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**How does water scarcity affect spatial and temporal patterns
of diatom community assemblages in Mediterranean streams?**

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Droughts affect diatom metacommunities in Mediterranean streams: the role of environmental and spatial factors

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3 **Droughts affect diatom metacommunities in Mediterranean streams: the role of**
4 **environmental and spatial factors**
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19 **ABSTRACT**
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22 Mediterranean streams are mostly characterized by intermittent flow regime, with droughts in
23 summer followed by floods in autumn. During droughts, the creation of lentic habitats (i.e.
24 lenticification process) and isolated pools in the riverbeds (i.e. fragmentation process) represents a
25 strong selective pressure on biotic communities. In these highly heterogeneous and disconnected
26 habitat patches, species sorting may be driven by stochastic mechanisms, as well as by
27 environmental filtering. In this work we investigated the selective mechanisms determining the
28 structure and composition of diatom communities during droughts in Mediterranean streams. This
29 work was conducted on five oligotrophic streams in the Ligurian Alps (NW-Italy), similar in terms
30 of physical-chemical parameters. Data were collected at least monthly from April to October 2014
31 in: 1) lentic sites, where the water flow became slower but was permanent during the hot season; 2)
32 fragmented sites, where the riverbed stretch dried out creating isolated pools. For each sampling
33 site, we collected six benthic diatom samples from different microhabitats. We examined which
34 factors, i.e. spatial or environmental, better explained the temporal and spatial variation of diatom
35 communities. We then calculated the turnover and nestedness components of dissimilarity by
36 comparing samples collected during moderate flow with samples obtained during the hot season.
37 We further investigated if the idiosyncrasy of diatom species could be explained by the ecological
38 niche width of species and/or by species traits. Our results showed a contribution of both
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3 environmental and spatial factors in determining species composition during drought, while the
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5 main selective mechanism resulted to be species replacement. The number of idiosyncratic species,
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7 i.e. those departing from the nested pattern, resulted to be more tolerant than nested species, while
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9 no differences were encountered in terms of species traits. According to our results, species
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11 replacement due to niche assembly rules seemed to be the dominating process in diatom benthic
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13 communities during drought. These results indicate that future climate change may drive the loss of
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15 specialist species, being replaced by more tolerant taxa. A better evaluation of species autecology
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17 could improve the application of Water Framework Directive (2000/60 EC) classification to
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19 Mediterranean streams.
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24 **Key-words:** intermittent streams, partial RDA, dissimilarity, nestedness, ecological niche
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27 **Running head:** drought effects on diatom metacommunities
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INTRODUCTION

The Mediterranean climate is characterized by seasonality and variability of rainfalls (Gasith & Resh, 1999; Sabater *et al.*, 2006) which often lead to river flow intermittency, i.e. lack of hydrological connectivity at multiple spatial scales (Larned *et al.*, 2010). Intermittency in Mediterranean rivers is highly predictable and can be summarized in three phases (Datry, Bonada & Heino, 2016). Firstly, flow cessation leads to the shift from lotic to lentic conditions, i.e. lenticification process. Afterwards, the total drying of some stretches causes fragmentation of the stream channel. The deepest pools become isolated habitat patches (Datry *et al.*, 2016; Sabater *et al.*, 2016) which differ from the main channel in terms of physical-chemical parameters: the temperature rises, the oxygen content lowers and nutrients become more concentrated (Lake, 2003). In a second moment, remnant pools progressively dry up, thus converting aquatic habitats into terrestrial ones (Datry *et al.*, 2016). The third and last phase is represented by the rewetting, that occurs suddenly and unpredictably, often as disruptive floods that reconnect all the isolated pools and change the streambed morphology (Lake, 2003).

Due to this hydrological cycle, Mediterranean intermittent streams are characterized by a marked spatial and temporal heterogeneity (Lake, 2000), thus representing meta-systems, i.e. a network of discrete populations, communities and ecosystems that are intermittently connected by gene, material and energy flows and individual dispersal (Larned *et al.*, 2010). As a consequence, biotic communities in Mediterranean streams represent metacommunities, defined as networks of local communities in which inter- and intra-community dispersal and interactions affect species persistence (Hanski, 1994; 1998). Since flow intermittency creates unique dynamics in streams, metacommunities in intermittent streams may show typical temporal and spatial patterns (Taylor, 1997; McAbendroth *et al.*, 2005; Bonada *et al.*, 2006). This is true especially during the first phase of flow cessation, when the lenticification and fragmentation processes convert connected communities into isolated local ones.

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3 The spatial and temporal patterns of metacommunities in Mediterranean streams may be explained
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5 by two coexisting paradigms, i.e. the island paradigm and the trait-environment paradigm (Weiher
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7 & Keddy, 2001). The former states that assembly rules are governed by dispersal-driven
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9 mechanisms, so the main focus is represented by stochastic processes like immigration and
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11 extinction (MacArthur & Wilson, 1967). The latter identifies niche assembly rules as the major
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13 force in determining community assemblages, emphasising species autecology and how
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15 environment filters species traits (Diamond, 1975). Within this context, Datry *et al.* (2016)
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17 underlined how lentication and fragmentation would cause a dominance of environmental filtering
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19 processes, including adaptation to lentic conditions, enhancing biotic interactions within contracting
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21 pools and stronger predator pressure. Conversely, the rewetting phase would be dominated by
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23 dispersal processes which allow organisms to colonize rewetted habitats. However, as noticed by
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25 Soinenen (2008), the two paradigms may not be mutually exclusive, since some traits may favour
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27 the ability of colonize new habitats or the autecology of a particular species may be related to the
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29 spatial structure it exhibits (McAbendroth *et al.*, 2005).
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34 As a result, great differences between local communities arise, especially in a series of disconnected
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36 habitat patches, thus increasing beta diversity in the metacommunity. Beta-diversity is a measure of
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38 the extent of similarity between community assemblage composition in different sites (Koleff,
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40 Gaston & Lennon, 2003) and it can generally be described as the combination of two dissimilarity
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42 components, namely turnover and nestedness (Harrison, Ross & Lowton, 1992; Baselga, 2010;
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44 Baselga, 2012). Turnover is a measure of species replacement, that occurs when species present in
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46 one site are absent in another one and they are replaced by other, while nestedness measures the
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48 degree to which communities of species-poor sites are a subset of species-rich sites, i.e. species loss
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50 or gain (Ulrich & Gotelli 2007; Ulrich, Almeida-Neto & Gotelli, 2009).
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54 Literature data show contrasting results when trying to define which mechanism is actually driving
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56 the structure of benthic biofilm metacommunities in temporary streams. In some cases, they
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58 indicate biological communities of temporary reaches as a subset of communities inhabiting
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3 permanent reaches, containing ubiquitous and highly mobile species (Datry *et al.*, 2014), thus
4 suggesting species loss. Conversely, in other works, data show how lotic communities are gradually
5 replaced by lentic and subaerial species (Stewart *et al.*, 2010; Tornés & Rhuï, 2013; Falasco, Piano
6 & Bona, 2016a). However, only presence data are normally considered for underpinning
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The aims of our work are to scrutinize on i) which paradigm better explains patterns of benthic diatom communities in Mediterranean streams (i.e. trait-environment or island paradigm) and ii) which mechanism drives their variation during droughts i.e. species loss or species replacement. In order to achieve these goals, we used diatoms as a model group considering not only presence but also abundance data. In a second moment we also evaluated iii) if environmental filtering processes mainly selected species based on their autecology or biological traits.

MATERIALS AND METHODS

Data collection

This study was conducted in five streams belonging to the Ligurian Alps hydroecoregion (HER 122; N-W Italy), comparable in terms of geology (mostly calcareous), climate and altitude, substratum size (mainly cobbles and pebbles) and water quality. In order to reduce the environmental variability among sites and focus only on physical disturbance induced by flow instability, we selected stretches with low nutrient inputs. To do this, we checked chemical data collected by the Environmental Protection Agency of Liguria (ARPAL) during the last ordinary surveys. All streams are permanent in the upper part of their course, but become temporary next to the mouth in the Ligurian Sea (Fig. 1). We performed five sampling campaigns from April to September 2014. The first was performed in spring (April: 17/04/2014), with moderate flow, while the other four campaigns were performed during the drought season, every month from the end of June to the end of September (June: 30/06/2014; July: 22/07/2014; August: 28/08/2014; September: 24/09/2014). Droughts in the selected rivers were mainly caused by rainfall scarcity and water uptakes (for further details see

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3 Falasco, Piano & Bona, 2016b). Starting from these considerations and from field observations
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5 performed during summer, we considered the sampling date as a proxy of the temporal hydrological
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7 disturbance, since we observed a progressive and gradual lenticification, fragmentation and isolation
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9 of stream stretches. Therefore, the sampling session of April represented our control session. We
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11 selected 2 sampling sections for each stream, representing two levels of hydrological disturbance
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13 (Fig. 1): i) an upstream section, where we observed only a progressive flow reduction during
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15 summer (lentic section, LS); ii) a downstream section, exposed to high hydrological fragmentation,
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17 with the creation of isolated pools during summer (fragmented section, FS).
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21 In each section, besides a standard sampling transect, we also identified five sampling plots
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23 (microhabitats, hereinafter MHs), defined as a circular area of 40 cm of diameter, representing the
24
25 highest heterogeneity in terms of flow velocity, water depth and isolation from the main river
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27 course. MHs were selected in order to detect differences in the response of diatom community to
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29 the spatial heterogeneity typical of Mediterranean rivers (Tornés & Sabater, 2010). Among them,
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31 isolated pools were considered in the data analyses as proxies of the loss of hydrological
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33 connectivity.
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37 We measured physical-chemical parameters in both transects and isolated MHs. In particular, we
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39 detected water dissolved oxygen (DO), oxygen saturation (%O₂), pH, temperature and conductivity
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41 by means of a multiparametric probe (Hydrolab mod. Quanta). Moreover, in each transect and MH
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43 we measured water depth and flow velocity with a current meter (Hydro-bios Kiel). The
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45 environmental matrix was finally composed of two types of variables: i) *physical-chemical*
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47 *variables*: DO, %O₂, pH, temperature and conductivity; and ii) *hydromorphological variables*:
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49 sampling date, sampling section (LS or FS), degree of the MH connection to the main channel
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51 (connected or isolated), water depth and flow velocity.
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55 Diatom samples in transects were collected in accordance with the standard procedure defined by
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57 the European Committee for Standardization (UNI EN 13946, 2003). We chose at least 5 cobbles
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59 from the main flow and we collected periphyton by scraping their upper surface by means of a
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3 toothbrush. Considering the MHs, we chose to sample only one single cobble as representative of
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5 each 40 cm diameter circular area. From each section, diatom samples from transect and MHs were
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7 kept separated and preserved in ethanol. In laboratory, samples were treated following the
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9 standardized method by cleaning them with hydrogen peroxide (30%) and HCl. Slides for the
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11 observation at the light microscope were mounted with Naphrax. We identified at least 400 valves
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13 in each sample. Diatom identification was based on several diatom floras and monographies, as well
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15 as recent taxonomic papers (Krammer & Lange-Bertalot 1986-1991 a, b; Krammer 1997 a, b, 2002,
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17 2003; Reichardt, 1999; Lange-Bertalot, 2001; Werum & Lange-Bertalot, 2004; Blanco *et al.*, 2010;
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19 Hofmann, Werum & Lange-Bertalot, 2011; Bey & Ector 2013; Falasco, Piano & Bona, 2013; Ector
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21 *et al.*, 2015).

22 23 24 25 26 27 **Statistical analyses**

28 29 Testing paradigms: island or environmental filter

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31 In order to test which paradigm, i.e. trait-environment and island paradigm, better explains diatom
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33 community patterns, we applied a Partial RDA to both abundance and presence data following the
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35 approach suggested in Peres-Neto *et al.* (2006) and De Bie *et al.* (2012).

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37 First, we constructed two biotic matrices both composed of 300 samples, one with the relative
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39 abundance of each recorded taxon in each sample (hereinafter abundance matrix), and the second
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41 with presence/absence data (hereinafter presence matrix).

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43 We then built up an environmental matrix [E] based on a parsimonious combination of
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45 environmental variables and a spatial matrix [S] with both the coordinates of the sampling sites (LS
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47 and FS for each river) and the spatial variables extracted by MEM analysis (Moran's Eigenvector
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49 Maps, see Dray, Legendre & Peres-Neto, 2006). The MEM analysis produces a set of orthogonal
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51 spatial variables that are derived from geographical coordinates of the study sites and that can be
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53 used as explanatory variables to model spatial relationships in community data. Given that
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55 intermittent streams lack hydrological connectivity, we here did not consider a directional spatial
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3 process for modelling a scenario whereby interactions among sampling locations would occur
4 through hydrological connections (AEM, Asymmetric Eigenvector Maps, Blanchet *et al.*, 2011).
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7 Conversely, we evaluated the scenario that spatial interactions among communities are taking place
8 through dispersal overland. We separately tested both the [E] and [S] matrices against the
9 abundance and the presence matrix and evaluated the jointed fraction of explained variance as well
10 as the variance explained by each matrix separately. With variation partitioning, we decomposed
11 total community variation into a purely spatial component (S|E) and a purely environmental
12 component (E|S). The magnitude of a significant environmental component (E|S) measures the
13 degree to which community variation is uniquely structured by the environment, i.e. species sorting
14 (Cottenie, 2005). The magnitude of a significant spatial component (S|E) is indicative for the
15 amount of spatial variation caused by dispersal limitation or stochastic events (Legendre &
16 Legendre, 1998). We tested the significance of both components by means of a Monte Carlo test
17 with 1000 permutations. We corrected estimates of explained variation for the number of predictor
18 variables and sampling sites (R^2 adjusted) following the procedure proposed by Peres-Neto *et al.*
19 (2006).

20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 Testing mechanisms: turnover or nestedness

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38 In order to test which dissimilarity component, i.e. turnover vs nestedness, would become dominant
39 with the progression of drought, pair-wise dissimilarities were calculated using the approach
40 suggested by Baselga (2013) on the abundance matrix. This framework consists of decomposing the
41 Bray–Curtis dissimilarity index (d_{BC}) into two additive components accounting for the balanced
42 variation in abundances (d_{BC-bal}) and abundance gradients (d_{BC-gra}). The balanced variation in
43 abundances (d_{BC-bal}) describes the variation in species density with the overall species density
44 remaining constant and corresponds to true species turnover (some individuals are substituted by
45 individuals of different species from site to site). The measure for abundance gradients (d_{BC-gra})
46 describes the decrease (or increase) in species density from one site to the other. This is equivalent
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3 to species nestedness, as some individuals may be lost from one site to the other without any
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5 substitution.

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7 For each of the three dissimilarity measures (d_{BC} , d_{BC-bal} and d_{BC-gra}) we calculated the pair-wise
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9 dissimilarities of all samples against the transect samples collected in April, which represent the
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11 control sampling occasion. In this way, we obtained a measure of the distance of each sample from
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13 the control communities in terms of d_{BC} , d_{BC-bal} and d_{BC-gra} .

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15 To analyse community dissimilarities on the presence matrix, we measured the degree of nestedness
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17 with the software ANINHADO (Guimaraes & Guimaraes, 2006). We computed the classical matrix
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19 temperature (T ; Atmar & Patterson, 1993), which can be interpreted as a thermodynamic measure of
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21 disorder, ranging from 0° in ordered systems (totally nested systems) to 100° in disordered systems
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23 (totally not nested systems). We considered the temperature value calculated for each sample
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25 (T_{sample}) as a measure of their nestedness and we extracted the T value for each species
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27 ($T_{species}$). We considered as idiosyncratic those species with a T value higher than the T value of
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29 the whole matrix. For each sample we calculated the percentage of idiosyncratic species
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31 ($\%idiosyncratic$), as an indirect measure of sample nestedness.

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33 In order to test the response of dissimilarity and nestedness measures against environmental
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35 variables, we performed Generalized Linear Mixed Models (GLMMs, in accordance with Zuur *et*
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37 *al.*, 2009) in R environment (R Core Team, 2015).

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39 Given the high correlation between environmental variables, we applied a Principal Component
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41 Analysis (PCA) in order to reduce the number of variables and synthetize them into orthogonal
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43 axes. Given that the sampling date (proxy of temporal hydrological disturbance), the isolation from
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45 the main river course and the sampling section (proxies of spatial hydrological disturbance) were
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47 categorical variables, we converted them into numerical variables to include them in the PCA.

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49 Scores were assigned in order to have increasing value with increasing hydrological disturbance.

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51 We tested the retained PCA axes (i.e. those explaining the highest percentage of variance) against
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53 our dependent dissimilarity variables — d_{BC} , d_{BC-bal} and d_{BC-gra} — via GLMMs. Given the spatial
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3 dependence of the data (two sections in each river), we applied the mixed procedure to include a
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5 grouping variable (site) nested in a second grouping variable (river) as random factors in order to
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7 account for the variation they introduced in our samples, rather than to test for their direct effect on
8
9 the dependent variables. The same procedure was repeated for the nestedness measures, i.e.
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11 *T_samples* and *%idiosyncratic*. GLMMs were fitted via the *lme4* R package (Bates *et al.*, 2014,
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13 version 1.0-6).
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15 16 Environmental filtering: autecology or species traits

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18 In order to test the third hypothesis, i.e. whether the filtering process would apply more to species
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20 autecology than to species traits, we verified if the *T_species* was related to species niche width or
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22 life-history traits.
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25 We firstly calculated the niche width of each species based on our data by means of the Outlying
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27 Mean Index (OMI) with the *ade4* R package (Dray & Dufour, 2007). This is a two-table ordination
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29 technique that positions species in a multidimensional space as a function of environmental
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31 parameters (Doledec *et al.*, 2000). The analysis returns the tolerance parameter, which measures the
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33 niche width, i.e. the amplitude in the distribution of each species along the sampled environmental
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35 gradients. Low values mean that a species is distributed across a limited range of conditions
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37 (specialist species), while high values imply that a species is distributed across habitats with widely
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39 varying environmental conditions (generalist species). The tolerance parameter (*tol*) was selected as
40
41 a proxy of species niche breadth. The OMI analysis was performed via the function “*niche*” in the
42
43 package *ade4* (Dray & Dufour, 2007) for the R software (R Core Team, 2015).
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49 Considering the species traits, we followed the procedure suggested by Elias *et al.* (2015) and we
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51 focused our attention on two traits, namely life-forms and biovolume. Within the life-form trait,
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53 four categories were considered: mobile, colonial, tube-forming and stalked. The mobile taxa have
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55 the ability of selecting the most suitable habitat. The colonial taxa are in constant contact within
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57 each other, thus being capable of surviving with less moisture. The tube-forming taxa are colonial
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59 taxa living in a mucilaginous protective structure within which they are able to move freely. The
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3 formation of this structure provides protection from desiccation, osmotic stress and intense light
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5 radiation. These three traits are thus expected to favour species survival during drought. Conversely,
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7 the stalked taxa are fixed to the substratum through a mucilage stalk and are potentially exposed to
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9 higher risk of desiccation. Considering biovolume, we expected small species to be favoured during
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11 drought given their higher capacity to live with less moisture, while large species have higher cell
12
13 surface exposed which reduces their capacity to live with less moisture. In addition to these two
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15 traits, we also considered aerophily since we expected more aerophilous taxa to be favoured during
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17 water scarcity compared to taxa strictly dependent from water.
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21 Classification of species based on these traits was derived from literature data. In particular, the
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23 classification based on life-forms and the attribution of the biovolume values were performed in
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25 accordance with Rimet & Bouchez (2012), while the classification of species based on aerophily
26
27 was performed in accordance with van Dam, Mertens & Sinkeldam (1994). Given the high
28
29 variability of biovolume values, we applied a log-transformation in order to achieve a
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31 homogenization of its distribution.
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34 We then tested the *T_species* against their niche breadth, life-form, biovolume and aerophily by
35
36 means of a linear regression, after log-transformation of *T* for achieving a normal error distribution.
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38 Data referring to life-history traits and temperature values for each species are reported in table S1.
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43 RESULTS

44 Testing paradigms: island or environmental filter

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46 The results of Partial RDA showed different results for the abundance and the presence matrices.
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49 Considering the abundance matrix, the Partial RDA revealed that variation among communities
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51 could be significantly explained by the environmental component, while the spatial component gave
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53 a much lower contribute, as demonstrated by the lower value of adjusted R^2 (Tab. 1).
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56 Environmental filtering mechanisms seem then to dominate the community structure in terms of
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58 species abundance. Opposite results were obtained for the presence matrix, for which the highest
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percentage of variance was explained by the spatial component, even if the environmental component also contributed in explaining species distribution (Tab. 1). Stochastic mechanisms then showed to play a major role when considering the species composition of communities.

Testing mechanisms: turnover or nestedness

The first three axes of the PCA explained the 72% of total variance and were then considered for subsequent analysis. Axis 1 and 3 explained 36% and 15% of variance respectively and were both positively correlated with the hydrological disturbance (Table 2). In particular, axis 1 was negatively correlated with water depth and positively correlated with the sampling section. Axis 3 was negatively correlated with dissolved oxygen and was positively correlated with the sampling section and with the isolation. Conversely, axis 2 explained 21% of variance and was negatively correlated with the hydrological disturbance (Table 2), since it was negatively correlated with conductivity, temperature, sampling section, sampling date and isolation, while it was positively correlated with dissolved oxygen.

Considering the abundance matrix, the observed Bray-Curtis dissimilarities showed, on average, a dominant turnover pattern in the sampled communities ($d_{BC} = 0.69 \pm 0.18$; $d_{BC-bal} = 0.67 \pm 0.19$; $d_{BC-gra} = 0.02 \pm 0.02$). Results of statistical models showed a significant positive relationship with axis 3 for the total Bray Curtis dissimilarity d_{BC} (Tab. 3 and Fig. 2a) and the turnover component d_{BC-bal} (Tab. 3 and Fig. 2b), while the nestedness component d_{BC-gra} was negatively correlated (Tab. 3 and Fig. 2c). These results underlie how the progression of water scarcity causes a turnover of the diatom community.

Considering the temperature metrics, results obtained from statistical models showed a significant effect of the hydrological disturbance. In particular, we observed a significant positive relationship between $T_samples$ and axis 1 and 3 (Tab. 3 and Figs. 2d and 2e), while $\%idiosyncratic$ was significantly affected by axis 2 (Tab. 3 and Fig. 2f). These results confirm what we obtained with the dissimilarity measures, showing that the nestedness of the community decreases with the progression of hydrological disturbance.

Environmental filtering: autecology or species traits

According to the results of the regression analysis (Tab. 4), the Temperature value of each species ($T_{species}$) is positively correlated with the niche width. Conversely, we could not find any significant effects of species traits. According to our results, the tolerance to drought seems to be linked to the ecological niche more than to species traits.

DISCUSSION

Mediterranean rivers are subjected to periodical intermittency of flow regime with highly predictable cycles of drought and rewetting (Bonada & Resh, 2013). The extent to which riverine communities differ in terms of species composition during an increasing drought may be linked both to the decrease of the hydrological connectivity, which restricts dispersal and mixing of freshwater organisms (Larned *et al.*, 2010), as well as to environmental harsh conditions which filter out maladapted species (Gutierrez-Cánovas *et al.*, 2015). We here demonstrated that environmental and spatial components both contribute in determining the composition of diatom communities. This is in accordance with recent research, which suggests that assemblages of microorganisms, and in particular of lotic diatoms, are both spatially structured and environmentally controlled (Heino *et al.*, 2010; Wetzel *et al.*, 2012; Fontaneto & Hortal, 2013; Göthe *et al.*, 2013; Heino *et al.*, 2015).

More in detail, the contribution of the environmental and spatial components is different when considering presence or abundance data. While the species composition is mainly explained by spatial factors, the environmental filter plays a major role in determining the local success of species. The role of environmental and spatial components on diatom diversity is often controversial. One view of microbial distributions, including diatoms, is that they have unlimited access to all sites within a region, particularly over a long time period, but they are selected by the environment (Ubiquity Hypothesis; Finlay, 2002; Fenchel & Finlay, 2004). In several cases it has been demonstrated that small passive dispersers, like diatoms, are more affected by environmental

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3 than spatial components (De Bie *et al.*, 2012; Padial *et al.*, 2014). However, if diatom species were
4 dispersed everywhere, they should be found at all sites with similar environmental conditions,
5 which is often not the case, leading to a large portion of variation explained by spatial factors
6 (Potapova & Charles, 2002; Vyverman *et al.*, 2007; Smucker & Vis, 2011; Sakeva *et al.*, 2016).
7 According to our results, the island paradigm better reflects distributional patterns of species
8 generated by dispersal limitation as a consequence of isolated habitat creation in Mediterranean
9 streams. Then, once that species have reached a patch, their relative ecological success is better
10 explained by the trait-environment paradigm.
11

12 Secondly, we demonstrated that the variation in diatom community composition along the drought
13 was mainly explained by the turnover component of dissimilarity, while the nestedness component
14 played a much minor role compared to the turnover component. Despite some contrasting results
15 found in literature (Datry *et al.*, 2014), this is in agreement with Rolls, Heino & Chessman (2016)
16 who showed a dominance of turnover processes in the dissimilarity partitioning on
17 macroinvertebrates and fish subjected to intermittent flow. Beta-diversity within a flow regime
18 should be low during non-drought phases for taxa that are strong dispersers because environmental
19 conditions are not harsh and organisms experience favourable high hydrological connectivity
20 between sites (Thomaz *et al.*, 2007; Larned *et al.*, 2010). Conversely, the turnover component of
21 dissimilarity increases with increasing intermittency (McAbendroth *et al.*, 2005; Soininen, 2008).
22 This pattern is furtherly strengthened by the higher number of idiosyncratic species in fragmented
23 sites than in lentic sites. Similar results were obtained by Tornés & Ruhí (2013), who observed a
24 higher percentage of idiosyncratic species in temporary streams compared to permanent ones in a
25 Mediterranean basin. Since the turnover component becomes dominant with the progression of
26 drought, we can hypothesize that resistance rather than resilience is the principal mechanism of
27 survival in these highly disturbed systems (Ledger *et al.*, 2008; Datry *et al.*, 2014; Acuña *et al.*,
28 2015).
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3 In Mediterranean regions, stream drying is a natural part of the hydrological cycle, thus stream biota
4 possess attributes adapted to tolerate or escape dry conditions (Bonada & Resh, 2013). These
5 attributes can include species traits, i.e. characterizing organisms in terms of their multiple
6 biological attributes (physiological, morphological, biochemical, structural, phenological,
7 behavioral) (Violle *et al.*, 2007), as well as aspects of their realized niche, such as environment
8 experienced over the geographic range or position in the trophic web (Bowler *et al.*, 2015). For
9 diatoms, our results demonstrated how the niche width of species better explains their idiosyncrasy
10 than biological traits, since idiosyncratic species are more generalists than the nested ones (Tornés
11 & Ruhi, 2013). While for macroinvertebrates drought selects adapted traits (Robson, Chester &
12 Austin, 2011), diatom communities seem more shaped based on their ecological tolerance (Boix *et*
13 *al.*, 2010). The main reason could be that they are directly influenced by nutrient availability and
14 water quality (Tornés *et al.*, 2007), which are in turn altered by hydrological intermittency (Gasith
15 & Resh, 1999; Lake, 2003).

34 CONCLUSIONS

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36 Overall, our results emphasize how the dispersal limitation may play a role in determining diatom
37 species composition, but then species success is driven by an environmental filtering processes
38 acting on species autecology (Tornés & Ruhi, 2013; Viktória *et al.*, 2014). Moreover, our results
39 suggest that coupling evaluations of diversity patterns, i.e. dissimilarity and functional responses,
40 may help in disentangling the selective mechanisms exerted by droughts in Mediterranean streams
41 on benthic diatoms. A better understanding of these mechanisms may give a comprehensive view of
42 the potential effects on biotic communities of flow intermittency, which is expected to increase in a
43 future climate change scenario. Given that biomonitoring of water quality in Mediterranean streams
44 is still challenging (Dallas, 2013), a better definition of the autecology of diatom species in
45 Mediterranean streams could represent a key aspect for a proper quality classification of this stream
46 typology.
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Supplementary information

Table S1: List of diatom species identified with their relative values of niche width and life-history traits.

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Table 1. Results of the pure environmental model (E|S) and the pure spatial model (S|E) obtained from the partial RDA applied to the abundance (a) and the presence/absence (b) matrices (DF = Degrees of Freedom, Adj-R² = adjusted R²).

(a) ABUNDANCE					
MATRIX	DF	Adj-R²	Variance	F	P
Environmental model (E S)	8	0.1010	0.0668	4.459	0.001
Spatial model (S E)	11	0.0441	0.0435	2.112	0.001
Residual	220	0.8330	0.4120		
(b) PRESENCE					
MATRIX	DF	Adj-R²	Variance	F	P
Environmental model (E S)	9	0.0776	0.0658	3.825	0.001
Spatial model (S E)	13	0.1497	0.1202	4.842	0.001
Residual	217	0.6895	0.4145		

Table 2. Loadings of each environmental variable to PCA components.

	Axis 1	Axis 2	Axis 3
Flow velocity			
Water depth	-0.982		
Conductivity		-0.705	-0.649
O₂ Saturation		0.425	-0.215
Dissolved Oxygen		0.296	-0.159
Temperature		-0.125	
pH			
Sampling section	0.176	-0.133	
Sampling date		-0.401	0.609
Isolation		-0.195	0.137

Table 3. Results of the test of the response of d_{BC} (total Bray-Curtis dissimilarity), d_{BC-bal} (balanced variation in species abundance), d_{BC-gra} (abundance gradient), $T_samples$ (temperature value for each sample) and $\%idiosyncratic$ (percentage of idiosyncratic species in each sample) towards the three selected PCA axes. Significant results are highlighted in bold.

Variable	PCA axis	Estimate	SE	t	P
<i>dBC-bray</i>	axis 1	0.011	0.015	0.723	0.47
	axis 2	-0.033	0.032	-1.032	0.303
	axis 3	0.261	0.039	6.693	< 0.001
<i>dBC-bal</i>	axis 1	0.010	0.015	0.638	0.525
	axis 2	-0.042	0.033	-1.280	0.202
	axis 3	0.261	0.040	6.562	< 0.001
<i>dBC-gra</i>	axis 1	0.001	0.001	0.538	0.591
	axis 2	0.002	0.002	0.175	0.241
	axis 3	-0.007	0.002	-3.102	0.002
<i>T_samples</i>	axis 1	0.173	0.066	2.605	0.010
	axis 2	0.174	0.175	0.990	0.323
	axis 3	2.251	0.216	10.40	< 0.001
<i>% idiosyncratic</i>	axis 1	-0.002	0.007	-0.376	0.707
	axis 2	-0.028	0.012	-2.337	0.020
	axis 3	-0.022	0.015	-1.506	0.134

Table 4. Results of the test for the response in the species temperature ($T_{species}$) towards niche width (Tol), species mobility (mobile), production of stalks (stalk), creation of colonies (colonial), creation of tube-forming colonies (tube), biovolume classes (biovolume) and degree of aerophily (aerophily) across the range of the species. Significant values are highlighted in bold.

Category	Variable	Estimate	SE	t	P
Autecology	Tol	0.2240	0.0977	2.292	0.023
	Mobile	0.3030	0.1986	1.525	0.129
	Stalk	0.2255	0.2127	1.060	0.291
Species traits	Colonial	0.0188	0.2014	0.093	0.926
	Tube	-0.0242	0.3818	-0.063	0.950
	Biovolume	-0.0511	0.0607	-0.842	0.401
	Aerophily	-0.0937	0.0574	-1.631	0.105

Review

Figure captions

Figure 1. Map of the five study streams and relative sampling sections (triangles = lentic sections, LSs; circles = fragmented sections, FSs).

Figure 2. Predicted values and confidence intervals (95%) for dependent variables in relation to PCA axes resulted significant from statistical models: (a) d_{BC} (total Bray-Curtis dissimilarity) vs PCA axis 3; (b) d_{BC-bal} (balanced variation in species abundance) vs PCA axis 3; (c) d_{BC-gra} (abundance gradient) vs PCA axis 3; (d) $T_samples$ vs PCA axis 1; (e) $T_samples$ vs PCA axis 3; (f) $\%idiosyncratic$ in relation to PCA axis 2.

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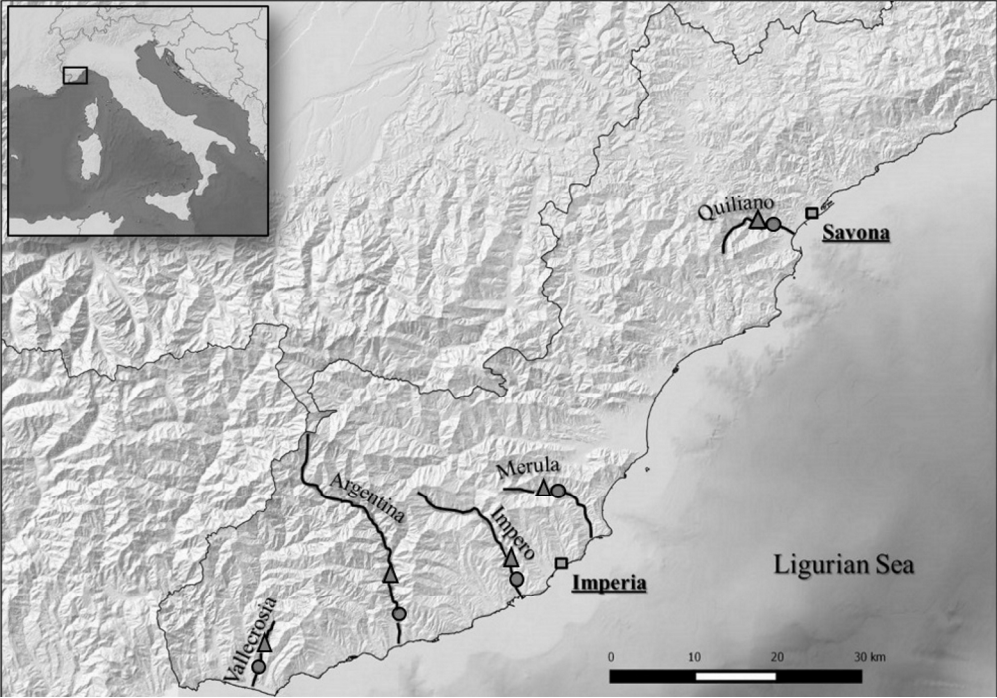


Figure 1. Map of the five study streams and relative sampling sections (triangles = lentic sections, LSs; circles = fragmented sections, FSs).

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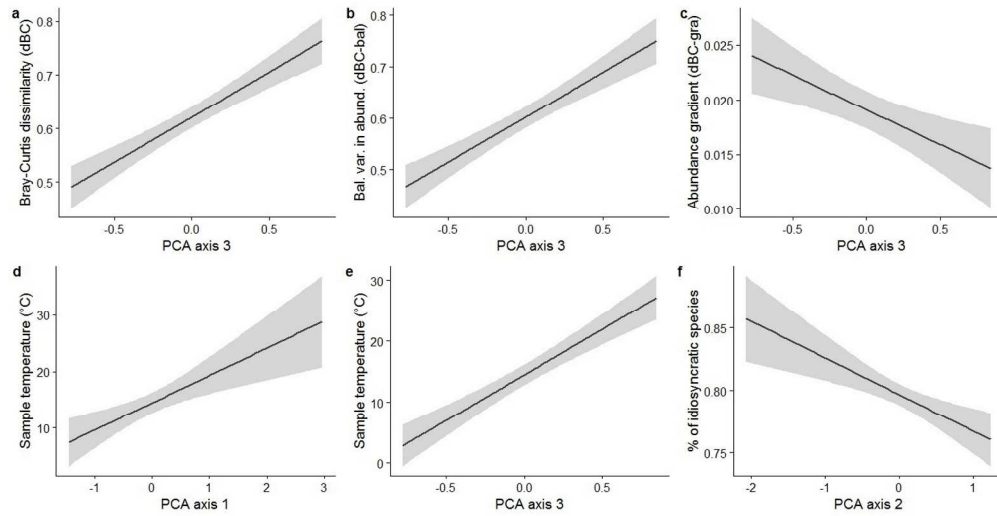


Figure 2. Predicted values and confidence intervals (95%) for dependent variables in relation to PCA axes resulted significant from statistical models: (a) dBC (total Bray-Curtis dissimilarity) vs PCA axis 3; (b) dBC-bal (balanced variation in species abundance) vs PCA axis 3; (c) dBC-gra (abundance gradient) vs PCA axis 3; (d) T_samples vs PCA axis 1; (e) T_samples vs PCA axis 3; (f) %idiosyncratic in relation to PCA axis 2.

Or Review

Table S1. List of diatom species identified with their relative values of tolerance (tol), life-forms (motile: 0 = not motile species, 1 = motile species; stalk: 0 = not stalked species, 1 = stalked species; colonial: 0 = non-colonial species, 1 = colonial species; tube: 0 = not tube-forming species, 1 = tube-forming species), aerophily (1 = never, or only very rarely, occurring outside water bodies, 2 = mainly occurring in water bodies, sometimes in wet places, 3 = mainly occurring in water bodies, also rather regularly on wet and moist places, 4 = mainly occurring on wet and moist, or temporarily dry places, 5 = nearly exclusively occurring outside water bodies), biovolume and nestedness temperature ($T_{species}$)

Species	tol	motile	stalk	colonial	tube	aerophily	biovolume	$T_{species}$
<i>Achnantheidium affine</i> (Grun) Czarnecki	9.9	0	0	0	0	0	163	15.31
<i>Achnantheidium lineare</i> W.Smith	9.2	0	0	0	0	0	46	33.91
<i>Achnantheidium atomoides</i> Monnier, Lange-Bertalot & Ector	6.5	0	0	0	0	0	34	12.1
<i>Achnantheidium catenatum</i> (Bily & Marvan) Lange-Bertalot	9.6	0	0	1	0	0	62	4.36
<i>Achnantheidium eutrophilum</i> (Lange-Bertalot)Lange-Bertalot	15.7	0	0	0	0	3	72	51.35
<i>Achnantheidium gracillimum</i> (Meister)Lange-Bertalot	19.1	0	0	0	0	0	97	13.05
<i>Achnantheidium jackii</i> Rabenhorst	4.6	0	0	0	0	0	72	10.3
<i>Achnantheidium latecephalum</i> Kobayasi	0.4	0	0	0	0	0	96	8.4
<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki	19.8	0	0	0	0	3	76	0
<i>Achnantheidium delmontii</i> Peres, Le Cohu et Barthes	6.4	0	0	0	0	0	NA	30.32
<i>Adlafia minuscula</i> (Grunow) Lange-Bertalot	9.7	0	0	0	0	4	64	14.98
<i>Achnantheidium minutissimum</i> (Kütz.) Czarnecki abnormal form	24.7	0	0	0	0	3	76	36.52
<i>Achnantheidium pyrenaicum</i> (Hustedt) Kobayasi abnormal form	10.2	0	0	0	0	0	106	43.45
<i>Achnantheidium pyrenaicum</i> (Hustedt) Kobayasi	14.3	0	0	0	0	0	106	7.61
<i>Achnantheidium straubianum</i> (Lange-Bertalot)Lange-Bertalot	11.3	0	0	0	0	3	36	25.84
<i>Achnantheidium subatomus</i> (Hustedt) Lange-Bertalot	8.9	0	0	0	0	0	61	3.71
<i>Achnantheidium subatomus</i> (Hustedt) Lange-Bertalot abnormal form	7.2	0	0	0	0	0	61	3.18
<i>Achnantheidium thienemannii</i> (Hustedt) Lange-Bertalot	4.9	0	0	0	0	0	87	7.52
<i>Amphora ovalis</i> (Kützing) Kützing var. <i>ovalis</i>	16.1	0	0	0	0	1	52858	6.72

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<i>Diadismis confervacea</i> Kützing var. <i>confervacea</i>	5.6	0	0	1	0	3	416	4.97
<i>Diadismis contenta</i> (Grunow ex V. Heurck) Mann	1.1	0	0	1	0	4	129	1.74
<i>Diatoma ehrenbergii</i> Kützing	13.6	0	0	1	0	1	2064	43.72
<i>Diatoma ehrenbergii</i> Kützing abnormal form	3.7	0	0	1	0	1	2064	7.71
<i>Didymosphenia geminata</i> (Lyng.)Schmidt morphotyp <i>geminata</i> Metzelt	6.8	0	1	1	0	0	10200	14.83
<i>Denticula kuetzingii</i> Grunow var. <i>kuetzingii</i>	12.9	1	0	0	0	3	337	54.63
<i>Diatoma moniliformis</i> Kützing	14	0	0	1	0	0	303	59.76
<i>Diatoma moniliformis</i> Kützing abnormal form	2.5	0	0	1	0	0	303	2.48
<i>Diploneis parma</i> Cleve sensu Krammer & Lange-Bertalot	0.1	0	0	0	0	0	1442	0.72
<i>Diploneis separanda</i> Lange-Bertalot	1	0	0	0	0	0	274	5.71
<i>Denticula tenuis</i> Kützing	5.7	1	0	0	0	3	337	50.14
<i>Diatoma vulgare</i> Bory	17.5	0	0	1	0	1	3033	31.71
<i>Diatoma vulgare</i> Bory abnormal form	16.2	0	0	1	0	1	3033	6.13
<i>Encyonema caespitosum</i> Kützing var. <i>caespitosum</i>	9.3	0	0	1	1	0	751	32.75
<i>Encyonopsis cesatii</i> (Rabenhorst) Krammer	28.1	0	0	0	0	3	679	15.53
<i>Encyonopsis microcephala</i> (Grunow) Krammer abnormal form	0.1	0	0	0	0	3	60	6.34
<i>Encyonopsis minuta</i> Krammer & Reichardt	18	0	0	0	0	0	304	15.41
<i>Encyonema lange-bertalotii</i> Krammer morphotype 1	1.7	0	0	1	1	0	1094	1.65
<i>Encyonema minutum</i> (Hilse in Rabh.) D.G. Mann in Round Crawford &	15.6	0	0	1	1	0	213	39.69
<i>Encyonema minutum</i> (Hilse in Rabh.) D.G. Mann abnormal form	1.2	0	0	1	1	0	213	2.5
<i>Encyonema ventricosum</i> (Agardh) Grunow in Schmidt & al.	16.6	0	0	1	1	0	185	60.94
<i>Eolimna minima</i> (Grunow) Lange-Bertalot	12.7	1	0	0	0	3	88	32.84
<i>Eolimna minima</i> (Grunow) Lange-Bertalot abnormal form	17.9	1	0	0	0	3	88	10.68
<i>Encyonema prostratum</i> (Berkeley) Kützing	0.4	0	0	1	1	1	8278	2.27
<i>Encyonema silesiacum</i> (Bleisch in Rabh.) D.G. Mann abnormal form	4.3	0	0	1	1	1	821	1.14

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<i>Gomphonema angustum</i> Agardh	4.3	0	1	0	0	0	1301	7.01
<i>Gomphonema capitatum</i> Ehr.	13.3	0	1	1	0	0	1150	9.94
<i>Gomphonema cymbelliclinum</i> Reichardt & Lange-Bertalot	15.7	0	1	0	0	0	289	23.42
<i>Gomphonema elegantissimum</i> Reichardt & Lange-Bertalot in Hofmann	8.1	0	1	0	0	0	360	27.43
<i>Gomphonema gracile</i> Ehrenberg	2.4	0	1	0	0	3	1095	4.74
<i>Gomphonema italicum</i> Kützing	6.9	0	1	1	0	0	1243	31.14
<i>Gomphonema lateripunctatum</i> Reichardt & Lange-Bertalot	16.2	0	1	0	0	3	1034	37.18
<i>Gomphonema micropus</i> Kützing var. <i>micropus</i>	11.2	0	1	0	0	3	855	33.12
<i>Gomphonema minutum</i> (Ag.)Agardh f. <i>minutum</i>	5.3	0	1	1	0	0	318	28.28
<i>Gomphonema olivaceum</i> (Hornemann) Brébisson var. <i>olivaceum</i>	6.2	0	1	1	0	1	510	41.26
GOMPHONEMA C.G. Ehrenberg	5.6	0	1	1	0	0	510	4.76
<i>Gomphonema parvulum</i> (Kützing) Kützing var. <i>parvulum</i> f. <i>parvulum</i>	17.2	0	1	0	0	3	331	44.21
<i>Gomphonema pumilum</i> var. <i>rigidum</i> Reichardt & Lange- Bertalot	5.9	0	1	0	0	0	270	4.08
<i>Gomphonema pumilum</i> (Grunow) Reichardt & Lange- Bertalot	3.9	0	1	0	0	0	270	43.76
<i>Gomphonema rhombicum</i> Fricke	19.1	0	1	0	0	0	1800	3.74
<i>Gomphonema tergestinum</i> (Grunow in Van Heurck) Schmidt in Schmidt	12.5	0	1	0	0	3	673	3.74
<i>Gomphonema tenoccultum</i> Reichardt	5.2	0	1	0	0	0	NA	1.37
<i>Gomphonema vidalii</i> Beltrami & Ector	3.6	0	1	0	0	0	NA	2.33
<i>Halamphora montana</i> (Krasske) Levkov	6.9	0	0	0	0	4	664	4.5
<i>Hippodonta pseudacceptata</i> (Kobayasi) Lange-Bertalot Metzeltin &	0.8	1	0	0	0	0	NA	1.96
<i>Halamphora veneta</i> (Kützing) Levkov	36.4	0	0	0	0	3	3543	0.29
<i>Karayevia clevei</i> (Grunow) Bukhtiyarova var. <i>clevei</i>	1.8	0	0	0	0	1	485	1.97
<i>Meridion circulare</i> (Greville) C.A.Agardh var. <i>circulare</i>	6	0	0	1	0	1	671	13.59
<i>Mayamaea permitis</i> (Hustedt) Bruder & Medlin	13.2	1	0	0	0	3	66	24.77
<i>Melosira varians</i> Agardh	17.4	0	0	1	0	2	3267	29.97

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<i>Navicula reichardtiana</i> Lange-Bertalot var. <i>reichardtiana</i>	10.6	1	0	0	0	0	176	26.71
<i>Nitzschia recta</i> Hantzsch in Rabenhorst	0.8	1	0	0	0	1	871	6.43
<i>Navicula subalpina</i> Reichardt	4.8	1	0	0	0	0	364	3.41
<i>Nitzschia solgensis</i> Cleve-Euler	0.1	1	0	0	0	4	259	0.7
<i>Navicula splendidula</i> Van Landingham	20	1	0	0	0	0	1161	7.28
<i>Nitzschia tabellaria</i> (Grunow) Grunow in Cl. & Grunow	3	1	0	0	0	3	289	14.96
<i>Navicula tripunctata</i> (O.F.Müller) Bory	13.6	1	0	0	0	3	966	60.41
<i>Navicula trivialis</i> Lange-Bertalot var. <i>trivialis</i>	36.5	1	0	0	0	3	1097	1.99
<i>Navicula veneta</i> Kützing	16.4	1	0	0	0	3	279	19.84
<i>Nitzschia costei</i> Tudesque, Rimet & Ector	1.2	1	0	0	0	0	170	6.72
<i>Nitzschia inconspicua</i> Grunow abnormal form	8.8	1	0	0	0	3	89	2.12
<i>Planothidium frequentissimum</i> (Lange-Bertalot)Lange-Bertalot	14.6	0	0	0	0	0	219	28.1
<i>Pseudostaurosira brevistriata</i> (Grun.in Van Heurck) Williams & Round	6.6	0	0	1	0	2	157	7
<i>Planothidium lanceolatum</i> (Brebisson ex Kützing) Lange-Bertalot	7.8	0	0	0	0	3	475	20.8
<i>Rhoicosphenia abbreviata</i> (C.Agardh) Lange-Bertalot	6.2	0	1	1	0	2	568	15.83
<i>Rhopalodia gibba</i> (Ehr.) O.Muller	2.4	1	0	0	0	3	185472	0.38
<i>Reimeria sinuata</i> (Gregory) Kociolek & Stoermer	9.1	0	1	0	0	3	406	14.7
<i>Reimeria uniseriata</i> Sala Guerrero & Ferrario	12.7	0	1	0	0	0	456	29.02
<i>Synedra acus</i> Kützing	14.8	0	0	1	0	0	467	21.57
<i>Stenopterobia anceps</i> (Lewis) Breb. ex V. Heurck ssp. <i>gigantea</i> Metzelti	0	1	0	1	0	0	NA	3.04
<i>Surirella angusta</i> Kützing	3	1	0	0	0	3	1315	5.43
<i>Surirella brebissonii</i> var. <i>kuetzingii</i> Krammer et Lange-Bertalot	0.8	1	0	0	0	3	1347	2.09
<i>Staurosira binodis</i> Lange-Bertalot in Hofmann Werum & Lange-Bertalot	10.2	0	0	1	0	2	166	7.11
<i>Sellaphora bacillum</i> (Ehrenberg) D.G.Mann	9.9	1	0	0	0	2	2129	8.12
<i>Simonsenia delognei</i> Lange-Bertalot	8.5	1	0	0	0	3	53	3.93

