Ecohydrology

WILEY

RESEARCH ARTICLE OPEN ACCESS

Investigating the Effects of Flow Regulation Combining Stream Geomorphology With Macroinvertebrate Ecology: A Case Study in the Orobic Alps (Italy)

Luca Bonacina | Riccardo Fornaroli | Valeria Mezzanotte | Giovanni Vezzoli

Department of Earth and Environmental Sciences (DISAT), University of Milano-Bicocca, Milan, Italy

Correspondence: Luca Bonacina (luc.bonacina@gmail.com; l.bonacina9@campus.unimib.it)

Received: 11 December 2024 | **Revised:** 8 July 2025 | **Accepted:** 10 July 2025

Keywords: bedload | functional traits | hydrological alterations | LIFE index | reservoir | sediment grain size distribution

ABSTRACT

Mountain streams exhibit hydrogeomorphological heterogeneity, which is further intensified by the presence of hydraulic infrastructure. Despite extensive research on the influence of hydrological conditions and flow regulation on ecology, there is a notable absence of holistic studies investigating stream dynamics from both geomorphologic and ecological perspectives. Our work seeks to address this gap by characterizing stream channels' morphology, sediment grain-size distribution and streambed lithological composition combined with an evaluation of bedload rates and an assessment of macroinvertebrate taxonomic composition and flow preferences. The study was conducted along the longitudinal profiles of two steep headwater streams of the Orobic Alps (Northern Italy), one regulated by reservoirs and the other unregulated. Five reaches were surveyed, with two for each stream, plus one below their confluence. The investigation unveiled a patchwork of geomorphological conditions and bedload rates across the five stream reaches examined. These variations, related to physiographic setting and flow regulation, were associated with differences in the taxonomic composition of macroinvertebrate assemblages and their flow preferences. In the stream regulated by reservoirs, a higher taxonomic richness and abundance of both limnephilic and reophilic taxa were observed compared with the unregulated stream. Below their confluence, the composition of the macroinvertebrate assemblage exhibited marked temporal variability, likely associated with the highly fluctuating hydromorphic conditions. Despite the lack of a detailed hydrological characterization, our study highlights the interconnectedness of geomorphology, bedload rates and macroinvertebrate responses under distinct hydrological conditions, providing complementary insights. Thus, we advocate for interdisciplinary studies to better unravel mountain watercourses dynamics.

1 | Introduction

Rivers are complex and dynamic systems with a strong influence on the territory; they transport water and materials and shape the landscape, acting on different spatial and temporal scales. Mountain regions produce a huge amount of sediments transported up to the ocean by the hydrographic network and provide the major water source (Milliman and Syvitski 1992). Moreover, headwaters control the denudation rate, the hillslope stability and the shaping of the valleys, and their action is transmitted downstream, affecting the whole drainage network (Wohl 2013; Larsen and Montgomery 2012). Lastly, mountain streams are unique environments that constitute a hotspot of biodiversity (Muhlfeld et al. 2011; Fochetti 2012; Jordan et al. 2016).

Hydraulic infrastructures such as dams, reservoirs and diversion channels disrupt the river continuity and alter the flow regime of water bodies, thereby modifying the magnitude, timing and frequency of natural flows (Zolezzi et al. 2009; Bocchiola 2014). Generally, watercourses regulated by a

Ecohydrology, 2025; 18:e70082
https://doi.org/10.1002/eco.70082

reservoir are characterized by a shrunken and simplified geomorphology, which directly impacts riparian habitats, resulting in smaller and less diverse riparian ecosystems compared with the larger and more complex ones found along unregulated reaches (Graf 2006). Impoundments affect the sediment cycling, promoting sedimentation and inducing a higher erosion below the dam (Anselmetti et al. 2007) as sediments remain trapped. According to the serial discontinuity concept (Stanford and Ward 1983), dams result in upstream–downstream shifts in biotic and abiotic patterns because of the modification of environmental conditions. Such alterations are caused by (i) flooding of the terrestrial habitats; (ii) changes in hydraulic conditions; (iii) retention of sediments, organic debris, chemical pollutants, nutrients and trophic resources; (iv) modification of water temperature and dissolved oxygen content; and (v) changes in channel geomorphology (Goldman 1976; Baxter 1977; Graf 2006).

From the beginning of the 20th century, several hydraulic infrastructures have been built on mountains for hydroelectric purposes. For instance, in Italy, there are more than 530 large reservoirs (dam high >15 m and with a volume $>10^6$ m^3) and around half are in the Alps (ISPRA 2019). Most of the reservoirs were designed exclusively for hydropower generation, even if there are impoundments for flood control and for irrigation and drinking water purposes too, especially in the Italian southern regions. Additionally, especially in the last years, some small reservoirs and mini/micro hydropower plants have been and are being installed for artificial snow and electricity production (Evette et al. 2011; de Jong 2015). The higher number of hydraulic infrastructures and their overdispersion throughout the whole Alpine chain, together with the strong human pressure in terms of land use, have modified the morphology of the valleys, the hydrography and the geography so that 'reference conditions' cannot be found even in small mountain creeks (Comiti 2012). Hydropower plants allowed the industrialization and the economic development of alpine countries during the 20th century, providing most of their energy needs (Hediger 2021). Even today, the hydroelectric sector accounts for over 20% of Italy's energy and more than 55% of Switzerland's, primarily relying on reservoirs (Permanent Secretariat of the Alpine Convention 2009). Nevertheless, impoundments significantly disrupt the sediment load in alpine regions, affecting the entire drainage network and leading to increased coastal erosion (Syvitski et al. 2005; Syvitski and Kettner 2007; Sadaoui et al. 2018). Hinderer et al. (2013) estimated that only 45% of the bedload sediments mobilized in headwater streams are exported out of the Alps, as the remaining 55% become trapped in artificial reservoirs (equating to around 43 Mt/year). Lastly, hydraulic infrastructures profoundly alter the ecology of alpine freshwater networks, promoting lentification and modifying the hydrologic regime of most alpine streams (Baxter 1977).

Among the different organisms that inhabit watercourses, macroinvertebrates represent a heterogeneous group primarily associated with the riverbed. Macroinvertebrate assemblages comprise numerous taxa, with various habitat preferences and life history strategies (Hauer and Lamberti 2017). Their taxonomic and functional diversity allows them to reflect responses to multiple stressors, including the presence of fine sediment, pollution, invasive species and hydrologic and thermal alterations. Consequently, macroinvertebrates serve as effective bioindicators (Holt and Miller 2011) and are frequently used to assess the ecological status of freshwater systems (Cañedo-Argüelles et al. 2020). Historically, macroinvertebrate ecological indices relied on the taxonomic structure of the community (presence/absence or abundance of some specific taxa according to their sensitivity to different stressors); however, over the last 30 years, indices based on functional traits (as the trophic role or the habitat preference) have also emerged (Statzner and Bêche 2010). These indices offer a deeper understanding of how biotic communities respond to a range of anthropogenic stressors, including hydrological alterations (Tupinambás et al. 2014; Dolédec et al. 2015). Scientific literature extensively documents the effects of flow regulation on macroinvertebrates that encompass changes in taxonomic and functional composition, taxa abundances, richness and diversity (Poff and Zimmerman 2010; Worrall et al. 2014; Mbaka and Mwaniki 2015; Wang et al. 2019; Trottier et al. 2022). Such impacts are driven by hydrological alterations but can be mediated by changes in sediment mobility and resource supply, modifications in channel morphology and habitat availability and variations in the water physico-chemical conditions, including alterations in oxygen concentration and water temperature (Baxter 1977; Petts and Gurnell 2005; Dewson et al. 2007; White, Hannah, et al. 2016; Petruzziello et al. 2021).

This study aims to assess the stream geomorphological conditions and the associated ecological responses of macroinvertebrate communities along a gradient of hydraulic features in a mountain catchment of the Orobic Alps (Northern Italy). The study involves a characterization of the stream channels' morphology, grain-size distribution and lithological composition of bedload sediments combined with an evaluation of the taxonomic composition of macroinvertebrate assemblages and their flow preferences. The survey was conducted along the longitudinal profiles of two steep headwater streams, one regulated by reservoirs and the other unregulated, and downstream of their confluence. We hypothesized that stream regulation, reducing hydrological variability, would decrease bedload mobility as dams dab floods (H1). Accordingly, we supposed that macroinvertebrate communities' composition would vary among stream reaches and that the flow response guilds of the assemblages would reflect the hydraulic alteration and the geomorphological conditions of each reach (H2).

2 | Materials and Methods

2.1 | Study Area

The study was conducted in the Goglio valley, an unglaciated catchment situated in the Orobic Alps (South-Alpine tectonic domain) of Northern Italy (Figure 1A), covering ~32 km^2 ranging from 500 to 2626 m a.s.l. The drainage basin is formed by a metamorphic basement consisting of gneiss and schists, overlain by lower Permian sedimentary and volcanic rocks (Formazione di Pizzo del Diavolo; Vulcanite del Monte Cabianca) and by upper Permian conglomerates and sandstones (Verrucano Lombardo) (Figure 1B). The climatic conditions are typical of a montane environment characterized by snowfall during winter (November–April), springtime runoff primarily from snowmelt (April–June) and floods mainly occurring in autumn (September–November). The Valgoglio catchment was

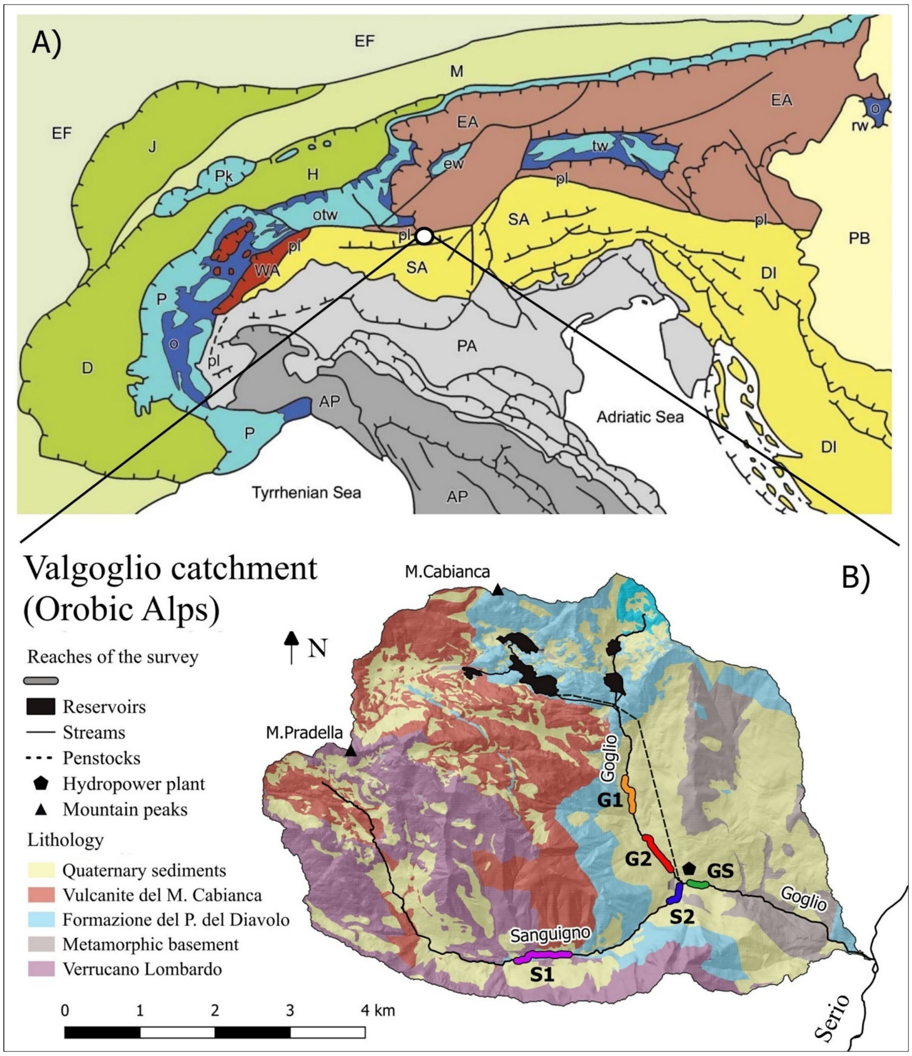

FIGURE 1 | (A) Tectonic map of Alps taken from Dal Piaz et al. (2003): (1) Europe-vergent collisional belt: (i) Western (WA) and Eastern (EA) Austroalpine; (ii) Penninic domain: continental and ophiolitic (o) nappes in western Alpine arc (P) and tectonic windows (otw: Ossola-Ticino, ew: Engadine, tw: Tauern, rw: Rechnitz); Prealpine klippen (Pk); (iii) Helvetic-Dauphinois (H-D) domain; (iv) Molasse foredeep (M); (v) Jura belt (J). (2) Southern Alps (SA), bounded to the north by the Periadriatic lineament (pl). Pannonian basin (PB), European (EF) and Po Valley-Adriatic (PA) forelands, Dinaric (DI) and Apenninic (AP) thrust-and-fold belts. (B) Lithological map of the Valgoglio catchment.

specifically selected for its unique features, comprising two main valleys, Goglio and Sanguigno, with similar environmental conditions in terms of lithology, land cover, altitude and area, but exhibiting contrasting hydrological regimes. Indeed, Goglio stream, regulated upstream by five artificial reservoirs built in the 1920s, contrasts sharply with the unaltered flow regime of Sanguigno stream. Originating from reservoirs situated on two wide glacial terraces at 2000 and 1750 m a.s.l., Goglio stream first courses through a very steep scarp, then crosses a less steep beech forest and finally enters the Serio River at 630 m a.s.l., approximately 7.5 km from the reservoirs. Conversely, Sanguigno stream begins at around 2200 m a.s.l. on the mountainside; it flows along a more constant slope, passing through an alpine meadow, and then crosses a steeper alders' wood before converging with Goglio at an altitude of 970 m a.s.l., roughly 7 km from its source (Figure 2A). Below the reservoirs, at ~1500 m a.s.l., the flow of Goglio stream remains very low and comprises mainly the environmental flow ($< 0.05\,\mathrm{m^3/s}$). Further down the valley, especially during the snowmelt season and fall events, its flow increases, primarily due to the contribution from unregulated tributaries. Upstream of the confluence, Sanguigno stream is diverted into Goglio stream (diversion limit $= 0.7\,\mathrm{m^3/s}$), which, in turn, is further diverted into the Aviasco hydropower plant (diversion limit $= 1.7\,\mathrm{m^3/s}$). Thus, the flow of the lower Goglio stream (downstream of the confluence with Sanguigno) depends on the management operations and generally corresponds to the ecological flow released by the Aviasco plant ($\sim 0.076\,\mathrm{m^3/s}$) (Figure 2B). The environmental flow refers exclusively to the hydrological component, defined as 10% of the mean annual natural flow. A seasonal modulation, ranging between 0.118 and $0.252\,\mathrm{m^3/s}$, was implemented only downstream of the Aviasco hydropower plant. Both stream channels exhibit characteristics of cascade morphology with steep-pool reaches, as defined by Montgomery and Buffington (1997), with a very steep hillslope (mean gradient of ~17% and 24% for Sanguigno and the upper Goglio, respectively). Active sediment sources predominantly include bare slopes, shallow landslides, eroded stream banks and minor debris-flow channels.

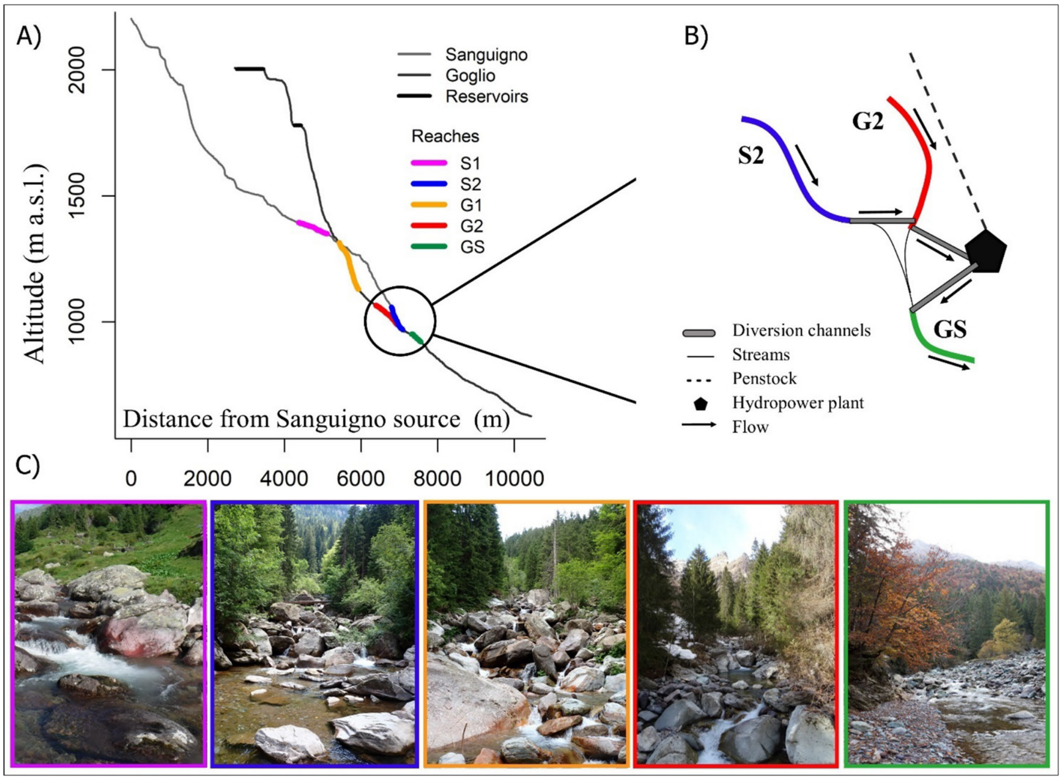

FIGURE 2 | (A) Longitudinal profiles of Sanguigno and Goglio streams, (B) schematic representation of the hydropower diversions and the stream confluence and (C) pictures of stream reaches taken from downstream to upstream (the colours of the border correspond to sites in Panel A).

Five stream reaches, ranging between 350 and 500 m in length, were selected for both the geomorphological characterization and the macroinvertebrate surveys. Reaches S1 and S2 were situated along Sanguigno stream, at mean altitudes of 1370 and 1000 m a.s.l., respectively, whereas reaches G1 and G2 were situated along Goglio stream at mean altitudes of 1200 and 1050 m a.s.l., respectively. The GS reach was located downstream of the confluence at a mean altitude of 940 m a.s.l. (Figure 2C).

2.2 | Channel Morphology and Sediment Characterization

In each reach, a cross-section was tracked at the bankfull level using a meter type and a meter stick. Additionally, one or two exposed stream bars were selected per reach to analyse the size and the lithology of the grains. Specifically, a minimum of 100 pebbles/cobbles, with a B-axis ranging from 8 to 256 mm, were randomly collected from a grid of the deposition bars (Wolman 1954); their intermediate axis (B-axis) was measured, and the lithology was classified into four groups: metamorphic rocks (e.g., mica schists), sedimentary rocks belonging to Formazione del Pizzo del Diavolo, volcanic rocks from the Cabianca Vulcanite and Verrucano Lombardo rocks. The channel morphology survey and the sediment characterization took place from autumn 2020 to summer 2021. Pebbles/cobbles size data were categorized based on the Buffington and Montgomery (1999) classification, and the grain size distribution was retrieved for each reach using a gamma regression to extrapolate the 5°, 16°, 50°, 84° and 95° percentiles. Prior to analysis, the B-axis of each percentile was converted into Psi ($\psi = \log_2(B)$; Krumbein 1934); subsequently, mean (M), sorting (σ), skewness (Sk) and kurtosis (K) metrics were calculated based on Folk and Ward (1957) to analyse the sediments distribution and understand riverine geomorphological processes. Moreover, the Shannon diversity index was applied to the five percentiles to assess streambed habitat heterogeneity in each reach. Lastly, the composition of the sediments was described through pie plots, illustrating the relative abundance of each lithology within every reach.

2.3 | Bedload Mobility and Yield

A first rough field assessment of the bedload mobility in each reach was conducted using the tracer method. This involved painting 100 in situ stones representative of the grain size distribution (10, 25, 30, 25 and 10 stones respectively for the 95°, 84°, 50°, 16° and 5° percentiles of each stream reach's grain size distribution), placing them on the surveyed exposed fluvial bars and monitoring their displacement after high-flow events accounting for the percentage of moved stones and the travelled distance. After each displacement, 100 newly painted stones were positioned on each bar. The bedload mobility surveys began in spring 2021 and ended in autumn 2021. The tracer method was chosen for its affordability, simplicity and ability to visually inspect surfaces, despite the low stones' recovery rate and the uncertain relation between displacement distance and grain size, particularly in steep headwater streams (Hassan and Ergenzinger 2005). Tracing natural clasts remains a common technique in stream sediment transport studies, especially in headstream channels, and as early as 1815 (more than one century before the first pioneers studied reported in scientific literature [Hassan and Ergenzinger 2005]), engineer Tadini conducted sediment transport experiments in the Orobic Alps, tracking pebbles of the Serio River (Tadini 1815). The bedload mobility was quantified at each survey event by combining the displacement of the tracers with the moved mass by the following metric, adapted from Townsend et al. (1997):

$$BEDLOAD\ MOBILITY = \frac{\sum_{i=1}^{n} {B^3}_i * d_i}{\sum_{i=1}^{n} {B^3}_i} \%$$

where B is the intermediate axis of the tracers and d is the displacement (0 for 'not moved' and 1 for 'moved'). Unrecovered stones were considered washed away. Since flow data were unavailable, the bedload mobility was associated with cumulated daily rain data measured by the weather station of Valcanale, located about 4 km as the crow flies from the Aviasco hydropower plant.

An approximate estimation of the bedload yield in each reach was computed using the equations proposed by de Vente et al. (2006) for Italian basins and Schlunegger and Hinderer (2003) for the Swiss Alps.

The annual area-specific sediment yield is determined by the catchment area (A) through the equation:

$AREA - SPICIFIC\ SEDIMENT\ YIELD = 103.6 * A^{0.28}$ (de Vente et al. 2006)

Additionally, the percentage of annual area-specific sediment yield attributed to bedload can be calculated using the equation:

$\%\,BEDLOAD\ YIELD = -5.06 * \log(\mathrm{A}) + 52.5$ (Schlunegger and Hinderer 2003)

and for the Valgoglio catchment, it is 39.

This estimation of the annual bedload yield was computed considering the basin area subtended by each section in two distinct scenarios: one accounting for the presence of reservoirs (current situation) and the other excluding reservoirs (reflecting the past situation when the Goglio reaches were fed by the entire catchment area). Note that these estimations do not aim to quantify the exact bedload yield but rather to compare relative differences among reaches and to assess the impact of dams on the downstream bedload discharge.

2.4 | Macroinvertebrate Assemblages

Macroinvertebrates were collected six times in each reach during the summers and falls of 2017 and 2018 using a Surber net ($0.10\,\mathrm{m}^2$, 500-μm mesh), following the standardized multihabitat sampling procedure (Barbour et al. 1999; Hering et al. 2012). Ten replicated samples were collected from different microhabitats (gravel/microlithal/mesolithal/macrolithal/megalithal) based on their relative coverage (only those covering at least 10% of the streambed surface were considered) and then pooled and stored in 96% ethanol. Taxa were identified at the family level using the standard keys, and the abundance of individuals of each taxon was annotated. Macroinvertebrate data were used to assess flow response guild, particularly focusing on quantifying the richness and abundance of taxa preferring slow and fast velocities through the application of the Family-level Lotic-invertebrate Index for Flow Evaluation (LIFE). This biomonitoring index, introduced by Extence et al. (1999), is based on the flow velocity preferences of invertebrate taxa, and it is commonly employed by UK regulatory bodies for establishing water abstraction licence conditions and monitoring macroinvertebrate responses to flow variability (Klaar et al. 2014). Taxa exhibiting preferences for moderate to rapid flow velocities ($> 0.2\,\mathrm{m/s}$) are classified as rheophilic (Groups I and II, Table A1), whereas those preferring slow flow velocities to standing waters ($v \leq 0.2\,\mathrm{m/s}$) are defined as limnephilic (Groups III and IV, Table A1) (White, Fornaroli, et al. 2021). Additionally, macroinvertebrate total abundance (individuals/m^2), taxa richness and Shannon–Wiener diversity were calculated as they are reliable indicators for assessing resilience mechanisms related to resource supply and the availability of refugia (Van Looy et al. 2019; Gething et al. 2020). A non-metric multidimensional scaling (nMDS) ordination, based on the Bray–Curtis dissimilarity, was performed to explore the dissimilarity of macroinvertebrate assemblages among reaches, and a permutational multivariate analysis of variance (PERMANOVA) was used to test for similarity among reaches. Such analyses were performed with the R *vegan* package using the *metaMDS* and *adonis2* functions (Oksanen 2022); Wisconsin double standardization and square root transformations were applied to the data. To examine significant differences in macroinvertebrate assemblage composition between each pair of reaches, pairwise comparisons were conducted using the *pairwise.adonis* function, applying Bonferroni corrections (Gething et al. 2020). The homogeneity of macroinvertebrate assemblages was assessed throughout the PERMDISP analysis by using the *betadisper* function in the R *vegan* package (Anderson et al. 2006; Oksanen 2022). This analysis compares the temporal beta diversity of each reach based on the Bray–Curtis distances. To address comparisons among treatments with a small number of samples, a bias.adjust (bias.adjust = TRUE, Stier et al. 2013) was employed, and the significance was assessed using the Tukey multiple comparisons test. The Kruskal–Wallis test, followed by Dunn's multiple-comparison test with Bonferroni correction, was performed to assess variations in LIFE index values, rheophilic and limnephilic taxa richness and abundance, macroinvertebrate total abundance, total taxa richness and Shannon–Wiener diversity among stream reaches. Spearman rank correlations were used to identify environmental variables that are more associated with site-averaged macroinvertebrate assemblage indices. All statistical analyses were performed using R project software (R Core Team 2020) and a significance level $\alpha < 0.05$.

3 | Results

3.1 | Channel Morphology and Sediment Characterization

The channel sections strongly differ among the investigated reaches. In the Sanguigno stream, the width increases from the upstream to downstream reaches, measuring 15 and 20 m respectively, accompanied by an elevation in maximum depth from 0.81 m (S1) to 1.95 m (S2). The slope also shows a notable rise, approximately 30% in S1 and 130% in S2. Conversely, the upper Goglio stream exhibits a reduction in size, with widths measuring 37 and 18.5 m (G1 and G2, respectively) and maximum depths of 3.95 m (G1) and 2.34 m (G2). The slope shows a decrease, about 250% in G1 and 50% in G2. Downstream from the confluence in GS, the Goglio stream widens considerably (width = 22.35 m) with a maximum depth of 3.37 m. This channel is constrained by a steep riverbank on the left hydrographic side, whereas the slope in this reach is approximately 40% (Figure 3A).

The upper Goglio stream (G1) exhibits wider sediments, measuring up to 256 mm in width, in contrast to the Sanguigno stream, where the maximum width is 180 mm (Figure 3B). Both streams display a gradual reduction in grain size across the D5,

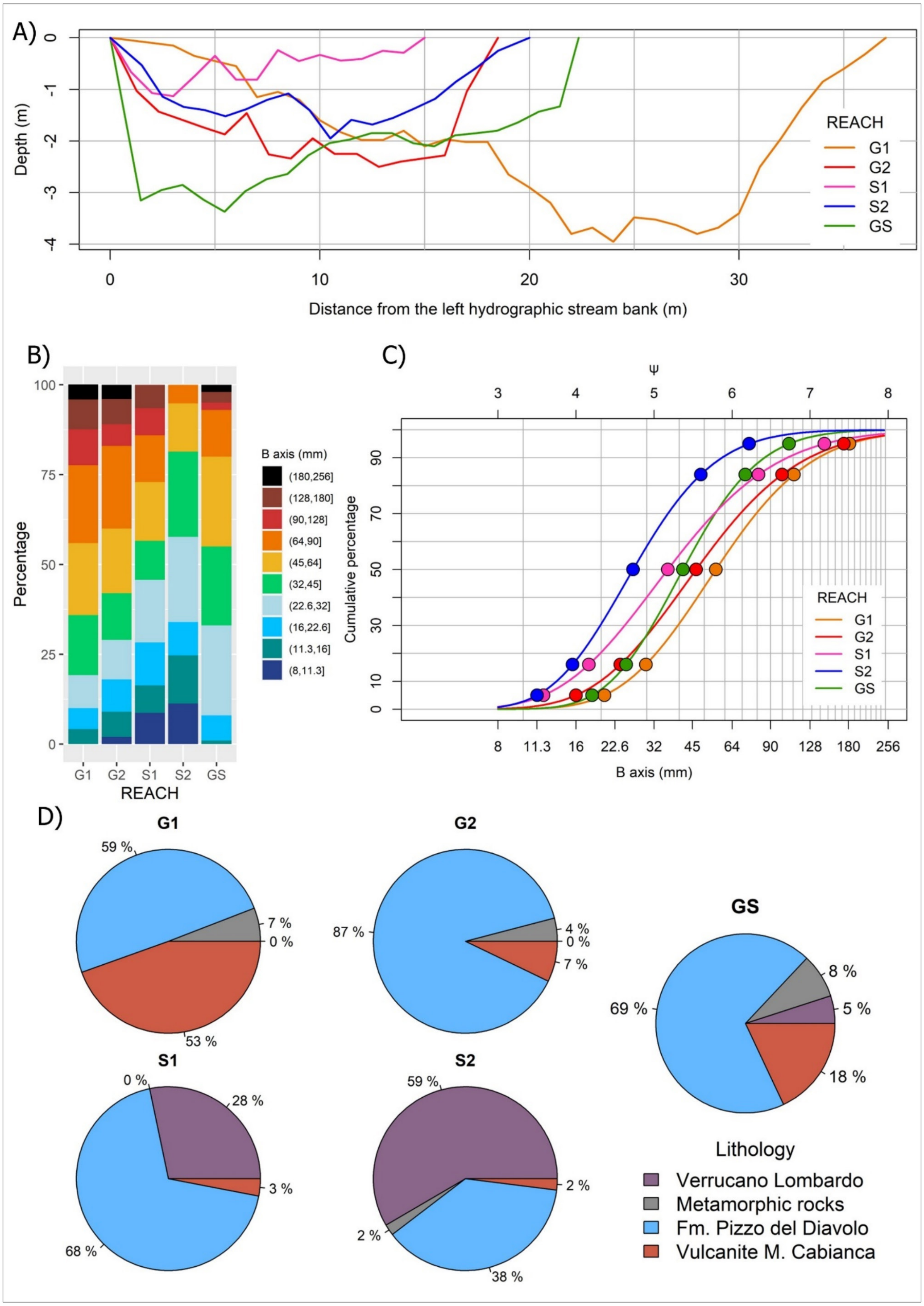

FIGURE 3 | (A) Stream channel sections; (B) relative percentage of each grain size class; (C) cumulative curves of the sediment grain size distribution with the 5°, 16°, 50°, 84° and 95° percentiles; and (D) pie plots reporting the relative percentage of each lithology in each reach.

D16, D50, D84 and D95 percentiles (Figure 3C). Nevertheless, below the confluence, the sediment grain size distribution lies intermediate between the G2 and S2 reaches, as is evinced by the D50, D84 and D95 percentiles, which are higher than those of G2 but lower than those of S2 (Figure 3B,C). On average, the upper Goglio stream has wider sediment sizes compared with Sanguigno, with mean values (*M*) ranging from 47.9 to 56.8 mm in G2 and G1, whereas S2 and S1 measure 27.1 and 37.4 mm, respectively. GS displays an intermediate sediment mean size of 42.0 mm. The grains in the upper reaches are classified as poorly sorted ($\sigma = 0.95$, 1.03 and 1.08 in G1, G2 and S1, respectively), whereas they exhibit moderate sorting in S2 and GS ($\sigma = 0.82$ and 0.76, respectively). Skewness values show minimal variation across reaches, indicating nearly symmetric grain size distribution (*Sk* ranging between 0.06 and 0.09). The kurtosis coefficient reveals a leptokurtic grain size distribution in all reaches (*K* ranging from 3.1 to 4.3) except for S1 ($K = 2.99$) (Table 1). The upper Goglio streambed consists of sedimentary rocks from the Formazione del Pizzo del Diavolo (59% and 87% in G1 and G2, respectively), Cabianca vulcanite (53% and 7% in G1 and G2, respectively) and metamorphic rocks (7% and 4% in G1 and G2%, respectively). In contrast, the Sanguigno streambed is mainly composed of sedimentary rocks belonging to Verrucano Lombardo (28% and 59% in S1 and S2, respectively) and the Formazione del Pizzo del Diavolo (68% and 38% in S1 and S2%, respectively), with metamorphic and volcanic rocks accounting for less than 5%. The GS streambed exhibits a lithological composition comprising Verrucano Lombardo (5%), metamorphic rocks (8%), volcanites (18%) and sedimentary rocks from the Formazione del Pizzo del Diavolo (69%) (Figure 3D).

TABLE 1 | Percentiles (*D*), mean (*M*), sorting (σ), skewness (*Sk*), kurtosis (*K*) and diversity (Shannon) metrics of the grain size distribution for each stream stretch and estimated bedload yield in the current and pre-dams' situations.

	G1	G2	S1	S2	GS
D5 (mm)	20.6	16.0	12.0	11.3	18.5
D16 (mm)	29.8	23.7	17.9	15.5	25.0
D50 (mm)	55.4	46.5	36.2	26.5	41.3
D84 (mm)	110.9	99.8	81.0	48.5	72.0
D95 (mm)	181.5	172.7	145.3	74.5	106.2
Mean (mm)	56.8	47.9	37.4	27.1	42.0
Sorting (σ)	0.950	1.039	1.089	0.823	0.764
Skewness (*Sk*)	0.072	0.083	0.092	0.076	0.063
Kurtosis (*K*)	3.776	3.332	2.993	3.576	4.330
Diversity (Shannon)	1.336	1.291	1.264	1.394	1.422
Current bedload yield (t/km^2*year)	53.09	62.09	71.18	79.82	89.57
Pre-dams' bedload yield (t/km^2*year)	78.38	82.23	71.18	79.82	99.71

3.2 | Bedload Mobility and Yield

During the bedload mobility survey period (from the 1st of April to the 1st of October 2021), no movement of painted stones was observed in G1, whereas movements occurred in other reaches following daily precipitation events exceeding ~90 mm (on the 3rd of August and on the 16th of September). Bedload mobility estimates indicated higher movement in S1 and S2 compared with G2, whereas GS displayed a marked variability in sediment mobilization, from 6% to 95% on the 3rd of August and the 16th of September, respectively (Figure 4).

According to the bedload yield estimations, currently, the upper Goglio stream transports a lower amount of bedload sediments compared with the Sanguigno (61.73 vs. 79.36 t/km^2*-year). By contrast, in the pre-dams' scenario, bedload sediment supply from the upper Goglio marginally exceeded that of the Sanguigno (81.75 vs. 79.36 t/km^2*year). The construction of the reservoirs reduced the bedload sediment by about 20%–25% in the upper Goglio and by 10% in the lower Goglio (Table 1).

3.3 | Macroinvertebrate Assemblages

The microhabitats surveyed for macroinvertebrate collection included megalithal (> 40 cm), macrolithal (20–40 cm), mesolithal (6–20 cm), microlithal (2–6 cm) and gravel (0.2–2 cm). The first three classes—megalithal, macrolithal and mesolithal—were roughly evenly represented, each accounting for 20%–30% and together comprising 70%–90% of the streambed. The distribution of sampled microhabitats closely reflects the grain size distribution observed in the sedimentation bars across the study reaches. Specifically, the upper reaches (G1 and S1) exhibited higher proportions of megalithal and macrolithal compared with the downstream reaches (G2 and S2). G1 had the lowest abundance of microlithal, whereas S2 was the only reach where gravel made up 10% of the streambed. The GS reach showed intermediate characteristics between the two streams, with 30% megalithal and no gravel (Figure 5).

Overall, macroinvertebrate assemblages strongly differ among sampled reaches (PERMANOVA: $R^2 = 0.216$, $p = 0.002$); within the non-metric multidimensional space, S1, S2, G1 and G2 reaches exhibit relatively distinct clusters (Figure 6). Pairwise PERMANOVA comparisons indicate that S1 differs from G1 and G2 but not from S2, and similarly, G1 differs from S1 and S2 but not from G2. However, G2 and S2 do not display significant differences, and likewise, the GS site does not significantly differ from the other reaches (Table A2). GS exhibits greater temporal variability in macroinvertebrate taxonomic composition (beta_div) compared with the other reaches, indicated by a wider dispersion of GS samples within the non-metric multidimensional space, with a multivariate distance to the centroid of 0.39 for GS, whereas approximately 0.33 for the other reaches (Figure 6).

On average, the LIFE index tends to be lower in the upper Goglio reaches (G1 and G2) compared with the Sanguigno ones (S1 and S2) (Figure 7A). Consistently, both limnephilic taxa richness and abundances exhibit slightly higher values in these upper Goglio reaches in comparison with the others (S1 and S2; $p > 0.05$ for all

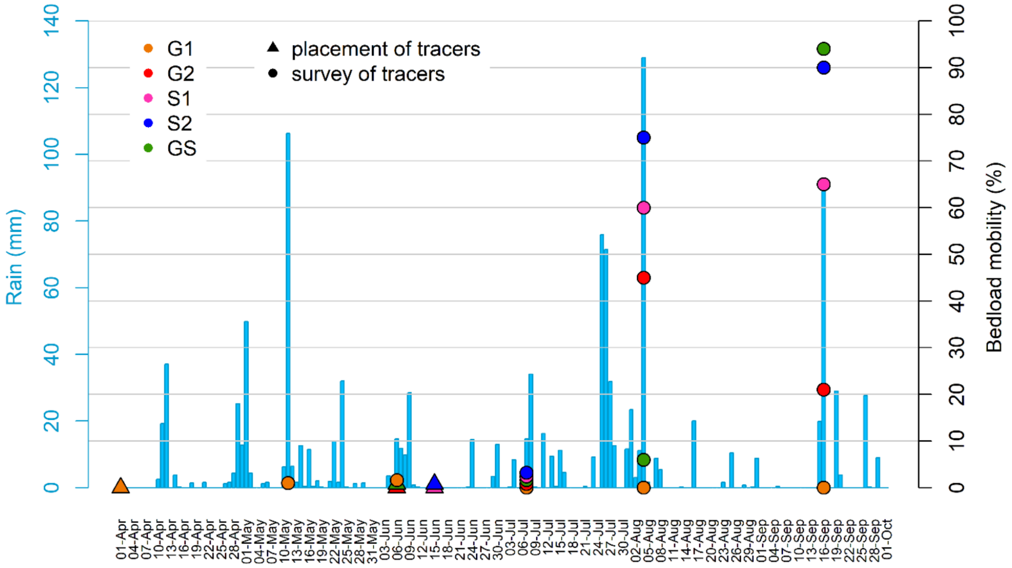

FIGURE 4 | Cumulated daily rain (mm) in the period 1st of April–1st of October 2021 and bedload mobility (%) estimated in each reach using the painted tracer method.

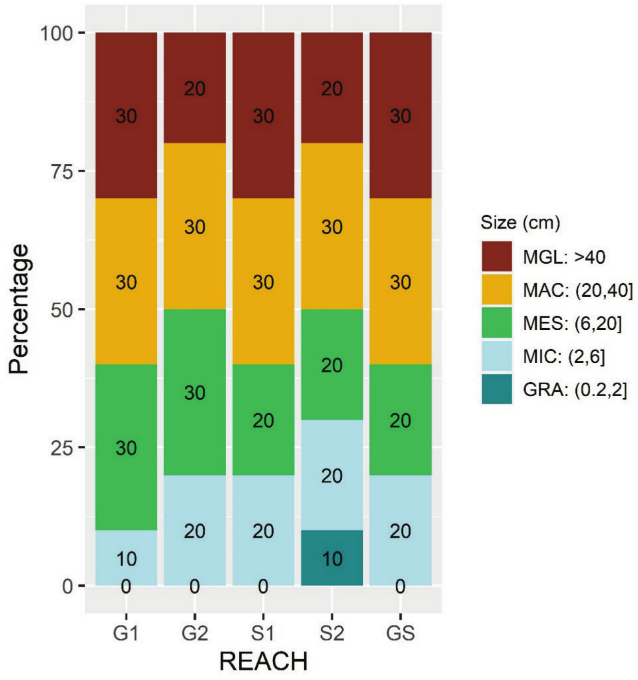

FIGURE 5 | Relative percentage of microhabitats surveyed for macroinvertebrate collection in each reach.

comparisons, Figure 7B,C). Conversely, both the richness of rheophilic taxa and the total taxa richness display higher values in the upper Goglio and lower values in the Sanguigno (Figure 7D,G). The abundance of rheophilic taxa and the total abundance exhibit minimal variability among stream reaches, displaying a consistent pattern (Figure 7E,F). However, the Shannon–Wiener diversity index strongly varies among reaches, with higher values observed in the upper Goglio and lower values in both the Sanguigno and lower Goglio ($p = 0.03$, Figure 7H). Lastly, the lower Goglio generally shows intermediate values between the two upstream channels (upper Goglio and Sanguigno) across all the studied macroinvertebrate indices (Figure 7).

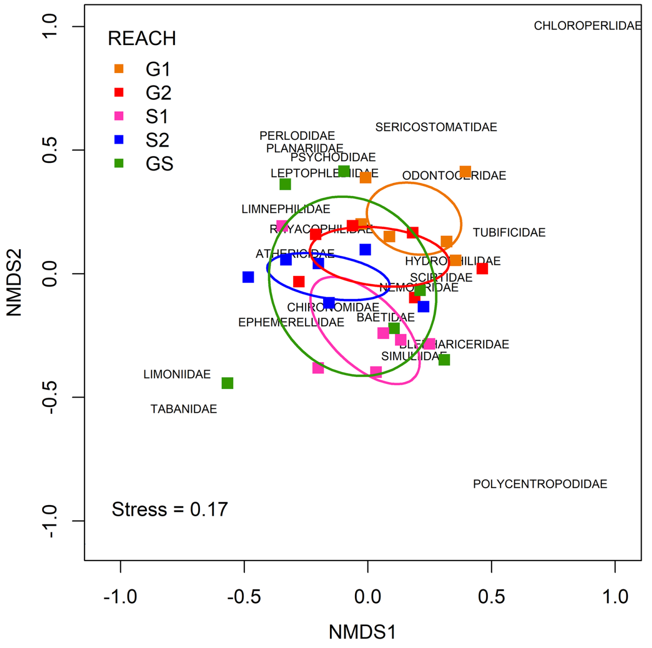

FIGURE 6 | Non-metric multidimensional scaling (nMDS) ordination plot for macroinvertebrate assemblages of the different reaches (6 samplings each reach). Shaded ellipses represent the 95% confidence interval surrounding the centroid of each reach in the ordination space. Each square represents the overall macroinvertebrate assemblage at each sampling. Macroinvertebrate families are indicated with uppercase labels, as weighted averages.

3.4 | Geomorphology and Bedload-Macroinvertebrate Relationships

Based on the Spearman rank correlations, several patterns emerged (Table 2). Total taxa richness, as well as the richness and abundance of limnephilic taxa, exhibits strong positive correlations with increasing substrate size, observed both in selected percentiles and mean substrate sizes. Conversely,

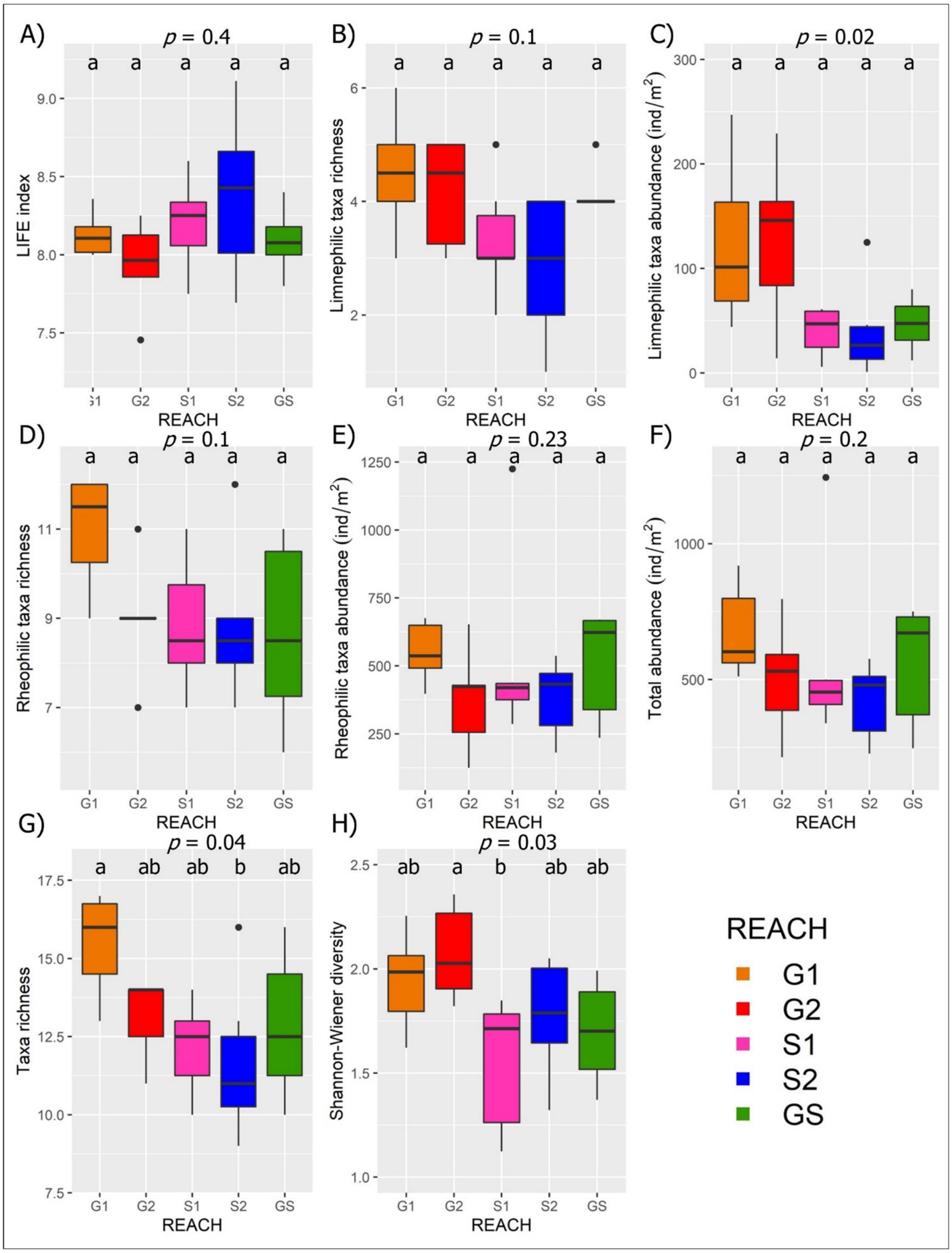

FIGURE 7 | Boxplots of (A) LIFE index, (B) limnephilic taxa richness, (C) rheophilic taxa richness, (D) limnephilic taxa abundances, (E) rheophilic taxa abundances, (F) macroinvertebrate total abundances, (G) taxa richness and (H) Shannon–Wiener diversity grouped by reach. The Bonferroni-corrected p-value of the Kruskal–Wallis test is reported above each plot and lowercase letters indicate which sites differed (Dunn's multiple comparison test, alpha = 0.05).

rheophilic taxa richness demonstrated a negative correlation with the estimated current bedload yield. Additionally, the temporal beta diversity of macroinvertebrate assemblages showed a negative correlation with the abundance of larger sediment size classes (D84 and D95) and a positive correlation with the estimated bedload yield. Weak or no correlations were found between any macroinvertebrate indices and sediment diversity (Shannon), sorting (σ), skewness (Sk) and kurtosis (K).

4 | Discussion

4.1 | A Gradient of Geomorphological Conditions

The survey of channel morphology, sediment grain size and lithological composition revealed diverse geomorphological conditions among the studied stream reaches, notably between the upper Goglio and Sanguigno streams. Both streams exhibit a decreasing sediment grain size from the upper to the lower reach,

TABLE 2 | Spearman coefficients and p-values of the correlations computed between morphological metrics (percentiles [D], mean, sorting, skewness, kurtosis and Shannon diversity and annual bedload yield) and macroinvertebrate community indices (LIFE, limnephilic taxa richness, rheophilic taxa richness, total taxa richness, limnephilic taxa abundance, rheophilic taxa abundance, total abundance, Shannon–Wiener and temporal beta diversity).

	D5 (mm)	D16 (mm)	D50 (mm)	D84 (mm)	D95 (mm)	Mean (mm)	Sorting (σ)	Skewness (Sk)	Kurtosis (K)	Diversity (Shannon)	Current bedload yield (t/km^2*year)
LIFE	$R=-0.60$ 0.28	$R=-0.60$ 0.28	$R=-0.70$ 0.19	$R=-0.50$ 0.39	$R=-0.50$ 0.39	$R=-0.70$ 0.19	$R<0.01$ 1	$R=0.20$ 0.75	$R=0.20$ 0.75	$R<0.01$ 1	$R=0.20$ 0.75
Limnephilic taxa richness	**$R=0.97$** **$p<0.01$**	**$R=0.97$** **$p<0.01$**	**$R=0.97$** **$p<0.01$**	$R=0.82$ 0.09	$R=0.82$ 0.09	**$R=0.97$** **$p<0.01$**	$R=-0.05$ 0.93	$R=-0.46$ 0.43	$R=0.46$ 0.43	$R=0.05$ 0.93	$R=-0.56$ 0.32
Rheophilic taxa richness	$R=0.36$ 0.55	$R=0.36$ 0.55	$R=0.67$ 0.22	$R=0.82$ 0.09	$R=0.82$ 0.09	$R=0.67$ 0.22	$R=0.46$ 0.43	$R=0.21$ 0.74	$R=-0.21$ 0.74	$R=-0.46$ 0.43	**$R=-0.97$** **$p<0.01$**
Total taxa richness	**$R=0.90$** **0.04**	**$R=0.90$** **0.04**	**$R=1$** **$p<0.01$**	**$R=0.90$** **0.04**	**$R=0.90$** **0.04**	**$R=1$** **$p<0.01$**	$R=0.10$ 0.87	$R=-0.30$ 0.62	$R=0.30$ 0.62	$R=-0.10$ 0.87	$R=-0.70$ 0.19
Limnephilic taxa abundance	$R=0.70$ 0.19	$R=0.70$ 0.19	**$R=0.90$** **0.04**	$R=0.80$ 0.10	$R=0.80$ 0.10	**$R=0.90$** **0.04**	$R=0.20$ 0.75	$R=-0.10$ 0.87	$R=0.10$ 0.87	$R=-0.20$ 0.75	$R=-0.60$ 0.28
Rheophilic taxa abundance	$R=0.50$ 0.39	$R=0.50$ 0.39	$R=0.30$ 0.62	$R=0.40$ 0.50	$R=0.40$ 0.50	$R=0.30$ 0.62	$R=0.10$ 0.87	$R=-0.20$ 0.75	$R=0.20$ 0.75	$R=-0.10$ 0.87	$R=-0.30$ 0.62
Total abundance	$R=0.70$ 0.19	$R=0.70$ 0.19	$R=0.60$ 0.28	$R=0.70$ 0.19	$R=0.70$ 0.19	$R=0.60$ 0.28	$R=0.30$ 0.62	$R=-0.10$ 0.87	$R=0.10$ 0.87	$R=0.30$ 0.62	$R=-0.50$ 0.39
Shannon–Wiener	$R=0.30$ 0.62	$R=0.30$ 0.62	$R=0.60$ 0.28	$R=0.50$ 0.39	$R=0.50$ 0.39	$R=0.60$ 0.28	$R<0.01$ 1	$R=-0.10$ 0.87	$R=0.10$ 0.87	$R<0.01$ 1	$R=-0.60$ 0.28
Temporal beta diversity	$R=-0.40$ 0.50	$R=-0.40$ 0.50	$R=-0.70$ 0.19	**$R=-0.90$** **0.04**	**$R=-0.90$** **0.04**	$R=-0.70$ 0.19	$R=-0.60$ 0.28	$R=-0.30$ 0.62	$R=0.30$ 0.62	$R=0.60$ 0.28	**$R=1$** **$p<0.01$**

whereas downstream of the confluence, the cumulative grain curve reflects the sediment contribution from both streams. Indeed, GS displays a more uniform sediment distribution as indicated by the lowest sorting and skewness coefficients and the highest kurtosis coefficient. Overall, the findings indicate a potentially greater carrying capacity in the upper Goglio compared with the Sanguigno, supported by several observations: (i) The upper Goglio exhibits a larger and more sculpted streambed, notably in G1, with a width of 37 m and a channel depth of 3.98 m; (ii) the sediment analysis reveals larger grain sizes (D5, D16, D50, D84 and D95) in G1 and G2 compared with S1 and S2; (iii) G2 displays poorer grain sorting ($\sigma = 1.039$) compared with S2 ($\sigma = 0.82$); (iv) moreover, the grain size distribution and lithological composition of GS strongly suggest a higher sediment supply originating from the Goglio rather than the Sanguigno. This is evident in the disparity between expected and observed percentages of grain sizes downstream of the confluence. Indeed, if Goglio and Sanguigno contributed equal amounts of bedload sediments, the percentage of grains lower than 22.6 mm (coming mostly from the Sanguigno) should be higher (~25%), and likewise, the percentage of grains larger than 22.6 mm (coming mostly from the Goglio) should be lower (~74%), but this is not the case (8% and 92%, respectively). Similarly, assuming an equal sediment supply, GS would display a higher percentage of sediments from the Verrucano Lombardo (30.5% instead of 5%) and a lower percentage of the others (62.5% of detritus belonging to the Formazione del Pizzo Diavolo compared with 69%, 3% of metamorphic rocks compared with 8% and 4.5% of volcanites compared with 18%). Such differences, indicating the contrasting hydrological and bedload regimes of the two headwater streams, seem to be related to the distinct physiographic conditions, as shown also in other contexts with contrasting geomorphological settings (Mao et al. 2009). Specifically, Sanguigno stream exhibits a gentler longitudinal profile when compared with the steeper gradient of Goglio stream. As shown by the longitudinal profile (Figure 2A), S1 lies within the mid-section of the valley on a glacier terrace with a 30% incline, dominated by step-pool unconfined reaches, interspersed with riffle-pool and cascade reaches. Subsequently, the following section displays a steep scarp (slope of 130%), primarily characterized by colluvial cascade reaches. In the first section, sediment supply seems constrained because of the unconnected gentle slides covered by meadows and trees, resulting in the formation of temporary sediment deposition bars. However, in the latter part, the channel morphology reflects high transport capacity but supply-limited conditions. Conversely, downstream of the reservoirs, the Goglio stream presents a very steep profile (slope of 250%), connected with lateral slopes and dominated by cascade reaches (G1). This section exhibits steep slides that convey a significant amount of sediments, including boulders. The morphological pattern then undergoes a sudden shift to a sinuous, unconnected channel with a lower gradient (slope of 50%); this part is marked by alternating steep pool and cascade reaches (G2) where an unregulated tributary flows into. As a result, finer sediment sizes prevail, leading to increased deposition bars within the bed morphology. Finally, downstream of the confluence, the Goglio stream exhibits a wider unconfined channel with a lower gradient (slope of 40%), predominantly characterized by riffle-pool reaches conducive to sediment deposition. Overall, the topographic and geological characteristics of the Valgoglio catchment contribute to the creation of a patchwork of geomorphological features within a limited area. This diversity likely fosters a wide array of biotic assemblages (Rice et al. 2001; Gething et al. 2020). Lastly, such heterogeneity, common in mountain catchments, reflects a multitude of processes related to erosion, deposition and transportation, which collectively shape the drainage network of the catchment (Wohl 2013).

4.2 | Sediment Conditions and Bedload Indicate Regulated Stream Channel Evolution

Experiments conducted using painted tracers revealed that in the upper Goglio, fewer stones moved compared with Sanguigno, indicating a lower bedload mobility, especially in G1. This contradicted the conclusion described in the previous paragraph. The experiments, despite their approximation, indicate the Sanguigno stream's higher susceptibility to bedload-mobilizing flow events, especially in S2, unlike the upper Goglio. Bedload mobilization in GS seems contingent on both upper streams' combined effect and consequently exhibits higher variation. These findings validate Hypothesis H1 and imply the reservoir altered Goglio's flow regime, reducing high flow event frequency and magnitude, thus decreasing hydrological variability. This change has reversed the sediment supply below the confluence, as supported also by bedload yield estimations computed in the current and past scenarios. Nevertheless, the grain size distribution of Goglio and the lithological composition in GS indicate that the streambed characteristics continue to mostly resemble conditions prior to reservoir construction, when powerful floods occurred, leading to the deposition of large cobbles onto the lateral bars. Yet, past the confluence, the hydrological and bedload patterns become more complex because of the interplay of reservoir dynamics and the Aviasco hydropower plant's influence on both Goglio and Sanguigno. Overall, the field survey and the bedload yield estimations provide complementary information, allowing for tracking Goglio stream's evolution over the past century, shaped by the construction of hydropower infrastructures.

4.3 | Macroinvertebrate Responses Reflect Hydro-Geomorphological Conditions

As hypothesized (H2), variations in the geomorphological and hydrological conditions among reaches have influenced the composition of macroinvertebrate assemblages, corroborating findings from prior studies (Katano et al. 2009; Guareschi et al. 2012; Theodoropoulos et al. 2017; Mathers et al. 2021). The NMDS plot illustrates distinct taxonomic compositions between macroinvertebrate communities in the upper Goglio and Sanguigno streams, consistent with pattern observed in studies comparing regulated and unregulated faunal assemblages (Poff and Zimmerman 2010; Mbaka and Mwaniki 2015; Krajenbrink et al. 2019). Additionally, NMDS shows a gradient of increasing similarity from upstream to downstream, aligning with the previously described variations in geomorphological features. Interestingly, the taxonomic composition of the GS macroinvertebrate assemblage exhibits a marked temporal variability, possibly linked to the highly fluctuating hydromorphic conditions. Notably, bedload yield negatively correlates with reophilic taxa richness and with the temporal beta diversity of communities, suggesting that increased transport rates and hydrological variability shape assemblage compositions, influencing certain taxa and amplifying temporal variations within the community (Gibbins et al. 2007, 2010). Consequently, the taxonomic composition of the macroinvertebrate assemblage in GS exhibits seasonal variations influenced by both the hydrological regime and incoming macroinvertebrate drift from upper reaches. These seasonal changes prompt GS's assemblage to more closely resemble either the composition found in the Sanguigno stream or those in the upper Goglio, depending on the specific season. The greater diversity, richness and abundance of macroinvertebrate families adapted to diverse water flow velocities observed in G1 and G2 reaches suggest highly suitable hydrological conditions (Petruzziello et al. 2021). The reservoirs, by attenuating high flow events downstream of the dam, result in reduced flow magnitude, lower hydrological variability and diminished bedload mobility (Anselmetti et al. 2007). These conditions foster the colonization of a broader range of taxa and impact macroinvertebrate functional traits, as evidenced in studies exploring macroinvertebrate responses to hydrological alterations (Monk et al. 2008; Dunbar et al. 2010; Theodoropoulos et al. 2017). In our case, the upper Goglio reaches display a higher abundance of limnephilic (Tabanidae, Tipulidae, Planaridae and Psychodidae) but also reophilic families (Chloroperlidae, Odontoceridae). The observed differences in macroinvertebrate taxonomic and flow response guilds composition across stream reaches align with the 'link discontinuity concept' (Rice et al. 2001). This theory proposes that at moderate spatial scales, variations in bed sediment due to tributary arrangements govern the longitudinal organization of faunal assemblages. Our findings support this idea, indicating that the presence of a tributary (in this case, Sanguigno) reversed habitat changes caused by the reservoir in the main stem (Goglio), a phenomenon also noted by Katano et al. (2009) in the Japanese Agi-gawa River. Additionally, our results are consistent with the serial discontinuity concept, highlighting differences in macroinvertebrate communities, both in taxonomy and flow response guilds, between unregulated and regulated streams (Stanford and Ward 1983).

5 | Final Remarks

Mountain streams undergo considerable fragmentation and hydrogeomorphological heterogeneity because of hydraulic infrastructure. Although the ecological impact of hydrological conditions and flow regulation has been extensively studied, a holistic assessment simultaneously evaluating both hydrogeomorphological conditions and biotic responses is lacking. Our study aimed to bridge this gap by providing insights into channel morphology, sediment grain size distribution, bedload rates and macroinvertebrate functional and taxonomic responses along a gradient of hydraulic features in mountain streams. The investigation reveals a patchwork of geomorphological conditions and bedload rates across the five examined stream reaches, particularly distinguishing the regulated and unregulated reaches and the reach below their confluence. Taxonomic and functional compositions of macroinvertebrate assemblages reflect these geomorphological variations, showing higher richness and abundance of both limnephilic and reophilic taxa in the regulated reaches and greater temporal diversity in community composition below the confluence, potentially influenced by high hydrogeomorphic fluctuations. Limitations arise because of unavailable flow data in the study area, hindering a detailed characterization of the hydrological regime. We partially addressed these limitations by characterizing sediment size distribution and conducting field experiments to assess bedload mobility as a proxy for high flow events and their impact on streambed sediments. However, the sediment size distribution primarily reflected the pre-dam conditions since only pebbles and cobbles have been considered, so caution should be considered in interpreting the results. Moreover, considering the site-specific influences of damming and tributaries on macroinvertebrate assemblages mediated by changes in hydrogeomorphic conditions, further research encompassing multiple reaches across a broader context is necessary to comprehend these distinct patterns. Yet, using a more detailed taxonomy, beyond the family level, may uncover clearer distinctions in both taxonomic and functional aspects. In conclusion, our study provides insights into geomorphological conditions and macroinvertebrate responses in streams with distinct hydrological conditions, indicating that an interdisciplinary approach deepens comprehension by providing complementary information. Further research investigating the interplay between hydrology, geomorphology, bedload rates and biotic responses is useful to better unveil mountain lotic systems.

Author Contributions

Conceptualisation, developing methods and conducting the field work: L.B., R.F., G.V. Data analysis: L.B., R.F. Writing of the manuscript and preparation of figures and tables: L.B. Manuscript editing: R.F., G.V. Founding: V.M.

Acknowledgements

We thank Antonio Petruzziello and Marco Mantovani for the assistance with macroinvertebrate sampling and Sandra Musitelli and Marta Freddi for helping us in the geomorphological survey, the grain size characterization and the lithological identification of the sediments. We are very grateful to Alberto Bonacina, Francesco Bonacina Andrea Alberti and Buck for their support in the bedload mobility experiments, and we sincerely thank Andrea Milani, Andrea Alberti, Daniele Bonacina and Anna Marinoni for their precious contribution to the creation of the video 'Water and Stones'. The clip, presenting the field activities conducted in the Valgoglio catchment, was created for the contest 'On the rocks' promoted by the Italian Geological Society and is available at https://www.youtube.com/watch?v=EgSMDRENU2E&t=12s

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Supporting information and raw data are included in the Appendix. The video 'Water and Stones' is available at https://www.youtube.com/watch?v=EgSMDRENU2E&t=12s.

References

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. "Multivariate Dispersion as a Measure of Beta Diversity." *Ecology Letters* 9: 683–693.

Anselmetti, F. S., R. Bühler, D. Finger, et al. 2007. "Effects of Alpine Hydropower Dams on Particle Transport and Lacustrine Sedimentation." *Aquatic Sciences* 69: 179–198.

Barbour, M. T., J. Gerritsen, S. D. Blaine, and J. B. Stribling. 1999. *Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates, and Fish*. Office of Water USEPA.

Baxter, T. M. 1977. "Environmental Effects of Dams and Impoundments." *Annual Review of Ecology and Systematics* 8: 255–283.

Bocchiola, D. 2014. "Long Term (1921-2011) Hydrological Regime of Alpine Catchments in Northern Italy." *Advances in Water Resources* 70: 51–64.

Buffington, J. M., and D. R. Montgomery. 1999. "A Procedure for Classifying Textural Facies in Gravel-Bed Rivers." *Water Resources Research* 35: 1903–1914.

Cañedo-Argüelles, M., C. Gutiérrez-Cánovas, R. Acosta, et al. 2020. "As Time Goes by: 20 Years of Changes in the Aquatic Macroinvertebrate Metacommunity of Mediterranean River Networks." *Journal of Biogeography* 47: 1861–1874.

Comiti, F. 2012. "How Natural Are Alpine Mountain Rivers? Evidence From the Italian Alps." *Earth Surface Processes and Landforms* 37: 693–707.

Dal Piaz, G. V., A. Bistacchi, and M. Massironi. 2003. "Geological Outline of the Alps." *Episodes* 26: 175–180.

de Jong, C. 2015. "Challenges for Mountain Hydrology in the Third Millennium." *Frontiers in Environmental Science* 3: 1–13.

de Vente, J., J. Poesen, P. Bazzoffi, A. V. Rompaey, and G. Verstraeten. 2006. "Predicting Catchment Sediment Yield in Mediterranean Environments: The Importance of Sediment Sources and Connectivity in Italian Drainage Basins." *Earth Surface Processes and Landforms* 31: 1017–1034.

Dewson, Z. S., A. B. W. James, and R. G. Death. 2007. "A Review of the Consequences of Decreased Flow for Instream Habitat and Macroinvertebrates." *Journal of the North American Benthological Society* 26: 401–415.

Dolédec, S., E. Castella, M. Forcellini, J. M. Olivier, A. Paillex, and P. Sagnes. 2015. "The Generality of Changes in the Trait Composition of Fish and Invertebrate Communities After Flow Restoration in a Large River (French Rhône)." *Freshwater Biology* 60: 1147–1161.

Dunbar, M. J., M. Warren, C. Extence, et al. 2010. "Interaction Between Macroinvertebrates, Discharge and Physical Habitat in Upland Rivers." *Aquatic Conservation: Marine and Freshwater Ecosystems* 20: 31–44.

Evette, A., L. Peyras, H. François, and S. Gaucherand. 2011. "Environmental Risks and Impacts of Mountain Reservoirs for Artificial Snow Production in a Context of Climate Change." *Journal of Alpine Research*.

Extence, C. A., D. M. Balbi, and R. P. Chadd. 1999. "River Flow Indexing Using British Benthic Macroinvertebrates: A Framework for Setting Hydroecological Objectives." *River Research and Applications* 15: 545–574.

Fochetti, R. 2012. "Italian Freshwater Biodiversity: Status, Threats and Hints for Its Conservation." *Italian Journal of Zoology* 79: 2–8.

Folk, R. L., and W. Ward. 1957. "Brazos River Bar: A Study in the Significance of Grain Size Parameters." *Journal of Sedimentary Petrology* 27: 3–26.

Gething, K. J., M. C. Ripley, K. L. Mathers, R. P. Chadd, and P. J. Wood. 2020. "The Influence of Substrate Type on Macroinvertebrate Assemblages Within Agricultural Drainage Ditches." *Hydrobiologia* 847: 4273–4284.

Gibbins, C., R. J. Batalla, and D. Vericat. 2010. "Invertebrate Drift and Benthic Exhaustion During Disturbance: Response of Mayflies (Ephemeroptera) to Increasing Shear Stress and River-Bed Instability." *River Research and Applications* 26: 499–511.

Gibbins, C., D. Vericat, and R. J. Batalla. 2007. "When Is Stream Invertebrate Drift Catastrophic? The Role of Hydraulics and Sediment Transport in Initiating Drift During Flood Events." *Freshwater Biology* 52: 2369–2384.

Goldman, C. R. 1976. "Ecological Aspects of Water Impoundment in the Tropics." *Revista de Biologia Tropical* 24: 87–112.

Graf, W. L. 2006. "Downstream Hydrologic and Geomorphic Effects of Large Dams on American Rivers." *Geomorphology* 79: 336–360.

Guareschi, S., C. Gutiérrez-Cánovas, F. Picazo, et al. 2012. "Aquatic Macroinvertebrate Biodiversity: Patterns and Surrogates in Mountainous Spanish National Parks." *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 598–615.

Hassan, M. A., and P. Ergenzinger. 2005. "Use of Tracers in Fluvial Geomorphology." In *Tools in Fluvial Geomorphology*, edited by M. Kondolf and H. Piégay, 397–423. Wiley.

Hauer, F. R., and G. A. Lamberti. 2017. In *Methods in Stream Ecology*, edited by F. R. Hauer and G. A. Lamberti, Third ed. Elsevier.

Hediger, W. 2021. Hydropower—A Key to Regional Development in the Swiss Alps. Pages 1–24 European Regional Science Association ERSA. Bozen.

Hering, D., P. F. Verdonschot, O. Moog, and L. Sandin, eds. 2012. *Integrated Assessment of Running Waters in Europe*, Vol. 175. Springer Science & Business Media.

Hinderer, M., M. Kastowski, A. Kamelger, C. Bartolini, and F. Schlunegger. 2013. "River Loads and Modern Denudation of the Alps—A Review." *Earth-Science Reviews* 118: 11–44.

Holt, E. A., and S. W. Miller. 2011. "Bioindicators: Using Organisms to Measure." *Nature* 3: 8–13.

ISPRA. 2019. Elaborazione ISPRA su dati del MIT-DG per le Dighe e l'Infrastrutture idriche ed elettriche e della PCM- Dipartimento di Protezione Civile. (https://indicatoriambientali.isprambiente.it/sys_ind/81)

Jordan, S., J. J. Giersch, C. C. Muhlfeld, et al. 2016. "Loss of Genetic Diversity and Increased Subdivision in an Endemic Alpine Stonefly Threatened by Climate Change." *PLoS One* 11: 1–13.

Katano, I., J. N. Negishi, T. Minagawa, H. Doi, Y. Kawaeuchi, and Y. Kavaba. 2009. "Longitudinal Macroinvertebrate Organization Over Contrasting Discontinuities: Effects of a Dam and a Tributary." *Journal of the North American Benthological Society* 28: 331–351.

Klaar, M. J., M. J. Dunbar, M. Warren, and R. Soley. 2014. "Developing Hydroecological Models to Inform Environmental Flow Standards: A Case Study From England." *Wiley Interdisciplinary Reviews: Water* 1: 207–217.

Krajenbrink, H. J., M. Acreman, M. J. Dunbar, D. M. Hannah, C. L. R. Laizé, and P. J. Wood. 2019. "Macroinvertebrate Community Responses to River Impoundment at Multiple Spatial Scales." *Science of the Total Environment* 650: 2648–2656.

Krumbein, W. C. 1934. "Size Frequency Distributions of Sediments." *Journal of Sedimentary Petrology* 4: 65–77.

Larsen, I. J., and D. R. Montgomery. 2012. "Landslide Erosion Coupled to Tectonics and River Incision." *Nature Geoscience* 5: 468–473.

Mao, L., M. Cavalli, F. Comiti, L. Marchi, M. A. Lenzi, and M. Arattano. 2009. "Sediment Transfer Processes in Two Alpine Catchments of Contrasting Morphological Settings." *Journal of Hydrology* 364: 88–98.

Mathers, K. L., C. Kowarik, C. Rachelly, C. T. Robinson, and C. Weber. 2021. "The Effects of Sediment Traps on Instream Habitat and Macroinvertebrates of Mountain Streams." *Journal of Environmental Management* 295: 113066.

Mbaka, J. G., and M. W. Mwaniki. 2015. "A Global Review of the Downstream Effects of Small Impoundments on Stream Habitat Conditions and Macroinvertebrates." *Environmental Reviews* 23: 257–262.

Milliman, J. D., and J. P. M. Syvitski. 1992. "Geomorphic Tectonic Control of Sediment Discharge to the Ocean: The Importance of Small Mountainous Rivers." *Journal of Geology* 100: 525–544.

Monk, W. A., P. J. Wood, D. M. Hannan, and D. A. Wilson. 2008. "Macroinvertebrate Community Response to Inter-Annual and Regional River Flow Regime Dynamics." *River Research and Applications* 24: 988–1001.

Montgomery, D. R., and J. M. Buffington. 1997. "Channel-Reach Morphology in Mountain Drainage Basins." *Bulletin of the Geological Society of America* 109: 596–611.

Muhlfeld, C. C., J. J. Giersch, F. R. Hauer, et al. 2011. "Climate Change Links Fate of Glaciers and an Endemic Alpine Invertebrate." *Climatic Change* 106: 337–345.

Oksanen J. 2022. Package 'vegan'.

Permanent Secretariat of the Alpine Convention 2009. Water and Water Management Issues. Report on the State of the Alps.

Petruzziello, A., L. Bonacina, F. Marazzi, S. Zaupa, V. Mezzanotte, and R. Fornaroli. 2021. "Effects of High-Altitude Reservoirs on the Structure and Function of Lotic Ecosystems: A Case Study in Italy." *Hydrobiologia* 848: 1455–1474.

Petts, G. E., and A. M. Gurnell. 2005. "Dams and Geomorphology: Research Progress and Future Directions." *Geomorphology* 71: 27–47.

Poff, N. L., and J. K. H. Zimmerman. 2010. "Ecological Responses to Altered Flow Regimes: A Literature Review to Inform the Science and Management of Environmental Flows." *Freshwater Biology* 55: 194–205.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. "Tributaries, Sediment Sources, and the Longitudinal Organisation of Macroinvertebrate Fauna Along River Systems." *Canadian Journal of Fisheries and Aquatic Sciences* 58: 824–840.

Sadaoui, M., W. Ludwig, F. Bourrin, and E. Romero. 2018. "The Impact of Reservoir Construction on Riverine Sediment and Carbon Fluxes to the Mediterranean Sea." *Progress in Oceanography* 163: 94–111.

Schlunegger, F., and M. Hinderer. 2003. "Pleistocene/Holocene Climate Change, Re-Establishment of Fluvial Drainage Network and Increase in Relief in the Swiss Alps." *Terra Nova* 15: 88–95.

Stanford, J. W. J., and J. V. Ward. 1983. *The Serial Discontinuity Concept of Lotic Ecosystems*. Ann Arbor Science Publishers.

Statzner, B., and L. A. Bêche. 2010. "Can Biological Invertebrate Traits Resolve Effects of Multiple Stressors on Running Water Ecosystems?" *Freshwater Biology* 55: 80–119.

Stier, A. C., S. W. Geange, K. M. Hanson, and B. M. Bolker. 2013. "Predator Density and Timing of Arrival Affect Reef Fish Community Assembly." *Ecology* 94: 1057–1068.

Syvitski, J. P. M., and A. J. Kettner. 2007. "On the Flux of Water and Sediment Into the Northern Adriatic Sea." *Continental Shelf Research* 27: 296–308.

Syvitski, J. P. M., C. J. Vörösmarty, A. J. Kettner, and P. Green. 2005. "Impact of Humans on the Flux of Terrestrial Sediment to the Global Coastal Ocean." *Science* 308: 376–380.

Tadini, G. A. 1815. Appunti di campo. Biblioteca Civica Angelo Mai, Bergamo.

Theodoropoulos, C., A. Vourka, A. Stamou, P. Rutschmann, and N. Skoulikidis. 2017. "Response of Freshwater Macroinvertebrates to Rainfall-Induced High Flows: A Hydroecological Approach." *Ecological Indicators* 73: 432–442.

Townsend, C. R., M. R. Scarsbrook, S. Doledec, and S. Dolédec. 1997. "Quantifying Disturbance in Streams: Alternative Measures of Disturbance in Relation to Macroinvertebrate Species Traits and Species Richness." *Journal of the North American Benthological Society* 16: 531–544.

Trottier, G., K. Turgeon, D. Boisclair, C. Bulle, and M. Margni. 2022. "The Impacts of Hydropower on Freshwater Macroinvertebrate Richness: A Global Meta-Analysis." *PLoS One* 17: 1–18.

Tupinambás, T. H., R. M. V. Cortes, S. G. Varandas, S. J. Hughes, J. S. França, and M. Callisto. 2014. "Taxonomy, Metrics or Traits? Assessing Macroinvertebrate Community Responses to Daily Flow Peaking in a Highly Regulated Brazilian River System." *Ecohydrology* 7: 828–842.

Van Looy, K., J. D. Tonkin, M. Floury, et al. 2019. "The Three Rs of River Ecosystem Resilience: Resources, Recruitment, and Refugia." *River Research and Applications* 35: 107–120.

Wang, J., L. Ding, J. Tao, C. Ding, and D. He. 2019. "The Effects of Dams on Macroinvertebrates: Global Trends and Insights." *River Research and Applications* 35: 702–713.

White, J. C., R. Fornaroli, M. J. Hill, et al. 2021. "Long-Term River Invertebrate Community Responses to Groundwater and Surface Water Management Operations." *Water Research* 189: 116651.

White, J. C., D. M. Hannah, A. House, S. J. V. Beatson, A. Martin, and P. J. Wood. 2016. "Macroinvertebrate Responses to Flow and Stream Temperature Variability Across Regulated and Non-Regulated Rivers." *Ecohydrology* 10: 1–21.

Wohl, E. 2013. *Mountain Rivers Revisited*. John Wiley & Sons.

Wolman, M. G. 1954. "A Method of Sampling Coarse River-Bed Material." *American Geophysical Union. Fall Meeting* 35: 951–956.

Worrall, T. P., M. J. Dunbar, C. A. Extence, C. L. R. Laizé, W. A. Monk, and P. J. Wood. 2014. "The Identification of Hydrological Indices for the Characterization of Macroinvertebrate Community Response to Flow Regime Variability." *Hydrological Sciences Journal* 59: 645–658.

Zolezzi, G., A. Bellin, M. C. Bruno, B. Maiolini, and A. Siviglia. 2009. "Assessing Hydrological Alterations at Multiple Temporal Scales: Adige River, Italy." *Water Resources Research* 45: 1–15.

Appendix

TABLE A1 | List of taxa with the associated LIFE score identifying rheofilic ($v > 0.2\,\mathrm{m/s}$) and limnephilic ($v \leq 0.2\,\mathrm{m/s}$) organisms.

Taxa	LIFE score	Flow response guild
Chloroperlidae	I	Rheophilic
Heptageniidae	I	
Odontoceridae	I	
Perlidae	I	
Perlodidae	I	
Philopotamidae	I	
Rhyacophilidae	I	
Baetidae	II	
Elmidae	II	
Ephemerellidae	II	
Hydropsychidae	II	
Leptophlebiidae	II	
Leuctridae	II	
Sericostomatidae	II	
Simuliidae	II	
Taeniopterygidae	II	
Dytiscidae	IV	Limnephilic
Hydraenidae	IV	
Hydrophilidae	IV	
Limnephilidae	IV	
Nemouridae	IV	
Planariidae	IV	
Planorbidae	IV	
Polycentropodidae	IV	
Scirtidae	IV	
Tipulidae	IV	

TABLE A2 | Pairwise PERMANOVA—Set of confidence intervals on the differences between the mean distance to centroid of the reaches with the specified family-wise probability of coverage. The intervals are based on the Studentized range statistic.

Comparison	R^2	F	p_{adj}
G1-S1	0.233	3.040	0.003
G1-S2	0.216	2.747	0.002
S2-S1	0.139	1.617	0.117
G2-G1	0.144	1.688	0.070
G2-S1	0.163	1.945	0.015
G2-S2	0.153	1.802	0.092
GS-S1	0.088	0.968	0.446
GS-S2	0.097	1.075	0.391
GS-G1	0.121	1.383	0.178
GS-G2	0.121	1.380	0.202

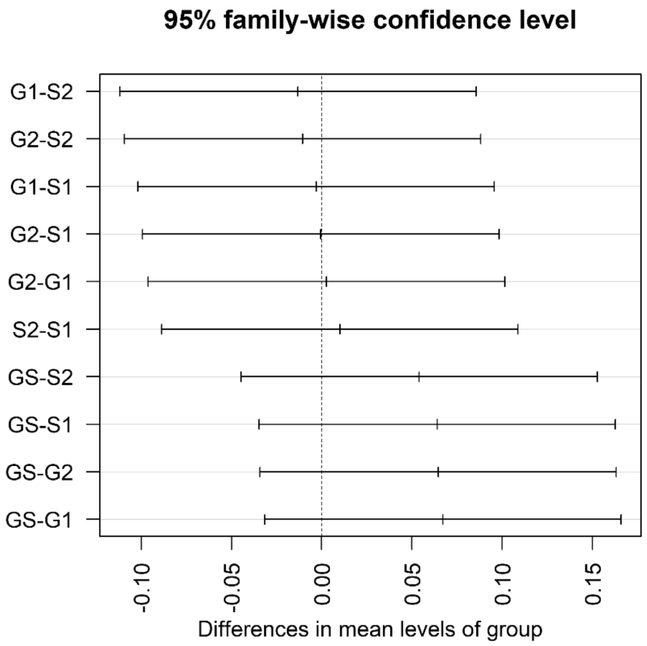

FIGURE A1 | PERMDISP—Set of confidence intervals on the differences between the mean distance to centroid of the reaches with the specified family-wise probability of coverage. The intervals are based on the Studentized range statistic.

TABLE A3 | PERMDISP—Set of confidence intervals on the differences between the mean distance to centroid of the reaches with the specified family-wise probability of coverage. The intervals are based on the Studentized range statistic.

Comparison	Difference	Lwr	Upr	p_{adj}
G1-S1	−0.00312	−0.10184	0.095597	0.999982
G1-S2	−0.01319	−0.11191	0.085526	0.994657
S2-S1	0.010071	−0.08865	0.108787	0.998121
G2-G1	0.002614	−0.0961	0.10133	0.999991
G2-S1	−0.00051	−0.09922	0.098211	1
G2-S2	−0.01058	−0.10929	0.08814	0.997726
GS-S1	0.064005	−0.03471	0.162721	0.341125
GS-S2	0.053934	−0.04478	0.15265	0.508325
GS-G1	0.067124	−0.03159	0.16584	0.29638
GS-G2	0.06451	−0.03421	0.163226	0.333616

TABLE A4 | Relative abundance (%) of grains collected in the littoral bars of the stream reaches according to B-axis size classes.

	Relative abundance (%)					
B-axis	**S1**	**S2**	**G1**	**G2**	**GS**	**Size (mm)**
2	0	0	0	0	0	(0,2]
8	8.7	11.3	0	2	0	(2,8]
11.3	7.6	13.4	4.2	7	1	(8,11.3
16	12	9.3	5.8	9	7	(11.3,16]
22.6	17.4	23.7	9.2	11	25	(16,22.6]
32	10.9	23.7	16.7	13	22	(22.6,32]
45	16.3	13.4	20	18	25	(32,45]
64	13	5.2	21.7	23	13	(45,64]
90	7.6	0	10	6	2	(64,90]
128	6.5	0	8.3	7	3	(90,128]
180	0	0	4.2	4	2	(128,180]
256	0	0	0	0	0	(180,256]

TABLE A5 | Abundance (ind/m^2) of macroinvertebrate taxa collected in the five stream reaches during summer and autumn of 2017 and 2018.

Sampler	Reach	Date	Chloroperlidae	Leuctridae	Perlidae	Perlodidae	Nemouridae	Taeniopterygidae	Baetidae	Heptageniidae	Ephemerellidae	Leptophlebiidae	Hydropsychidae	Limnephilidae
Luca	G1	26/07/2018	0	0	6	50	80	0	137	243	0	0	170	1
Luca	G1	10/10/2018	0	12	1	0	63	0	140	121	1	12	67	0
Antonio	G1	14/07/2017	0	1	4	0	76	0	229	128	0	0	100	0
Antonio	G1	23/08/2017	0	25	1	0	44	0	74	147	12	0	73	0
Antonio	G1	13/09/2017	24	3	3	3	14	0	235	167	0	2	22	0
Antonio	G1	19/10/2017	0	41	6	6	86	0	240	172	0	24	109	36
Luca	G2	26/07/2018	0	65	17	24	80	0	254	123	24	0	1	1
Luca	G2	10/10/2018	0	13	1	0	66	0	134	41	0	0	60	15
Antonio	G2	13/07/2017	0	14	5	0	47	0	207	56	0	0	44	0
Antonio	G2	22/08/2017	0	3	4	0	124	0	24	22	0	0	15	0
Antonio	G2	13/09/2017	0	8	3	1	7	0	75	34	1	1	7	0
Antonio	G2	19/10/2017	0	13	1	0	66	0	134	41	0	0	60	15
Luca	GS	26/07/2018	0	61	0	0	29	0	88	63	16	0	0	1
Luca	GS	10/10/2018	0	62	3	36	1	0	20	217	0	12	235	24
Antonio	GS	13/07/2017	0	94	0	0	0	0	264	205	0	0	5	0
Antonio	GS	22/08/2017	0	18	0	0	36	0	108	194	0	0	7	0
Antonio	GS	13/09/2017	0	6	2	0	8	0	125	41	0	0	16	0
Antonio	GS	19/10/2017	0	62	3	36	1	0	20	217	0	12	235	24
Antonio	S1	13/07/2017	0	33	26	0	2	0	163	91	0	0	3	1
Antonio	S1	22/08/2017	0	2	1	0	45	0	120	108	13	0	5	0
Antonio	S1	14/09/2017	0	3	1	0	2	0	212	170	1	0	14	0
Antonio	S1	19/10/2017	0	7	41	2	15	0	482	636	0	3	39	1
Luca	S1	26/07/2018	0	115	4	0	12	0	139	111	0	0	15	0
Luca	S1	10/10/2018	0	13	4	0	0	0	61	146	0	0	138	37
Antonio	S2	13/07/2017	0	7	1	0	1	0	79	128	0	0	1	8
Antonio	S2	22/08/2017	0	33	9	0	94	0	95	182	12	0	11	0
Antonio	S2	13/09/2017	0	4	0	0	21	0	65	48	0	1	31	12
Antonio	S2	19/10/2017	0	40	2	0	1	0	62	109	24	0	196	0
Luca	S2	26/07/2018	0	66	1	12	13	0	139	159	15	13	39	13
Luca	S2	10/10/2018	0	40	2	0	1	0	62	109	24	0	196	0

(Continues)

TABLE A5 | (Continued)

Sampler	Reach	Date	Odontoceridae	Philopotamidae	Polycentropodidae	Rhyacophilidae	Sericostomatidae	Dytiscidae	Elmidae	Scirtidae	Hydraenidae	Hydrophilidae	Athericidae	Blephariceridae
Luca	G1	26/07/2018	0	14	0	26	14	0	15	13	2	12	49	0
Luca	G1	10/10/2018	1	2	0	2	0	0	26	15	6	0	26	0
Antonio	G1	14/07/2017	0	1	0	6	3	0	19	6	4	3	0	84
Antonio	G1	23/08/2017	1	6	0	3	3	0	148	3	0	15	0	36
Antonio	G1	13/09/2017	0	1	0	9	8	0	104	10	2	18	0	0
Antonio	G1	19/10/2017	0	4	0	55	1	0	12	39	51	35	0	145
Luca	G2	26/07/2018	0	0	0	28	0	0	117	12	26	0	79	12
Luca	G2	10/10/2018	0	64	0	64	0	0	26	12	40	0	16	0
Antonio	G2	13/07/2017	0	4	0	1	0	0	52	1	0	16	59	12
Antonio	G2	22/08/2017	0	0	0	6	0	0	51	26	36	43	0	12
Antonio	G2	13/09/2017	0	0	0	22	0	0	46	0	2	5	1	0
Antonio	G2	19/10/2017	0	64	0	64	0	0	26	12	40	16	0	38
Luca	GS	26/07/2018	0	13	0	13	0	1	1	0	1	0	1	13
Luca	GS	10/10/2018	0	14	0	50	5	0	16	1	37	0	17	0
Antonio	GS	13/07/2017	0	1	1	1	1	0	19	26	1	3	3	37
Antonio	GS	22/08/2017	0	0	0	5	0	0	0	13	12	3	5	1
Antonio	GS	13/09/2017	0	1	0	3	0	0	15	1	2	1	0	12
Antonio	GS	19/10/2017	0	14	0	50	5	0	16	1	37	17	0	3
Antonio	S1	13/07/2017	0	0	0	0	0	0	34	13	19	6	2	15
Antonio	S1	22/08/2017	0	6	0	0	0	0	5	1	6	1	0	24
Antonio	S1	14/09/2017	0	2	0	3	0	0	8	0	2	2	0	39
Antonio	S1	19/10/2017	0	2	0	2	0	0	10	0	3	0	0	48
Luca	S1	26/07/2018	0	0	0	2	0	0	2	1	48	0	0	0
Luca	S1	10/10/2018	0	1	0	38	0	0	38	0	24	0	25	0
Antonio	S2	13/07/2017	0	0	0	2	0	0	25	0	2	2	5	0
Antonio	S2	22/08/2017	0	33	0	1	0	0	18	0	0	31	0	12
Antonio	S2	13/09/2017	0	3	0	7	0	0	17	0	12	1	2	2
Antonio	S2	19/10/2017	0	0	0	26	0	0	13	0	0	13	10	0
Luca	S2	26/07/2018	0	12	0	2	0	0	78	12	1	0	25	0
Luca	S2	10/10/2018	0	0	0	26	0	0	13	0	0	0	13	0

(Continues)

TABLE A5 | (Continued)

Sampler	Reach	Date	Chironomidae	Limoniidae	Simuliidae	Tabanidae	Tipulidae	Planariidae	Psychodidae	Lumbriculidae	Lumbricidae	Tubificidae	Ancylidae
Luca	G1	26/07/2018	77	0	1	1	0	72	0	0	2	0	0
Luca	G1	10/10/2018	13	0	12	0	2	28	0	3	1	0	0
Antonio	G1	14/07/2017	0	0	0	0	0	0	0	0	1	2	0
Antonio	G1	23/08/2017	0	0	0	1	0	0	0	0	1	1	0
Antonio	G1	13/09/2017	1	0	0	0	0	0	0	87	26	11	0
Antonio	G1	19/10/2017	13	1	2	0	0	0	0	0	37	0	0
Luca	G2	26/07/2018	5	14	0	0	0	24	0	25	3	0	0
Luca	G2	10/10/2018	38	13	25	0	0	36	0	127	0	0	0
Antonio	G2	13/07/2017	1	0	37	0	0	0	0	0	0	0	0
Antonio	G2	22/08/2017	2	0	0	0	0	0	0	0	3	0	0
Antonio	G2	13/09/2017	5	0	2	0	0	0	1	1	1	0	0
Antonio	G2	19/10/2017	13	0	25	0	0	0	0	36	127	0	0
Luca	GS	26/07/2018	12	38	0	12	0	0	0	0	0	0	0
Luca	GS	10/10/2018	0	2	0	0	0	0	0	0	0	0	0
Antonio	GS	13/07/2017	31	0	0	0	0	0	0	0	15	0	0
Antonio	GS	22/08/2017	22	0	325	0	0	0	0	0	0	0	0
Antonio	GS	13/09/2017	2	0	26	0	0	0	0	0	13	1	0
Antonio	GS	19/10/2017	2	0	0	0	0	0	0	0	0	0	0
Antonio	S1	13/07/2017	3	0	12	0	0	0	0	0	0	0	0
Antonio	S1	22/08/2017	1	0	26	0	0	0	0	0	0	0	0
Antonio	S1	14/09/2017	17	0	2	0	0	0	0	0	0	0	0
Antonio	S1	19/10/2017	3	0	1	0	0	0	0	0	0	0	0
Luca	S1	26/07/2018	87	26	36	0	0	0	0	0	0	0	0
Luca	S1	10/10/2018	75	0	0	0	0	0	0	0	0	0	0
Antonio	S2	13/07/2017	1	0	0	0	0	0	0	0	0	0	0
Antonio	S2	22/08/2017	4	0	0	0	0	0	0	0	0	12	0
Antonio	S2	13/09/2017	3	0	5	0	0	0	0	0	0	1	0
Antonio	S2	19/10/2017	2	0	0	0	0	0	0	0	2	0	0
Luca	S2	26/07/2018	116	16	1	0	0	0	0	2	0	0	0
Luca	S2	10/10/2018	0	2	0	0	0	0	0	2	0	0	0

(Continues)