RESEARCH ARTICLE

WILEY

Quantifying the ecological effects of water abstraction in Alpine streams through flume simulations

Francesca Vallefuoco[1,2] ⬦ | Maria Cristina Bruno[1] ⬦ | Guido Zolezzi[2] ⬦ | Stefano Larsen[1] ⬦

[1]Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy

[2]Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy

Correspondence
Maria Cristina Bruno, Research and Innovation Centre, Fondazione Edmund Mach, Via E. Mach 1, I-38098 San Michele all'Adige, Italy.
Email: cristina.bruno@fmach.it

Abstract

Water abstraction by small hydropower plants is a growing human pressure on Alpine stream ecosystems. Using a set of seminatural streamside flumes, we investigated the response of benthic invertebrate communities to a 50% experimental reduction of the natural discharge. We collected EPT taxa from upstream (control) and downstream (flow reduction) sections of the flumes before starting the simulations, and after 1 and 3 weeks of simulated flow reduction, while also collecting invertebrates drifting from each section every 24–48 h. Despite an initial (i.e., before simulation) difference in benthic densities and diversity between controls and treatments, these metrics changed and differed over time, with the reduced flow section becoming more diverse and with less individuals. Taxonomic composition differed between flow types, with a short-term (1 week after the beginning of flow reduction) increase of taxonomic heterogeneity. There was no evidence that flow reduction affected functional diversity and homogenized functional composition of the communities. Drift composition differed between flow types with drift rates and richness lower under reduced flow. Functional dispersion was always significantly lower in the drift collected in low-flow conditions where drift propensity was significantly higher for animals preferring medium to fast currents, living temporarily attached to the substrate and feeding as passive filterers; drift propensity was slightly lower for organisms moving as crawlers. Hence, short-term taxonomic and functional changes in benthic invertebrate communities with reduction in flow are likely related to behavioural responses such as drift, thus providing insight on the potential mechanisms underlying community-level effects of water abstraction.

KEYWORDS
drift, functional traits, macroinvertebrates, residual flows, small hydropower plants

1 | INTRODUCTION

Water abstraction for human needs is projected to increase globally to satisfy growing water demands, while at the same time representing one of the most challenging anthropogenic pressures on freshwater bodies worldwide (Dewson et al., 2007). As other hydromorphological pressures, water abstraction from streams and rivers is one of the main drivers of ecological degradation, even when water

pollution is not a particular concern (European Environment Agency [EEA], 2018). This is especially the case for Alpine streams, in which human activities are mainly affecting the river hydromorphology. In Alpine systems, the main source of water abstraction (Alpine Convention, 2009) is represented by hydropower, with smaller shares of human water demands associated with industry, agriculture, artificial snow production and drinking water.

In the Alpine region, recent increases in water abstractions have been associated with the widespread development of small hydropower plants triggered mainly by the economic incentives to promote energy production from renewable sources (Platform Water Management in the Alps, 2011). The large majority of the recent hydropower plants are small in size (capacity generally <10 MW), localized, with no or very small storage capacity (i.e., run of the river), and most often dewater a river stretch by means of a water diversion (Couto & Olden, 2018). Such dewatering can be very severe during drought periods (Wu et al., 2010). Recent assessments suggest that these small diversion systems (referred to as SDHPs in the following) produce proportionally (i.e., by unit of energy produced) more detrimental ecological effects than large facilities (Abbasi & Abbasi, 2011; Kelly-Richards et al., 2017; Kibler & Tullos, 2013). In fact, reduced flows normally alter the physical habitat of the stream reach, with reduced flow velocities, depths and potentially increased streambed siltation (Ward & Stanford, 1979). Hence, while lacking some of the effects associated with large reservoirs (e.g., emission of greenhouse gases and thermopeaking), SDHPs reduce hydrologic connectivity and alter natural sediment and flow regimes (Couto & Olden, 2018). Furthermore, SDHPs generally occur in smaller rivers and headwaters (Kibler & Tullos, 2013), which further increases their ecological impacts, given the importance of headwater streams in maintaining hydrologic connectivity, harbouring biodiversity and supporting ecosystem integrity at regional scales (Larsen et al., 2021; Meyer et al., 2007).

The most documented consequences of water abstractions and flow alterations caused by SDHPs are related to fish fauna (e.g., Bakken et al., 2021), with numerous studies showing decreased fish density and biomass in impacted reaches (Couto & Olden, 2018 and reference therein; Levin & Tolimieri, 2001). Conversely, the response for other organism groups and effects on the trophic structure remain unclear. For instance, no clear patterns emerged for the response of benthic invertebrates to flow alteration, with both decreases and increases in diversity observed (Poff & Zimmerman, 2010). Predicting the response of primary and secondary consumers to future SDHP development is paramount as they drive instream carbon processing and represent key links in the riverine food chain. However, despite substantial effort from the scientific community (Poff & Zimmerman, 2010), the development of quantitative relationships between flow alteration caused by SDHPs and ecological response has remained limited (Couto & Olden, 2018).

As already stated by James and Suren (2009), monitoring the impact of reduced flows per se on invertebrate communities upstream and downstream of abstraction points can be challenging, due to the potential synergistic effects of changes in other variables (e.g., temperature, oxygen concentration, conductivity) caused by

water abstraction. Such difficulties can be overcome by using experimental channels in which flows can be closely manipulated without causing large alterations to other physicochemical variables and the ecological effect of flow reduction can be singled out and analysed in detail. In fact, experimental flow manipulation is a relevant approach to understanding the impacts of low reduction on instream habitat and communities (Dewson et al., 2007). For this reason, in this study, we used a set of semi-artificial flumes to replicate the operation of a SDHP, by simulating an upstream reach with undisturbed (higher) flow and a downstream reach with residual flow. Scope of our research was to assess if and how short-term flow reduction affected the taxonomic and functional composition of benthic invertebrates, with particular focus on the Ephemeroptera, Plecoptera and Trichoptera (EPT), which are good indicators of environmental conditions in streams (Barbour et al., 1996; Lenat, 1988). Specifically, we hypothesized that flow reduction would lead to short-term changes in the functional and taxonomic composition of EPT communities, namely, a decrease in density and diversity and an increase in the relative density of taxa with preferences for lower velocity conditions, and a decline in the relative density of more sensitive taxa, resulting in a taxonomic and functional homogenization (decline in beta-diversity). Taxonomic and functional changes in the benthos were interpreted in light of taxa-specific responses in drift dynamics.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

The study was conducted using a set of five metal flumes installed on the right bank of the second-order Fersina Stream (46°04′33″ N; 11°16′27″ E), at an elevation of 580 m asl, in Trentino Province, Northeastern Italy (more details on the study site in Bruno, Cashman, et al., 2016; Gruppuso et al., 2021) (Figure S1). Each one of the five 20-m-long, 30-cm-wide, 30-cm-tall metal flumes is fed by the same 1 m^3 loading tank that collects water directly diverted from the stream. Discharge in each flume can be controlled by a sluice gate at the inlet. This setting allows benthic macroinvertebrate colonization mainly by incoming drift (Doretto et al., 2018), supplemented by aerial deposition of eggs by adults. The flume bottom is covered with a 20-cm-thick layer of fluvial cobbles (approx. 10 cm diameter) and, below that, a layer of gravel and sand deposited naturally by the water flow. This layer that cannot be considered a proper hyporheic zone as it is very thin and overlays the metal bottom of the flumes. We used three flumes for the simulation; a faucet was installed at half-length of each flume that, when open, would allow to withdraw a maximum of 5 L s^{-1}, thus dividing the flume in an upstream 10 m section at the initial higher flow and a downstream 10 m section with a reduced discharge. The flumes were kept at a baseflow of approximately 5 L s^{-1} from 1 April 2017 (i.e., the year preceding the simulations); 1 month before starting the experiment, on 23 August 2018, we manipulated the inlet sluice gates of each flume to establish an inflow of 7 L s^{-1} which was kept constant throughout the experimental period. On the

same date, in each flume section, we deployed 10 slotted circular baskets (kitchen colanders, 24 cm diameter, 11 cm depth) filled with substrate collected from the flumes to mimic the grain size distribution of the surrounding flume substrate, which was scraped to remove the invertebrates before inserting it into the baskets. The baskets underwent natural colonization by macroinvertebrates for 35 days. On 28 September, 1 month after setting the discharge at 7 L s^{-1}, we collected benthic samples before starting the water abstraction simulations (samples coded S0) by randomly removing three baskets (each one representing one replicate) from each flume/section, for a total of 3 (replicates) $\times$ 3 (flumes) $\times$ 2 (sections) = 18 baskets (Figure S2). Benthic invertebrates were removed from individual stones, filtered through a 350-μm mesh, transferred to a 70% ethanol solution and carried to the laboratory for identification. We started the water abstraction simulations after collecting the benthic samples, by opening the mid-flume lateral faucets to let approximately 5 L s^{-1} of water out from each flume; as a result, the downstream section of each flume had a reduced discharge of approximately 2 L s^{-1} which was kept for the remaining of the simulation. A second and a third set of 18 samples (samples coded S1 and S2, respectively) were collected on 4 October and 18 October, that is, respectively, after 1 and 3 weeks from the beginning of the flow reduction treatment, applying the same procedure as described for S0 (Figure S2). We used drift nets (350-μm mesh) fixed to a square metal frame which was tightly fitting into the flume to prevent further colonization and collect all benthic invertebrates drifting in and out of each section. Drift nets were placed upstream and downstream of each flume section immediately after collecting the benthic samples at S0 and before opening the faucets and remained in the flumes for the whole experimental period (Figure S2). Drift samples were collected approximately every 24–48 h from 28 September to 14 October (samples d1 to d13). In order to avoid invertebrates to cross sections during the net manipulations, before removing each drift net containing the collected invertebrates, we placed a second drift net a few cm downstream, and we carefully set it in place after removing the upstream one. One set of drift samples was retained and analysed due to time constraints and assuming that pattern observed in one flume reflect the overall drift dynamics, as already observed in other simulations conducted in the flumes (Bruno, Carolli, & Maiolini, 2016; Bruno, Cashman, et al., 2016).

On each sampling occasion, and for each flume and flume section, we measured physical and chemical parameters of surface water such as temperature (°C), oxygen concentration (mg L^{-1}), conductivity (μS m^{-1}), pH, turbidity (NTU) with a multi-parameter portable meter (Profi-Line pH/Cond 3320, WTW GmbH and Co., Weilheim, Germany); flow velocity (at 60% total depth from water surface) was recorded by using a digital water velocity meter (Global Water Flow Probe, College Station, Texas, USA).

A consistency check on the experimental flow setting was performed before removing the second set of baskets (i.e., on 4 October). Flow velocity and depth were measured along three cross-sections (at lateral distances 7, 15 and 23 cm from each side) located above three randomly-selected baskets from each flume/section. A manual hydrometer was used to measure the local flow depth, as the

difference between the water and bed surfaces readings in the same point, while surface flow velocity was measured with a hand-held Surface Velocity Radar (Welber et al., 2016). Actual discharge was calculated from the bottom height that could be controlled at each sluice gate, through previously validated rating curves derived for each flume. The local Froude numbers (Fr) were calculated to each coupled depth (D) and velocity (U) measurement using the formula $\frac{U}{\sqrt{gD}}$, which theoretically applies for a horizontal rectangular channel (Chanson, 2004).

2.2 | Macrobenthos processing

Overall, we collected 54 benthic samples and 13 drift samples. Only EPT were retained for the analyses. For these orders, functional traits are available to the genus/species level. In the laboratory, instars of EPT were identified to the species or genus level, when possible, following Campaioli et al. (1994, 1999), Tachet et al. (2010) and Waringer and Graf (2011). Information on functional traits were retrieved from www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2015). The functional traits chosen (Table 1) to assess the impacts of flow reduction relate to the habitat preference and colonization modalities (dispersal, substrate and flow velocity preference, locomotion and substrate relation, hence ability to avoid drift), physiology (resistance to desiccation, respiration) and trophic habits (feeding type) of each taxon. Affinities of each taxon to each trait category were standardized between 0 and 1 using a fuzzy coding procedure (Chevene et al., 1994). Fuzzy coding data were then converted to percentages of affinity for each trait category by weighting each category by species relative density to obtain a matrix of proportion of each trait category within each trait (Laliberté et al., 2014). This procedure partitions, for each trait, the densities of the species into the different trait category they expressed (an example is provided in S1).

Benthic densities of each taxon were expressed as the ratio of counts to total sampled surface, represented by the basket area (i.e., as taxon density, expressed as N. ind m^{-2}). Drift was expressed as drift rate, which represents the number of benthic invertebrates drifting each hour from the defined benthic surface area subject to the treatment of control flow (expressed as N. ind h^{-1}), and as drift propensity, which provides a measure of drift standardized by the benthic density of the source population, calculated as drift density/benthic density. To do so, because drift was collected approximately every 24 h, and benthos only on Days 7 (i.e., S1) and 21 (i.e., S2), we calculated the total drift density (expressed as N. ind m^{-3}) from Days 1 to 7, and from Days 8 to 21, and divided, respectively, for the average benthic densities at S1 and S2. Benthic densities, drift rates and drift propensities were used to calculate the respective taxonomic and functional datasets which were used for the statistical analysis.

2.3 | Statistical analyses

For each sample, we calculated the following community metrics: densities (N. ind m^{-2}), taxonomic richness (expressed as S = number of

TABLE 1 List of functional traits selected for the analysis, as retrieved from www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2015)

Parameter typology	Parameter name	Abbreviation	Trait category and explanation
H	Substrate (preferendum)[a]	sub-fbcp	Flags/boulders/cobbles/pebbles
		sub-grvl	Gravel
		sub-sand	Sand
		sub-silt	Silt
		sub-macp	Macrophytes
		sub-micp	Microphytes
		sub-twro	Twigs/roots
		sub-odli	Organic detritus/litter
		sub-mud	Mud
H	Current preference[b]	curr-ind	Indifferent: No preference for a certain current velocity
		curr-lrp	Limnophile to rheophyle: Preferably occurring in standing waters but regularly occurring in slowly flowing streams
		curr-lib	Limnobiont: Occurring only in standing waters
		curr-lip	Limnophile: Preferably occurring in standing waters; avoids current; rarely found in slowly flowing streams
		curr-rlp	Reophyle to limnophile: Usually found in streams; prefers slowly flowing streams and lentic zones; also found in standing waters
		curr-rhb	Rheobiont: Occurring in streams; bound to zones with high current
		curr-rhp	Rheophile: Occurring in streams; prefers zones with moderate to high current
H	Current velocity (preferendum)[a]	vel-null	$<5\ cm\ s^{-1}$
		vel-slow	$5–25\ cm\ s^{-1}$
		vel-medium	$25–50\ cm\ s^{-1}$
		vel-fast	$>50\ cm\ s^{-1}$
L	Locomotion and substrate relation[a]	loc-wsw	Full water swimmer
		loc-crw	Crawler
		loc-bur	Burrower (epibenthic)
		loc-int	Interstitial (endobenthic)
		loc-tat	Temporarily attached
L	Dispersal[a]	disp-aer-act	Aerial active
		disp-aer-pas	Aerial passive
		disp-aq-act	Aquatic active
		disp-aq-pas	Aquatic passive
L	Feeding type[c]	feed-gra	Grazers/scrapers: Feed from endolithic and epilithic algal tissues, biofilm, partially POM, partially tissues of living plants
		feed-shr	Shredders, feed from fallen leaves, plant tissue, CPOM
		feed-gat	Gatherers/collectors: Feed from sedimented FPOM
		feed-pff	Passive filter feeders: Feed from suspended FPOM, CPOM, prey; food is filtered from running water, e.g., by nets or specialized mouthparts
		feed-pre	Predators, feed from prey
L	Resistance forms[a]	res-coc	Cocoons
		res-did	Diapause or dormancy
		res-egg	Eggs, gemmula, statoblasts
		res-non	None

TABLE 1 (Continued)

Parameter typology	Parameter name	Abbreviation	Trait category and explanation
L	Respiration[a]	resp-gil	Gills
		resp-teg	Tegument

Note: For parameters typology: H = habitat parameters, L = life and body related parameters.
[a]Tachet et al. (2010).
[b]Schmedtje and Colling (1996).
[c]Moog (1995).

taxa and d = Margalef taxa richness), Hill–Shannon diversity (N1, computed as effective number of species of order q = 1; Jost, 2006; Roswell et al., 2021) and functional dispersion (FDis). FDis was chosen as a measure of functional diversity that is mathematically independent from taxa richness and was calculated with the FD package in R (Laliberté et al., 2014; Laliberté & Legendre, 2010). Individual community-weighted mean trait profiles were also examined.

To quantify the effect of the experimental flow reduction, we compared assemblages of control (i.e., upstream flume sections) and reduced flow treatments (i.e., downstream flume sections) according to the BACI framework. Hence, we used a generalized linear mixed model (GLMM) including 'time' (S0 = sample pre flow reduction; S1 = first sample post and S2 = second sample post) and 'treatment' (control vs. flow reduction) as fixed factors, where a significant interaction of 'time × flow' was considered indicative of experimental effects. We also included 'flume' identity as a random factor to account for the multiple observations within flumes. The glmmTMB function was used to model changes in taxonomic and functional metrics. Trait profiles were expressed as proportions and were modelled using a beta-distribution, which in most cases was better supported than a simple Gaussian or binomial distribution based on AIC values.

To quantify changes in composition, we calculated a similarity matrix based on Bray–Curtis similarity of the log(x + 1) transformed density of each taxon. We ran multifactorial permutational analysis of variance (PERMANOVA, Anderson & Walsh, 2013) as in the BACI approach described above, that is, with a crossed 'time × flow' design. For significantly differing factors, we tested pairwise PERMANOVA comparisons and used the similarity percentage analysis (SIMPER) (Clarke, 1993) to identify the species which contributed the most to the Bray–Curtis dissimilarity between control and reduced flow samples (Anderson et al., 2008), including in the analysis those taxa with a contribution to dissimilarity of at least 3%. Finally, we applied the principal coordinates analysis (PCoA) to the Bray–Curtis distances of log(x + 1) transformed densities to visualize the changes in composition over treatment and time in multivariate space. To test the hypothesis that experimental flow reduction led to taxonomic homogenization (reduced beta-diversity) we used the bedisper function to calculate the distance of each sample to the associated factor centroid (time and treatment) in multivariate space. Differences between control and treatment flow types were analysed using the GLMM BACI framework previously described.

Similarly, to quantify changes in functional compositional, we used the community-weighted mean trait profile (expressed as proportions) to calculate a similarity matrix based on the Bray–Curtis similarity, and we run the same PERMANOVA and SIMPER analyses as for the taxonomic dataset. To assess and visualize changes in the functional composition of communities, we run a fuzzy correspondence analysis (FCA) (Chevene et al., 1994) based on the community-level trait proportions using the dudi.fca function in ade4 R package (Chevene et al., 1994). Again, we used the bedisper function to calculate the distance of each sample to the associated factor centroids (time and flow) in multivariate space, to test the hypothesis that experimental flow reduction led to functional homogenization. Differences between flow types were then analysed using the GLMM BACI framework as previously described.

Drift was analysed to assess changes over time, and between reduced flow and control section, for the following metrics: drift rate (N. ind h^{-1}), taxonomic richness (expressed as S, number of species), Hill–Shannon diversity (N1) and functional dispersion (FDis). Differences between reduced flow and control sections were tested with a Mann–Whitney *U* test. We also produced a community-weighted mean trait proportion matrix using the same procedure as for the benthic samples. The log(x + 1) transformed drift rate and the drift traits proportions were used to calculate similarity matrices based on Bray–Curtis index and to run one-way PERMANOVAs for the factor treatment. Finally, we run a PCoA and a FCA to visualize differences and trends in taxonomic and functional composition in drift, respectively.

Statistical analyses were performed using the softwares R (version 3.6.2, R Core Team, 2019), PRIMER version 7 (Clarke & Gorley, 2015) with the PERMANOVA+ add-on package (Anderson et al., 2008) and Statistica ver. 13.3 (TIBCO Software Inc., 2017).

3 | RESULTS

3.1 | Hydrological and physicochemical parameters

The difference between the mean flow velocities of control and reduced flow sections were strongly significant (*T*-test *p* < 0.001). Froude number was less than unity in both sections (i.e., 0.69 ± 0.25 in controls and 0.66 ± 0.38 in treatments; *T*-test *p* value >0.05), which corresponds to a subcritical flow condition (i.e., flow dominated by
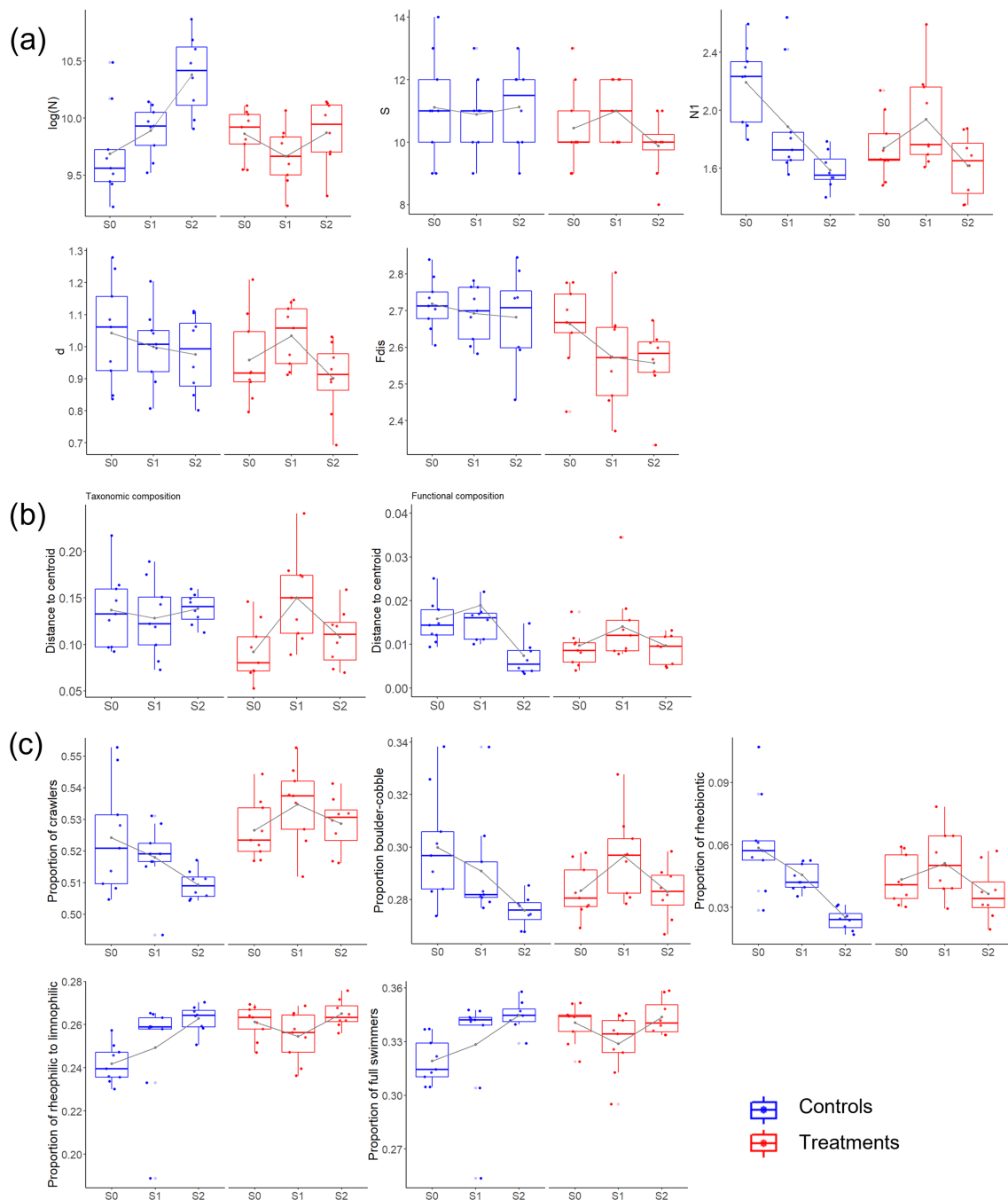
FIGURE 1   Box plots related to the GLMM tests, of (a) the benthic community metrics, (b) the distance of each sample from the centroid in the taxonomic and functional matrices and (c) the functional traits of benthic invertebrates identified by the SIMPER analysis as most contributing to dissimilarities between samples for the three sampling dates, in control and reduced flow flume sections, where the interaction in the GLM models 'time × treatment' was significant (for explanation of traits see Table 1). N = total density (N. ind m^{-2}); S = total number of taxa; d = Margalefs richness; N1 = Hills diversity Index; FDis = functional dispersion. Box = 25–75 percentiles, line = median; whisker = non-outlier range; points = single values. Grey lines join the points that represent the model predictions from the GLMs

gravitational over inertial forces, with mild oscillations of the water surface). The consistency check showed an average discharge of 4.8 (±1.12) L s^{-1} with an average velocity of 0.55 (±0.053) m s^{-1} in the control sections and an average discharge of 2.3 (±0.97) L s^{-1} with an average velocity of 0.38 (±0.065) m s^{-1} in the reduced flow sections, that is, a decrease in discharge of about 50% in the treatments.

The values of the physicochemical parameters (Table S1) were very similar between control and reduced flow sections of each flume, and among flumes. Changes over time were minimal: from S0 to S2, the average temperature increased almost 1°C, conductivity of 6.3 μS cm^{-1}, turbidity of 0.2 NTU and oxygen concentration and % saturation remained almost constant.
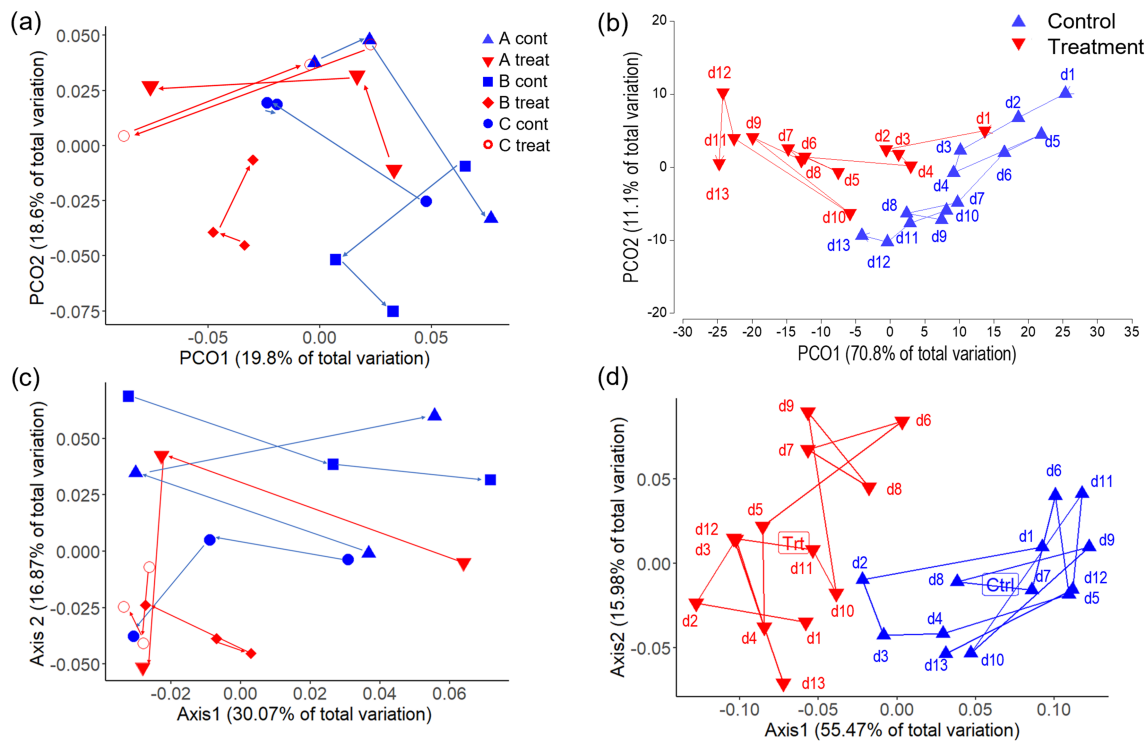
FIGURE 2 Principal coordinates analysis (PCoA) plot of (a) benthic invertebrate assemblages, centroids of each flume/flow; (b) drift assemblages. Fuzzy correspondence analysis (FCA) of the functional traits composition of (c) benthic invertebrates assemblages, centroids of each flume/flow; (d) drifting assemblages, with centroids (labelled) of reduced flow (=Trt) and control (=Ctrl) section. Arrows represent temporal trajectories (i.e., from S0 to S1, to S2 for benthos, from d1 to d13 for drift)

3.2 | Taxonomic changes of benthic communities

We collected a total of 51,619 EPT individuals in the artificial substrates, corresponding to 21,240 ind m^{-2}. *Baetis* spp. was the most abundant taxon, representing 88.7% and 87% in the controls and reduced flow treatments, respectively. Hydropsychidae and *Epeorus* sp. were also very abundant in both control and treatment sections. Together with *Baetis* spp, they comprised more that 94% of the total abundance.

Communities in the reduced flow and control sections differed at Time 0: The reduced flow sections had lower median Hill–Shannon diversity and species number and richness and higher densities. Differently from what was observed in the controls, where benthic densities increased over time (density S2/S1 = 1.5), in the reduced flow sections, densities decreased at S1, and increased only from S1 to S2 (density S2/S1 = 1.1) (Figure 1a). Conversely, benthic Hill–Shannon diversity did not decline in reduced flow as observed in control conditions, but rather, diversity had a small increase at S1 (Figure 1a). These two metrics differed significantly between controls and reduced flow treatments at S1 and S2 (Table 3). The two species richness metrics did not show any significant treatment, time or treatment by time effects.

The PCoA (Figures 2a and S3a) explained 38.4% of the total taxonomic variation; the centroids showed a separation between the control and reduced flow samples. The GLMM analysis of the distance of each sample from the centroid (Table 3) indicated a significant interaction flow × time at time S1. Indeed, the plots (Figure 1b) showed that the reduced flow samples had a more homogeneous taxonomic composition than the control ones before starting the simulations (i.e., at S0); after 1 week with reduced flow (i.e., at S1 in treatments) benthic invertebrates communities become taxonomically more heterogeneous but returned to a more homogeneous condition after one more week (i.e., at S2). The PERMANOVA analyses (Table 4) showed that the assemblages differed in composition over the treatment factor ($p = 0.001$), whereas there was no effect of interaction by flow and time on the taxonomic composition.

The results of the SIMPER analysis showed that differences between control and treatment sections were due to higher density of Trichoptera Hydropsychidae, *Rhyacophila* spp., Glossosomatidae, Limnephilidae and Hydroptilidae, and the Plecoptera *Perlodes* sp. and *Protonemura* sp. and the Ephemerellidae *Serratella ignita* in the control sections, where *Rhyacophila* spp., Limnephilidae, Hydropsychidae and *Perlodes* sp. decreased from S1 to S2, and Glossosomatidae, *Serratella ignita*, Hydroptilidae and *Protonemura* sp. increased from S1 to S2 (Table 2 and Figure S4). Conversely, the reduced flow sections were characterized by higher densities of *Sericostoma* spp. which increased from S1 to S2, and *Rhithrogena* sp., Leptophlebiidae, *Ecdyonurus* sp. and *Dinocras* sp. which decreased from S1 to S2 (Table 2 and Figure S4).

TABLE 2 Benthos densities and drift rate overall, in control and reduced flow sections

Benthos density (ind m^{-2})	Total overall	Total controls	Total treatments	Controls—treatments	SIMPER	Controls, S1 to S2	Treatments, S1 to S2
Baetis spp.	18,658	20,323	16,993	3330			
Hydropsychidae	790	1237	343	894	6.19 (C)	Decrease	
Epeorus sp.	637	545	730	−185			
Rhyacophila spp.	391	486	295	192	4.06 (C)	Decrease	
Leuctra sp.	277	281	272	9			
Nemoura sp.	255	226	284	−58			
Ecdyonurus sp.	64	52	77	−25	4.69 (T)		Decrease
Glossosomatidae	50	66	34	32	10.32 (C)	Increase	
Sericostoma spp.	34	34	34	0	8.52 (T)		Increase
Leptophlebiidae	23	21	26	−6	8.95 (T)		Decrease
Dinocras sp.	12	12	12	−1	7.43 (T)		Decrease
Rhithrogena sp.	12	12	12	0	7.37 (T)		Decrease
Serratella ignita	11	12	10	2	6.99 (C)	Increase	
Hydroptilidae	5	7	2	5	4.31 (C)	Increase	
Limnephilidae	5	7	2	6	3.79 (C)	Decrease	
Perlodes sp.	4	7	1	7	3.70 (C)	Decrease	
Protonemura sp.	4	5	3	2	4.22 (C)	Increase	
Goeridae	3	5	1	4			
Polycentropodidae	2	3	0	3			
Heptagenia sp.	1	1	2	−1			
Electrogena sp.	1	0	2	−2			
Psychomyiidae	1	2	0	2			
Amphinemura sp.	0	0	1	−1			
Nemurella picteti	0	0	1	−1			
Odontoceridae	0	1	0	1			
Lepidostomatidae	0	0	0	0			
DRIFT RATE (ind h^{-1})	**Total overall**	**Total control**	**Total treatment**	**Control—treatment**		**Control, S1 to S2**	**Treatment, S1 to S2**
Baetis spp.	593.91	390.69	203.22	187.47			
Hydropsychidae	27.31	21.83	5.48	16.35		Increase	
Epeorus sp.	6.11	2.89	3.22	−0.34			
Rhyacophila spp.	4.74	2.22	2.52	−0.30		Increase	
Leuctra sp.	6.29	3.69	2.61	1.08			
Nemoura sp.	2.40	1.48	0.92	0.57			
Ecdyonurus sp.	0.44	0.20	0.24	−0.04			Decrease
Glossosomatidae	4.25	3.77	0.48	3.29		Increase	
Sericostoma spp.	0.52	0.24	0.28	−0.05			Increase
Leptophlebiidae	0.14	0.12	0.03	0.09			Decrease
Dinocras sp.	0.06	0.03	0.03	0.00			Decrease
Rhithrogena sp.	0.09	0.06	0.03	0.03			Increase
Serratella ignita	0.26	0.22	0.04	0.18		Decrease	
Hydroptilidae	1.39	1.27	0.12	1.15		Decrease	
Limnephilidae	0.70	0.60	0.10	0.51		Increase	
Protonemura sp.	0.22	0.15	0.07	0.07		Decrease	
Goeridae	0.37	0.33	0.04	0.29			
Lepidostomatidae	0.40	0.40	0.0000	0.02			

TABLE 2 (Continued)

DRIFT RATE (ind h^{-1})	Total overall	Total control	Total treatment	Control–treatment	Control, S1 to S2	Treatment, S1 to S2
Odontoceridae	0.08	0.08	0.0000	0.00		

Note: For those taxa which differed in the SIMPER benthic analysis by the flow factor, last two columns: increase or decrease from S1 to S2 in controls and reduced flow sections. Column 'SIMPER' = % contribution to averaged squared Euclidean distance; in brackets: flume sections where the density in the analysis was higher (C = controls; T = reduced flow treatments). Treatments: reduced flow sections.

3.3 | Functional changes of benthic communities

Functional diversity (FDis) (Figure 1a) was higher and constant over time in the control sections, whereas in the reduced flow sections, it decreased from S0 but did not vary significantly over treatment by time (Table 3). The PERMANOVA analyses (Table 4) showed that the functional composition differed over the treatment factor ($p = 0.002$), but not over time, or between S0 and S1–S2 within each flow type (i.e., time × treatment not significant).

The FCA (Figures 2c and S3b) explained 47.0% of the total variation in functional composition and a partial separation of controls and flumes samples. The GLMM analysis of the distance of each sample from the centroid (Table 3 and Figure 1b) shows no evidence that the flow reduction was associated with functional homogenization. Rather, a progressive decline in beta-diversity occurred in the control sections, while a short-term (S1) increase (heterogenization) was observed in the treatment section following flow reduction. The SIMPER analysis for the flow factor showed that the most relevant traits (i.e., those contributing at least 3% of dissimilarity between groups, which together accounted for 70.7% of the total dissimilarity, Figures 1c and S5) refer to flow preference (organisms preferring slow/lentic zones or medium to high currents), substrate preference (organisms living on coarse substrates), locomotion and substrate relation (organisms living as crawlers, living temporarily attached to the substrate, moving as full water swimmers), feeding traits (feeding as gatherers/collectors of FPOM, grazers, passive filter feeders or as predators) and resistance forms (with resting eggs or with no resistance forms to desiccation). The results of the GLMM models (Table 3) for each of these traits identified the following significant 'time × treatment' interactions (Figure 1c and Table S2): taxa moving as full swimmers (taxa with high affinities to the trait: *Baetis* spp.) and preferring slow/lentic zones (rheophilic to limnophilic such as *Baetis* spp., Glossosomatidae, Limnephilidae and *Sericostoma* spp.) did not increase over time in the reduced flow sections, contrary to what was observed in control conditions, but they decreased at the beginning of reduced flow treatment (S1) to increase again after two more weeks (S2). Conversely, animals moving as crawlers (for instance, *Amphinemura* sp., *Dinocras* sp., *Ecdyonurus* sp., *Epeorus* sp., *Leuctra* sp., Limnephilidae, *Nemoura* sp., *Perlodes* sp., *Protonemura* sp. *Rhithrogena* sp. and *Sericostoma* spp.), preferring fast currents (i.e., rheobiontic, such as *Epeorus* sp., *Rhyacophila* spp., *Rhithrogena* sp.) and coarse substrata (*Ecdyonurus* sp., *Epeorus* sp., Glossosomatidae, *Heptagenia* sp., Hydropsychidae, *Rhithrogena* sp. and *Rhyacophila* spp.) did not decline

over time in treatments, contrarily to what was observed in control conditions, but rather increased at the beginning of low-flow treatment (S1) and after two more weeks (S2) returned to values similar to S0.

3.4 | Taxonomic changes of drifting communities

We collected a total of 19,870 specimens of EPT in the drift, corresponding to a total drift rate of 645 ind h^{-1}. Drift rate differed significantly between treatments and controls (Mann–Whitney, $p = 0.002$); drift rate was always higher and more variable in the control section; in both sections, the highest values were recorded on the first sampling date, that is, 23 h from the beginning of the experiment, and drift rate decreased over time in both sections (Figure 3). Drift rate was higher from the beginning of the flow reduction simulation to the date of benthic sampling S1 (4 October, i.e., Drift Samples 1 to 5) than from S1 to S2 (18 October i.e., Drift Samples 6 to 13) in both treatment and control, with higher drift rates in the control (mean drift rate at S1 and S2, respectively, 12 and 27 ind h^{-1} in reduced flow section, 24 and 48 ind h^{-1} in control). The number of drifting taxa was significantly lower in the reduced flow samples (Mann–Whitney, $p = 0.002$) (Figure 3). Hill–Shannon diversity was similar between reduced flow and control sections, except in the last three sampling days, when drift of the reduced flow samples was less diverse than in the control; diversity slightly increased over time in the drift collected from both reduced flow and control samples. The total drift propensity calculated at S1 and S2 was higher in the control where it slightly increased over time from 36 to 38; in the reduced flow section, drift propensity was lower and slightly decreased from S1 (26) to S2 (25).

The PCoA (Figure 2b) showed differences in drift composition between the reduced flow and control samples and a temporal shift in composition. The PERMANOVAs analysis confirmed the significant effect of flow (pseudo-$F = 14.67$, $p = 0.001$) on the composition of drifting assemblages, as already recorded for the benthos. *Baetis* spp. was the most abundant drifting taxon, representing 91.4% of overall drift. Hydropsychidae and *Epeorus* sp. followed in density in the reduced flow drift samples, summing up to 3.97%, and Hydropsychidae and Glossosomatidae in the control ones, summing up to 5.95% of the total.

For the benthic taxa identified as most contributing to the differences between reduced flow and control sections (SIMPER,

TABLE 3 Results of GLMM models applied to (1) the benthic community metrics, (2) the distance of each sample from the centroid in the taxonomic and functional matrices and (3) the functional traits proportion matrix (traits codes as in Table 1)

			Estimate	Std. error	z value	Pr(>|z|)	
1	S (total number of taxa)	Time S1 × treatment	0.778	0.805	0.967	0.334	
		Time S2 × treatment	−0.583	0.829	−0.703	0.482	
	N (total density)	Time = S2	0.689	0.133	5.170	<0.001	
		Time S1 × treatment	−0.399	0.183	−2.180	0.029	*
		Time S2 × treatment	−0.680	0.189	−3.610	0.000	***
	Hills diversity	Time = S1	−0.306	0.120	−2.549	0.011	*
		Time = S2	−0.607	0.124	−4.902	<0.001	***
		Treatment	−0.452	0.120	−3.769	0.000	***
		Time S1 × treatment	0.505	0.170	2.973	0.003	**
		Time S2 × treatment	0.484	0.175	2.764	0.006	**
	Margalefs richness	Time S1 × treatment	0.119	0.079	1.509	0.131	
		Time S2 × treatment	0.011	0.082	0.136	0.892	
	FDis (functional dispersion)	Time S1 × treatment	−0.063	0.063	−1.010	0.312	
		Time S2 × treatment	−0.069	0.064	−1.070	0.286	
2	Taxonomic composition (distance from centroids)	Treatment	−0.045	0.016	−2.825	0.005	**
		Time S1 × treatment	0.067	0.023	2.972	0.003	**
		Time S2 × treatment	0.015	0.023	0.634	0.526	
	Functional composition (distance from centroids)	Time = S2	−0.771	0.248	−3.107	0.002	**
		Treatment	−0.5	0.222	−2.248	0.025	*
		Time S1 × treatment	0.194	0.296	0.655	0.512	
		Time S2 × treatment	0.771	0.353	2.181	0.029	*
3	Full water swimmers	Time = S2	0.115	0.036	3.185	0.001	**
		Treatment	0.096	0.035	2.748	0.006	**
		Time S1 × treatment	−0.094	0.049	−1.903	0.057	
		Time S2 × treatment	−0.101	0.051	−1.981	0.048	*
	Substrate: flags/boulders/cobbles	Time = S2	−0.117	0.033	−3.570	0.000	***
		Treatment	−0.080	0.032	−2.510	0.012	*
		Time S1 × treatment	0.107	0.045	2.380	0.017	*
		Time S2 × treatment	0.115	0.047	2.470	0.013	*
	Crawlers	Time = S2	−0.060	0.020	−2.950	0.003	**
		Time S1 × treatment	0.058	0.028	2.065	0.039	*
		Time S2 × treatment	0.068	0.029	2.364	0.018	*
	Reophyle to limnophile	Time = S2	0.111	0.032	3.430	0.001	***
		Time S1 × treatment	−0.075	0.044	−1.690	0.091	
		Time S2 × treatment	−0.091	0.045	−2.000	0.046	*
	Rheobiont	Time = S1	−0.264	0.127	−2.080	0.038	*
		Time = S2	−0.879	0.157	−5.590	0.000	***
		Treatment	−0.314	0.128	−2.450	0.014	*
		Time S1 × treatment	0.434	0.183	2.380	0.017	*
		Time S2 × treatment	0.697	0.214	3.250	0.001	**

Note: Only the significant predictor variables and their interactions are listed (statistical significance is marked with asterisks).

Figure S5), drift rate and drift propensity (Figure 4 and Table 2) were higher in the treatment for *Sericostoma* spp. and *Rhyacophila* spp. Drift rate was also higher in treatment for *Ecdyonurus* sp. which, however, had higher drift propensity in the controls. Drift rate and propensity were significantly lower in the treatment flume for *Serratella ignita* (*p* = 0.049) and Hydroptilidae (*p* < 0.01). Drift rate was significantly lower and propensity higher for Hydropsychidae (*p* < 0.01) and Glossosomatidae (*p* < 0.01).

TABLE 4 Results of PERMANOVA analyses on taxa densities and traits proportional densities of benthic communities

Factor	Pseudo-F or T (for pairwise)	p (perm)	N perm
PERMANOVAs of densities			
Treatment	3.3807	0.001	997
Time	1.0964	0.349	996
Time × treatment	0.6294	0.816	997
PERMANOVAs of trait densities			
Treatment	6.7054	0.002	999
Time	3.7681	0.005	999
Time × treatment	2.089	0.052	999

Note: Factor BA: before (S0) versus after (S1 and S2); factor CI: control versus impact (reduced flow).

3.5 | Functional changes of drifting communities

The functional dispersion of drifting assemblages (FDis, Figure 3) was always significantly lower (Mann–Whitney, $p < 0.001$) in the drift collected from the reduced flow section (Figure 3). The first and second axes of the FCA (Figure 2d) explained 71.45% of the total variance in trait composition of the drifting community; functional composition differed between reduced flow and control (PERMANOVA, factor 'flow' pseudo-$F = 5.2481$, $p = 0.011$), for which the functional composition never overlapped over Axis 1.

The traits identified as most contributing to the differences between flow types in the benthic samples by the SIMPER analysis were analysed for the drift (Figure 5 and Table S2). In reduced flow conditions, drift rate (Table S2) and propensity were significantly higher for animals preferring fast currents (Mann–Whitney, $p < 0.001$ for rheobiontic taxa); drift rate was significantly higher ($p = 0.002$), but propensity was slightly lower for organisms moving as crawlers; conversely, in reduced flow conditions, drift rate was significantly lower and drift propensity higher for passive filterers ($p = 0.005$), organisms living temporarily attached to the substrate ($p < 0.001$) and preferring medium current velocity ($p < 0.001$). For the remaining traits, differences in drift rate and propensity between treatment and control were negligible.

4 | DISCUSSION

4.1 | Importance and limitations of eco-hydraulic flume simulations

Flow reduction caused by small diversion hydropower plants is one of the most widespread anthropogenic impacts in mountain streams (e.g., Copeman, 1997; McKay & King, 2006). Although the magnitude of water abstraction varies across SDHP types, it inevitably leads to the contraction of aquatic habitats downstream the diversion point, altering the environmental condition with effects on the biotic component (Couto & Olden, 2018; González et al., 2018; Jesus et al., 2004; Kelly-Richards et al., 2017). These impacts have gained scientific interest in recent times, as the worldwide transition to renewable energy technologies is causing a boom in SDHP construction (Couto & Olden, 2018; Habets et al., 2018). In our experiment, we successfully manipulated the flow and reduced the original discharge by 50%, which represent a good approximation of the reduction caused by a typical water abstraction feeding small diversion hydropower plants in upland streams (e.g., Copeman, 1997; McKay & King, 2006).

The use of semi-artificial flumes directly fed from a stream, as employed in this study, allows for a natural colonization of invertebrates thus recreating natural conditions in terms of community composition and main resources, including deposition of fines and organic matter, growth of periphyton and moss. This type of flumes, therefore, provides a model system to test for environmental impacts and alterations. Given the structure of the flumes, which prevent a complex representation of hydromorphological alterations, and the short time span of the experiment, our simulations provided a simplified model because (i) the control (upstream) sites were discharged with constant high flow, thus lacking the natural flow dynamics; (ii) the flow reduction in the treatment sites did not cause a contraction of the available habitat, as the wetted width did not change due to the uniform morphology of the flume; and (iii) for the 3 weeks of the experiment, control and impact sections did not receive drifting fauna, whereas real low-flow impacted sites receive drifting invertebrates which contribute to change benthic composition. Although we did not fully simulate the effects of flow reduction compared to a control site under natural flow regime, this experiment allowed us to (i) exclude the effect of natural disturbances, such as peak flows that would confound the effects of water diversion. This allowed the examination of temporal trends associated with the prolonged reduced flow conditions; (ii) rule out the effect of habitat contraction and associated stranding and/or aggregation of invertebrates, which often results from the reduced discharge; and (iii) assess how the persistence of low flows can change the benthic assemblages through animal removal by drift following several days of disturbance (by excluding recolonization from upstream and therefore of 'new' individuals experiencing reduced flow for shorter time spans).

Despite the limitation inevitably linked to small-scale simulations of large-scale processes, our results can help detect changes in invertebrate communities associated with SDHP operations, focusing on the exclusive effect of changes in flow, and on the resulting emigration by drift. Because manipulative experiments allow overcoming
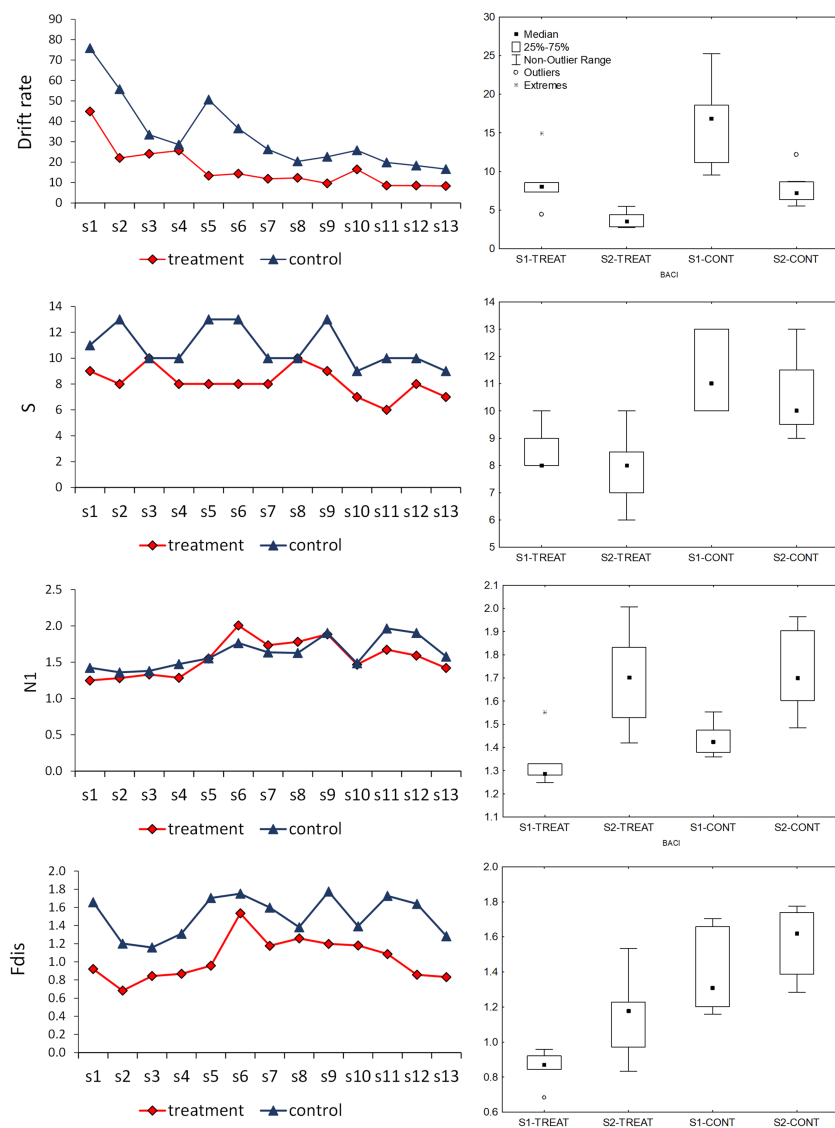
FIGURE 3 Temporal variations of the taxonomic metrics of drifting invertebrates, in control and reduced flow flume sections. N = total density (N. ind m^{-2}); S = total number of taxa; N1 = Hill–Shannon diversity; FDis = functional dispersion
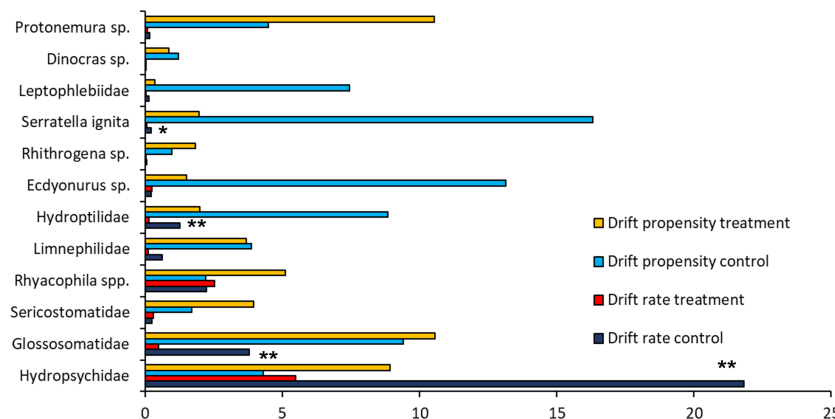

FIGURE 4 Total drift, expressed as drift rate and drift propensity, in the control and reduced flow section. Only those taxa identified by the SIMPER analysis as most contributing to dissimilarities for factor flow in benthic samples were analysed. Taxa which significantly differed in drift rate between control and reduced flow are marked with asterisk

important issues arising in field studies, such as the lack of pre-impact data, appropriate reference sites and the presence of multiple interacting pressures (Dewson et al., 2007), artificial flumes have been successfully used for investigating the response of benthic organisms to

environmental alterations, especially those difficult to isolate and quantify in the field (Lancaster & Ledger, 2015; Ledger et al., 2011, 2012; Poff et al., 2003). These same flumes have been used to simulate other types of physical alterations related to hydropower
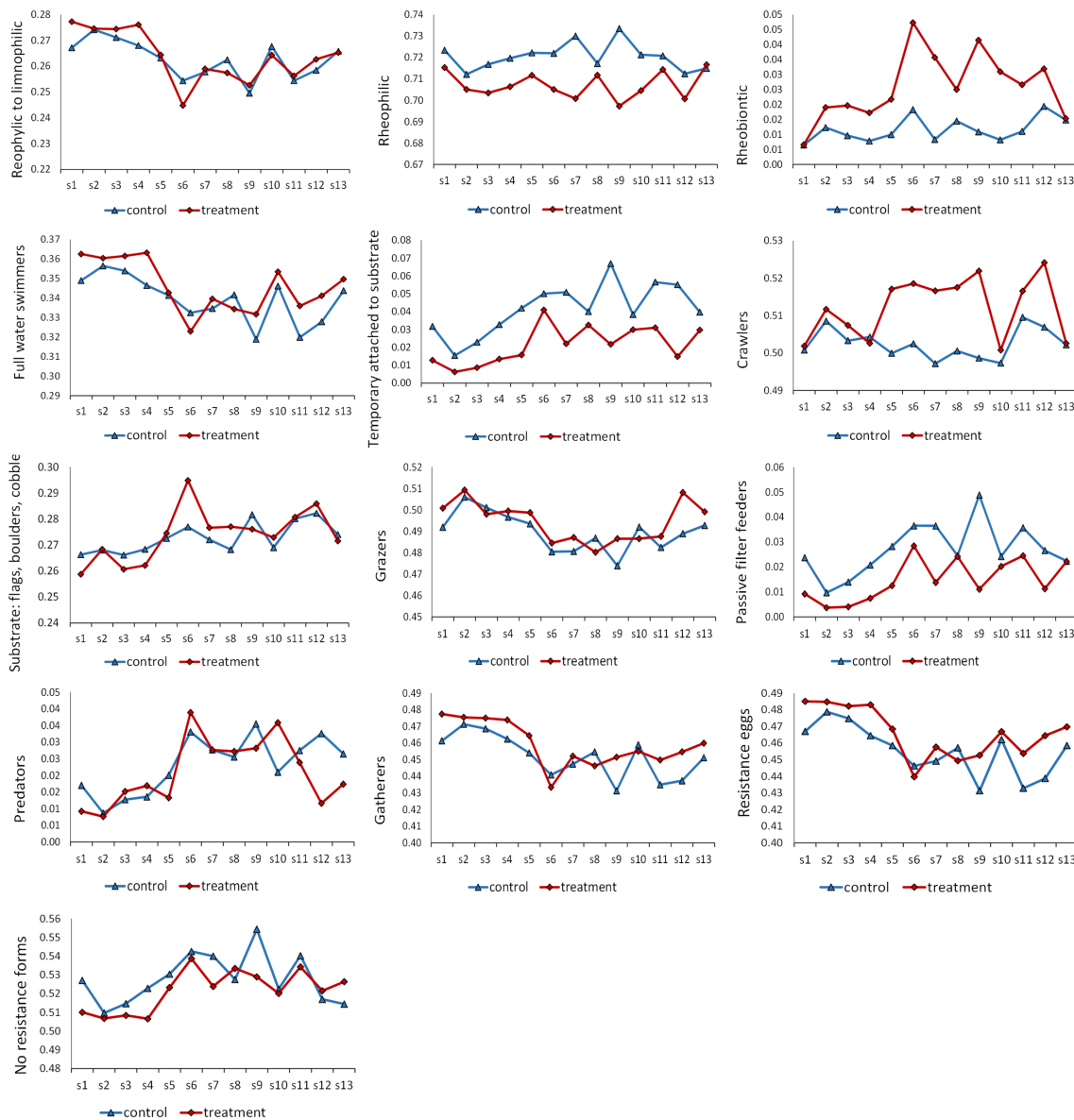
FIGURE 5 Temporal trends of the functional traits (calculated as proportion of each trait category over each trait parameter) of drifting invertebrates most contributing to dissimilarities between benthic samples (see Table 2), in control and reduced flow flume section

schemes (namely, hydropeaking and thermopeaking) and to assess the responses in benthic communities, in particular, drift responses to such disturbances (Bruno et al., 2013; Bruno, Cashman, et al., 2016; Carolli et al., 2012). We are therefore confident that our flume system provides an appropriate model to test for the effects of flow reduction.

We used artificial substrates (baskets) to collect benthic invertebrates. Artificial samplers only record the community that develops during the sampling period, which is determined by individuals that colonized the baskets via drift or crawling from the bottom substrate. Dispersal frequencies and distances covered by colonizers determine overall population structure in streams (Harrison & Hastings, 1996; Sharpe & Downes, 2006) and clearly influence the composition and abundance of taxa on artificial substrates. This likely increased the

stochasticity in the density and composition of invertebrates in each substrate/flume, both in pre-simulation conditions (i.e., S0) and during the simulations (i.e., S1 and S2). This may in part explain the initially differing composition between control and treatment sections and the changes occurring in the control sections during the experiment.

4.2 | Changes in benthic communities induced by flow reduction

Results from our experiment indicate that flow reduction can alter the taxonomic and functional structure of benthic EPT communities, but in ways that are not necessarily in line with theoretical expectation. We can exclude ecological effects due to changes in physicochemical

parameters (dissolved oxygen, pH, conductivity and temperature) as no differences in such parameters were observed between control and reduced flows; the ecological effects observed were only due to changes in flow velocity and water depth. Because we did not simulate a reduction in habitat availability (i.e., the wetted area remained unchanged, as the bed of the flumes was always submerged), and the flumes do not provide relevant instream refugia, such as pools and saturated hyporheic sediments (Gruppuso et al., 2021), changes in benthic densities during the experiment were not due to recolonization from the hyporheos or reduced habitat availability. Rather, invertebrate densities and community composition responded to reduced flow through changes in the drift intensity and dynamics, as also observed elsewhere (Dewson et al., 2007). Reduced flow can increase benthic densities because the rate of catastrophic drift decreases as water velocity declines (Dewson et al., 2007; James et al., 2008) and drift becomes predominantly behavioural. Because during flow reductions, behavioural drivers generally dominate drift dynamics (Naman et al., 2016), the drift responses of EPT to the sudden decreases in flow is the most likely explanation for the observed short-term changes in benthic composition (Poff & Ward, 1991), which reflected taxon-specific sensitivities and flow velocity preferences (e.g., Poff et al., 2006; Rader, 1997; Tachet et al., 2010).

In our flumes, EPT communities differed between reduced flow and control sections before starting the simulations, when the reduced flow sections had more individuals but were less diverse. Despite this, different drift dynamics during flow reduction were evident and led to effects on benthic assemblages, namely, in the control sections where flow was higher, drift rate over time, and drift propensity at S1 and S2 were higher (and propensity slightly increasing from S1 to S2) than in the reduced flow section (where propensity slightly decreased from S1 to S2) as expected; however, benthic densities increased over time not only in the reduced flow sections but also in the control ones. The mechanisms leading to such unexpected changes could possibly be related to invertebrates movement within the flumes and to the distances travelled before gaining contact with the artificial substrates (predominantly ruled by their rate of entrainment in drift, increased with the higher flow condition, and swimming abilities). In the flumes, EPT nymphs entrained by catastrophic drift have been shown to regain contact with the substrate within a distance of 4–10 m (Bruno, Carolli, & Maiolini, 2016); hence, in our experiment, they were able to perform several short-distance movements by drift and settle into the benthic substrates, possibly with higher rates in the control sections, thus explaining the stronger increases in substrates densities recorded there. Effects of flow reduction on density and diversity were already evident after 1 week and continuing for two more weeks. In the treatment sections, flow reduction led to a short-term (i.e., 1 week) decrease in benthic density and increase in Hill–Shannon and beta-diversity (heterogenization) of the EPT assemblages; however, these effects were short lived, and Hill–Shannon and beta-diversity returned to initial levels after 3 weeks. Contrary to what hypothesized, the results do not support the hypothesis that flow reduction can lead to overall taxonomic homogenization and reduction in diversity. Low flows in permanent streams can affect taxonomic diversity as rheophilic taxa are eradicated due to the loss of fast-flow habitat types such as riffles (McIntosh et al., 2002). However, richness reduction can be modest or absent if the diversity of habitats is relatively preserved during decreases in flow (Wood & Petts, 1999), as it was the case in our flumes and in naturally homogeneous stream sections (Wood & Petts, 1994).

In our study, changes in taxonomic composition showed by the PCO were non-random with respect to the functional identity of the taxa involved and shown by the FCA. Although taxonomic diversity increased with flow reduction, a decline in functional diversity (FDis) was evident in the treatment sections, albeit non-significant, whereas changes where negligible in controls. At the same time, however, flow reduction did not result in functional homogenization of the community after 3 weeks. That is, assemblages did not converge to similar functional composition across samples despite declines in local FDis. If anything, control sections appeared more functionally homogeneous at the end of the experiment. These results highlight the importance of examining both alpha- and beta-diversity when assessing functional responses. Overall, our findings do not parallel recent field and experimental investigations on the effects of low flows. In particular, studies in Alpine streams (Piano et al., 2020) revealed a significant reduction of functional diversity in intermittent reaches and suggested that flow intermittency may exert a stronger pressure on benthic invertebrate communities in Alpine relative to Mediterranean streams, where the drying phase is a natural part of the hydrological cycle (Leigh et al., 2016). Indeed, the natural flow regime of the Fersina Stream in the study reach does not include frequent droughts, and hence, the invertebrate assemblages colonizing the flumes were not expected to be drought-tolerant. In mountain streams, benthic communities are dominated by rheophilic taxa that do not tolerate low-flow velocity, due to their trophic and physiological requirements. Piano et al. (2020) recorded a replacement of taxa preferring medium- to fast-flowing oligotrophic waters by taxa adapted to lentic habitats in recently intermittent Alpine streams. In our experiment, flow reduction led to a decline in the proportion of 'rheophilic to limnophilic' taxa, according to the GLMM. However, other responses are difficult to interpret and may be related to the short-term and simplified setting of the experiment. For instance, the immediate increase in the proportion of crawlers and taxa associated with boulders–cobbles was not expected under reduced flow, although animals with this suite of functional characteristics would likely increase their movement on the substrate under low-flow conditions in search of more favourable conditions and might have become abundant on the substrates. It has to be noted, however, that some of the apparent effects of the experiment, as emerged from the GLMM analysis (time × treatment interaction), are likely due to changes occurring 'naturally' in the control section but not in treatments. These include, for instance, a steady increase of full water swimmers in the benthos collected from the control substrates (again, suggesting a higher movement by drift within the flumes, elicited by the higher flows maintained in the control sections), as well as the large increase in overall density.

Interestingly, we did not observe any clear response of feeding traits to the experimental flow reduction. In a recent flow reduction

experiment of over 2 months, González and Elosegi ([2021](#)) recorded a decline of functional dispersion in the benthos and suggested that under water abstraction, assemblages would lose the ability to perform the variety of original functions as trophic resources become more homogenous. They attributed these effects to changes in leaf-litter accumulation in the treated sections. Because we blocked the incoming flow of CPOM via drift nets, the lack of observed effects of flow reduction on feeding traits may be partly due to the lack of effects on leaf-litter accumulation.

4.3 | Drift dynamics related to flow reduction

Behavioural (i.e., active) drift can increase following rapid experimental flow reductions, as animals attempt to avoid conditions insufficient to meet their nutritional or physiological needs (James et al., [2008](#); Naman et al., [2016](#), and references therein). In the case of water abstraction, drift densities often increase immediately after the start of low-flow conditions (e.g., Dewson et al., [2007](#); James et al., [2008](#)), indicating a behavioural response. This was also observed in the treatment flume, where drift rates were highest within 24 h from the start of the flow reduction. James et al. ([2008](#)) and James and Suren ([2009](#)) performed an experiment in streamside channels, where they simulated flow reductions of approximately 50% and 75%, and reported increased drift during the first three nights of artificial low flows, and a return to normal values after 1 week. In the present experiment, drift rate decreased over time in both treatment and control, but it was higher in the control section, where the higher flow and shear stress might have induced both passive and active drift. Nonetheless, invertebrates under the reduced flow treatment probably decreased their rate of passive drift, but increased the rate of active drift to avoid the unfavourable conditions, as also suggested by results of González et al. ([2018](#)), who simulated flow reduction of 90% in a first-order stream in northern Spain, and reported increased active drift as a response to the stressful conditions, so that the impacted reach was converted to a net exporter of invertebrates.

In our study, drift rate was lower, less taxonomically and functionally diverse in the reduced flow than in the control section. However, drift responses are clearly species specific and depend also on the composition of the source benthic communities (González et al., [2018](#)). In fact, in our study, emigration by drift in the two sections was not evenly distributed among taxa and traits. Most of the taxa tended to drift more (as measured by high drift rate) where they were abundant in the benthos (as measured by high drift propensity and rate). This was the case of *Sericostoma* spp. and *Rhyacophila* spp. which had higher drift propensities and rates in the reduced flow conditions. This suggests a co-occurrence of density dependent, passive (accidental) drift occurring while individuals move on the substrate surface in search of food and of optimal microhabitat conditions and of an active (behavioural) entry into the water column to escape unfavourable conditions (Naman et al., [2016](#), and references therein). *Sericostoma* and *Rhyacophila* were reported by González et al. ([2018](#))

as, respectively, increasing and decreasing in drift densities with a 90% flow reduction but no significant increases/decreases in drift rate; however, intentional/active drift propensity of *Rhyacophila* sp. is reported to be rare but to increase with flow reduction (Rader, [1997](#)). Conversely, a group of taxa drifted less (lower drift rate) and with lower propensity in the reduced flow condition (this was the case of *Serratella ignita* and Hydroptilidae and, to a lesser extent, *Dinocras* sp., Leptophlebiidae and Limnephilidae). The drift density of *Serratella* and one Leptophlebiidae and Perlidae taxa are similarly reported as decreasing with reduced flow, although with no differences in their drift rate by González et al. ([2018](#)); all these taxa rarely drift actively but can increase their drift propensity as a predator-avoidance strategy (Rader, [1997](#)), although this response was probably not relevant in our flumes as the most abundant predator, *Rhyacophila* spp., drifted out of the same flumes. Hence, the main type of drift for these taxa in our experiment must be passive, which is known to occur with less intensity with low flows.

A second group of taxa tended to persist for short time in the drift (low drift rates) in reduced flow conditions although their propensity to drift was high there, suggesting multiple drift re-entry occasions followed by high settling rates; this occurred for Hydropsychidae, Glossosomatidae, *Rhithrogena* sp. and *Protonemura* sp. For these taxa, as for those above, intentional, active drift is rare or occasional and mostly induced by predators and, for Hydropsychidae, also by flow reduction (Rader, [1997](#)). Lastly, in low-flow conditions *Ecdyonurus* sp. tended to persist in the drift more (high drift rates) although its propensity to drift was low, suggesting that each drift re-entry occasion was accompanied by a low tendency to resettle on the substrate. *Ecdyonurus torrentis* was reported by Oldmeadow et al. ([2010](#)) to display behavioural responses to prolong drift by posturing with the body and limbs extended horizontally at a velocity of velocity of $0.20\,\mathrm{m\,s^{-1}}$ roughly comparable to the one of our reduced flow section.

Drift entry and settling abilities of invertebrates are difficult to assess, and their taxon-specific dynamics are still poorly known (Bruno, Carolli, & Maiolini, [2016](#)). Distances travelled before regaining contact with the substrate are determined by the physical constraints imposed by the hydraulic environment on the morphological and mechanical swimming abilities of organisms, the decisions individuals make regarding whether to terminate or prolong drift and their settling efficiency (Rader, [1997](#)). In our experiment, multiple settling and drift re-entry events could have occurred, because Hydropsychidae, *Rhithrogena* sp., *Sericostoma* spp., *Ecdyonurus* sp. and *Rhyacophila* spp. when drifting in the flumes, can settle within 10 m, within less than 1 min (Bruno, Carolli, & Maiolini, [2016](#)).

Overall, the GLMM analysis of the functional composition provided interesting results related to the traits associated with drift responses in the different flow conditions. The taxa preferentially drifting (i.e., higher drift propensities) from each section were those less adapted to the respective flow conditions: taxa preferring medium to high flows, living temporarily attached to the substrate tended to leave the reduced flow section, whereas those living as crawlers drifted preferentially out of the higher flow section.

5 | CONCLUSIONS

Alpine streams are heavily impacted by flow regulation, hydropower development and increased water abstraction to fulfil multiple societal needs (López-Rodríguez et al., 2019; Wohl, 2006), while the effects of climate change are likely to further exacerbate the hydrological stress (Bruno et al., 2019). The objective of this experiment was to examine the short-term responses of benthic invertebrates to hydrological alteration associated with water abstractions in low-order mountain streams, as relatively few empirical studies investigated the influence of reduced flows on the abiotic and biotic properties of permanent streams (Dewson et al., 2007). Our experiment simulated the sudden decrease in flow caused by small diversion hydropower systems. Although artificial flumes represent simplified systems, our results offer some evidence of the taxonomic and functional implications for benthic invertebrate communities, likely mediated by drift responses, thus providing information on the potential mechanisms underlying patterns of community-level effects to water abstraction. Because recolonization from upstream and retreating into the hyporheic zone was not possible due to the experimental setting, any change in composition and densities derived from drift dynamics. If the effects of water abstraction are already detectable with a 50% flow reduction (i.e., at a simulated residual flow much higher than the one usually occurring in Alpine streams), and on a small and morphologically simplified benthic surface, the extrapolation of our results to the larger scales and complex morphologies of natural streams implies that the impacts of flow reduction on biotic assemblages and ecosystem processes can be severe. Additionally, in Alpine watersheds, where often several small hydropower plants withdraw water along the same watercourse, more research is needed to appraise the cumulative and synergistic impacts of flow alterations on downstream communities.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Francesca Vallefuoco https://orcid.org/0000-0002-3180-0487
Maria Cristina Bruno https://orcid.org/0000-0001-7860-841X
Guido Zolezzi https://orcid.org/0000-0003-2807-7387
Stefano Larsen https://orcid.org/0000-0002-6774-1407

REFERENCES

Abbasi, T., & Abbasi, S. A. (2011). Small hydro and the environmental implications of its extensive utilization. *Renewable & Sustainable Energy Reviews, 15*, 2134–2143. https://doi.org/10.1016/j.rser.2010.11.050

Alpine Convention. (2009). *Report on the State of the Alps #2. Water and water management issues*. Permanent Secretariat of the Alpine Convention.

Anderson, M., & Walsh, D. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs, 83*, 557–574. https://doi.org/10.1890/12-2010.1

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E.

Bakken, T. H., Harby, A., Forseth, T., Ugedal, O., Sauterleute, J. F., Halleraker, J. H., & Alfredsen, K. (2021). Classification of hydropeaking impacts on Atlantic salmon populations in regulated rivers. *River Research and Applications*, 1–13. https://doi.org/10.1002/rra.3917

Barbour, M. T., Gerritsen, J., Griffith, G. E., Frydenborg, R., McCarron, E., White, J. S., & Bastian, M. L. (1996). A framework for biological criteria for Florida streams using benthic macroinvertebrates. *Journal of the North American Benthological Society, 15*, 185–121. https://doi.org/10.2307/1467948

Bruno, D., Belmar, O., Maire, A., Morel, A., Dumont, B., & Datry, T. (2019). Structural and functional responses of invertebrate communities to climate change and flow regulation in alpine catchments. *Global Change Biology, 25*, 1612–1628. https://doi.org/10.1111/gcb.14581

Bruno, M. C., Carolli, M., & Maiolini, B. (2016). Settling distances of benthic invertebrates in a sediment mobilization simulation in semi-natural flumes. *Journal of Limnology, 75*, 180–192. https://doi.org/10.4081/jlimnol.2015.1324

Bruno, M. C., Cashman, M. J., Maiolini, B., Biffi, S., & Zolezzi, G. (2016). Responses of benthic invertebrates to repeated hydropeaking in semi-natural flume simulations. *Ecohydrology, 9*, 68–82. https://doi.org/10.1002/eco.1611

Bruno, M. C., Siviglia, A., Carolli, M., & Maiolini, B. (2013). Multiple drift responses of benthic invertebrates to interacting hydropeaking and thermopeaking waves. *Ecohydrology, 6*, 511–522. https://doi.org/10.1002/eco.1275

Campaioli, S., Ghetti, P. F., Minelli, A., & Ruffo, S. (1994). *Manuale per il riconoscimento dei macroinvertebrati delle acque dolci italiane* (Vol. I). Provincia Autonoma di Trento.

Campaioli, S., Ghetti, P. F., Minelli, A., & Ruffo, S. (1999). *Manuale per il riconoscimento dei macroinvertebrati delle acque dolci italiane* (Vol. II). Provincia Autonoma di Trento.

Carolli, M., Bruno, M. C., Siviglia, A., & Maiolini, B. (2012). Responses of benthic invertebrates to abrupt changes of temperature in flume simulations. *River Research and Applications, 28*, 678–691. https://doi.org/10.1002/rra.1520

Chanson, H. (2004). *Environmental hydraulics of open channel flows*. Elsevier Butterworth-Heinemann. https://doi.org/10.1016/B978-075066165-2.50034-5

Chevene, F., Dolédec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology, 31*, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology, 18*, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K. R., & Gorley, R. N. (2015). *Getting started with PRIMER v7*. PRIMER-E Ltd.

Copeman, V. A. (1997). The impact of micro-hydropower on the aquatic environment. *Water Environment Journal, 11*, 431–435. https://doi.org/10.1111/j.1747-6593.1997.tb01376.x

Couto, T. B. A., & Olden, J. D. (2018). Global proliferation of small hydropower plants—Science and policy. *Frontiers in Ecology and the Environment, 16*, 91–100. https://doi.org/10.1002/fee.1746

Dewson, Z. S., James, A. B. W., & Death, R. G. (2007). A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society*, *26*, 401–415. https://doi.org/10.1899/06-110.1

Doretto, A., Piano, E., Falasco, E., Fenoglio, S., Bruno, M. C., & Bona, F. (2018). Investigating the role of refuges and drift on the resilience of macroinvertebrate communities to drying conditions: An experiment in artificial streams. *River Research and Applications*, *34*, 777–785. https://doi.org/10.1002/rra.3294

European Environment Agency. (2018). *European waters—Assessment of status and pressures 2018*. EEA Report No 7/2018. European Environment Agency, Publications Office of the European Union.

González, J. M., & Elosegi, A. (2021). Water abstraction reduces taxonomic and functional diversity of stream invertebrate assemblages. *Freshwater Science*, *40*(3), 524–536. https://doi.org/10.1086/716201

González, J. M., Recuerda, M., & Elosegi, A. (2018). Crowded waters: Short-term response of invertebrate drift to water abstraction. *Hydrobiologia*, *819*, 39–51. https://doi.org/10.1007/s10750-018-3620-1

Gruppuso, L., Doretto, A., Piano, E., Falasco, E., Bruno, M. C., Bona, F., & Fenoglio, S. (2021). Effects of flow intermittence on ecosystem processes in mountain streams: Are artificial and field experiments comparable? *Fundamental and Applied Limnology*, *195*, 39–59. https://doi.org/10.1127/fal/2021/1367

Habets, F., Molenat, J., Carluer, N., Douez, O., & Leenhardt, D. (2018). The cumulative impacts of small reservoirs on hydrology: A review. *Science of the Total Environment*, *643*, 850–867. https://doi.org/10.1016/j.scitotenv.2018.06.188

Harrison, S., & Hastings, A. (1996). Genetic and evolutionary consequences of metapopulation structure. *Trends in Ecology & Evolution*, *11*, 180–183. https://doi.org/10.1016/0169-5347(96)20008-4

James, A. B. W., Dewson, Z. S., & Death, R. G. (2008). The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, *24*, 22–35. https://doi.org/10.1002/rra.1052

James, A. B. W., & Suren, A. M. (2009). The response of invertebrates to a gradient of flow reduction– An instream channel study in a New Zealand lowland river. *Freshwater Biology*, *54*, 2225–2242. https://doi.org/10.1111/j.1365-2427.2009.02254.x

Jesus, T., Formigo, N., Santos, P., & Tavares, G. (2004). Impact evaluation of the Vila Viçosa small hydroelectric power plant (Portugal) on the water quality and on the dynamics of the benthic macroinvertebrate communities of the Ardena River. *Limnetica*, *23*, 241–256. https://doi.org/10.23818/limn.23.21

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kelly-Richards, S., Silber-Coats, N., Crootof, A., Tecklin, D., & Bauer, C. (2017). Governing the transition to renewable energy: A review of impacts and policy issues in the small hydropower boom. *Energy Policy*, *101*, 251–264. https://doi.org/10.1016/j.enpol.2016.11.035

Kibler, K. M., & Tullos, D. D. (2013). Cumulative biophysical impact of small and large hydropower development in Nu River, China. *Water Resources Research*, *49*, 3104–3118. https://doi.org/10.1002/wrcr.20243

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. Retrieved from https://cran.r-project.org/web/packages/FD/

Lancaster, J., & Ledger, M. E. (2015). Population-level responses of stream macroinvertebrates to drying can be density-independent or density-dependent. *Freshwater Biology*, *60*, 2559–2570. https://doi.org/10.1111/fwb.12643

Larsen, S., Comte, L., Filipa Filipe, A., Fortin, M.-J., Jacquet, C., Ryser, R., Tedesco, P. A., Brose, U., Erős, T., Giam, X., Irving, K., Ruhi, A., Sharma, S., & Olden, J. D. (2021). The geography of metapopulation synchrony in dendritic river networks. *Ecology Letters*, *24*, 791–801. https://doi.org/10.1111/ele.13699

Ledger, M. E., Edwards, F. K., Brown, L. E., Milner, A. M., & Woodward, G. (2011). Impact of simulated drought on ecosystem biomass production: An experimental test in stream mesocosms. *Global Change Biology*, *17*, 2288–2297. https://doi.org/10.1111/j.1365-2486.2011.02420.x

Ledger, M. E., Harris, R. M., Armitage, P. D., & Milner, A. M. (2012). Climate change impacts on community resilience: Evidence from a drought disturbance experiment. *Advances in Ecological Research*, *46*, 211–258. https://doi.org/10.1016/B978-0-12-396992-7.00003-4

Leigh, C., Bonada, N., Boulton, A. J., Hugueny, B., Larned, S. T., Vander Vorste, R., & Datry, T. (2016). Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers. *Aquatic Sciences*, *78*, 291–301. https://doi.org/10.1007/s00027-015-0427-2

Lenat, D. R. (1988). Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *Journal of the North American Benthological Society*, *7*, 222–233. https://doi.org/10.2307/1467422

Levin, P., & Tolimieri, N. (2001). Differences in the impacts of dams on the dynamics of salmon populations. *Animal Conservation*, *4*, 291–299. https://doi.org/10.1017/S1367943001001342

López-Rodríguez, M. J., Muñoz, C. M., Ripoll-Martín, E., & de Figueroa, J. M. T. (2019). Effect of shifts in habitats and flow regime associated to water diversion for agriculture on the macroinvertebrate community of a small watershed. *Aquatic Ecology*, *53*, 1–13. https://doi.org/10.1007/s10452-019-09703-6

Mcintosh, M. D., Benbow, M. E., & Burky, J. (2002). Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications*, *18*, 569–581. https://doi.org/10.1002/rra.694

McKay, S. F., & King, A. J. (2006). Potential ecological effects of water extraction in small, unregulated streams. *River Research and Applications*, *22*, 1023–1037. https://doi.org/10.1002/rra.958

Meyer, J. L., Strayer, D. L., Wallace, J. B., Eggert, S. L., Helfman, G. S., & Leonard, N. E. (2007). The contribution of headwater streams to biodiversity in river networks. *JAWRA Journal of the American Water Resources Association*, *43*, 86–103. https://doi.org/10.1111/j.1752-1688.2007.00008.x

Moog, O. (1995). *Fauna Aquatica Austriaca—A comprehensive species inventory of Austrian aquatic organisms with ecological notes*. Federal Ministry for Agriculture and Forestry, Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2016). Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1292–1305. https://doi.org/10.1139/cjfas-2015-0363

Oldmeadow, D. F., Lancaster, J., & Rice, S. P. (2010). Drift and settlement of stream insects in a complex hydraulic environment. *Freshwater Biology*, *55*, 1020–1035. https://doi.org/10.1111/j.1365-2427.2009.02338.x

Piano, E., Doretto, A., Mammola, S., Falasco, E., Fenoglio, S., & Bona, F. (2020). Taxonomic and functional homogenisation of macroinvertebrate communities in recently intermittent Alpine watercourses. *Freshwater Biology*, *65*, 2096–2107. https://doi.org/10.1111/fwb.13605

Platform Water Management in the Alps. (2011). *Situation report on hydropower generation in the alpine region focusing on small hydropower*. Permanent Secretariat of the Alpine Convention.

Poff, N. L., Allan, J. D., Palmer, M. A., Hart, D. D., Richter, B. D., Arthington, A. H., Rogers, K. H., Meyer, J. L., & Stanford, J. A. (2003). River flows and water wars: Emerging science for environmental decision making. *Frontiers in Ecology and the Environment*, *1*, 298–306. https://doi.org/10.1890/1540-9295(2003)001[0298:RFAWWE]2.0.CO;2

Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: Trait-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*, 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Poff, N. L., & Ward, V. (1991). Drift responses of benthic invertebrates to experimental streamflow reduction in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 1926–1936. https://doi.org/10.1139/f91-229

Poff, N. L., & Zimmerman, J. K. S. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

R Development Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rader, R. B. (1997). A functional classification of the drift: Traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 1211–1234. https://doi.org/10.1139/f97-025

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*, 321–338. https://doi.org/10.1111/oik.07202

Schmedtje, U., & Colling, M. (1996). *Ökologische Typisierung der aquatischen Makrofauna*. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft.

Schmidt-Kloiber, A., & Hering, D. (2015). www.freshwaterecology.info—An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, *53*, 271–282. https://doi.org/10.1016/j.ecolind.2015.02.007

Sharpe, A. K., & Downes, B. J. (2006). The effects of potential larval supply, settlement and post-settlement processes on the distribution of two species of filter-feeding caddisflies. *Freshwater Biology*, *51*, 717–729. https://doi.org/10.1111/j.1365-2427.2006.01526.x

Tachet, H., Bournaud, M., Richoux, P., & Usseglio-Polatera, P. (2010). *Invertébrés d'eau douce - systématique, biologie, écologie*. CNRS Editions.

TIBCO Software Inc. (2017). Statistica (data analysis software system), version 13. http://statistica.io

Ward, J., & Stanford, J. (1979). Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In J. V. Ward & J. A. Stanford (Eds.), *The ecology of regulated streams* (pp. 35–55). Springer. https://doi.org/10.1007/978-1-4684-8613-1_4

Waringer, J., & Graf, W. (2011). *Atlas of central European Trichoptera larvae/Atlas der Mitteleuropäischen Köcherfliegenlarven*. Erik Mauch Verlag.

Welber, M., Le Coz, J., Laronne, J. B., Zolezzi, G., Zamler, D., Dramais, G., Hauet, A., & Salvaro, M. (2016). Field assessment of noncontact stream gauging using portable surface velocity radars (SVR). *Water Resources Research*, *52*, 1108–1126. https://doi.org/10.1002/2015WR017906

Wohl, E. (2006). Human impacts to mountain streams. *Geomorphology*, *79*, 217–248. https://doi.org/10.1016/j.geomorph.2006.06.020

Wood, P. J., & Petts, G. E. (1994). Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management*, *9*, 303–316. https://doi.org/10.1002/rrr.3450090410

Wood, P. J., & Petts, G. E. (1999). The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes*, *13*, 387–399. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:3<387::AID-HYP745>3.0.CO;2-R

Wu, N. C., Jiang, W. X., Fu, X. C., Zhou, S. C., Li, F. Q., & Cai, Q. H. (2010). Temporal impacts of a small hydropower plant on benthic algal community. *Fundamental and Applied Limnology*, *177*, 257–266. https://doi.org/10.1127/1863-9135/2010/0177-0257

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.