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Combining taxonomic, functional and biomonitoring metrics to evaluate the recovery of alpine stream macroinvertebrate communities after an extreme flood

Niccolò Talluto · Ilaria Bonalumi · Annalisa Givonetti · Paola Emma Botta · Pancrazio Bertaccini · Giuseppe Roberto Pisaturo · Livia Servanzi · Silvia Quadroni · Alberto Doretto

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Abstract Floods are usually recognized as a natural disturbance of lotic ecosystems shaping riverine communities. Although benthic macroinvertebrates display morphological and behavioural adaptations to cope with flood-related conditions, the diversity and density of these organisms are generally reduced after a flood. Understanding the mechanisms and timing of the post-flood recovery of macroinvertebrate communities assumes a key importance in aquatic ecology, but our current knowledge is limited by the restricted number of studies as well as the metrics used to evaluate the success in recovery. In this study, the temporal recovery of macroinvertebrate communities in the Anza River (northwestern Italy) after an extreme flood was evaluated by analysing a multifaceted set of taxonomic, functional, and biomonitoring metrics. The taxonomic composition of macroinvertebrate communities changed over time along with a significant increment in the percentage of fine sediment in the substrate immediately after the flood. Overall, richness and density metrics significantly declined after the flood but, within 9 months, they approached or even exceeded the before-flood values. Functional richness and functional evenness, instead, decreased over time and, after nine months, did not recover to the before-flood values. Although the considered biomonitoring indices were significantly reduced by the flood, they differed in the post-flood recovery outcome. Since floods are expected to be more frequent in the next future due to climate change, the results of this study provide evidence on which metrics drive the post-flood recovery of macroinvertebrate communities with potential insights for disentangling the impacts of natural and anthropogenic pressures on river ecosystems.

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N. Talluto · I. Bonalumi · A. Givonetti · A. Doretto (✉)
Department for Sustainable Development and Ecological Transition, University of Eastern Piedmont, Piazza Sant'Esuebio 5, 13100 Vercelli, Italy
e-mail: alberto.doretto@uniupo.it

P. E. Botta · P. Bertaccini
Dipartimento Territoriale del Nord-Est, Agenzia Regionale per la Protezione dell'Ambiente – Arpa Piemonte, Via IV Novembre 294, 28887 Omegna Crusinallo, Italy

G. R. Pisaturo
Faculty of Engineering, Free University of Bozen-Bolzano, Via B. Buozzi 1, 39100 Bolzano, Italy

L. Servanzi · S. Quadroni
Department of Theoretical and Applied Sciences, University of Insubria, Via J.H. Dunant 3, 21100 Varese, Italy

A. Doretto
Alpine Stream Research Center – ALPSTREAM, 12030 Ostana, Italy

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Introduction

Flow can be widely recognized as the "master variable" of rivers insofar as it affects and regulates all the other physical variables of lotic ecosystems (Poff et al. 1997). For instance, river flow is directly linked to the water depth and velocity, which, in turn, determine the physical habitat for riverine species and their spatial distribution. Flow is also directly involved in several hydro-morphological processes of rivers, including the sediment erosion, transport, and deposition, the substrate stability, and the chemical exchanges with the hyporheic zone (Allan and Castillo 2007). Therefore, flow plays an important role in shaping riverine communities because of its direct and indirect effects on all the other components of the lotic ecosystem (Extence et al. 1999; Mathers et al. 2020; Laini et al. 2022a). Moreover, except for regulated rivers (Šarauskienė et al. 2021; Zargari et al. 2023), flow usually varies seasonally and yearly depending on the climatic and hydrological conditions so that periods characterized by baseflow, low flow, and floods generally succeed over time (Suren et al. 2006; Belmar et al. 2011; Doretto et al. 2020a).

In the Alpine setting, floods usually occur in spring, autumn, and sometimes summer due to snow and ice melting, seasonal patterns in precipitation, and their additive effects (Brown et al. 2003; Parajka et al. 2010; Bard et al. 2015; Quadroni et al. 2021). From an ecological perspective, floods act as natural disturbances that affect the structure, composition as well as temporal stability of riverine communities. All riverine biota is expected to be adapted to the river flow and its variation, but this latter factor assumes a particular importance for bottom-associated organisms, such as benthic macroinvertebrates. Owing to their strong relationship with the near-bed habitat, including hydraulic and sediment conditions, benthic macroinvertebrates have been proved to be particularly sensitive to the flow-related changes, especially in terms of water velocity and turbulence (Rempel et al. 1999; Su et al. 2019). For instance, some mayflies and midges (e.g. Heptageniidae and Blephariceridae) have specific morphological adaptations that allow them to resist to the current, at least until a certain extent, such as pronounced dorso-ventral flattening, elliptical shape of the head, and suckers (Fenoglio et al. 2020). Other macroinvertebrate taxa, instead, find shelter inside the finer grained substrate (e.g. Chironomidae) or produce cases that function as ballast (e.g. Limnephilidae) (Death 2008). Another behavioural strategy to resist flood events consist of moving within the hyporheic zone, which increases the chances of fast recovering after the disturbance (Stubbington 2012). However, this vertical migration is mostly suitable for small-sized and interstitial macroinvertebrate species (Milner et al. 2018).

In general, previous research has proven that floods reduce the richness and density of macroinvertebrates (Ledger et al. 2006; Rempel et al. 1999; Pažourková et al. 2021; Robinson et al. 2023). Hajdukiewicz et al. (2018) found also that a flood event homogenized the taxonomic composition of macroinvertebrate communities of natural and canalized river stretches, thus eliminating the differences between the two river types. While increased water velocity, turbulence, and turbidity have likely short-term negative impacts on benthic macroinvertebrates during the initial stages of a flood by scouring and dislodging them from the substrate, the massive deposition of fine sediment may likely impair macroinvertebrate communities on medium to long-term even after the flood. In Alpine rivers, fine sediment can be particularly harmful for macroinvertebrates because, beyond the direct negative effects on the anatomical parts, by filling the interstices on the substate, it hinders the gas exchanges between the surficial and hyporheic zones, reduces the habitat heterogeneity, and affects the availability of energetic inputs such as in-stream primary production and organic detritus (Kreutzweiser et al. 2005; Kondolf et al. 2014; Wohl et al. 2015; Folegot et al. 2021).

Therefore, predicting the timing and outcome of the post-flood recovery of macroinvertebrate communities is difficult and challenging because of the influence of several context-dependent factors, such as the local environmental features, the presence of refuges, the size of the watercourse, the presence and distance of pristine sites that may serve as sources of new colonizers, and the land use of the surrounding area including the effects of other anthropogenic pressures (Death 2008; Greenwood and Booker 2015). Moreover, several authors have demonstrated that even the availability of food resources as well as the biotic interactions play important roles in driving the post-disturbance trajectories of macroinvertebrate communities (Van Looy et al. 2019). While previous studies focused mainly on richness, density, and taxonomic composition (Rader et al. 2008; Pažourková et al. 2021), these community attributes may be not adequate because they could not catch the variability associated with the multifaceted aspects of the recolonization dynamics (Death 2010). The trait-based approach can provide useful insights due to the hypothesised link between species traits and local environmental conditions but, to date, this approach mainly consists of analysing differences in the abundance of the functional feeding groups. For instance, Marino et al. (2024) monitored the recovery of macroinvertebrates in a low-order stream after an exceptional flood and found that collector–gatherers peaked immediately after the flood and, then, the proportions of all groups aligned to the before-flood values over time. However, functional feeding groups only focus on the trophic relationships of benthic taxa so that their abundance can be affected by seasonal variations in the food resources. To this end, functional metrics such as functional richness, dispersion, and evenness may likely be more informative than single trait modalities; yet, their application in studies dealing with the post-flood recovery of macroinvertebrates is still limited.

Since river ecosystems are typically affected by multiple stressors (Schinegger et al. 2012; Dudgeon 2019), a correct assessment of the sources and mechanisms of variation in the biodiversity is fundamental to better disentangle the effects of natural and anthropogenic pressures. Beyond advancing our knowledge on the ecological and biological processes that drive the post-disturbance dynamics, it may also allow to refine biomonitoring approaches and indices, which have been rarely tested in relation to floods (but see Smith et al. 2019; Gholizadeh 2021).

This study was aimed at monitoring the temporal recovery of benthic macroinvertebrate communities on the Anza River (northwestern Italy) after an extreme flood by analysing simultaneously taxonomic, functional and biomonitoring metrics. Differences in the candidate metrics over time, including one sampling before the flood and six post-event campaigns, were statistically tested with the specific goal of evaluating their sensitivity to the flood. In particular, we hypothesised that all the selected metrics would decline suddenly after the flood, before recovering over time; and we expected that taxonomic metrics (i.e. richness and density) would recover faster than functional and biomonitoring metrics. Also, the correlations among the candidate metrics and between these latter ones with the local environment variables were statistically examined to evaluate which factors drove the post-flood recovery of macroinvertebrate communities in the study area. To this end, we hypothesised that the amount of deposited fine sediment and organic matter, as well as their temporal variation, would have a significant impact on how macroinvertebrates respond to flooding.

Materials and methods

Study area

This study was conducted on the Anza River, located in the Anzasca Valley (Verbano-Cusio-Ossola Province, Piedmont Region, northwestern Italy; Fig. 1a, 1b). The valley (35 km long; total surface area = 257.60 km^2) is mainly made up of metamorphic rocks, including gneiss, orthogneiss, diorites. Its upper limit is represented by the Monte Rosa massif, while downstream the valley ends at the confluence between the Anza River and the Toce River. Three different sampling sites were selected: one was approximately 1 km upstream of the Ceppo Morelli Dam (Locality Campioli, 931 m.a.s.l., hereafter C site), while the other two sites were located approximately 350 m (D1 site) and 2 km (D2 site) downstream of the dam, respectively (Fig. 1c). The Ceppo Morelli Dam was built in 1929 for hydroelectric power generation: it is 39 m tall with the maximum regulation height at 780.75 m a.s.l., while the crest length is 37 m. When it was created, the dam had a volume of 400,000 m^3 but its storing capacity decreased over time due to the sediment accumulation so that, nowadays, it is approximately 100,000 m^3. Since 2024, the sampling sites have been included in the framework of activities of a National Research Project dealing with the response of benthic macroinvertebrates to sediment flushing operations from dams in Alpine rivers (i.e. FluEMMA PRIN project). A sediment flushing operation from the Ceppo Morelli Dam was originally planned in July–August 2024, but in June 2024 an extreme flood occurred in

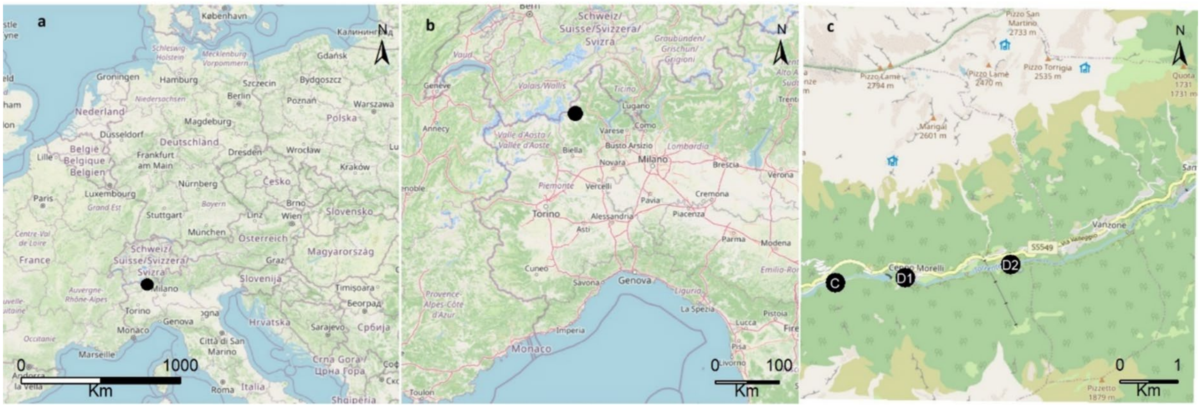


Fig. 1 Map of the study area. In **a** and **b**, black dot indicates the location of the Anza River in northwestern Italy. In **c**, black dots indicate the location of the sampling sites

the area of study so that this operation was cancelled. Therefore, data collected in the sampling sites before this event were used as benchmark to monitor the post-flood recovery of the benthic macroinvertebrate communities in the Anza River.

Description of the extreme flood event

From Saturday 29th to Sunday 30th June 2024 an extremely intense precipitation event occurred in the area of study because of the mixing of cold and pre-existing warm, humid air masses at high altitude. The two closest weather monitoring stations of the Local Agency for Environmental Protection (hereafter ARPA Piemonte), located in Macugnaga—Pecetto and Macugnaga—Rifugio Zamponi, recorded precipitation values of 179 and 177.6 mm, respectively. The maximum cumulative values for the durations of 3 and 6 h corresponded to recurrency times of 100 and 200 years, respectively (data from ARPA Piemonte). Data gained from the ARPA Piemonte gauge station on the Anza River, located in San Carlo con Vanzone, about 3.5 km downstream from the sampling sites, showed that, on 29th June the hydrometric height of the Anza River approached the danger level (2 m), and then it returned below the warning level in the late morning of Sunday 30th June. Moreover, other two intense rainfall events occurred on 5th September 2024 and in October 2024 (17th–27th), despite their magnitude was slightly lower than the previous one. As a consequence, all these rainfall events caused sharp increments of the discharge of the Anza River (Fig. 2a and 2b).

Data collection

Macroinvertebrate and environmental data were gained from seven sampling campaigns over a 11-month period. Pre-flood data were collected in each sampling site on 30th May 2024, while six post-flood sampling campaigns took place from July 2024 to March 2025. To better evaluate the temporal recovery of the benthic macroinvertebrate communities as well as the physical habitat, especially in the immediate period after the flood, the first three sampling campaigns were performed monthly: namely on 22nd July, 26th August, and 30th September 2024. The last three campaigns, instead, were performed every two months: 27th November 2024, 5th February, and 27th March 2025.

At each site, a representative 30-m long river reach was selected for the collection of the abiotic and biological data. Dissolved oxygen (mg/L), pH, electrical conductivity (µs/cm) and temperature (°C) were measured at each site with a multiparametric probe (Hanna, mod. HI98194).

The McNeil corer (McNeil and Ahnell 1964) was used to obtain quantitative data on the settled sediments per unit area. Three 1L samples of turbid water were collected by using a resuspension technique (see Espa et al. 2013; Quadroni et al. 2024) on three different spots: one upstream, one central, and one downstream. Samples were returned in laboratory where

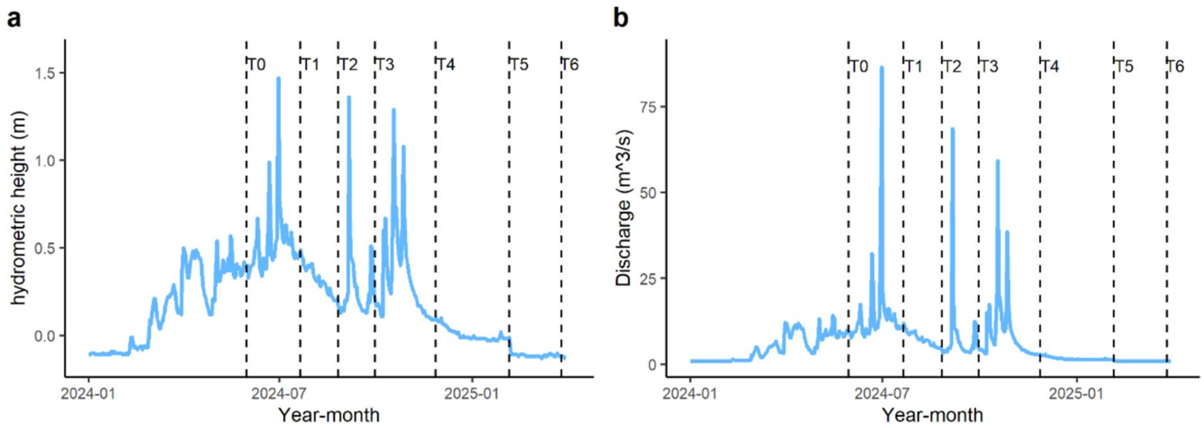


Fig. 2 Graphs illustrating the temporal variation in the: **a** hydrometric height (m) and **b** daily discharge (m^3/s) of the Anza River recorded from 1st January 2024 to 31st March 2025 in the gauge station located in San Carlo con Vanzone (around 3.5 km downstream from the sampling sites). Vertical dotted lines indicate the sampling campaigns (T0–T6)

they were analysed following the gravimetric method (APAT IRSA-CNR 2003) by filtering 100 mL (50 mL for very turbid samples) on cellulose filters (nominal porosity of 0.47 µm) and weighing them after drying in an oven at 105 °C for 2 hours. The mass of settleable solids per unit area (g/m^2) was calculated considering the filtered volume and the volume of the turbid water in the sampler, and then by dividing the mass of the sediment by the cross-sectional area of the corer. Moreover, in order to characterize the grain size composition of the substrate, three 1 L samples of the bottom substrate were taken in the same spots where the McNeil corer was used. In laboratory, these samples were dried in an oven at 105 °C overnight and subsequently sieved with an automatic sieve composed of the following mesh sizes: 16 mm, 8 mm, 4 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, and 63 µm. The portion of sediment selected from each sieve was weighed and, finally, the percentage weight of fine sediment (<2 mm—Wood and Armitage 1997; Harper et al. 2017) was calculated for each sample.

In compliance with the Water Framework Directive (WFD, 2000/60/EC) as well as the Italian Decrees D.Lgs. 152/2006 and D.M. 260/2010, ten quantitative samples of benthic macroinvertebrates were collected by using a Surber net (area = 0.1 m^2; mesh-size = 500 µm; Doretto et al. 2020b) and adopting multi-habitat proportional sampling scheme. For each Surber sample, the water depth (cm) and velocity (m/s) were measured with a flow meter (Scubla, mod. N.01.200), while the type of mineral substrate (e.g. microlithal, mesolithal, etc.) was visually assessed by the same operators. Benthic macroinvertebrates were preserved in 90% ethanol and delivered to the laboratory where they were counted and identified to genus (Plecoptera and Ephemeroptera) or family level by using dichotomous keys for the Italian and European fauna (Campaioli et al. 1994, 1999; Tachet et al. 2010).

To better characterize the availability of energetic inputs for macroinvertebrates, data on the instream primary production and Coarse Particulate Organic Matter (CPOM) were obtained for each site. One composite periphyton sample was collected by selecting a cobble associated with each Surber sample and scratched it with a toothbrush across an area of 10 cm^2. Periphyton was conserved in a dark bottle and transported to the laboratory, where chlorophyll-a was analysed within 24 h after collection following the standard method (APAT IRSA-CNR 2003). From each periphyton sample, 100 mL were filtered using a glass-fiber filter (nominal porosity 0.7 µm), then chlorophyll-a was extracted using acetone (Sigma-Aldrich, #179124). The detection of absorbance values was carried out using the spectrophotometer (Shimadzu, UV-1800) at wavelengths of 750 nm, 665 nm, 664 nm, 647 nm, and 630 nm both before and after acidification (HCl 0.1 M, Sigma-Aldrich, #320331). Once absorbance values were obtained, the concentration of chlorophyll-a normalized for the filtered volume was calculated by applying the standard formula (APAT IRSA-CNR 2003). The amount of

CPOM, instead, was obtained from the Surber samples by separating all the fragments of organic detritus during the macroinvertebrate sorting in laboratory. Then, CPOM samples were dried in an oven (105 °C for 24 h) and weighted (see Piano et al. 2020).

Statistical analyses

All the statistical analyses (significance threshold: p-value < 0.05) were performed with the R software (R Core Team 2025; Wickham et al. 2024; Kassambara 2025) by using both basic and specific functions as illustrated below. For each site, the total macroinvertebrate community was obtained by pooling together the 10 Surber samples (3 sites X 7 sampling campaigns = 21 observations) so that all the statistical analyses were run on this latter dataset.

Non-Metric Multidimensional Scaling (NMDS) and Permutational Analysis of Variance (PERMANOVA) were applied to visualize and test for differences in the taxonomic composition of macroinvertebrate communities among sites and sampling campaigns (*mds* and *adonis2* functions, "vegan" R package; Oksanen et al. 2015). In these multivariate analyses, the Bray–Curtis dissimilarity index was used as distance measure. Moreover, to better evaluate whether the macroinvertebrate community composition was statistically affected by environmental variables, these latter ones were plotted as arrows in the NMDS ordination graph and tested for significance with the function *envfit* of the "vegan" R package (Oksanen et al. 2015). With this respect, the following environmental variables were considered: pH, water temperature, electrical conductivity, dissolved oxygen, average water velocity and depth, average amount of CPOM and concentration of chlorophyll-a, the average amount of settled (i.e. McNeil data) and fine (i.e. grain-size data) sediments, the maximum and average river discharge, and the coefficient of variation of the river discharge. These latter three hydraulic variables were calculated on the 30-day period before each sampling campaign.

Total beta diversity and its nestedness (i.e. loss/gain of taxa) and turnover (i.e. taxa replacement) components, as theorized by Baselga (2010), were calculated with the function *beta.multi* of the "BAT" R package (Cardoso et al. 2022) to evaluate the sources of variation in the taxonomic composition among sites on each sampling campaign. Moreover, the function *momentum* of the "distantia" R package (Benito and Birk 2020) was used to visualise which taxa mostly contributed to the dissimilarity or similarity in the temporal trajectories of macroinvertebrate communities among sites. This latter analysis is based on the psi score, which normalizes the cumulative sum of distances between two or more time series by the cumulative sum of distances between their consecutive samples to generate a comparable dissimilarity score (Benito and Birk 2020). In this study, the psi score was calculated for each taxon with high positive and negative values indicating strong contribution of that taxon to the among-site dissimilarity and similarity, respectively, of macroinvertebrate communities over time.

In addition to the multivariate analyses, a set of different and multifaceted metrics were taken into consideration to monitor the post-flood recovery of macroinvertebrate communities. The total taxon richness, EPT (Ephemeroptera, Plecoptera and Trichoptera) richness, total macroinvertebrate density (N. individuals/m^2), and EPT density were selected as taxonomic metrics due to their wide application in river ecology and biomonitoring (Chang et al. 2014; Buss et al. 2015; Roccatello et al. 2025). By using the traits classification of Tachet et al. (2010) for riverine macroinvertebrates, the following functional metrics were calculated: functional richness, functional evenness, and functional dispersion ("biomonitoR" R package; Laini et al. 2022b). Functional richness indicates the amount of functional space filled by the community, while functional evenness describes how evenly the abundance of taxa is distributed in the functional trait space (Villéger et al. 2008). Functional dispersion, instead, quantifies the spread of the taxa in the trait dimensional space (Laliberte and Legendre 2010). Finally, the STAR_ICMi and SILTES indices were selected as biomonitoring metrics. In Italy, STAR_ICMi is the official biomonitoring index based on macroinvertebrate communities to assess the ecological status of running waters in compliance with the WFD. It is a multi-metric, but generic, index composed of six sub-metrics, i.e. the Average Score Per Taxon (ASPT), number of Ephemeroptera, Plecoptera and Trichoptera families, total number of macroinvertebrate families, 1 minus the relative proportion of Gastropoda, Oligochaeta, and Diptera (1-GOLD), Shannon index, and the logarithm of the abundance of selected Ephemeroptera, Plecoptera, Trichoptera, and Diptera taxa plus one (Log10_Sel_EPTD + 1) (Erba et al. 2020; Bo et al. 2023). Based on the reference values for both STAR_ICMi and its sub-metrics listed in the Italian Ministerial Decree D.M. 260/2010, the ecological assessment is expressed into five classes: High, Good, Moderate, Poor, and Bad. Similarly, SILTES is multi-metric index composed of three sub-metrics: the taxon richness, EPT richness, and the proportion of macroinvertebrates associated with large mineral substrates (i.e. Community Weighted Mean of trait value for coarse mineral substrate). Yet, unlike STAR_ICMi, SILTES is a stressor-specific index recently developed to evaluate the impacts associated with fine sediment deposition (Doretto et al. 2018, 2021, 2022). Thus, these two biomonitoring indices were included in the analysis to evaluate if they were coherently able to detect the impacts associated with the flood and the consequent recovery of macroinvertebrate communities. As we expected that the extreme flood impacted in a similar manner the three sampling sites, significant differences in the taxonomic, functional, and biomonitoring metrics among sampling campaigns were tested by applying Generalized Linear Models (GLMs) or Linear Models (LMs) using the *glm* and *lm* functions, respectively. In all models, the metrics were included as response variables, while the factor “Time” was included as fixed effect. GLMs with Poisson or negative binomial (in case of overdispersion) distributions were used for count data, namely richness and density metrics. LMs, instead, were used for functional and biomonitoring metrics. Prior performing the regression models, proportion metrics (i.e. functional richness, functional evenness, and SILTES index) were logit-transformed (*logit* function in “car” R package; Fox et al. 2024).

Finally, Principal Component Analysis (PCA; function *prcomp*) was run to examine the relationships between the selected metrics and the environmental parameters. To this end, also the sub-metric of the STAR_ICMi and SILTES were included in this multivariate analysis. Therefore, PCA served for evaluating how the macroinvertebrate metrics were positively or negatively associated with the environmental variables with the ultimate goal of providing more information on the temporal recovery of macroinvertebrate communities.

Results

Sediment and energetic inputs

Before the flood, the average amount of settled sediments was similar among all sampling sites and it was always lower than 50 g/m^2 (Fig. 3a). After one month since the flood (T1), a sharp increment was observed only in C, while in the downstream sites (D1 and D2) it still remained similar to that observed on T0. A further increase was recorded on T2 in all sites, especially in D1, then the amount of settled sediments decreased over time achieving values comparable to the before-flood condition, despite a less-pronounced peak in D2 on T5 (Fig. 3a). Similar results were also found by the analysis of the grain size composition. Before the flood, the average percentage of fine sediment in the substrate was lower than 9% in all sites and, as expected, it abruptly increased within the first two months since the flood, ranging from 80.82% in C on T1 to 47.79% in D1 on T2 (Fig. 3b). Then, while it decreased over time in C, some fluctuations were recorded in D1 and D2. On T6, after 9 months from the flood, the percentage of fine sediment in the substrate still remained higher than before-flood values in all sites (19.03% in C, 73.93% in D1, and 50.67% in D2).

On T0, the average amount of CPOM differed among the sites and ranged from 3.81 g in C to 1.34 g in D2 (Fig. 3c). Immediately following the flood, the amount of CPOM was drastically reduced in all sites but since T3 it increased again over time, especially in D1 and D2. Around 9 months after the flood (i.e. T6), the average amount of CPOM was almost fourfold higher in D2 (3.85 g) than C (0.95 g). Similarly, the amount of chlorophyll-a differed among the sites before the flood: the highest value was recorded in D2 (14.63 mg/m^2), followed by D1 (6.10 mg/m^2), and C (3.20 mg/m^2). It was reduced by the flood in all sites until T3 and, after peaking on T4 and T5, the amount of chlorophyll-a further declined on T6 (Fig. 3d). The peak in primary production observed in autumn (T4–November) and winter (T5–February) was due to the combined effect of reduced riparian vegetation shading and increased abundance of the macroalga *Hydrurus foetidus*, as previously documented in other alpine streams (Quadroni et al. 2024).

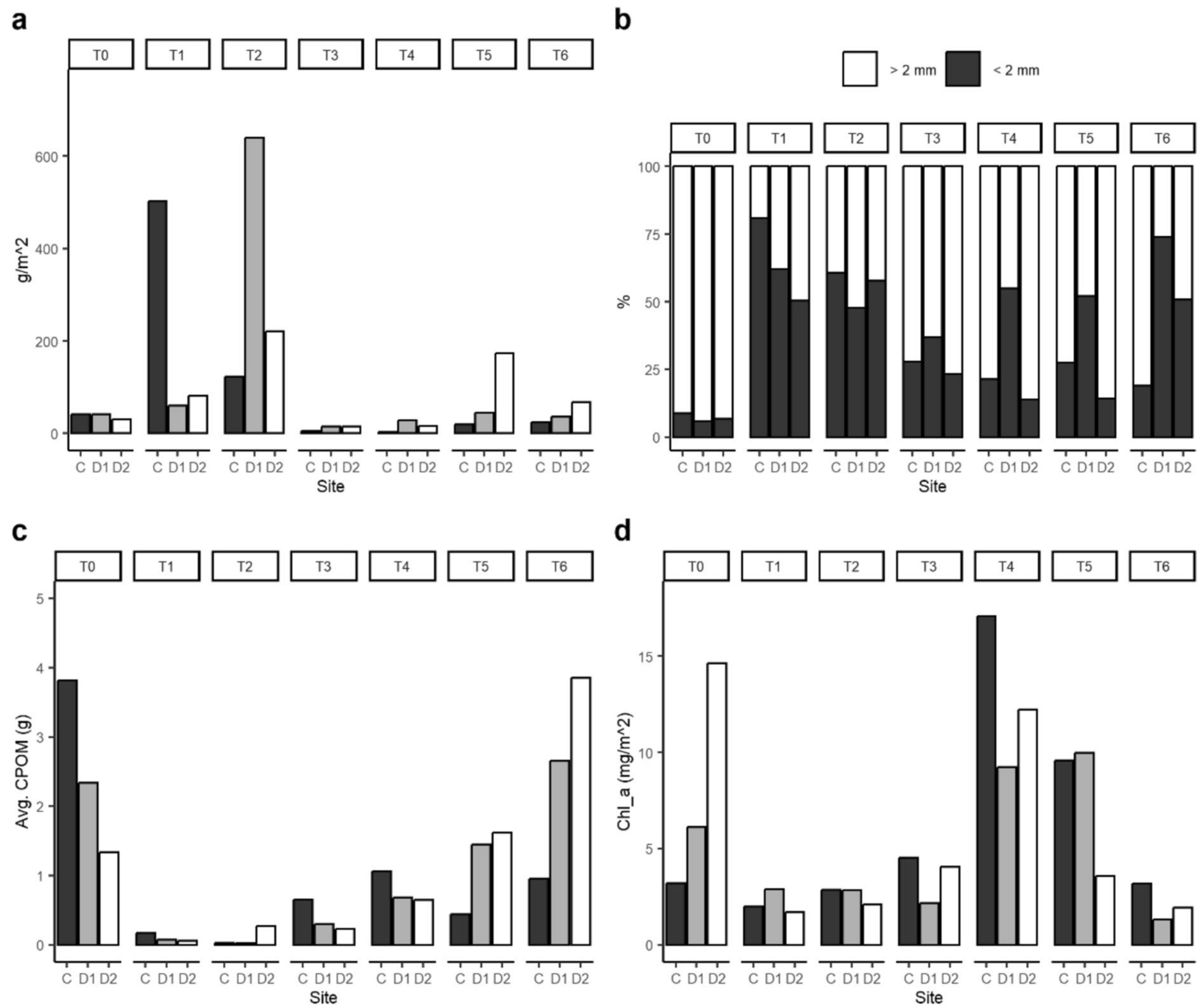


Fig. 3 Bars illustrating: **a** the average amount of settled sediments, **b** the percentage of fine and coarse sediment in the substrate, **c** the average amount of CPOM, and **d** the amount of chlorophyll-a in the sampling sites (C, D1, D2) on each sampling campaign (TO–T6)

Benthic macroinvertebrate communities

A total of 39,323 macroinvertebrates belonging to 49 different taxa were collected (Table S1). Chironomidae, *Baetis*, and *Leuctra* were the most abundant taxa and together accounted for 86% of the total macroinvertebrates. The average number of taxa per sample was 7 (± 3.76 SD), while the average density (n. individuals/m^2) was 1873 (± 1702 SD).

The multivariate analysis showed that the taxonomic composition of macroinvertebrate communities significantly varied among sites ($F_{2,12} = 2.448$; p-value $= 0.032$) and sampling campaigns ($F_{6,12} = 5.591$; p-value < 0.001). The before-flood communities clearly separated from the other ones and were located in the bottom-left part of the NMDS ordination plot, while the communities sampled on T1, T2 and T3 were mostly oriented in the upper part of the plot (Fig. 4a). Starting from T4, the taxonomic composition of macroinvertebrate communities tended to approach again the one observed on T0 without, however, reaching a full recovery. Among the environmental variables analysed, only the average percentage of fine sediment (p-value $= 0.021$), water velocity (p-value $= 0.037$), and the amount of CPOM (p-value $= 0.044$) had a significant effect on

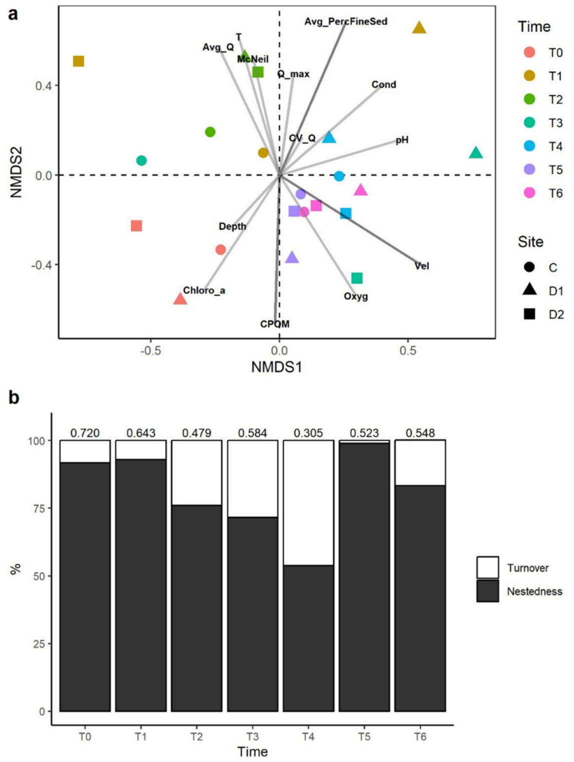


Fig. 4 NMDS ordination plot **a** showing the variation in the taxonomic composition of macroinvertebrate communities between sites (symbols) and sampling campaigns (T0–T6; colours). Arrows and labels indicate the environmental parameters: Vel = water velocity, Depth = water depth, CPOM = coarse particulate organic matter, Chloro_a = amount of chlorophyll-a, pH, Cond = electrical conductivity, T = water temperature, Oxyg = dissolved oxygen, McNeil = amount of settled sediments, Avg_PerFineSed = percentage of fine sediment in the river bed, Avg_Q = average discharge, CV_Q = coefficient of variation for river discharge, Q_max = highest value of river discharge. Black arrows (Avg_PerFineSed, Vel, CPOM) indicate significant environmental parameters, while grey arrows are for not-significant parameters. Stacked bars **b** displaying the percentage contribution of nestedness (i.e. gain/loss of taxa) and turnover (i.e. taxa replacement) to total beta diversity (numbers above the bars)

the taxonomic composition of macroinvertebrate communities; while the other environmental variables were not significant (Table S2). The percentage of fine sediment increased with positive values of the NMDS2 axis, thus indicating that macroinvertebrate communities sampled immediately after the flood were associated with higher percentages of fine sediment in the river substrate. On the contrary, the amount of CPOM and the water velocity negatively correlated with the NMDS2 axis and these two environmental parameters were mostly associated with the T0, T5, and T6 macroinvertebrate communities (Fig. 4a).

Total beta diversity among sampling sites varied over time with the highest (0.720) and the lowest (0.305) values observed on T0 and T4, respectively (Fig. 4b). The gain/loss of taxa (i.e. nestedness) was the component of the beta diversity that mainly explained the compositional differences of macroinvertebrate communities across sampling sites. The percentage contribution of nestedness to total beta diversity was always higher than 50% and ranged from 99% on T5 to 53.8% on T4. On the contrary, the taxa replacement (i.e. turnover) poorly explained the compositional differences in the taxonomic composition of macroinvertebrate communities, despite a growing percentage contribution of turnover was observed from T2 (24%) to T4 (46.2%) (Fig. 4b).

When looking at the role of each taxon, we found that 25 taxa accounted for the dissimilarity in the temporal trajectories of macroinvertebrate communities among sampling sites (Fig. 5). Among these, *Serratella ignita*, Athericidae, *Rhithrogena*, *Leuctra*, and Psychodidae were the macroinvertebrates that exerted the highest contribution (i.e. positive psi scores). On the contrary, 18 taxa showed similar temporal variations in their occurrence and density across the sampling sites, thus contributing to increase the similarity in the temporal trajectories of macroinvertebrate communities in the area of study (i.e. negative psi scores). Among these, Blephariceridae, *Baetis*, Nematoda, Elmidae, *Nemoura*, and Limoniidae were the most relevant ones (Fig. 5).

On average, taxon richness declined from T0 to T1 and remained significantly lower than the before-flood values until T4 (Fig. 6a). Then, it increased again but on T5 and T6 taxon richness was still lower than that observed on T0, despite these differences were not significant. None of the sites fully recovered to the before-flood values: the total number of taxa dropped from 28, 25 and 25 in C, D1 and D2, respectively, to 23, 15 and 22, respectively (Fig. 6b). Even the EPT (Ephemeroptera, Plecoptera and Trichoptera) richness was significantly reduced immediately after the flood but, unlike taxon richness, it rapidly recovered over time insofar as since T4 the EPT richness was, on average, similar to the before-flood values (Fig. 6c). However, when looking at each sampling

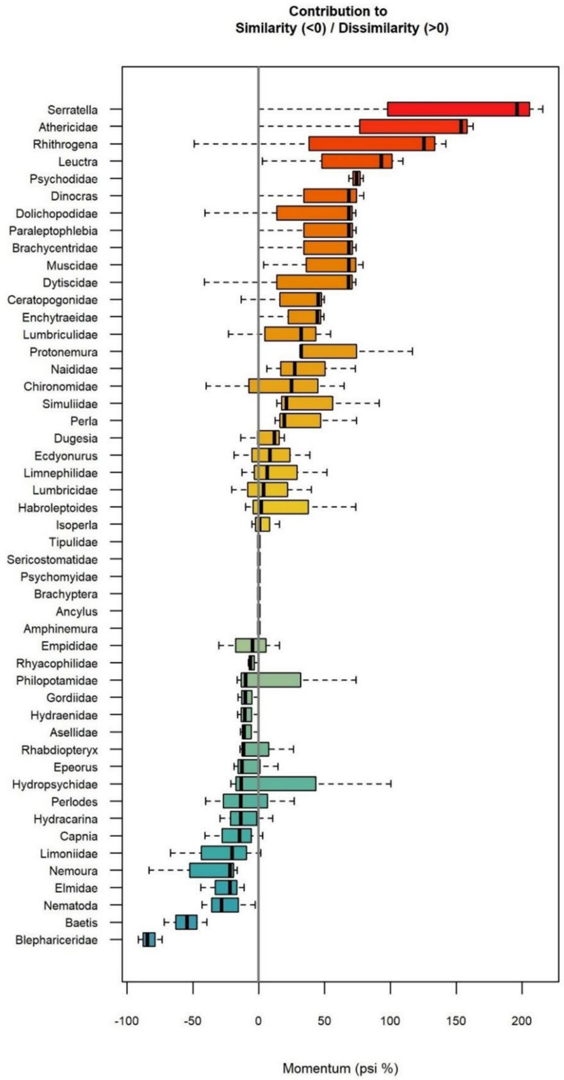


Fig. 5 Boxplots illustrating the average psi score of each macroinvertebrate taxon. High positive and negative values indicating strong contribution of that taxon to dissimilarity and similarity, respectively, of macroinvertebrate communities

site, we found that C and D2 sites fully recovered to or even exceeded the before-flood values, while in D1 the total EPT richness (8 taxa) still remained lower than that recorded on T0 (11 taxa) (Fig. 6d).

Both the total density and EPT density significantly varied among sampling campaigns (Fig. 6e and 6g), with very similar temporal trends across sites (Fig. 6f and 6h). Compared to T0, both these density metrics were significantly reduced by the flood but they rapidly recovered over time so that they exceeded the before-flood values on the last two sampling campaigns (T5 and T6). Moreover, the temporal fluctuations in the density metrics were largely due to the genus *Baetis*, which was one of the most abundant taxa in this study (Table S1).

Similar to the taxonomic richness metrics, the functional richness declined from T0 to T1 but this reduction was not significant (Fig. 7a). Except for an increment on T3, this functional metric remained, on average, constant over time and never recovered to the before-flood values. However, when looking at each site divergent temporal trends for this metric were found (Fig. 7b). Compared to the value observed on T0, in C the functional richness slightly decreased immediately after the flood, peaked on T3, decreased again on T4 and T5, and finally exceeded the before-flood value. In the downstream sites, instead, the functional richness was strongly reduced by the flood and, after some fluctuation, it did not recover to the before-flood values at the end of the study (T6). On average, no significant variations in the functional dispersion were observed among sampling campaigns (Fig. 7c) but clear, contrasting patterns among sampling sites were observed (Fig. 7d). In C the total functional dispersion was slightly reduced immediately after the flood, and then it increased again and remained almost constant until T6. On the contrary, in D1 the total functional dispersion was 0.21 before the flood, and it dropped to 0.13 and 0.12 on T2 and T3, respectively. After recovering to 0.21 on T4, functional dispersion slightly decreased on the last two sampling campaigns to 0.18. In D2, instead, the opposite trend was observed: staring from 0.13 on T0, the functional dispersion increased to 0.19 after the flood, dropped to 0.13 on T3 and finally it increased over time until 0.21 at the end of the study (Fig. 7d). No significant variations in the functional evenness were detected among sampling campaigns (Fig. 7e). Although some differences among sites, this functional metric remained almost constant before and after the flood until T3; then it progressively declined over time and such reduction was observed in all sites (Fig. 7f).

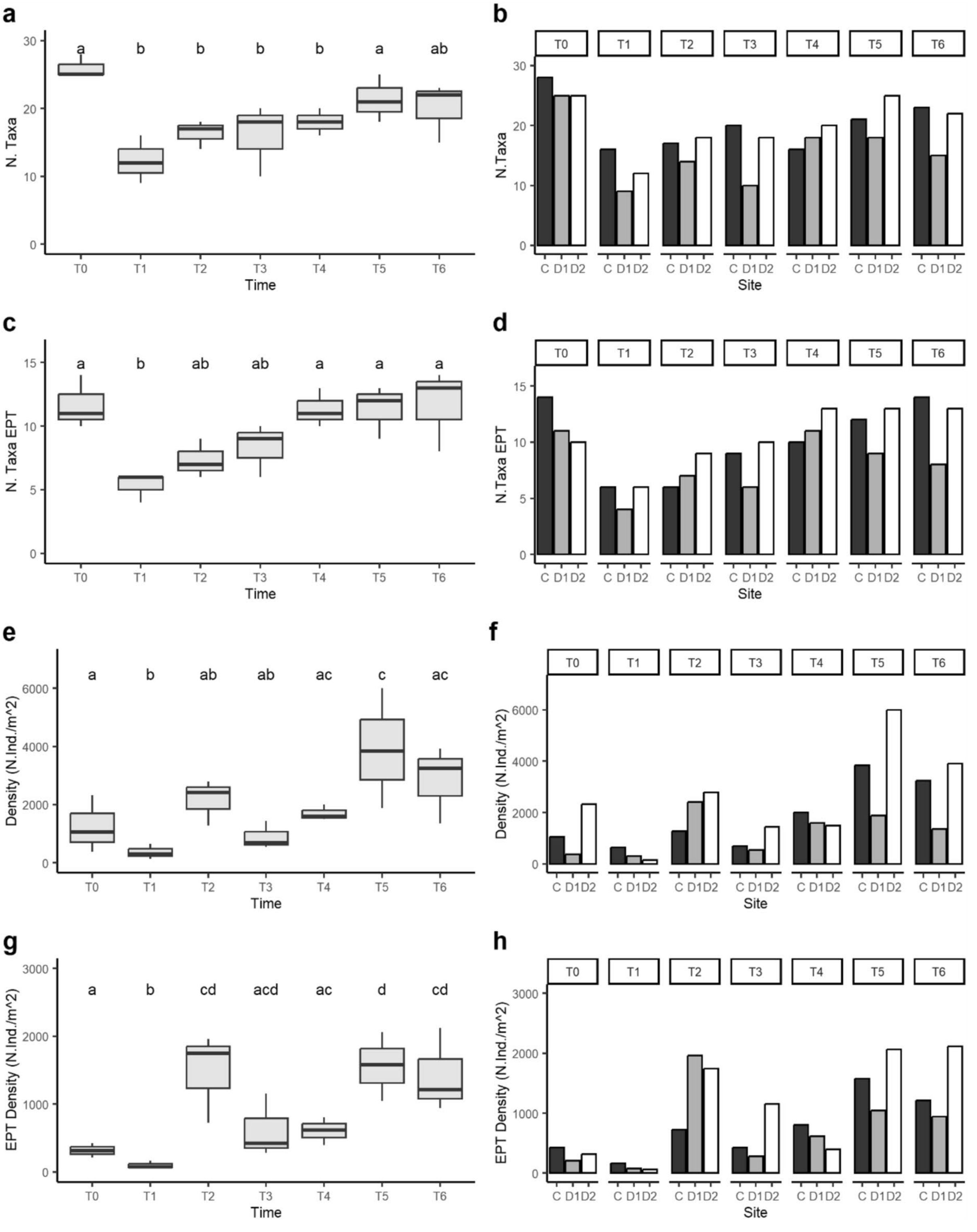
STAR_ICMi significantly declined from T0 to T1 and, then, it slowly increased over time reaching, on average, similar values to those observed before the flood on T5 and T6 (Fig. 8a). When looking at the ecological status assessment, before the flood C and D1 fall into the “Good” quality class; while D2 was classified as "Moderate" (STAR_ICMi = 0.708), despite it was very close to the threshold discriminating "Good" and "Moderate" (i.e. ≥ 0.71). Immediately after the flood, the sharp decline in the STAR_ICMi values lowered the ecological status class to "Moderate" and "Poor" for C and D1, respectively, while D2 still remained "Moderate". Except for a few cases, from T2 to T5, the ecological status class mostly remained "Moderate" in all sites. On T6, instead, all sites reached the "Good" class, thus indicating full recovery (Fig. 8b). Similar to the STAR_ICMi, also the SILTES index significantly declined from T0 to T1 as a consequence of the flood and, then, it slowly increased over time (Fig. 8c). At the end of the study (T6), the SILTES index was, on average, still lower than T0, despite this difference was not significant (Fig. 8c). However, while in C and D2 a progressive recovery over the time from T2 to T6 was observed for this index, in D1 SILTES peaked on T4 and then decreased again on the last two sampling campaigns (Fig. 8d).

Overall, the first two axes of PCA accounted for 55.25% of the total variance associated with the environmental variables and macroinvertebrate metrics with PC1 and PC2 explaining 39.45% and 15.80%, respectively (Fig. 9). PC1 was positively correlated with the biomonitoring indices (i.e. STAR_ICMi and SILTES) and their richness as well as EPT-based metrics. Among the environmental variables, positive values of PC1 were correlated with increased CPOM, water velocity and dissolved oxygen; while negative values of PC1 were correlated with the flow- and sediment-related variables (Fig. 9). On the contrary, positive values of PC2 were associated with enhanced functional richness and functional evenness, while negative values were correlated with the electrical conductivity, CWM_Coarse, 1-GOLD, and to a minor extent with the sediment-related variables. In the PCA ordination plot, the before-flood samples separated from the others and were oriented in the top-right corner. These samples were also associated with increased values of the biomonitoring indices (i.e. STAR_ICMi and SILTES), taxonomic and functional richness-based metrics, and energetic inputs (CPOM and Chlorophyll-a). Post-flood samples, instead, were mostly oriented along the PC1 axis with samples from T1 to T3 being associated with the flow- and sediment-related variables (i.e. left part of the ordination plot), while the samples from T4 to T6 were oriented in the right part of the plot, thus indicating their strong association with the density- and richness-based metrics as well as the biomonitoring indices. Despite the clear temporal shift, none of the post-flood samples approached the T0 ones (Fig. 9).

Discussion

Rivers are typically considered as heterogenic and dynamic ecosystems where biological communities vary across spatial and temporal gradients according to the environmental and anthropogenic pressures (Larsen et al. 2019; Fornaroli et al. 2020; Burgazzi et al. 2020). Floods act as natural disturbances affecting the diversity and composition of riverine communities and, in recent years, an increase in the irregularity of precipitations has been observed owing to climate change with, in turn, a growing frequency of severe and flashy floods (Hosseinzadehtalaei et al. 2020). Such disturbances sum up to those caused by anthropogenic alterations on rivers so that researchers and local authorities need to correctly quantify the response as well as the temporal recovery of riverine biodiversity to these disturbances.

This study was designed to shed light on the post-flood trajectories of benthic macroinvertebrate communities by analysing changes in both taxonomic composition and several, multifaceted metrics with the ultimate aim of providing evidence on the temporal recovery. As expected, our results showed that the taxonomic composition of macroinvertebrate communities significantly changed after the flood and these shifts were driven by reductions in the richness and density of macroinvertebrates, especially among EPT taxa. Also, in this study, the average percentage of fine sediment (< 2 mm) in the substrate significantly increased immediately after the flood, thus confirming the negative impacts of fine sediment deposition on benthic macroinvertebrates associated with flood events. Nevertheless, the richness and density of macroinvertebrates, on average, recovered to or even exceeded the values recorded before the flood within 9 months, despite some differences observed among sampling sites. The taxonomic composition of macroinvertebrate communities progressively shifted over time and, at the end of the study, approached again that of the before-flood sampling campaign, thus providing signals of recovery.

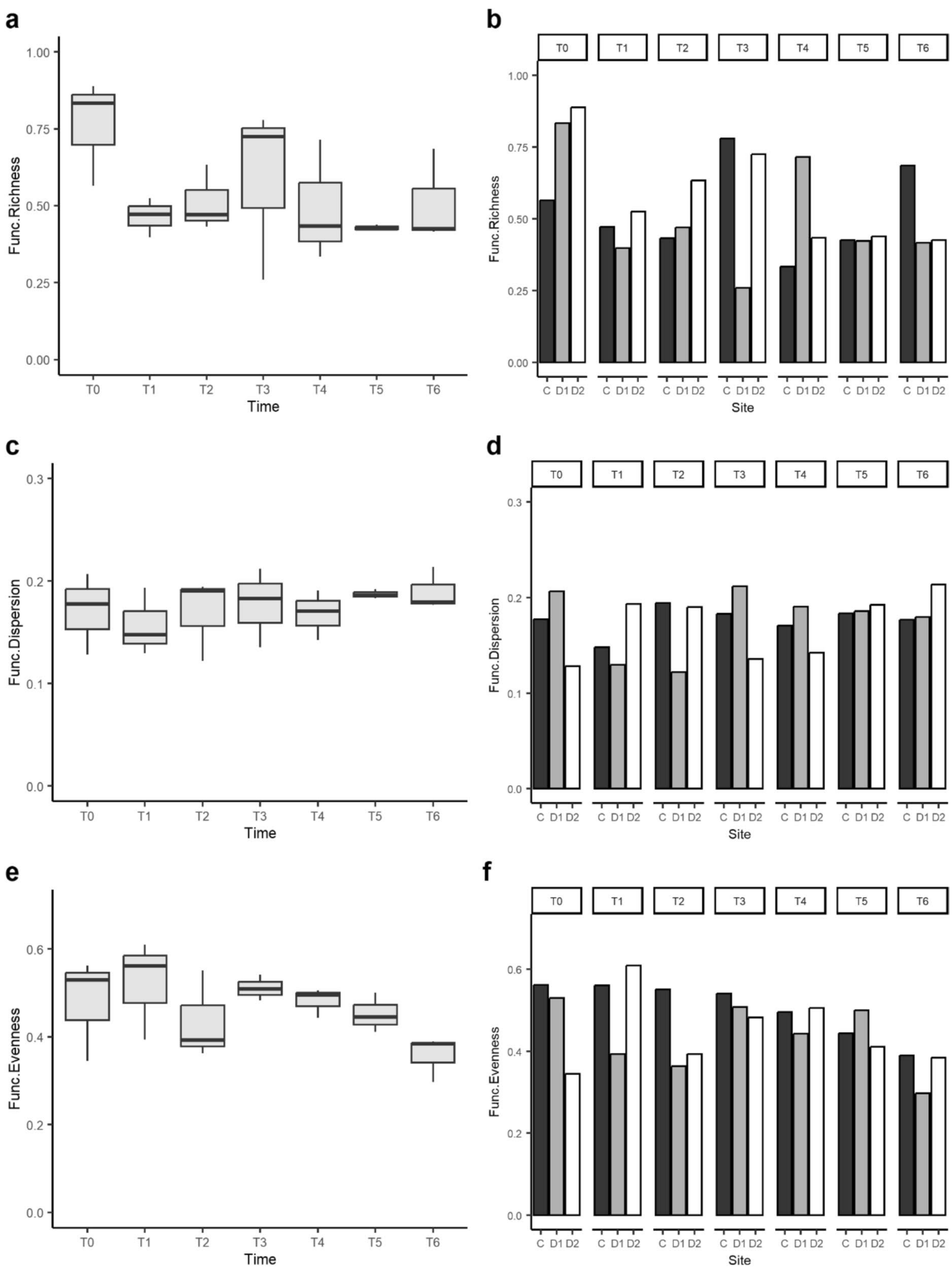

a
N. Taxa
a b b b b a ab
T0 T1 T2 T3 T4 T5 T6
Time
b
T0 T1 T2 T3 T4 T5 T6
N.Taxa
C D1 D2
Site
c
N. Taxa EPT
a b ab ab a a a
Time
d
N.Taxa EPT
Site
e
Density (N.Ind./m^2)
a b ab ab ac c ac
Time
f
Density (N.Ind./m^2)
Site
g
EPT Density (N.Ind./m^2)
a b cd acd ac d cd
Time
h
EPT Density (N.Ind./m^2)
Site

◂**Fig. 6** Boxplots illustrating the variation in: **a** taxon richness, **c** EPT (Ephemeroptera, Plecoptera, Trichoptera) richness, **e** total density, and **g** EPT density among sampling campaigns (T0–T6). Black horizontal line = median; upper and lower box edges = 3rd and 1st quartile, respectively; vertical lines = whiskers (± 1.5 interquartile distance). Bars illustrate the values of: **b** taxon richness, **d** EPT richness, **f** total density, and **h** EPT density for each site (C, D1, D2) and on each sampling campaign (T0–T6)

Overall, these results are similar to those gained in previous studies and highlight how riverine macroinvertebrate communities are generally resilient, even in relation to extreme floods (Greenwood and Booker 2015; Woodward et al. 2015; Milner et al. 2018). Similar findings were also found when looking at the response of benthic macroinvertebrates to flow releases or sediment pulses from dams in Alpine rivers (Crosa et al. 2010; McMullen and Lytle 2012; Quadroni et al. 2016; Robinson et al. 2018, 2023). Despite these latter ones are man-induced and, usually, they have lower magnitude and intensity than natural floods, some parallels in the temporal variation of macroinvertebrate communities can be identified. For instance, Robinson et al. (2004) performed repeated water releases from a reservoir to restore the natural flow regime in an Alpine stream and found that, despite initial decrement, macroinvertebrate communities fast recovered over time.

A possible reason explaining the relatively rapid recovery observed here is that our sampling sites were near-pristine and located in a study area with scarce or negligible anthropogenic pressures in the upstream catchment. According to the theoretical framework proposed by Van Looy et al. (2019), natural areas as well as the connectivity with undisturbed and pristine communities, which may provide new colonizers through dispersal routes, are expected to facilitate the resilience of biological communities. This seems to apply to our study: in fact, all sites could have benefited from the recolonization of macroinvertebrates by drift from upstream river reaches, especially in C and also in D2 because of a small tributary joining the Anza River between the D1 and D2 sites. On the contrary, D1 site was located 350 m downstream the Ceppo Morelli Dam in a very narrow and confined river segment so that the ability of dispersing macroinvertebrates to reach this site is supposed to be limited. This aspect potentially explains why, at the end of this study (T6), total taxon richness and EPT richness in D1 remained lower than the before-flood values, and suggests that the Ceppo Morelli Dam could have interfered with the effects of the flood and the post-disturbance recolonization process of benthic macroinvertebrates. Moreover, we found that the mayfly genus *Baetis* and the midge families Chironomidae and Simuliidae were the dominant taxa in the macroinvertebrate communities within the first 3 months after the flood, confirming their role as fast and pioneer colonizers after a disturbance, as found in previous studies (Robinson et al. 2004; Rader et al. 2008; Salmaso et al. 2020). These findings suggest that the dispersal by drift was likely the main mechanism of post-flood recolonization in our study, while it could be assumed that the role of the hyporheic zone was limited due to the substrate erosion and, then, fine sediment deposition during and after the flood.

Previous results were further confirmed by the analysis of the beta diversity and its nestedness and turnover components. The gain/loss of taxa (i.e. nestedness scenario) was the main component that explained the compositional differences among sites and this was coherent with the temporal variation in the richness metrics observed here. However, we found a growing contribution of taxa replacement (i.e. turnover) from T2 to T4, which corresponded to the period when two additional floods occurred in the area of study. While these floods did not significantly reduce the richness and density of benthic macroinvertebrates, it seems that such repeated disturbances increased the dissimilarity among the macroinvertebrate communities from one site to another one by enhancing the taxa replacement. This aspect assumes particular relevance in the context of climate change, given the predicted increase in the frequency of extreme hydrological events in the next future. Our results suggest that repeated, closely-spaced floods may cause stream macroinvertebrate communities to become more dissimilar. These findings disagree with those of previous studies showing that repeated disturbances, such as floods, sediment flushing operations, and droughts, caused homogenization of the taxonomic composition of macroinvertebrate communities (Hajdukiewicz et al. 2018; Piano et al. 2020; Folegot et al. 2021). However, these latter studies were carried out on different temporal scales compared to our experiment, in which results may be likely explained by the dispersal-related processes


a
Func.Richness
1.00
0.75
0.50
0.25
0.00
T0 T1 T2 T3 T4 T5 T6
Time
b
T0 T1 T2 T3 T4 T5 T6
Func.Richness
C D1 D2
Site
c
Func.Dispersion
0.3
0.2
0.1
0.0
Time
d
Func.Dispersion
Site
e
Func.Evenness
0.6
0.4
0.2
0.0
Time
f
Func.Evenness
Site

◀**Fig. 7** Boxplots illustrating the variation in the: **a** functional richness, **c** functional dispersion and **e** functional evenness among sampling campaigns (T0–T6). Black horizontal line = median; upper and lower box edges = 3rd and 1st quartile, respectively; vertical lines = whiskers (± 1.5 interquartile distance). Bars illustrate the values of: **b** functional richness, **d** functional dispersion and **f** functional evenness at each site (C, D1, D2) and on each sampling campaign (T0–T6)

affecting the sites with C and D2 being more prone to be colonized by drifting macroinvertebrates than site D1.

When evaluating the response of benthic macroinvertebrate communities to disturbances, it should be recognised that the temporal recovery may be context-dependent because of the influence of several co-occurring factors. For instance, natural disturbances, such as droughts and floods, may act differently and interact with local conditions in various ways. The response of benthic macroinvertebrate communities to a single, extreme flood event may differ from that occurring under repeated flooding. Similarly, given the strong relationship between species phenology and seasonality in Alpine streams, the post-flood trajectories of macroinvertebrate communities may be affected by the timing of floods. Therefore, to advance the current knowledge on the post-flood recovery of benthic macroinvertebrates, future studies should be carried out over multiple timescales, ranging from season to multiple years, as well as across a gradient of frequency (i.e. from a single event to repeated floods) and intensity.

When looking at the functional metrics, no statistically significant results arose. However, we found that functional richness and functional evenness decreased over time and, at the end of the study, they were generally lower than the before-flood values. Overall, these results suggest that functional metrics recovered slower than taxonomic richness and macroinvertebrate density, thus indicating that after 9 months since the flood the ecological niches offered by the sampling sites were probably not restored at all. Such a hypothesis seems to be corroborated by the results here obtained especially for the downstream sites (D1 and D2), where at the end of the study the percentage of fine sediment in the substrate still remained far higher than that recorded before the flood. Again, these findings suggest that the Ceppo Morelli Dam could have interfere with the post-flood recolonization of benthic macroinvertebrates in the downstream sections. Although it should be expected that functional metrics vary seasonally along with temporal variations in key environmental variables of temperate Alpine streams, to date, the lack of previous research dealing with the temporal changes in functional richness, dispersion and evenness of macroinvertebrate communities in pristine and impacted rivers makes any comparisons and interpretations difficult and speculative. One limitation of this study is that the final sampling campaign (T6) was carried out in early spring (March 2025), whereas the before-flood sampling campaign was conducted in late spring (May 2024). It is therefore possible that the weak and incomplete recovery of the functional diversity metrics was, in part, due to these seasonal differences. However, given that on T6 a significant percentage fine sediment was found at the sampling sites downstream of the Ceppo Morelli Dam, it should be hypothesised that functional diversity of benthic macroinvertebrates was primary affected and slowed by the flood-related environmental conditions rather than other factors. Overall, our study stresses the importance of future research on the temporal variation in the functional richness, dispersion and evenness under natural and anthropogenic conditions.

The application of biomonitoring indices showcased both similar and contrasting results. While STAR_ICMi and SILTES were successful in detecting a significant decline immediately after the flood, their post-disturbance trends resulted in different outcomes. Based on STAR_ICMi, at the end of the study a full recovery was observed in all sampling sites as each of them achieved the "Good" ecological status class. By contrast, SILTES index depicted a substantial recovery only for the C and D2 sites, while in D1 this index remained far lower than the before-flood value. Such differences may be explained by the sensitivity of the sub-metrics composing these biomonitoring indices, as clearly illustrated in our multivariate (PCA) analysis. Although both indices were strongly associated with the richness metrics, STAR_ICMi appeared to be particularly affected by the EPT-based metrics including EPT family richness, ASPT, and Log10(Sel_EPTD + 1). Since in this study a full recovery to the before-flood values was found for the EPT richness, it may be hypothesised that the effective and rapid gain of EPT taxa during the post-flood recolonization positively affected all the sub-metrics based on these sensitive macroinvertebrates, that in turn contributed to increase the numeric value of

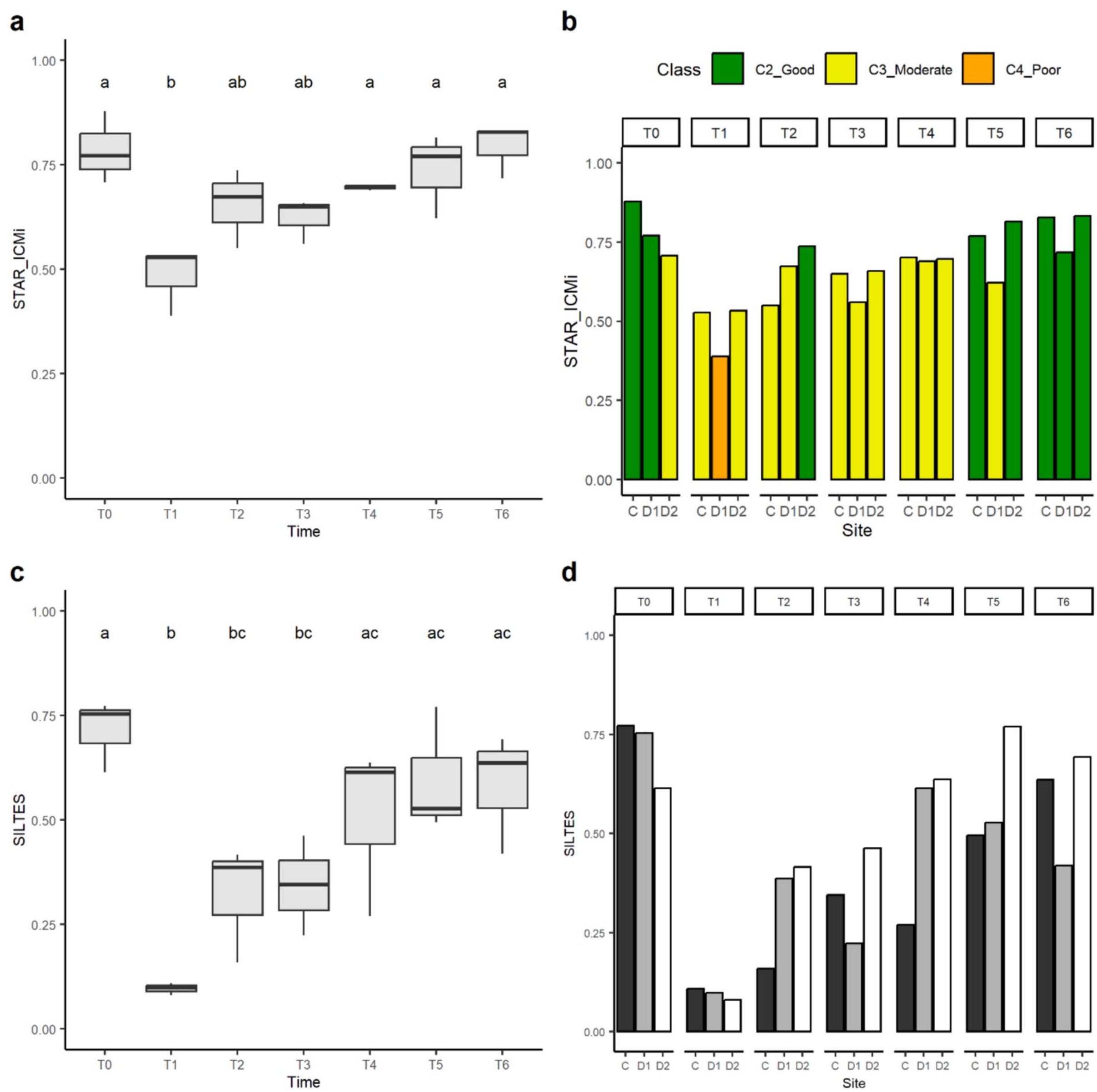


Fig. 8 Boxplots illustrating the variation in the: **a** STAR_ICMi, and **c** SILTES index among sampling campaigns (T0–T6). Black horizontal line = median; upper and lower box edges = 3rd and 1st quartile, respectively; vertical lines = whiskers (± 1.5 interquartile distance). Bars illustrate the values of the **b** STAR_ICMi and **d** SILTES index at each site (C, D1, D2) and on each sampling campaign (T0–T6)

STAR_ICMi. EPT richness is also one of the metrics composing the SILTES index, along with the total taxon richness and the proportion of macroinvertebrates preferring coarse mineral substrates (here represented by the metric CWM_Coarse). Nevertheless, our results showed that SILTES index was likely more conservative than STAR_ICMi in evaluating the post-flood recovery of macroinvertebrate communities, especially in site D1, and these findings agree with those obtained from the multivariate (NMDS) analysis, functional metrics, and environmental variables. Being a stressor-specific index designed to assess the impacts of siltation, previous studies have demonstrated that SILTES was able to detect the

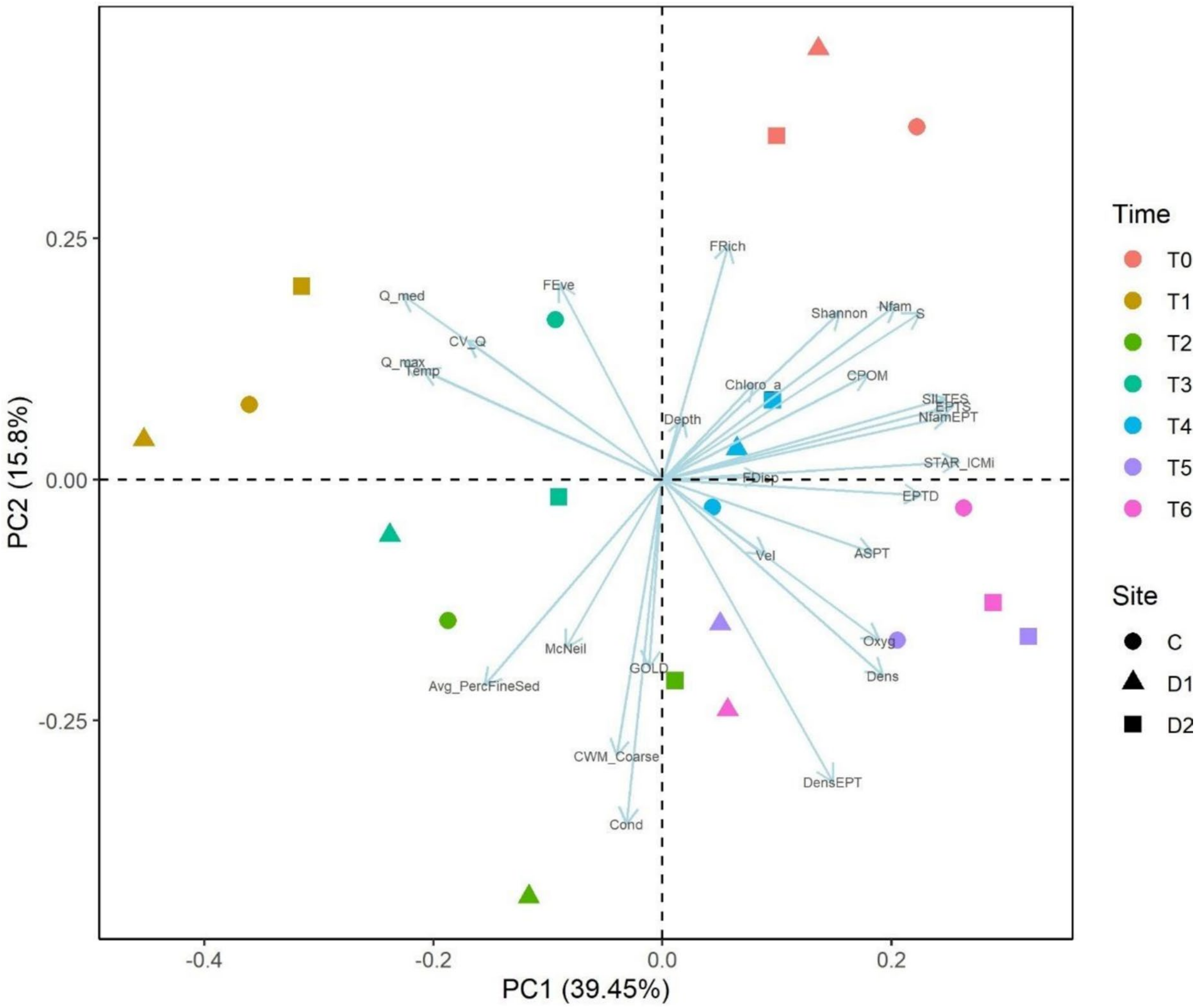


Fig. 9 Principal Component Analysis (PCA) ordination plot. Symbols indicate the sampling sites (C, D1 and D2); colours indicate the sampling campaigns (T0–T6). Light blue arrows and labels indicate the environmental parameters and macroinvertebrate metrics: Vel = water velocity, Depth = water depth, CPOM = coarse particulate organic matter, Chloro_a = amount of chlorophyll-a, Oxyg = dissolved oxygen, Cond = electrical conductivity, Temp = water temperature, McNeil = amount of settled sediments, Avg_PerFineSed = percentage of fine sediment in the substrate, Avg_Q = average discharge, CV_Q = coefficient of variation for river discharge, Q_max = highest value of river discharge, S = taxa richness, Dens = total density, EPTS = EPT richness, DensEPT = EPT density, FRich = functional richness, FDisp = functional dispersion, FEve = functional evenness, SILTES = SILTES index, CWM_Coarse = Community Weighted Mean of trait value for coarse mineral substrate (this is a sub-metric of the SILTES index), STAR_ICMi = STAR_ICMi index. Sub-metric: Nfam = number of macroinvertebrate families, NfamEPT = number of EPT families, Shannon = Shannon index, ASPT = Average Score per Taxon, EPTD = Log10(Sel_EPTD + 1), GOLD = 1-GOLD

impacts of fine sediment deposition on macroinvertebrate communities (Doretto et al. 2018, 2019, 2021, 2022), as it did occur in this study especially in D1.

To conclude, monitoring the response of riverine communities to changes in flow is an irreplaceable aim for correctly managing and preserving river ecosystems. While in the last decades a relevant research effort has been carried out to develop macroinvertebrate-based metrics to assess the impacts of drying conditions (Chadd et al. 2017; Burgazzi et al. 2025) or the ecological preferences of taxa for water velocity (Extence et al. 1999; Theodoropoulos et al. 2017; Laini et al. 2022a), studies testing the sensitivity of biomonitoring metrics to evaluate the post-flood recovery are still underrepresented in scientific literature (but see Smith et al. 2019; Gholizadeh 2021; Chattopadhyay et al. 2021). By providing a multifaceted but seldom adopted approach, this study offers insights on the temporal recovery of Alpine macroinvertebrate communities after an extreme flood in terms of taxonomic and functional diversity. Therefore, the results obtained in this study may serve as a useful benchmark to compare the timing and mechanisms of resilience of macroinvertebrates to floods across biomes and geographical settings. Moreover, our results may contribute to refine the current biomonitoring approaches in order to better discriminate the impacts associated with natural and anthropogenic disturbances, with the ultimate goal of improving our knowledge on the effects of multiple stressors on river ecosystems.

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Author contributions NT: data collection, data analysis, writing—original draft, writing—review and editing. IB: data collection, writing—review and editing. AG: data collection, writing—review and editing. PEB: conceptualization, writing—review and editing. PB: conceptualization, writing—review and editing. GRP: funding acquisition, conceptualization, writing—review and editing. LS: data collection, writing—review and editing. SQ: funding acquisition, conceptualization, writing—review and editing. AD: funding acquisition, conceptualization, data collection, data analysis, writing—original draft, writing—review and editing.

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Data availability Authors declare that data are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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