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Environmental filtering and limiting similarity as main forces driving diatom community structure in Mediterranean and continental temporary and perennial streams

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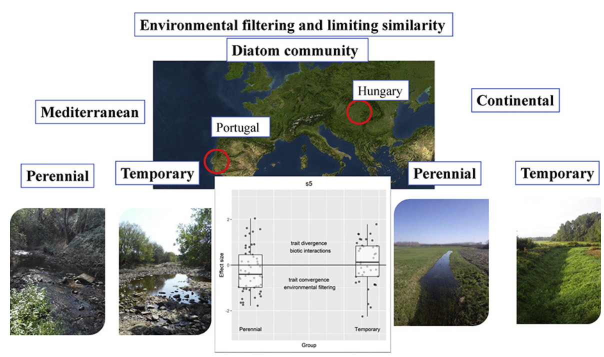
HIGHLIGHTS

- We studied trait composition of diatom assemblages in perennial and temporary streams.
- Trait differences in the two types of streams were greater in the continental region.
- Environmental filtering and limiting similarity shape community structure.
- Unpredictable drying up (continental) has more drastic effects than predictable one.
- The time-for-adaptation and in part the stress-dominance theories have been supported.

GRAPHICAL ABSTRACT



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ABSTRACT

Climatic extreme events such as droughts (unpredictable), dry periods (predictable) or even flush floods, threaten freshwater ecosystems worldwide. The filtering mechanisms of these events and their strength on communities, however, can be different among regions. While time-for-adaptation theory defines whether or not water scarcity can be considered as disturbance, the stress-dominance theory predicts an increase in importance of environmental filtering and a decrease in the role of biotic interactions in communities with increasing environmental stress. Here, we tested whether environmental filtering (leading to trait convergence) or limiting similarity (leading to trait divergence) is the main assembly rule shaping the structure and trait composition of benthic diatom assemblages in Mediterranean (Portuguese) and continental (Hungarian) temporary and

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perennial streams. We assumed that the trait composition of diatom assemblages in the two stream types would be less different in the Mediterranean than in the continental region (addressed to time-for-adaptation theory). We also hypothesized that trait composition would be shaped by environmental filtering in the Hungarian streams while by biotic interactions in Portuguese streams (addressed to stress-dominance theory). Our results supported our first hypothesis since traits, which associated primarily to temporary streams were found only in the continental region. Our findings, however, only partially proved the stress-dominance hypothesis. In the continental region, where drying up of streams were induced by unpredictable droughts, biotic interactions were the main assembly rules shaping community structure. In contrast, environmental filtering was nearly as important as limiting similarity in structuring trait composition in the Mediterranean region during the predictable dry phase with no superficial flow. These analyses also highlighted that drought events (both predictable and unpredictable ones) have a complex and strong influence on benthic diatom assemblages resulting even in irreversible changes in trait composition and thereby in ecosystem functioning.

1. Introduction

In the last century, freshwater became one of the most valuable goods in the world (Green et al., 2015). Freshwater in sufficient quantity and adequate quality is essential for healthy functioning of natural ecosystems and has a variety of ecosystem services to society (Francis, 2011; Jefferies et al., 2012). Freshwaters are fundamental resources for food production, drinking water services, industrial activities, transportation, human well-being services and also for nutrient cycling and maintenance of biodiversity, among others (Francis, 2011). Freshwater ecosystems, however, are under increasing pressures from anthropogenic activities and natural hazards (Dudgeon et al., 2006; Francis, 2011; Skoulikidis et al., 2017) and now, they are considered to be "the most endangered ecosystems worldwide" (Dudgeon et al., 2006).

In the last 50 years, the frequency and the intensity of extreme weather events including droughts and flash floods increased worldwide (IPBES, 2019). These extremities strongly threaten terrestrial, marine and freshwater ecosystems causing biodiversity loss and decrease in their functioning at local scale (IPBES, 2019). Drying up of freshwaters seems to be a typical example for disturbances, independently of their natural or anthropogenic origin. The time scale of dryness, however, is a key factor assessing whether this event is a disturbance or not (Poff et al., 1997; Acuña et al., 2017). In general, the naturally re-occurring predictable water shortage allows organisms to develop adaptations and strategies to overcome the critical environmental periods. In contrast the unpredictable human-induced drying up of waters and dry events with extraordinary magnitudes (even the natural ones) have strong influence on ecosystem structure and function (Acuña et al., 2017).

Drought-induced water scarcity is a direct driver causing reversible or even irreversible changes in freshwater ecosystems by changing the water flow conditions (e.g. Acuña et al., 2017; Stubbington et al., 2017). Depending on the surface flow conditions, lotic freshwaters can be classified as perennial (characterized by continuous flow) and temporary (characterized by drying up for a part of the year) (Skoulikidis et al., 2017). Temporary streams are widespread in arid, semi-arid and Mediterranean regions, but they are also common in oceanic climate regions (Stubbington et al., 2017). In the continental region, however, recurring drying up of formerly permanent streams began only in the last decades due to the effects of simultaneously acting human activities and climate change (B-Béres et al., 2019).

In the context of community assembly droughts can be considered as strong environmental filters. These filters operate on the traits or trait combinations of species rather than on the species themselves (McGill et al., 2006; Díaz et al., 2007; Zorger et al., 2019), and results in trait convergence within the assemblages. However, the decrease in trait diversity does not necessarily coincide with a decrease in species richness. There can be several species in the assemblages, which share almost identical traits, resulting in high functional redundancy. This functional redundancy gives stability to the systems, because species losses (caused by disturbances, competition or demographic stochasticity) do not bring losses in functioning. Species that successfully pass through the environmental filter have similar trait combinations, and due to this similarity they become exposed to strong biotic interactions. These interspecific interactions can be even more pronounced within the community if traits filtered are directly related to resources (including food and shelter). In these highly competitive environments, only those species, which differ remarkably in some relevant characteristics, can coexist (trait divergence within assemblages) (MacArthur and Levins, 1967; Pásztor et al., 2016). Thus, trait composition of the assemblages refers to the leading assembly rules (Götzenberger et al., 2012). To recognize these rules the most appropriate traits or trait combinations must be selected, which are responsive to disturbing effect (Zorger et al., 2019). Exclusion of responsive traits from analyses might lead to misunderstand the results and to draw incorrect findings. The strength of the environmental and biotic filters strongly depends on the abiotic characteristics of the habitats. This notion has been conceptualized in the stress dominance hypothesis, which states that composition is shaped by environmental filtering in harsh environmental conditions e.g. under extraordinary flow regimes, while biotic interaction plays pivotal role in formation of assemblages in benign environments (Grime, 1977; Weiher and Keddy, 1995; Coyle et al., 2014). However, harshness cannot be evaluated on an absolute scale. Extraordinary climatic events that caused drying up of streams can be assumed as harsh conditions in the continental region. Although, in Mediterranean region, the predictable dry periods cannot be considered as natural characteristics of the systems, at a longer historical timescale there is enough time for adaptation of the communities. This phenomenon was conceptualized in the time-for-adaptation theory by Acuña et al. (2017). Thus, while unpredictable droughts are strong filters in the continental region, periodically reoccurring dry periods have less severe impacts on the assemblages of Mediterranean streams, where biotic interactions can be supposed to be the major mechanisms structuring communities.

Benthic diatom assemblages as primary producers contribute significantly to the food webs in lotic ecosystems, especially in small streams (Kireta et al., 2012). Thus, changes in their structure induced by water shortage will finally influence the whole ecosystem (Stubbington et al., 2017). While studies on community structure or biodiversity dynamics of diatoms in temporary streams are considered as priority topics in Mediterranean regions (e.g. Novais et al., 2014; Falasco et al., 2016; Piano et al., 2017; Stubbington et al., 2019), only limited information is available on communities of benthic algae in drying waters in the continental region (B-Béres et al., 2019). It has been demonstrated that independently of ecoregions, aerophilous and/or terrestrial taxa can be characteristic in temporary streams (Falasco et al., 2016; B-Béres et al., 2019). However, considerable differences in trait composition can also be shown between Mediterranean and continental regions (Falasco et al., 2016; B-Béres et al., 2019). These differences may suggest that the strength of the water shortage-induced filtering mechanisms on benthic diatom communities differ among ecoregions.

Here, we tested whether environmental filtering or limiting similarity is the main assembly rule shaping trait composition of diatom assemblages in Mediterranean and continental perennial and temporary streams.

According to the above-mentioned "time-for-adaptation" theory (Acuña et al., 2017) and "stress-dominance" theory (Coyle et al., 2014) we addressed the following research hypotheses:

(i) Benthic diatom assemblages of perennial and temporary streams in the continental region show larger compositional differences than those in the Mediterranean region.
(ii) Independently of the water regime, environmental filtering is the decisive assembly rule within diatom assemblages in continental streams, while trait composition is shaped by biotic interactions in the Mediterranean region.

2. Materials and methods

2.1. Sampling area

A total of 92 sites (39 temporary and 53 perennial) were sampled in southern and central Portugal belonging to the Ribeiras do Algarve (17), Guadiana (12), Mira and Sado (13), and Tejo (50) watersheds (Fig. 1). Sampling was carried out during spring 2006, under flowing conditions. The hydrological regime was determined by using a surface runoff model within a geographic information system (INAG, 2008). The studied streams belong to the R 17–20 river types (Solheim et al., 2019), and were subject to low anthropogenic pressure, based on REFCOND (2003) criteria and organized by the National Water Institute (INAG), such as land use in the watershed, urban area, presence and characteristics of the riparian vegetation, sediment loads, hydro-morphological alterations, changes in river connectivity caused by the presence of dams, toxicity, acidification and organic contamination.

In Hungary, the driest period shifted from winter to the growing season (summer) during the last decades (Bartholy et al., 2014), and the frequency of unpredictable droughts increased. Therefore, many formerly perennial streams were dried up recurrently in the last decade. These streams are referred as temporary and can be characterized by alternating dry and flowing phases within a year. However, there were several streams with irregular drying pattern, which made their characterization difficult. In some years, the flow conditions are permanent, while in others some stream reaches completely dry up during periods with no precipitation. Thus, here we defined the sampling events themselves "temporary" or "perennial" depending on the permanence of flow conditions. Accordingly, altogether 26 sites were sampled in the Eastern part of Hungary during spring from 2008 to 2015 in the course of the WFD-based national biomonitoring program (Fig. 1). In this period, a total of 96 samplings were conducted of which 71 have been considered as "temporary" and 25 have been considered as "perennial". The sampling was defined as temporary when only pools were present or no water was found in the streambed in the previous autumn. The studied lowland streams are calcareous with coarse or medium sized sediment, in small or medium sized catchments (R-05 Broad types, Solheim et al., 2019). In the region, the agricultural activity is intense, thus the ecological status of the streams was moderate (web 1, n.d.). Since in Hungary, continuous monitoring and collection of background data/information in some small temporary streams have begun very recently (van Dam et al., 2007), no information is available in the sampling period on topics such as pre-drought community composition, presence or absence of refugia during the drought, the duration of drying up, the velocity of water retreat, etc.

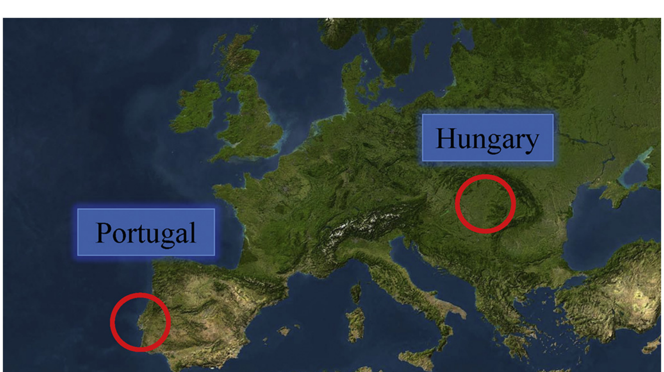

Fig. 1. The study area in Portugal and in Hungary.

2.2. Sample collection and preparation

All the samples were collected in the flowing phase of the streams. The sampling and preservation were performed according to the European standard (EN, 2003). In Portugal, the samples were collected from stones and cobbles while in Hungary, periphytic diatom samples were collected from emergent macrophytes (*Phragmites australis* (Cav.) Trin ex. Steud., or *Typha* spp.) as characteristic substrate types in the lowland area of the Carpathian Basin. Since some diatom species prefer certain substrate types (e.g. *Cocconeis placentula* ssp. favors plants as microhabitat; Soininen and Eloranta, 2004), we excluded problematic samples from the analyses in a pre-sorting process. According to the European standard (EN, 2003), hot hydrogen-peroxide method was used for the preparation of diatom valves and Naphrax resin was used for embedding. At least 400 diatom valves were counted and identified at least to species but also subspecies level using Leica DMRB (in Hungary) and Leica DMRX (for Portuguese samples) microscopes with 1000–1600-fold magnification. The identification of diatom taxa was carried out using references and also up-to-date literatures (Krammer and Lange-Bertalot, 1997a, 1997b; Krammer and Lange-Bertalot, 2004a, 2004b; Potapova and Hamilton, 2007; Bey and Ector, 2013 in PO and HU; Stenger-Kovács and Lengyel, 2015 in HU; the series 'Diatoms of Europe', 'Iconographia Diatomologica', 'Bibliotheca Diatomologica' and relevant taxonomic papers in PO).

2.3. Data processing and analyses

Altogether 168 and 299 taxa were found, respectively in the Portuguese and the Hungarian streams (Supplementary Table 1). According to Rimet and Bouchez (2012) diatom taxa were classified into 23 trait categories referring as traits in the paper (Table 1). Based on these traits species can be assigned one of to four guilds, to five cell size categories, to twelve life form groups, and mobility, spreading and colonization as binary categories.

The reliability of divergence/convergence analysis is based solely on the recorded traits, presence of non-recorded traits in assemblages might lead to unidentified relationships. Here, the most ecologically relevant 23 diatom traits were involved in the analyses that significantly indicate habitat diversity (see more in review Tapolczai et al., 2016). Other traits, such as formation of resting spores, or resting cysts, that enable taxa to endure disturbed environments are very rare in freshwater diatoms (Kaczmarska et al., 2013; Lange et al., 2016). Thus, these traits were excluded from analyses.

2.4. Statistical analyses

Two data matrix were prepared: one for taxonomic analysis with 188 samples and 378 taxa; another for traits analysis with 378 taxa and 23 traits. The calculation of convergence or divergence of traits follows the null model approach similarly to Lhotsky et al. (2016). We used Rao's quadratic entropy (RaoQ) (Botta-Dukát, 2005) as test statistic. RaoQ is the mean dissimilarity between two species weighted by the product of their relative abundances. First, we calculate the RAoQ test statistics, to 9999 random samples, created from the original species pool. Then, we repeated the same analysis for the real samples. Differences in trait distributions between the real and random communities were characterized

Table 1
Applied morphological and functional traits and their categories.

Type of traits	Trait categories
Guilds	Low profile
	High profile
	Motile
	Planktic
Cell size	S1: 5–99 μm^3
	S2: 100–299 μm^3
	S3: 300–599 μm^3
	S4: 600–1499 μm^3
	S5: ≥1500 μm^3
Life forms	Adnate
	Pedunculate
	Pad
	Stalk
	Non-colonial
	Colonial
	Mucous tubule colony
	Filament colony
	Zig-zag colony
	Rosette colony
	Ribbon colony
	Arbuscular colony
Mobility	Mobile
Spreading and colonization	Pioneers

by the p-values of the applied t-test. Probit transformed p-values were used as 'effect size values' (ES), which indicate the higher probability of trait divergence or convergence (Botta-Dukát, 2018). Positive ES values indicate that **competition** is the leading assembly rule, while negative ones refer to the leading role of **environmental filtering**. The positive values mean that the resident species in the assemblages have highly different values of the given trait than those in the random assemblages. In the case of negative ES values the resident species have more similar trait values than those in the randomised populations because species having highly different trait values are filtered out by the environment. This combination of test statistic and randomization algorithm allows detecting both trait convergence due to environmental filtering, and trait divergence due to limiting similarity (Botta-Dukát and Czúcz, 2016; Götzenberger et al., 2016).

We used the Student's t-test to show the significant differences in ES values from zero for the whole dataset. For visualizing the differences between perennial and temporary streams, we used box-plot approach with jitter plots and the significance of the differences between these two groups was tested with Mann-Whitney U test.

The entire procedure sketched out above was repeated for each trait independently.

Additional, two Principal Components Analyses (PCA) were performed to complement the interpretation of the ecological traits in perennial and temporary streams. For these analyses, we used the community weighted mean (CWM) approach, which expresses the mean trait value in the community weighted by the relative abundances of the species matrix of both, Hungarian and Portuguese datasets.

All statistical analyses and graphs were performed under R environment, with the relevant packages (vegan, tidyverse and ade4) (Dray and Dufour, 2007; Oksanen et al., 2019; R Core Team, 2019).

For the comparison of the taxonomic composition between the two regions, we used a Non-metric Multidimensional Scaling (NMDS) using the Jaccard coefficient of similarity. Since the Jaccard coefficient is based on binary distances and focuses on the similar taxa occurring in the two datasets. For the comparison of the trait compositions between the two regions, we used the community-weighted mean (CWM) matrix, in which the mean trait values in the community were weighted by the relative abundances of the species. An NMDS using the Bray-Curtis coefficient of dissimilarity was then produced. The multivariate statistical software Canoco 5 (ter Braak and Šmilauer, 2002) was used for the analysis.

3. Results

3.1. Traits–water regime relationships

3.1.1. General findings

Independently of the water regime, taxonomy-based NMDS analysis indicated clear separation between the diatom assemblages in the two ecoregions (Fig. 2), while the trait-based NMDS analysis showed a greater overlap among them (Fig. 3). Small size, pioneer and/or low profile guild taxa were characteristic of the Mediterranean region (no separation was observed according to water regime) and of the temporary streams in the continental region. Different types of colonial taxa seemed to prefer more likely the perennial streams independently of the ecoregion. Medium or large sized and/or motile taxa were, however, dominant in the continental streams independently of the water regime types (Fig. 3).

3.1.2. Ecoregional differences

Based on the trait composition of benthic diatoms, the N-PCA analysis performed for the first two components indicated only slight differences in the importance of water regime in explaining the functional composition of assemblages (63.38% in the continental region and 61.66% in the Mediterranean region). Characteristic traits of the two water regime types could be clearly identified in the continental region. However, occurrence of this kind of specific traits was not characteristic in the Mediterranean region. In the continental region, diatom communities in temporary streams were characterized by small size (S1) and/or pioneer taxa belonging mainly to low profile guild. Most of these taxa attached by stalk to the substrates. In contrast, different

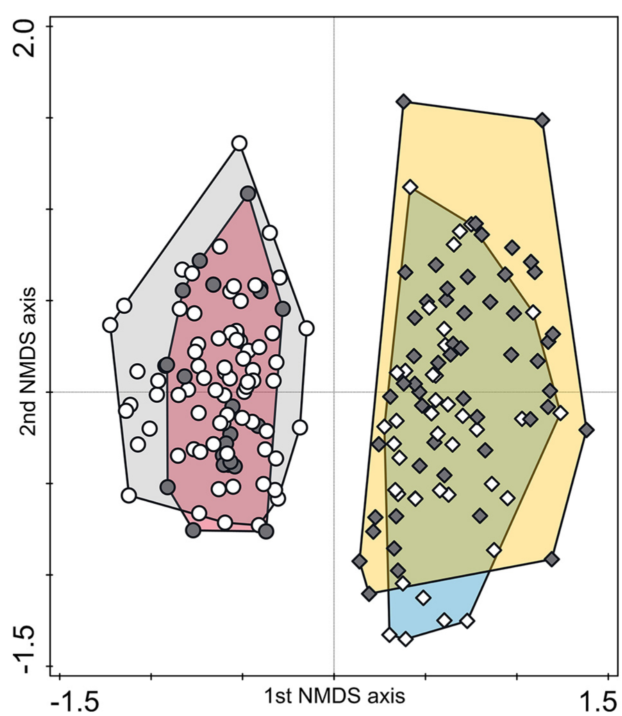

Fig. 2. Results of the species-based NMDS analysis of the diatom communities in streams of the continental and Mediterranean streams. The first and second axes explained 46.67% and 28.46% of the total variance, respectively. Temporary streams in the continental region are marked with white circles (their covered area is grey). Perennial watercourses in the continental region are marked with grey circles (their covered area is red). Temporary streams in the Mediterranean region are marked with white diamond (their covered area is blue). Perennial watercourses in the Mediterranean region are marked with grey diamond (their covered area is yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

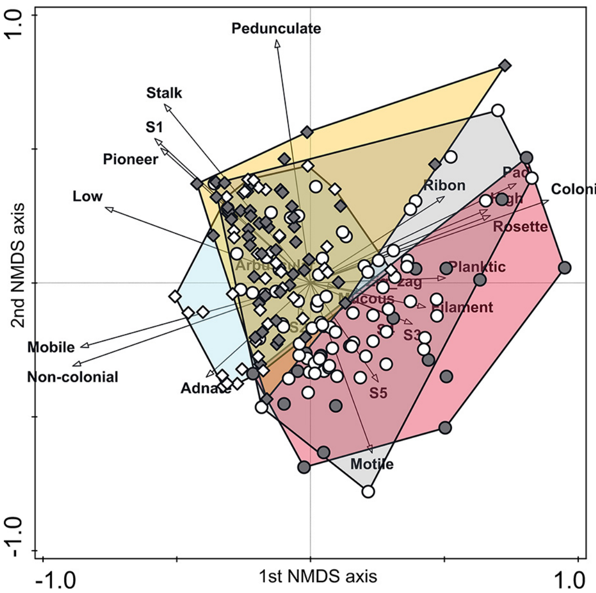

Fig. 3. Results of the trait-based NMDS analysis of the mean trait profiles of diatom assemblages in streams of the continental and Mediterranean regions for the first two axes. The first and second axes explained 52.94% and 30.15% of the total variance, respectively. Temporary streams in the continental region are marked with white circles (their covered area is grey). Perennial watercourses in the continental region are marked with grey circles (their covered area is red). Temporary streams in the Mediterranean region are marked with white diamond (their covered area is blue). Perennial watercourses in the Mediterranean region are marked with grey diamond (their covered area is yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

types of colonial, high profile taxa were characteristic for perennial streams (Fig. 4, Supplementary Table 2).

In the Mediterranean region, the perennial streams were mostly preferred by high profile, mostly colonial (in different types) taxa attached to substrate by pad, while there were no traits which could clearly indicate the temporary regime (Fig. 5).

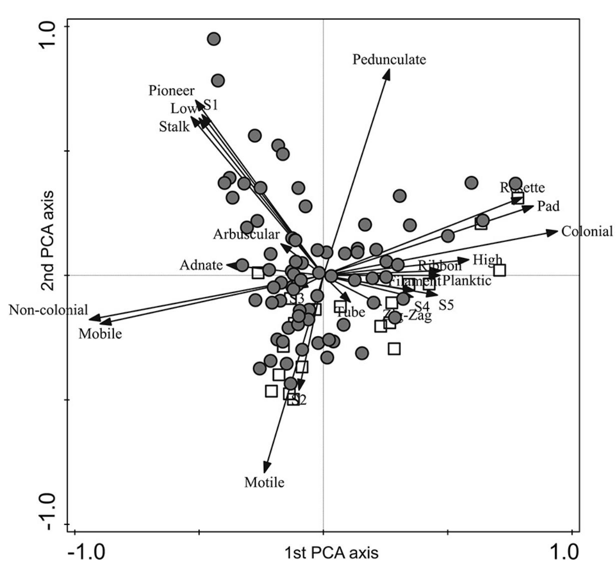

Fig. 4. Results of the PCA analyses of the mean trait profiles of diatom communities in Hungarian streams (continental region). The first and second axes explained 28.78% and 15.61% of the total variance, respectively. Temporary streams are marked with grey circles. Perennial watercourses are marked with squares.

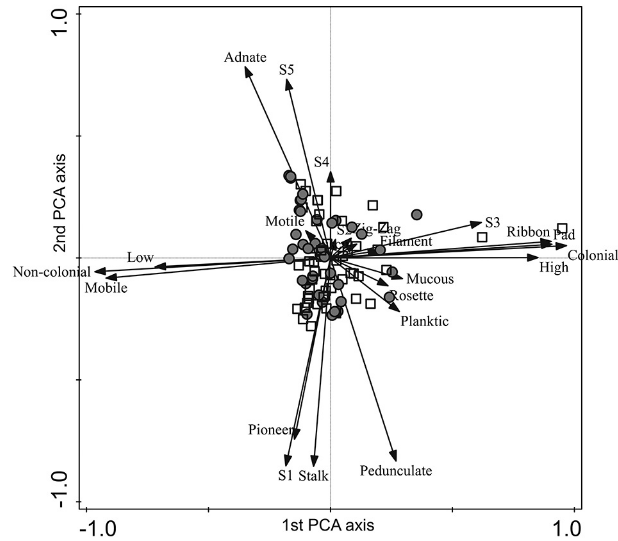

Fig. 5. Results of the PCA analyses of the mean trait profiles of diatom communities in Portuguese streams (Mediterranean region) for the first two components. The first and second axes explained 28.53% and 17.91% of the total variance, respectively. Temporary streams are marked with grey circles. Perennial watercourses are marked with squares.

3.2. Distribution of the effect size (ES) values in comparison with the null model in the continental region

In the continental region, the results of Mann-Whitney tests indicated that the ES values of adnate, low profile guild, pioneer, S1 and stalk traits were significantly higher in temporary streams than in perennial streams (Table 2). In contrast, significantly higher ES values were found in perennial streams than in temporary ones in the case of traits like S5 (Fig. 6, Table 2).

Regardless the water regimes, in the continental region nine traits were characterized by non-random distribution (low profile guild, S3, S4, adnate, pioneer and filament, zig-zag, rosette and arbuscular colonies;

Table 2
The significance of the difference in effect size values between perennial and temporary streams, based on Mann-Whitney *U* test. Significant differences are highlighted in bold (↑↓ indicates the increase or decrease in ES values of temporary streams compared to perennial ones).

Traits	*p* values	
	Continental region	Mediterranean region
Low profile	**0.000** ↑	0.950
High profile	0.184	0.204
Motile	0.431	0.637
Planktic	0.090	0.598
s1	**0.002** ↑	0.333
s2	0.228	0.185
s3	0.343	**0.0188** ↓
s4	0.298	0.106
s5	**0.013** ↓	0.051
Adnate	**0.003** ↑	0.765
Pedunculate	0.309	0.919
Pad	0.924	0.777
Stalk	**0.032** ↑	0.629
Non-colonial	0.706	**0.021** ↑
Colonial	0.512	**0.022** ↓
Mucous tubule colony	0.163	**0.002** ↓
Filament colony	0.170	0.431
Zig-zag colony	0.932	0.288
Rosette colony	0.798	0.783
Ribbon colony	0.809	0.427
Arbuscular colony	0.597	0.151
Mobile	0.664	0.055
Pioneer	**0.045** ↑	0.582

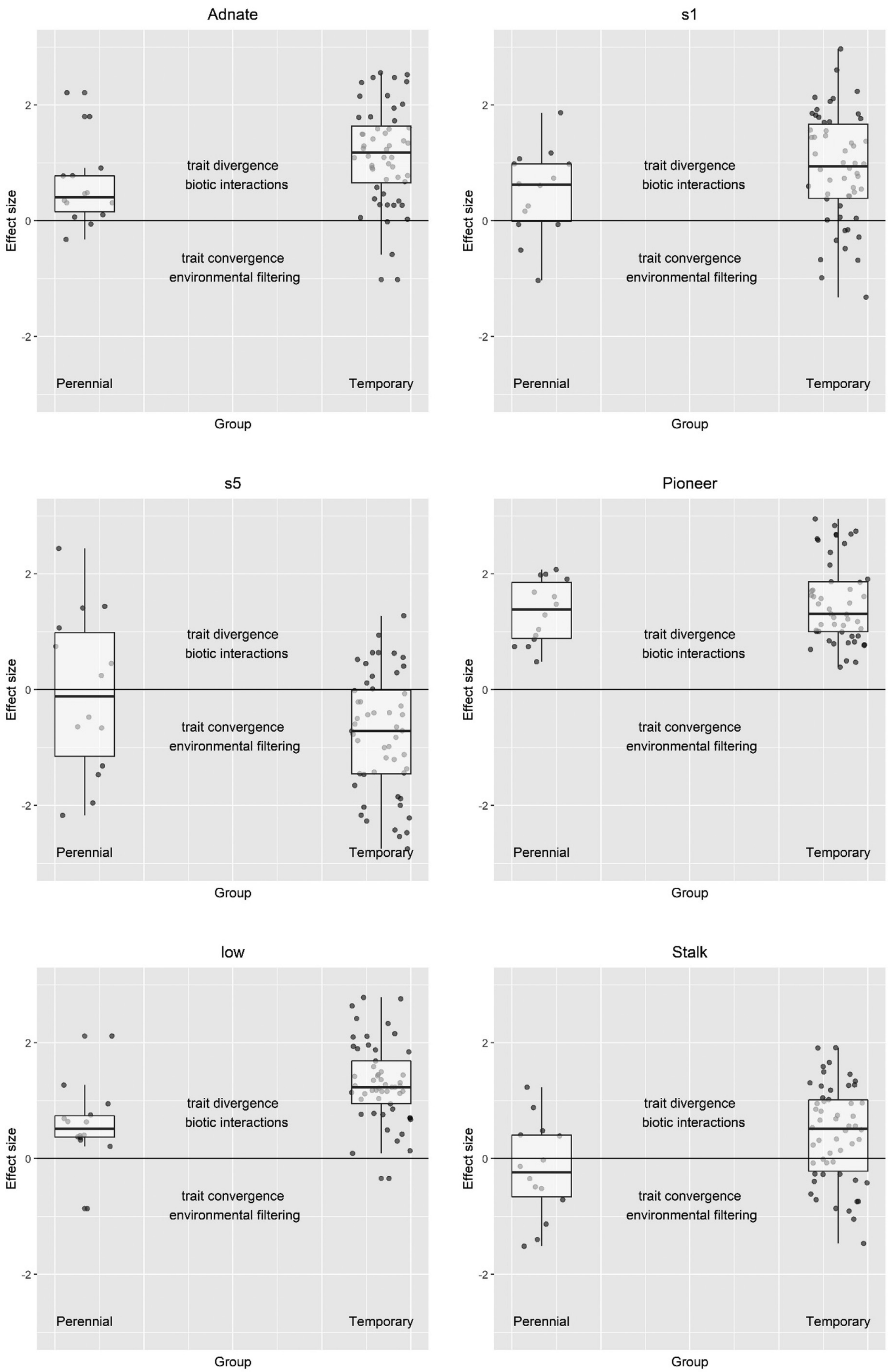
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Table 3
Results of the test on the effect size values from random distribution (0 value), the table includes the mean ES values and the *p*-value of the *t*-test; significant differences highlighted in red (in both water regimes), red and bold (exclusively in temporary streams), black and bold (exclusively in perennial streams).

	Continental region				Mediterranean region			
	ES values		p values		ES values		p values	
	perennial	*temporary*	*perennial*	*temporary*	*perennial*	*temporary*	*perennial*	*temporary*
Low profile	0.706	1.460	0.000	0.000	0.494	0.464	0.000	0.010
High profile	0.161	-0.150	0.523	0.138	-0.519	-0.666	0.000	0.000
Motile	-0.095	-0.345	0.746	**0.018**	-0.839	-0.861	0.000	0.000
Planktic	0.361	-0.043	**0.050**	0.702	-0.444	-0.393	0.000	0.001
s1	0.250	0.852	0.111	**0.000**	0.939	0.723	0.000	0.000
s2	0.283	-0.037	0.170	0.766	-0.003	-0.183	0.975	0.166
s3	0.454	0.642	0.015	0.000	0.014	-0.413	0.912	**0.002**
s4	-0.720	-0.473	0.002	0.000	-0.412	-0.165	**0.001**	0.229
s5	-0.190	-0.924	0.502	**0.000**	-0.215	0.157	0.210	0.354
Adnate	0.622	1.319	0.000	0.000	0.978	0.990	0.000	0.000
Pedunculate	0.241	0.481	0.313	**0.000**	-0.296	-0.226	0.082	0.303
Pad	0.174	0.144	0.536	0.303	-0.642	-0.687	0.000	0.000
Stalk	-0.013	0.456	0.946	**0.000**	0.384	0.411	**0.004**	0.071
Non-colonial	0.126	0.019	0.681	0.879	-0.583	-0.988	0.000	0.000
Colonial	0.207	0.016	0.531	0.894	-0.632	-1.173	0.000	0.000
Mucous tubule colony	0.170	-0.071	0.531	0.193	0.474	0.099	**0.000**	0.259
Filament colony	1.611	1.318	0.000	0.000	0.682	0.750	0.000	0.000
Zig-zag colony	0.217	0.210	0.023	0.000	0.819	0.734	0.000	0.000
Rosette colony	1.430	1.362	0.000	0.000	0.425	0.444	0.000	0.000
Ribbon colony	-0.220	-0.159	0.445	0.140	-0.466	-0.574	0.001	0.000
Arbuscular colony	4.753	4.753	0.000	0.000	0.301	0.365	0.001	0.000
Mobile	0.364	0.248	0.181	**0.039**	-0.539	-0.932	0.001	0.000
Pioneer	1.254	1.757	0.000	0.000	2.141	2.121	0.000	0.000

Table 3). Additionally, six traits showed also non-random distribution in temporary streams, while only the distribution of the planktic trait differed significantly from random in perennial streams (Table 3). In both stream water regime types, the means of ES values of traits like adnate, arbuscular, filamentous, low profile guild, pioneer, rosette colony, S3 and zig-zag colony were significantly higher than zero, indicating higher probability of trait divergence (biotic interactions). In contrast, the mean ES values of S4 trait were significantly lower than zero, related to a higher probability of convergence (environmental filtering). In the temporary streams of the continental region, traits like mobile, pedunculate, S1 and stalk were characterized by mean ES values >0, while mean ES values <0 are related to motile and S5 traits. In the case of planktic trait, the mean ES value >0 indicated higher probability of trait divergence in perennial streams (Table 3).

3.3. Distribution of the effect size (ES) values in comparison with the null model in the Mediterranean region

In the Mediterranean region, higher ES values of S3, colonial and mucous tube colony traits were more characteristic in perennial than in temporary streams (Fig. 7, Table 2). Only the ES values of non-colonial trait were significantly higher in temporary streams than in perennial ones (Table 2).

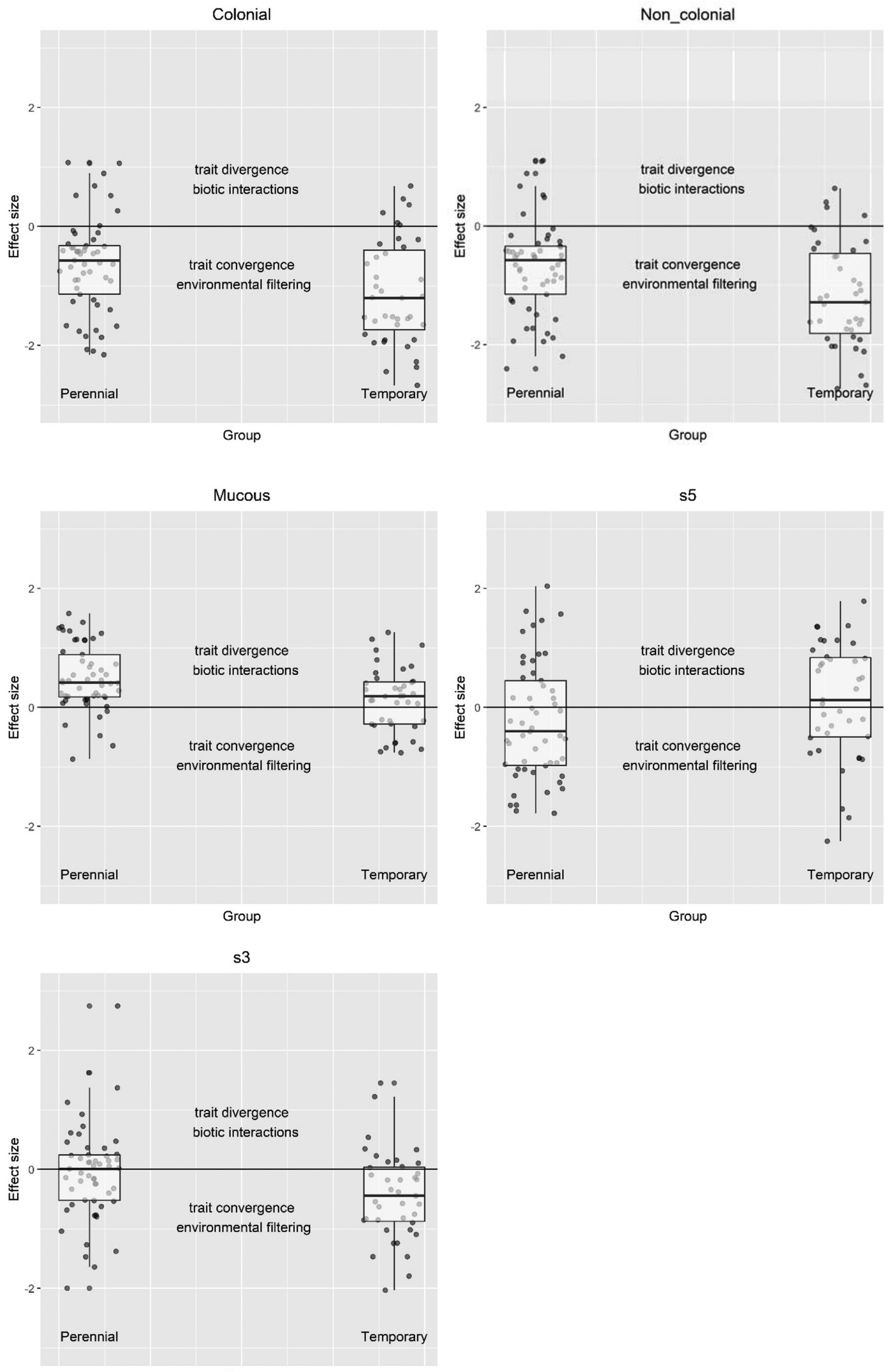
In the Mediterranean region, *t*-tests indicated non-random distribution of sixteen traits in both stream water regime types. There was only one trait (S3) which distribution differed from random exclusively in temporary streams, while non-random distribution characterized S4, stalk and mucous tube colony traits in perennial streams. In both stream water regime types, the mean ES values of traits like adnate, arbuscular, filamentous, low profile guild, pioneer, S1, rosette and zig-zag colony were significantly larger than 0, indicating higher probability of trait divergence. In contrast, significantly <0 mean values, characterized traits like colonial, high profile and motile guilds, mobile, non-colonial, pad, planktic and ribbon referring to higher probability of trait convergence. In the case of S3 trait, the mean ES values were significantly <0, indicating higher probability of environmental filtering in temporary streams. In perennial streams, significantly <0 mean ES values characterized the S4 trait, while the mean ES values of stalk and mucous tube colony traits were significantly >0. (Table 3).

4. Discussion

4.1. Ecoregional differences in trait composition - general findings

Traditionally, diatoms are considered as cosmopolitan taxa and might have a wide geographical distribution (Soininen and Niemela, 2002). Recent studies, however, emphasize that many species have rather limited distribution (Kociolek et al., 2017; Sakaeva et al., 2016). Furthermore, ecoregional differences in climate, soil or in geology can further modify the species responses to general water characteristics (e.g. nutrient supply, light conditions, etc.) (Besse-Lototskaya et al., 2011), highlighting strong microevolutionary pressure on taxa (Soininen et al., 2016). Thus, the clear separation of taxonomic composition between the ecoregions studied here was expected. The overlap in trait composition, however, was more pronounced due to the strong similarity among diatom assemblages in the continental temporary, in the Mediterranean temporary and in the Mediterranean perennial streams. Independently the water regime, Novais et al. (2014) also found high trait-based similarity in the Mediterranean region. However, they also highlighted the taxonomic differences between water regime

Fig. 6. The distribution of effect size values in perennial and temporary streams in the continental region (Hungary).


Colonial
Effect size
2
0
-2
trait divergence
biotic interactions
trait convergence
environmental filtering
Perennial
Temporary
Group
Non_colonial
Effect size
2
0
-2
trait divergence
biotic interactions
trait convergence
environmental filtering
Perennial
Temporary
Group
Mucous
Effect size
2
0
-2
trait divergence
biotic interactions
trait convergence
environmental filtering
Perennial
Temporary
Group
s5
Effect size
2
0
-2
trait divergence
biotic interactions
trait convergence
environmental filtering
Perennial
Temporary
Group
s3
Effect size
2
0
-2
trait divergence
biotic interactions
trait convergence
environmental filtering
Perennial
Temporary
Group

types, indicating the importance of temporary streams in biodiversity conservation. Traits, which were dominant in the Mediterranean region (small size, pioneer, low profile), were also characteristics in the continental temporary streams. Despite the fact, that taxa with different traits or trait combinations can cope with the same unpleasent circumstances (Le Bagousse-Pinguet et al., 2017; Pinho et al., 2019), our results clearly indicated the aprior benefits of the mentioned diatom traits in the continental and Mediterranean temporary and the Mediterranean perennial streams (detailed explanations of similarities of Mediterranean watercourses see in the next chapter).

Assessing the influence of water regime on colonial forms we found that depending on the complexity of the colonies, taxa are able to tolerate either stable, predictable conditions (simple colony) or unpredictable environments (complex colony) (Passy, 2002; Passy and Larson, 2011). Independently the ecoregions, colonial taxa preferred perennial streams to temporary ones in our study. Obviously, perennial water regime creates more stable conditions for assemblages comparing to temporary waters. Droughts and dry periods, however, can change the hydrological, physical and chemical conditions in these perennial streams. Even in the Mediterranean region, the strength and the duration of the dry period cannot be predicted from period to period.

Although nutrient enrichment can usually stimulate taxa in all guilds, high nutrient supply is especially favorable for members of the motile guild (Passy, 2007; Passy and Larson, 2011). Here we found, that independently of the water regime, richness and proportion of motile guild were higher in the continental than in the Mediterranean ecoregion. One reliable reason of this phenomenon is, that the studied lowland streams in the continental region were exposed to intense agricultural activity and their ecological status was moderate, while streams in the Mediterranean region were under low anthropogenic pressure. Furthermore, the decreasing water coupled with increasing nutrient concentrations in the dry period can significantly enhance the ratio of motile taxa, especially of the large ones, in the assemblages of the continental region (Kókai et al., 2015). Another possible reason of the above-mentioned phenomenon could be the use of different substrate types for sampling in the two ecoregions (stones vs emergent macrophytes). Although the substrate type can significantly influence the taxonomic and trait structure of communities, several studies have demonstrated the similarity between guild composition of diatom assemblages on epiphytic and epilithic substrates (Poulickova et al., 2004; Passy, 2007). Both of them are usually favored by high and low profile taxa.

4.2. Water regime influence on trait distribution – time-for-adaptation theory

Time scale of droughts and dry periods, i.e. the historical occurrence of these events, define the direction and strength of compositional changes in assemblages during these events. An intense influence of dryness on assemblages may be present in regions where these dry events with extraordinary magnitude do not fall within the annual average hydrological variations. In contrast, assemblages could adapt to the harsh circumstances of water scarcity in regions, where these conditions are expected (Acuña et al., 2017). Thus, more pronounced trait-based compositional differences in diatom assemblages were hypothesized between perennial and temporary streams in the continental than in the Mediterranean region. Although our results supported this hypothesis, they have encouraged us to rethink the adaptation theory in terms of diatoms. It was unexpected, that the importance of water regime in formation of functional composition was quite similar in the two ecoregions (61.66% in the Mediterranean vs. 63.38% in the continental region). In Hungary, however, the two hydrological regimes (perennial vs. temporary) clearly separated from each other and characteristic traits in these regimes have been recognized. In contrast, no traits clearly characterized the temporary streams in the Mediterranean region. Since nutrient supply and water quality were very similar in the studied Mediterranean streams, our results also reinforced that in such systems drying up in the dry period can be considered as an intense natural process influencing biodiversity and shaping community's structure (Novais et al., 2014; Piano et al., 2017; Tornes and Ruhi, 2013). Generally, it is hard to identify changes in adaptation strategies of microorganisms, especially in the field (Berthon et al., 2011; Tapolczai et al., 2016; B-Béres et al., 2017). The very similar trait composition in the Mediterranean streams, however, suggested that benthic diatoms have already adapted at community level to recurrent dry period by strong trait selection. Traits that have superior competitive abilities in marginally disturbed but nutrient rich environments (e.g. motile guild) were influenced by strong selective pressure here. In contrast, the resource poor habitats predictably disturbed by dry periods ensured the persistence of other traits (low profile, small size, pioneer) supporting survival during these conditions. Despite the community level adaptation of benthic diatoms to the recurrent dry periods in the Mediterranean region, annual changes in trait composition were obviously controlled by important factors such as the duration of the dry period, the pre-dry period community composition, the presence or absence of residual pools, the herbivorous pressure by macroinvertebrate grazers and even by the velocity of water retreat. Finally, our findings in the Mediterranean region (i.e. similar trait composition independently of the water regime) also reinforce the notion that disturbing effects increase the convergence of traits within assemblages highlighting the influence of environmental filtering on communities (Zorger et al., 2019).

Traits indicating permanent habitat, however, could be identified in both ecoregions. Colonial and high profile traits were characteristic of perennial stream communities independently of the region. Our findings denote the robustness of these traits as indicators of permanent habitat. Taxa having these characteristics prefer stable physical and chemical environments (Tapolczai et al., 2016; B-Béres et al., 2017) and also tolerate the grazing pressure (Passy, 2007). In addition, colonial and high profile taxa prefer stable substrates such as macrcophytes and stones, where they are less exposed to dislodgement (Passy, 2007).

As we mentioned above, small size generalists, including pioneers belonging to the low profile guild, dominated the temporary streams in Hungary. These mostly r-selected taxa are well-known as indicators of physically disturbed environments (Biggs et al., 1998; Passy, 2007). Their stress-tolerant character means that these taxa are capable of prevailing under extreme and even contrasted water regime conditions: either high current velocity or floods (Stenger-Kovács et al., 2006; Passy, 2007; B-Béres et al., 2014) or drying up of waters (Novais et al., 2014; B-Béres et al., 2019); either high light (Leira et al., 2015; Kókai et al., 2019) or low light conditions (Liess et al., 2009; Stenger-Kovács et al., 2013). In Hungary, the flow conditions of sampling in spring were followed by the drying up of temporary streams in summer. In addition, high light conditions were characteristic in dry periods, while low light availability was present during the flowing phase in spring. These circumstances were ideal for the colonization and fast reproduction of the small, r-strategist taxa.

4.3. Main assembly rules in the Mediterranean and continental region – stress-dominance theory

Independently of the geographical location, drying up in streams creates a very unique but also very constraining and selecting environment for populations. According to the stress-dominance theory

Fig. 7. The distribution of effect size values in perennial and temporary streams in the Mediterranean region (Portugal).

(Weiher and Keddy, 1995), environmental filtering could have a leading role in shaping community structure during dry periods and droughts compared to biotic interactions. It may be especially true in the continental region, where drying up of streams is mostly unpredictable. Here, the main factor leads to drying up, is the unpredictable annual distribution of the precipitation. In the last century, the annual precipitation decreased in the region parallel to an increase in the number of extreme precipitation days (Bartholy and Pongrácz, 2005), while the driest period shifted to the summer period (Bartholy et al., 2014). Additionally, agricultural activities as watering strengthen the negative effects of natural processes. In the Mediterranean region, however, effects of drying up may be less pronounced, since the assemblages are better adapted to these periodically reoccurring events (Acuña et al., 2017). Therefore, when formulating our hypothesis, we also considered the time-for-adaptation theory and we hypothesized a more pronounced environmental filtering effect in the continental than in the Mediterranean region. Furthermore, we also supposed that biotic interactions would play pivotal role in structuring of diatom assemblages in the Mediterranean region. Our results only partially supported this hypothesis: The main assembly rule was limiting similarity in the Hungarian streams resulting in strong biotic interaction within the assemblages and leading to trait divergence (rejecting stress-dominance hypothesis). But dryness influenced differently the diatom assemblages in the two water regime types because their trait composition significantly differed between temporary and perennial streams. In temporary streams, benthic algae had to regularly face dryness. Those taxa which were not able to tolerate these conditions, were filtered out rapidly from communities (e.g. large size and/or stalk or motile), while algae having the suitable traits (e.g. small size and/or pedunculated) were able to survive. Because in the continental region, the continuous monitoring of temporary streams and the collection of their background data have begun very recently, we have no information about important topics such as the community structure before, during and after drying up, the presence or absence of refugia during the drought, the duration of drying up. Therefore, the stability of the selected trait composition is unknown in these streams. The results, however, highlight a strong environmental filtering caused by drying up of streams. In contrast, taxa living in perennial streams were strongly affected by decreasing water supply and probably increasing nutrient supply. Although in this study, we did not examine the changes of physical and chemical parameters, our previous results have shown that droughts induce an increase in the concentration of nutrients in small lowland perennial streams (Kókai et al., 2015). In addition, the agricultural activity is basically intense in the region. The elevated nutrient concentrations are able to strengthen the negative impact of agriculture on communities. Thus, the dominance of colonial taxa, characterizing the perennial streams here, might also refer to elevated nutrient content, since most of those taxa prefer eutrophic conditions (van Dam et al., 1994 updated 2011). In addition, these circumstances also favor motile taxa, which have higher competitive abilities in nutrient-rich environments (Passy, 2007).

In the Mediterranean region, the ES values of most traits differed from 0. This highlights the importance of limiting similarity and environmental filtering in structuring the assemblages. Both temporary and perennial streams were mainly dominated by taxa with traits providing competitive advantage under physically disturbed and/or nutrient poor environments (ES values >0). The ES values of traits that characterized diatom assemblages of perennial streams (pad, high profile) were significantly lower than 0. Such values indicate the higher probability of trait convergence due to the major role of environmental filtering in trait selection. In contrast, ES values of some other traits characteristic of perennial streams (different colonial types) or usually characteristic of temporary streams were significantly higher than 0 indicating the higher importance of biotic interactions in structuring assemblages. Although these results supported only partially the stress dominance hypothesis, they clearly highlighted that the dry period is a very strong and complex environmental factor in the Mediterranean region that probably drives diatom community composition in combination with other factors (e.g. light, low nutrient supply, etc.).

5. Conclusion

Our findings have highlighted the ecoregional differences of drying up-induced filtering mechanisms on benthic diatom communities. While characteristic combinations of traits under both temporary and perennial aquatic regimes could be recognized in the diatom assemblages of the continental region, no traits were specifically associated to the diatom assemblages of temporary streams in the Mediterranean region. Our results, however, also pointed out the robustness of traits indicating perennial streams since almost the same combination of traits has characterized this aquatic regime in both ecoregions. Our results have also demonstrated that environmental filtering and limiting similarity play a pivotal role in structuring benthic diatom assemblages in both regions. Our findings, however, have only partially supported the stress-dominance hypothesis (importance of environmental filtering increases with increasing environmental stress; Grime, 1977; Weiher and Keddy, 1995). In Hungary, limiting similarity was the main force structuring communities denoting and resulting in a strong biotic interaction within assemblages, while both environmental filtering and limiting similarity controlled the trait composition of diatom assemblages in Portugal. These results have highlighted the complexity of drought-induced influences on benthic diatoms regardless of ecoregional differences.

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CRediT authorship contribution statement

Gábor Várbíró: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization.**Gábor Borics:**Writing - original draft, Writing - review & editing, Investigation.**Maria Helena Novais:** Writing - original draft, Writing - review & editing, Investigation. **Maria Manuela Morais:**Conceptualization, Writing - original draft, Writing - review & editing, Investigation.**Frédéric Rimet:**Writing - original draft, Writing - review & editing.**Agnès Bouchez:**Conceptualization, Writing - original draft, Writing - review & editing.**Kálmán Tapolczai:** Writing - original draft, Writing - review & editing.**István Bácsi:**Writing - original draft, Writing - review & editing.**Philippe Usseglio-Polatera:** Writing - original draft, Writing - review & editing.**Viktória B-Béres:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Investigation, Data curation.

Declaration of competing interest

The authors declare that there is no conflict of interest.

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