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**Taxonomic and functional homogenisation of macroinvertebrate communities in recently intermittent Alpine watercourses**

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1 **Patterns in taxonomic and functional diversity highlight the “mediterraneization”**  
2 **of macroinvertebrate communities in recently intermittent Alpine watercourses**

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11  
12 **Abstract**

- 13 1. Mountain streams are currently shifting from perennial to intermittent regime due to the combined  
14 effect of climate change and local anthropogenic pressures. Studies on the effect of flow  
15 intermittency on macroinvertebrates are as yet inconclusive due to the large heterogeneity in  
16 geographical areas and spatial scales at which this relationship has been investigated. Given that  
17 flow intermittency is a recently documented phenomenon in the Alps, only few studies have  
18 investigated functional and taxonomical diversity of benthic invertebrate communities in recently  
19 intermittent Alpine streams.
- 20 2. We used a hierarchical sampling design to investigate patterns in taxonomic and functional  
21 diversity of benthic invertebrate communities in 13 recently intermittent Alpine streams in NW-  
22 Italy. In each of these streams, we sampled in April 2017 benthic communities in two reaches with  
23 different hydrological conditions: a control reach, with permanent flow, and an intermittent reach,  
24 which recently experienced non-flow periods in summer.

- 25 3. We tested for the response of taxonomic richness at multiple spatial scales by partitioning total  
26 diversity into the average richness of local communities and the richness due to variation  
27 among local communities both within and among reaches. By partitioning total diversity ( $\gamma$ ) into  
28 its local ( $\alpha$ ) and turnover ( $\beta$ ) components we showed a decrease in local and regional species  
29 richness both within and among reaches, whereas variation among communities was significantly  
30 lower in intermittent reaches only at the reach scale.
- 31 4. The analysis of the multidimensional trait space of macroinvertebrates in reaches with different  
32 hydrological conditions further revealed a significant reduction of functional diversity, dispersion,  
33 and evenness in intermittent reaches. There was trait overdispersion in intermittent reaches, as  
34 these hosted both typical Alpine taxa and organisms adapted to flow intermittency. In particular,  
35 we observed the replacement of taxa with aquatic respiration and preferring medium- to fast-  
36 flowing oligotrophic waters by taxa adapted to lentic habitats and with larval dormancy phases.
- 37 5. These results provide strong support that recent flow intermittency determines drastic changes of  
38 benthic invertebrate communities in Alpine streams which are facing a “mediterraneization”  
39 process. Our work highlights the importance of considering multiple spatial scales and of  
40 integrating taxonomic and functional diversity to thoroughly assess the impacts of flow  
41 intermittency.

42 **Keywords:** flow intermittency, drying, diversity partitioning, nestedness, functional traits

43

44

45 **INTRODUCTION**

46 Stream ecosystems are particularly sensitive to climate change, as changes in precipitations,  
47 temperature and evaporation direct translate in shifts in river flow regimes and their physical conditions  
48 (Lake, 2003). The raising of water temperatures and the disruption of hydrologic cycles, further  
49 exacerbated by anthropogenic activities (e.g. deforestation, water capture, streambed alterations; Wohl,  
50 2006) can lead, in turn, to stochastic events (Scheffer et al., 2001), like floods and droughts. The observed  
51 and predicted climate warming is also increasingly associated to changes in distribution and phenology of  
52 biota (Heino et al., 2009; Whitehead et al., 2009).

53 Among flow-related disturbances, water scarcity, and consequent riverbed desiccation, is one of  
54 the most pressing environmental issues related to climate change, with expected drastic consequences on  
55 biodiversity (Lake, 2003). The necessity of understanding such complex dynamics have recently pushed  
56 more and more researchers to study the effect of flow intermittency on the taxonomic richness of benthic  
57 invertebrate communities. Yet contrasting results have so far been obtained, as either negative  
58 relationships (Datry et al., 2014; Leigh & Datry, 2017; Datry et al. 2016a), no relationship (Bonada et al.,  
59 2007; Bogan et al. 2015; Datry et al., 2016b; Leigh et al., 2016) or fluctuating relationships (Bogan et al.  
60 2017) were observed. This heterogeneity of results suggests that the effect of flow intermittency may  
61 strongly depend on the scale at which this trend is studied. Specifically, in streams experiencing flow  
62 intermittency, we can observe the local extinction of species lacking traits conferring resistance (e.g.  
63 desiccation-resistant stages) or resilience (e.g. plurivoltine taxa). This may cause a shift in community  
64 composition, whereby either only a subset of tolerant species from the original pool will persist *in situ* or  
65 less adapted species will be replaced by a new set of species more tolerant to flow intermittency. These  
66 two processes, often acting hand-in-hand, determine variations in nestedness and turnover components of  
67  $\beta$ -diversity, respectively, and may ultimately result in biotic homogenisation of intermittent reaches and a  
68 reduction of the total taxonomic diversity at the regional scale (Socolar et al. 2016).

69 As anticipated, variations in taxonomic composition further reflect changes in the organization of functional  
70 space [functional diversity (FD); Petchey & Gaston, 2002], due to the selection of species based on their

71 biological traits related to physiology, behaviour, feeding strategy or dispersal (MacLean & Beissinger,  
72 2017). A reduction in total diversity of traits and their dispersion should translate in a functional  
73 homogenization of aquatic communities due to the depletion of less tolerant species, i.e. environmental  
74 filtering (e.g. Elias et al., 2015; Leigh et al., 2016; Brown et al., 2018). Therefore, a nuanced understanding  
75 of the underlying mechanisms shaping the structure of lotic communities in a flow intermittency regime is  
76 best achieved by simultaneously looking at multiple spatial scales and diversity measures (Bruno et al.,  
77 2019; Van Looy et al., 2019). While similar comprehensive studies have been performed in Mediterranean  
78 streams, where flow intermittency is part of their natural hydrological cycle (García-Roger et al., 2013),  
79 little is known in other biogeographic areas where streams are changing from perennial to intermittent  
80 regimes as a result of anthropogenic activities, therefore generating novel community trajectories (Bogan  
81 et al. 2015).

82 Alpine streams are expected to be particularly affected by flow intermittency, because they are fed  
83 at least partially by snowfields and glaciers, which are rapidly disappearing (Gobiet et al., 2014). Moreover,  
84 they host specialized organisms adapted to a narrow range of environmental conditions (McGregor et al.  
85 1995). In these lotic systems, summer flow cessation periods are increasing, especially at the mid-latitudes,  
86 as they are warming at a rate two to three times faster than the global average (Hansen et al., 2005;  
87 Pederson et al., 2011). The rapid shrinkage of glaciers and snowpack (Rauscher et al., 2008) anticipates the  
88 hydrological peak in spring and induces modifications in both thermal and hydrological regimes as well as in  
89 sediment transport (Brighenti et al., 2019). Moreover, mountainous streams are suffering the heavy flow  
90 regulation, hydropower and increased water abstraction aimed to fulfill local human needs e.g., agricultural  
91 use, drinking water and energy production (Wohl, 2006; López-Rodríguez et al., 2019). The combined  
92 effects of both climate change and anthropogenic disturbance are changing mountain streams from  
93 perennial to temporary systems (Bruno et al., 2019), alternating non-flow events and rewetting phases  
94 (Fenoglio et al., 2010), bringing new challenges to the conservation and management of these ecosystems.  
95 In this context, periodic flow intermittency represents a major threat for stream macroinvertebrates in  
96 mountainous lotic ecosystems (e.g. Doretto et al., 2018; Piano et al., 2019a; Piano et al., 2019b), whose  
97 resistance and resilience abilities are expected to be limited compared to their counterpart in the

98 Mediterranean region, where the drying phase is a natural part of the stream hydrological cycle (Leigh et  
99 al., 2016; Vannucchi et al., 2013). Investigating the effects of flow intermittency on Alpine benthic  
100 invertebrate communities is therefore pivotal to understand how this phenomenon is changing their  
101 communities and to predict potential threats in the near future.

102 We here investigated the effects of flow intermittency on Alpine benthic invertebrate communities  
103 using a hierarchical sampling design, wherein a permanent reach, located upstream, and intermittent  
104 reach, located downstream, were selected within 13 Alpine streams in SW-Alps recently facing summer  
105 flow intermittency. Within each reach we sampled macroinvertebrates in seven patches differing in near-  
106 bed conditions. Following modern standards in community ecology analyses (e.g. Pavoine et al., 2011;  
107 Jarzyna & Jetz, 2018), we estimate multiple facets of taxonomic and functional diversity at both reach and  
108 basin scale to evaluate how hydrological disturbance affects the assemblage composition of benthic  
109 invertebrate communities. Specifically, we tested whether: (i) flow intermittency causes taxa loss at local  
110 and/or at regional scale; (ii) communities in intermittent sites represent either a subset of taxa usually  
111 inhabiting permanent reaches or they are composed by different taxa; and (iii) changes in taxonomic  
112 composition are mirrored in the functional diversity due to the filtering of taxa with particular combinations  
113 of traits. By assuming that flow intermittency is a major cause of species loss (e.g. Datry et al., 2017;  
114 Samways et al., 2020) and considering that the overall pool of species in Alpine streams is expected to be  
115 mainly composed by taxa not adapted to drying (e.g. Doretto et al., 2018, 2020a; Piano et al., 2019a), we  
116 made the following hypotheses: (i) taxonomic diversity should decrease in intermittent sites at both reach  
117 and basin; (ii) variation in taxa composition among permanent and intermittent reaches is best explained  
118 by taxa loss (i.e., nestedness) than by taxa replacement (i.e. turnover); and (iii) loss of taxa displaying  
119 particular trait combinations should directly lead to a reduction of functional diversity and a general  
120 rearrangement of the total functional space.

## 121 **MATERIALS AND METHODS**

### 122 **Sampling design**

123            This study was conducted in 13 low to mid-order streams, experiencing dewatering events since  
124 2011 in multiple reaches. The study streams were selected based on our previous knowledge (Fenoglio et  
125 al., 2007) integrated with available historical hydrological data provided by the local Environmental  
126 Protection Agency (ARPA). The study streams are all located in the hydroecoregion of SW-Alps (HER 4,  
127 Piemonte, NW Italy; Wasson et al. 2007), thus they are characterized by comparable geology, climate,  
128 topology and altitude (Moog et al., 2004). In each stream, we selected two 30 m long sampling sections,  
129 differing in their hydrological regime: i) an upstream reach, with permanent water throughout the year  
130 (hereinafter UP); and ii) a downstream reach, experiencing dewatering events during summer (hereinafter  
131 DOWN). In the study area, flow intermittency events lasted on average two months since 2011, with the  
132 riverbed almost completely dry for several kilometres (ARPA, 2013; personal observations). Stream drying  
133 was caused by the reduction in precipitations, and consequently of snow accumulation, and the parallel  
134 increase in water abstraction for human needs. UP and DOWN reaches were located within 10 km, in order  
135 to reduce variations in environmental parameters (as demonstrated in Piano et al., 2019) and changes in  
136 community composition attributable to geographical distance rather than differences in flow regimes. Both  
137 permanent and intermittent sites were identified in the bottom of the valleys. Sampling site elevation was  
138 on average 489 m a.s.l., ranging from 307 and 656 m, and permanent and intermittent reaches within the  
139 same stream differed on average of 70 m in their elevation (min = 19 m; max = 155 m). Sampling was  
140 performed in April 2017 under moderate flow conditions ( $Q_{\text{mean}} = 3.98 \pm 4.56 \text{ m}^3\text{s}^{-1}$ ) occurring in both  
141 reaches, approximately six months after water flow resumption in the DOWN reach (Hydrological bulletins,  
142 [www.arpa.piemonte.it](http://www.arpa.piemonte.it)).

### 143            **Data collection**

144            In each sampling site, we selected seven sampling patches representative of the different  
145 conditions of flow velocity, water depth and substrate composition occurring within each section (7  
146 samples x 2 reaches x 13 streams = 182 samples). In each patch, we measured flow velocity at 0.05 m from  
147 the bottom and water depth with a current meter (Hydro-bios Kiel). We used a gravelometer to estimate  
148 percentages of different substratum sizes based on the Wentworth's grain size classification (Wentworth,

149 1922): boulders (> 256 mm), cobbles (64–256 mm), gravel (2–64 mm), and fine sediment (< 2 mm). One  
150 benthic sample was collected in each sampling patch, using a Surber sampler (250  $\mu\text{m}$  mesh size; 0.062m<sup>2</sup>  
151 area), and preserved in 75% ethanol (see Doretto et al., 2020a).

152 In the laboratory, macroinvertebrates were sorted from the substrate, counted and identified to  
153 the family or genus level according to Campaioli et al. (1994, 1999). Each taxon was then assigned to: i) a  
154 functional feeding group (FFG) based on its morpho-behavioral mechanisms of food acquisition (shredders,  
155 scrapers, predators, collector-gatherers, and filterers); ii) a biological group based on its life-history traits  
156 (size, life-cycle, respiration, reproduction, and locomotion); and iii) an ecological group based on its  
157 ecological requirements (transversal and longitudinal distribution, preferred substrate and current  
158 velocity). FFGs were assigned based on the classification provided by Merritt et al. (2017), whereas  
159 biological and ecological groups were assigned based on the classification proposed by Usseglio-Polatera et  
160 al. (2000), who grouped together taxa showing similar combinations of life-history traits (biological groups)  
161 and ecological preferences (ecological groups). We preferred this approach as it allowed us to synthesize all  
162 the most important life-history and ecological traits within few categories.

### 163 **Data analysis**

164 We conducted all analyses in R (R Core Team, 2019).

165 Taxonomic diversity. In order to test our first hypothesis (H1), we partitioned the total taxonomic richness  
166 into its underlying components both within and among reaches. First, we decomposed the total diversity of  
167 each stream ( $\gamma_w$ ) into its within-reach diversity components (hereafter “reach scale”), namely average local  
168 taxa richness of the seven patches within a reach ( $\alpha_w$ ) and the variation among these communities ( $\beta_w$ ) (Fig.  
169 1). We therefore obtained 13 values of each diversity component, one for each stream. In a second step,  
170 we calculated the among-reach diversity components (hereafter “basin scale”), namely: i) average local  
171 diversity ( $\alpha_a$ ), obtained by averaging the total taxa richness of each reach; ii) total diversity ( $\gamma_a$ ), calculated  
172 as the total number of taxa observed at the basin scale; and iii) the variation in taxa richness ( $\beta_a$ ) among  
173 reaches (Fig. 1). We therefore obtained a single value for each diversity component. Variation in taxa  
174 composition among local communities ( $\beta$ -diversity) was calculated with the additive formula as the



175 difference between  $\gamma$ - and  $\alpha$ -diversity (Anderson et al., 2011). Therefore, variation in taxa composition  
176 within reaches ( $\beta_w$ ) is calculated as the difference between  $\gamma_w$  and  $\alpha_w$ , while variation in taxa composition  
177 among reaches ( $\beta_a$ ) is calculated as the difference between  $\gamma_a$  and  $\alpha_a$ . Being calculated with this formula,  $\beta$ -  
178 diversity expresses the number of species that accumulates at regional level as a result of differences  
179 between sites at local level. Differences in taxa richness among permanent and intermittent reaches at the  
180 reach scale was tested with a paired t-test. On the other hand, differences in taxa richness at basin scale  
181 were tested with null modelling, by permuting samples over the two hydrological categories as only a single  
182 value for permanent and intermittent reaches was produced. Significant differences between streams can  
183 thus be obtained by comparing the observed value of the taxa richness to the null expectation where  
184 hydrological categories (permanent vs intermittent) are randomly permuted across the sampling sites  
185 (Legendre & Legendre, 1998).

186 In order to test our second hypothesis (H2), we decomposed total beta diversity, here intended as the  
187 dissimilarity between communities in UP and DOWN sites ( $\beta_{total}$ ) into its turnover ( $\beta_{repl}$ ) and nestedness  
188 ( $\beta_{rich}$ ) components with the function *beta* in the BAT package (Cardoso et al., 2020). We decomposed beta  
189 diversity within UP and DOWN reaches and we thus obtained 13 values of total beta diversity, turnover and  
190 nestedness for UP and DOWN sites, respectively, and we tested for differences between UP and DOWN  
191 sites with a paired t-test.

192 Functional diversity. In order to test our third hypothesis, we examined variation in functional  
193 diversity between benthic invertebrate communities in UP vs DOWN using functional  $n$ -dimensional  
194 hypervolumes (Mammola & Cardoso, 2020) as implemented in the BAT package (Cardoso et al., 2020). We  
195 constructed the community functional hypervolume for each reach with the *hypervolume* package (Blonder  
196 et al., 2014; Blonder, 2019). Since functional traits of benthic invertebrates here considered are categorical,  
197 we used the approach proposed by Carvalho & Cardoso (2018) to incorporate categorical variables in the  
198 hypervolume estimation procedure. We applied a Gower dissimilarity measure to the complete trait matrix  
199 and extracted orthogonal morphological axes through Principal Coordinate Analysis (PCoA). We retained  
200 the first three PCoA axes (43% Variance explained) to construct hypervolumes using a gaussian kernel  
201 estimator (Blonder et al., 2018) and a default bandwidth for each axis. In turn, we estimated functional  $\alpha$

202 diversity, functional dispersion and functional evenness based on the approach by Mammola & Cardoso  
203 (2020). To further inspect functional turnovers among permanent and intermittent reaches, we estimated  
204 functional  $\beta$ -diversity following Carvalho & Cardoso (2018). This approach computes a pairwise  
205 decomposition of the overall differentiation among kernel hypervolumes into two components: the  
206 replacement of space between hypervolumes ( $\beta$ -replacement) and net differences between the amount of  
207 space enclosed by each hypervolume ( $\beta$ -richness) (see Cardoso et al., 2014 and Mammola & Cardoso, 2020  
208 for further details). As we had seven values for each reach within each flow category, we tested for  
209 significant differences between UP and DOWN reaches using linear mixed models (LMMs), with the flow  
210 intermittency category (UP vs DOWN) as independent variable and stream identity as a random factor. We  
211 included the latter to account for spatial dependence of the data (sampling reaches nested within streams)  
212 (Zuur et al., 2009).

213 To investigate which combination of traits is selected in UP and DOWN sites, we evaluated the  
214 functional contribution of each taxon (observation) within communities to the functional space and  
215 originality of each taxon within both UP and DOWN reaches. Taxa with high values of contribution provide  
216 rare combinations of traits within the community thus contributing the most to the overall functional  
217 diversity of the community (Pavoine et al., 2005; Violle et al., 2017), whereas taxa with high originality  
218 values are the ones contributing the most in determining the functional dispersion of the community  
219 (Mammola & Cardoso, 2020).

220

## 221 **RESULTS**

### 222 **Taxonomic diversity**

223 We observed a significant decline in taxa diversity from UP to DOWN reaches both within and  
224 among reaches (Fig. 2a). When considering diversity within reaches, we could detect a significant decrease  
225 in all diversity components, indicating that flow intermittency reduces both local ( $\alpha_w$ :  $t = 4.85$ ,  $P < 0.001$ )  
226 and total ( $\gamma_w$ :  $t = 6.06$ ,  $P < 0.001$ ) diversity within reaches from UP to DOWN sites, as well as taxa variation  
227 among habitat patches within reaches ( $\beta_w$ :  $t = 4.26$ ,  $P = 0.001$ ). When considering diversity among reaches,

228 we could detect a significant decline in both local ( $\alpha_d$ :  $P < 0.001$ ) and total ( $\gamma_d$ :  $P < 0.001$ ) diversity  
229 components from UP to DOWN sites, but not in terms of taxa variation ( $\beta_d$ :  $P = 0.333$ ).

230 By partitioning total  $\beta$ -diversity, here intended as the dissimilarity among community matrices,  
231 into its turnover and nestedness components, we observed a higher contribution of nestedness than  
232 turnover in both UP and DOWN sites (UP:  $\beta_{total} = 0.69$ ,  $\beta_{repl} = 0.19$ ,  $\beta_{rich} = 0.50$ ; DOWN:  $\beta_{total} = 0.66$ ,  $\beta_{repl} =$   
233  $0.21$ ,  $\beta_{rich} = 0.45$ ), although no significant differences between UP and DOWN sites were observed  
234 (turnover:  $t = -0.507$ ,  $P = 0.621$ ; nestedness:  $t = 1.05$ ,  $P = 0.313$ ). This suggests that the contribution of the  
235 two components is equal in the two hydrological levels (Fig. 2b).

236

### 237 **Functional diversity**

238 Results of the LMMs showed that all functional metrics significantly differ between UP and DOWN  
239 reaches (Tab. 1).  $\alpha$ -diversity, dispersion and evenness were significantly lower in DOWN than in UP reaches  
240 (Fig. 3). When considering  $\beta$ -diversity, we observed significantly higher values in pairwise comparisons  
241 between communities in DOWN reaches, whereas communities in UP reaches were in general more similar  
242 to one another, suggesting trait overdispersion in sites experiencing flow intermittency. In DOWN reaches  
243 the  $\beta$ -richness component was more preponderant than in UP reaches, whereas the  $\beta$ -replacement was  
244 higher in UP reaches. When evaluating the contribution of each taxon, we inferred that Tipulidae (Diptera)  
245 was the taxon contributing the most to the functional space in UP reaches, and *Perla* (Plecoptera, Perlidae)  
246 in DOWN reaches. In other words, Tipulidae contributed with unique traits in UP sites, while *Perla*  
247 contributed with unique traits in DOWN sites.

248

### 249 **DISCUSSION**

250 According to our results, flow intermittency is causing a decline in macroinvertebrate taxonomic  
251 richness at both reach and basin scale, suggesting that this phenomenon, which is expected to increase in  
252 frequency in the near future in Alpine streams (Brighenti et al., 2019), will represent a threat for Alpine  
253 stream biodiversity.

254           Decomposing the total diversity into its taxonomic components allowed us to obtain a more  
255 detailed view on which of the two main mechanisms, i.e. species filtering (alpha diversity) and biotic  
256 homogenization (beta diversity components) (Socolar et al. 2016), and at which spatial scale, is affecting  
257 macroinvertebrate assemblages. We could highlight that the overall decline in macroinvertebrate richness  
258 is mainly due to local diversity reduction among and within reaches. In particular, at the reach scale, local  
259 macroinvertebrate communities are impoverished and become more homogeneous. Conversely, we did  
260 not record a significant difference in taxonomic variation among reaches between permanent and  
261 intermittent sites. These results are partially supported by García-Roger (2013), who found that variation in  
262 intermittent streams during the wet season is accounted by both the microhabitat (in systems with pools  
263 during the dry season) and the stream (in systems where the riverbed completely dries during the dry  
264 season) scale. The lack of taxonomic variation among reaches observed in our study might indicate that the  
265 biotic homogenization of macroinvertebrate communities caused by flow intermittency, which is a  
266 relatively new phenomenon in the investigated streams, has not become pervasive yet. However, this  
267 result should be interpreted with caution as we here identified our taxa at the family to genus levels,  
268 preventing to infer whether a homogenization process is ongoing at species level too.

269           When analysing the contribution of nestedness and turnover components, we could detect that  
270 variation among local communities is mainly due to richness difference in both permanent and intermittent  
271 reaches, while taxa replacement seemingly played a minor role, in accordance with the fact we sampled  
272 during the base flow regime. In fact,  $\beta$ -diversity should be low during non-drought phases and dominated  
273 by nestedness as organisms experience favourable high hydrological connectivity between sites (Larned et  
274 al., 2010). Conversely, the turnover component of dissimilarity increases with increasing intermittency (  
275 Tornés & Ruhì, 2013; Piano et al., 2017; Aspin et al., 2018). Although we did not record significant  
276 differences in the relative contribution of these two components in permanent and intermittent reaches,  
277 we observed a slightly higher contribution of turnover in intermittent than permanent sites. Despite some  
278 contrasting results found in literature (Datry et al., 2014), this is in agreement with Rolls et al. (2016) who  
279 showed a dominance of turnover processes in the dissimilarity partitioning on macroinvertebrates and fish  
280 subjected to intermittent flow. This may be due to the environmental filter imposed by physical and

281 chemical alterations associated with stream drying—lentification with the creation of isolated pools, where  
282 organisms experience oxygen reduction and increase in nutrient concentration, fine sediment deposition  
283 and biotic interactions (Lake, 2003)—that causes the replacement of the most sensitive taxa by tolerant  
284 ones (Dolédec et al., 2017).

285         Functional diversity patterns showed that reaches experiencing flow intermittency are less  
286 functionally diverse than permanent ones, with communities in intermittent sites showing lower diversity,  
287 variability and a less homogeneous distribution of functional traits. Opposite results were obtained by  
288 Belmar et al. (2019) in Mediterranean streams, where they did not observe any significant effect of flow  
289 intermittence on functional diversity. These different outcomes may indicate that flow intermittency exerts  
290 a stronger environmental pressure on benthic invertebrate communities in mountainous lotic ecosystems  
291 than in Mediterranean streams. In fact, the overall pool of macroinvertebrates in Alpine areas lacks  
292 functional traits to cope with flow intermittency, which are present in their counterpart in the  
293 Mediterranean region, where the drying phase is a natural part of the stream hydrological cycle (Leigh et  
294 al., 2016; Vannucchi et al., 2013). On the other hand, the analysis of functional  $\beta$ -diversity showed how  
295 intermittent reaches experience trait overdispersion, and this is mainly due to a net difference in the  
296 amount of space enclosed by the trait space rather than replacements of traits. In other words,  
297 communities in intermittent streams are composed by taxa that show a subset of the entire pool of  
298 functional traits, but this subset is different depending on the reach considered. Similar results were  
299 obtained by Dolédec et al. (2017), as they observed that Mediterranean taxa, which have to cope with  
300 higher hydrological variability, may perform more diverse functional roles than temperate taxa and  
301 intermittent streams show higher functional variability than permanent systems within the Mediterranean  
302 area. This may be due to the fact that intermittent sites are colonized by species with traits adapted to flow  
303 intermittence even during baseflow conditions leading to the coexistence of taxa displaying a wide range of  
304 traits. The variation in trait composition among reaches can be explained by the high variability of lotic  
305 systems experiencing flow intermittency, which in turn affect the community assemblages through  
306 stochastic extinctions and colonization (Datry et al., 2016).

307           The analysis of taxa contribution to the functional diversity allowed us to highlight which trait  
308 combination is less typical in permanent and intermittent reaches. We observed that Tipulidae shows  
309 unique traits for the environmental conditions in permanent sites, whereas *Perla* shows unique traits for  
310 environmental conditions in intermittent sites, confirming the results that we obtained in related studies  
311 (Doretto et al., 2018; Doretto et al., 2020b; Piano et al., 2019a). In other words, Tipulidae and *Perla* traits  
312 are atypical (and possibly maladaptive) for permanent and intermittent stretches, respectively. Tipulidae is  
313 a monovoltine, crawler taxon, living in slow flowing waters, such as side-arms or near the banks, whose  
314 larvae have a dormancy phase, whereas *Perla* is a large-sized, monovoltine, crawler taxon, with aquatic  
315 respiration, preferring oligotrophic, cold, fast-flowing waters (Usseglio-Polatera et al., 2000; Merritt et al.,  
316 2017). Large semivoltine taxa with long larval life are expected to be unable to survive in periodically dry  
317 environments, while fast growing, plurivoltine organisms are adapted to complete their life cycle in less  
318 than one year, emerging just before the loss of surface water (Corbet et al., 2006; López-Rodríguez et al.,  
319 2009a, b; Bonada & Dolédec, 2018). Small body size is another trait that increases the survival in  
320 intermittent reaches as reduced dimensions allow fast development and population growth (Bonada et al.  
321 2007). The shift from rheophilous to lentic taxa has also been recorded in literature (e.g. Acuña et al., 2005;  
322 Pace et al., 2013; Chessmann, 2015), as flow intermittency is usually associated with lentication and  
323 consequent oxygen reduction (Lake, 2003), which may compromise the survival of many taxa, especially in  
324 mountainous lotic ecosystems where organisms have to be adapted to high flow velocities and the  
325 pronounced oligotrophy (Fenoglio et al., 2010). In addition, it should be noted that, compared to other  
326 exclusively lotic organisms, Tipulidae larvae can survive even in terrestrial habitats if characterized by  
327 sufficient moisture (Pritchard, 1983), thus being naturally tolerant to intermittent regimes.

328           Overall, our results demonstrate that benthic invertebrate biodiversity is threatened at both local  
329 and regional scale, whereas the biotic homogenization process is still ongoing. We can therefore suggest  
330 that macroinvertebrate communities are currently facing an ongoing “mediterraneization process”, which  
331 is still in progress, and the results of the analyses of functional diversity support this hypothesis. In fact, a  
332 more in-depth analysis of their functional diversity revealed that Alpine streams are currently facing the  
333 extinction of rheophilous organisms, typical of fast-flowing, well-oxygenated waters, which are gradually

334 replaced by lentic taxa, with life-traits that confer adaptations to flow intermittency. As the frequency and  
335 magnitude of anthropogenic and climatic droughts in the mountain areas are predicted to increase  
336 (Brighenti et al., 2019), further studies should be performed in the next future to prevent the loss of  
337 specialized benthic species, their functional diversity, and the key role they play in the riverine ecological  
338 network.

339

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351

#### 352 **Data Availability Statement**

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

355

#### 356 **Conflict of Interest Statement**

357 The authors declare no conflict of interest.

358

359

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564 **Tables**

565 Table 1. Mean values with standard deviation in brackets of functional diversity measures in  
 566 permanent (UP) and intermittent (DOWN) sites, and estimated parameters (Est), with standard errors (SE)  
 567 in brackets, and p-values (P) of LMMs performed on functional metrics (FD = functional  $\alpha$ -diversity; Fdis =  
 568 functional dispersion; Feve = functional evenness) to test for differences between UP and DOWN sites. All  
 569 comparisons are significant.

Functional measures	UP	DOWN	BEst $\pm$ SE	P
FD	0.20 ( $\pm$ 0.10)	0.13 ( $\pm$ 0.13)	-0.071 ( $\pm$ 0.014)	< 0.001
Fdis	0.53 ( $\pm$ 0.04)	0.49 ( $\pm$ 0.06)	-0.053 ( $\pm$ 0.006)	< 0.001
Feve	0.17 ( $\pm$ 0.06)	0.13 ( $\pm$ 0.09)	-0.039 ( $\pm$ 0.014)	0.007
$\beta$ -diversity ( $\beta$ -replacement + $\beta$ - richness)	0.63 ( $\pm$ 0.14)	0.74 ( $\pm$ 0.15)	0.119 ( $\pm$ 0.003)	< 0.001
$\beta$ -replacement	0.25 ( $\pm$ 0.16)	0.19 ( $\pm$ 0.18)	-0.062 ( $\pm$ 0.004)	< 0.001
$\beta$ -richness	0.38 ( $\pm$ 0.24)	0.56 ( $\pm$ 0.29)	0.181 ( $\pm$ 0.006)	< 0.001

570

571 **Figure captions**

572 Figure 1. Schematic overview of the calculated diversity components ( $\alpha_w$  = local diversity within  
573 reaches;  $\alpha_a$  = local diversity among reaches;  $\beta_w$  = variation among local communities within reaches;  $\beta_a$  =  
574 variation among local communities among reaches;  $\gamma_w$  = total diversity within reaches;  $\gamma_a$  = total diversity  
575 among reaches) to test the effect of flow intermittency (UP = orange; DOWN = light blue) within- (reach  
576 scale) and among stretches (basin scale).

577 Figure 2. a) diversity partitioning of total diversity in the study area into its within- and among  
578 reaches components in UP and DOWN reaches ( $\alpha_w$  = dark grey;  $\beta_w$  = medium grey;  $\beta_a$  = light grey); b)  
579 decomposition of  $\beta$ -diversity into its nestedness (dark grey) and turnover (light grey) components in in UP  
580 and DOWN reaches.

581 Figure 3. a–c) Functional richness (a), dispersion (b) and evenness (c) of benthic invertebrate  
582 communities in permanent (UP) and intermittent (DOWN) reaches; d–f) Density of functional  $\beta$ -diversity  
583 values for pairwise comparison of communities in permanent (UP) and intermittent (DOWN) reaches. Total  
584 functional  $\beta$ -diversity (d) is split in two components:  $\beta$ -replacement (e) is turnover in functional  
585 composition explained by replacement of space between hypervolumes, and  $\beta$ -richness (f) is the turnover  
586 in functional composition explained by net differences between the amount of space enclosed by each  
587 hypervolume (Carvalho & Cardoso, 2018; Mammola & Cardoso, 2020).