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Stay with the flow: how macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought

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3 1 **Stay with the flow: how macroinvertebrate communities recover during the rewetting phase in**
4 2 **Alpine streams affected by an exceptional drought**
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8 4 Short running title: Resilience of macroinvertebrates to droughts in Alpine streams
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For Peer Review

1
2
3 **Abstract**
4

5 24 Drought occurrence is affecting an increasing number of lotic ecosystems worldwide due to the
6
7 25 combined effects of climatic and anthropogenic pressures. Unlike naturally intermittent rivers,
8
9 26 where the drying phase is a part of the annual flow regime, water scarcity in Alpine rivers represent
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11 27 a relatively recent phenomenon and, therefore, a major threat for the biodiversity of these lotic
12
13 28 ecosystems, but the response of aquatic communities to this disturbance is still poorly investigated.
14
15 29 Here, we present the results on the recovery of stream macroinvertebrates in two Alpine streams
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17 30 after a supra-seasonal drought. As water resumed, a total of ten sampling sessions were carried out
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19 31 and temporal patterns in diversity, density and taxonomic composition of benthic communities as
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21 32 well as in the percentage of functional feeding groups were investigated.
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23 33 We found that the resistance of invertebrate communities in Alpine streams is generally low:
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25 34 drought significantly reduced the diversity and density of macroinvertebrates. Conversely, our
26
27 35 results suggest that the passive dispersal by drift from the upstream river sections seems the main
28
29 36 mechanism that promotes the post-drought recovery. Nevertheless, this resilience ability appears
30
31 37 to be stream-specific and influenced by intrinsic stream characteristics, including the flow
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33 38 permanence and distance from the nearest upstream perennial reach. This work sheds light on the
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35 39 impacts of climatic and human-induced droughts on benthic invertebrate communities and assumes
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37 40 a primary importance to predict their future composition in relation to the intensification of flow
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39 41 intermittency in Alpine areas under the current global change scenario.
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40 **Keywords:** benthic invertebrates, Alpine streams, water scarcity, recolonization, biodiversity,
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1. Introduction

Climate change is currently one of the most relevant challenges for habitat and species conservation worldwide because the raising in air temperature and alterations in the precipitation regimes are responsible for the habitat loss and fragmentation, changes in species phenology and enhanced rates of biodiversity loss (Dawson, Jackson, House, Prentice, & Mace, 2011; Mantyka-pringle, Martin, & Rhodes, 2012). The increased frequency and magnitude of hydrological extremes, such as floods and droughts, are among the main consequences of these phenomena for lotic ecosystems (Beniston, 2012; Heino, Virkkala, & Toivonen, 2009; Middelkoop et al., 2001; Ledger, & Milner, 2015; Whitehead, Wilby, Battarbee, Kernan, & Wade, 2009; Wu, & Johnson, 2019).

Alpine streams are expected to be extremely sensitive to the effects of droughts because the Alps are one of the most impacted areas by climate change and, at the same time, water abstraction is an increasing pressure (Fenoglio, Bo, Cucco, Mercalli, & Malacarne, 2010; Gorbach, Shoda, Burky, & Benbow, 2014; McKay, & King, 2006; López-Rodríguez, Márquez Muñoz, Ripoll-Martín, & Tierno de Figueroa, 2019). Under similar conditions, drought occurrence represents a major threat for stream macroinvertebrates, as documented by some authors (Bonada, Doledec, & Statzner, 2007; Calapez, Elias, Almeida, & Feio, 2014; Doretto et al., 2018b; Durance, & Ormerod, 2007; Fenoglio, Bo, Cucco, & Malacarne, 2007; Ledger, Brown, Edwards, Milner, & Woodward, 2013; Piano et al. 2019a; Pinna et al., 2016; Smith, McCormick, Covich, & Golladay, 2017; Storey, 2016).

A growing attention is paid by river ecologists on the resistance and resilience mechanisms of benthic organisms to face the drying phase (Chester, & Robson, 2011; Fritz, & Dodds, 2004; Robson, Chester, & Austin, 2011; Aspin et al., 2019). However, the resistance ability of aquatic invertebrates to drought in Alpine streams is generally considered limited, compared to the aquatic biota of other geographical regions, such as the Mediterranean area, where the drying phase is a natural part of the annual flow regime (Leigh et al., 2016; Tierno de Figueroa, López-Rodríguez, Fenoglio, Sánchez-Castillo, & Fochetti, 2013). Benthic communities in Alpine streams, therefore, are generally considered more resilient than resistant (Doretto et al., 2018b), but scientific evidence on this is still limited.

In a recent publication, Van Looy et al. (2019) developed a general framework to explain the resilience of aquatic communities to disturbance in streams, including droughts, based on the relative and combined role of three main drivers: resources competition and/or facilitation, recruitment and refugia. Firstly, the access or limitation to food resources affect the response of aquatic communities in terms of trophic and biotic relationships, acting as the major driver of the

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3 77 post-disturbance recovery especially where the energetic inputs are pulsed- or patchy-distributed
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5 78 (Richardson & Sato, 2015). In this context, ameliorative effects of large amount of organic matter
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7 79 on macroinvertebrate communities have been reported also in relation to other physical
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9 80 disturbances, such as siltation (Doretto et al., 2017). Second, recruitment (i.e. the gain of individuals
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11 81 by the dispersal from adjacent habitat sources) is expected to play a primary contribution in highly
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13 82 connected river networks, resulting in a faster post-drought recovery (Flower, 2004; Ledger &
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15 83 Hildrew, 2001). Finally, habitat heterogeneity promotes the presence of in-stream refugia (mainly
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17 84 pools and the hyporheic zone) that can be exploited by the benthic taxa, according to their
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19 85 ecological traits, to survive under drying conditions (Boulton 2003; Chester & Robson, 2011;
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21 86 Fenoglio, Bo, & Bosi, 2006; Otermin, Basaguren, & Pozo, 2002; Verdonschot, Oosten-Siedlecka,
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23 87 Braak, & Verdonschot, 2015; Wood, Boulton, Little, & Stubbington, 2010).
24
25 88 In this study we monitored the post-drought recovery of macroinvertebrate communities in two
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27 89 Alpine streams affected by a supra-seasonal drought (Lake, 2003) and discussed the results in
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29 90 relation to the contribution of food resources, recruitment and refugia. In particular, temporal
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31 91 patterns in composition and diversity of benthic invertebrate communities were evaluated during
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33 92 the water resumption (hereafter rewetting phase) and compared to the upstream permanent
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35 93 reaches. Our hypotheses were that: i) the invertebrate recruitment, especially in terms of
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37 94 recolonization by drift from the upstream sections would be the main mechanism of resilience in
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39 95 our streams, while ii) the resource availability would have a minor role. As the supra-seasonal
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41 96 drought was one of the most prolonged ever reported for the Italian Alps, lasting for more than 5
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43 97 months, we expected a negligible effect of the in-stream refugia (i.e. pools and hyporheic zone). In
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45 98 addition, we postulated that the recovery process would be affected by stream-specific
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47 99 characteristics, especially in relation to hydrology stability and flow persistence.

100 101 **2. Materials and methods**

102 *2.1 Area of study*

103 The sampling area is located in the Cottian Italian Alps (Northwestern Italy), where we examined
104
105 the post-drought recovery in two lotic systems, namely the Po and Pellice rivers, which originate at
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107 2,022 and 2,387 m.a.s.l. respectively. The former is the longest Italian watercourse: it runs for 652
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109 Km until the Adriatic Sea with a drainage basin of approximately 71,000 Km². The latter is the
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111 principal tributary of the Po river within the Alpine area and runs for 55 Km (drainage area: 974 Km²)

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3 108 before its confluence (Fig. 1). They represent two good case studies as they have good water and
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5 109 biological qualities but with stretches recently affected by drought.

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7 110 On each river, two sampling sites were selected: a perennial stretch (P), with permanent flow
8
9 111 throughout the year, and an intermittent stretch (I) experiencing recurrent drought events since
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11 112 2011 (ARPA, 2013; Piano et al., 2019a; 2019b), due to the joint effect of climate change and
12
13 113 consequent water abstraction to fulfill human needs. At this scale of investigation, the Po and Pellice
14
15 114 are 5-order rivers (Strahler, 1957), with the substrate dominated by coarse mineral elements and a
16
17 115 pluvio-nival hydrological regime. Also, the land use is very similar between these two streams: more
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19 116 than 90% is represented by natural areas, while agricultural and urbanized areas on average account
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21 117 for 8% and 1.5% (Table 1).

22 118 23 119 *2.2 Data collection*

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25 120 In 2017, Northwestern Italy experienced the most severe summer droughts ever reported. In the
26
27 121 lower sections of the Po and Pellice rivers, including the intermittent sites here considered, surface
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29 122 water ceased in July and August 2017 respectively (Falasco, Piano, Doretto, Fenoglio, & Bona, 2018)
30
31 123 and resumed only in January 2018, after conspicuous rainfalls (see Supplementary Materials Fig.
32
33 124 SM1). Although a marked reduction of the river discharge, the upstream perennial sites were
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35 125 characterized by the continued permanence of running surface water during this period.

36 126 As water resumed, a total of ten sampling dates were carried out in the intermittent sites to monitor
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38 127 the post-drought recovery of benthic communities, covering a 3-month period (Table 2). To better
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40 128 describe the first phases of the recolonization process, samples were initially collected every 3 days,
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42 129 while at the end of the sampling period benthic invertebrates were sampled every two weeks.
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44 130 Moreover, since we expected that the upstream perennial stretches acted as sources of organisms
45
46 131 during the recolonization process, macroinvertebrates were sampled also in the perennial sites on
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48 132 two selected occasions, namely on 19th January and 22th March 2018. These samplings allow to
49
50 133 obtain an overview of macroinvertebrate communities, at the beginning and at the end of the
51
52 134 studied period.

53 135 On each sampling occasion, dissolved oxygen concentration (mgL^{-1}), oxygen saturation (%), pH,
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55 136 water temperature ($^{\circ}\text{C}$) and electrical conductivity (μScm^{-1}) were measured with a multiparametric
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57 137 probe (Hydrolab mod. Quanta). Water depth (cm) and water velocity (ms^{-1}) were measured for each
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59 138 sample using a flowmeter (Hydro-bios Kiel). Moreover, the composition of the substrate within the
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61 139 area delimited by the Surber sampler was visually estimated. Based on the Wentworth's grain size

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3 140 classification (1922), the percentages of boulders (>256 mm), cobbles (256-64 mm), gravel (64-2
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5 141 mm) and fine sediment (<2 mm) were estimated by the same operator. Macroinvertebrates were
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7 142 collected using a Surber sampler (0.05 m², 250 µm mesh-size) and three samples were taken on
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9 143 each sampling occasion, with the only exception represented by 23th February, when no samples
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11 144 were collected in the intermittent site of the Po river because the stream bed was completely dry
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13 145 (Table 2). Samples were preserved in 70% ethanol and returned in laboratory for the sorting under
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15 146 a stereo-microscope. Specimens were counted and systematically identified to genus
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17 147 (Ephemeroptera and Plecoptera) or family level using the taxonomic keys for the Italian
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19 148 macroinvertebrate fauna (Campaioli, Ghetti, Minelli, & Ruffo, 1994; 1999), and also classified into
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21 149 functional feeding groups (FFGs: collector-gatherers, filterers, predators, scrapers and shredders;
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23 150 Merritt, Cummins, & Berg, 2008).

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2.3 Statistical analyses

27 153 Significant differences in the environmental parameters between the perennial and intermittent
28
29 154 sampling sites (i.e. Pellice I vs Pellice P and Po I vs Po P) as well as between rivers (i.e. Pellice and
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31 155 Po) over the monitored period were visualized by means of Principal Component Analysis (PCA) and
32
33 156 tested with Permutational Analysis of Variance (PERMANOVA). The water temperature, pH,
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35 157 electrical conductivity, dissolved oxygen and the mean value of the water velocity, depth and
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37 158 percentage of the four substrate classes was calculated for each sampling site on each date and
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39 159 included in this analysis. To meet the assumptions of normality, percentage data were square-
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41 160 root(arcsin) transformed prior performing the PCA, which was run using the “prcomp” function in
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43 161 the basic package of R. The “adonis” function in the *vegan* R package (Oksanen et al. 2015) was
44
45 162 used, instead, to perform the PERMANOVA analysis, for which the Euclidean distance was applied.
46
47 163 Changes in the taxonomic composition of benthic communities between sampling occasions and
48
49 164 sites were initially visualized by means of a Non-metric Multidimensional Scaling (NMDS). This
50
51 165 multivariate analysis was performed using the function “metaMDS” in the *vegan* R package
52
53 166 (Oksanen et al. 2015). Surber samples were used as separate replicates: raw data about the
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55 167 abundance of macroinvertebrates were square-root transformed and then a Bray-Curtis
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57 168 dissimilarity index was applied. PERMANOVA was run to test for significant differences in relation
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59 169 to the “time” (as days from the water return) and “site” (Pellice P, Pellice I, Po P and Po I) factors.
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61 170 Generalized Additive Models (GAMs) were used to assess the non-linear response of the community
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63 171 metrics over the time, expressed in terms of days from the water return. Prior to perform the

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3 172 statistical models, data exploration was carried out according to Zuur, Ieno & Elphick (2010) and
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5 173 outliers were removed. Four taxonomical metrics were considered: the total taxa richness, total
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7 174 density of macroinvertebrate (number of individuals m^{-2}) as well as EPT (Ephemeroptera, Plecoptera
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9 175 and Trichoptera) richness and density. In addition, the percentage of each functional feeding group
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11 176 and the ratio between scrapers and total collectors were also taken into account. The latter
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13 177 parameter has been proposed as an ecosystem indicator for the prevalence of autotrophy (i.e.
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15 178 grazing) or heterotrophy (i.e. detritus chain) in rivers (Cummins, Merritt, & Andrade, 2005). Samples
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17 179 collected in the perennial sites were not included in the regression models, but the mean value of
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19 180 each metric was calculated to better interpret the observed patterns.

20 181 All the GAMs were carried out using the “gam” function in the *mgcv* R package (Wood & Wood,
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22 182 2015): a Poisson distribution was used for count data, while the negative binomial distribution was
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24 183 alternatively used in case of overdispersion. The binomial distribution was instead applied for the
25
26 184 percentage variables. All the analyses were performed with the statistical software R (R
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28 185 Development Core Team, 2018).

31 187 **3. Results**

32 188 *3.1 Environmental parameters*

33
34 189 The first and the second axes of PCA accounted for 25.6% and 22.5% respectively of the variance
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36 190 associated to the environmental parameters, for a cumulative percentage equal to 48.1% (Fig. 2).
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38 191 The first axis (PC1) was positively correlated with the electrical conductivity and negatively
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40 192 correlated with the pH and water velocity. By contrast, the second axis (PC2) was positively
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42 193 correlated with the percentage of cobbles and the dissolved oxygen, while it was negatively
43
44 194 correlated with the percentage of sand, water depth and water temperature.

45 195 In general, samples from the Pellice river were mainly oriented in the top-left part of the plot and
46
47 196 showed a less pronounced dispersion, while samples from the Po river were oriented in the bottom-
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49 197 right part of the graph and showed a higher dispersion. Nevertheless, PERMANOVA did not show
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51 198 significant differences in the environmental parameters among sampling sites ($P = 0.184$) and rivers
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53 199 ($P = 0.056$), despite the p-value in this latter case was close to the significant threshold.

54 200 55 56 201 *3.2 Macroinvertebrates*

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58 202 A total of 12,570 macroinvertebrates were collected, belonging to 38 different taxa (Supplementary
59
60 203 Materials: Table SM1). Plecoptera, Ephemeroptera and Diptera were the orders with the highest

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3 204 number of taxa (8), followed by Trichoptera (6), Coleoptera and Oligochaeta (2), Odonata,
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5 205 Tricladida, Crustacea and Nematomorpha (1). In general, *Baetis* sp., *Rhithrogena* sp.,
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7 206 Hydropsychidae, Chironomiidae and Simuliidae were the dominant taxa in the perennial and
8
9 207 intermittent sites of both rivers. The average number of taxa per sample was 10, while the mean
10
11 208 number of individuals per sample was 182.

12 209 Results of the NMDS and PERMANOVA analyses showed a significant effect of the factors “time”
13
14 210 ($F_{9,45} = 3.311$; $P < 0.001$) and “site” ($F_{3,45} = 7.302$; $P < 0.001$) on the composition of macroinvertebrate
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16 211 communities (Fig. 3). Invertebrate samples collected in the intermittent site of the Pellice river
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18 212 (Pellice I) showed a similar taxonomical composition, as they clustered together in the central part
19
20 213 of the plot. Moreover, a partial overlap with the composition of the upstream perennial site (Pellice
21
22 214 P) was observed. On the contrary, macroinvertebrate communities in the intermittent site of the Po
23
24 215 river (Po I) showed the highest dispersal indicating a significant variation in the taxonomic
25
26 216 composition over the time. Samples from this site were mostly oriented in the left-side of the plot
27
28 217 and did not overlap with samples collected in the upstream permanent site (Po P).

29 218 When looking at the temporal variation of the diversity and density of macroinvertebrates during
30
31 219 the rewetting phase, we found significant differences between the two rivers (Table 3). Total
32
33 220 richness in the Pellice river significantly increased over the time, from 8 to 14 taxa (Fig. 4a, Table 3),
34
35 221 despite it was lower than that of the upstream perennial site (18 taxa). Conversely, the total richness
36
37 222 in the Po river slightly increased within the first 20 days of rewetting and then it markedly dropped
38
39 223 (Fig. 4a). The average number of taxa recorded in the intermittent and permanent sites of the Po
40
41 224 river at the end of the study were 5 and 20 respectively.

42 225 Similar results were obtained for the EPT richness, which showed opposite trends in the two rivers
43
44 226 (Fig. 4b, Table 3). The number of EPT taxa significantly increased since the water resumption and
45
46 227 completely approached the same value of the upstream permanent site (10 taxa). By contrast, EPT
47
48 228 richness progressively decreased in the Po river and at the end of the sampling period was quite
49
50 229 lower than that in the upstream permanent site (11 taxa).

51 230 Significant temporal variations in the density of macroinvertebrates were also observed in both
52
53 231 rivers (Table 3). In the Pellice river the total density of macroinvertebrates significantly increased
54
55 232 over time, from 2,000 to approximately 5,000 individuals m^{-2} after 73 days of rewetting (Fig. 4c).
56
57 233 However, it was still lower than the average density recorded in the perennial section (7,700
58
59 234 individuals m^{-2}). Conversely, total density of macroinvertebrates in the Po river peaked around 25
60
61 235 days after the water resumption but then it collapsed (Fig. 4c). The numerical gap with the upstream

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3 236 site (6,400 individuals m^{-2}) was high, despite the increment on the last sampling occasion. As EPT
4
5 237 taxa were numerically dominant in this study, the temporal variation of EPT density closely
6
7 238 resembled that observed for the total density, especially in the Po river (Fig. 4d, Table 3). The EPT
8
9 239 density in the Pellice river, instead, showed a sharp increase after 20 days from the water
10
11 240 resumption and then stabilized around a value of 3,500 individuals m^{-2} , that was comparable to the
12
13 241 average EPT density in the perennial site (4,290 individuals m^{-2}).

14 242 With exception of shredders, percentages of functional feeding groups significantly varied over the
15
16 243 time (Table 3). On average, collector-gatherers were the most abundant group in the Pellice river
17
18 244 (34%) followed by filterers (32%), despite these two groups showed some fluctuations (Fig. 5a). Also,
19
20 245 the percentage of scrapers was high (29%) and relatively constant over the time (Fig. 5a), while a
21
22 246 general increase was observed for predators during the rewetting phase but, on average, they
23
24 247 accounted for less than 4%.

25 248 Benthic communities in the Po river were almost exclusively dominated by collector-gatherers (50%)
26
27 249 and scrapers (40%): the former were more abundant on the first and last sampling occasions
28
29 250 respectively, while the latter were numerically abundant on the intermediate sampling occasions
30
31 251 (Fig. 5b). The percentage of filterers was generally low (8%), despite this functional group peaked
32
33 252 after 31 and 45 days from the water resumption (Fig. 5b). Predators were recorded only on few
34
35 253 sampling occasions in the Po river and no significant trends were observed for this group (Fig. 5b,
36
37 254 Table 3). Most representative taxa of each functional feeding group are listed in Table SM1
38
39 255 (Supplementary Materials).

40 256 Changes in the ratio between the scrapers and total collectors (i.e. shredders, collector-gatherers
41
42 257 and filterers) were observed only in the Po river, where this indicator rapidly increased during the
43
44 258 initial stages of the rewetting phase, peaked around 20 days, and then it decreased at the end of
45
46 259 the study (Fig. 5c, Table 3).

40 260 41 42 43 44 45 46 47 261 **4. Discussion**

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49
50 262 In a review on the response of riverine communities to disturbance, Death (2010) pointed out that,
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52 263 in general, benthic communities recover rapidly because they are more resilient rather than
53
54 264 resistant. In this study we monitored the post-drought recovery of macroinvertebrate communities
55
56 265 after a supra-seasonal drought in two Alpine streams and our findings corroborate this statement.
57
58 266 Drought significantly reduced the diversity and density of invertebrate communities, especially
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60 267 regarding the most sensitive invertebrates, like EPT taxa, and confirmed our hypothesis for which

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2
3 268 the resistance of Alpine macroinvertebrates to this disturbance is quite scarce, as demonstrated
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5 269 previously (Doretto et al., 2017; Fenoglio et al., 2007; Herbst, Cooper, Medhurst, Wiseman, &
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7 270 Hunsaker, 2019; Piano et al., 2019a). Moreover, this limited resistance could be explained by the
8
9 271 negligible contribution provided by in-stream refugia because of the drought intensity and length.
10
11 272 Unlike other studies, where pools and the hyporheic zone have been recognized to be primary
12
13 273 drivers of the post-drought recovery of benthic organisms (Vander Vorste, Malard, & Datry, 2016;
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15 274 Verdonschot et al., 2015), the prolonged drying conditions here observed probably nullified the
16
17 275 suitability of such refugia. Indeed, pools disappeared in our intermittent sites and also the survival
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19 276 of macroinvertebrates in the moist interstitial spaces appears unlikely under similar circumstances.
20
21 277 To confirm this, data acquired by a piezometer showed that, in the intermittent site of the Po river,
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23 278 water was 2.5 m below the ground level for the majority of the time from July to December 2017
24
25 279 (unpublished data, see Supplementary Materials Fig. SM2). Our results showed that the passive
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27 280 recolonization by drift from the upstream section was probably the main factor facilitating the
28
29 281 recovery of macroinvertebrates in Alpine streams, according to the results of other authors (Doretto
30
31 282 et al., 2018; Flower, 2004).
32
33 283 However, marked differences were found among the two examined lotic systems, thus supporting
34
35 284 the role of recruitment in macroinvertebrate community resilience to exceptional droughts. In the
36
37 285 Pellice river we observed a progressive and significant increase in all the diversity metrics since the
38
39 286 water resumption and multivariate analysis indicated a partial overlap in the community
40
41 287 composition of permanent and intermittent sites. As water resumed in this river, no relevant
42
43 288 changes in flow and environmental conditions were observed among sampling occasions. This
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45 289 aspect, combined with the shorter distance from the upstream nearest permanent site, probably
46
47 290 explains the recovery dynamics here documented, as pointed out by other authors (Bogan,
48
49 291 Boersma, & Lytle, 2015; Fritz & Doods, 2004). On the contrary, the rewetting process in the Po river
50
51 292 was strongly influenced by the precipitation amount (Supplementary Materials Fig. SM1): after a
52
53 293 steady raise in flow, the riverbed shrank over the time and dried completely around 45 days from
54
55 294 the water resumption with flowing water that re-established only on the last sampling occasions.
56
57 295 As a consequence, richness and density of macroinvertebrates generally peaked within the first 20
58
59 296 days and then collapsed, while even after 73 days the taxonomical composition of the intermittent
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297 and permanent sites was still different. In addition, also the greater distance between these two
298 sampling stations probably explains why an appreciable recovery was not reached in this lotic
299 ecosystem.

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3 300 Van Looy et al. (2018) indicated also that the resource competition/facilitation plays an important
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5 301 role on the resilience after a disturbance of riverine communities. Although we did not assess
6
7 302 directly the food availability and biotic interactions, temporal changes in the percentages of FFGs
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9 303 and ratio between scrapers and total collectors were examined. FFGs have been widely invoked to
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11 304 indirectly infer riverine ecosystem attributes and their use in biomonitoring is currently growing
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13 305 (Cummins et al., 2005; Doretto, Piano, Bona & Fenoglio, 2018; Merritt, Fenoglio & Cummins, 2017).
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15 306 Temporal patterns for FFGs were found for both rivers but, interestingly, significant variations in the
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17 307 ratio between scrapers and total collectors were observed only in the Po river. This ratio was here
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19 308 used as an indicator of the prevalence of autotrophy or heterotrophy, and our results suggest that
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21 309 probably the availability and quality of periphyton and organic matter were not influential factors
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23 310 in the Pellice river (Falasco et al., in preparation), while they affected, at least partially, the
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25 311 recolonization process in the Po river.

25 312 To conclude, this work stresses the importance of the recolonization by drift as the main mechanism
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27 313 for the post-drought recovery of macroinvertebrates in Alpine streams. This is in accordance with
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29 314 conceptual framework proposed by Van Looy et al. (2018), for which the recruitment from adjacent
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31 315 habitat sources is usually the main drivers of community resilience in connected river network. As
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33 316 the intermittent and permanent sites in this study were located few kilometers aside, we assume
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35 317 that this condition applied to our results. However, we also demonstrated that river-specific
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37 318 attributes, such as local climate conditions, hydrology and the distance from the nearest upstream
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39 319 perennial site can strongly influence the recovery process. Given the predicted increment in the
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41 320 frequency and magnitude of anthropogenic and climate droughts in the mountain areas, the results
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43 321 of this study offer important information for the management and conservation of Alpine streams
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45 322 and their biota.

45 323 46 47 324 **Data Availability Statement (DAS)**

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49 325 The data that support the findings of this study are available from the corresponding author upon
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51 326 reasonable request.

52 53 327 54 328 **References**

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495 **Tables**

496

497 Table 1. Geographical information of the sampling sites.

River	Site	Coordinates	% Natural areas	% Agricultural areas	% Urbanized areas	Elevation (m.a.s.l.)	Distance between stations (Km)
Po	Perennial	367119E; 4945951N	93	6	1	474	5.5
	Intermittent	372959E; 4943103N	89	10	1	246	
Pellice	Perennial	364293E; 4963123N	92	6	2	422	3.1
	Intermittent	366638N; 4964043E	92	6	2	378	

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3 500 Table 2. Scheme of the sampling activity. Date = sampling date, Days = days from the water return
 4 501 in the intermittent sites.

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Date	Days	Pellice sites		Po sites	
		Perennial	Intermittent	Perennial	Intermittent
12 th January 2018	3	-	Sampling	-	Sampling
16 th January 2018	7	-	Sampling	-	Sampling
19 th January 2018	10	Sampling	Sampling	Sampling	Sampling
23 th January 2018	14	-	Sampling	-	Sampling
30 th January 2018	21	-	Sampling	-	Sampling
1 st February 2018	23	-	Sampling	-	Sampling
9 th February 2018	31	-	Sampling	-	Sampling
23 th February 2018	45	-	Sampling	-	Dry
9 th March 2018	59	-	Sampling	-	Sampling
22 th March 2018	73	Sampling	Sampling	Sampling	Sampling

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Table 3. Statistics of the GAMs for the macroinvertebrate community. Int = intercept, SE = standard error, z = z-value, t= t-value, River = studied rivers (i.e. Pellice, Po), χ^2 = Chi-square, F = F-value, P = p-value. Significant values are in bold.

Metric	Int	SE	z	River	χ^2	P
Taxa richness	2.214	0.046	48.370	Pellice	3.895	0.048
				Po	5.208	0.129
Total density	7.661	0.062	123.000	Pellice	10.520	0.020
				Po	111.730	<0.001
EPT richness	1.791	0.057	31.650	Pellice	3.827	0.050
				Po	3.319	0.238
EPT density	7.171	0.062	115.000	Pellice	21.700	<0.001
				Po	121.500	<0.001
% Collector-gatherers	-0.735	0.035	-21.010	Pellice	347.500	<0.001
				Po	152.200	<0.001
% Filterers	-0.637	0.036	-17.500	Pellice	549.700	<0.001
				Po	261.000	<0.001
% Predators	-4.064	0.119	-34.150	Pellice	48.078	<0.001
				Po	4.839	0.188
% Scrapers	-1.076	0.036	-30.010	Pellice	61.030	<0.001
				Po	215.950	<0.001
% Shredders	-4.335	0.121	-35.940	Pellice	5.986	0.055
				Po	2.214	0.137
Metric	Int	SE	t	River	F	P
Scrapers/Total collectors	0.605	0.061	9.905	Pellice	0.406	0.527
				Po	4.193	0.013

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3 509 **Figure captions**

4
5 510 Fig. 1. Sampling sites and elevational range of the sub-basins of the Pellice and Po rivers.

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7 511
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9 512 Fig 2. PCA ordination plot. Labels indicate: river (Pe = Pellice, Po = Po), type of site (P = Permanent,
10 513 I = Intermittent) and sampling occasion expressed as days from the water return. Ellipses represent
11 514 standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river,
12 515 dashed line = Po river).

13 516
14
15 517 Fig 3. NMDS ordination plot. Symbols represent the type of site (I = intermittent, P = perennial) for
16 518 each river. Colors represent the sampling occasions, indicated as number of days since the water
17 519 return. Ellipses represent standard deviations around the centroids of sampling sites of the two
18 520 rivers (solid line = Pellice river, dashed line = Po river).

19 521
20 522 Fig 4. Generalized Additive Models (GAMs) for (a) total taxa richness, (b) EPT richness, (c) total
21 523 density of macroinvertebrates and (d) EPT density. Black lines represent the predicted values of the
22 524 models, while the dashed lines represent 95% confidence interval.

23 525
24
25 526 Fig 5. Bars indicate the percentage of functional feeding groups in the (a) Pellice and (b) Po rivers on
26 527 each sampling occasion, expressed as days from the water return. GAMs for the ratio between
27 528 scrapers and total collectors during the rewetting phase (c): black lines represent the predicted
28 529 values of the models, while the dashed lines represent 95% confidence interval.

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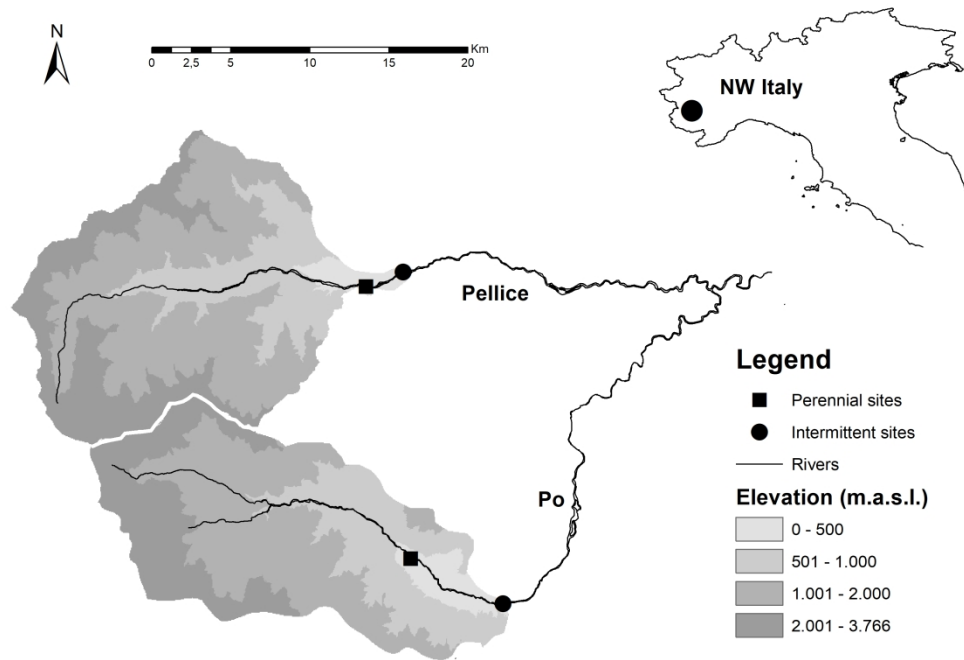


Fig. 1. Sampling sites and elevational range of the sub-basins of the Pellice and Po rivers.

296x209mm (300 x 300 DPI)

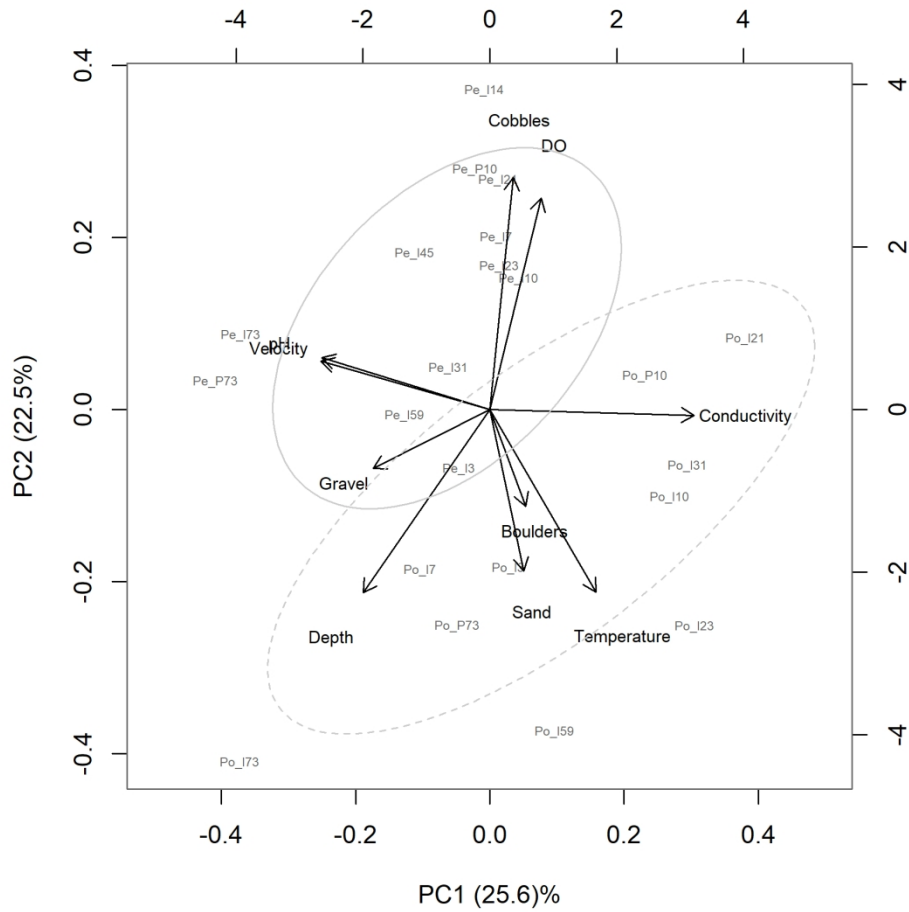


Fig 2. PCA ordination plot. Labels indicate: river (Pe = Pellice, Po = Po), type of site (P = Permanent, I = Intermittent) and sampling occasion expressed as days from the water return. Ellipses represent standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river, dashed line = Po river).

169x169mm (300 x 300 DPI)

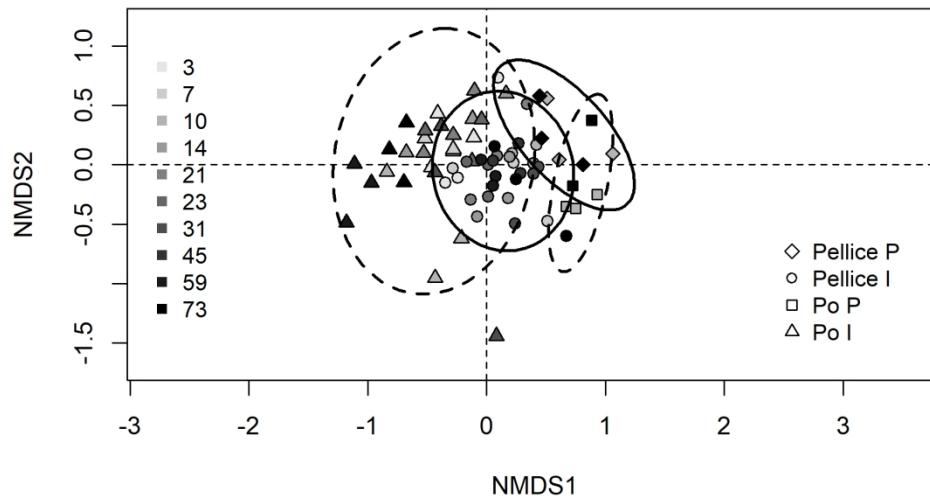


Fig 3. NMDS ordination plot. Symbols represent the type of site (I = intermittent, P = perennial) for each river. Colors represent the sampling occasions, indicated as number of days since the water return. Ellipses represent standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river, dashed line = Po river).

169x109mm (300 x 300 DPI)

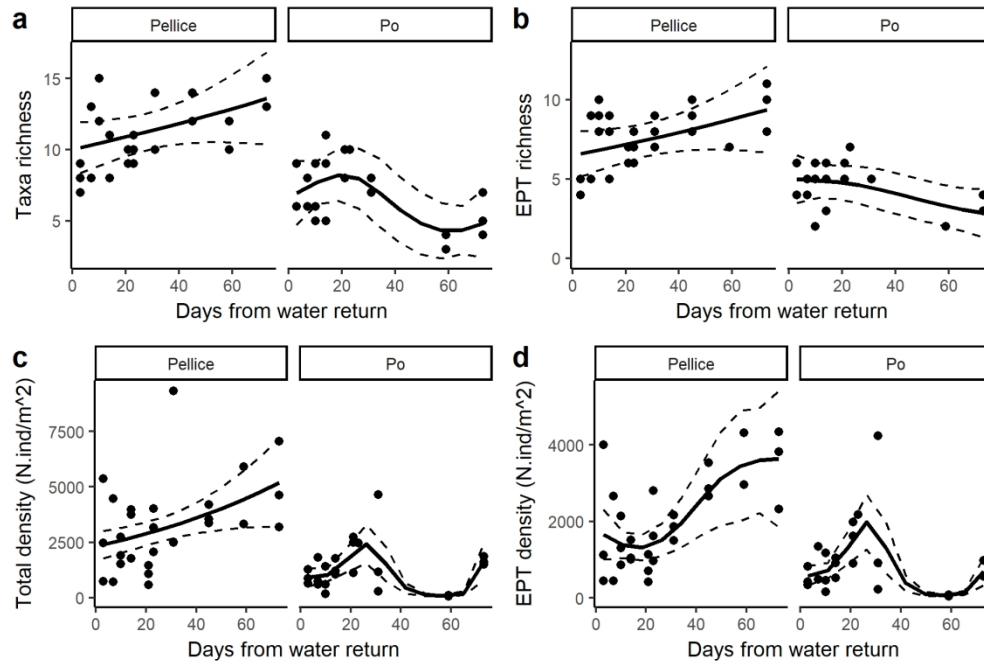


Fig 4. Generalized Additive Models (GAMs) for (a) total taxa richness, (b) EPT richness, (c) total density of macroinvertebrates and (d) EPT density. Black lines represent the predicted values of the models, while the dashed lines represent 95% confidence interval.

169x114mm (300 x 300 DPI)

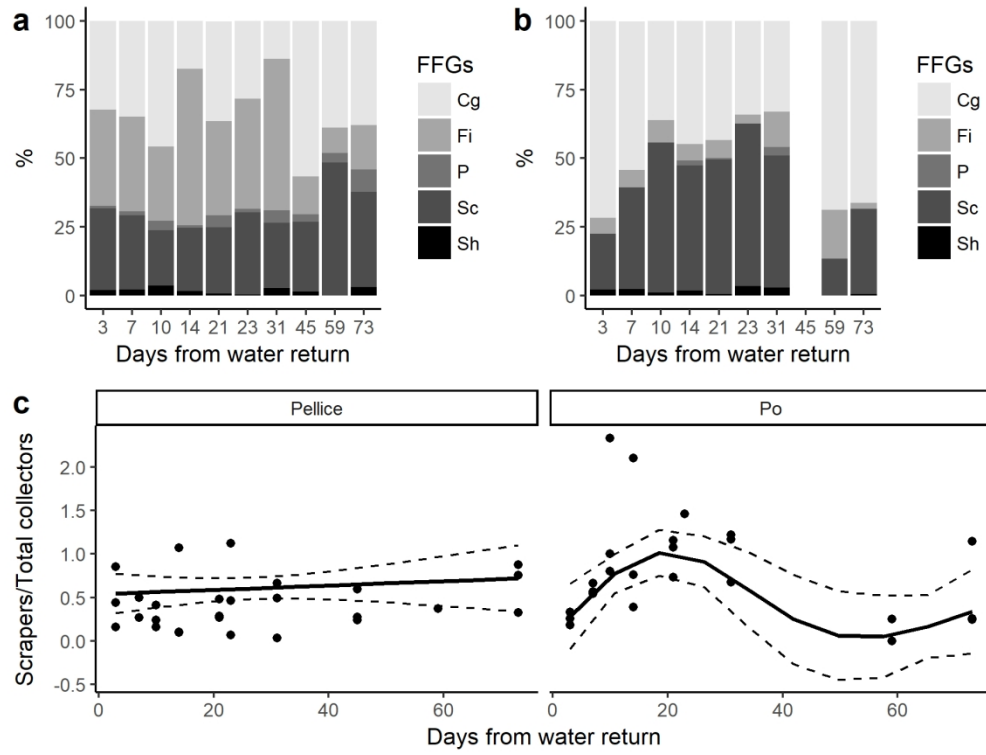


Fig 5. Bars indicate the percentage of functional feeding groups in the (a) Pellice and (b) Po rivers on each sampling occasion, expressed as days from the water return. GAMs for the ratio between scrapers and total collectors during the rewetting phase (c): black lines represent the predicted values of the models, while the dashed lines represent 95% confidence interval.

169x129mm (300 x 300 DPI)