositional differences. Shapiro-Wilk test was used to determine the distribution (normal or non-normal) of our variables. In case of normal distribution, Welch's test or one-way ANOVA and in case of non-normal distribution, Mann-Whitney or Kruskal-Wallis test was used to compare the environmental background and diversity characteristics between permanent and intermittent streams and between hydrological phases of intermittent streams (i.e. flowing, standing and dry phases) using Past software (version 4.17; Hammer et al., 2001).

3. Results

3.1. Environmental background

In general, from the 18 physical and chemical parameters involved in the analyses, the BOD and pH conditions and the ammonium-nitrogen supply were good in the studied waters, while the oxygen supply, conductivity, chloride ion concentration and especially the phosphate content indicated moderate or poor quality (Supplementary Table 4).

A total of eight parameters were found to be significantly different ($p < 0.05$) between permanent and intermittent streams. Conductivity (COND), total dissolved solids (TDS), chemical oxygen demand (COD_{Mn}), sulphate and soluble silicate were found to be significantly higher in intermittent streams, while nutrients such as ammonium-, nitrate- and nitrite-nitrogen were higher in permanent streams (Supplementary Fig. 1a-h).

With regard to the hydrological phases in intermittent streams, there is a significant difference in the oxygen balance between the flowing and standing phases. The flowing phase typically exhibits higher levels of oxygen (DO and O_2%; Supplementary Fig. 2a, b), indicating a more favourable status in these environments (Supplementary Table 4). In contrast, elevated water temperatures, as well as higher levels of chemical oxygen demand and phosphate concentration were observed in the standing phase (Supplementary Fig. 2c-e).

3.2. Water body type differences – permanent vs. intermittent

3.2.1. Taxa and trait composition, biodiversity

A total of 275 taxa were found in permanent and intermittent streams. With one exception, all of them were identified to at least species level (Supplementary Table 5). 134 taxa were found in both water types, while 83 taxa occurred only in permanent streams and 65 exclusively in intermittent streams.

The taxonomy-based NMDS analysis revealed a distinct difference in diatom composition between permanent and intermittent streams (Fig. 2a). This finding was confirmed by the PERMANOVA analysis ($p = 0.0001$). The trait-based NMDS analyses also demonstrated separation of the diatom trait composition between permanent and intermittent streams (Fig. 2b), which was confirmed by the PERMANOVA analyses ($p = 0.0474$). However, it should be noted that the permanent sites occupy a subset of the space of the intermittent sites. Additionally, the intermittent sites occupy more space, indicating greater variability among the samples.

A high number of taxa were found to be indicative of permanent streams ($n = 69$), and a further 32 taxa were identified as indicator members of intermittent streams (Supplementary Table 6). Most of these taxa exhibited low relative abundances; however, many of them were dominant in the waters. As for indicative traits, permanent streams were characterised by the following trait categories: rounded (LW1-LW2) and elongated (LW6) shapes, moderate size (S3), filamentous life form and planktic guild. In contrast, small (S2) and large (S4) size and moderately elongated shapes (LW3-LW4) categories were indicative of intermittent streams (Supplementary Table 6). This means, that *inter alia*, the presence of round (*Stephanocyclus meneghinianus* (Kützing) Kulikovskiy, Genkal and Kociolek) or narrow, elongated (*Fragilaria radians* (Kützing) D.M.Williams and Round, *Ulnaria acus* (Kützing) Aboal and *Ulnaria danica* (Kützing) Compère and Bukhtiyarova) planktic species, as well as the filamentous *Melosira varians* C.Agardh, was indicative of permanent watercourses. It should be noted that *Navicula* and *Nitzschia* s.l. species, which prefer eutrophic conditions, as well as halophilic

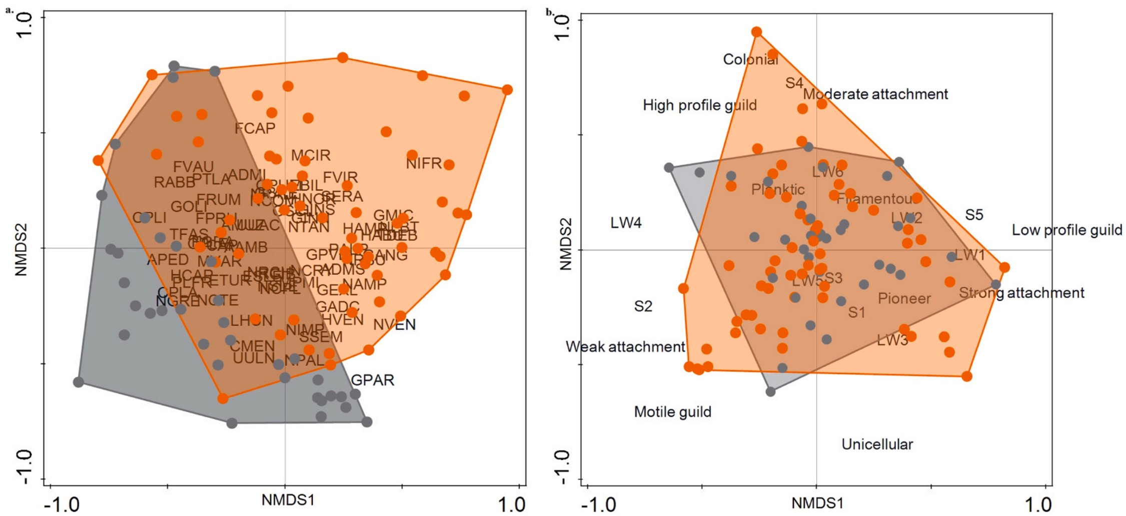

Fig. 2. Taxonomic composition (a) and trait composition (b) of different water body types according to NMDS. The four-letter OMNIDIA codes in Fig. 2a represent the species (Supplementary Table 3). Permanent streams are marked with grey circles (their covered area is grey), intermittent streams are marked with orange circles (their area is orange).

Tryblionella spp. (except *T. debilis* Arnott ex O'Meara), were also characteristic of these streams. In contrast, almost half of the taxa indicative of intermittent streams belongs to the high profile guild. This includes both large or small sized colonial (e.g. *Eunotia bilunaris* (Ehrenberg) Schaarschmidt, *Eunotia formicina* Lange-Bertalot, *Fragilariforma virescens* (Ralfs) D.M.Williams and Round, and *Gomphonema micropus* Kützing) and unicellular *Gomphonema* species. Most of the other taxa were moderately elongated, motile *Navicula* s.l. and *Nitzschia* s.l. species which prefer even eutrophic environments. In addition to the aforementioned species, aerophilous taxa such as *Humidophila contenta* (Grunow) R.L.Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot and Kopalová, *Halamphora normanii* (Rabenhorst) Levkov, *Hantzschia abundans* Lange-Bertalot, *Nitzschia hantzschiana* Rabenhorst, *Pinnularia brebissonii* (Kützing) Rabenhorst and *Tryblionella debilis* were also indicative of intermittent waters.

In terms of biodiversity, permanent streams had significantly higher taxa numbers and functional diversity compared to intermittent streams. However, no difference in effective Shannon's H biodiversity was observed between these watercourses (Fig. 3).

3.2.2. Conservation status and vulnerability

A total of six endangered diatom species were identified in this study (2.2 % of the total taxa number). According to the Red List used, three species are classified as "highly endangered" and three are categorised as "endangered" (Table 1).

We identified species listed on the Red List in nearly 40 % of the samples, totaling thirty-nine samples (n_{total}=42 data records: $n_{intremittent}$=33 data records; $n_{permanent}$=9 data records). Four species were recorded exclusively in intermittent watercourses, one species were found in both water types, and one species were found exclusively in permanent streams (Table 1). The relative abundances of most species were below 5 %, but one species (*Gomphonema parvulius* (Lange-Bertalot and E.Reichardt) Lange-Bertalot and E. Reichardt) exceeded this threshold at least once. While this species was found in both permanent and intermittent streams, it was only dominant in the latter. Additionally, the relative abundance of two other taxa (*Fragilariforma nitzschioides* (Grunow) Lange-Bertalot, and *Nitzschia gisela* Lange-Bertalot) surpassed 1 % at least once. These species were exclusively found in intermittent streams. Two species, including *F. nitzshioides*, were identified in a single sample. In contrast, two species, *G. parvulius* and *N. gisela* were recorded in at least 10 samples, accounting for over 10 % of the total.

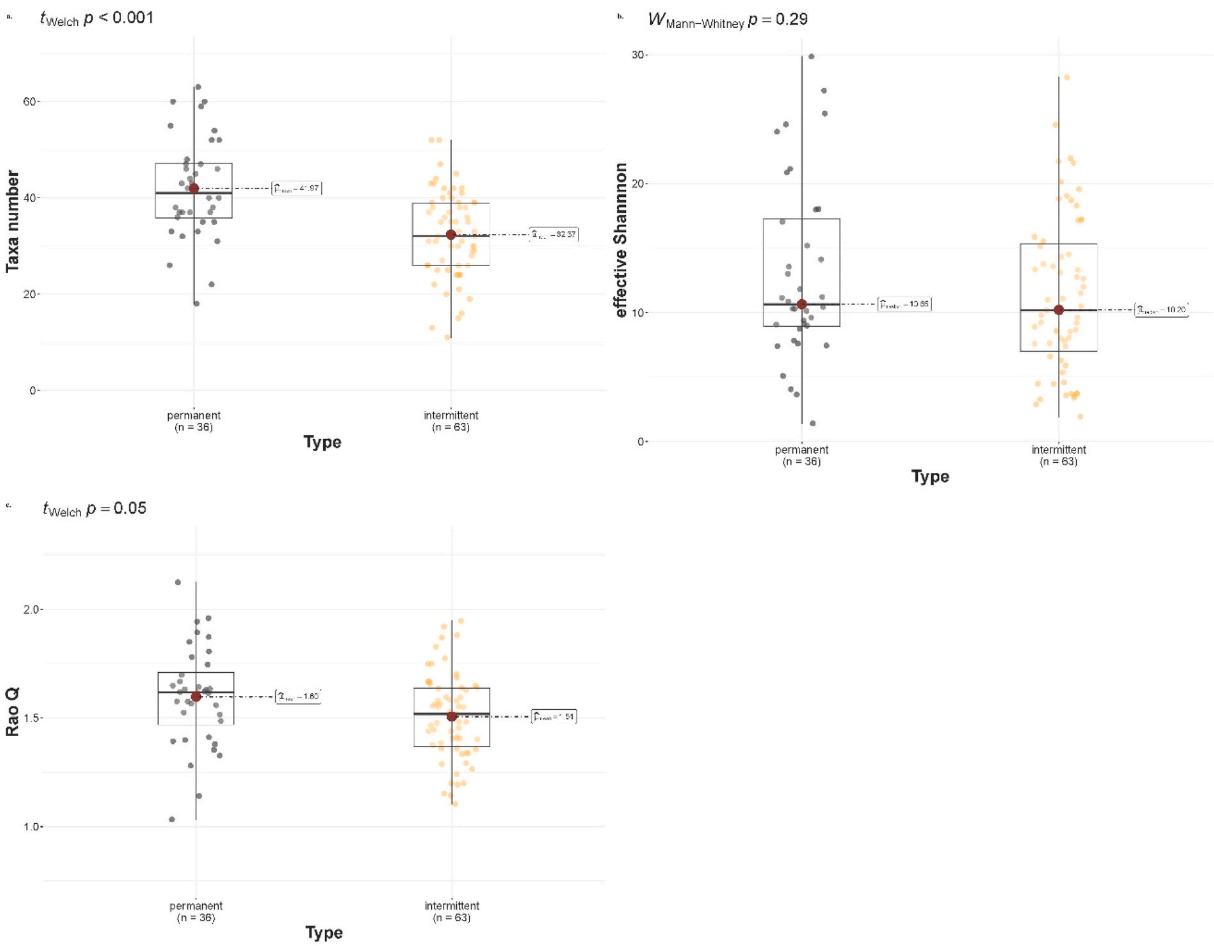

Fig. 3. Biodiversity in different water body types. (a) Taxa number (b) Shannon's H biodiversity (effective Shannon) and (c) Functional diversity (Rao Q). Grey circles - permanent streams; orange circles - intermittent streams.

Table 1
According to Hofmann et al. (2018), the conservation status of Red List' benthic diatom species identified is categorised as follows: highly endangered and endangered. In addition, the occurrence and maximum of relative abundance of these species in different water body types (permanent vs intermittent) and hydrological phases (flowing, standing and dry).

Species	Conservation status	max. rel. ab.	Number of occurrence	Permanent	Intermittent		
					flowing	standing	dry
Achnanthidium rosenstockii	highly endangered	0.0068	3	0	0	1	2
Caloneis tenuis	endangered	0.0095	2	0	0	0	2
Cymbella tumidula	highly endangered	0.0024	1	1	0	0	0
Fragilariforma nitzschioides	endangered	0.0118	1	0	1	0	0
Gomphonema parvulius	endangered	0.0603	23	8	3	8	4
Nitzschia gisela	highly endangered	0.0218	12	0	2	5	5

3.3. *Hydrological phases in intermittent streams – flowing, standing, dry phases*

3.3.1. *Taxa and trait composition, biodiversity*

A total of 196 diatom taxa were recorded in the three hydrological phases. All of these were identified to at least species level (Supplementary Table 5). Furthermore, it is notable that more than 40 % of the species (n = 85) were found in all phases. A comparable number of taxa were exclusively recorded in either flowing (n = 12) or standing (n = 16) phases. Conversely, 36 taxa were exclusively found in dry phases. The taxonomy-based NMDS analysis demonstrated a clear distinction in diatom composition between hydrological phases (Fig. 4a). This finding was confirmed by the PERMANOVA analysis (p = 0.0004).

All of the studied 22 trait categories were found in the phases. The PERMANOVA analysis revealed that the overall trait composition of the phases differed from each other (p = 0.0457; Fig. 4b). However, the paired test confirmed that this difference was attributed to the composition of the assemblages during the flowing phase (flowing vs. standing – p = 0.0301; flowing vs. dry – p = 0.0125), with no significant difference observed between the standing and dry phases (p = 0.6297).

The number of indicator species was almost identical in the hydrological phases ($n_{flowing}$=16, $n_{standing}$=15 and n_{dry}=17) (Supplementary Table 7). However, it should be noted that the number of indicative traits differed considerably between the hydrological phases. The flowing phase was indicated by four trait categories as large size (S4), moderately attached, colonial and high profile guild. Here, the presence of colonial *Fragilaria* and *Diatoma* species, as well as unicellular *Gomphonema* species, was notable. In addition, the presence of the colonial, large *Meridion circulare* (Greville) C.Agardh was also observed. In contrast, only the unicellular category was indicative of the standing phase, while the filamentous and unicellular categories were indicative of the dry phase. In the standing phase, small and medium-sized *Navicula* and *Nitzschia* sl. species, and stalk-forming *Gomphonema* species, were characteristic. Most of the unicellular taxa, which were indicative of the dry phase, belong to the motile guild. Many of these are moderately elongated (LW2-LW4). Filamentous taxa, which were found during the dry phase, were mostly planktic *Aulacoseira* species.

Despite the compositional differences in diatom assemblages between hydrological phases, no biodiversity loss was detected in this study. Neither taxonomic nor functional diversity metrics differed significantly (p > 0.05).

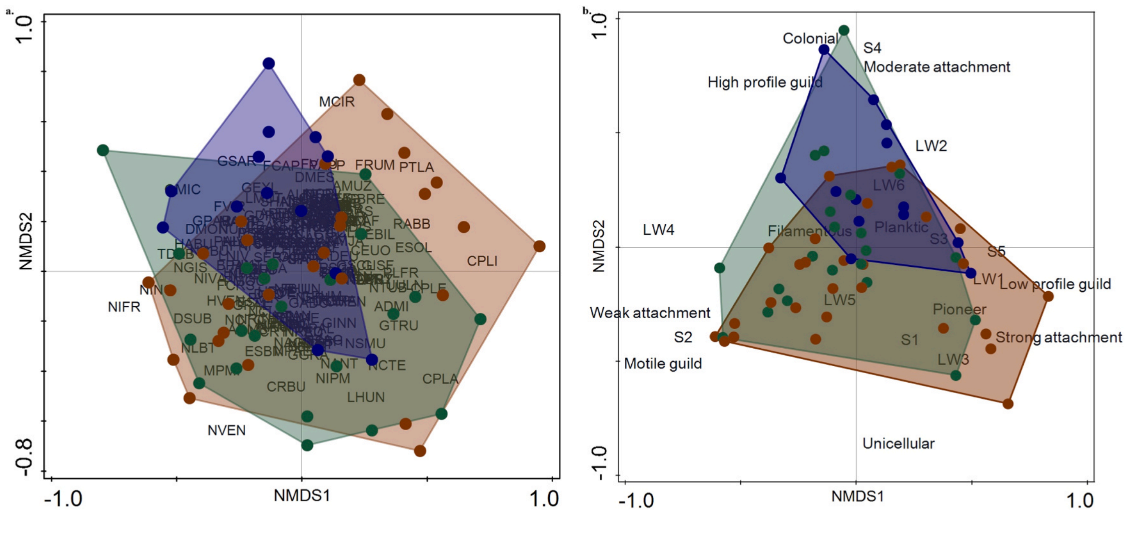

Fig. 4. Taxonomic composition (a) and trait composition (b) of hydrological phases in intermittent streams according to NMDS. The four-letter OMNIDIA codes in Fig. 3a represent the species (Supplementary Table 3). Flowing phases are marked with blue circles (their covered area is blue), standing phases are marked with green circles (their covered area is green), dry phases are marked with brown circles (their covered area is brown).

3.3.2. Conservation value and vulnerability

A total of five endangered taxa were identified in intermittent streams (data records: $n_{flowing}=6$, $n_{standing}=14$ and $n_{dry}=13$); of these, four species were found exclusively in these watercourses (see in 3.2.2 Section). According to the Red List, three species are classified as "highly endangered" and two species as "endangered" (Table 1). It is worth noting that two species were recorded in only one hydrological phase ($n_{flowing}=1$ - *F. nitzschioides*, and $n_{dry}=1$ - *Caloneis tenuis* (W.Gregory) Krammer). The relative abundance of only two taxa was low (less than 1 %). Two species, however, were slightly abundant (>1 %): *F. nitzschioides* (1.18 %) and *N. gisela* (2.18 %). Additionally, *G. parvulius* was dominant on two occasions during the sampling period, both times in the standing phase.

4. Discussion

4.1. Compositional changes

Hydrological extremes, such as floods (B-Béres et al., 2014; Lukács et al., 2021), reduced water levels (Kókai et al., 2015; Nemes-Kókai et al., 2023), and stream drying (Novais et al., 2020; Tornés et al., 2021; Witteveen et al., 2020), impose significant disruptions on aquatic communities. These disturbances ultimately lead to the emergence, or even the dominance, of taxa that are either tolerant of or specifically adapted to these altered conditions (Sabater et al., 2016, 2017; Timoner et al., 2014). Here, we revealed significant compositional differences between water types at both taxonomic and trait levels. However, it should be noted that the diatom composition of permanent waters was a subset of that found in intermittent waters, indicating that intermittent streams support a broader ecological spectrum by encompassing both taxa typical of stable hydrological conditions and those adapted to drying. This also highlights the potential refuge function of intermittent streams. Permanent watercourses were characterized by two distinct types of planktic species: round (centric) and narrow, elongated (fragilaroid). Their presence in the periphyton can be attributed to several factors closely linked to water level and flow conditions, such as post-flood sedimentation or the rapid sedimentation of algal cells as water levels decrease during drought periods (B-Béres et al., 2014, 2017). In our study, planktic trait and several planktic species were key indicators of permanent watercourses for two main reasons: (1) their reliance on stable water columns for their life cycle (Reynolds, 2006), and (2) reduced summer water levels in small permanent streams promote faster settling of planktic cells from the shrinking water column. It is worth noting that motile species such as *Navicula* and *Nitzschia* s.l., which prefer eutrophic conditions, were also common in permanent watercourses. This clearly reflects that these waters flow through agricultural areas and small settlements (B-Béres et al., 2019; Solheim et al., 2019). Numerous studies have demonstrated a positive correlation between motile taxa and the nutrient load in water (revised by Stenger-Kovács and B-Béres, 2024), observable at local (e.g. B-Béres et al., 2014; Passy and Larson, 2011), regional (e.g. Berthon et al., 2011; Budnick et al., 2021), and global (Soininen et al., 2016) scales. Strictly aquatic halophilic species (e.g., *Tryblionella hungarica* (Grunow) Frenguelli and *T. levidensis* W.Smith) have also been identified as indicator species in permanent watercourses, suggesting that extreme weather, such as prolonged summer droughts, also have a significant impact on the community structure by elevated ion concentrations due to lower water levels (B-Béres et al., 2019; Kókai et al., 2015).

In contrast to permanent waters, our results revealed much greater structural variability in intermittent streams. These waters were characterized by the presence of small, moderately elongated nitzschoid and naviculoid species. Cell size is not only a feature that can be easily identified under a microscope and is relatively simple to quantify in diatoms, but it also holds significant ecological relevance. Smaller species, including pioneer diatoms, typically exhibit strong dispersal abilities (Passy, 2007; Rimet and Bouchez, 2012), crucial following floods or flash floods in intermittent streams (Lukács et al., 2021). However, the phenomenon we found has a different background. The high proportion of small taxa in intermittent streams can be attributed not only to the reappearance of water but also to their ability to survive periods of desiccation. During drying, small, motile and mobile species can easily retreat into the mud, between the sediment grains, where they can survive the water-poor conditions (McKew et al., 2011; Novais et al., 2020; Witteveen et al., 2020). Additionally, their moderately elongated shape further supports this adaptation (Stenger-Kovács et al., 2018). Interestingly, large species also indicated intermittent waters in this study. Indicative species associated with this group include high-profile, large-stalked *Gomphonema* species. Their presence is probably linked to the extensive macrophyte cover (Nemes-Kókai et al., 2024) characteristic of these waters. In addition, the colonial *M. circulare* was also found in the drying waters. This species is characteristic of Hungarian small streams, particularly during winter and early spring. Aerophilous taxa, commonly found in drying habitats, were similarly indicative (B-Béres et al., 2019, 2022; Falasco et al., 2016; Novais et al., 2014; Sabater et al., 2016, 2017).

As previously mentioned, the composition of the diatom assemblages varied significantly across the different hydrological phases - flowing, standing, and dry. During the flowing phase, large, colonial taxa (e.g., rheophilic *D. mesodon* and *M. circulare*) were indicative, favouring well-oxygenated and relatively nutrient-poor waters (Lekesiz et al., 2024; Rott et al., 1999). In our study, such an environment was characteristic of the flowing phase. Traits such as moderate attachment and the high-profile guild were also indicative characteristics, which were exhibited, either partially or fully, by the species in question. It is debated which hydrological phase the above-mentioned traits and the species exhibiting them (e.g., *Gomphonema* and *Fragilaria* species in our study) are characteristic of. It seems that the specific combination of traits (guild + life form + attachment type + colony type, if present) may play a more decisive role than any individual trait on its own (Novais et al., 2020; Tornés et al., 2021). Here, the extensive macrophyte cover (Kókai et al., 2015) and the relatively slow flow typical of lowland watercourses likely contributed to making these traits and species indicative of the flowing phase. In our study, the standing phase was primarily indicated by the unicellular trait, including both motile naviculoid and nitzschioid taxa, and stalk-forming *Gomphonema* species. Motility correlates with reduced water flow, siltation, and sedimentation (B-Béres et al., 2017; Elias et al., 2015; Lange et al., 2016; Novais et al., 2020; Tornés et al., 2021). Mucilaginous, stalk-forming *Gomphonema* species are also characteristic of the standing phase (Falasco et al., 2016; Tornés et al., 2021), although their abundance may decrease during pool formation (Novais et al., 2020). The dry phase was characterized by unicellular taxa, most of which were motile, with many exhibiting a moderately elongated shape. These traits enable species to migrate from the surface to the deeper sediment layers in the event of complete desiccation (McKew et al., 2011). Another key indicator of the dry phase was the filamentous category, which during this phase was predominantly represented by planktic *Aulacoseira* species. These species were likely deposited from the water column, i.e. from the plankton.

4.2. Biodiversity changes

Intermittent streams are unique habitats that combine lotic, lentic and terrestrial conditions. Their biodiversity is shaped locally by the duration of the dry phase (Tornés et al., 2021) and the spatial extent of the drought (Acuña et al., 2017; Pumo et al., 2016). As large-scale, recurring droughts have not historically occurred in the Pannonian Ecoregion (Várbíró et al., 2020), local communities remain poorly adapted, and drying events can significantly reduce diversity. In our study, although intermittent streams had fewer taxa and lower functional diversity, the effective Shannon's H index showed no difference from permanent waters. This suggests that while species loss had already begun in the intermittent waters (indicated by the lower number of taxa), the assemblages were not dominated by one or a few species (as reflected by the lack of difference in effective Shannon's H. Community structure in intermittent streams of this region is primarily shaped by biotic interactions (Várbíró et al., 2020), which become more influential after the environmental filtering effects of drying and desiccation. The lower RaoQ in intermittent streams, which might indicate reduced functional richness due to habitat filtering, supports this notion. Although no traits were lost during stream' drying, certain taxa with specific trait combinations may have been filtered out, which could be reflected in the lower RaoQ value.

Although the hydrological phases differed taxonomically, biodiversity metrics did not show significant changes, implying that compositional differences have not yet translated into reduced diversity.

4.3. Nature conservation aspects: background and applications

Despite their economic and social importance (Kaletová et al., 2019), freshwater ecosystems are often overlooked in policy and conservation planning, especially intermittent watercourses (Reid et al., 2019). Recent studies suggest that including Red List diatom species both from permanent and intermittent streams in analyses could improve ecological status assessment metrics and further highlight the importance of these assemblages – and ultimately the ecosystems they inhabit – for water management and conservation planning (Cantonati et al., 2020). To achieve this, however, it is necessary to reconsider our sampling protocols, particularly in relation to the standing phase (intermittent streams). As this phase is known to provide potential refuges for rheophilic species and even endangered lacustrine taxa (Falasco et al., 2016; Novais et al., 2020). However, determining the appropriate level of protection and applying the IUCN Red List, which is primarily designed to assess the vulnerability of macroscopic organisms, presents a significant challenge when it comes to microorganisms, including algae (Juráň and Kaštovský, 2019). Since a national Red List specifically for diatoms was not available, we used the Hofmann et al. (2018) diatom Red List for Germany database in our analyses.

A significant proportion of the samples, nearly 40 %, contained red-listed species. It is important to note that the drying waters harboured almost four times as many endangered species as the permanent waters. These species accounted for 2.2 % of the taxa identified (n = 6 species). Similar to findings in the Mediterranean region (Novais et al., 2020), several species were observed at specific sampling points across multiple sampling occasions. The mucilaginous, stalk-forming endangered *Gomphonema parvulius*, which was found in both stream types, was only dominant in the intermittent streams (during the standing phase). It is well-known that the *Gomphonema* species have the ability to withstand a range of environmental challenges due to their unique physical characteristics: their slimy stalks provide resilience against water scarcity during drought conditions, as well as elevated conductivity and salt concentration (McKew et al., 2011; Sabater et al., 2017).

Regarding the hydrological phases, more data records of endangered species were found in the standing and dry phases than in the flowing phase. *Caloneis tenuis*, found exclusively in the dry phase, is an aerophilous species that also tolerates the ion concentration that occurs during drying (Mertens et al., 2025). In contrast, *Fragilaria nitzschioides*, which was only present during the flowing phase, is able to survive in dry conditions but prefers oligotrophic environments (Almeida et al., 2017). In our study, phosphate concentrations were significantly lower in the flowing phase compared to the standing phase, which may help explain this observation.

The studied small watercourses, regardless of water supply, are locally and regionally important for biodiversity conservation. Additionally, the more detailed analysis of the data highlighted that intermittent streams, due to their diverse habitats, play a key role in this process, and their importance is expected to increase. Given the vulnerability of surface waters (Skoulikidis et al., 2017), climate projections (Babka et al., 2018; IPCC Intergovernmental Panel on Climate Change, 2014; ITM Climate Change Report, 2020), the increasing rates of species extinctions (Juráň and Kaštovský, 2019), and the existing gaps in our understanding of microscopic organisms (Juráň and Kaštovský, 2019; Naselli-Flores and Padisák, 2023), urgent development of ecoregional (national), continental, and global red lists for algae is essential. Changes in the nature of many watercourses (e.g., from permanent to intermittent) are now inevitable. As many permanent watercourses shift toward intermittency, assessing their current - though already altered - state is critical. This may be the last opportunity to define a baseline, including endangered species and at-risk habitats, before full transformation occurs.

4.4. Environmental background

For stream communities, flow-generated disturbances (e.g., flowing vs. standing phases in intermittent streams) or stress caused by prolonged drying of the stream bed cannot be interpreted in isolation, without considering how fundamental physical and chemical properties of the water change (Magand et al., 2020). Since these properties, even on their own, strongly shape community structure and biodiversity, understanding shifts in benthic diatom assemblages across permanent and intermittent streams and through different hydrological phases requires knowledge of them.

Our results showed significant differences in physical and chemical parameters among watercourses with differing water supplies, as well as between distinct hydrological phases. Inorganic nitrogen concentrations were higher in permanent watercourses likely due to nutrient leaching from the surrounding agricultural and residential areas (River Basin Management Plan Report Suppl.6.1., 2021, River Basin Management Plan Report Suppl.6.3., 2021). Conversely, intermittent stream showed elevated conductivity (COND), total dissolved solids (TDS) and chemical oxygen demand (CODMn) levels which can be explained by water level reduction and flow cessation, facilitating concentration (Magand et al., 2020).

Environmental conditions varied notably across the hydrological phases. The oxygen balance was more favourable during the flowing phase than in the stagnant phase, due to the continuous flow-driven oxygen diffusion (Magand et al., 2020; Padisák, 2005). Furthermore, the flowing phase typically coincided with the cooler winter and spring months, which further enhanced the solubility of oxygen in the water (Magand et al., 2020; Padisák, 2005). It is widely acknowledged that water temperature fluctuations in a watercourse are influenced by a variety of factors, including flow, water depth, solar radiation, shading, and TSS concentration, among others (Brown and Hannah, 2008). In our study, the higher temperature observed during the standing phase can largely be attributed to the fact that this phase is primarily, though not exclusively, typical of watercourses during the warmer summer months. Furthermore, the no-flow condition also plays a significant role in enhancing the warming effect. In the standing phase, the elevated chemical oxygen demand (COD) reflects an organic matter load, which also can be attributed to the lack of flow, as it allows organic debris to accumulate. Given the significant macrophyte cover in the examined watercourses, the presence of decaying plant matter, and the reduced oxygen supply (see in Sections 3.1 and 4.1), effectively explain the elevated COD levels (Kiss et al., 2024). In intermittent streams, nutrient levels often undergo significant changes during the drying process (Magand et al., 2020; Novais et al., 2020; Kiss et al., 2024). In our study, phosphate concentration alone differed significantly, with higher levels recorded in the standing phase, likely due to the low and decreasing water level resulting from increased evaporation, leading to concentration.

5. Conclusions

We investigated the impact of drying and desiccation on the benthic diatom communities in small lowland watercourses within the Pannonian Ecoregion. We compared the assemblage structure, biodiversity, and conservation value (including Red List species) of intermittent streams with those of watercourses having similar characteristics but a constant water supply. Additionally, we were the first in the region to examine the differences in assemblage structure and diversity across the three hydrological phases typical of intermittent streams - the flowing, standing, and dry phases - as well as their conservation significance. Our study revealed significant differences in assemblage structure between watercourses with varying water supplies (permanent vs. intermittent). The impact of stream drying on biodiversity was apparent in certain metrics; however, our findings also show that desiccation did not lead to the overdominance of any single species in the affected watercourses. The observed decline in functional diversity suggests that it may be combinations of traits, rather than individual traits, that are being filtered out of the assemblages. Nonetheless, this hypothesis requires further validation in future studies. Our studies also highlighted that despite the significant differences in the structure of assemblages between hydrological phases, there has not yet been a decrease in diversity. This suggests that the duration of the drying of the streams during the studied period did not exceed the required threshold value for this. We were the first to investigate the conservation biological value of intermittent waters in the region, focusing on diatom communities. Our findings indicate that, regardless of water supply constancy, small watercourses in the Great Hungarian Plain possess significant conservation value. However, intermittent watercourses contribute even more to this value, mainly due to the diverse habitats present during the standing phase and the unique conditions found in the dry phases.

CRediT authorship contribution statement

István BÁCSI: Writing – original draft, Data curation. **Zsuzsanna NEMES-KÓKAI:** Investigation, Data curation. **Stefánia KISS:** Writing – original draft, Visualization, Formal analysis. **B-Béres Viktória:** Writing – original draft, Visualization, Resources, Investigation, Funding acquisition, Data curation, Conceptualization. **Péter TÖRÖK:** Writing – original draft. **Júlia SZELES:** Visualization, Investigation. **Csilla STENGER-KOVÁCS:** Writing – original draft. **Gábor BORICS:** Writing – original draft. **Enikő T-KRASZNAI:** Writing – original draft, Investigation. **Kamilla MÁRTON:** Investigation. **Áron LUKÁCS:** Writing – original draft, Investigation.

Ethical statement

No human participants and animals were involved in the research.

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.

Acknowledgements

The project was financially supported by the National Research, Development and Innovation Office - NKFIH FK 132 142 (VBB), NKFIH KKP 144068 (PT) and NKFIH – K137950 (Cs S-K), by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences BO-00458-20-8 (VBB), by the EKÖP-24-3 University Research Scholarship Program of the Ministry for Culture and Innovation from the Source of the National Research, Development and Innovation Fund (SK). We are thankful to Tamás Bozóki for preparation of the map (Fig. 1).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03858.

Data availability

Data will be made available on request.

References

Acuña, V., Hunter, M., Ruhí, A., 2017. Managing temporary streams and rivers as unique rather than second-class ecosystems. Biol. Conserv 211, 12–19. https://doi.org/10.1016/j.biocon.2016.12.025.

Almeida, P.D., Wetzel, C.E., Morales, E.A., Ector, L., Bicudo, D.C., 2017. New species and combinations on fragilariforma (Bacillariophyta) from tropical freshwater environments. Fottea 17, 277–292. https://doi.org/10.5507/fot.2017.006.

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. 58, 626–639. https://doi.org/10.1139/f01-004.

ASTM D859-00, 2000. ASTM Standard test method for silica in water.

Babka, B., Futó, I., Szabó, S., 2018. Seasonal evaporation cycle in oxbow lakes formed along the tisza river in Hungary for flood control. Hydrol. Process 32, 2009–2019. https://doi.org/10.1002/hyp.13126.

B-Béres, V., Török, P., Kókai, Z., Krasznai, E.T., Tóthmérész, B., Bácsi, I., 2014. Ecological diatom guilds are useful but not sensitive enough as indicators of extremely changing water regimes. Hydrobiologia 738, 191–204. https://doi.org/10.1007/s10750-014-1929-y.

B-Béres, V., Török, P., Kókai, Z., Lukács, Á., T-Krasznai, E., Tóthmérész, B., Bácsi, I., 2017. Ecological background of diatom functional groups: comparability of classification systems. Ecol. Indic. 82, 183–188. https://doi.org/10.1016/j.ecolind.2017.07.007.

B-Béres, V., Tóthmérész, B., Bácsi, I., Borics, G., Abonyi, A., Tapolczai, K., Rimet, F., Bouchez, Á., Várbíró, G., Török, P., 2019. Autumn drought drives functional diversity of benthic diatom assemblages of continental intermittent streams. Adv. Water Resour. 126, 129–136. https://doi.org/10.1016/j.advwatres.2019.02.010.

B-Béres, V., Kókai, Z., Várbíró, G., Mustazhapova, G., Csabai, Z., Pernecker, B., Borics, G., Bácsi, I., Boda, P., 2022. Flow intermittence drives the benthic algal composition, biodiversity and Diatom-Based quality of small hilly streams in the pannonian ecoregion, Hungary. Front. Ecol. Evol. 10, 834548. https://doi.org/10.3389/fevo.2022.834548.

Berthon, V., Bouchez, A., Rimet, F., 2011. Using diatom life-forms and ecological guilds to assess organic pollution and trophic level in rivers: a case study of rivers in south-eastern France. Hydrobiologia 673, 259–271. https://doi.org/10.1007/s10750-011-0786-1.

Bey, M.Y., Ector, L., 2013. Atlas des diatomées des cours d'eau de la région Rhône-Alpes.

ter Braak, C.J.F., Smilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). ⟨www.canoco.com⟩, Ithaca NY, USA.

Brown, L.E., Hannah, D.M., 2008. Spatial heterogeneity of water temperature across an alpine river basin. Hydrol. Process 22, 954–967. https://doi.org/10.1002/hyp.6982.

Budnick, W.R., Mruzek, J.L., Larson, C.A., Passy, S.I., 2021. The impacts of nutrient supply and imbalance on subcontinental co-occurrence networks and metacommunity composition of stream algae. Ecography 44, 1109–1120.

Cantonati, M., Kelly, M.G., Demartini, D., Angeli, N., Dörflinger, G., Papatheodoulou, A., Armanni, D.G., 2020. Overwhelming role of hydrology-related variables and river types in driving diatom species distribution and community assemblage in streams in Cyprus. Ecol. Indic. 117, 106690.

Crabot, J., Mondy, C.P., Usseglio-Polatera, P., Fritz, K.M., Wood, P.J., Greenwood, M.J., Bogan, M.T., Meyer, E.I., Datry, T., 2021. A global perspective on the functional responses of stream communities to flow intermittence. Ecography 44, 1511–1523. https://doi.org/10.1111/ecog.05697.

Da Silva, W.J., Jahn, R., Ludwig, T.A.V., Hinz, F., Menezes, M., 2015. Typification and taxonomic status re-evaluation of 15 taxon names within the species complex *cymbella affinis/tumidula/turgidula* (Cymbellaceae, Bacillariophyta). PhytoKeys 53, 1–25. https://doi.org/10.3897/phytokeys.53.4782.

Datry, T., 2012. Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: effects of duration of dry events. Freshw. Biol. 57, 563–574. https://doi.org/10.1111/j.1365-2427.2011.02725.x.

Datry, T., Larned, S.T., Fritz, K.M., Bogan, M.T., Wood, P.J., Meyer, E.I., Santos, A.N., 2014. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. Ecography 37, 94–104. https://doi.org/10.1111/j.1600-0587.2013.00287.x.

Death, R.G., Fuller, I.C., Macklin, M.G., 2015. Resetting the river template: the potential for climate-related extreme floods to transform river geomorphology and ecology. Freshw. Biol. 60, 2477–2496. https://doi.org/10.1111/fwb.12639.

Douglas, S., Xue, J., Hardison, A., Liu, Z., 2023. Phytoplankton community response to a drought-to-wet climate transition in a subtropical estuary. Limnol. Oceano 68, S187–S201. https://doi.org/10.1002/lno.12348.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species:the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Elias, C.L., Calapez, A.R., Almeida, S.F.P., Feio, M.J., 2015. From perennial to temporary streams: an extreme drought as a driving force of freshwater communities. Mar. Freshw. Res. 66, 469. https://doi.org/10.1071/MF13312.

EN 13946, 2014. Water quality. Guidance for the routine sampling and preparation of benthic diatoms from rivers and lakes.

EN 14407, 2014. Water quality. Guidance for the identification and enumeration of benthic diatom samples from rivers and lakes.

Falasco, E., Piano, E., Bona, F., 2016. Diatom flora in Mediterranean streams: flow intermittency threatens endangered species. Biodivers. Conserv 25, 2965–2986. https://doi.org/10.1007/s10531-016-1213-8.

Felföldy, L., 1987. A biológiai vízminősítés. 4. Javított és bővített kiadás. In: Vízügyi Hidrobiológia, 13. VGI.

Gál, B., Weiperth, A., Farkas, J., Schmera, D., 2020. The effects of road crossings on stream macro-invertebrate diversity. Biodivers. Conserv 29, 729–745. https://doi.org/10.1007/s10531-019-01907-4.

Gallart, F., Cid, N., Latron, J., Llorens, P., Bonada, N., Jeuffroy, J., Jiménez-Argudo, S.-M., Vega, R.-M., Solà, C., Soria, M., Bardina, M., Hernández-Casahuga, A.-J., Fidalgo, A., Estrela, T., Munné, A., Prat, N., 2017. TREHS: an open-access software tool for investigating and evaluating temporary river regimes as a first step for their ecological status assessment. Sci. Total Environ. 607–608, 519–540. https://doi.org/10.1016/j.scitotenv.2017.06.209.

Gómez, R., Arce, M.I., Baldwin, D.S., Dahm, C.N., 2017. Water physicochemistry in intermittent rivers and ephemeral streams. in: Intermittent Rivers and Ephemeral Streams. Elsevier, pp. 109–134. https://doi.org/10.1016/B978-0-12-803835-2.00005-X.

Guiry, M.D., Guiry, G.M., 2025. AlgaeBase. World-wide electronic publication, University of Galway. 〈https://www.algaebase.org〉.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis [www document]. Palaeontol. Electron. 〈https://palaeo-electronica.org/2001_1/past/issue1_01.htm〉.

Hofmann, G., Werum, M., Lange-Bertalot, H., 2006. Diatomeen im Süßwasser-Benthos von mitteleuropa. A.R.G. Gantner Verlag K.G.

Hofmann, G., Lange-Bertalot, H., Werum, M., Klee, R., 2018. Rote Liste der limnischen Kieselalgen. Naturschutz und Biologische Vielfalt.

HungaroMet Climate Data Series, 2025. 〈https://met.hu/en/eghajlat/magyarorszag_eghajlata/eghajlati_adatsorok/Debrecen/adatok/eves_adatok/〉 (accessed 26 March 2025).

IPCC Intergovernmental Panel on Climate Change, 2014. Climate change 2014. Mitigation of climate change. Summary for policy makers and technical summary.

ITM Climate Change Report, 2020 Report on the scientific assessment of the potential impacts of climate change on the Carpathian Basin. in Hungarian. 〈https://banyasz.hu/images/klimapolitika/Jelent%C3%A9s%20az%20%C3%A9ghajlat%C3%A1ltoz%C3%A1s%20K%C3%A1rp%C3%A1t-medenc%C3%A9re%20gyakorolt%20esetleges%20hat%C3%A1sainak%20tudom%C3%A1nyos%20%C3%A9rt%C3%A9kel%C3%A9s%C3%A9r%C5%91l.pdf〉(accessed 26 March 2025).

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Juráň, J., Kaštovský, J., 2019. The procedure of compiling the red list of microscopic algae of the Czech Republic. Biodivers. Conserv 28, 2499–2529. https://doi.org/10.1007/s10531-019-01792-x.

Kaletová, T., Loures, L., Castanho, R.A., Aydin, E., Gama, J.T.D., Loures, A., Truchy, A., 2019. Relevance of intermittent rivers and streams in agricultural landscape and their impact on provided ecosystem Services—A Mediterranean case study. IJERPH 16, 2693. https://doi.org/10.3390/ijerph16152693.

Kalogianni, E., Vourka, A., Karaouzas, I., Vardakas, L., Laschou, S., Skoulikidis, N.Th, 2017. Combined effects of water stress and pollution on macroinvertebrate and fish assemblages in a Mediterranean intermittent river. Sci. Total Environ. 603–604, 639–650. https://doi.org/10.1016/j.scitotenv.2017.06.078.

Kiss, S., Nemes-Kókai, Z., Lukács, Á., Bácsi, I., T-Krasznai, E., Márton, K., B-Béres, V., 2024. Aquatic phases have a stronger effect on lotic benthic Diatoms than human-induced microhabitat variability. Hydrobiologia 851, 897–914. https://doi.org/10.1007/s10750-023-05405-1.

Kókai, Z., Bácsi, I., Török, P., Buczkó, K., T-Krasznai, E., Balogh, C., Tóthmérész, B., Béres, V., 2015. Halophilic diatom taxa are sensitive indicators of even short term changes in lowland lotic systems. Acta Bot. Croat. 74, 287–302. https://doi.org/10.1515/botcro-2015-0025.

Krammer, K., Lange-Bertalot, H., 1997b. Bacillariophyceae 1. In: Naviculaceae, Gerloff, H., Heynig, J.H., Mollenhauer, D. (Eds.), Süsswasserflora Von Mitteleuropa. Elsevier, Heidelberg.

Krammer, K., Lange-Bertalot, H., 1997a. Bacillariophyceae 2, bacillariaceae, epithemiaceae, surirellaceae. In: Gerloff, H., Heynig, J.H., Mollenhauer, D. (Eds.), Süsswasserflora Von Mitteleuropa. Elsevier, Heidelberg.

Krammer, K., Lange-Bertalot, H., 2004b. Bacillariophyceae 3, centrales, fragilariaceae, eunotiaceae. In: Gerloff, H., Heynig, J.H., Mollenhauer, D. (Eds.), Süsswasserflora Von Mitteleuropa. Spektrum Akademischer Verlag, Heidelberg.

Krammer, K., Lange-Bertalot, H., 2004a. Bacillariophyceae 4, achnanthaceae. Kritische erganzungen zu achnanthes s.l., navicula str., gomphonema. Gesamt literaturverzeichnis teil 1–4. In: Gerloff, H., Heynig, J.H., Mollenhauer, D. (Eds.), Süsswasserflora Von Mitteleuropa. Spektrum Akademischer Verlag, Heidelberg.

Lakatos, M., Bihari, Z., Izsák, B., Szentes, O., 2021. Globális és hazai éghajlati trendek, szélsőségek változása: 2020-as helyzetkép. Sci. Secur 2, 164–171. https://doi.org/10.1556/112.2021.00037.

Lancaster, J., Ledger, M.E., 2015. Population-level responses of stream macroinvertebrates to drying can be density-independent or density-dependent. Freshw. Biol. 60, 2559–2570. https://doi.org/10.1111/fwb.12643.

Lange, K., Townsend, C.R., Matthaei, C.D., 2016. A trait-based framework for stream algal communities. Ecol. Evol. 6, 23–36. https://doi.org/10.1002/ece3.1822.

Lange-Bertalot, H., Steindorf, A., 1996. Liste der limnischen Kieselalgen (Bacillariophyceae) Deutschlands. Schriftenreihe für BfN, Bonn and Bad Godesberg.

Lekesiz, Ö., Çelekli, A., Yavuzatmaca, M., Dügel, M., 2024. Determination of ecological statuses of streams in the ceyhan river basin using composition and ecological characteristics of Diatoms. Environ. Sci. Pollut. Res. 31, 34738–34755. https://doi.org/10.1007/s11356-024-33518-0.

Lukács, Á., Bácsi, I., Nemes-Kókai, Z., Borics, G., Várbíró, G., T-Krasznai, E., B-Béres, V., 2021. Strong influence of climatic extremes on diversity of benthic algae and Cyanobacteria in a lowland intermittent stream. Ecohydrology 14, e2286. https://doi.org/10.1002/eco.2286.

Magand, C., Alves, M.H., Calleja, E., Datry, T., Dörflinger, G., England, J., Gallart, F., Gomez, R., Jorda-Capdevila, D., Marti, E., Munne, A., Pastor, A.V., Stubbington, R., Tziortzis, I., Von Schiller, D., 2020. Intermittent rivers and ephemeral streams: what water managers need to know. Zenodo. https://doi.org/10.5281/ZENODO.3888474.

McKew, B.A., Taylor, J.D., McGenity, T.J., Underwood, G.J.C., 2011. Resistance and resilience of benthic biofilm communities from a temperate saltmarsh to desiccation and rewetting. ISME J. 5, 30–41. https://doi.org/10.1038/ismej.2010.91.

Mertens, A., van der Wal, J., Verweij, G., Pex, B., van Dulmen, A., van Dam, H., 2025. A revised list of diatom ecological indicator values in the Netherlands. Ecol. Indic. 172, 113219.

Messager, M.L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., Datry, T., 2021. Global prevalence of non-perennial rivers and streams. Nature 594, 391–397. https://doi.org/10.1038/s41586-021-03565-5.

MSZ 12750-6, 1971. Testing of surface waters. Determination of all solved and floating matter content.

MSZ 1484-13, 2009. Water quality. Part 12: Determination of nitrate and nitrite. Content by spectrophotometric method.

MSZ 1484-15, 2009. Water quality. Part 15: Determination of chloride content by argentometric titration method.

MSZ 448-13, 1983. Ivóvízvizsgálat – Szulfátion meghatározás.

MSZ EN 1899-2, 2000. Water quality. Determination of biochemical oxygen demand after n days (BODn) - Part 2: Method for undiluted samples (ISO 5815:1989, modified).

MSZ EN ISO 6878, 2004. Water quality. Determination of phosphorus. Ammonium molybdate spectrometric method.

MSZ ISO 7150-1, 1992. Water quality. Determination of ammonium. Part 1: Manual spectrometric method.

Naselli-Flores, L., Padisák, J., 2023. Ecosystem services provided by marine and freshwater phytoplankton. Hydrobiologia 850, 2691–2706. https://doi.org/10.1007/s10750-022-04795-y.

Nemes-Kókai, Z., Kovács, K., Borics, G., Mayer, R., Novák, Z., Robotka, Á.G., József, J., Érczes, K., Lukács, Á., B-Béres, V., 2023. Continuous precipitation loss induced more pronounced compositional and diversity changes in the lotic phytobenthos than one-off drought events. Ecol. Indic. 148, 110051. https://doi.org/10.1016/j.ecolind.2023.110051.

Nemes-Kókai, Z., Borics, G., Csépes, E., Lukács, Á., Török, P., T-Krasznai, E., Bácsi, I., B-Béres, V., 2024. Role of microhabitats in shaping diversity of periphytic diatom assemblages. Hydrobiologia. https://doi.org/10.1007/s10750-023-05336-x.

Németh, J., 1998. A Biológiai Vízminősítés Módszerei. Vízi Természet- és Környezetvédelem. Környezetgazdálkodási Intézet, Budapest.

Novais, M.H., Morais, M.M., Rosado, J., Dias, L.S., Hoffmann, L., Ector, L., 2014. Diatoms of temporary and permanent watercourses in Southern Europe (Portugal). River Res. Appl. 30, 1216–1232. https://doi.org/10.1002/rra.2818.

Novais, M.H., Morales, E.A., Penha, A.M., Potes, M., Bouchez, A., Barthès, A., Costa, M.J., Salgado, R., Santos, J., Morais, M., 2020. Benthic diatom community dynamics in Mediterranean intermittent streams: effects of water availability and their potential as indicators of dry-phase ecological status. Sci. Total Environ. 719, 137462. https://doi.org/10.1016/j.scitotenv.2020.137462.

Padisák, J., 2005. Általános limnológia: egyetemi tankönyv. ELTE Eötvös Kiadó, Budapest.

Passy, S.I., 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. Aquat. Bot. 86, 171–178. https://doi.org/10.1016/j.aquabot.2006.09.018.

Passy, S.I., Larson, C.A., 2011. Succession in stream biofilms is an environmentally driven gradient of stress tolerance. Microb. Ecol. 62, 414–424. https://doi.org/10.1007/s00248-011-9879-7.

Potapova, M., Hamilton, P.B., 2007. Morphological and ecological variation within the achnanthidium minutissimum (Bacillariophyceae) species complex. J. Phycol. 43, 561–575. https://doi.org/10.1111/j.1529-8817.2007.00332.x.

Pumo, D., Caracciolo, D., Viola, F., Noto, L.V., 2016. Climate change effects on the hydrological regime of small non-perennial river basins. Sci. Total Environ. 542, 76–92. https://doi.org/10.1016/j.scitotenv.2015.10.109.

Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theor. Popul. Biol. 21, 24–43. https://doi.org/10.1016/0040-5809(82)90004-1.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94, 849–873. https://doi.org/10.1111/brv.12480.

Reynolds, C.S., 2006. The Ecology of Phytoplankton, 1st ed. Cambridge University Press. https://doi.org/10.1017/CBO9780511542145.

Rimet, F., Bouchez, A., 2012. Life-forms, cell-sizes and ecological guilds of Diatoms in european rivers. Knowl. Manag. Aquat. Ecosyst. 01. https://doi.org/10.1051/kmae/2012018.

River Basin Management Plan Report Suppl.1.1, 2021. ⟨https://vizeink.hu/vizgyujto-gazdalkodasi-terv-2019-2021/vgt3-elfogadott/#up01⟩ (accessed 26 March 2025).

River Basin Management Plan Report Suppl.6.1, 2021. ⟨https://vizeink.hu/vizgyujto-gazdalkodasi-terv-2019-2021/vgt3-elfogadott/#up01⟩ (accessed 26 March 2025).

River Basin Management Plan Report Suppl.6.3, 2021. ⟨https://vizeink.hu/vizgyujto-gazdalkodasi-terv-2019-2021/vgt3-elfogadott/#up01⟩ (accessed 26 March 2025).

River Basin Management Plan Report Suppl.6.4, 2021. ⟨https://vizeink.hu/vizgyujto-gazdalkodasi-terv-2019-2021/vgt3-elfogadott/#up01⟩ (accessed 26 March 2025).

Rott, E., Pipp, E., Pfister, E., Van Dam, H., Ortler, K., Binder, N., Pall, K., 1999. Indikationslisten für Aufwuchsalgen in österreichischen Fliessgewässern. Teil 2: Trophieindikation (sowie geochemische Präferenzen, taxonomische und toxikologische Anmerkungen). Wasserwirtschaftskataster, Bundesministerium f.Land-u. Forstwirtschaft, Vienna.

Sabater, S., Timoner, X., Borrego, C., Acuña, V., 2016. Stream biofilm responses to flow intermittency: from cells to ecosystems. Front. Environ. Sci. 4. https://doi.org/10.3389/fenvs.2016.00014.

Sabater, S., Timoner, X., Bornette, G., De Wilde, M., Stromberg, J.C., Stella, J.C., 2017. Chapter 4.2 - the biota of intermittent rivers and ephemeral streams: algae and vascular plants. In: Datry, T., Bonada, N., Boulton, A. (Eds.), Intermittent Rivers and Ephemeral Streams. Academic Press, pp. 189–216. https://doi.org/10.1016/B978-0-12-803835-2.00016-4.

Skoulikidis, N.T., Sabater, S., Datry, T., Morais, M.M., Buffagni, A., Dörflinger, G., Zogaris, S., Del Mar Sánchez-Montoya, M., Bonada, N., Kalogianni, E., Rosado, J., Vardakas, L., De Girolamo, A.M., Tockner, K., 2017. Non-perennial Mediterranean rivers in Europe: status, pressures, and challenges for research and management. Sci. Total Environ. 577, 1–18. https://doi.org/10.1016/j.scitotenv.2016.10.147.

Soininen, J., Jamoneau, A., Rosebery, J., Passy, S.I., 2016. Global patterns and drivers of species and trait composition in Diatoms: global compositional patterns in stream Diatoms. Glob. Ecol. Biogeogr. 25, 940–950. https://doi.org/10.1111/geb.12452.

Solheim, L.A., Globevnik, L., Austnes, K., Kristensen, P., Moe, S.J., Persson, J., Phillips, G., Poikane, S., Van De Bund, W., Birk, S., 2019. A new broad typology for rivers and lakes in Europe: development and application for large-scale environmental assessments. Sci. Total Environ. 697, 134043. https://doi.org/10.1016/j.scitotenv.2019.134043.

Stenger-Kovács, C., Lengyel, E., 2015. Taxonomical and distribution guide of Diatoms in soda pans of central Europe. Stud. Bot. Hung. 46, 3–203. https://doi.org/10.17110/StudBot.2015.46.Suppl.3.

Stenger-Kovács, C., Körmendi, K., Lengyel, E., Abonyi, A., Hajnal, É., Szabó, B., Buczkó, K., Padisák, J., 2018. Expanding the trait-based concept of benthic Diatoms: development of trait- and species-based indices for conductivity as the master variable of ecological status in continental saline lakes. Ecol. Indic. 95, 63–74. https://doi.org/10.1016/j.ecolind.2018.07.026.

Stenger-Kovács, C., B-Béres, V., 2024. Guilds for Diatoms: history and future prospects. In: Maidana, N.I., Licursi, M., Morales, E. (Eds.), Diatom Ecology. Wiley, pp. 233–279. https://doi.org/10.1002/9781394174898.ch8.

Stubbington, R., England, J., Wood, P.J., Sefton, C.E.M., 2017. Temporary streams in temperate zones: recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. WIREs Water 4. https://doi.org/10.1002/wat2.1223.

Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., Munné, A., Pařil, P., Pešić, V., Tziortzis, I., Verdonschot, R.C.M., Datry, T., 2018. Biomonitoring of intermittent rivers and ephemeral streams in Europe: current practice and priorities to enhance ecological status assessments. Sci. Total Environ. 618, 1096–1113. https://doi.org/10.1016/j.scitotenv.2017.09.137.

Timoner, X., Borrego, C.M., Acuña, V., Sabater, S., 2014. The dynamics of biofilm bacterial communities is driven by flow wax and wane in a temporary stream. Limnol. Oceano 59, 2057–2067. https://doi.org/10.4319/lo.2014.59.6.2057.

Tornés, E., Colls, M., Acuña, V., Sabater, S., 2021. Duration of water flow interruption drives the structure and functional diversity of stream benthic Diatoms. Sci. Total Environ. 770, 144675. https://doi.org/10.1016/j.scitotenv.2020.144675.

Trábert, Z., Tihamér Kiss, K., Várbíró, G., Dobosy, P., Grigorszky, I., Ács, É., 2017. Comparison of the utility of a frequently used diatom index (IPS) and the diatom ecological guilds in the ecological status assessment of large rivers. Fundam. Appl. Limnol. 189, 87–103. https://doi.org/10.1127/fal/2016/0933.

Truchy, A., Csabai, Z., Mimeau, L., Künne, A., Pernecker, B., Bertin, W., Pellizzaro, F., Datry, T., 2023. Citizen scientists can help advance the science and management of intermittent rivers and ephemeral streams. BioScience 73, 513–521. https://doi.org/10.1093/biosci/biad045.

Várbíró, G., Borics, G., Novais, M.H., Morais, M.M., Rimet, F., Bouchez, A., Tapolczai, K., Bácsi, I., Usseglio-Polatera, P., B-Béres, V., 2020. Environmental filtering and limiting similarity as main forces driving diatom community structure in Mediterranean and continental temporary and perennial streams. Sci. Total Environ. 741, 140459. https://doi.org/10.1016/j.scitotenv.2020.140459.

Wellman, J.C., Combs, D.L., Cook, S.B., 2000. Long-Term impacts of bridge and culvert construction or replacement on fish communities and sediment characteristics of streams. J. Freshw. Ecol. 15, 317–328. https://doi.org/10.1080/02705060.2000.9663750.

Witteveen, N.H., Freixa, A., Sabater, S., 2020. Local and regional environmental factors drive the spatial distribution of phototrophic biofilm assemblages in Mediterranean streams. Hydrobiologia 847, 2321–2336. https://doi.org/10.1007/s10750-020-04258-2.