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# Strong influence of climatic extremes on diversity of benthic algae and cyanobacteria in a lowland intermittent stream

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## Abstract

Freshwater ecosystems are threatened by the global change-induced extreme climatic events worldwide. The unpredictable changes in water supply create strongly disturbed environments and ultimately result in diversity changes. Here, we studied the formation of benthic algal and cyanobacterial assemblages under intermediately disturbed (IDC) and highly disturbed conditions (HDC) in a small lowland intermittent stream. We addressed our hypotheses to the Intermediate Disturbance Theory supposing that intermediate frequencies or intensities of disturbances maximise diversity independently of its level. We expected a larger influence of extremes in water supply on functional than on taxonomic and phylogenetic diversity. Our results only partially proved our first hypothesis highlighting the (i) importance of short-time but intense disturbing effect on biofilm formation and trait composition under IDC period and (ii) the instability within the assemblages caused by large and opposing influences during HDC. Although extreme weather events caused trait extremes (supporting second hypothesis), they did not result in a decrease in functional richness (rejecting the second hypothesis). These findings in accordance with the insurance hypothesis clearly stress that a system with high functional redundancy can keep its functionality even under drastic hydrological conditions and the accompanying loss of species.

**KEYWORDS**
benthic algae and cyanobacteria, biodiversity changes, climatic extremes, highly disturbed conditions, intermediately disturbed conditions, intermittent streams

# 1 | INTRODUCTION

Natural and artificial ecosystems are both increasingly pressured by global change and its effect on climatic patterns and land-use (IPCC, 2014). In the last decades, extreme climatic events such as heavy rainfalls and droughts, are becoming more frequent in space and time (Pendergrass & Knutti, 2018; Wilhite & Glantz, 1985). In freshwater ecosystems, these events lead to uneven spatial and temporal occurrence of precipitation patterns and result in severe floods or dry periods (Döll et al., 2018; Döll & Schmied, 2012; Raymond et al., 2013; von Schiller et al., 2014). Changes in climatic patterns and flow conditions can modify the biophysical environment and can act as harsh environmental filter on assemblages (Várbíró et al., 2020). Aquatic organisms are selected by these filtering effects (Botta-Dukát & Czúcz, 2016), resulting in compositional and structural changes at a higher community level, which is ultimately expressed in diversity changes (Acuña et al., 2017; Bellard et al., 2012; Stubbington et al., 2017). In fluvial ecosystems, at local scale, taxonomic diversity is usually lower in highly dynamic environments than under permanent flow conditions (Stubbington et al., 2017). However, taxonomic diversity represents only one level of biotic diversity, which can be considered as the sum of taxonomic, phylogenetic, genetic and ecological diversity (van der Spoel, 1994) and it also includes functional diversity (Tilman, 2001).

Although benthic algae and cyanobacteria play a pivotal and multifaceted role in fluvial ecosystems, (Stevenson, 2014), recent studies on rivers in the Carpathian Basin demonstrated that independently of the physiographic river types, benthic assemblages are especially endangered by extreme flow events (B-Béres et al., 2014, 2019; Kókai et al., 2015; Stenger-Kovács et al., 2013; Trábert et al., 2017). Changes in taxonomic and/or trait composition induced by flash floods or dry events have an effect on the whole ecosystems, including assemblages of fishes, invertebrates, macrophytes and benthic algae and cyanobacteria (Datry, 2012; Morán-López et al., 2012; Robson & Matthews, 2004; Robson et al., 2008; Soria et al., 2017, Tornés & Ruhí, 2013; Tornés & Sabater, 2010; Westwood et al., 2006). Under stable flow condition, the formation of a mature biofilm generally takes ~4 weeks (Tapolczai et al., 2016). During its succession the taxonomic composition of the biofilm is obviously determined by the local and regional species pool and also the colonisation success of taxa living or immigrating here. But the actual taxa composition is quite unpredictable mainly because of the interactions among species with very similar demands. At functional level, however, the succession is more deterministic and easier to predict (Passy & Larson, 2011). Direction of the succession is strongly influenced by the stability of environmental conditions. After the initial colonisation period that is affected primarily by physical disturbances, the formation of assemblages is mainly driven by biotic interactions in benign environment (Coyle et al., 2014; Grime, 1973, 1977; Passy & Larson, 2011; Weiher & Keddy, 1995). Unexpected extreme flow events, however, create strongly disturbed environments (Acuña et al., 2017). Flash floods caused by short but heavy rainfalls can result in immediate damage and drifting away of taxa (B-Béres et al., 2016; Lukács et al., 2018; Stenger-Kovács et al., 2013). Although these events can decrease the taxonomic diversity within the community in short term (Ács & Kiss, 1993), the vacant niches can initiate re-colonisation processes (B-Béres et al., 2016; Lukács et al., 2018). After extreme flow events, stable environmental conditions are needed for the formation of mature biofilm. In accordance with the Intermediate Disturbance Hypothesis (IDH; Connell, 1978) intermediate frequencies and/or intensities of disturbances maximise diversity. Frequency and/or intensity of climatic extremes is increasing worldwide (IPCC, 2014) resulting in unpredictable water regime and potential changes in the composition of benthic algal and cyanobacterial assemblages. But until now, only limited information is available on how taxonomical and functional diversity of benthic algae and cyanobacteria changes during colonisation under different frequencies of disturbance.

We aimed to highlight the importance of extremes in water flow conditions on structuring of benthic algal and cyanobacterial assemblages, thus here formation of these assemblages was studied under intermediately disturbed (IDC) and highly disturbed conditions (HDC) in a small lowland astatic stream. Diversity changes at different levels were monitored during colonisations to test our hypotheses addressed to the above mentioned Intermediate Disturbance Hypothesis and colonisation theory.

(i) We hypothesized that the benthic algal and cyanobacterial assemblages display higher diversity under intermediately disturbed than under highly disturbed conditions independently of the level of diversity (taxonomic-, functional- and phylogenetic diversities).

(ii) We also hypothesized that extreme flow events (i.e., floods or non-flow periods) result in extremes in trait composition of benthic algae and cyanobacteria and have larger influence on functional diversity than on taxonomic and phylogenetic ones.

# 2 | MATERIALS AND METHODS

## 2.1 | Study area and experiment design

Samples were collected in the upper section of a small continental lowland stream (Tócó) in Eastern Hungary (Debrecen, EOVX: 254755; EOVY: 839873). Based on the dataset of the Hungarian Meteorological Service, the average annual temperature was 10.5°C, the total annual precipitation was 549 mm and the total annual sunshine duration was 2054 hours here between 1981 and 2010 (met.hu). The studied stream belongs to the R-05 Broad type (Solheim et al., 2019): its catchment area is small (89 km$^2$; vizugy.hu/1), its basic geology is calcareous, its altitude is less than 200 m. In general, the physical and chemical conditions are good in the sampling site and there is no organic pollution (vizugy.hu/2).

According to the information and typology of 2nd River Basin Management Plan (vizugy.hu/1), Tócó is an intermittent stream. It has an irregular drying pattern, that is, depending on the precipitation its flow conditions can be permanent in a year (e.g., in 2010—observation of authors), while in other years the stream can completely dry up especially in summer and early autumn (e.g., in 2012 and in 2013—observation of authors). Since in Hungary, the perennial-intermittent

typological shift of streams like Tócó is a new phenomenon, the collection of their background information has begun very recently. Therefore, there is no exact data about the number of dry days or the duration of non-flowing and flowing periods.

The streambed of Tócó consists mostly of fine organic matter and is highly covered by macrovegetation (mostly *Phragmites australis*, *Typha* spp., *Berula* spp.) and allochthonous coarse particulate organic matter (CPOM) from the riparian area.

Addressing the study questions required the use of completely new and empty surfaces. Since the composition of artificial substrate can influence significantly the structure and/or diversity of benthic algal assemblages (Barbiero, 2000; Cattaneo & Amireault, 1992; Kröpfl et al., 2006), substrate type should be selected very carefully. Here, we strived to imitate natural conditions during colonisation, therefore we applied semi-artificial wooden slides as substrates. The chemical composition of this substrate type is very similar to the naturally available substrates in this stream (Papp, 2010). The surface area of the wooden slides was 32 cm$^2$, dimensions of the slides were 6 cm in length, 2 cm in weight and 0.5 cm in height. Altogether three chains of wooden slides were placed to the streambed and three slides were collected at each sampling event (one slide per chain). Each chain contained 36 wooden slides. The duration of our study was 84 days (from 15.03.2014 to 06.06.2014) and at the end of the samplings, the stream dried up. Altogether 93 samples were collected during the study period. The timetable of sampling was performed after some modification according to Ács et al. (2000). In order to capture the rapid compositional changes occurring in early successional state, frequency of the sampling decreased in time: hourly in the first 9 hr; daily in the first week; twice a week until the 35th day and from the 35th day weekly to the end of the study.

Water depth (WD) was measured by tape line (cm) each sampling time. Simultaneously water velocity (WV) also was measured by SonTek FlowTracker Handheld-ADV (USA) (m/s). Nevertheless, at the last two sampling times (30.05.2014 and 06.06.2014) measurements of velocity could not be performed, because the water depth was too low for the flow tracking device. At these times, the stream had already partially dried up. While the chains of wooden slides were in a pool, the streambed was dry right below the sampling area. The condition of streambed was checked again in 13.06.2014. That time, the stream has completely dried up. Precipitation data (mm/day) for the study period was provided by the Hungarian Meteorological Service.

## 2.2 | Microscopic analysis and data processing

The collected wooden slides were preserved in Lugol's solution (CEN 13946, 2003). We used toothbrushes to remove the biofilm from the slides in the laboratory. Biofilms from the three replicates were analysed separately. Taxonomic composition of algal and cyanobacterial assemblages was determined at species or genus level (see more below) by analysing 1-mL biofilm suspension examined under a 400 × microscope (Leica DMIL, Wetzlar, Germany) following the

classification described by Ettl, 1983; Grigorszky et al., 1999; Javornický, 2003; Kadlubowska, 1984; Komárek, 2013; Komárek & Anagnostidis, 1998, 2005; Krammer & Lange-Bertalot, 1997a, 1997b, 2004a, 2004b; Németh, 1997a, 1997b; Schmidt & Fehér, 1998, 1999, 2001; Uherkovich et al., 1995. The microscopic analyses were performed according to the CEN 15204 (2006) standard. Since only single cells of algae or cyanobacteria might be counted as cells, while colonies, coenobia and filaments should be treated as single units and not counted as individual cells according to the CEN 15204 (2006) standard, a minimum of 400 algal and cyanobacterial units (specimens with chloroplasts) were counted by performing random transect under light microscope. The algal and cyanobacterial units, that is, single cells, colonies, coenobia or filaments, were defined according to the CEN 15204 (2006) standard. Since the aim of this study was to examine the whole algal and cyanobacterial assemblages including diatoms, non-diatoms and cyanobacteria, undigested samples were used for microscopic analyses. According to the CEN 15204 (2006) standard, taxa were identified to species or genus level depending on the confidence level of identification (Table S1).

Algae and cyanobacteria were grouped into 14 classes corresponding to four larger trait groups (Lukács et al., 2018). The four groups were defined by the cell size, life-form, attachment type and mobility. Taxa were assigned to five cell size classes according to Berthon et al. (2011) by using the dataset of Rimet and Bouchez (2012). Since this database contains only diatom taxa, it was complemented by size data of non-diatoms according to the Hungarian National Phytoplankton Database. According to Rimet and Bouchez (2012) and Lange et al. (2016) three life-form classes were differentiated; unicellular, colonial and filamentous. Taxa were classified into three attachment categories (Lange et al., 2016): such as weakly, moderately and strongly attached. Taxa were assigned to three mobility classes (non-mobile, fast moving and slow moving) according to Rimet and Bouchez (2012). The database of Rimet and Bouchez (2012) was complemented with the mobility data of non-diatoms.

## 2.3 | Statistical analyses

Number of observed taxa in the samples was considered as taxa richness. Taxonomic diversity of the assemblages has been also expressed in Effective Shannon's H values (Jost, 2006). Using effective Shannon's H in analyses is a simple but powerful method to compare the true diversities of two or more assemblages (Beck & Schwanghart, 2010; Morris et al., 2014; Stuart-Smith et al., 2013). Effective Shannon's H is simply the exponential of Shannon's H, which is calculated as follows:

$$\text{Effective Shannon's H} := \exp(H_{Sh})$$

where $H_{Sh}$ is the Shannon index, which can be calculated by the following formula:

$$H_{Sh} = -\sum_{i=1}^{S} p_i \log p_i$$

where $p_i$ is the proportion of the $i_{th}$ taxon.

We used the PAST software for the calculation of the Shannon index (version 3.25; Hammer et al., 2001).

Functional approaches provide comprehensive picture about the structuring of assemblages and endangerment of ecosystem functioning (Abonyi et al., 2018; Mason et al., 2005), thus, describing the taxa distribution in the niche space, the main components of functional diversity were measured (Laliberté & Legendre, 2010; Mason et al., 2005; Villéger et al., 2008). These metrics are functional richness (FRich), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). These diversity components represents (i) the amount of niche space occupied by taxa (FRich), (ii) the evenness of abundance distribution in occupied niche space (FEve), (iii) the position of clusters of taxa' function in the niche space (FDiv), and (iv) the main distance of all taxa from the abundance weighted centroid of traits in trait space (FDis).

The metrics FRic, FEve and FDiv were calculated according to Villéger et al., 2008, while FDis was estimated as described in Laliberte and Legendre 2010. For the calculation of these functional diversity metrics, R environment was used (Laliberté & Legendre, 2010; version 3.5.2; R Core Team, 2019).

To test how closely taxa are related to each other in the assemblages we used a phylogenetic diversity measure D(T) based on Chao et al., 2014. This measure provides the effective number of phylogenetic entities, which in this case is the number of unit-length branches of a phylogenetic tree weighted by the relative abundance of taxa. For the calculation of these values, we used PAST software (version 3.25; Hammer et al., 2001).

Additionally, two Principal Components Analyses (PCA) were performed to complement the interpretation of taxa and trait composition in IDC and HDC periods. For these analyses, we used the relative abundances of taxa and the community weighted mean (CWM) approach, which expresses the mean trait value in the community weighted by the relative abundances of the taxa matrix. The multivariate statistical software Canoco 5 (ter Braak & Šmilauer, 2002) was used for these analyses.

Altogether 23 water depth and 23 water velocity data were used to differentiate the periods of intermediately (IDC) and highly disturbed conditions (HDC). Considering these hydrological data the first period from day 0 to day 22 could be considered as IDC (based on 12–12 data of variables), and the second period from day 23 to day 84 as HDC (based on 11–11 data of variables). To examine the extent of parameter fluctuations, we tested the range and standard deviation of water depth values and the absolute values in differences of water velocity values between each sampling for the two periods.

To test the differences in diversity between the IDC and HDC periods one-way analysis of variance (ANOVA) was used ($p < 0.05$). To explore the relationships between environmental parameters and indices, we used the Pearson correlation test for the two periods separately. We also tested relationships between the different indices by Pearson correlation method. Tests were performed for the two phases separately. All of these statistical analyses were performed in R environment (version 3.5.2; R Core Team, 2019).

# 3 | RESULTS

## 3.1 | Changes of environmental conditions in IDC and in HDC periods

The total precipitation was 94 mm during sampling period. A rainy period started on the 23rd day of the experiment (7.4.2014) which finally resulted in changes in the hydrological conditions (water depth and water velocity) (Table 1 and Figure S1). Periods of intermediately disturbed conditions (IDC) and highly disturbed conditions (HDC) were separated by these differences in water depth and water velocity between the consecutive sampling events (IDC: days 0–22nd; HDC: days 23rd–84th; Figure S1). While the two periods differed significantly in water depth ($p = 0.01$), marginally significant difference were found in water velocity under IDC and HDC ($p = 0.05$) (Figure S2). In the IDC period, there were only two rainy days with altogether 7 mm rainfall: one was on the first day, when the precipitation was 1 mm, and another 6 mm rain fell on the 10th day. In contrast, it rained 19 times with 87 mm precipitation in the HDC period. Maximum rainfall per day was 16 mm. The maximum value of precipitation, which preceded the following sampling events, was 36 mm (between the sampling events on the 56th and 63rd days; Figure S1). A dry period started on the 65th day with 2 mm total precipitation to the end of the experiment. Finally, this drought resulted in the drying up of the stream.

## 3.2 | Changes of assemblages composition and diversity in IDC and in HDC periods

### 3.2.1 | Taxa composition, taxonomic diversity and phylogenetic diversity

A total of 68 algal and cyanobacterial taxa were recorded in the samples: 40 to species, 26 to genus level and two to higher taxonomical level. There were only partial overlap in species pool between IDC and HDC periods. Altogether 35 taxa were identified in both (22 diatoms and 13 non-diatoms; Table S1). In contrast, 21 taxa including 6 diatoms and 15 non-diatoms, were recorded exclusively in IDC and 12 taxa were found only in HDC period (6–6 diatoms and non-diatoms; Table S1). The PCA analysis also indicated clear differences in the importance of hydrological regime in explaining the taxonomical composition of assemblages (Figure 1). The eigenvalues of the PCA were 0.366 and 0.087, while taxa and hydrological regime correlation was 60% for all canonical axes. Even though these clear differences in taxa composition, diatoms dominated in both periods (average value: 89% in IDC and 94% in HDC; $p = 0.00$). Independently of the periods, *Achnanthidium minutissimum* and *Navicula* species were dominant in assemblages but their relative abundance increased significantly in HDC (ADMI: max. 7.7% in IDC and 37.6% in HDC; NASP: max. 23% in IDC and 35% in HDC; $p = 0.00$ in both cases). Whereas filamentous green algae were also abundant in biofilms in IDC, their relative abundance significantly decreased in HDC (average

**TABLE 1** Summary of data sets of water depth, velocity and precipitation during the intermediately disturbed and the highly disturbed conditions

| | IDC | | | HDC | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Water depth (cm) | Velocity (diff) (m/s) | Precipitation (mm) | Water depth (cm) | Velocity (diff) (m/s) | Precipitation (mm) |
| Minimum | 13.000 | 0.000 | 0.000 | 4.000 | 0.008 | 0.000 |
| Maximum | 16.000 | 0.041 | 6.000 | 18.000 | 0.092 | 16.000 |
| Mean | 15.583 | 0.016 | 0.304 | 11.9091 | 0.035 | 1.426 |
| Range | 3.000 | 0.041 | 6.000 | 14.000 | 0.084 | 16.000 |
| Standard deviation | 0.954 | 0.013 | 1.231 | 4.188 | 0.026 | 3.361 |



**FIGURE 1** Results of the Principal Components Analyses (PCA) analysis of taxa composition of benthic algal and cyanobacterial assemblages. Four letter codes indicate the 68 taxa identified in the samples (see list and codes in Table S1). Intermediately disturbed conditions are marked with white circle. Highly disturbed conditions are marked with grey squares
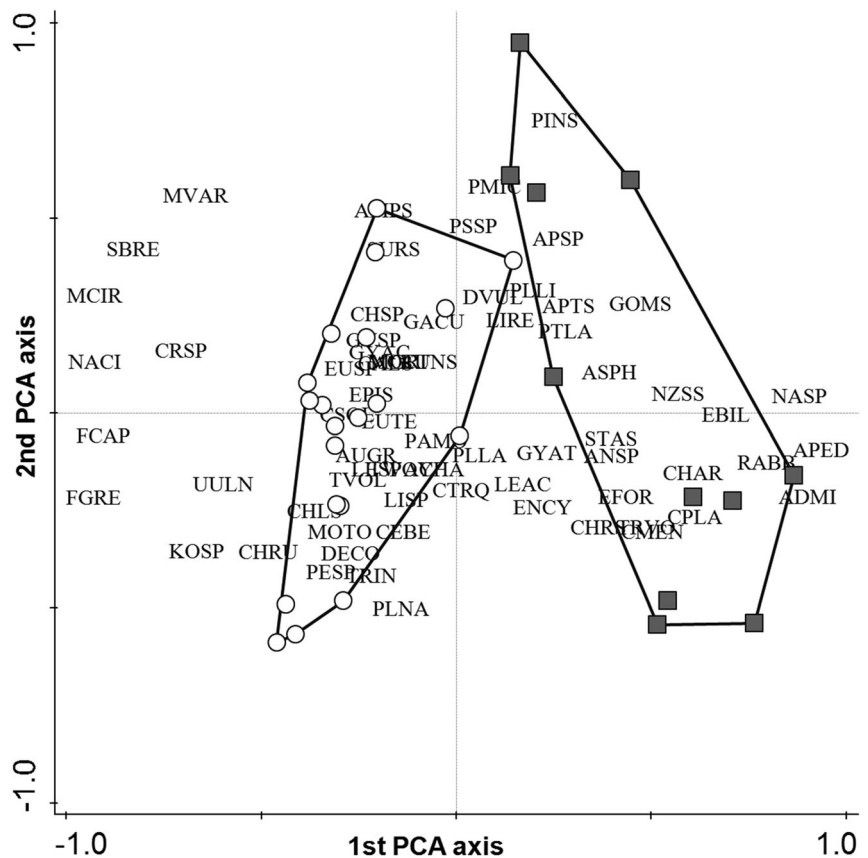
values: 2.9% and 0.5%; $p = 0.00$). Among other eukaryotic algae, mainly unicellular euglenoids and cryptomonads, euplanktic green algae and metaphytic taxa, in addition different cyanobacteria formed the assemblages (Table S1).

Despite of the clear taxonomical differences between IDC and HDC periods, it did not have significant influence on taxa number ($p = 0.91$) (Figure 2a). In contrast, effective Shannon's H values responded significantly to the extreme changes in environmental parameters ($p = 0.01$), indicating higher diversity during IDC (Figure 2b).

Changes in taxonomical composition over time, that is, taxa replacement, resulted in a strong significant difference in phylogenetic diversity between the two periods characterised by different disturbance conditions ($p = 0.01$). D(T) values were higher under IDC than in HDC (Figure 3).

### 3.2.2 | Trait composition and functional diversity

Based on trait composition of benthic algae and cyanobacteria, the PCA analysis revealed clear differences between IDC and HDC periods (Figure 4). The eigenvalues of the PCA were 0.513 and 0.192, while trait composition and hydrological regime correlation was 86% for all canonical axes. Large size, non-mobile, filamentous taxa, mainly green algae, and fast moving taxa such as euglenoids and cryptomonads characterised the IDC period. In contrast, small
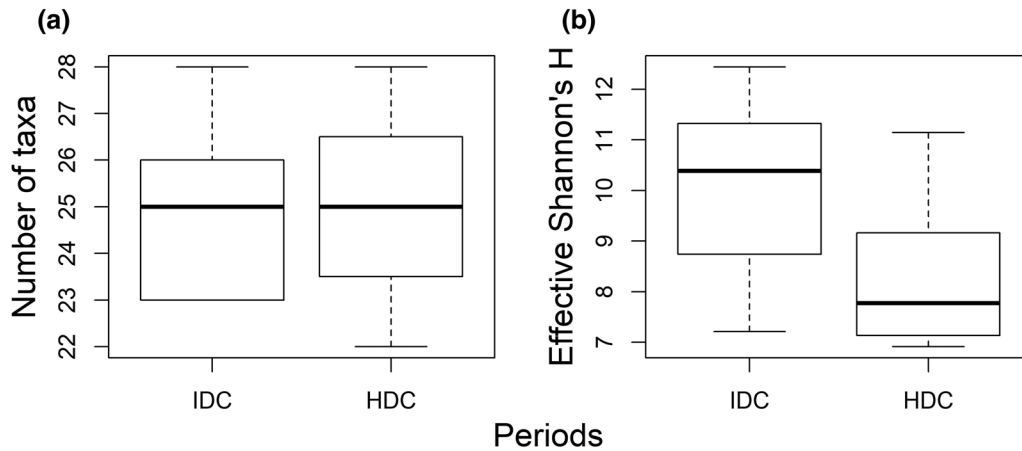
**(a)**



**(b)**



Periods

**FIGURE 2** Number of taxa (a) and effective Shannon's H (b) during the intermediately disturbed and the highly disturbed conditions results of analysis of variance (ANOVA) tests were $p = 0.91$ in the case of number of taxa and $p = 0.01$ in the case of effective Shannon's H
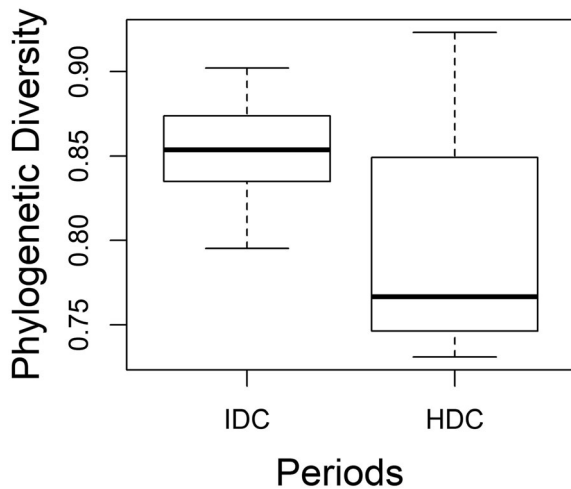


**FIGURE 3** Phylogenetic diversity during the intermediately disturbed and the highly disturbed conditions results of analysis of variance (ANOVA) tests were $p = 0.01$

unicellular algae with different attachment type (mainly diatoms such as *A. minutissimum* and *Navicula* sp.) were abundant in HDC period (Figure 4). The heavy rain on the 10th day in IDC period resulted in changes in trait composition. It significantly decreased the abundances of filamentous algae and cyanobacteria and the fast moving non-diatoms ($p < 0.01$ in both cases). In HDC period, drought started on the 65th day and induced significant changes in biofilm, trait composition shifted to strongly attached small species ($p < 0.01$).

Despite the clear separation of trait compositions between the periods, the influence of environmental changes on functional diversity metrics was different (Figure 5). Those metrics, which reveal de facto the number of functional niche space filled by the taxa (FRich) and regularity in the distribution of the mean traits (FEve) did not respond significantly to the changes in hydrological regime over time ($p = 0.34$ and $p = 0.09$) (Figure 5a,b). In contrast, high difference was found in FDiv values of IDC and HDC periods ($p = 0.00$; Figure 5c).

Furthermore, FDis differed significantly too in the two periods ($p = 0.04$; Figure 5d). FDiv was higher during HDC period than in IDC, whereas FDis showed the opposite pattern.

### 3.3 | Correlation of environmental parameters and indices

Results of the Pearson correlation test showed that almost all indices correlated with water depth to a higher extent than with velocity for the two periods (exceptions: FRic and FEve under HDC, Figure 6). Weak correlations to water depth and velocity were found only in the case of D(T) during IDC (coefficient under ±0.3) (Figure 6a). In this period, FDiv was positively correlated to both water depth and water velocity. Furthermore, the values of correlation coefficients were higher than 0.3 in relation to water velocity only in the cases of FRic (0.44), S (0.40) and FDiv (0.33) under IDC period (moderate correlations; Figure 6a). During the HDC period, diversity metrics such as FDiv, FDis, effective H and D(T) showed the strongest correlations with environmental parameters, especially with water depth (Figure 6b). In this period, FDiv correlated negatively both to water depth ($-0.49$) and to current velocity ($-0.35$) (Figure 6b).

### 3.4 | Correlation of indices

During IDC period, significant negative correlations were found only between D(T) vs S ($-0.30$) and D(T) vs FEve ($-0.40$). In contrast, strong positive correlation (higher than 0.70) was observed between FDiv vs FDis (0.96), FRic vs S (0.83), effective Shannon H vs FDiv (0.83) and effective Shannon H vs FDis (0.87) (Figure 7a).

Under HDC, FDiv was the only index that showed negative correlation with almost all indices, except FEve (0.30). The strongest correlations were observed between FRic vs S (0.78), FDiv vs FDis ($-0.74$),

**FIGURE 4** Results of the Principal Components Analyses (PCA) analysis of the main trait profiles of benthic algal and cyanobacterial assemblages. Intermediately disturbed conditions are marked with white circle. Highly disturbed conditions are marked with grey squares
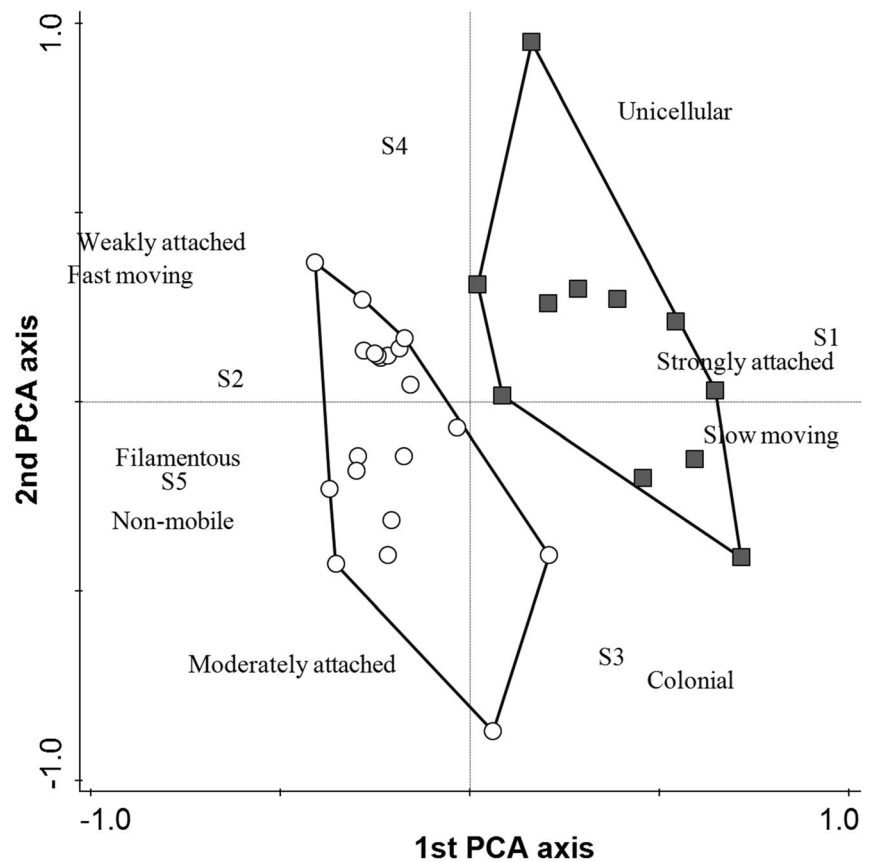


effective Shannon H vs FDiv (−0.81), effective Shannon H vs FDis (0.96), FDis vs D(T) (0.95) and effective Shannon H vs D(T) (0.94) (Figure 7b).

## 4 | DISCUSSION

### 4.1 | Diversity changes under IDC and HDC–IDH theory

Our results revealed clear differences in benthic algal and cyanobacterial assemblages of Tócó stream between IDC and HDC periods even though the benthic flora was dominated by diatoms independently the hydrological regime. Intermediately disturbed conditions were favoured by large sized, weakly attached, filamentous algae including green algae too. Previous works also suggested that stable conditions in water regime can maintain higher abundance of these organisms (Lange et al., 2016; Witteveen et al., 2020). These conditions enable large taxa to settle down fast into the biofilm and prevent them from drifting (Ács et al., 2000). Witteveen et al. (2020) also pointed out that low canopy cover can be an important factor for presence of weakly attached filamentous green algae. Here, the high abundance of these forms was more likely due to above mentioned factors (stable hydrological regime and fast settlement), but the canopy cover was also low in this period. In the HDC period, which was characterised with unpredictable

flow conditions resulted by rainy and dry phases, taxa composition shifted to dominance of small, unicellular strongly attached or even fast moving diatoms. These traits ensure taxa advantages during physically disturbed conditions caused by share effect or even sedimentation (Lange et al., 2016; Passy, 2007; Rimet & Bouchez, 2012; Stenger-Kovács et al., 2006).

Taxonomic and phylogenetic diversities—with the exception of number of taxa—were significantly higher in the first period of our study (IDC). These results supported our first hypothesis and were in accordance with the Intermediate Disturbance Hypothesis (IDH; Connell, 1978), which emphasised that periods free from extremes contribute to the development of diverse communities. In contrast, extreme water regime (drought and flash floods) results in a negative local impact on the diversity of assemblages (Acuña et al., 2017; Stubbington et al., 2017). Here, effective Shannon and phylogenetic diversity values showed a clear decrease during HDC. This diversity loss was due to the dominance of small diatom taxa, such as the typically pioneer, unicellular, strongly attached *Achnanthidium minutissimum* and the unicellular but weakly attached and mobile *Navicula* species. The tolerance of *A. minutissimum* against disturbances is a well-known phenomenon: its small size makes this species a fast and efficient coloniser even under low supply and it is adapted well to the shear forces caused by water flow as well as the extremes in light intensity (B-Béres et al., 2014; Schmidt et al., 2018; Stenger-Kovács et al., 2006). Most of the *Navicula* species that dominated the benthos in the HDC period were small-sized organisms. This result is
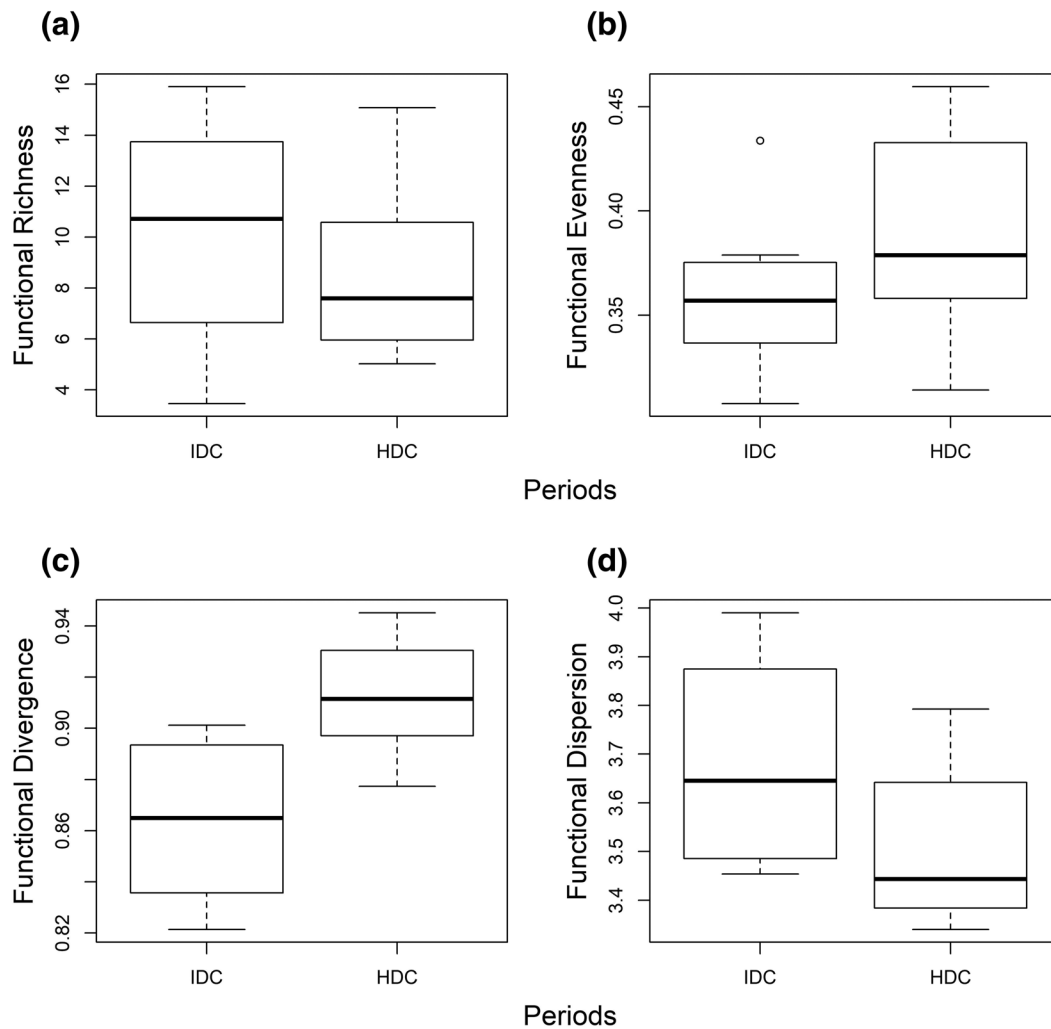
**FIGURE 5** Functional richness (a), functional evenness (b), functional divergence (c) and functional dispersion (d) during the intermediately disturbed and the highly disturbed conditions results of analysis of variance (ANOVA) tests were $p = 0.35$ in the case of FRich, $p = 0.09$ in the case of FEve, $p = 0.00$ in the case of FDiv and $p = 0.039$ in the case of FDis

in accordance with previous observations of Lange et al. (2016). They recorded strong positive correlation between sedimentation caused by drying up and abundance of small, motile taxa.

In contrast to taxonomic and phylogenetic-based analyses, changes of trait-based functional diversity metrics did not support our first hypothesis. The only exception was FDis, which was significantly higher in IDC than HDC and which is sensitive to the dominance of trait values. FRich and FEve, on the other hand, did not differ significantly between the two periods. These results highlighted that even in the case of the small species pool that characterised the studied stream and even in the case of high dominance of diatoms, the function of assemblages was not damaged by the climatic extremes that caused disturbed conditions. But it has to be stressed, that post-drought effects on the structure of the assemblages were not studied here. FDiv was higher under HDC than in IDC, indicating extreme functional characteristics of dominant taxa such as *A. minutissimum* and *Navicula* sp. in HDC period. Mason et al. (2005) clearly suggest

that functional divergence may change without any change in functional richness. In our case, this phenomenon was probably due to the following reasons: (i) At the start of the colonisation experiment (IDC period), a relatively large number of filamentous green algae detached from the mature biofilm in the area and appeared in our samples. Despite the slow settling of small unicellular algae such as *A. minutissimum* or *Navicula* sp., they have a competitive advantage over the others due to their other characteristics (e.g., active mobility or strong attachment; Berthon et al., 2011). Thus, in the beginning of the colonisation, unicellular, small diatoms were also present in large numbers in the samples. Therefore, a diverse assemblage emerged in the initial period with high FDiv values. (ii) Although there was no significant amount of precipitation in the IDC period (7 mm), 6 mm of it fell at once on day 10 during a major storm. This reduced significantly the number of filamentous algae and cyanobacteria and the fast moving non-diatoms within the biofilm. These taxa did not disappear from the assemblage, only the distribution of traits changed and a

**FIGURE 6** Correlation plots of index values and environmental parameters under intermediately disturbed condition (a) and under highly disturbed conditions (b). Definition of correlation strengths were: Absolute deviation (±) 0.3 from zero was weak correlation; between 0.3 and 0.7 there was moderate correlation; and above 0.7 the correlation was considered strong
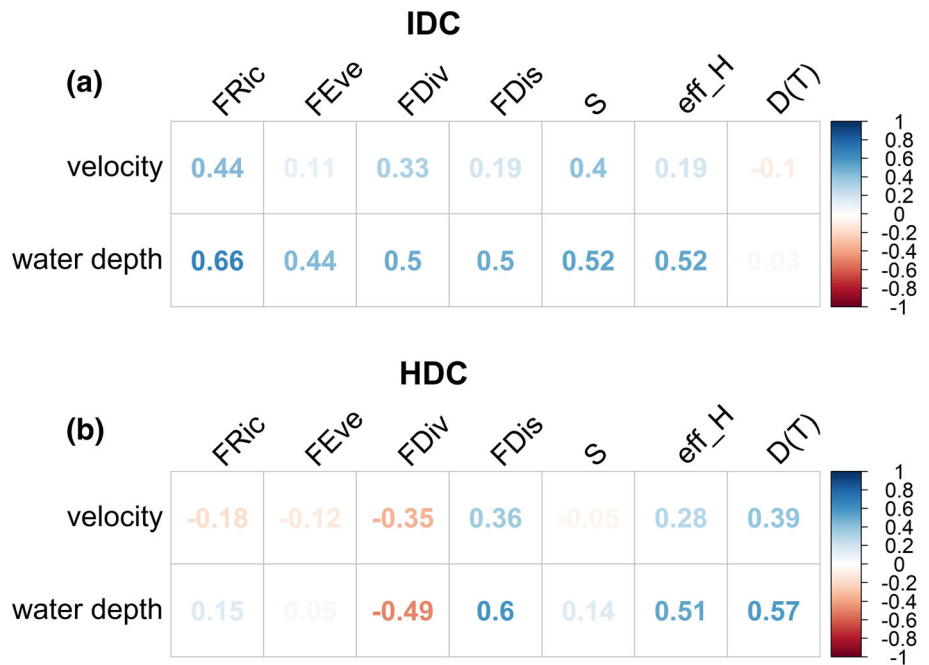


taxa-replacement has begun resulting in a decrease in FDiv values. These values were not able to grow until the beginning of the HDC period. (iii) In contrast to the IDC period, the HDC started with a prolonged heavy rainy period. In these days the rapid changes in FDiv values were probably due to the highly fluctuating water regime that repeatedly reorganised the assemblages. After this rainy period, the composition of the assemblages became stable and the formation of a mature biofilm began, coinciding with a permanent growth in FDiv values. The colonisation process was finally interrupted by the beginning of the dry period, which reduced functional diversity and resulted in a sharp increase in the dominance of taxa tolerating the drought induced disturbances (small sized, slow moving, strongly attached).

## 4.2 | Biofilm formation under IDC and HDC— Colonisation theory

While the species pool is mainly determined by historical and geographical factors such as origin, age, climate, altitude, etc., local factors have a much greater influence on the trait composition of the community (Soininen et al., 2016). Thus, the colonisation success of a specimen depends on whether it has characteristics contributing to its settlement and survival in a given environment or not (Ács & Kiss, 1993; B-Béres et al., 2014, 2016; Stenger-Kovács et al., 2013). Extreme physical disturbance (e.g., floods or drying up) significantly rearranges the composition of benthic algal and cyanobacterial assemblages, typically shifting them towards to the dominance of one group. Since extreme flow events act as main drivers of aquatic organisms, only those one with specific adaptive capabilities (functional traits) persist under these conditions (Larson & Passy, 2012). Therefore, we assumed that HDC periods have more pronounced effect on functional diversity metrics than on taxonomic ones. The results only partially supported

our hypothesis, since not only functional diversity—with the exception of FRich—but taxonomic and phylogenetic diversities also differed significantly in the two periods (see above the explanation regarding to the results of taxonomic and phylogenetic diversities). The FRich did not differ significantly between the two periods, that is, the number of unoccupied niches did not increase in the HDC period. Supposedly, the changes that occurred during the study were not strong enough to filter out functional roles fulfilled by individual traits or trait groups (Valdivia et al., 2017). This finding provides an example of the phenomenon when higher functional redundancy enables the system to keep its functionality even in the case of stochastic species or taxa loss (Biggs et al., 2020; Yachi & Loreau, 1999).

In contrast, environmental changes were strong enough to cause significant differences both in FDiv and FDis values between the IDC and HDC periods. FDiv was higher during disturbed conditions than in IDC. These results are clearly related to the prevalence of extreme traits under HDC. High FDiv values besides trait extremes assume efficient resource use and low competition (Mason et al., 2005) (see above the reasoning). Since FDis is the abundance weighted mean distance of traits from the abundance weighted centroid of traits in the trait space, it clearly refers to changes in dominance relations. In contrast to FDiv, FDis was positively correlated with water depth not only in IDC but also in the HDC period. The fact, however, that FRich did not correlate with water depth during this period (HDC) highlighted that the traits did not disappear from the system only their proportions changed. However, we note that, we did not study how the system behaved during the dehydrated period or after the water had returned. This information could nuance the situation, since we pointed out in our previous study that the drying up of streams result in clearly lower FRich even after water returns to the systems compared to the functional richness of small streams with a stable water regime (B-Béres et al., 2019). Thus, disturbed conditions finally lead to
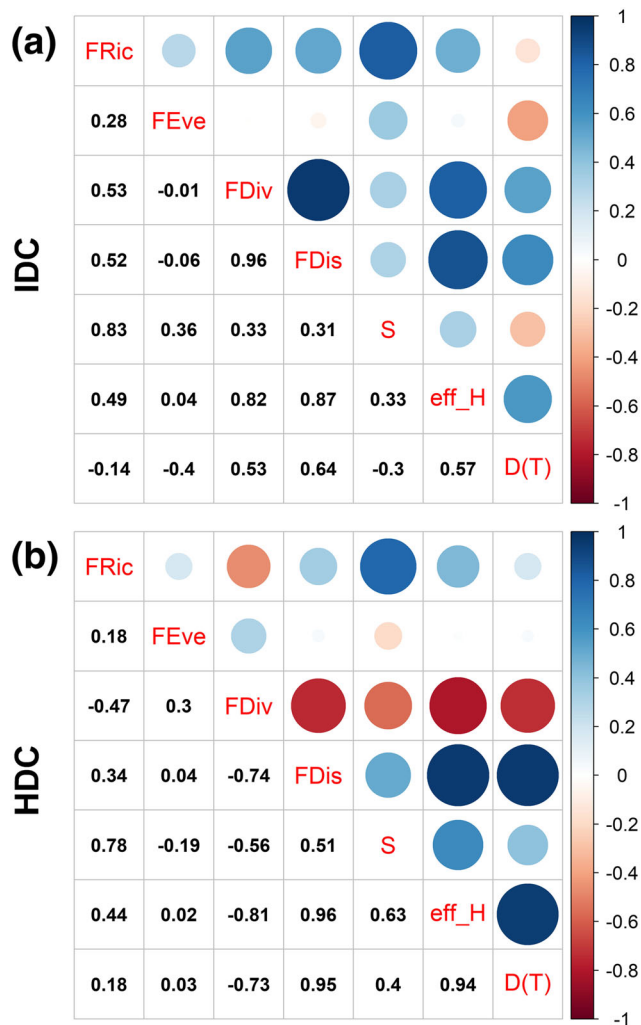
**FIGURE 7** Correlations between diversity indices under intermediately disturbed condition (a) and under highly disturbed conditions (b). Definition of correlation strengths were absolute deviation (±) 0.3 from zero was weak correlation; between 0.3 and 0.7 there was moderate correlation; and above 0.7 the correlation was considered strong

species or taxa loss, loss of phylogenetic diversity, and ultimately loss of functional diversity if environmental conditions do not improve. Since benthic algae and cyanobacteria are one of the most important primary producers in intermittent streams with fluctuating water level (Robson et al., 2008; Robson & Matthews, 2004), their compositional changes have a major impact on the consumers. An algal and cyanobacterial community of closely related taxa with a few extreme traits can ultimately lead to a decline in the diversity and/or biomass of consumer community (Blanco & Ector, 2009). The permanence of changes in community structure is mainly determined by the length and intensity of the environmental extremes. According to even the most optimistic scenarios, frequency of these events will increase in the next decades (IPCC, 2014). Thus, the recognition of nature protection value of intermittent streams, the biodiversity conservation in these ecosystems and the modelling of the expected processes are the challenges of science and applied technologies in the upcoming years.

## 5 | CONCLUSIONS

Our results pointed out the applicability of intermediate disturbance theory only for taxonomical and phylogenetic diversities of benthic algae and cyanobacteria in a lowland intermittent stream with small catchment area. The results did not support this theory, clearly suggesting (i) the importance of a short-time but intense disturbing effect on assemblages in stable period resulting a destabilisation in trait composition; and (ii) fluctuation and instability within the assemblages caused by extreme and opposite influences during the disturbed period. Our findings also highlighted that extreme flow events basically changed both taxonomical and functional composition of benthic algal and cyanobacterial assemblages shifting them to trait extremes. The results, however, stressed only the expression of proportional changes in trait composition, not the disappearances of traits from the system, reinforcing that ecosystems with high functional redundancy can keep their functionality even under the pressure of extreme flow events resulting stochastic changes in taxa composition. Thus, carefully performed water management and protection strategies are needed to preserve both taxonomical and functional diversities in lowland intermittent streams at the ecoregion.

## CONFLICT OF INTEREST
The authors declare that there is no conflict of interest.

## DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.