



Flow intermittency negatively affects three phylogenetically related shredder stoneflies by reducing CPOM availability in recently intermittent Alpine streams in SW-Italian Alps

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Abstract Several Alpine streams are currently facing recurrent summer drying events with detrimental consequences on stream detritivores, i.e., shredders, due to negative effects via changes the organic matter (CPOM) availability. We examined the ecological requirements of three phylogenetically related shredder genera belonging to the family of Nemouridae (Plecoptera), namely *Nemoura*, *Protonemura* and *Amphinemura*, in 14 Alpine streams recently facing recurrent summer flow intermittency events. We evaluated the overlap among their ecological niches measured in terms of hydraulic stress, substrate composition, changes in CPOM availability and

competition with other shredder taxa (i.e., presence of individuals of other shredders) and we examined potential changes in their ecological niches between permanent and intermittent sites. The ecological niches of *Protonemura* and *Amphinemura* overlap broadly, but not with *Nemoura*, suggesting only partial potential competition. The reduced CPOM availability decreased the individual abundance of the three genera in intermittent sites, where they consistently preferred microhabitats with high CPOM availability and low competition with other shredder taxa, possibly due to food limitation. Overall, our results emphasize how the negative effect of flow intermittency on shredders in Alpine streams is mainly due to the decrease in CPOM availability, with consequent potential bottom up effects on stream ecosystem functionality.

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Introduction

Mountain low order lotic systems have always been characterized by highly predictable natural hydrological and geomorphological dynamics, with an increase in water flow and fine sediments in summer, during snow melting, and a minimum discharge in winter (McGregor et al., 1995). The recurrent occurrence of flow intermittency is currently becoming one of the

most dramatic threats to mountain streams (Fenoglio et al., 2010; Brighenti et al., 2019), which are changing from perennial to temporary systems. These newly temporary streams are characterized with recurrent non-flow events, occurring in summer, followed by rewetting phases in late autumn (Fenoglio et al., 2010) due to the interactive effects of both climate change and anthropogenic disturbance (Belmar et al., 2019; Bruno et al., 2019). These recurrent drying events are expected to alter the distribution of lotic biota by influencing physical conditions and distribution of trophic resources (e.g., Calapez et al., 2014; Elias et al., 2015; Milner et al., 2017; Doretto et al., 2018; Falasco et al., 2018; Piano et al., 2019a; Doretto et al., 2020a).

Stream detritivores, which feed on fragments of leaf litter and other plant detritus (i.e., shredders, sensu Merritt et al., 2017), represent a key component in the lotic food web of mountain streams (Boyero et al., 2012). In fact, small, upland, snow melt driven streams in temperate regions are mainly heterotrophic ecosystems, as most of the energetic support is allochthonous (Vannote et al., 1980) and originate from terrestrial plant organic matter, such as dead leaves introduced during autumn abscission in forested areas (e.g., Petersen & Cummins, 1974; Webster & Meyer, 1997; Merritt et al., 2017) or grass fragments in arctic-alpine areas (Fenoglio et al., 2014; Taylor & Andrushchenko, 2014). In particular, detritivores have evolved to take advantage of pulsed organic matter inputs (Benstead & Huryn, 2011), having their life cycles synchronized with the autumnal litter fall (Fenoglio et al., 2005). Early instars take advantage of the organic matter that enters the streams and feed on CPOM until individuals are ready to emerge as winged adults in late spring/early summer (Cummins et al., 1989; Bo et al., 2013; Ferreira et al., 2013). This enables shredder biomass and body size to increase throughout the winter and to reach a maximum in early spring, just before the adult insects emerge from the water before the expected increase in flow due to snow melt (González & Graça, 2003; Fenoglio et al., 2005; Tierno de Figueroa et al., 2009; Bo et al., 2013).

Therefore, as flow intermittency events occur in summer, they are expected to impact shredders during the oviposition and early instars, greatly reducing their survival and abundance, but also because recurrent drying events significantly alter organic matter processing, as already observed in Mediterranean streams

(e.g., Abril et al., 2016). For instance, surface flow disappearance usually reduces the decomposition rate especially in dry streambed sediments, where the activity of Ingoldian fungi, bacteria and invertebrates are inhibited by emersion (Corti et al., 2011; Receveur et al., 2020). In addition, lower flow velocity reduces the removal of fine sediments, with consequent high fine sediment deposition, which can alter the quality and quantity of resources, in terms of both reduced in-stream production, due to the abrasion of autotrophic biofilms (Henley et al., 2000; Bona et al., 2016), and allochthonous coarse organic matter availability through burial (Doretto et al., 2016). On top of that, such dramatic consequences on organic matter availability and decomposition may persist even after several months following flow resuming, because of the so-called “drying memory” (Datry et al., 2011; Pinna et al., 2016), thus affecting also the late instars of shredders (Piano et al., 2019a). Physical alterations and consequent changes in food resources induced by flow intermittency thus represent strong environmental filters that may influence the ecological niche of shredders. Although some studies investigated the effect of flow intermittency on the diversity of this trophic group in Alpine streams (e.g., Fenoglio et al., 2007; Doretto et al., 2018; Piano et al., 2019a), little is known about how these events may alter the ecological parameters that determine the niches of shredder taxa.

Here, we investigated the influence of flow intermittency, CPOM availability, hydromorphological parameters and competition on the distribution and the ecological niche of three phylogenetically related shredder genera, namely *Nemoura*, *Protonemura* and *Amphinemura*, belonging to the Nemouridae (Plecoptera) family. We focused our attention on these genera as they are expected to be particularly sensitive to flow intermittency due to their life-history and ecological traits, as they are medium-sized, monovoltine crawlers, with aquatic respiration, preferring fast flowing waters and coarse substrates (Usseglio-Polatera et al., 2000; Tachet et al., 2010). We conducted our study in fourteen streams in Italian SW-Alps experiencing summer flow intermittency since 2011, where we evaluated the distribution of our focal genera during base flow conditions in April 2017, when shredder larvae reach their maximum density and size. This work is part of the research project NOACQUA dedicated to the investigation of

the effect of flow intermittency on the biodiversity and ecosystem processes in mountain Italian streams, which has already published data on other macroinvertebrate groups (i.e., scrapers, see Piano et al., 2019b). We hypothesized that: (i) the ecological niches of the three examined genera overlap, thus suggesting possible exploitative competition; (ii) flow intermittency negatively affects their abundances; and (iii) recurrent drying events change their ecological niches.

Materials and methods

Sampling design

This study was conducted in fourteen low order streams located in the hydroecoregion of SW Alps (HER 4, Piemonte, NW Italy; Wasson et al., 2007), characterized by similar geology, climate and altitude. Study streams were selected based on our experience and available historical data on their hydrology (ARPA – local Environmental Protection Agency). In each stream, we selected two sampling reaches differing in their hydrological regime: (i) a control section, with permanent water during the whole year (hereinafter PS); (ii) an intermittent section, which experiences drying events during summer (hereinafter IS) caused by factors acting at both global (i.e., climate change) and local (i.e., water abstraction) scales. In particular, ISs have already been facing summer drying lasting on average two months since 2011, with the riverbed almost completely dry for several kilometers (ARPA, 2013). We selected PSs within 10 km upstream of the ISs to reduce environmental variation between the two reaches. At the same time, due to the low drift propensity of Nemouridae (e.g., Bruno et al., 2013), permanent and intermittent sites within the same stream may be considered independent sampling units. Sampling site elevation was on average 489 m a.s.l., ranging from 307 m and 656 m, and permanent and intermittent reaches within the same stream differed on average of 70.2 m in their elevation (min = 19 m; max = 155 m). We performed our sampling campaign in April 2017, before summer snow melt (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, which allowed us to sample shredders at their latest instars and in the period of

their maximum biomass. Water flow in ISs had resumed in November 2016 after a heavy rain event, ending the dry period (Hydrological bulletins, www.arpa.piemonte.it).

In each reach we selected seven independent sampling patches within 30 m long stream section of longitudinal distribution, overall spaced at least 5 m apart, which were randomly selected to cover different habitat conditions of flow velocity, water depth and substrate composition (7 samples \times 2 reaches \times 14 streams = 196 samples). In each patch, which consisted of a surface of 0.062 m², i.e., the area of the Surber sampler, we measured flow velocity (0.05 m from the bottom) and water depth with a current meter (Hydro-bios Kiel) and we visually estimated percentages of different substratum sizes measured with a gravelometer following the classification of Wentworth, namely boulders (> 256 mm), cobbles (64–256 mm), gravel (2–64 mm) and fine sediment (< 2 mm). One sample was collected in each sampling patch, by using a Surber sampler (250 μm mesh size; 0.062 m² area) and we collected both the retained CPOM and macroinvertebrates (Doretto et al., 2020b). Collected samples were preserved in plastic jars with 75% ethanol. In the laboratory, CPOM was washed through a 250 μm mesh sieve to eliminate mineral detritus and subsequently separated from macroinvertebrates. The material was subsequently air dried for 24 h, oven dried (105°C) for 24 h, and then weighed with an electronic balance (accuracy 0.001 g). The CPOM mass, expressed as mg/m², was then considered a proxy of CPOM availability in subsequent analyses. 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 shredder taxa were considered for further analysis (see Table S1 and Fig. S1 for a complete checklist of shredders collected in this study). The numbers of individuals of the three genera *Nemoura*, *Protonemura* and *Amphinemura* were used as dependent variables in our analyses, while we used the number of individuals of the other shredder taxa as a proxy for inter-specific competition.

Statistical analyses

All statistical analyses were performed with R software (R Core Team, 2019). In a preliminary step, we calculated the Froude number (Gordon et al., 1992)

and the Substrate Index (SI, modified by Quinn & Hickey, 1994 after Jowett et al., 1991) to obtain synthetic measures of hydraulic stress and substrate composition. The Froude number is a measure of hydraulic turbulence, hence high values correspond to erosive microhabitats. It is calculated as: $v/\sqrt{(d \times g)}$, where v = flow velocity, measured as m/s, d = 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; Bo et al., 2017; Piano et al., 2019b).

Ecological niches of *Nemouridae*

In order to characterize the ecological niches of *Nemouridae*, we compared the overall (i.e., independent of streams and sections) ecological niches of the examined genera based on abundance data in both PS and IS sites to investigate whether their ecological requirements overlap, thus suggesting possible exploitative competition. To perform this, we calculated their ecological niche as their multidimensional Hutchinsonian hypervolume with a kernel density estimation (KDE) procedure via the *hypervolume* R package (Blonder, 2015) based on the Froude number, SI, CPOM mass and the number of other shredder taxa measured at each Surber sample. All variables were standardized before this analysis to achieve the same dimensionality for all axes and 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, and we set a threshold that included 100% of the total probability density. We then calculated the intersection between the hypervolumes and their overlap statistics for each pair of genera via the *hypervolume_set* and *hypervolume_overlap_statistics* R commands, respectively (Blonder, 2015). Overlap statistics include the Jaccard and Sorensen similarity indices, which range from 0 to 1 (0 = no overlap; 1 = complete overlap).

Effects of flow intermittency on the ecological niches of *Nemouridae*

To test the effect of flow intermittency on the ecological niches of *Nemouridae*, we first checked whether environmental and biotic parameters, namely Froude number, SI, CPOM mass and the abundance of individuals belonging to shredders (hereinafter Competition), and abundances of the three examined genera differed between PSs and ISs with the non-parametric Wilcoxon test repeated for each variable.

In a second step, we assessed whether flow intermittency affects the ecological niche of the three examined genera by means of the Outlying Mean Index (OMI) analysis performed on PS and IS sites separately. The OMI is a two-table ordination technique that can be implemented even with low number of individuals, such as those observed in our work. It positions the sampling units in a multidimensional space as a function of environmental parameters and the distribution of species in this space represents their realized niches (Dolédec et al., 2000). It is based on the concept of marginality, i.e., the distance between the mean habitat conditions observed in the sampling sites where the taxon is present and the mean habitat conditions across the study area. Taxa with high marginality occur in atypical habitats within the study area, while those with low marginality occur in typical habitats within the study area. Besides the marginality, the OMI analysis also calculates the tolerance of each taxon, which is calculated as the niche breadth, namely the amplitude in the distribution of each species along the sampled environmental gradients. Low tolerance values mean that a species is distributed across a limited range of conditions (specialist species), while high tolerance values imply that a species is distributed across habitats with widely varying environmental conditions (generalist species). 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, 2019).

Results

All the three genera of *Nemouridae* typical of the Alpine area, namely *Nemoura*, *Protonemura* and *Amphinemura*, were present in the samples and were

generally more abundant in PS than in IS sites. We collected 492 Nemouridae, 450 individuals in PS sites and 72 individuals in IS sites, recorded in 11 and 6 reaches, respectively. Among the three genera, *Protonemura* resulted the most abundant and widely distributed genus, with 264 individuals recorded in 13 out of 28 reaches, with higher occurrence and abundance in PS (Occurrence = 8 reaches; Abundance = 225 individuals) than IS sites (Occurrence = 5 reaches; Abundance = 39 individuals). *Amphinemura* was slightly less abundant than *Protonemura*, with a total of 236 individuals of *Amphinemura*, 205 in PS sites and 31 in IS sites, recorded in 10 reaches and 4 reaches, respectively, for a total of 14 reaches. *Nemoura* showed the lowest occurrence and abundance, with only 22 individuals collected, 20 in PS sites and 2 in IS sites, recorded in 8 and 2 reaches, respectively, for a total of 10 reaches. Of the 28 investigated reaches, 11 had no Nemouridae, 2 had only one genus, 10 hosted 2 genera and 5 reaches accounted for the three examined genera.

Ecological niches of Nemouridae

Among the three examined genera, *Protonemura* showed the highest dimension of the four-dimensional hypervolume (559.4), followed by *Amphinemura* (353.0) and *Nemoura* (248.8). The three hypervolumes partially overlap (Fig. 1) as demonstrated by the Jaccard and Sorensen similarity indices (Table 1). Although *Nemoura* has the smallest hypervolume, about 50% of its ecological niche is unique and does not overlap with that of *Protonemura* and *Amphinemura* (Unique 1 values at the first and second line, respectively in Table 1). The highest overlap value is observed between the ecological niches of *Amphinemura* and *Protonemura* (Table 1). The overlap between ecological niches (Fig. 1) indicates that the unique portion of *Nemoura* niche is mainly determined by the fact that it is not limited by the presence of other shredder taxa (Competition), but it seems to be the most limited by the amount of organic matter (CPOM). *Amphinemura* and *Protonemura* show an opposite pattern compared to *Nemoura*, as they occupy all ecological niches determined by CPOM while they are limited by the competition with other shredder taxa (Fig. 1). When considering the Froude number and the Substrate Index, the ecological niches of the three genera broadly overlap, suggesting that

they have similar requirements in terms of hydromorphological conditions (Fig. 1).

Effects of flow intermittency on the ecological niches of Nemouridae

The Wilcoxon test highlighted significant differences among PS and IS sites for all the three genera, as PS sites had higher abundances and more favorable habitat conditions than in IS sites (Table 2), and among PS and IS sites in terms of Substrate Index, CPOM mass, and Competition, while no differences were observed for the Froude number (Table 2). In particular, our results highlight how PS sites have significant higher values of SI, CPOM and Competition than IS sites.

To evaluate how flow intermittency affects the ecological preferences of the three examined genera, we performed the OMI analysis, which showed how responses to hydrological intermittency seems to be genera-specific.

In PS sites, *Amphinemura* showed the highest marginality and tolerance values, thus being the genus that occupies the most marginal microhabitats, whereas *Nemoura* showed the lowest marginality, which means that it occupies the most typical microhabitats in permanent sites (Table 3). When considering tolerance, *Amphinemura* showed the highest values, thus having the widest niche, while *Protonemura* showed the lowest tolerance values, thus being the genus with the narrowest niche in permanent sites (Table 3). In IS sites, *Nemoura* has the highest marginality, thus occupying the most marginal microhabitats in intermittent sites, whereas *Protonemura* has the lowest marginality value, thus occurring in the most typical microhabitats of intermittent sites (Table 3). When considering niche width, *Amphinemura* resulted the genus with the widest niche, as it had the highest tolerance value, whereas *Protonemura* has the narrowest niche as demonstrated by the fact that it has the lowest tolerance value (Table 3).

When considering the role of environmental variables, *Nemoura* was positively affected by Froude number (0.31), Competition (0.55), and weakly by CPOM mass (0.10), but negatively by SI (− 0.22) in PS sites (Table 4 and Fig. 2a), while it is positively affected by CPOM mass (0.23) and negatively by Competition (− 0.28), Froude (− 0.76) and SI (− 1.06) in IS sites (Table 4 and Fig. 2b). *Protonemura*

Fig. 1 Bi-plots showing the two-dimensional aspects of the estimated four-dimensional hypervolumes in a pair-wise comparison among the three genera. The colored points for each genus reflect the centroids (large points), original observations (intermediate points) and the stochastic points sampled from the inferred hypervolume (small points). All variable are standardized

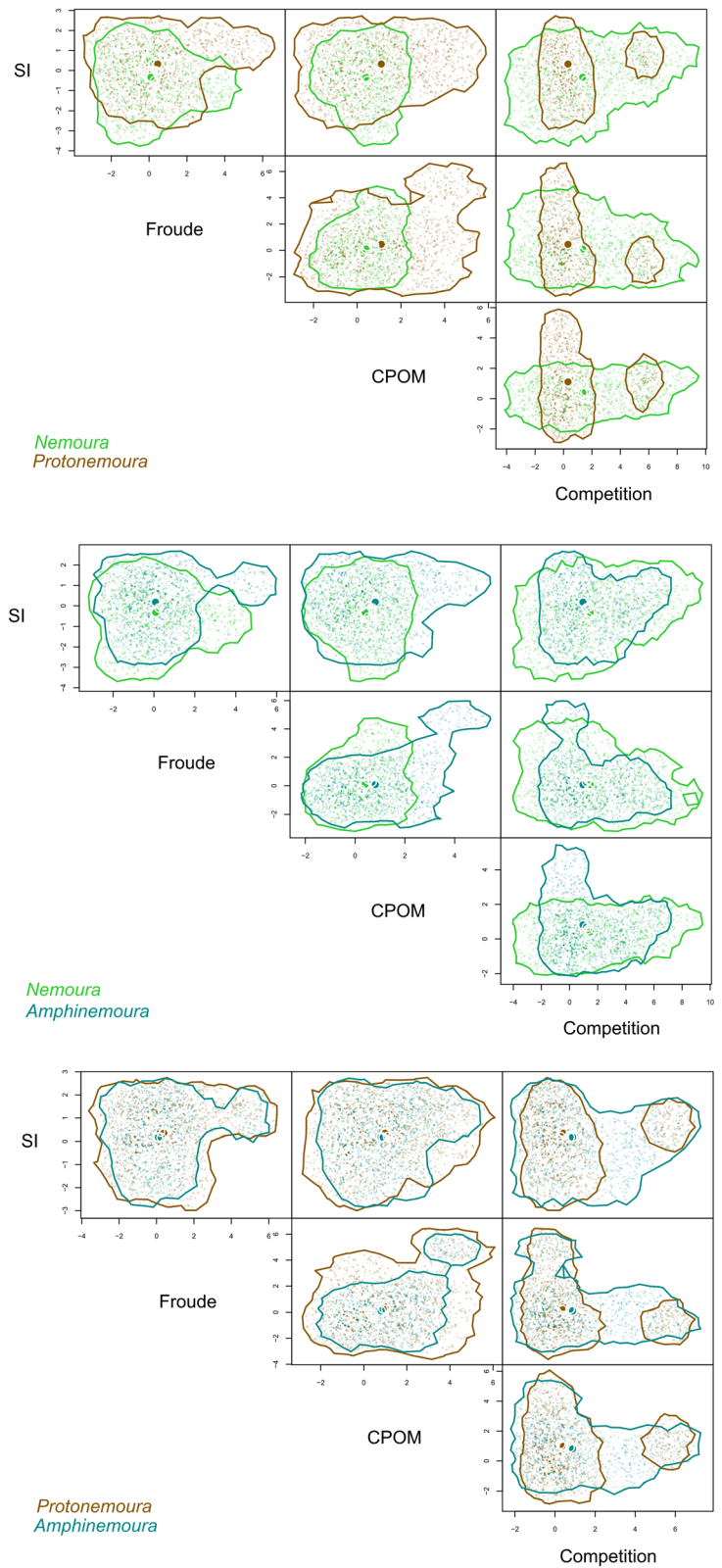


Table 1 Average values and standard deviations for environmental parameters and abundance of the three examined genera in PS and IS sections

Parameter	PSs	ISs	Wilcoxon test
Froude number	0.35 ± 0.18	0.31 ± 0.21	V = 2915; P = 0.083
Substrate Index	6.30 ± 0.49	6.07 ± 0.59	V = 2854; P = 0.005
CPOM mass (g/m ²)	14.2 ± 14.2	9.68 ± 11.8	V = 3030; P = 0.032
Competition (n/m ²)	130 ± 6.67	29.5 ± 77.6	V = 1714; P < 0.001
<i>Nemoura</i> (n/m ²)	3.23 ± 11.8	0.32 ± 2.26	V = 52; P = 0.013
<i>Protonemura</i> (n/m ²)	37.1 ± 151	6.45 ± 25.3	V = 445; P < 0.001
<i>Amphinemura</i> (n/m ²)	33.7 ± 80.5	5.16 ± 19.2	V = 790.5; P < 0.001

Significant results are reported in bold

Table 2 Results of the hypervolume overlap statistics for the three pairs of genera examined here

Parameter	Jaccard	Sorensen	Unique 1	Unique 2
<i>Nemoura</i> vs <i>Protonemura</i>	0.27	0.43	0.62	0.51
<i>Nemoura</i> vs <i>Amphinemura</i>	0.40	0.57	0.52	0.31
<i>Protonemura</i> vs <i>Amphinemura</i>	0.50	0.67	0.37	0.29

The Jaccard and Sorensen similarity indices provide a measure of the niche overlap, ranging from 0 (no overlap) to 1 (complete overlap), whereas the Unique 1 and Unique 2 represent the fractions of the hypervolume that are exclusive of the first and second species in the pair, respectively

Table 3 Niche parameters of Nemouridae genera

PS/IS	Genus	Inertia	OMI	Tol	Rtol	P
PS sites	<i>Nemoura</i>	5.24	0.46	1.36	3.43	0.425
	<i>Protonemura</i>	2.23	0.06	0.43	1.74	0.979
	<i>Amphinemura</i>	4.84	0.74	1.48	2.62	0.024
IS sites	<i>Nemoura</i>	3.24	1.84	0.68	0.71	0.272
	<i>Protonemura</i>	6.34	0.71	0.87	4.76	0.198
	<i>Amphinemura</i>	5.14	0.77	1.80	2.56	0.173

Inertia = variance or weighted sum of squared distances to the origin of the environmental axes; OMI = contribution of the outlying mean index (marginality) to the total inertia; Tol = contribution of tolerance to the total inertia; Rtol = residuals; P P value of the Monte Carlo test for the OMI. Significant results are reported in bold

Table 4 Eigenvalues of projected environmental variables and examined genera on OMI axes in PS and IS sites

Environmental variables	PS sites		IS sites	
	Axis 1	Axis 2	Axis 1	Axis 2
Froude number	0.18	0.63	0.03	0.29
Substrate Index	− 0.46	− 0.02	− 0.70	− 0.67
CPOM mass (g)	− 0.31	− 0.57	− 0.71	0.68
Competition	0.42	0.51	0.07	0.09
Genera				
<i>Nemoura</i>	− 0.47	3.51	0.78	1.99
<i>Protonemura</i>	0.28	0.95	− 1.00	− 0.82
<i>Amphinemura</i>	1.44	− 0.09	− 1.01	1.11

was positively affected by Froude number (0.14) and negatively affected by SI (− 0.17), while it showed an extremely low influence of CPOM mass (− 0.06) and Competition (− 0.05) (Table 4 and Fig. 2a) in PS sites. In IS sites, it showed a positive relationship with CPOM (0.41) and SI (0.71), whereas it is negatively affected by Competition (− 0.11) and Froude (− 0.17) (Table 4 and Fig. 2b). *Amphinemura* is favored by Competition (0.61), followed by CPOM mass (0.45), and SI (0.38), but it is weakly negatively affected by

Froude number (− 0.14) (Table 4 and Fig. 2a) in PS sites. In IS sites, it is positively correlated with CPOM mass (0.80), Froude (0.12) and SI (0.35), while it is not affected by Competition (− 0.01) (Table 4 and Fig. 2b).

Therefore, *Nemoura* shifts from reophilous microhabitats with finer substrates, high hydraulic stress and competition in permanent sites towards microhabitats with finer substrates, high CPOM availability and low competition and hydraulic stress in intermittent sites. *Protonemura* prefers microhabitats with finer

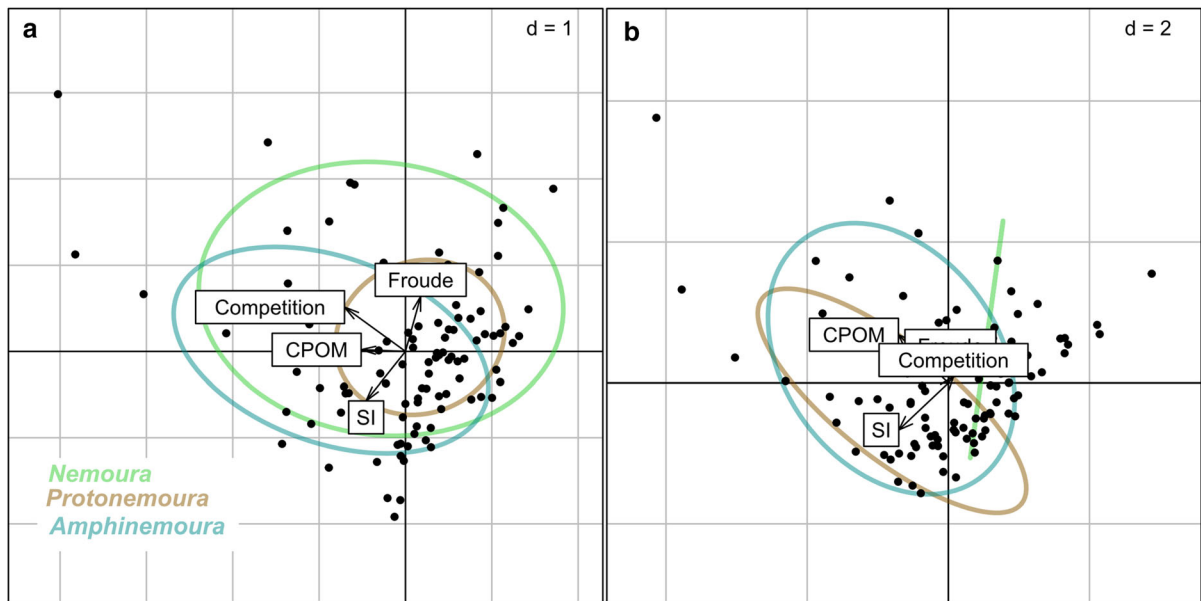


Fig. 2 Projection of environmental variables on the axis of OMI analysis and representation of ecological niches of the three examined genera in: **a** PS sites (axis 1 = 92.0% of total explained variance, and it represents a gradient of increasing competition and decreasing coarseness of the substrate; axis 2 = 7.82% of the total explained variance, and it is a gradient of decreasing CPOM mass and increasing hydraulic stress); and

b IS sites (axis 1 = 82.7% of total explained variance, and it represents a gradient of decreasing CPOM mass and SI; axis 2 = 12.5% of total explained variance, and it represents a gradient of decreasing SI and increasing CPOM mass). The *d* value reported in the top right corner of the pictures represents the measure of one square along the two axes

substrates and high hydraulic stress in permanent sites, whereas it is mainly found in microhabitats with coarser substrates, high CPOM availability and low hydraulic stress and competition in intermittent sites. *Amphinemoura* selects microhabitats with coarser substrates and high competition and CPOM availability in permanent sites, while it is not affected by competition in intermittent sites.

Discussion

We here evaluated the role of flow intermittency in shaping the niche of three coexisting phylogenetically related shredders in Alpine streams recently facing summer seasonal drying events. As summer drying may strongly affect the CPOM processing, by altering the decomposition by fungi and bacteria, and availability, as high fine sediment deposition buries CPOM, in the subsequent months, we here tested whether and how flow intermittency affects the three shredder genera belonging to the Nemouridae family, namely *Nemoura*, *Protonemoura* and *Amphinemoura*. By first

highlighting how these three genera share similar ecological requirements, we then demonstrated a clear negative effect of flow intermittency on both the abundance and ecological preferences of *Nemoura*, *Protonemoura* and *Amphinemoura*.

Ecological niches of Nemouridae

As we expected differences in the ecological requirements of Nemouridae, we first examined whether the examined genera differed in the dimension of their realized ecological niches and whether they overlap in their ecological requirements. Our results displayed only a partial overlap of the niche hypervolumes of the three genera, partially confirming our first hypothesis. Although our model organisms were found to co-occur in similar hydromorphological conditions, they differ in their niche dimension especially in terms of CPOM availability and potential competitive pressure. *Nemoura* displayed the smallest niche, but it also showed the highest unique component, which can be due both to competitive exclusion and the capacity to exploit atypical habitats. The results of the OMI analysis

support this second hypothesis as *Nemoura* occupied the most atypical habitats in intermittent sites. In addition, this genus is also possibly the most negatively affected by flow intermittency as its tolerance decreases from perennial to intermittent sites. We can hypothesize that this can be due to the fact that some species within this genus, such as *Nemoura cinerea*, display semivoltine populations (Fochetti et al., 2009). Voltinism has been recognized as one of the most sensitive traits (Bonada & Doledec, 2018) to flow intermittency as shifts from semivoltinism to multivoltinism have been observed from perennial to intermittent hydrological regimes in Mediterranean streams (López-Rodríguez et al. 2009a, b). In fact, plurivoltine species can overcome the negative effects of flow intermittency events on individuals inhabiting the stream during summer by producing multiple generations per year. Conversely, individuals semivoltine species, i.e., completing their life cycle in more than 1 year, have to face the drying up of the riverbed, thus being strongly affected by these events.

Although being highly sensitive to flow intermittency, *Protonemura* and *Amphinemura* resulted to be less influenced by flow intermittency than *Nemoura*, possibly because species belonging to these genera are mainly monovoltine (Fochetti et al., 2009), and their life cycle allows them to escape flow intermittency events by emerging before their occurrence. This hypothesis of a similar response of these two genera to flow intermittency is further supported by the fact that their ecological niches broadly overlap. Although having the widest niche, the results of the OMI analysis suggest that *Protonemura* is outcompeted by *Amphinemura*, which has the highest tolerance in both permanent and especially in intermittent sites. Although being negatively affected by flow intermittency, as demonstrated by the lower number of individuals in intermittent compared to permanent sites, *Amphinemura* was the most tolerant genus to flow intermittency among the three Nemouridae genus studied. This can be due to the lower body size dimensions of this genus compared to *Nemoura* and *Protonemura* (Fochetti et al., 2009) as small body size is also a common attribute of macroinvertebrate taxa living in intermittent streams because smaller individuals have display fast development and population growth, which allow to complete the life cycle before the water disappears (Bonada et al. 2007).

Effects of flow intermittency on the ecological niches of Nemouridae

When considering the effect of flow intermittency on the three examined genera, our results showed that abundances of the three genera were lower in intermittent than in permanent reaches, in agreement with our second hypothesis. This is in accordance with the results observed in a related study performed in the same study area, where we observed a significant negative effect of flow intermittency on the relative abundance of scrapers taxa (Piano et al., 2019a). This reduction is due to the lower availability of organic matter in intermittent than in permanent sites, which is in turn potentially determined by the lower retention capacity of the riverbed substrate in intermittent sites. In fact, although the flow had recovered since 6 months at the sampling moment, we still observed a significant lower value of the substrate index in intermittent sites, indicating that sites experiencing recurrent drying events are characterized with finer substrates than perennial sites. Heavy fine sediment accumulation (i.e., clogging) is strictly associated with flow reduction and droughts, because lower water velocity prevent the export of fine sediments (Dewson et al., 2007; Rolls et al., 2012), thus reducing the retention capacity of the substrate. In addition, the high fine sediment deposition can alter the quantity of energy inputs, as it affects the amount of autotrophic production (Henley et al., 2000; Bona et al., 2016) and allochthonous coarse organic matter availability in Alpine streams (Doretto et al., 2016, 2017). In particular, the burial of leaf litter by sediments reduces availability of this resource and alters the composition of the microbial community involved in its degradation (Receveur et al., 2020), with consequent negative effects on shredder invertebrates (Danger et al., 2012).

When focusing on the differences in ecological niches of the three genera between permanent and intermittent sites, the relationship with CPOM is weak in permanent sites, except for *Amphinemura*, but it becomes consistently and highly positive in intermittent sites, suggesting food limitation under flow intermittency conditions. Competition with other shredders positively influences the examined genera in permanent sites, except for *Protonemura*, suggesting that in permanent sites, where CPOM availability is high, different shredder taxa can coexist. Conversely, in intermittent sites, competition with other

shredders has a consistent weak negative effect, possibly because the access to trophic resources is dominated by exploitative competition among shredder taxa due to food limitation, with detrimental effects on Nemouridae. Our suggestion is supported by Tierno de Figueroa & Lopez-Rodriguez (2019) reviewed how Nemouridae are highly dependent on CPOM, even if some species can act as collector-gatherers (Lopez-Rodriguez et al., 2010).

While the role of CPOM availability and competition in determining the ecological niches in permanent and intermittent sites is consistent among the three examined genera, the role of the hydromorphological parameters is more controversial. When considering the Froude number, *Nemoura* and *Protonemura* were favored in reophilous microhabitats in permanent but not in intermittent sites, whereas *Amphinemura* was weakly affected by this factor. Our sampling sites are located in mountain streams, where near-bed hydraulic stress is naturally high. In these conditions, CPOM usually accumulates when particles hit an obstruction, such as a rock, log or vegetation, where the hydraulic stress is lower (Hoover et al., 2006; Quinn et al., 2007). Therefore, at microhabitat level, hydraulic conditions have an indirect effect on the examined genera, with high Froude numbers likely negatively affecting the occurrence of shredder taxa as often associated with low CPOM retention. We can suggest that in permanent sites, where there is no food limitation, *Nemoura* and *Protonemura* better thrive in fast flowing conditions, which represent optimal habitats for Nemouridae (Usseglio-Polatera et al., 2000), whereas in intermittent sites they select suboptimal habitats, where the CPOM concentration is expected to be higher (Quinn et al., 2007).

Given that microhabitats with low flow velocity are deposition areas not only of CPOM but also of fine sediments (Quinn et al., 2007), the substrate preference can also indirectly affect the examined genera by conditioning the availability of CPOM. In fact, we observed again contrasting results among the three examined genera, and even between permanent and intermittent sites for *Protonemura*, which could be ascribed to the relationship between CPOM availability and substrate composition. In fact, *Protonemura* is mainly found on finer substrates in permanent sites whereas it shifts on coarser substrates in intermittent sites. This change can be due to the food limitation in

intermittent sites, where *Protonemura* selects microhabitat with coarser substrates that have a higher retention capacity of CPOM. The relationship of *Nemoura* and *Amphinemura* with this parameter corroborates this hypothesis, as *Amphinemura*, which shows the stronger association with CPOM in both permanent and intermittent sites, has a consistent positive relationship with the Substrate Index, whereas *Nemoura*, which is the genus with the lowest association with CPOM in both permanent and intermittent sites, consistently prefers finer substrates.

Conclusions

Overall, our results emphasize how stream physical parameters, resource availability and their interaction play a key role in determining the distribution and the ecological niche of shredders in Alpine streams. Recurrent drying events negatively affect the examined genera, which are less represented in ISs than in PSs, and the narrower niches in ISs than in PSs, and their niche shift in ISs furtherly corroborate this hypothesis. According to our results, the negative effect of flow intermittency is mainly due to the reduced availability of CPOM compared to permanent sites confirming previous findings in other temperate geographical areas (Datry et al., 2011; Pinna et al., 2016). Consequently, water flow reduction and recurrent drying events are expected to reduce shredder biodiversity by altering the availability of their energetic inputs, with potential dramatic effects on stream ecosystem functionality (e.g., Ledger et al., 2008; Datry et al., 2011; Piano et al., 2019b). In fact, the expected decrease in allochthonous trophic resources will likely cause a bottom-up effect in the food web, directly influencing the survival, growth and reproduction of invertebrate shredders. Further investigations in mountain areas are thus required in the next future to better unravel how the interaction between flow intermittency and CPOM availability may affect shredders in lotic ecosystems.

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