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PRIMARY RESEARCH PAPER

The role of recurrent dewatering events in shaping ecological niches of scrapers in intermittent Alpine streams

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Abstract Several Alpine streams are currently changing from perennial to intermittent systems with expected detrimental consequences on benthic invertebrates, through the alteration of hydrological conditions, substrate composition, and trophic resources. We examined the ecological niche of three phylogenetically-related scraper macroinvertebrates, namely *Ecdyonurus*, *Epeorus,* and *Rhithrogena* (Ephemeroptera, Heptageniidae) experiencing recurrent summer dewatering events in perennial and intermittent stretches in 13 Alpine streams. We evaluated the overlap among the ecological niches of the three examined taxa in terms of hydraulic stress, substrate coarseness, and total primary production and we investigated their ecological preferences in perennial and intermittent sites. Our results showed a broad overlap of their ecological niches, suggesting exploitative competition among the examined taxa. Their ecological niches were smaller in intermittent than perennial sites, pointing out a reduction of available microhabitats. All groups were favored by substrate coarseness and total primary production in reach types, while the hydraulic stress showed an opposite effect in perennial (negative) and intermittent (positive) sites. Overall, our results emphasize how stream physical parameters play a key role in determining the ecological niche of Heptageniidae and underline how benthic communities in intermittent sections of previously perennial Alpine streams are currently under pressure.

Keywords Heptageniidae · Chlorophyll *a* · Froude number · Substrate Index · Physical disturbance

Introduction

Streams are dynamic ecosystems, often facing natural hydrological and geomorphological changes that might rearrange near-bed conditions, potentially reducing the availability of suitable microhabitat for some species, while increasing it for others (Gore et al., 2001). In mountainous low-order lotic systems these phenomena are usually highly predictable, with an increase in water flow and fine sediments in summer, during snow melting, and a minimum discharge in winter (McGregor et al., 1995). However,

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the increasing human pressure has been intensifying physical disturbance in these streams (Wohl, 2006) with detrimental consequences on benthic biota (Bona et al., 2008; Bruno et al., 2013; Doretto et al., 2016, 2017, 2019). For instance, clogging caused by the huge increase of fine sediments caused by human activities currently represents one of the most important and pervasive concern for mountainous lotic environments, especially because they are naturally characterized by coarse substrates (Bo et al., 2007; Bona et al., 2016; Doretto et al., 2016, 2017). Another current threat to mountainous lotic systems is the enhanced frequency of extreme flow events (i.e., droughts and floods) due to Climate Change and exacerbated by human activities (Brighenti et al., 2019). In particular, summer flow cessation periods are increasing in mountainous regions at the mid-latitudes, because they 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 (Rauscher et al., 2008). These changes anticipate the hydrological peak in spring and induce modifications in thermal and hydrological regimes as well as sediment transport (Brighenti et al., 2019), thereby modifying hydrogeomorphological, physical, and chemical conditions downstream (Hannah et al., 2007) causing cascading effects on the structure and function of aquatic communities (Milner et al., 2017). 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, characterized by recurrent non-flow events followed by rewetting phases (Fenoglio et al., 2010) as a consequence of interactive effects of both climate change and anthropogenic disturbance (Belmar et al., 2019; Bruno et al., 2019). Periodic flow intermittency is expected to alter the distribution of benthic invertebrates by influencing physical conditions and distribution of trophic resources (e.g., Datry et al., 2011; Acuña et al., 2015; Piano et al., 2017; Chessman, 2018).

From an evolutionary standpoint, near-bed hydraulic conditions and substratum composition represent strong selective pressures for benthic invertebrates (Rempel et al., 2000; Jowett, 2003; Mérigoux & Dolédec, 2004). Near-bed hydraulic conditions are of critical importance for benthic invertebrates (Statzner et al., 1988), which need to find a compromise between the energy costs of maintaining position in turbulent environments, the benefits of acquiring food and oxygen and dispersal (Chessman, 2018). The stream benthos is also dependent on substratum characteristics, whereby stable substrates provide a good supply of shelters and food resources increasing richness and abundance of benthic invertebrates (e.g., Minshall, 1984; Boulton et al., 1998; Bona et al., 2016; Doretto et al., 2017). Conversely, huge amounts of fine sediments, which are often a byproduct of human activities, impact benthic macroinvertebrates due to abrasion, clogging and burial (Fenoglio et al., 2007; Jones et al., 2012; Bona et al., 2016) and reducing refuge availability and the amount of food resources (Doretto et al., 2017). Hydraulic and substratum conditions therefore represent major physical gradients along which the benthic community is organized. However, coexistence of multiple species with the same ecological requirements translates into strong competitive interactions, especially when species are phylogenetically-related and thus share the same trophic niche and competitive abilities (Leibold & Chase, 2017). Consequently, interspecific competition for food may also influence the abundance and distribution of aquatic taxa. Likely, physical conditions and food availability are key factors in outlining the ecological niche of macroinvertebrates in streams (Resh et al., 1988).

The ecological niche of a species can be defined as the range of ecological conditions in which this species can survive, grow, reproduce, and maintain a viable population (Hutchinson, 1957). In streams, it is mainly influenced by physical factors acting at multiple spatial scales (Statzner et al., 1988; Quinn & Hickey, 1994; Heino et al., 2003). At regional and global scale, the investigation of the ecological niche considers distribution patterns of species along large geographical and environmental gradients, such as variation in precipitations and temperature, to elucidate their bioclimatic ranges and biogeographic history (e.g., Boyero et al., 2011). At smaller scale, local environmental conditions become the most important factors explaining species coexistence and their competition for space and resources (Chesson, 2000; Chase & Leibold, 2003). In particular, water flow and particle size have been recognized to play a major role in the spatial distribution of macroinvertebrate organisms at within-site scale (e.g., Statzner et al., 1988; Wellnitz, 2015; Bo et al., 2016).

Evidence in literature (Fenoglio et al., 2007; Datry et al., 2011; Doretto et al., 2018; Piano et al., 2019) suggests that specialized feeders, namely shredders, i.e., invertebrates feeding on coarse allochthonous organic fragments, and scrapers, i.e., invertebrates feeding on autochthonous biofilm, were often more negatively affected by dewatering events than generalist collectors and predators, in accordance with the assumptions of the River Continuum Concept (RCC, Vannote et al., 1980). In particular, dewatering events likely affect scrapers by preventing the establishment of mature periphytic biofilms (Wood & Petts, 1999), by promoting heterotrophy (Acuña et al., 2015) and by altering fatty acid composition in the biofilm (Guo et al., 2016). Although some studies investigated the response of this trophic group to flow intermittency in Alpine streams (e.g., Fenoglio et al., 2007; Doretto et al., 2018; Piano et al., 2019), little is known about the role of dewatering events in shaping ecological niches of scrapers.

We here investigated the ecological niche of three phylogenetically-related genera of scrapers, namely *Ecdyonurus*, *Epeorus* and *Rhithrogena* (Ephemeroptera, Heptageniidae) in 13 streams in Italian SW Alps, where summer non-flow events, lasting on average two months, have been recorded since 2011. In particular we aimed at: (i) shedding light on ecological niche requirements at within-site scale of the three most common genera of Heptageniidae in Italian Alpine streams; (ii) investigating the potential interspecific competition among the three examined taxa; and (iii) exploring potential effects of recurrent non-flow events on their niche partitioning.

Materials and methods

Sampling design

This study was conducted in 13 low-order streams located in the hydroecoregion of SW Alps (HER 4, Piemonte, NW Italy; Wasson et al., 2007), showing similar characteristics in terms of geology, climate, and altitude. In this area, streams flow on siliceous substrates and are characterized by a nivo-pluvial regime (Fig. S1). Several stretches are already facing seasonal hydrological alterations in summer due to the interactive effect of reduction in precipitations and the consequent increase in water abstraction for human needs. In particular, the stream selection was made based on our expertise and historical data (ARPA—Environmental Protection Agency of Piemonte) regarding their hydrology and confirmed by recognized fishermen (i.e., ATAAI—Associazione Tutela Ambienti Acquatici e Ittiofauna). According to these data, selected streams have been already facing seasonal summer droughts lasting two months since 2011, with the riverbed almost completely dry in some stretches at least 30 m long, as a combination of climatic factors and anthropogenic pressures, namely increasing water abstraction, e.g., for hydroelectric power generation, drinkable waters, irrigation, and snow generation (Borroni, 2011; ARPA, 2013).

In each of the selected stream, we sampled and compared an intermittent and a perennial section in subalpine reaches during baseflow conditions to investigate differences as a result of possible cumulative effects of non-flow events. In each stream, we then selected two sampling sections differing in their hydrological regime: (i) a control section, with permanent water during the whole year (hereinafter CON section); and (ii) a disturbed section, which experiences drought during summer (hereinafter DIS section). CON sections were identified within 10 km upstream of the DIS section to reduce environmental variation between the two stretches (mean distance = 4.7 km). The selected sections were distributed over a 510 m elevational range, with the lowest and the highest sections located at 308 and 847 m.a.s.l. respectively (see Table S1 for an environmental characterization of sampling sections). We performed our sampling campaign in April 2017 (6 months after the last drying period), under moderate flow (Q_{mean} = 3.98 ± 4.56 m^3/s) in both sections. All samples were collected within 15 days to minimize temporal variation of organism distribution related to seasonality and temperature. Water flow in DIS sections had resumed in November 2016 after a heavy rain event, interrupting the dewatering period of the streams (Hydrological bulletins, www.arpa.piemonte.it).

In each stretch we collected three Surber samples, selected within the streambed in order to cover different conditions of flow velocity, water depth, and substrate composition (3 samples × 2 stretches x 13 streams = 78 samples). Each Surber sampled a patch in which we measured flow velocity (0.06 m from the bottom) and water depth with a current meter (Hydro-bios Kiel). Percentages of different substratum sizes (rocks, boulders, cobbles, gravel, sand) were recorded at each point by using a gravelometer and their coverage was visually estimated. 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. Only data referred to Heptageniidae were considered for further analysis.

To obtain synthetic measures of hydraulic stress and substrate composition, we calculated the Froude number (Gordon et al., 1992) and the Substrate Index (SI, modified by Quinn & Hickey, 1994 after Jowett et al., 1991). The Froude number is a measure of hydraulic turbulence, hence high values correspond to rheophilous microhabitats. It is calculated as: $v/\sqrt{(d \times g)}$, where v is the flow velocity, measured as m/s, d is the water depth, measured as m, and g is the gravity acceleration. The SI quantifies the coarseness of the substrate composition, with high values corresponding to coarse substrates and it is calculated as: $0.8 \times$ %Rocks $+ 0.7 \times$ %Boulders $+ 0.6 \times$ %Cobbles $+ 0.5 \times$ %Gravel $+ 0.4 \times$ %Sand. We focused our attention on these parameters since they have already been successfully used to describe the physical niche of benthic invertebrates (e.g., Lamouroux et al., 2004; Mesa, 2010). In addition, we expected that these parameters would affect the distribution of the three examined genera, which are medium-sized, monovoltine crawlers, preferring coarse rheophilous substrates, on which they feed on the periphytic biofilm (Tachet et al., 2010).

In order to quantify the scraper food availability we measured the amount of periphyton biomass. Within each Surber sample, we selected one cobble where we took three measures of epilithic chlorophyll *a* with the BenthoTorch®. This instrument is a Pulse Amplitude Modulated (PAM) fluorimeter emitting light pulses at three different wavelengths (470, 525, and 610 nm), recording the response of cyanobacteria, diatoms, and green algae at 690 nm wavelength (Kahlert & McKie, 2014). We then selected the median value of chlorophyll *a* concentration for each autotrophic group, and we calculated the total chlorophyll *a* concentration as the sum of their values as an explanatory variable and a proxy for resource availability for subsequent analyses.

Statistical analysis

All statistical analyses were performed with R software (R Core Team, 2017).

To investigate whether the three examined taxa displayed similar ecological niches, we first built their multidimensional niche hypervolumes (sensu Hutchinson, 1957) using a set of variables referring to hydrological conditions, substrate composition, and trophic resources. We then assessed their potential competition by calculating the overlap between the resulting geometrical solids. Finally, we compared their niches in permanent and intermittent sites.

Among the three genera of Heptageniidae recorded in our samples, *Rhithrogena* resulted the most abundant and widely distributed taxon, followed by *Epeorus* and *Ecdyonurus* (Table 2). Before proceeding with the analysis of the ecological niches of examined taxa, we investigated whether hydrological stress (Froude number), substrate coarseness (Substrate Index) and periphyton biomass (total chlorophyll *a* concentration) differed between CON and DIS sites by means of the non parametric Wilcoxon test for paired data.

Niche hypervolume

In a first step, we compared the overall ecological niches of the examined taxa based on presence data in both CON and DIS sites to investigate whether their ecological requirements overlap, thus suggesting possible exploitative competition. To perform this, we calculated their ecological niche *sensu* Hutchinson (1957) via the *hypervolume* R package (Blonder, 2015) based on the Froude number, SI, and total chlorophyll *a* measured at each Surber sample. This approach relies on a kernel density estimation (KDE) procedure, which permits to quantify the multidimensional Hutchinsonian hypervolume and to assess the intersection between the hypervolumes of two taxa (mathematical details in Blonder et al., 2014). Before the analysis, we standardized all variables in order to achieve the same dimensionality for all axes following the assumptions of the algorithm. The hypervolume was calculated with the hypervolume_gaussian R command (Blonder, 2015), which constructs a hypervolume based on a Gaussian kernel density estimate. We standardized the choice of bandwidth for each variable through a Silverman estimator (Silverman,

1992) as recommended by Blonder et al. (2014), and we set a threshold that included 100% of the total probability density. The intersection between the hypervolumes and their overlap statistics were obtained via the hypervolume_set and hypervolume_overlap_statistics R commands respectively (Blonder, 2015) for each pair of taxa, for a total of three pairs. Overlap statistics include the Jaccard and Sorensen similarity indices, which range from 0 to 1 (0 = no overlap; 1 = complete overlap).

Outlying Mean Index (OMI)

In a second step, we examined whether recurrent dewatering events alter the ecological niche of the three examined taxa by means of the Outlier Mean Index (OMI) analysis on CON and DIS sites separately. The OMI is a two-table ordination technique that positions the sampling units in a multidimensional space as a function of environmental parameters (Dolédec et al., 2000). The distribution of species in this space represents their realized niches and considers two aspects: marginality and tolerance. The marginality measures the distance between the mean habitat conditions used by a taxon and the mean habitat conditions across the study area. Taxa with high values of OMI have marginal niches (occur in atypical habitats within the study area), whereas those that get low values have non-marginal niches (occur in typical habitats within the study area). The tolerance measures the niche breadth, which means the amplitude in the distribution of each species along the sampled environmental gradients. Low values mean that a species is distributed across a limited range of conditions, while high values imply that a species is distributed across habitats with widely varying environmental conditions. The OMI analysis were performed via the function "niche" in the package *ade4* (Chessel et al., 2004; Dray & Dufour, 2007; Dray et al., 2007) for the R software (R Core Team, 2017).

Results

The observed values of environmental parameters observed in this study in both CON and DIS sites are reported in Table 1. The Wilcoxon test highlighted significant differences among CON and DIS sites in terms of Substrate Index (P = 0.008) and Froude number (P = 0.015), while no differences were observed for total chlorophyll *a* (P = 0.873).

Among the three genera of Heptageniidae recorded in our samples, *Rhithrogena* resulted the most abundant and widely distributed taxon, followed by *Epeorus* and *Ecdyonurus* (Table 2).

Niche hypervolume

Among the three examined taxa, *Epeorus* showed the highest dimension of the three-dimensional hypervolume (184.7), whereas *Ecdyonurus* and *Rhithrogena* displayed lower and similar values (*Ecdyonurus* = 128.2; *Rhithrogena* = 131.5). The three hypervolumes remarkably overlap (Fig. 1) as demonstrated by the

Table 1 Average values (mean) and standard deviations (SD) for environmental parameters in CON and DIS sites

	CON sites (mean ± SD)	DIS sites (mean ± SD)
Flow velocity (m/s)	0.63 ± 0.36	0.42 ± 0.32
Water depth (m)	0.29 ± 0.14	0.27 ± 0.11
Rocks (%)	0.26 ± 1.60	0.77 ± 2.70
Boulders (%)	48.7 ± 30.4	29.0 ± 32.5
Cobbles (%)	38.8 ± 25.0	46.1 ± 23.9
Gravel (%)	9.36 ± 15.6	15.5 ± 18.2
Sand (%)	2.56 ± 5.49	8.33 ± 15.1
Chl-*a* diatoms (μg/cm^2)	2.14 ± 3.24	1.61 ± 1.50
Chl-*a* cyanobacteria (μg/cm^2)	0.21 ± 0.29	0.15 ± 0.15
Chl-*a* green algae (μg/cm^2)	0.01 ± 0.03	0.01 ± 0.05
Froude number	0.38 ± 0.20	0.26 ± 0.18
Substrate Index	6.33 ± 0.50	5.97 ± 0.58
Total chl-a	2.35 ± 3.33	1.77 ± 1.53

Table 2 Number of samples (*N* samples) and abundance of individuals (*N* individuals) recorded in perennial (CON) and intermittent (INT) sites, as well as their total values (Tot) in the study area, for the three examined genera

Taxon	Site	*N* samples	*N* individuals
Rhithrogena	CON	25	157
	INT	22	101
	Tot	47	258
Epeorus	CON	18	120
	INT	6	19
	Tot	24	139
Ecdyonurus	CON	14	69
	INT	4	6
	Tot	18	75

similarity indices (*Ecdyonurus* vs *Epeorus*: Jaccard = 0.64, Sorensen = 0.78; *Ecdyonurus* vs *Rhithrogena*: Jaccard = 0.66, Sorensen = 0.79; *Epeorus* vs *Rhithrogena*: Jaccard = 0.65; Sorensen = 0.79).

Outlying Mean Index (OMI)

The first two axes of the OMI analysis were selected and they accounted for the 99.4% and 100% of total explained variance in CON and DIS sites, respectively.

In CON sites, the first and second axes contributed for the 79.2% and 20.2% to the total explained variance, respectively (Table 3). *Ecdyonurus* and *Epeorus* showed the highest and lowest marginality values (%OMI) respectively, while they have similar values of tolerance (%Tol). *Rhithrogena* had the narrowest niche (%Tol) (Table 4). *Ecdyonurus* is negatively affected by Froude number (− 0.72), but positively by SI (0.46), while total chlorophyll *a* has a positive low influence (0.02). The main environmental variables favoring *Epeorus* are total chlorophyll *a* (0.24) and SI (0.23), while Froude number has a low but negative effect (− 0.08) (Fig. 2). *Rhithrogena* is favored especially by total chlorophyll *a* (0.54) followed by SI (0.30), but it is negatively affected by Froude number (− 0.62) (Fig. 2).

In DIS sites, the first axis alone contributed for the 87.5%, while the second axis contributed for the 12.5% to the total explained variance (Table 3). *Ecdyonurus* resulted as the most tolerant taxon (%Tol), showing also the lowest marginality value (%OMI) (Table 3). *Epeorus* is characterized with the highest marginality value (%OMI), while *Rhithrogena* showed the lowest tolerance value (%Tol) (Table 4). The three taxa all positively correlate with Froude number, with *Rhithrogena* (0.56) showing the highest correlation, followed by *Epeorus* (0.35) and *Ecdyonurus* (0.14). The SI has a highly positive effect on *Epeorus* (0.72) and a weak positive correlation with *Ecdyonurus* (0.14) and *Rhithrogena* (0.11) (Fig. 2). Total chlorophyll *a* positively affects the three taxa, even if its effect is more evident on *Rhithrogena* (0.33) and *Epeorus* (0.17) than on *Ecdyonurus* (0.06) (Fig. 2).

Discussion

We here revisited the role of interspecific competition in shaping the general geometry of the niche of three coexisting phylogenetically-related scrapers in mountainous streams recently facing seasonal dewatering events. In agreement with our predictions, our model organisms were found to co-occur in similar environmental conditions and were negatively affected by recurrent dewatering events, since they are less represented in DIS than in CON sites.

Correlation among taxa and OMI axes indicated that all three environmental variables (Froude number, Substrate Index, and total chlorophyll *a* concentration) were important in explaining the spatial distribution of macroinvertebrates within microhabitats. Several studies underlined that the examined taxa prefer rheophilous microhabitats with coarse mineral substrates (Rempel et al., 2000; Usseglio-Polatera et al., 2000; Mérigoux & Dolédec, 2004; Beauger et al., 2006; Wellnitz, 2015) and our results partially confirmed previous findings.

On one hand, we observed a positive consistent effect of the Substrate Index on the three examined taxa. In particular, this environmental feature was highly positively correlated with occurrence of *Ecdyonurus* and *Epeorus* in perennial and intermittent sections respectively. It should be noted that, although the flow had recovered since 6 months at the sampling moment, significant differences were observed in terms of Substrate Index among CON and DIS sites, with the former displaying more coarse substrates than the latter, possibly as a consequence of fine sediment deposition due to the dewatering event (average ± SD

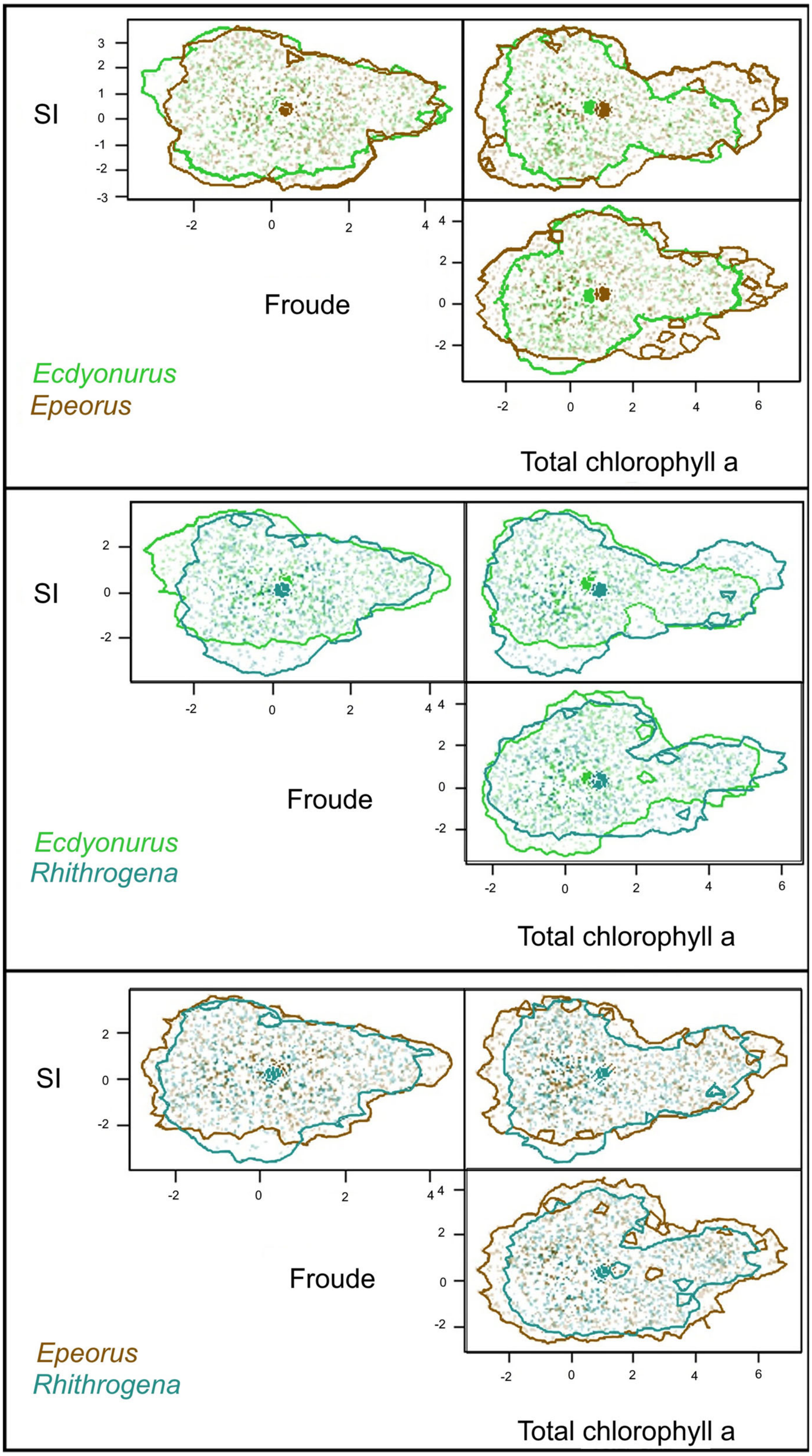

Fig. 1 Pair plots showing the estimated three-dimensional hypervolumes for the three examined taxa. The colored points for each taxon reflect the centroids (large points), original observations (intermediate points) and the stochastic points sampled from the inferred hypervolume (small points). All variable are standardized

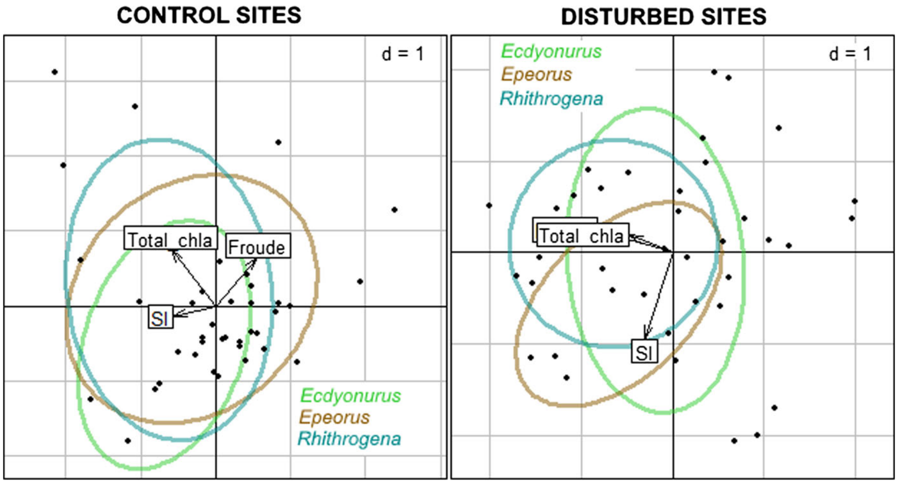

Fig. 2 Projection of environmental variables on the axis of OMI analysis in CON (left panel) and DIS (right panel) sites and representation of ecological niches of the three examined taxa. Values of distances among one square and the other along the two axes are determined by the d value reported in the top right corner of the pictures

Table 3 Correlation values between OMI axes and both environmental variables and examined taxa in CON and DIS sites

	CON sites		DIS sites	
	Axis 1	Axis 2	Axis 1	Axis 2
Environmental variables				
Froude number	0.56	0.65	– 0.82	0.25
Substrate Index	– 0.57	– 0.14	– 0.31	– 0.95
Total chlorophyll *a*	– 0.60	0.75	– 0.47	0.20
Taxa				
Ecdyonurus	– 0.69	– 0.52	– 0.19	– 0.09
Epeorus	– 0.32	0.09	– 0.59	– 0.57
Rhithrogena	– 0.62	0.22	– 0.65	0.10

Table 4 Niche parameters of Heptageniidae taxa

CON/DIS	Taxon	Inertia	%OMI	%Tol	%Res
CON sites	*Ecdyonurus*	3.46	21.4	30.3	48.3
	Epeorus	3.66	3.20	30.2	66.7
	Rhithrogena	4.13	10.4	25.3	64.3
DIS sites	*Ecdyonurus*	2.20	2.00	26.5	71.5
	Epeorus	3.29	20.4	25.1	54.6
	Rhithrogena	3.35	12.9	17.1	70.0

Inertia variance or weighted sum of squared distances to the origin of the environmental axes, *%OMI* percentage of variability of outlying mean index (marginality), *%Tol* percentage of variability of tolerance index, *%Rtol* residuals (%)

%Sand: CON sites = 2.56% ± 5.49; DIS sites = 8.33% ± 15.1). In fact, fine sediment accumulation is strictly associated with flow reduction and droughts, because lower water velocity enables more sediments to settle out of suspension (Dewson et al., 2007; Rolls et al., 2012).

On the other hand, the role of the hydrological stress is controversial. Heptageniidae display morphological adaptations to fast currents, i.e., flat head and femora (Weissenberger et al., 1991) and abdominal gills that overlap to form friction pads (Ditsche-Kuru & Koop, 2009). In addition, their abdominal gills are largely immobile, making Heptageniidae nymphs unable of generating effective ventilatory movements. Consequently, they are likely physiologically restricted to fast-flow waters with high oxygen exchange rates (Baumer et al., 2000). Surprisingly, examined taxa were favored by high hydraulic stress in intermittent sites, but this relationship was opposite in perennial sites. In particular, *Rhithrogena* was strongly disturbed by high hydraulic stress in perennial sites, despite being known as an extremely rheophilous taxon (Rempel et al., 2000; Mérigoux & Dolédec, 2004; Beauger et al., 2006). Evidence in literature suggests that this inverse relationship might be due to different grazing rates at different flows, which may also vary within the same family. For instance, Poff et al. (2003) showed an increasing grazing rate with increasing flow velocity for the caddisfly *Glossosoma verdona* Ross, 1938, but Wellnitz et al. (2001) observed an opposite trend for the related species

Agapetus boulderensis Milne, 1936. We might hypothesize that differences in flow velocity among perennial and intermittent sites are responsible of altered grazing efficiency with consequent inconsistent relationship among the examined taxa and hydraulic stress. In addition, the architecture and taxonomic composition of periphyton is shaped by stream current. Microhabitats differing in their flow velocity may host periphytic mats on which some grazers can feed and forage more effectively than others. For instance, thin biofilms are more readily consumed by some species (Wellnitz & Poff, 2012), while thicker mats may hinder grazer movements across substrates (Hoffman et al., 2006). Also, current-mediated periphytic structure also has the potential to foster positive interactions among grazers if one grazer's foraging facilitates another's access to algal food (Wellnitz & Poff, 2012). A comprehensive investigation of these aspects in recently temporary streams may, therefore, improve our ability to predict the effect of flow changes on macroinvertebrates.

Availability of trophic resources positively affected the distribution of the three examined taxa. In particular, *Rhithrogena* and *Epeorus* were strictly linked to the total chlorophyll *a* concentration, whereas this relationship was less evident for *Ecdyonurus*. This pattern might result from different ecological preferences of the three examined taxa. For instance, low water velocity and turbulence allow the accrual of algae, with consequent high abundance of scrapers (Manfrin et al., 2016). Conversely, light attenuation in deeper areas may reduce periphyton growth and thus food availability for scrapers (Quinn & Hickey, 1994; Mérigoux & Dolédec, 2004).

As their ecological niches broadly overlapped, we may expect that the interaction among the three examined taxa results in exploitative competition. This is particularly true in DIS sites, where their niches are smaller compared to CON sites, suggesting how dewatering events likely reduce the availability of suitable niches and, consequently, enhance competition among coexisting taxa.

In our streams, *Epeorus* resulted to be the most competitive taxon among Heptagenidae, as demonstrated by the widest hypervolume, and this is particularly true in perennial sites, where it showed the lowest marginality value. The lower hypervolumes suggest that in perennial stretches *Rhithrogena* and *Ecdyonurus* are less competitive. Among them, *Rhithrogena* seems the most specialized taxon since it had the narrowest niche both in permanent and intermittent sections. On the contrary, *Ecdyonurus* had its optimal niche in intermittent sites, where it had the lowest marginality. In fact, interestingly, while showing similar niche width, *Epeorus* and *Ecdyonurus* were characterized by opposite marginality values in perennial and intermittent sites, with the former being favored in perennial sites and viceversa. We might hypothesize that, in intermittent sites, the less competitive taxon, namely *Ecdyonurus*, replaces *Epeorus*, which outcompetes *Ecdyonurus* in hydrologically stable sites. Another explanation could be found in the different flow conditions between perennial and intermittent sites. In fact, we observed higher values of Froude number in perennial than in intermittent sites, which are due to higher values of flow velocity. Several studies indicated *Epeorus* and *Rhithrogena* among the most rheophilic organisms (Rempel et al., 2000; Mérigoux & Dolédec, 2004; Beauger et al., 2006; Wellnitz, 2015), whereas *Ecdyonurus* showed preference for intermediate or low flow velocity (Mérigoux & Dolédec, 2004; Beauger et al., 2006).

However, flow velocity and water depth, here summarized into Froude number, showed opposite effects on examined taxa in perennial and intermittent sections, whereas the positive relationship between their occurrence and total chlorophyll *a* concentration is consistent across sampling sites. This pattern seems therefore to corroborate the hypothesis of lower competition ability of *Ecdyonurus* compared to *Rhithrogena* and *Epeorus,* which emerged from the hypervolume and marginality values. This hypothesis is furtherly supported by Peralta-Maraver et al. (2017), who recently analyzed the gut content of several macroinvertebrate taxa, among which the three Heptageniidae examined in this study. Their results showed how *Ecdyonurus* is less dependent on periphytic biofilm, which compose on average the 50% of its diet, than *Epeorus* and *Rhithrogena*, whose 68% of their average diet is composed by periphytic biofilm. Interestingly, *Ecdyonurus* can alternatively feed on allochthonous organic detritus, which represents on average 22% of its diet, and this happens especially when the three taxa temporally coexist.

We can thus suggest that *Ecdyonurus* is more generalist and less competitive than *Epeorus* and *Rhithrogena* in the access to trophic resources. However, translating these observations into interspecific competition among Heptageniidae for trophic resources should be interpreted with caution. Although our data suggest that *Epeorus* and *Rhithrogena* outcompeted *Ecdyonurus* in the access to trophic resources in perennial flow conditions, their high mobility could allow them to partition their trophic niche. In fact, mayflies are extremely agile crawlers on surfaces exposed to fast current and they can move from one area to another, eating only small amounts of algae at each location (Hill & Knight, 1987). Moreover, spatial segregation within the periphyton mat may also occur, with some taxa feeding mainly on tightly attached forms and others preferring superficial layers (Tall et al., 2006). Further investigations should be therefore performed to shed light on this point.

Overall, our results emphasize how stream physical parameters play a key role in determining the ecological niche of Heptageniidae. Although we did not highlight any difference between perennial and intermittent sections in terms of substrate and trophic resource preferences, recurrent dewatering events negatively affect the examined taxa, which are less represented in DIS than in CON sites and the controversial role of hydraulic stress corroborates this hypothesis. In addition, flow reduction is strictly associated with fine sediment accumulation, because lower water velocity enables more sediments to settle out of suspension (Dewson et al., 2007; Rolls et al., 2012). Both phenomena may in turn alter primary productivity and algae composition (Bona et al., 2012, 2016; Piano et al., 2017) with consequent detrimental effects on scrapers. These phenomena will reduce the availability of suitable conditions for the three examined taxa, as demonstrated by the narrower niches in DIS than in CON sites. Since taxa living in previously perennial streams do not have evolved adaptations to dewatering events, they are likely exposed to higher risk of extinction compared to organisms living in Mediterranean streams, which naturally include extreme variations of flow discharge in their hydrological cycle (Fenoglio et al., 2010). In addition, Alpine and mountainous streams are affected by a variety of different human pressures that may alter and sometimes almost destroy these ecosystems (Wohl, 2006). In particular, the increasing water abstraction, e.g., for hydroelectric power generation, drinking, irrigation, and snow generation, add up to the global climate change effects, is exacerbating the effects of flow reduction on mountainous streams (Maiolini and Bruno, 2007). Water flow reduction and dewatering events are expected to have dramatic consequences on stream ecosystem functionality by altering the availability of energetic inputs (e.g., Ledger et al., 2008; Datry et al., 2011; Piano et al., 2017; Falasco et al. 2018). The expected decrease in autochthonous trophic resources will likely cause a bottom-up effect in the food web, directly influencing the survival, growth, and reproduction of invertebrate scrapers. The reduced grazing pressure may also favor the bloom of toxic cyanobacteria, whose growth is enhanced by water flow reduction and temperature increase (Piano et al., 2017).

Since low-order mountainous streams are currently facing alterations caused by flow intermittency, further investigations in mountain areas are required in the next future to better unravel these processes.

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