



If Alpine streams run dry: the drought memory of benthic communities

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Abstract

Several mountain streams are currently changing from perennial to temporary regimes due to increasing water abstraction and global climate change with expected detrimental effects on stream biodiversity and functionality. We here examined whether macroinvertebrates and diatoms, experiencing recurring non-flow periods, showed alterations even after complete flow resumption in 13 mountain streams in SW Italian Alps. Benthic communities were sampled after complete flow resumption in April 2017 in a control section, with permanent flow, and in an intermittent section, which experiences recurrent non-flow periods during summer, in each stream. We tested for differences in terms of taxonomic composition, diversity and functional groups between permanent and temporary sections. Our results showed a significant alteration of benthic invertebrate, but not diatom communities in temporary sections. Different species composition and low diversity values in temporary sections were due to the replacement of monovoltine taxa, with aquatic respiration, preferring medium to fast flowing, oligotrophic waters by plurivoltine taxa, with aerial respiration preferring lentic habitats. Such results provide some insights into the mechanisms by which non-flow periods impact Alpine streams, and further investigations in mountain areas are required in the future to better unravel the repercussions on stream ecosystem processes.

Keywords Diatoms · Macroinvertebrates · Hydrological intermittency · Functional traits

Introduction

Stream ecosystems have been recognized as extremely sensitive to climate change, because of the raising of water temperatures and the disruption of hydrologic cycles (Heino et al. 2009; Whitehead et al. 2009; Fenoglio et al. 2010). Changes in precipitations, temperature and evaporation determine shifts in river flow regimes and groundwater recharge (IPCC 2013), with consequences for the temporal and spatial distribution of biodiversity and ecosystem processes in streams and rivers (Acuña and Tockner 2010;

Datry et al. 2016). This climatic alteration can lead to extreme flow events, like floods and non-flow events, which can be exacerbated by anthropogenic activities (e.g. deforestation, water capture, streambed alterations; Fenoglio et al. 2010; Ledger and Milner 2015). Among flow regime alterations, riverbed desiccation is one of the most pressing environmental issues related to climate change (Wilhite 2000). In Mediterranean streams, non-flow events represent natural component of their hydrologic cycle. Therefore, freshwater biota in temporary streams is physically, chemically and biologically shaped by sequential, predictable and seasonal non-flow events (Boulton et al. 2014). Therefore, freshwater biota of periodically temporary environments shows adaptations and strategies to survive dry periods (e.g. desiccation-resistant stages or colonization of hyporheic environment; Boulton and Lake 1992; Fenoglio et al. 2006; Bonada et al. 2007a; López-Rodríguez et al. 2009a; Souffreau et al. 2010). This is in accordance with the *natural flow regime paradigm*, which states that the structure and function of a lotic ecosystem, and the adaptation of its constituent aquatic species, are determined by the pattern of temporal variation in river

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flows (Poff et al. 1997; Lytle and Poff 2004). However, consequences of desiccation on aquatic organisms are expected to be different in temperate streams, where this phenomenon is quite recent and communities are still not adapted (Calapez et al. 2014; Elias et al. 2015).

Among these, Alpine and in general mountain streams are becoming increasingly affected by intermittent flow (Beniston 2012; Chiogna et al. 2016). In the Alpine areas, low flows normally occur during winter and are caused by snow accumulation and freezing processes (Veza et al. 2010; Fenoglio et al. 2015). However, summer non-flow periods are becoming more common since mountainous regions in the mid-latitudes are warming at a rate two to three times faster than the global average (Hansen et al. 2005; Pederson et al. 2011), causing rapid shrinkage of glaciers and snowpack (Hall and Fagre 2003; Rauscher et al. 2008). Moreover, these lotic ecosystems are suffering the heavy flow regulation, hydropower and increased water abstraction aimed to fulfill local human needs (e.g. agricultural use, drinking water, etc). As a consequence, mountain streams are changing from perennial to temporary systems with expected long-term detrimental effects on stream biodiversity and functionality (Durance and Ormerod 2007; Fenoglio et al. 2007; Leigh et al. 2016a; Pinna et al. 2016).

From an evolutionary perspective, by influencing mortality rates, desiccation represents a primary selective pressure on aquatic communities (Lytle and Poff 2004). These strong environmental filters are expected to differentially affect species from the regional pool by either favouring species that can tolerate drying conditions and/or disfavouring species lacking resistance or resilience mechanisms to the disturbance, in accordance with the *habitat templet theory* (Southwood 1977, 1988; Townsend and Hildrew 1994). On one hand, in naturally intermittent Mediterranean streams, stretches experiencing drying likely have, on average, less diverse communities than those of nearby perennial sites (e.g. Datry et al. 2014), because of the exclusion of the most sensitive species (but see Bonada et al. 2007a for contrasting results in a large scale analysis). On the other hand, such environmental filtering is expected to cause turnover among perennial and intermittent stretches due to substitution of non-adapted taxa by disturbance-tolerant species (Myers et al. 2015). Both phenomena may result in biotic homogenisation of temporary streams due to the loss of rare and specialised species and the gain of tolerant species (Socolar et al. 2016). Selection process due to desiccation is likely to favour particular traits (Webb et al. 2010; Luck et al. 2012) conferring resistance (i.e. set of traits that enable organisms to survive during non-flow periods) and/or resilience (set of traits that enable organisms to recolonize and recruit after non-flow events). A trait is defined as a characteristic that reflects a species adaption to its environment (Menezes et al. 2010) which can be morphological or physiological

attributes measured at the individual level (Violle et al. 2007; Webb et al. 2010), or aspects of the realized niche of the species (Bowler et al. 2015). Exploring shifts in the functional profile of a community could therefore shed light into species-disturbance relationships (McGill et al. 2006) but also into their repercussion on the ecosystem functionality. Depending on which traits are extirpated, such trait shifts may, in fact, have severe effects on ecological functions, with a wide range of potential impacts on functional processes (Hooper et al. 2005; Cardinale et al. 2012).

Alterations in community diversity and functional traits might be temporary, depending on the recovery capacity of aquatic organisms: species highly resilient or resistant to drying are able to recover within a few weeks or months, therefore limiting long-term effects of desiccation (Rincon and Cressa 2000; Fritz and Dodds 2004; Vander Vorste et al. 2016). However, some taxa might not be able to recover so quickly, with cumulative detrimental effects on diversity and functionality over the years. For instance, Datry et al. (2011), in the Albarine river (France), found persistent differences in shredder density among intermittent and permanent sections long after flow resumption, underlining the so-called “drying memory” of the system. Therefore, the assessment of non-flow effects needs to consider not only immediate but also long-term impacts.

We here investigated the long-term effects of drying events (“drying memory”) on benthic organisms, in thirteen Italian Alpine streams, where summer non-flow events, lasting two months, have been recorded since 2011. In particular, we compared the response of two different communities, i.e. macroinvertebrates and diatoms, to highlight potential differences in their recovery capacity, since they are known to exhibit differential responses to stream alteration, like metal pollution (Hirst et al. 2002; De Jonge et al. 2008), physical alterations (Bona et al. 2008) or siltation (Bona et al. 2016). In each of these streams, we sampled and compared an intermittent and a perennial stretch during base-flow conditions to quantify differences as a result of eventual cumulative effects of non-flow events. We here assumed that aquatic communities in intermittent sites would have reached a complete recovery if their composition and diversity was comparable to that of communities sampled in perennial sites. Such comparison allowed us to investigate differences between diatoms and macroinvertebrates as well as underlying selection mechanisms, i.e. species loss versus species replacement, due to filtering of non-adapted species and/or gain in generalist species. In this context, we hypothesized that: (i) recovery capacity differs between benthic invertebrates and diatoms due to their different reproduction rates and dispersal capacities (Elias et al. 2015); (ii) cumulative effects of non-flow events on benthic communities mainly result in species loss processes and (iii) species loss is due to the depletion of non-adapted taxa.

Materials and methods

Sampling design

This study was conducted in thirteen low order streams belonging to the SW Alps hydroecoregion (HER 4, Piemonte, NW Italy; Wasson et al. 2007, Fig. 1), therefore comparable in terms of geology, climate and altitude to reduce confounding factors. Such hydroecoregion includes Cottian and Maritime Alps, whose streams are characterized by a nivo-pluvial regime. In consequence, several stretches are already facing seasonal hydrological alterations in summer because of reduction in precipitations and the following increase in water abstraction for human needs.

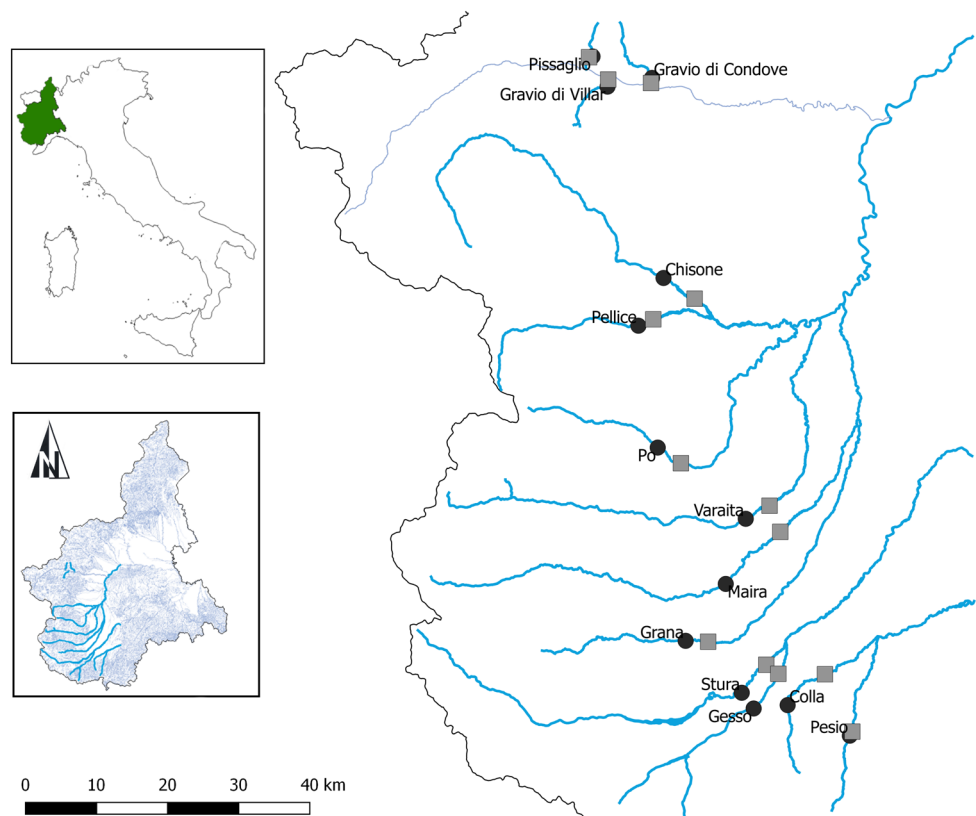
We selected two sampling sections for each stream, with different levels of hydrological disturbance: (i) a control section, with permanent water during the whole year (hereinafter CON section); (ii) an intermittent section, which experiences non-flow periods during summer (hereinafter DIS section). CON sections were consistently located upstream, therefore representing a potential source of organisms for DIS sections after flow resumption. Selected streams were chosen based on interviews to fishermen (Associazione Tutela Ambienti Acquatici

e Ittiofauna) and on the data provided by the ARPA - Environmental Protection Agency of Piedmont, according to which these streams have been already facing seasonal summer non-flow events lasting two months since 2011, with the riverbed almost completely dry in their DIS sections, as a combination of climatic factors and anthropogenic pressures (A.A.V.V. 2011; Borroni 2011; ARPA 2013). CON sections were identified within 10 km upstream of the DIS section to reduce environmental variability between the two stretches (Fig. 1). To verify if a “drying memory” phenomenon occurred in benthic invertebrate and/or in diatom communities after the complete flow resumption, we performed our sampling campaign in April 2017 (6 months after the drying period), under moderate flow ($Q_{\text{mean}} = 3.98 \pm 4.56 \text{ m}^3/\text{s}$) occurring in both sections. Water flow in DIS sections had resumed in November 2016 after a heavy rain event, interrupting the dewatering period of the streams (Hydrological bulletins, <http://www.arpa.piemonte.it>).

Data collection

In each sampling stretch, we collected a set of 13 local environmental variables. Water physical and chemical parameters (water dissolved oxygen, oxygen saturation, pH, water temperature, conductivity) were measured with

Fig. 1 Map of the thirteen study streams with respective sampling sites (circles = CON sites; squares = DIS sites)



a multiparametric probe (Hydrolab mod. Quanta). Additionally, to check the water quality, water samples were collected from the middle of the water course in each sampling section. The samples were then analysed with standard spectrophotometric (Perkin Elmer, Lambda 35) methods for soluble reactive and total phosphorus (APHA 1998), ammonium (Koroleff 1970), nitrate (APHA 1998) and total nitrogen (APHA 1998).

In each stretch we defined five microhabitats spaced at least 5 m apart, where we measured flow velocity (0.05 m from the bottom) and water depth with a current meter (Hydro-bios Kiel) and we visually estimated the % of six classes of substratum (boulders, cobbles, pebbles, gravels, sand and silt). These microhabitats were selected following the Italian multihabitat sampling method (Buffagni and Erba 2007). One sample of macroinvertebrates was collected in each microhabitat, for a total of five samples in each stretch, using a Surber sampler (250 μm mesh size; 0.062 m^2 area). Collected samples were conserved into plastic jars with 75% ethanol. In the laboratory, all benthic invertebrates were identified according to Campaioli et al. (1994, 1999) to the family or genus level and counted. Based on their trophic strategies and their biological and ecological requirements, macroinvertebrates were classified into the Functional Feeding Groups (FFGs—Merritt et al. 2017) and biological and ecological groups (Usseglio-Polatera et al. 2000) respectively. Macroinvertebrates are classified into Functional Feeding Groups based on their morpho-behavioral mechanisms of food acquisition (Merritt et al. 2017). Biological and ecological groups were defined by Usseglio-Polatera et al. (2000) by grouping together taxa displaying similar biological (e.g. size, life-cycle, respiration, reproduction, dispersal, locomotion) and ecological (transversal and longitudinal distribution, preferred substrate and current velocity, trophic status) traits respectively.

For benthic diatoms, one sample for each stretch was collected, brushing 3 different cobbles, covering at least an area of 10 cm^2 (European Committee for Standardization 2003), chosen in correspondence of three of the five microhabitats and merged together in a unique sample for subsequent analyses (see Falasco et al. 2018). Diatoms were identified mainly according to reference floras Krammer and Lange-Bertalot (1986, 1988, 1991a, b) as well as on recent bibliography including series of Diatoms of Europe Iconographia Diatomologica and relevant scientific papers (Krammer and Lange-Bertalot 1986, 1988, 1991a, b; Krammer 1997a, b, 2002, 2003; Reichardt 1999; Lange-Bertalot 2001; Werum and Lange-Bertalot 2004; Blanco et al. 2010; Hofmann et al. 2011; Bey and Ector 2013; Falasco et al. 2013; Ector et al. 2015). Diatom species were then assigned to one category of life-form based on classification provided by Rimet and Bouchez (2012) and to one eco-morphotype,

which combines the ecological guilds with size classes, based on the classification provided by B-Béres et al. (2017).

Data analysis

To test whether aquatic communities completely recovered after desiccation, we compared the composition and diversity of aquatic communities between DIS and CON sections. We assumed that aquatic communities in intermittent sections would have reached a complete recovery if their composition and diversity was comparable to that of communities sampled in perennial sections. All statistical analyses were performed using R software (R Core Team 2017).

Environmental variables at CON and DIS stretches

To explore potential differences between CON and DIS stretches with respect to environmental conditions, we performed a Principal Component Analysis (PCA) using the 13 habitat variables. A Permutational Multivariate Analysis of Variance PERMANOVA (Anderson 2001) was then applied to the environmental dissimilarity matrix based on Euclidean distances to test for differences between CON and DIS stretches with the function “adonis” in the *vegan* package (Oksanen et al. 2015). Statistical significance was tested via 9999 random permutations with the ID of each stream as stratum.

Community composition

We first visually inspected whether taxa dissimilarity differs among CON and DIS sections by means of a Principal Coordinate Axes (PCoA) using the Bray-Curtis dissimilarity index. We then tested whether dissimilarity in taxa composition between CON and DIS was significantly different from a random distribution with a PERMANOVA. Statistical significance was tested via 9999 random permutations with the stream identity as stratum. Both analyses were conducted with the *vegan* package (Oksanen et al. 2015). We then performed the Indicator Species Analysis (Dufrêne and Legendre 1997) with the function “multipatt” in the *indicspecies* package (De Cáceres and Legendre 2009) to identify which taxa are more specifically linked to CON and DIS stretches for both diatoms and benthic invertebrates.

α -, β - and γ -Diversity

To test whether differences between CON and DIS sections were due to taxa loss (α - and γ -diversity) or species replacement (β -diversity), we followed the approach proposed by Xiao et al. (2018). We decomposed taxa richness of benthic invertebrates and diatoms into local (α) and total (γ) diversity, wherein local diversity is obtained as the average

value of taxa richness at each sampling section and total diversity is given by the total number of encountered taxa in the entire sampling area. Beta diversity was calculated with the Whittaker's multiplicative formula as the ratio between gamma and alpha diversity. Statistical significance was calculated through a non-parametric, randomization test, where the null expectation of each metric is defined by permuting sampling sections between treatments and recalculating the taxa richness for each permutation. Significant differences between treatments can thus be obtained by comparing the observed value of the taxa richness to the null expectation when treatments are randomly permuted across the sampling sites (Legendre and Legendre 1998). At the α scale where there are replicate plots to summarize over, we calculated the ANOVA F -statistic as our test statistic for the observed values and we compared it with the distribution of F -statistics obtained for each permutation. At the γ scale, for which we only have a single value for each treatment (and therefore cannot use the F -statistic), we compared the observed absolute difference between the treatments with the distribution of those obtained from permutations (see McGlinn et al. 2018 for further details). These statistical analyses were performed with the R package *mobr* (Xiao et al. 2018).

Functional profile of benthic communities in CON and DIS sections

To check whether differences between CON and DIS sections were due to selective environmental filtering of some functional traits, we considered functional feeding groups (FFGs), ecological and biological groups (Usseglio-Polatera et al. 2000) for benthic invertebrates, whereas for diatoms we evaluated life-forms (Rimet and Bouchez 2012) and eco-morphotypes (B-Béres et al. 2017). We calculated this set of functional metrics as the community-level weighted means of trait values, with the function "functcomp" of the *FD* package (Laliberté and Legendre 2010; Laliberté et al. 2014). This function builds a site-by-trait matrix by multiplying the site-by-species matrix with a species-by-trait matrix. For continuous and ordinal traits, like diatom body size, this function calculates the mean trait value of all species present in the community weighted by their relative abundances. For nominal and binary traits, like FFGs, ecological and biological groups for benthic invertebrates and life-forms and ecological guilds for diatoms, the relative abundance of taxa belonging to each individual class is returned. In addition, such comparison was applied also to those taxa potentially most threatened by desiccation. For benthic invertebrates, we focused on the EPT (Ephemeroptera, Plecoptera, Trichoptera) taxa richness because they are a key component of benthic assemblages in Alpine streams and sensitive to flow variability (Laini et al. 2018). For benthic diatoms, we considered the Red List (RL) taxa richness

because it showed to be negatively affected by desiccation in Mediterranean streams (Falasco et al. 2016a). Significant effects of hydrological conditions on functional metrics were tested by means of a one-way ANOVA with the stream identity as error stratum. Data were log-transformed to achieve normal distribution and homoscedasticity of residuals.

Results

Environmental parameters (Table S1) were comparable across the investigated streams and between the two sampling sections. The first two axes of the PCA explained 40.5% of the total variance in the environmental variables across all sites (Fig. 2). The first axis (22.8%) represents a gradient of rheophily, being positively correlated with flow velocity, % cobbles, oxygen saturation and dissolved oxygen, and negatively with % pebbles and temperature. The second axis (17.7%) represented a streambed sediment gradient, being negatively correlated with % pebbles, % sand and positively correlated with % cobbles and pH. PERMANOVA showed that environmental variables did not differ between CON and DIS sections (PERMANOVA, $P=0.111$, Table 1).

The PCoA depicted differences in species composition between CON and DIS sections for benthic invertebrates (Fig. 3a), whereas this pattern was not evident for diatoms (Fig. 3b). These patterns revealed significant differences between CON and DIS sections for benthic invertebrates

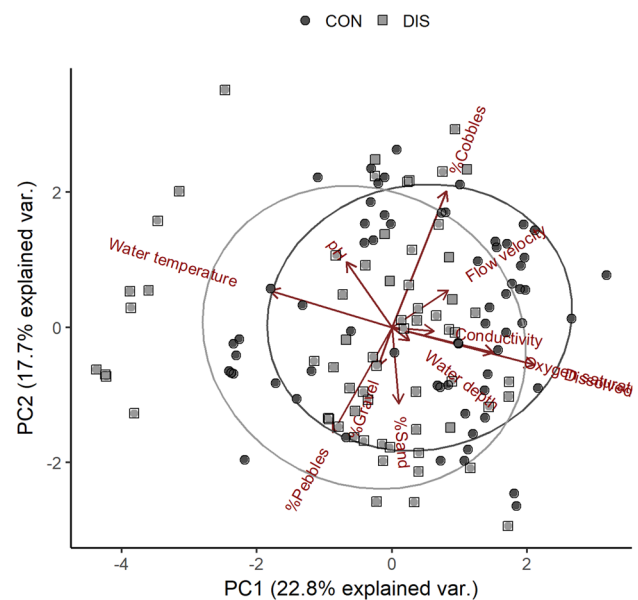


Fig. 2 Result of the PCA. Points represent each single sample while arrows represent the loadings of each environmental variable included in the analysis. Ellipses represent standard deviations around the centroids of the two groups

Table 1 Results of the Indicator Species Analysis for benthic invertebrates

CON sites	IndVal	P
Rhyacophilidae	0.645	0.001
<i>Epeorus</i> spp.	0.639	0.001
<i>Ecdyonurus</i> spp.	0.586	0.001
<i>Amphinemura</i> spp.	0.575	0.001
<i>Leuctra</i> spp.	0.524	0.017
<i>Protonemura</i> spp.	0.492	0.011
<i>Isoperla</i> spp.	0.487	0.007
Sericostomatidae	0.460	0.002
<i>Dinocras</i> spp.	0.445	0.011
Blephariceridae	0.416	0.001
Odontoceridae	0.313	0.034
<i>Perla</i> spp.	0.304	0.036
DIS sites	IndVal	P
Naididae	0.762	0.001

(PERMANOVA, $F_{1,128} = 5.84$; $P < 0.001$) but not for diatoms (PERMANOVA, $F_{1,24} = 0.692$; $P = 0.072$).

The Indicator Species Analysis identified 12 indicator taxa in CON sections and 1 indicator taxon of DIS sections for benthic invertebrates (Table 1), whereas no indicator species were identified for diatoms.

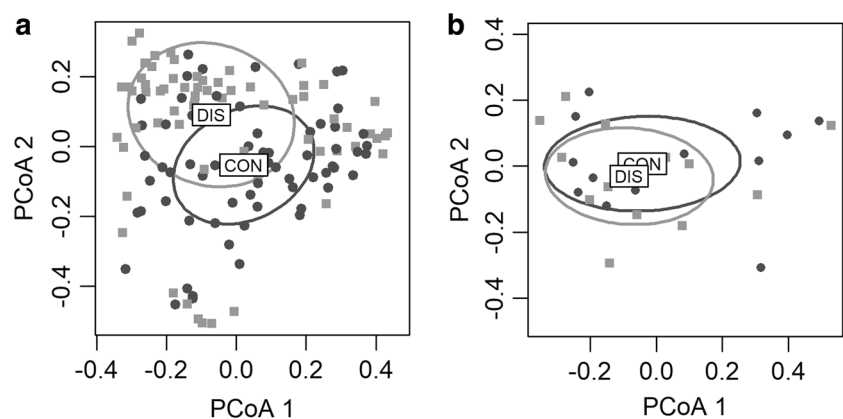
The results of the diversity partitioning showed significant effects of the hydrological conditions on macroinvertebrate taxa richness at both alpha and gamma scale (Fig. 4a), which drops from an average value of 11.6 in CON stretches to 8.58 in DIS stretches. Conversely, we did not find statistical differences in any of the diversity metric considered between CON and DIS sites for diatoms (Fig. 4b).

Considering the community functional profile of benthic invertebrates, we found significant effects of the hydrological conditions on EPT richness (Table 2; Fig. 5a) and FFG composition (Table 2; Fig. 6), with particularly evident impacts on predators, scrapers and shredders. In CON sites, the abundances of predators, scrapers and shredders are on

average 4%, 8% and 9%, respectively, but drop to 3%, 6% and 3% in DIS sites. Conversely, results showed a significant effect of hydrological conditions on collector-gatherers (Table 2; Fig. 6), with higher values in DIS (70%) compared to CON sites (59%), whereas no significant effects (Table 2; Fig. 6) were recorded for filter-feeders (20% in CON sites and 18% in DIS sites). Significant negative effects of non-flow hydrological conditions were observed for organisms preferring medium to fast flowing, oligotrophic waters and living on coarse mineral substrata and vegetation (ecological groups A and C; Table 2; Fig. 6). Percentages of individuals belonging to ecological groups A and C showed significant lower values in DIS than in CON stretches, dropping from 12% and 21–6% and 13% respectively. For taxa preferring lentic habitats (ecological group F), we observed a significant increase from CON (36%) to DIS (48%) sites (Table 2; Fig. 6). Significant effects of hydrologic conditions were also recorded for several biological groups (Table 2; Fig. 6). Percentages of semivoltine organisms, large-sized predators and crawlers (biological group d), monovoltine organisms, medium-sized shredders and crawlers with aquatic respiration (biological group f), and small to medium-sized swimmers or crawlers, with aerial respiration (biological group g), showed a significant decreasing pattern (Table 2; Fig. 6) from CON (2%, 15% and 9% respectively) to DIS (1%, 8% and 4% respectively) stretches. Conversely, plurivoltine, small-sized organisms (biological groups h and e) showed significant higher values in the DIS (11% and 76% respectively) than in CON (5% and 64% respectively) sites (Table 2; Fig. 6).

Considering the community functional profile of benthic diatoms, we could not detect any significant effect of hydrological conditions on red list species abundance (Table 2; Fig. 5b) and on functional groups (Table 2), except for high profile species of size class 4, which resulted more abundant in DIS than in CON sites.

Fig. 3 Ordination of the sampled benthic invertebrate (a) and diatom (b) communities according to the first two PCoA axes (Dark grey circles = CON sites; light grey squares = DIS sites). Ellipses represent standard deviations around the centroids of the two groups



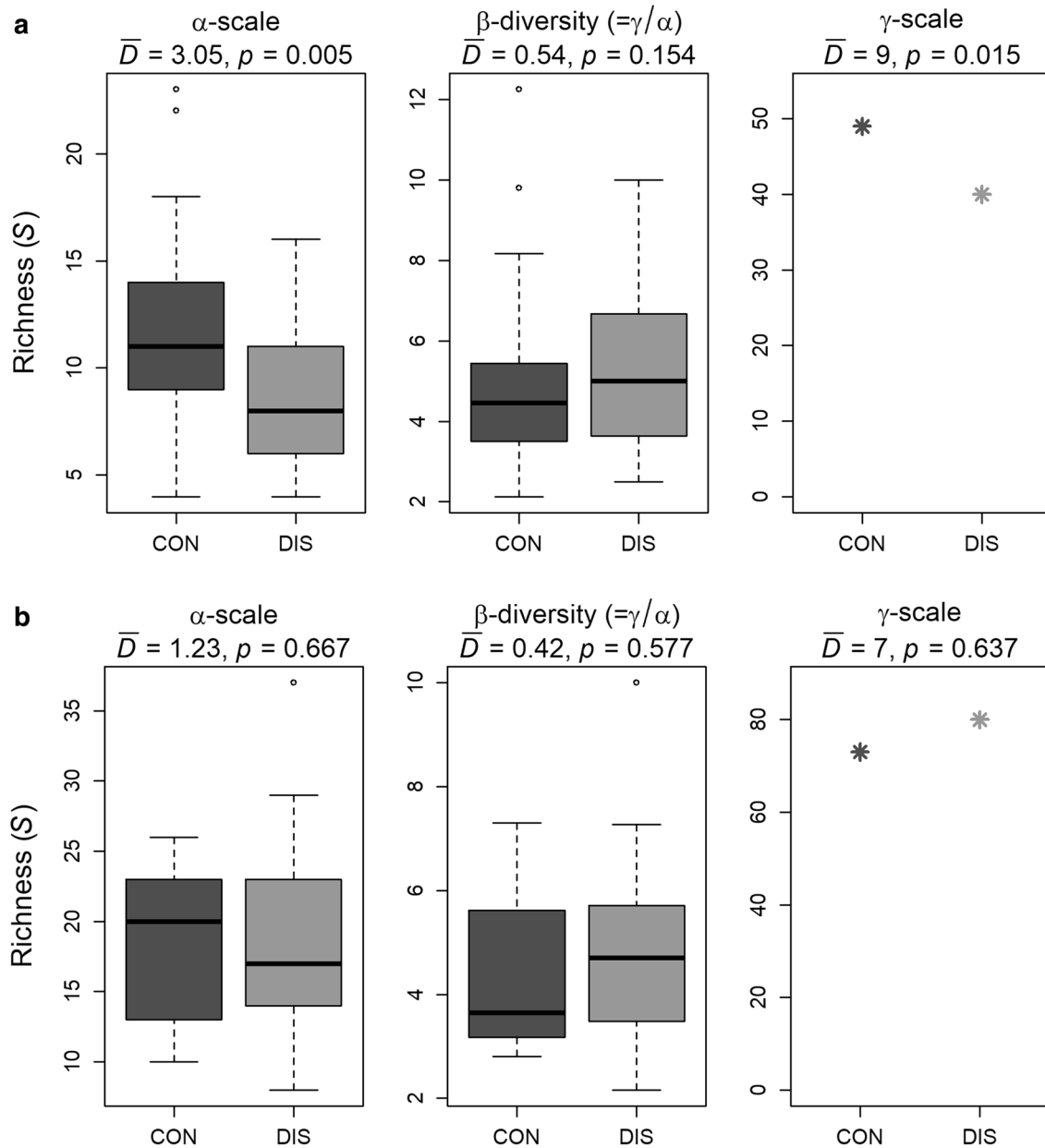


Fig. 4 Diversity metrics for benthic invertebrates (a) and diatoms (b) at the α (i.e., single stretch), beta (i.e., between stretches), and γ (i.e., all stretches) scales. The p -values are based on 999 permutations of the treatment labels

Discussion

Alpine and mountainous streams are affected by multiple pressures that often cause the alteration and sometimes even the almost complete destruction of these ecosystems (Wohl 2006). In particular, increasing water abstraction (e.g. for hydroelectric power generation, drinkable waters, irrigation and snow generation) combined with the global climate change effects have severe repercussions on Alpine streams, with increasing frequency of non-flow events in previously perennial systems (Fenoglio et al. 2010). Such

events are expected to affect biotic communities, whose composition changes substantially during non-flow periods, but recovers quite rapidly after water returns (Lake 2003; Fowler 2004). However, this might not be true in recently temporary streams, where biotic communities still lack adaptations to such extreme events. Although environmental variables in permanent and intermittent sites were similar in our study, we recorded differences in benthic community diversity and composition, which could be ascribed to the long-term effects of desiccation. This result clearly strengthens the role of biological communities in

Table 2 Results of the one-way ANOVA performed on functional traits. Significant results are reported in bold

Benthic invertebrates	$F_{1,128}$	P
<i>Taxonomic metrics</i>		
EPT richness	57.33	< 0.001
<i>FFG</i>		
Shredders	17.4	< 0.001
Scrapers	4.32	0.040
Predators	8.93	0.003
Coll-gath	10.8	0.001
Filterers	1.42	0.237
<i>Ecological groups</i>		
Eco A	18.2	< 0.001
Eco B	1.78	0.185
Eco C	13.0	< 0.001
Eco D	0.366	0.546
Eco E	1.81	0.181
Eco F	20.5	< 0.001
<i>Biological groups</i>		
Bio b	1.53	0.219
Bio c	0.116	0.734
Bio d	7.88	0.006
Bio e	5.70	0.019
Bio f	17.1	< 0.001
Bio g	23.7	< 0.001
Bio h	9.01	0.003
Diatoms	$F_{1,24}$	P
<i>Taxonomic metrics</i>		
RL taxa	0.732	0.409
<i>Life-forms</i>		
Mucous	3.22	0.098
Adnate	0.082	0.779
Pad	1.69	0.219
Stalk	0.129	0.726
Free	0.071	0.794
Solitary	0.295	0.597
Colonial	0.261	0.619
<i>Eco-morphotypes</i>		
Low1	1.61	0.228
Low2	2.57	0.135
Low3	0.900	0.362
Low4	0.923	0.356
Low5	0.147	0.708
High1	0.732	0.409
High2	0.928	0.354
High3	4.48	0.056
High4	10.63	0.007
High5	2.43	0.145
Motile1	0.172	0.686
Motile2	1.28	0.281
Motile3	0.456	0.512
Motile4	2.53	0.138
Motile5	2.08	0.175

assessing ecological conditions as their response integrates temporal aspects. Our results revealed that in recently temporary Alpine streams benthic macroinvertebrates, but not diatoms, reflect a negative effect of water intermittency, confirming earlier findings in Mediterranean (Boix et al. 2010) and other temperate regions (Calapez et al. 2014; Elias et al. 2015).

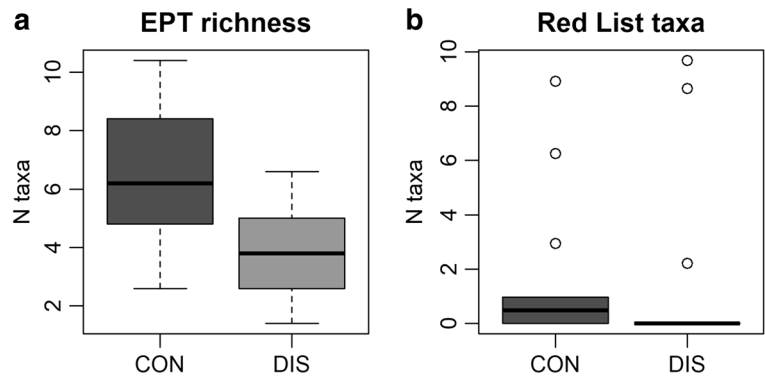
Benthic invertebrate response

Our results depicted how river reaches experiencing non-flow periods supported different and less species-rich communities compared to perennial reaches. These results suggest that the shift in macroinvertebrate community composition was partly determined by a species filtering process, such that only a limited set of species—with particular trait combinations—can survive in the intermittent sections, similarly to Giam et al. (2017).

To further investigate whether desiccation favours tolerant-disturbance species or species that share particular traits, we tested whether communities in perennial and intermittent river reaches differed in their functional trait composition. In accordance with literature (Dewson et al. 2007; Datry et al. 2014), we observed that taxa depletion in intermittent sites was mainly driven by the loss of the EPT (Ephemeroptera, Plecoptera and Trichoptera) taxa, which represent the dominant groups in the Alpine streams and the most sensitive taxa as well. Likewise, several EPT taxa can be found almost exclusively in perennial sections, as demonstrated by the Indicator Species Analysis. Consistent results were obtained by Doretto et al. (2018) who conducted a manipulative experiment in artificial flumes located in Eastern Italian Alps. In the cited work, taxonomic richness of benthic invertebrates and EPT richness decreased after two consecutive non-flow events.

Considering the response in terms of biological groups of benthic invertebrates, large semivoltine taxa with long larval life, such as *Dinocras* sp., *Perla* sp. and *Athericidae*, which are unable to survive in periodically dry environments, showed lower values in intermittent than in perennial sections. Conversely, small, fast growing, plurivoltine organisms, such as *Chironomidae*, *Simuliidae* and *Baetis* sp., showed an opposite trend. Voltinism has been recognized as one of the most sensitive traits (Bonada and Dolédec 2018) and a shift from multivoltinism to semivoltinism has been observed from perennial to intermittent hydrological regimes in Mediterranean streams (Corbet et al. 2006; López-Rodríguez et al. 2009a, b): in particular, these authors demonstrated that species inhabiting temporary habitats complete their life cycle in less than 1 year, emerging just before the loss of surface water. However, in Alpine streams, where non-flow events are human-induced, the match between

Fig. 5 Boxplots representing differences in EPT richness (a) of benthic invertebrates and Red List species abundance (b) of diatoms between CON and DIS sites



life-history adaptation and non-flow periods might be lost with severe consequences for species survival. Similarly, small body size is also a common attribute of macroinvertebrate taxa living in temporary Mediterranean streams, since

reduced dimensions allow fast development and population growth (Bonada et al. 2007b). These attributes assure higher survival rates in temporary watercourses, where life-cycle has to be completed before water disappears.

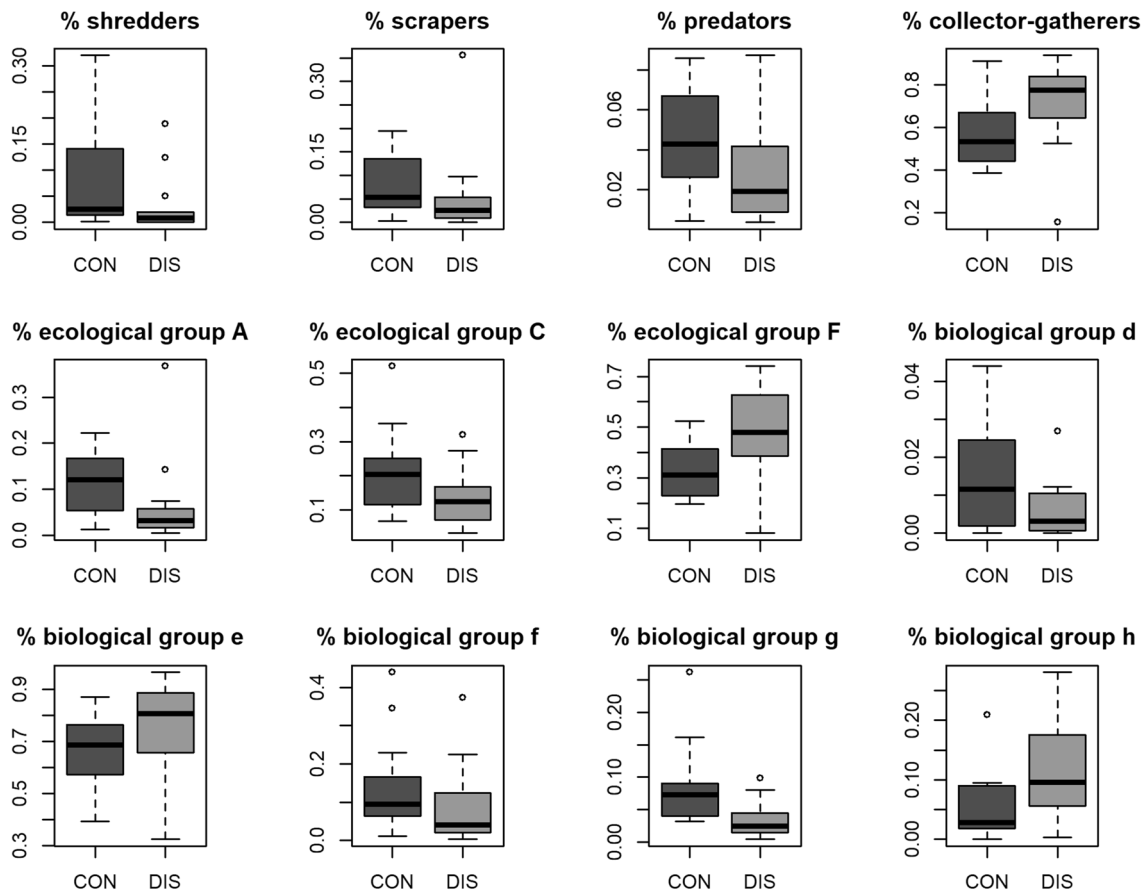


Fig. 6 Boxplots representing differences in functional groups between CON and DIS sites for benthic invertebrates. Only significant results are reported. Ecological group A: rheophilous organisms preferring coarse mineral substrates in oligotrophic and cold waters; ecological group C: organisms living on mineral substrates or vegetation at slow or medium current velocities; ecological group F: organisms living in lentic and stagnant habitats. Biological group d: semivoltine, large-

sized predators and crawlers, with aerial dispersal; biological group e: small to medium-sized plurivoltine crawlers with aquatic respiration; biological group f: monovoltine, medium-sized shredders and crawlers with aquatic respiration; biological group g: small to medium-sized swimmers or crawlers, with aerial respiration; biological group h: monovoltine burrowers, deposit-feeders

When looking at ecological niches, we could observe that rheophilous taxa preferring coarse substrata, such as *Epeorus* sp. and *Rithrogena* sp., decreased from perennial to intermittent sites, while there was an increase of lentic taxa, mainly Chironomidae, able to survive in environments with fluctuating water levels. This is in accordance with Acuña et al. (2005), Pace et al. (2013) and Chessmann (2015), who depicted negative effects of desiccation on rheophilous taxa in Mediterranean streams.

Our results on macroinvertebrates confirm early findings of Fenoglio et al. (2007) who observed similar responses along a gradient of desiccation in a study on the Po river. However, as they developed their work during the lenticification phase, it remained less clear to what extent such functional alteration of benthic invertebrate community was transient or persistent in time. Since we here sampled intermittent sections six months after water returned, our data strongly suggest the long-term effect of non-flow events on macroinvertebrate communities in Alpine streams. Moreover, with the analysis of functional groups, we could reveal that desiccation does not only filter non-adapted taxa, but this taxonomic loss is at least partly compensated by positive selection of tolerant species. This desiccation-driven replacement of species mirrors the effects of climatic change, whose impacts have been reported for many taxonomic groups (Parmesan and Yohe 2003; Hickling et al. 2006).

Our results also demonstrate that non-flow events in Alpine streams alter macroinvertebrate functional feeding groups, with possible repercussions on the ecosystem functionality. We here highlighted how specialised functional feeding groups, such as shredders and scrapers, mainly represented by Limnephilidae and Heptageniidae respectively, decreased from perennial to intermittent sections. Conversely, the generalist group of collector-gatherers, including *Baetis* sp. and Chironomidae, increased. This suggests that drying events can persistently alter the composition of macroinvertebrate assemblages in streams and this might be particularly true for non-adapted Alpine communities. The absence of water disrupts some ecological processes, such as the microbial breakdown of allochthonous inputs (Boulton and Lake 1992). In this context, Wensch et al. (2017) demonstrated how the loss of shredder benthic taxa may significantly alter the decomposition rate of leaf litter in streams with consequent alteration of ecosystem functionality. Such results are critical also because flow reduction and desiccation are strictly associated with heavy fine sediment accumulation (i.e., clogging), since lower water velocity enables more sediment to settle out of suspension (Dewson et al. 2007; Rolls et al. 2012). Such phenomenon is also responsible for altering the organic material decomposition (Doretto et al. 2016, 2017), exponentially increasing the negative effect of non-flow events on stream nutrient

cycling. Although intermittent flow might prevent the establishment of permanent periphytic biofilms (Wood and Petts 1999), this explanation is not plausible to justify the strong reduction of scrapers in intermittent sections observed in our study, since we could not record any clear response of benthic diatoms. However, in our sites, scrapers are mainly represented by the family Heptageniidae, which includes extremely rheophilous organisms (Usseglio-Polatera et al. 2000). Therefore, they are probably negatively affected more by flow reduction than by trophic processes. In addition, desiccation promotes heterotrophy (Acuña et al. 2015) and alter fatty acid composition (Sanpera-Calbet et al. 2017) in the biofilm, likely affecting scrapers (Guo et al. 2016). Further investigations in this sense could unravel mechanisms behind this pattern.

Benthic diatom response

Diatoms show a rapid recovery after non-flow regime in this study, given that after 6 months since the water returned diatom community in intermittent stretches is comparable to that found in perennial sites. This result was also confirmed by the analysis of the most sensitive taxa, i.e. Red List taxa, since we could not find any significant pattern. Within biofilm, diatoms are probably the most sensitive component since other groups, such as cyanobacteria and green algae, better cope with desiccation (Piano et al. 2017a). In this context, in Mediterranean streams a clear response of diatoms to stream lenticification and fragmentation processes occurring during non-flow periods has been highlighted: for instance, river shrinkage causes the loss of Red List diatom taxa (Falasco et al. 2016a), with increasing proportions of motile (Falasco et al. 2016b) and tolerant (Piano et al. 2017b) species, and similar results were also reported by Falasco et al. (2018a) in Alpine streams. Considering colonization processes during rewetting phases, Artigas et al. (2012) observed a faster recolonization on bare substrates in a Mediterranean temporary stream, in comparison to a slow gradual recovery in a Central European river. Similarly, Souffreau et al. (2010) demonstrated that acclimatization increases the tolerance of diatom strains to desiccation, underlying how non-flow events can have a stronger negative impact on diatom communities in recently temporary rivers than in Mediterranean regions. Despite recovery might take more than 90 days in pristine streams (Falasco et al. 2018b), diatom communities recovered faster after a non-flow event in comparison with macroinvertebrates, probably due to their shorter life cycles and higher physiological adaptation to dryness (Calapez et al. 2014). Moreover, the high dispersal capacity of diatoms (Robson et al. 2008) combined with their fast reproduction rates guarantee a rapid recovery after desiccation (i.e. mass effect, Mouquet and Loreau 2003). The analysis of their functional groups confirmed results

obtained from diversity and community composition, since communities in intermittent sites showed no significant variations in ecological guilds, size and lifeforms compared with the perennial stretches.

Although changes in species diversity and composition as well as in functional groups were more clearly detected for benthic invertebrates than for diatoms, translating these observations as stronger invertebrate versus diatom response to long-term desiccation effects should be interpreted with caution. Although diatoms and invertebrates were sampled in an equal number of sites, the higher number of replicates within each site collected for macroinvertebrates could potentially lead to higher statistical power to detect invertebrate than diatom responses. Further investigations are required to shed light on this point.

Conclusions

Our results emphasize how the functional-based approach can help in unravelling the ecological responses of stream benthic communities to non-flow events. Our predictions of a persistent effect of desiccation on benthic communities was rejected for diatoms, but was confirmed for macroinvertebrate assemblages. Moreover, we disentangled the additive effect of two mechanisms on benthic invertebrates, which may act with varying intensities depending on the considered functional aspects. Species loss represents the dominant mechanism, since non-adapted species are filtered out, as confirmed by a reduction in species richness. On the other hand, species replacement also plays a role since small, plurivoltine taxa, preferring lentic habitats and feeding on streambed sediment are favoured in intermittent sections. Such results underlay how benthic communities in intermittent sections of Alpine streams are currently facing alterations caused by flow intermittency and further investigations in mountainous areas are required in the next future to better unravel these processes. In particular, even if we did not record significant differences between permanent and intermittent sites in terms of environmental parameters, results of the PCA showed how intermittent sites are slightly warmer than permanent ones. Temperature increasing values likely associated with low flows might represent a disrupting mechanism, especially in cold arctic streams, as highlighted by Heino et al. (2009). The effect of water warming on benthic communities should be investigated in Alpine streams, which are in some respect environmentally similar to arctic streams. Moreover, since alterations in benthic invertebrate functional groups could possibly have repercussions on periphyton composition (e.g. scraper decrease), despite at present no alterations were recorded for diatom community, monitoring both benthic communities will be essential to disentangle functional changes in the lotic food web.

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