



Flow Intermittence Drives the Benthic Algal Composition, Biodiversity and Diatom-Based Quality of Small Hilly Streams in the Pannonian Ecoregion, Hungary

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Climate change is putting increasing pressure on flowing waters. Drastic water level fluctuations in rivers or drying up of small and medium-sized streams all contribute to the biodiversity crisis threatening freshwater ecosystems. Benthic diatoms are important elements of biofilm in small streams. However, knowledge on the relationship between benthic diatoms and flow intermittence is incomplete, especially in regions recently impacted by recurrent drying. Thus, we investigated benthic diatom flora of small intermittent, hilly streams in the warm temperate region of Europe (the Pannonian Ecoregion). Our hypotheses were addressed to compositional changes, biodiversity loss and diatom-based ecological assessment. The results revealed clear flow intermittence-induced differences in taxa and trait composition of diatoms. Altogether six species for the dry phase and three species in the aquatic phase were identified as indicative ones by using indicator value analyses. In contrast to water regime induced changes in assemblages, there was a seasonal overlap in taxa and trait composition. During the study period, the drying up of streams did not result in significant biodiversity loss either at taxa or trait levels. Functional dispersion, however, reduced significantly by summer. Overall, neither the hydrological regime nor seasonal changes had a significant effect on diatom-based quality indices, except for the Rott trophic index (TID index). The TID index values were significantly lower in dry phases than in aquatic ones. These results suggested that the drying up of streams has a very complex influence on benthic diatoms. It seems that taxonomical and functional redundancy can reduce the negative impact of short-time flow intermittence on assemblages. As a practical benefit, the results are the first to support the use of diatom-based quality indices in the assessment of flow intermittence in the temperate region.

Keywords: flow intermittence, small hilly streams, temperate region, water quality indices, aquatic ecosystem, compositional changes

INTRODUCTION

Over the past decades, biodiversity loss has become a major problem facing humanity and as it is constantly worsening it threatens ecosystems functioning and human well-being (Díaz et al., 2006; He et al., 2019; Crabot et al., 2021; Thompson et al., 2021). Although freshwaters are one of the most diverse ecosystems, integrity loss of communities here is an increasing trend that poses a challenge to biodiversity conservation (Dudgeon et al., 2006; Reid et al., 2019). Climate change and its impact on freshwater biodiversity is one of the 12 threats named by Reid et al. (2019) endangering the entire ecosystem from specimen to community level resulting in, inter alia, reduction in cell/body size, changes in phenology, changes in species distribution, spread of invasive or non-native species or even disease outbreaks (see more in Reid et al., 2019). Rapid and extreme changes in water regime, increasing water temperature, drying of small water bodies and nutrient concentration during drying are just some of the influences that can result in irreversible transformations in freshwater ecosystems (see more in Magand et al., 2020).

As climate change, water abstraction or even land use resulted in a shift of perennial watercourses becoming intermittent ones in the last 5 decades, small streams all around the world are increasingly threatened by flow cessation (Messenger et al., 2021). According to the latest IPCC report (IPCC, 2021), there is high probability of increase in extreme climatic events, including severe droughts will occur in the near future. These events will result in an increase in the number of intermittent streams and the duration of non-flow periods. In the Mediterranean regions characterized by an intra-annual moisture deficit, a number of intermittent streams can be considered as natural elements of the landscape (Sabater et al., 2016; Acuña et al., 2017). In contrast, the intermittent shift of formerly perennial streams to an intermittent state is a relatively new phenomenon in the warm temperate region, where the summers are hot and there are no significant seasonal differences in precipitation¹ (B-Béres et al., 2019; Várbíró et al., 2020). Independently of the historical background of intermittent streams, i.e., drying is a new phenomenon or it dates back to the ancient times, these watercourses constitute a very large fraction of river networks and their number is probably underestimated (Sabater et al., 2016).

Intermittency is a strong pressure on organisms. Populations living in intermittent streams are either able to adapt to dry conditions or they disperse to a new area or become extinct from the given ecosystem (Falasco et al., 2016a; Sabater et al., 2016; Stubbington et al., 2017). Thus, these watercourses can be usually considered as lower diversity areas during the aquatic phase compared to permanent waters. However, appearance of lentic and terrestrial species in assemblages during intermittence can result in higher taxonomical and functional variability here (Stubbington et al., 2017). But intermittence is a strong environmental pressure that induces diversity changes during drying of streams. The replacement of taxa is quite intense then, the appearance of lentic and terrestrial taxa in

assemblages first results in an increase of diversity in pools (Stubbington et al., 2017; Novais et al., 2020). But finally the increase in biotic interactions within these assemblages and the ongoing drying of pools lead to the decrease in biodiversity (Stubbington et al., 2017).

Freshwater benthic diatoms are one of the most abundant algal groups in the biofilm of streams (Pan et al., 1999), thus they play a key role in these ecosystems as primary producers and also as a food source for herbivores (Kireta et al., 2012). Since they are sensitive indicators of environmental stressors (McCormick and Cairns, 1994), they provide valuable information on the ecological quality of waters (Water Framework Directive – EC, 2000). In addition, in the last few years, an increasing number of studies have shown that benthic diatoms respond sensitively to drying of waters (Novais et al., 2014, 2020; Falasco et al., 2016a; Piano et al., 2017; B-Béres et al., 2019; Stubbington et al., 2019; Várbíró et al., 2020; Tornés et al., 2021). Previous studies pointed out that diatom indices can be useful metrics comparing the ecological quality of intermittent streams in different phases (Barthès et al., 2015; Novais et al., 2020). In a comprehensive study, Novais et al. (2020) validated that values of diatom-based metrics from dry and from previous aquatic phases are comparable and showed no significant differences. There is no doubt, however, that drying of streams results in compositional modifications within assemblages (Novais et al., 2014, 2020; Falasco et al., 2016a; Piano et al., 2017; B-Béres et al., 2019; Várbíró et al., 2020; Tornés et al., 2021). Flow cessation and drying of streams create very harsh conditions for benthic algae and finally result in a decrease in biodiversity (Sabater et al., 2017; B-Béres et al., 2019; Novais et al., 2020; Várbíró et al., 2020; Tornés et al., 2021). Although taxonomical or functional redundancy seems to be able to balance this negative effect (Novais et al., 2020; Lukács et al., 2021), latest studies suggest that this phenomenon is highly dependent on the duration of the dry periods not only in the case of diatoms (Tornés et al., 2021), but also in macroinvertebrate assemblages (Crabot et al., 2021). Others pointed out that the time scale of dry periods is crucial in determining the extent of compositional changes. Drying of streams has a stronger negative influence on benthic diatom assemblages in regions where the flow intermittence is a new phenomenon than in regions with historical occurrence of intermittent streams (Várbíró et al., 2020). Our knowledge of flow intermittence – benthic diatom relationship, however, is incomplete in regions recently impacted by recurrent drying. It is especially true in the Pannonian Ecoregion, the largest part of which belongs to Hungary. Approximately 10,000 watercourses are registered here, but less than 10% of them are monitored regularly by the Water Framework Directive-related (WFD) National Biomonitoring System² (Stubbington et al., 2018). Very small streams with a catchment area less than 10 km² are not included in this biomonitoring system. Thus, we have no information on how many of these small streams are affected by drying in the region. Our knowledge of how these streams contribute to the maintenance of biodiversity of benthic flora is also incomplete. Therefore, we started to study benthic diatom

¹<http://koeppen-geiger.vu-wien.ac.at>

²www.vizeink.hu

assemblages of these very small intermittent streams in the last few years focusing first on the southern hilly part of the region. Our main aim was to investigate the impact of drying up on stream diatom assemblages. We hypothesized the following:

- (H1) Assemblages composition – Dry and aquatic phases of streams can be characterized by compositional differences at both taxonomical and trait levels. It is also assumed that indicator taxa could be identified in both phases.
- (H2) Biodiversity – Drying of streams coincides with the loss of diversity.
- (H3) Diatom-based assessment of water quality – Only slight differences in diatom-based quality are assumed between the different water regimes.

MATERIALS AND METHODS

Sampling Area and Environmental Parameters

A total of 30 diatom samples were collected from 13 sampling sites on 8 very small intermittent streams in spring and summer in 2019 (Figure 1 and Supplementary Table 1). The streams are located in the southern part of Hungary within the Mecsek Mountains. The local climate is quite special here since Mediterranean impacts can also prevail beside continental ones resulting in a moderately cool and moderately dry climate in the region (Ács et al., 2015). Thus, this area can be characterized by 650–750 mm of mean annual precipitation, 7–10°C of mean annual temperature and more than 2000 h of total annual sunshine duration (Ács et al., 2015; Mezősi, 2017).

The catchment areas of each studied stream are less smaller than 10 km². They are hilly streams, their bedrock is calcareous or red sandstone (Petőczi stream) and the sediment size is coarse to medium. In all but one sampling site (Szentkatalin), the cover of aquatic macrovegetation is also negligible. Most of the streams run through forests; where characteristic tree taxa are mostly beech, oaks, poplars, birch and robinia.

In this study, altogether 11 samples were collected from dry streambed. Hereinafter they will be referred to as the dry phase. There was flowing or standing water in the streambed in 19 sampling events. After we proved that there were no differences in composition and in diversity and also in ecological status indices between these two conditions (Supplementary Table 2; see details in Statistical analyses subchapter) we handled these 19 sampling events together as an aquatic phase.

At sampling sites where surface water could be found in the streambed (aquatic phase), a total of 10 physical and chemical parameters were measured. Water temperature (T - °C), pH and conductivity (COND - $\mu\text{S cm}^{-1}$) were measured in the field with a portable-multi-parameter digital meter (HQ30d, Germany). The water samples were kept at 4°C in a cooler bag during transportation to the laboratory for further analyses. Nutrient and chloride contents were determined according to international and national standards (NO_3^- -N in mg L^{-1} – MSZ 1484-13:2009, 2009; NO_2^- -N in $\mu\text{g L}^{-1}$ –

MSZ 1484-13:2009, 2009; NH_4^+ -N in $\mu\text{g L}^{-1}$ – MSZ ISO 7150-1:1992, 1992; PO_4^{3-} -P in mg L^{-1} – MSZ EN ISO 6878:2004, 2004 and Cl^- in mg L^{-1} – MSZ 1484-15:2009, 2009). Total suspended solids (TSS in mg L^{-1} – MSZ 12750-6:1971, 1971) and total dissolved solids (TDS in mg L^{-1} – Németh, 1998) were measured according to national standard and proposal. Based on the nutrient concentrations and other physical and chemical parameters of the streams, the anthropogenic impact on them was negligible (Supplementary Table 3).

Sample Collection, Preparation and Identification

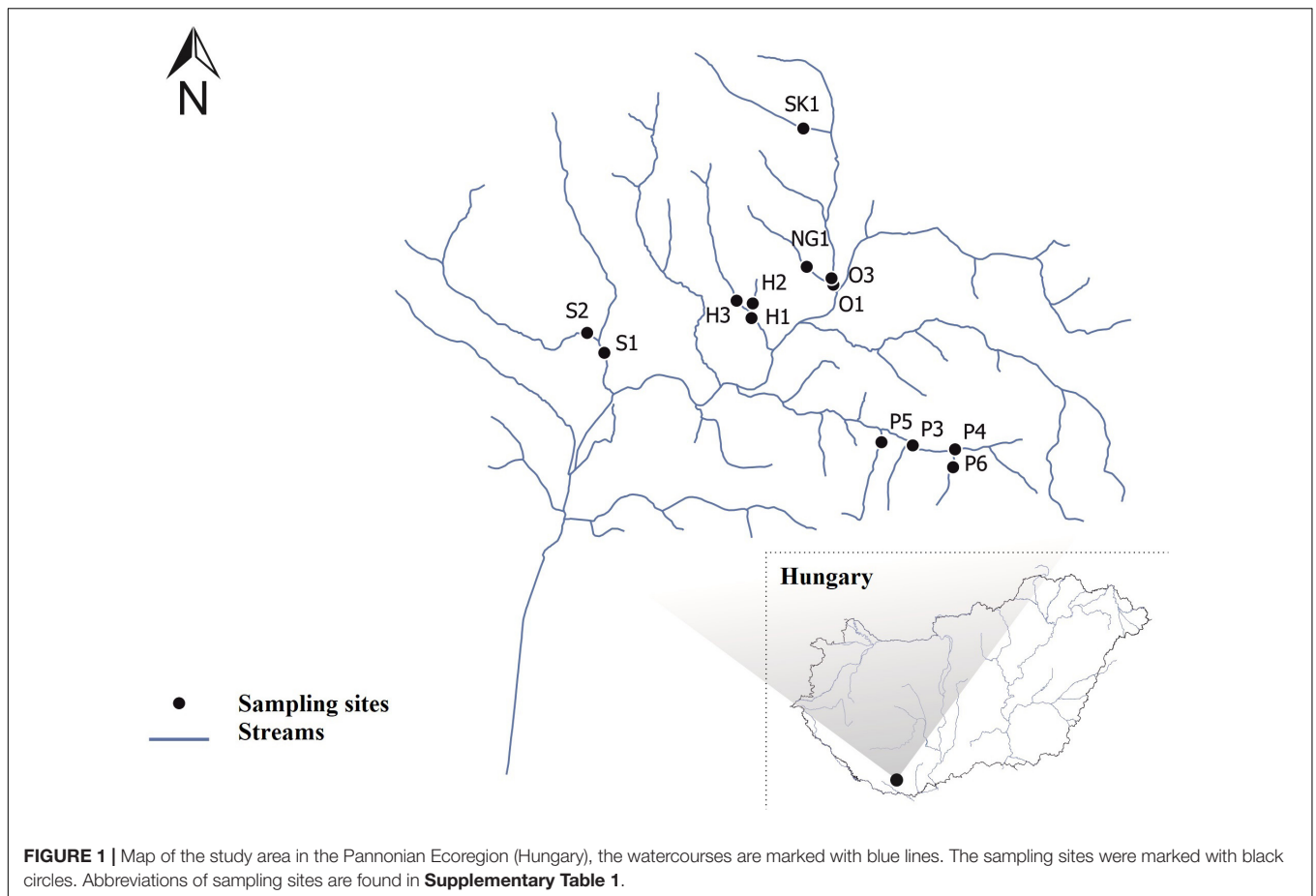
In flowing conditions, sampling was done according to the European standard (EN 13946, 2014). In pools, when more than one pool was detected, composite samples were collected with the proviso that at least 5 cobbles should be used as substrate per pool. In the dry phase, 5–10 cobbles were sampled from the middle of the streambed. Independently of the aquatic states, when cobbles were not found in the streambed, we used the most characteristic substrates for collecting diatom samples (pebbles, emergent or submerged macrophytes, branches). Substrates were cleaned by toothbrushes and diatom samples were preserved by Lugol's solution according to the recommendation of European standard (EN 13946, 2014). Diatom valves were prepared by hot hydrogen-peroxide method (EN 13946, 2014) and valves were embedded into Naphrax® (EN 14407, 2014). At least 400 valves were counted and identified using a Leica DMRB microscope (1000–1600-fold magnification). The identification of diatoms was carried out using up-to-date and relevant literatures: Krammer and Lange-Bertalot (1997a,b, 2004a,b), Potapova and Hamilton (2007); Bey and Ector (2013), Stenger-Kovács and Lengyel (2015).

Data Processing and Statistical Analyses

Diatom taxa were classified into 27 trait categories including cell size according to Berthon et al. (2011), guild, life-form and attachment type according to Rimet and Bouchez (2012) and length and width (L/W) ratio according to Stenger-Kovács et al. (2018); Supplementary Table 4). We applied moisture preference of taxa proposed by van Dam et al. (1994) updated in 2011 (Supplementary Table 4). Additionally, taxa were referred to as pioneer according to Rimet and Bouchez (2012; Supplementary Table 4). The number of categories within traits were 5, 4, 3, 3, 6, and 5, respectively; Table 1.

The number of taxa observed in the samples was considered as taxa richness (Taxa_S). Effective Shannon's H values (Jost, 2006) was calculated to compare the “true diversities” of assemblages (Beck and Schwanghart, 2010; Stuart-Smith et al., 2013; Morris et al., 2014). Effective Shannon's H is the exponential of Shannon's H. Taxa richness and Shannon's H were calculated by using the Past software package (version 4.08; Hammer et al., 2001).

The main components of diversity metrics as functional richness (FRich), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) were calculated by using “FD” R software package in R



(Laliberté and Legendre, 2010; Laliberté et al., 2014; version 3.5.2; R Core Team, 2019).

To identify the indicative species of sites' groups with similar drying characteristics, we performed indicator value analysis based on relative abundances of taxa (IndVal; Dufrêne and Legendre, 1997). For the calculation of these values, R package "indicspecies" was used (v1.7.9; De Cáceres and Legendre, 2009).

Altogether four indices were calculated to assess the diatom-based ecological quality of streams: Specific pollution sensitivity index (IPS; Coste, 1982), Rott's trophic index (TID; Rott et al., 1999), Rott's saprobic index (SID; Rott et al., 1997) and the Hungarian phytobenthos metric (IPSITI; Várбірó et al., 2012). While SID can assess organic load, TID is sensitive for trophic level. The IPS and IPSITI aim to assess both trophic and saprobic states. All of them are based on the weighted average equation of Zelinka and Marvan (1961) modified by Coste (1982).

$$\text{index} = \frac{\sum_{j=1}^n p_j \times s_j \times v_j}{\sum_{j=1}^n p_j \times v_j}$$

p_j : relative abundance of counting units of "j" taxon in sample.

s_j : sensitivity of "j" taxon (optimum).

v_j : tolerance/indicator value of "j" taxon.

Diatom indices IPS, SID, and TID were calculated by using OMNIDIA software package (version 5.2; Lecoince et al., 2003),

while ISPITI is the arithmetic mean of these three indices. The final values of indices vary between 1 (worse quality) to 20 (best quality).

In the first step, we applied Mann-Whitney test for testing significant differences in diversity and diatom metrics between flowing and standing conditions. We also performed Non-metric Multi-dimensional Scaling (NMDS) with Bray-Curtis distance by applying CANOCO 5.0 software package to compare the taxa and trait composition of streams in flowing and standing aquatic conditions (ter Braak and Šmilauer, 2002). These tests proved that there were no differences in either the studied metrics or the composition of these streams. Thus, as we mentioned above, these two conditions were merged and sampling events were handled as aquatic phase in further analyses.

Comparing the taxa and trait composition in dry and aquatic phases, and also in spring and summer, four NMDSs with Bray-Curtis distance were performed. Here, we used the relative abundances of taxa and the community weighted mean (CWM) matrix, in which the main values of traits in the community were weighted by the relative abundances of the taxa matrix.

One-way ANOVA tests were used to compare the diversity characteristics and also diatom-based water qualities between dry and aquatic phases and also between the two seasons. The fixed factors were the phase-type or the season, while the dependent

TABLE 1 | Applying functional traits and their categories and key references.

Traits	Trait categories		References
Cell size (μm^3)	S1	5–99	Berthon et al., 2011
	S2	100–299	
	S3	300–599	
	S4	600–1499	
	S5	≥ 1500	
Guilds	Low profile		Rimet and Bouchez, 2012
	High profile		
	Motile		
	Planktic		
Life-forms	Unicellular		
	Filamentous		
	Colonial		
Attachment	Weakly		
	Moderately		
	Strongly		
Length/width ratio	LW1	<2	Stenger-Kovács et al., 2018
	LW2	2–3	
	LW3	4–5	
	LW4	6–11	
	LW5	12–19	
	LW6	≥ 20	
Moisture preference	Strictly aquatic	AQU	van Dam et al. (1994) updated in 2011
	Occasional aerophile	AOC	
	Aquatic-subaerial	WSA	
	Aerophile	AER	
	Terrestrial	TER	
Spreading	Pioneer		Rimet and Bouchez, 2012

variables were taxa_S, effective Shannon's H, FRich, FEve, FDIV, FDis and the diatom indices as IPS, TID, SID, and IPSITI.

RESULTS

Taxa Composition

A total of 208 diatom taxa were identified in the samples: 206 to species and 2 to genus level (**Supplementary Table 5**).

According to the taxonomy-based NMDS analysis (stress value: 0.089), there was only partial overlap in diatom taxa pools between dry phase and aquatic phase (**Figure 2A**). While altogether 106 taxa were recorded in both water types, 24 taxa were found exclusively during dry phase and 78 taxa were identified exclusively during aquatic phase (**Supplementary Table 5**). The different hydrological regime of small streams explained 82.17% of the variance in the taxa composition of benthic diatom assemblages for the first two canonical axes (**Figure 2A**). The eigenvalues of the first and second axes were 0.577 and 0.245. The diatom taxa *Diadasmus contenta*, *Meridion circulare*, *Planothidium lanceolatum*, *Reimeria sinuata* and

R. uniseriata characterized the assemblages of streams with dry streambed, while *Cocconeis* species, *Navicula* and *Nitzschia* sensu lato species, *Gomphonema pumilum* and *Halamphora* species as *H. montana* and *H. normanii* characterized the assemblages of streams where water was present (**Figure 2A**). *Diadasmus contenta*, *Meridion circulare*, *Navicula veneta*, *Frustulia vulgaris*, *Luticola ventricosa* and *Nitzschia liebetruithii* were significant indicators of dry-phase assemblages ($p < 0.05$), while *Gomphonema pumilum*, *Gomphonema angustatum* and *Navicula lanceolata* were indicative of aquatic phase ($p < 0.05$, in case of *G. pumilum*: $p < 0.01$).

According to the NMDS analysis, a considerable seasonal overlap in taxa composition was found (**Figure 2B**). From those taxa, which were recorded in spring, 39 taxa were not found in summer. In contrast, altogether 74 taxa were recorded exclusively in summer. Some of them were dominant in summer such as *Cocconeis placentula*, *Halamphora normanii*, *Placoneis paraelginensis* and *Sellaphora pseudopupula*.

Trait Composition

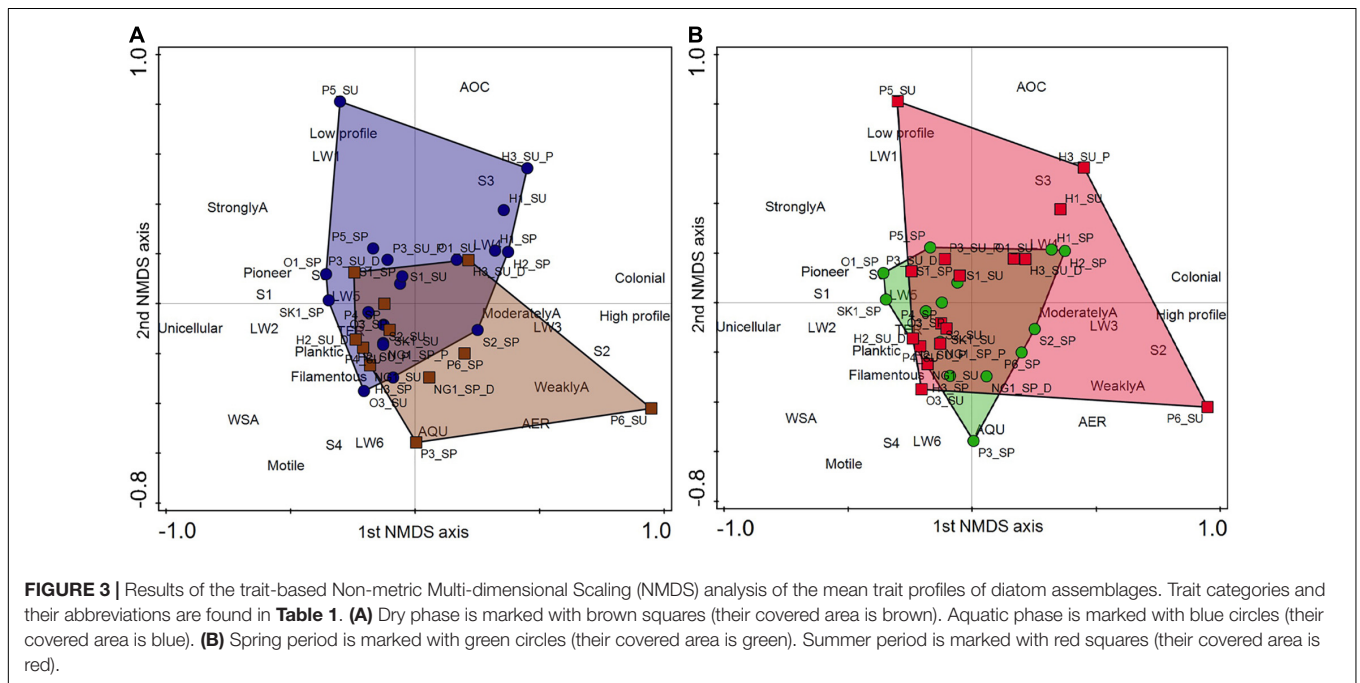
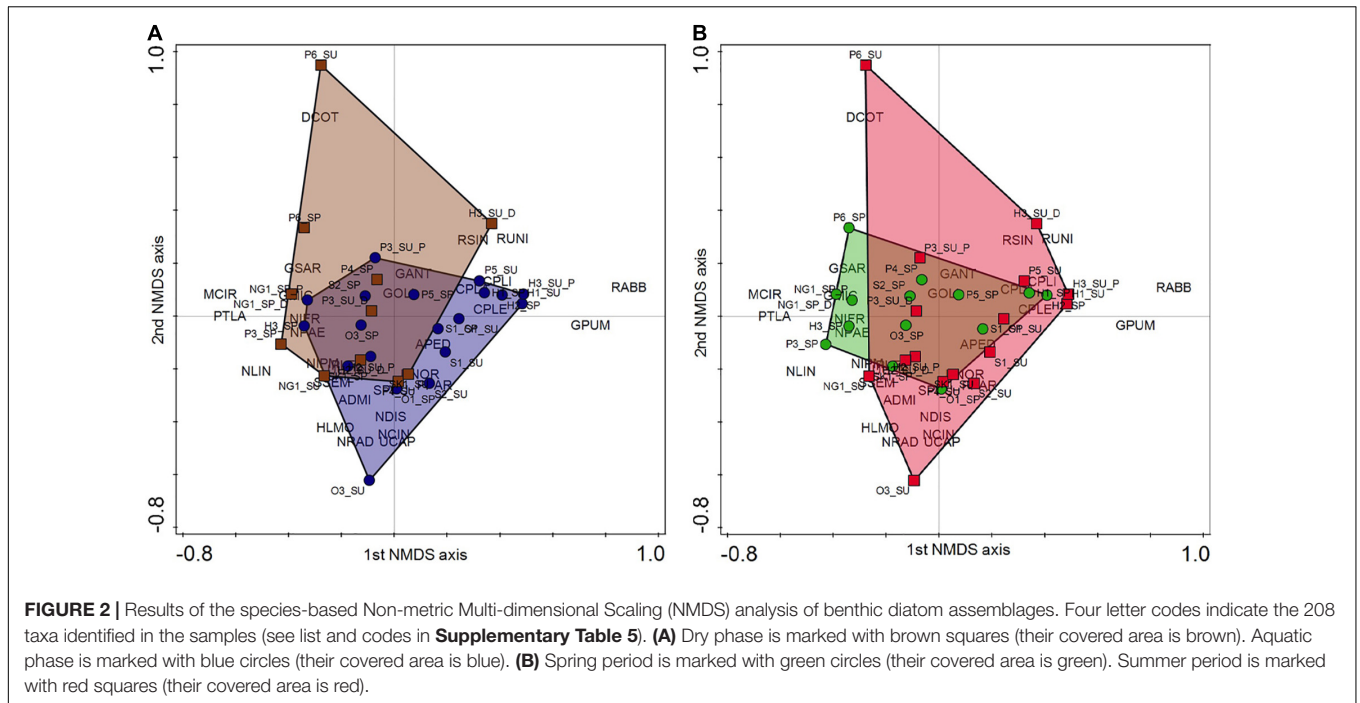
Based on the trait composition of diatom assemblages the NMDS (stress value: 0.088) analysis revealed clear differences between dry phase and aquatic phase (**Figure 3A**). The eigenvalues of NMDS were 0.559 and 0.238, while the hydrological regime and trait composition correlation was 79.74 with the first two canonical axes. The dry phase was characterized by trait categories as high profile guild, S2 size, colonial, moderate or weak attachments and aerophilic, but surprisingly, non-aerophilic category was also characteristic here. In contrast, low profile guild, small (S1) or medium size (S3), unicellular, pioneer and more or less rounded forms (LW1 and LW2) were dominant in aquatic phase. In addition, here, WSA (aquatic-subaerial) and AOC (occasional aerophile) spreading trait groups characterized this phase (**Figure 3A**).

Similarly to the taxonomy-based analysis, a less pronounced difference in trait composition was found between spring and summer (**Figure 3B**). All trait categories were found in both seasons, only their proportion was different. In summer, the following trait categories characterized the assemblages: high profile guild and/or S2 size and/or colonial category and/or low profile guild and/or LW1 category.

Biodiversity and Diatom Indices

Although both taxa and trait composition of benthic assemblages of the two phases clearly separated, hydrological regimes studied here did not result in significant differences either in the taxonomy-, or in the trait-based diversity metrics ($p > 0.05$; **Figure 4**). Despite the seasonal overlap in taxa and trait composition, the FDis was reduced significantly by summer ($p = 0.012$). The other diversity metrics, however, did not show seasonal differences ($p > 0.05$; **Supplementary Figure 1**).

In the case of TID index, we found strong positive correlation between diatom-based ecological quality and hydrological regime: it was significantly lower in streams with dry streambed than in aquatic phase ($p = 0.0122$; **Figure 5B**). Overall, neither hydrological regime nor seasonal changes resulted in significant



differences in the other indices ($p > 0.05$; **Figure 5** and **Supplementary Figure 2**).

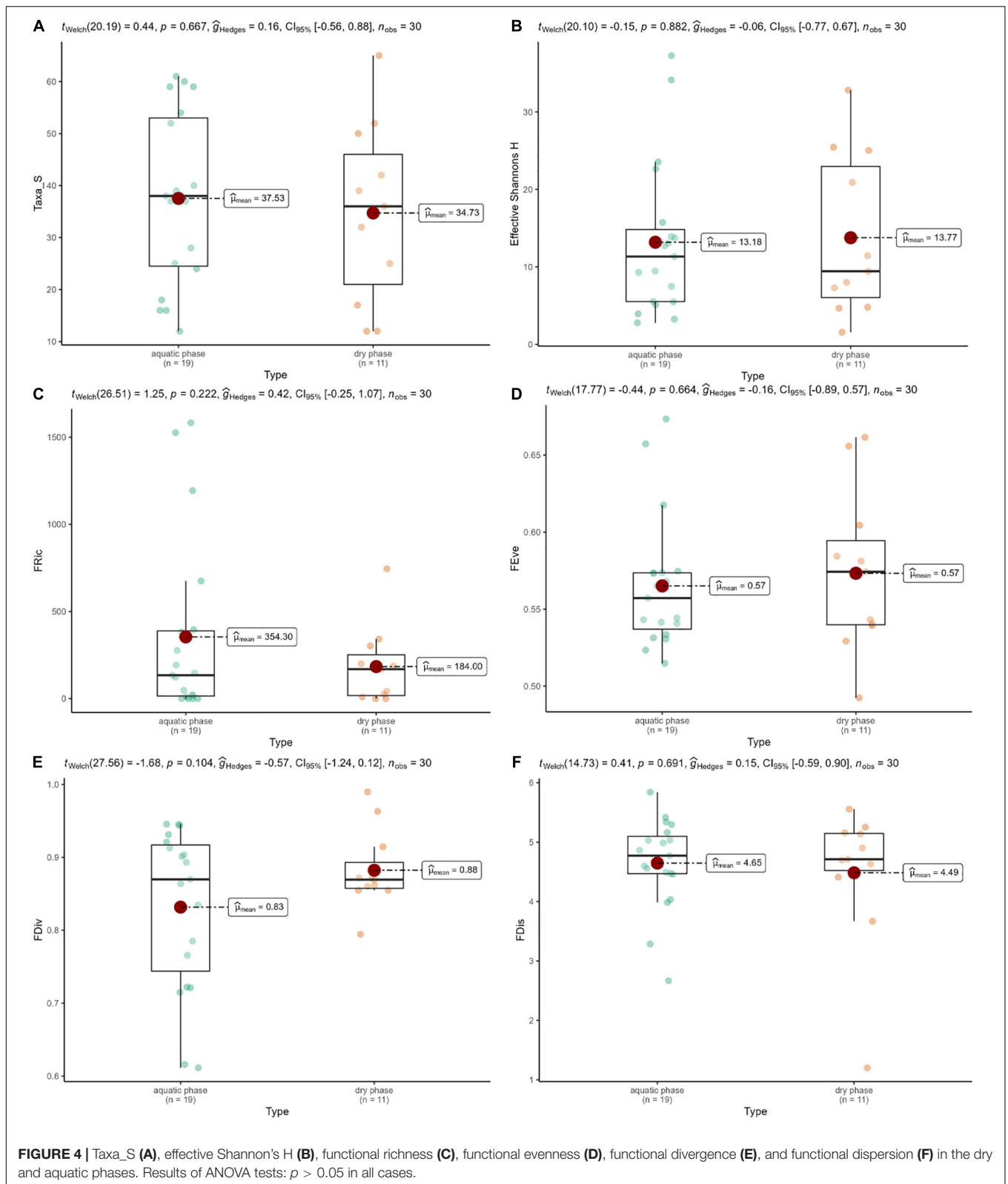
DISCUSSION

Compositional Changes

Intermittent small streams provide a variety of services to human communities and they contribute to the integrity of river

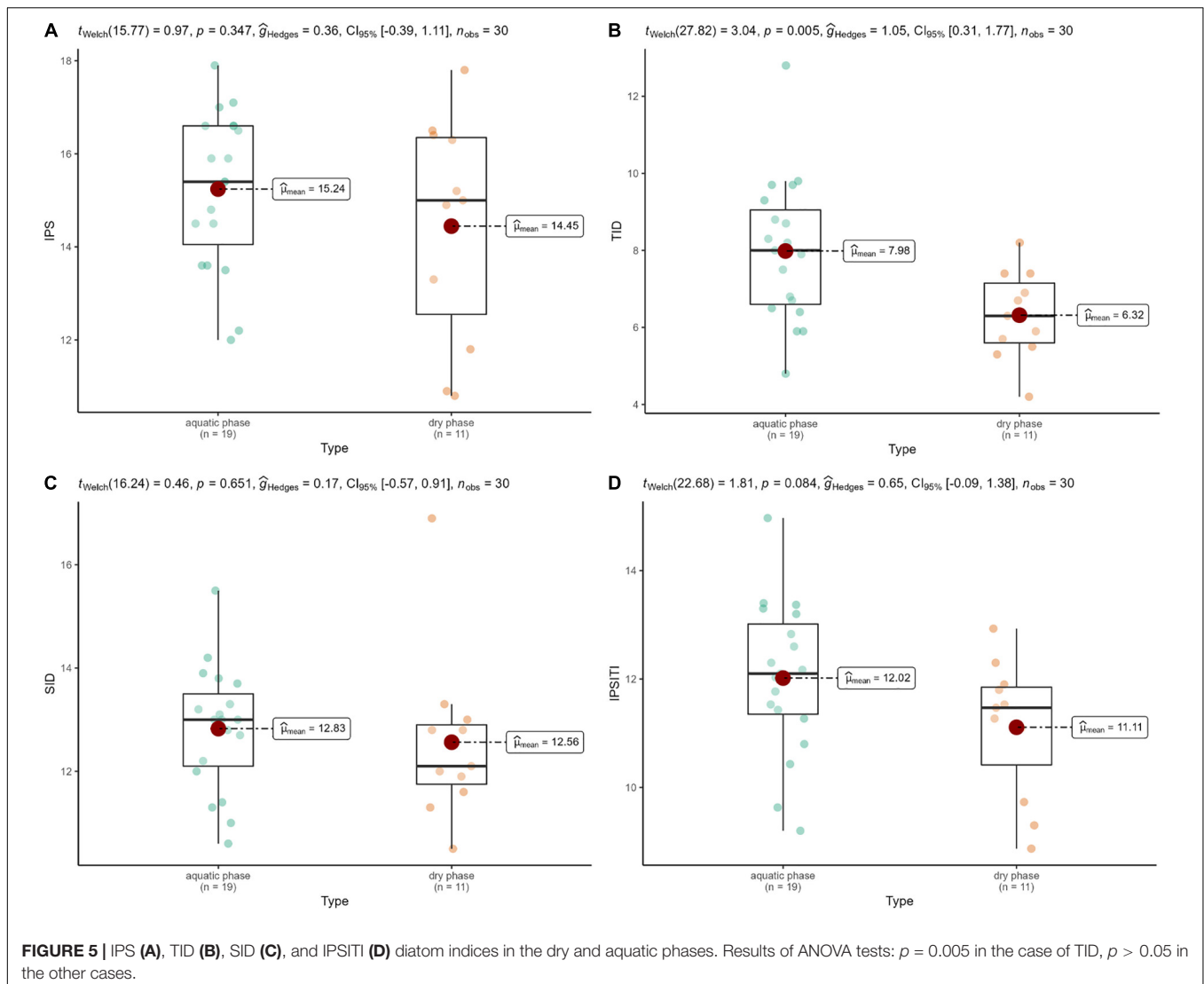
networks (see more in Magand et al., 2020). The assemblages living here are special compared to permanent flowing waters, since lentic and terrestrial species appear regularly beside lotic taxa during intermittence (Stubbington et al., 2017). Additionally, intermittence requires special adaptation strategies, thus, functional composition of diatom assemblages continuously changes during drying up of streams (Sabater et al., 2017).

Here, we hypothesized that there would be clear compositional differences between streams with dry streambed (dry phase)



and streams in aquatic phase both in terms of taxonomical and trait levels. We also assumed that indicator taxa could be identified in both phases. The results supported our hypotheses.

We found clear, hydrological regime induced compositional differences both at taxonomy and trait levels and indicative species could be recorded too. Periphytic algae, including diatoms



sensitively indicated the intermittence independently of the ecoregion (Novais et al., 2014, 2020; B-Béres et al., 2016, 2019; Falasco et al., 2016a; Várбірó et al., 2020; Lukács et al., 2021).

In this study, mainly colonial taxa belonging to high profile guild dominated the dry phase (but see *Meridion circulare* – low profile guild taxa). Current evidences about the dominance of high profile guild and colonial forms in intermittent streams are inconsistent among studies (Falasco et al., 2016a; Novais et al., 2020; Várбірó et al., 2020). These traits can support survival in permanent waters, where obviously the environmental conditions, especially the water regime, are more stable than in intermittent streams (Várбірó et al., 2020). Novais et al. (2020) also found, that the relative abundances of the high profile guild are higher during aquatic (flow) phase than in dry phase.

In contrast to high profile guild, colonial lifestyle, especially in case of those colonial taxa which form mucous tube can be advantageous in intermittent streams (Falasco et al., 2016a) and during dry phase (Sabater et al., 2017). In our study, mucilage-forming taxa were not dominant during the dry phase, only

non-tube forming colonial taxa such as *Diademesma contenta*. Although *Frustulia vulgaris*, which forms a mucous tube, was one of the indicator species of dry phase, this species was never dominant in samples.

Beside the above mentioned taxa, aerophilous and/or motile species were revealed as indicative species in dry phase. Appearance of aerophilous taxa in intermittent streams is a well-known phenomenon (Novais et al., 2014; Falasco et al., 2016a; Sabater et al., 2016, 2017; B-Béres et al., 2019). Similar to high profile guild and colonial taxa, it is not easy to ascribe the members of motile guild into a water regime phase or type, i.e., they are diverse in their habitat preferences with respect to water phase. Motile taxa can be considered as physical disturbance indicators, since their dominance within assemblages usually increases with siltation and in depositional habitats (Falasco et al., 2016b; Novais et al., 2020), which are common during intermittence. Additionally, motile taxa are able to migrate from the sediment surface to the deeper, wet layers during drying. After rewetting, they return to the surface and colonize it relatively

fast (McKew et al., 2011). Our previous studies, however, pointed out that intermittence is a strong selective pressure for motile taxa independently from the ecoregions (Várbíró et al., 2020) and this guild is characteristic for permanent streams in the Pannonian Ecoregion (B-Béres et al., 2019). Here, indicator species of dry phase belonging to motile guild were small sized and aerophilous or subaerial taxa. These characteristics together and their additive ecological benefits made survival possible for diatoms bearing these traits.

A further indicator species was the low profile and colonial *Meridion circulare* during dry phase, which was often dominant in streams with dry streambed (max. 36%). This species is usually found in small streams in winter and spring (Stenger-Kovács et al., 2013). In this study, *M. circulare* was more abundant in spring than in summer. But this species, as a member of the low profile guild, tolerates the physical disturbances which can be characteristic during intermittence. We believe these two characters (favor low temperature and tolerate disturbances) lead to the high number of *M. circulare* in streams with dry streambed in spring. In summer, its relative abundance decreased in the dry phase too, pointing out a more significant temperature-dependent than intermittence-dependent appearance of this taxon.

In this study, streams in aquatic phase were dominated mostly by pioneer category (e.g., *Achnanthydium minutissimum* and *Amphora pediculus*) and/or low profile guild, small and medium sized, unicellular taxa (e.g., *Planothidium lanceolatum*, *Reimeria sinuata*, and *R. uniseriata*) belonging usually to WSA or AOC spreading trait groups. It is a well-known phenomenon that physical disturbance is indicated by small sized, unicellular, low profile taxa (Berthon et al., 2011; B-Béres et al., 2019; Novais et al., 2020). In intermittent streams right after the rewetting of the streambed, these traits, i.e., small size, low profile guild, unicellular and/or pioneer, support the fast spreading of species and colonization of habitats. In our study, the relative lack of aquatic macrovegetation can enhance the chance for spreading of species bearing these traits.

Moisture preference should be an important trait in intermittence studies, since it clearly refers to the tolerance of water shortage. However, Novais et al. (2020) pointed out that most taxa they found in Portuguese streams do not have clear moisture preference. Here, more than 71% of the taxa related to WSA or AOC moisture categories meaning that these taxa are able to tolerate aerophilic conditions for a while. These taxa were characteristic in aquatic phase, while true aerophilic taxa preferred dry phase, as we mentioned above.

Mostly unicellular, stalk-forming *Gomphonema* species were indicative of aquatic phase. Long peduncle i.e., stalk provides an opportunity for taxa to live in the upper layers of biofilm. This life-form subserves an efficient access to light and nutrients but it exposes taxa to high flow disturbances (Passy, 2007). Here, most of the studied streams run through forests. Thus, there is no significant anthropogenic impact on them and their nutrient content is relatively low. In addition, flow conditions in the aquatic phase are comparatively stable. These circumstances, as we mentioned above, favor stalk-forming taxa.

Biodiversity Changes

We hypothesized that biodiversity would be reduced in the dry phase. The results, however, did not confirm our assumption. Neither taxonomical nor functional diversity metrics changed significantly due to drying. These results suggest that taxonomical and functional redundancies were able to compensate for biodiversity loss. Although these results are in accordance with observations of Novais et al. (2020), they contradict the very recent results of studies by Crabot et al. (2021) and Tornés et al. (2021). Crabot et al. (2021) and Tornés et al. (2021) highlighted that functional redundancy decreases with flow intermittence. But this decrease is time-dependent, the longer the dry period the smaller the protective effect of the functional redundancy on assemblages. In our study, the duration of the dry period of streams was very variable (from 7 to 266 days), however, in most cases, it was lower than 50 days, which is lower than the threshold of duration resulting in diversity reduction in the paper of Tornés et al. (2021). They found a significant decrease in biodiversity only after 50 days. Crabot et al. (2021) also noted that any 10% increase in flow intermittence results in a 5% decrease in functional redundancy. In our case, the annual flow intermittence does not reach the 10% in most cases.

Independently of the water regime, a slight decrease in FDis was revealed in summer. The FDis is strongly connected to the dominance of the trait values (Laliberté and Legendre, 2010). Because other metrics like FDiv and FRich did not change significantly, decrease in FDis did not reveal a shift of assemblages' composition to extreme traits, and traits did not disappear, only their proportions changed. This was probably due to the biotic interactions that might be stronger during summer. Since proportion of other algal groups, e.g., green algae, cyanobacteria, usually increases in summer (Biggs and Stokseth, 1996; Suren et al., 2003) resulting in an enhanced resource competition and thus, a biotic pressure on diatoms.

Changes in Diatom Indices

Almost 10,000 watercourses are registered in Hungary (Stubbington et al., 2018), but less than 10% of them are monitored regularly². This means that there is no information about the risk of vulnerability or the risk of intermittence as well as the ecological quality for more than 9000 small Hungarian watercourses. These ecosystems, however, are strongly endangered both by anthropogenic and natural impacts including climatic extremes. To the best of our knowledge, this paper is the first where diatom-based ecological quality of very small intermittent hilly streams were studied in the Pannonian Ecoregion. Since there is no diatom index for evaluating the status of these streams, altogether four diatom indices regularly used in WFD-based biomonitoring in Hungary (Várbíró et al., 2012) were analyzed here. Based on former studies by Falasco et al. (2016b) and by Novais et al. (2020), only slight differences in diatom indices were hypothesized between aquatic and dry phases. The results supported our hypothesis, since drying up of streams had significant negative influence only on TID, while water regime had no impact on the other three diatom indices. The stability of the studied indices points out their applicability

in ecological status assessment of intermittent streams. However, it has to be highlighted that much more sampling sites including permanent ones as well as differently loaded sites should be involved in the analyses. Our study is only the first step in this way, but the results are encouraging. These diatom indices were developed mostly for assessing anthropogenic impact on permanent waters with larger catchment areas than the waterbodies studied here. Nevertheless, our results suggest that these indices are stable enough to assess the status of very small permanent streams even in dry phase. We think that the higher values of TID in the aquatic phase were attributable to the higher proportion of small, pioneer taxa considered as indicators of good or excellent waters. These taxa, as we mentioned above, are good colonizers and tolerate physical disturbances caused by rewetting. Analyzing this diatom index together with the others can be a good way to indicate both nutrient supply and climate-induced influences on benthic diatom assemblages in small intermittent streams in the Pannonian Ecoregion.

CONCLUSION

Here, we examined the influence of flow intermittence on benthic diatom communities in very small hilly streams (catchment area <10 km²) in the Pannonian Ecoregion. While the results revealed strong water regime dependent differences in taxa and trait composition of assemblages, no seasonal separation was found. However, our findings have highlighted that short-term drying up of streams might not necessarily cause biodiversity loss. It seems that taxonomical and functional redundancy could prevail. In contrast, decrease in functional dispersion in summer suggests proportional changes in trait values. But it has to be stressed that traits did not disappear from the system, and assemblages were not pushed to dominance of extreme traits. In this study, we first analyzed the usability of diatom-based quality indices in the assessment of drying up of small streams in this region. We showed that these metrics are useful tools for ecological evaluation of streams even in the dry phase. As we noted, these streams are strongly endangered to become episodic. However, it is not a simple shift from permanence to intermittency, the lengthening of the dry-phase in the future might result in irreversible compositional changes and significant diversity loss, threatening the entire aquatic ecosystem not just benthic algae. Thus, any knowledge, which supports their

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ecological role in this region, can help to save them and their valuable microflora.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

VB-B: conceptualization, data curation, project administration, supervision, and roles/writing – original draft. ZK, GV, GM, and VB-B: formal analysis and visualization. VB-B, PB, and ZC: funding acquisition. ZK, VB-B, IB, PB, and BP: investigation. VB-B, IB, and GV: methodology. PB, GB, ZC, and VB-B: resources. VB-B, PB, ZC, BP, GB, GV, and IB: writing – review and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.834548/full#supplementary-material>

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