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Leakage from Traditional Irrigation Systems and Groundwater Upwelling Buffer the Impact of Heavy Streamflow Diversion on Benthic Biodiversity

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Abstract
Headwater streams are biodiversity-rich yet highly vulnerable ecosystems, especially in Mediterranean mountain regions where hydrological regimes are increasingly altered by irrigation and climate change. We assessed the effects of flow reduction by traditional irrigation weirs on benthic macroinvertebrate communities in five headwaters within the National–Natural Park of Sierra Nevada. We sampled upstream (reference) and downstream (flow-impacted) sites of the weirs in spring and autumn. We also quantified stream physicochemical characteristics and macroinvertebrates, and evaluated changes in their community structure. Flow reduction downstream of the abstraction points was severe (76–98% of discharge in upstream reaches), yet downstream reaches remained without significant water chemical alteration, and flow — although minimal — was perennial through the year due to seepage from ditches and upwelling groundwater. Macroinvertebrate density was substantially reduced downstream, particularly in spring (≈50% lower). While local (α) and interlocal (β) diversities and community composition did not differ significantly between reach types, flow reduction consistently impaired regional (γ) diversity. Moreover, taxa richness of collectors and several biotic indices — based on Ephemeroptera, Plecoptera, and Trichoptera — significantly decreased in flow-impacted sites. These findings support incorporating EPT-based metrics to enhance the sensitivity of ecological quality assessments in mountain rivers. Overall, maintaining hydrological connectivity through leaky traditional irrigation systems appears pivotal for mitigating further losses of local biodiversity, particularly in impacted reaches that lack groundwater inflow. Furthermore, since even moderate local diversity losses can accumulate to reduce regional diversity, preserving as many stream reaches as possible with natural, or modified flow compatible with biodiversity conservation, is mandatory, particularly in biodiversity hotspots.

Keywords Biotic indices · Ecological quality · Macroinvertebrates · Mountain streams · Water abstraction · Hydrological connectivity · Irrigation ditches

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1 Introduction

Freshwater ecosystems are among the most biodiverse habitats on Earth (Dudgeon 2019) and the most threatened ecosystems globally (Albert et al. 2021). Despite their small size, headwater streams remain a primary conservation concern within freshwater networks due to their disproportionate influence on maintaining biodiversity (Finn et al. 2011), ecosystem functioning, and ecological connectivity (Angeler et al. 2023; Lowe and Likens 2005) at the river network scale.

Hydrological alterations are the most common impacts in mountain headwaters (Wohl 2006). In Mediterranean mountains, flow regimes are extensively modified by irrigated agriculture and climate change (Carlson et al. 2024). This situation is remarkably persistent in semiarid mountains, such as Sierra Nevada (SE Spain), where ancient irrigation systems have been integrated into natural hydrological networks for centuries, forming socio-ecological systems in which natural processes and human practices have co-shaped hydrological regimes (Civantos et al. 2023). These ditches, locally called *acequias de careo*, were conceived to divert streamwater during snowmelt, to convey water to irrigated areas, and to regulate basin resources by recharging slope aquifers (Martos-Rosillo et al. 2019). These traditional ditches are intended to coexist with biodiversity conservation, being even framed as nature-based solutions (Jódar et al. 2022). However, the effects of water diversion on riverine biodiversity of these ancient irrigated landscapes — often typified as biodiversity hotspots (Arroyo et al. 2022) — remain critically understudied. Investigating this is imperative to reconcile flow diversion with biodiversity conservation under a changing climate (Martín-Ortega et al. 2011).

Benthic macroinvertebrates, considered key indicators of freshwater ecosystem health (Carter et al. 2017), can be highly sensitive to anthropogenic reductions in flow (Palmer and Ruhi 2019). Flow reduction alters the physical habitat and tends to reduce its heterogeneity (Dewson et al. 2007a). Furthermore, altered flows may exacerbate additional stressors—such as thermal extremes, low dissolved oxygen, nutrient enrichment, or contaminant accumulation—thereby creating compounding effects on aquatic communities (Sabater et al. 2018). These processes can promote taxonomic and functional homogenisation of communities (Liu et al. 2022), thereby reducing β-and γ-diversity.

The impacts of flow alteration on macroinvertebrates remains empirically inconsistent. While the Poff and Zimmerman (2010) review reported declines in abundance and diversity under both reduced and elevated flows, the meta-analysis by Sabater et al. (2018) found overall adverse effects. Such inconsistency likely arises from pooling highly heterogeneous flow-modifying structures: large dams induce complex hydrological and physicochemical changes (Sabater et al. 2018), whereas small impoundments generally exert minimal effects on most stream-water physicochemical variables (Mbaka and Wanjiru Mwaniki 2015). Experimental field studies have reported contrasting responses. While the only microcosm channel experiment reported clear linear declines in both local species richness and density, along with major changes in community composition (Aspin et al. 2019), other studies applying fixed flow reductions (ranging from 50% to >85%) reported weak or context-dependent responses (Dewson et al. 2007a; González and Elosegi 2021; Rhoades et al. 2025; Vallefuoco et al. 2022). Detected effects typically involved declines in sensitive

taxa—i.e. predators (Cowell et al. 2025), scrapers (McKay and King 2006), and shredders (Mollá et al. 2017)—with abrupt trophic shifts triggered by riffle dewatering (Aspin et al. 2019), and diet homogenization which reduced functional dispersion (González and Elosegi 2021; but see Vallefuoco et al. 2022).

Despite this growing body of knowledge, the consequences of flow reduction on community taxonomic homogenization across spatial scales —and their associated impacts on β- and γ-diversity—remain poorly understood (Rolls et al. 2018).

Here, we examine the effects of flow diversion by *careo*-irrigation ditches on benthic macroinvertebrate communities from headwaters of the National-Natural Park of Sierra Nevada (Spain). We compared upstream-reference (above the diversion) and downstream-impacted (below the diversion) communities in five headwaters affected by these ditches, using samples collected in two seasons: during spring thaw and in autumn after a prolonged dry period. The following hypotheses are proposed: H1. Flow reduction by ditches will lead to decreased density (H1a) and α-diversity (H1b) of macroinvertebrate communities, particularly when high-magnitude diversions occur and when interacting with other stressors; H2. Flow reduction, if substantial, will lead to the loss—or greater declines in abundance—of the most sensitive species (e.g., predatory and shredding taxa); H3. Downstream-impacted sites will exhibit a more homogeneous community composition, resulting in lower β- and γ-diversity— relative to upstream-reference sites, due to the exclusion of sensitive taxa and the dominance of stress-tolerant ones.

Understanding these dynamics is essential for guiding sustainable water management in climate-vulnerable regions of high conservation value.

2 Materials and Methods

2.1 Study Area and Experimental Design

We studied five headwater streams (first to second order) located in the southern face of the Sierra Nevada Natural and National Park (Alpujarra region, southeastern Spain) (Figure S1), a critical biodiversity hotspot in the Mediterranean region (Arroyo et al. 2022), designated as a Biosphere Reserve (1986). The climate is Mediterranean high-mountain, characterized by cold-wet winters and hot-dry summers, with pronounced climate change effects (Pardo-Igúzquiza et al. 2024). In each of the five selected streams, a ditch diverted water by means of small, rudimentary weirs made of loose rocks and gravel gathered from the river itself. Diversion sites were located at altitudes of 1800–2000 m a.s.l., ca. on the boundary between the National and the Natural Parks. The National Park occupies the highest elevations, allowing low-density livestock grazing despite its stringent Spanish legal protection. In contrast, the Natural Park, at lower altitudes, is subject to less restrictive regulations (low-intensity agriculture and pastoralism are permitted) contingent upon alignment with conservation objectives. Therefore, water diversion is the primary impact at this altitude, while catchment land-use impacts are negligible.

The system of *careo*-irrigation ditches in this region has been documented since the Early Middle Ages (8th–10th centuries) (Martos-Rosillo et al. 2019). Its primary function

is to collect snowmelt and rainfall-derived runoff in headwater reaches—particularly during spring— and distribute it throughout the upper parts of the slopes to artificially recharge aquifers in weathered fractured hard rocks. This extends the availability of water resources in the lowlands of the river basin during the dry season, when water demand for agricultural and urban uses is higher (Zakaluk et al. 2024). Since the beginning of the 21st century, particularly in several valleys of the Alpujarra region (i.e., Bérchules and Mecina, Table 1), agricultural intensification—mainly tomato crops grown under plastic mesh—has spread within the Natural Park at nearly 1900 m a.s.l. This shift has exponentially increased irrigation water requirements, prompting structural and operational changes in the original *careo*-irrigation ditches (Jódar et al. 2022).

In each selected stream (Figure S1), we studied two reaches: upstream (reference) and downstream (impacted) of the water diversion point. Both reaches were relatively close to each other (Table 1) to avoid tributary water contributions between the sites. Our objective was to keep similar conditions between paired sites within each stream, except for discharge magnitude and dynamics. However, characteristics such as bankfull channel morphometry and bed substrate composition (mostly narrow bankfull channel and gravel–cobble–boulder dominated) slightly changed between upstream and downstream reaches in Bérchules and Nechite (wider bankfull channel with scattered alluvial deposits downstream). Moreover, accessibility constraints determined the distance between each reach and the water diversion point, leading to variability across the streams (Table 1).

Table 1 Location and physical characteristics of the studied stream sites in the southern face of Sierra Nevada (Southeast of Spain)

Stream	Sampling site relative to the point of water diversion	Geographic coordinates	Altitude (m a.s.l.)	Wetted channel width (m) mean ± SE	Distance between sampling site and diversion point (m)	Riparian canopy cover (%)
Cáñar	upstream	36°58'29''N, 3°24'29''W	1864	2,8 ± 1,2	63	69
	downstream	36°58'26''N, 3°24'30''W	1845	0,6 ± 0,4	32	63
Bérchules	upstream	37°02'18''N, 3°12'08''W	1994	2,5 ± 1,1	146	3
	downstream	37°02'13''N, 3°12'13''W	1975	0,4 ± 0,2	58	1
Mecina	upstream	37°03'21''N, 3°07'51''W	1859	1,9 ± 0,7	885	19
	downstream	3702'19''N, 3°08'02''W	1655	0,3 ± 0,1	10	18
Nechite	upstream	37°04'23''N, 3°05'29''W	1851	0,8 ± 0,3	132	6
	downstream	37°04'12''N, 3°05'21''W	1798	0,3 ± 0,2	248	12
Laroles	upstream	37°04'08''N, 3°02'52''W	1837	1,7 ± 0,8	13	65
	downstream	37°03'54''N, 3°02'43''W	1785	0,4 ± 0,3	450	79

2.2 Physical and Chemical Characterisation of Streams

Streamflow and physicochemical properties of water were measured at upstream-reference and downstream-impacted reaches throughout one year from November 2022. We conducted 7–12 measurements of the wetted channel width and instantaneous streamflow per reach, including the dates when macroinvertebrates were sampled (see below), using the salt-dilution method (EasyFlow flowmeter, JDC Electronic). We aimed to ensure that these measurements represented both the low and high flow conditions. Moreover, in each site we installed (submerged, fixed to the bottom) a water level and temperature data logger (HOBO™, model U20L-02) to obtain continuous records (hourly). We constructed rating curves, the relationship between water level height and instantaneous volumetric flow, to estimate continuous discharge. Estimated uncertainties for both the gauging method and streamflow sensors were ≤5% (Zakaluk et al. 2024).

Using these continuous records, we estimated for each stream, the proportion of discharge reduced downstream the weir, assuming that the difference in flow between upstream and downstream reaches roughly represents the withdrawn flow. Discharge measurements in the irrigation ditches were abandoned following the theft and vandalism of essential data loggers. The short distance between sections minimized the errors inherent to this proxy (upstream-downstream flow difference). This approximation, however, impeded further differentiation of downstream flow gains (seepage from ditches, groundwater upwelling) or losses (evapotranspiration, infiltrating surface water).

We compared mean discharge between upstream and downstream reaches within each season using a Wilcoxon signed-rank test (*wilcox.test* function of the 'stats' package; R Core Team, 2024). Differences in the magnitude of the net flow reduction among seasons were assessed using Kruskal-Wallis tests (*kruskal.test* function of the 'stats' package) followed by Dunn's test for multiple comparisons (dunnTest function of the 'FSA' package; Ogle et al. 2015).

For water temperature we calculated the daily mean, minimum, maximum, and mean daily thermal amplitude. Differences in these values between up- and downstream reaches within seasons were assessed using the Wilcoxon test (*see above*).

Discrete field measurements of pH, electrical conductivity, dissolved oxygen ($n=6$), and dissolved nutrients ($n=4$) of stream water were taken throughout the annual cycle, including the two dates of macroinvertebrate sampling (see details in Supp. Mat., Methods S1).

2.3 Macroinvertebrates Sampling, Diversity and Biotic Indices

Benthic macroinvertebrates were collected by kick-sampling with a hand net (250 µm mesh size) during two seasons: autumn (November-December 2022) and spring (May-June 2023). We followed standard procedures for evaluating macroinvertebrate communities and river ecological quality using multimetric indices (MAGRAMA, 2013), with some modifications (Methods S2).

We determined regional richness (ϒ-diversity) and its two components—local (reach-level) taxa richness (α-diversity) and the change in assemblage composition among individual reaches, interlocal (β-diversity)—for the sets of streams (within and across the two reach types). All diversities were calculated for the entire data set and separately for each reach type and sampling season.

We determined α-diversity as taxa richness, number of taxa collected in a given sample, and Shannon-Weaver diversity (Magurran 2004).

We performed interlocal diversity (β-diversity) and its partition into the components species replacement (β-Repl) and abundance difference (Ab-Diff) using the Ruzicka dissimilarity index (equivalent to the Jaccard coefficient for quantitative data) (Podani et al. 2013). We determined the local contribution to β-diversity (LCBD) as described by Legendre and De Cáceres (2013). The LCBD measures the uniqueness of macroinvertebrate community composition across sites; thus, high values of this metric indicate sites with unusual taxonomic combinations and high conservation value (Legendre 2014; Legendre and De Cáceres 2013). The partition of β-diversity was performed using the *beta.div.comp* function and LCBD of each sample was computed using the *beta.div* function (Legendre and De Cáceres 2013) from the R package *adespatial* (Dray 2025).

Taxa accumulation smoothed curves were used to estimate γ-diversity. For each group of reaches, samples were randomized ($n = 999$) with replacement to obtain the Mao Tau estimator of rarefied 'observed' richness. The smoothed curves of 'observed' taxa were ln (x + 1)-transformed. The resulting linear regressions were tested for differences in slope and intercept using ANCOVA, with the number of samples as a covariate and the reach group as a fixed factor.

To provide a unified framework linking local (α), interlocal (β), and regional (γ) diversity, we applied additive diversity partitioning following Lande (1996), where regional richness is $\gamma = \alpha + \beta$. Local diversity (α) was calculated as the mean taxa richness per sample, regional diversity (γ) as the total observed taxa richness within each reach group (upstream and downstream) and season, and the β component of regional richness was calculated as $\gamma - \alpha$.

We calculated 14 biotic indices (seven qualitative and seven quantitative; Table S1) to evaluate the local ecological quality of each stream reach, following the criteria of the European Water Framework Directive.

In all cases, we compared the density of total macroinvertebrates and functional feeding groups (FFG), values of taxonomic richness and diversity (α and β), taxa richness of each FFG, and ecological quality indices (EQI) between upstream and downstream reaches using the Wilcoxon signed-rank test for paired samples (see above).

2.4 Differences in Community Composition Between Stream-Reach Types

We performed a non-metric Multi-Dimensional Scaling (NMDS) ordination to visualize the magnitude of differences between groups of stream reaches (upstream-reference vs. downstream-impacted) in macroinvertebrate assemblage composition. The ordination was based on a Bray-Curtis similarity matrix of Hellinger-transformed taxa abundance data to reduce the effects of very high abundances.

We used the Analysis of Similarity (ANOSIM) to assess the magnitude and statistical significance (randomization by 9999 sample permutations) of the differences in macroinvertebrate assemblage composition between types of stream reaches (upstream vs. downstream). When the ANOSIM test (Global R) for differences between groups was significant ($p < 0.05$), we used Indicator Value (IndVal; Dufrêne and Legendre 1997) to identify taxa significantly associated with groups, using the R package 'indicspecies' (De Cáceres and Legendre 2009), using 999 permutations. Taxa were considered significant indicators of a type of reach when $p < 0.05$.

A power analysis was conducted using the *pwr.t.test* function of the 'pwr' R package (Champely 2020) to assess the sensitivity of our sampling design. For a paired design ($n = 5$), a significance level of 0.05 and a desired power of 0.80, the minimum detectable effect

size (Cohen's d) was estimated at 1.68. Therefore, for the biological variables analysed, we calculated effect sizes (Hedge's g) to complement null-hypothesis testing by providing information on the magnitude and direction of differences. Effect sizes were calculated using the *cohen.d* function of "effsize" R package (Torchiano 2020), and accounting for the paired structure of the sampling design. Effect sizes were estimated separately for each season. We compared downstream (impacted) against upstream (reference) reaches, such that positive values indicate higher values downstream, whereas negative values indicate higher values upstream. Effect sizes of 0.20–0.49, 0.50–0.79 and ≥0.80 were considered small, medium and large, respectively (Cohen 1988).

All statistical analyses were carried out in R version 4.0.5 (R Development Core Team 2024), except for γ-diversity, which was computed using EstimateS v9.1 (Colwell 2013).

3 Results

3.1 Physical and Chemical Characteristics

Mean streamflows of the five streams were consistently higher in upstream-reference compared to downstream-impacted reaches regardless of the season (Fig. 1). This pattern indicated persistent flow reduction through the year. Indeed, during all surveys, we observed the weirs diverted a high proportion of flow, and only limited surface flow passed through

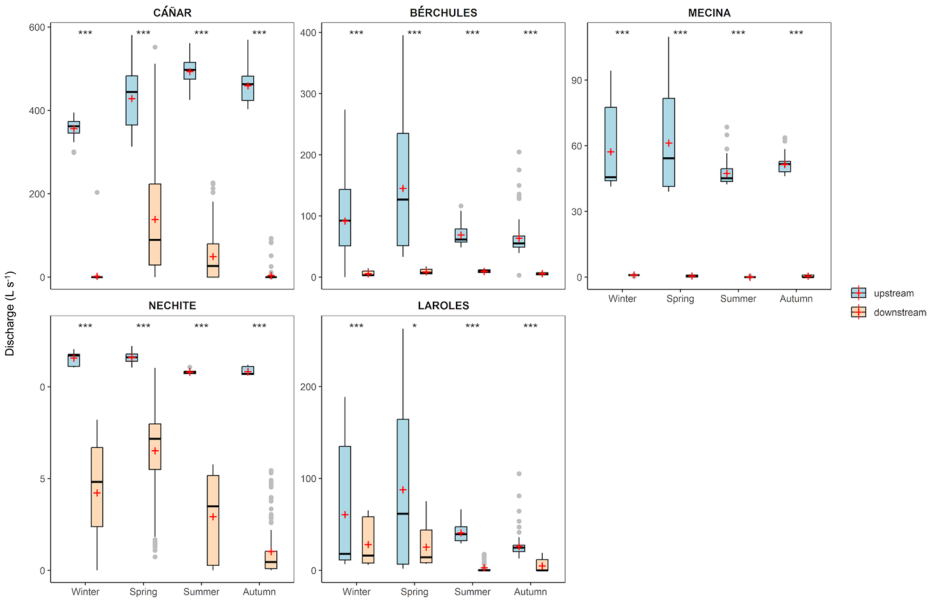

Fig. 1 Box-and-whisker plots of streamflow (L s^{-1}) measured throughout the seasons along the study period in each of the five streams assessed. Box represents median and the interquartile range (25–75%), whiskers are the range, crosses are the mean and dots are outliers. Symbols stand for comparisons between upstream and downstream reaches in each season. Different symbols (ns, $p>0.05$; *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$) indicate levels of significance based on linear models. Note that each plot shows a different scale to improve visualization

because of leakage within the dams` unconsolidated materials. Seasonal mean flow differences between up and downstream reaches (proxy of withdrawn water volume by ditches) depended on the particular discharge magnitude of each stream, which ranged from a maximum value of ca. 500 L s^{-1} in Cáñar to a minimum of ca. 5 L s^{-1} in Nechite (Fig. 1). Proportional flow reduction was particularly high in Cáñar, Mecina, and Bérchules, with mean values over 0.85 throughout the year, except in Cáñar during winter (Fig. 2). Such reductions result in flows below 10 L s^{-1} at downstream reaches (Fig. 1). Lower proportional values of flow reduction were detected in Laroles and Nechite, with mean values ranging from 0.41 to 0.44 in spring to 0.76 and 0.91 in autumn, respectively (Fig. 2). In Nechite, despite not exhibiting the highest proportional flow reduction, absolute values of mean flow in the downstream reach always ranged between 1 and 6 L s^{-1}, due to the natural low mean flow measured in the upstream reach all year round (ca. 10–12 L s^{-1}) (Fig. 1). Despite these high magnitudes of flow reduction, downstream reaches remained perennial, thus maintaining longitudinal flow connectivity during the study period.

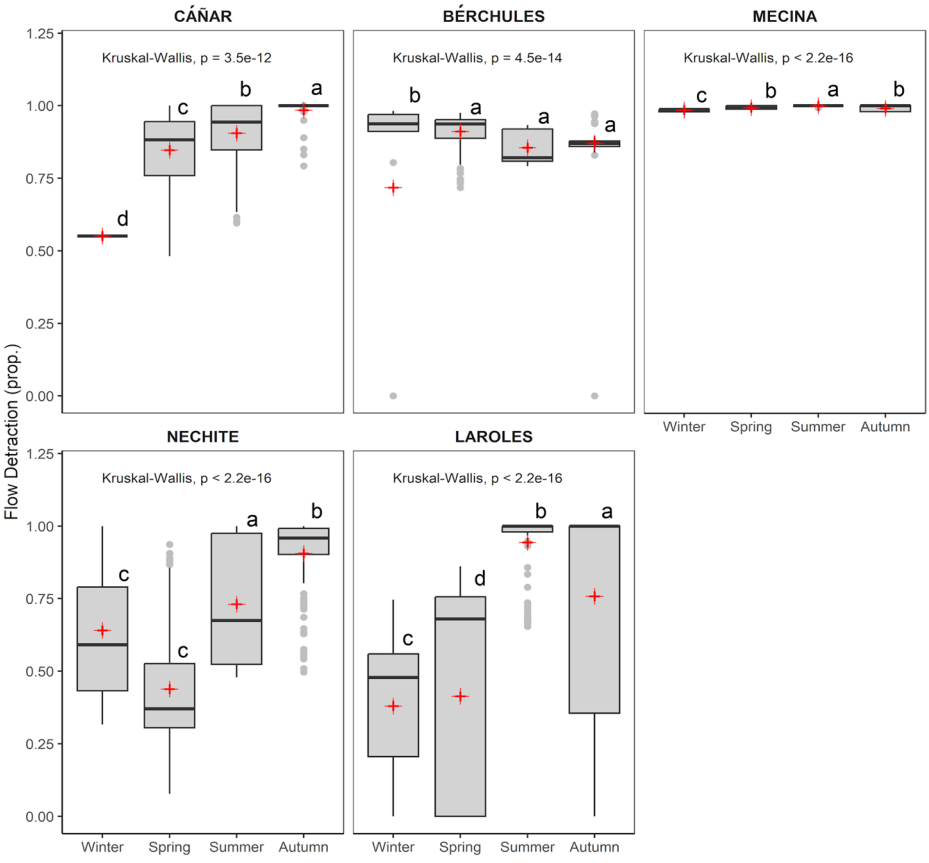

Fig. 2 Seasonal flow diversion (proportion) in each of the five studied streams. Box represents median and the interquartile range (25–75%), whiskers are the range, crosses are the mean and dots are outliers. Different letters ($p<0.05$) indicate significant differences between seasons according to rank-based linear models

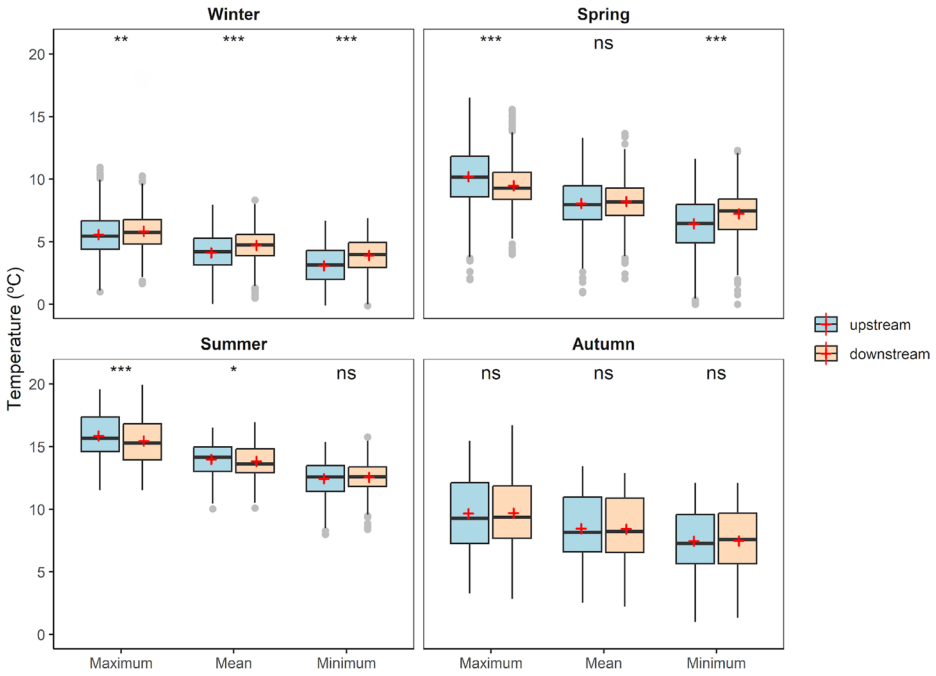

Fig. 3 Box-and-whisker plots for average maximum, mean and minimum water temperatures (°C) measured throughout the seasons along the year of study in upstream and downstream reaches ($n = 5$ streams). Box represents median and the interquartile range (25–75%), whiskers are the range, crosses are the mean and dots are outliers. Symbols stand for comparisons between upstream and downstream reaches. Different symbols (ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$) indicate levels of significance of differences based on linear models

Continuous stream temperature records (Fig. 3) and daily thermal amplitudes (Figure S1) indicate a stronger groundwater influence downstream than upstream. This influence is supported by significantly higher downstream winter temperatures despite lower discharge at these sites (Figs. 3, S2). Furthermore, lower summer maxima and means (Fig. 3), coupled with reduced spring daily fluctuations (Figs. 3, S2), confirm that groundwater recharges sustain these baseflows. The exception was Laroles (Figure S2), likely due to the greater distance between the weir and the downstream reach, which prolonged atmospheric heat exchange.

Overall, water physicochemistry was similar across reach types (Figure S3). Slightly lower oxygen content and higher salinity were recorded in downstream reaches, as expected in a streamflow dominated by groundwater, but these differences were not statistically significant (Figure S3). Only total dissolved N—despite overall low concentrations—showed significantly higher values in upstream reaches, suggesting a stronger influence of surface runoff at these sites.

3.2 Changes in the Macroinvertebrate Community Between Upstream-Reference and Downstream-Impacted Reaches

The mean total macroinvertebrate density was 3.5-fold higher in spring and 1.4-fold higher in autumn at upstream relative to downstream sites (Fig. 4A), with medium effect sizes in

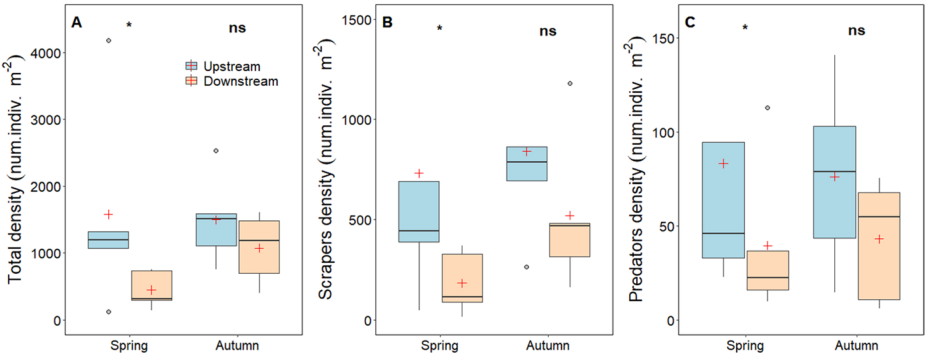

Fig. 4 Densities (num. ind. / m2) of (**A**) total macroinvertebrates, (**B**) scrapers and (**C**) predators, measured in upstream and downstream reaches ($n=5$ streams) during spring and autumn seasons. Box represents median and the interquartile range (25–75%), whiskers are the range, crosses are the mean and dots are outliers. Symbols stand for comparisons between upstream and downstream reaches. Different symbols (ns, $p>0.05$; *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$) indicate levels of significance based on the Wilcoxon signed-rank test for paired samples

both seasons (Hedges' g = -0.53 and −0.57, respectively), although differences were only statistically significant in spring. All functional groups contributed to these differences in density, showing consistent higher densities upstream in both seasons with effect sizes ranging between −0.18 and −0.73 in spring and between −0.18 and −0.77 in autumn (Fig. 4B and C, Table S2).

Local (α) and interlocal (β) diversities showed similar values at both upstream and downstream reaches (Fig. 5). Local diversity—measured as taxa richness or Shannon diversity (Fig. 5A and B)— tended to be higher in upstream reaches during spring, although effect sizes were small for both metrics ($g<0.3$; Table S2). The pronounced intragroup dispersion observed in downstream sites likely prevented the detection of significant differences. Taxa richness of each FFG was only statistically higher in upstream reaches during spring for collector-gatherers, with a medium effect size (g = -0.52; Table S2). However, collector-filterers exhibited a large effect size in spring (g = -1.08; Table S2) indicating a potential higher richness in upstream reaches. Mean interlocal diversity as β-diversity (with low-moderate values between >0.2 and <0.4) or LCBD (Fig. 5C and D, respectively) did not show clear differences between reach-groups, with similar values of partitioning between species replacement and abundance difference (nestedness). However, this second component reached a higher proportion in the spring samples, particularly at upstream reaches (ca. ⅔) (Fig. 5C).

Rarefaction taxa curves for both seasons (Fig. 6) indicated a significantly higher number of accumulated taxa at the regional scale (γ-diversity) in upstream reaches, similar to that for the whole set of sites, compared to downstream reaches.

When additive diversity partitioning ($\gamma=\alpha+\beta$) was applied, the relative contributions of the α and β components to observed regional richness were similar between upstream and downstream reaches in both seasons (Table S3). The slightly higher observed γ-diversity of upstream reaches was associated primarily with higher local richness in spring, whereas both α and β components contributed positively in autumn.

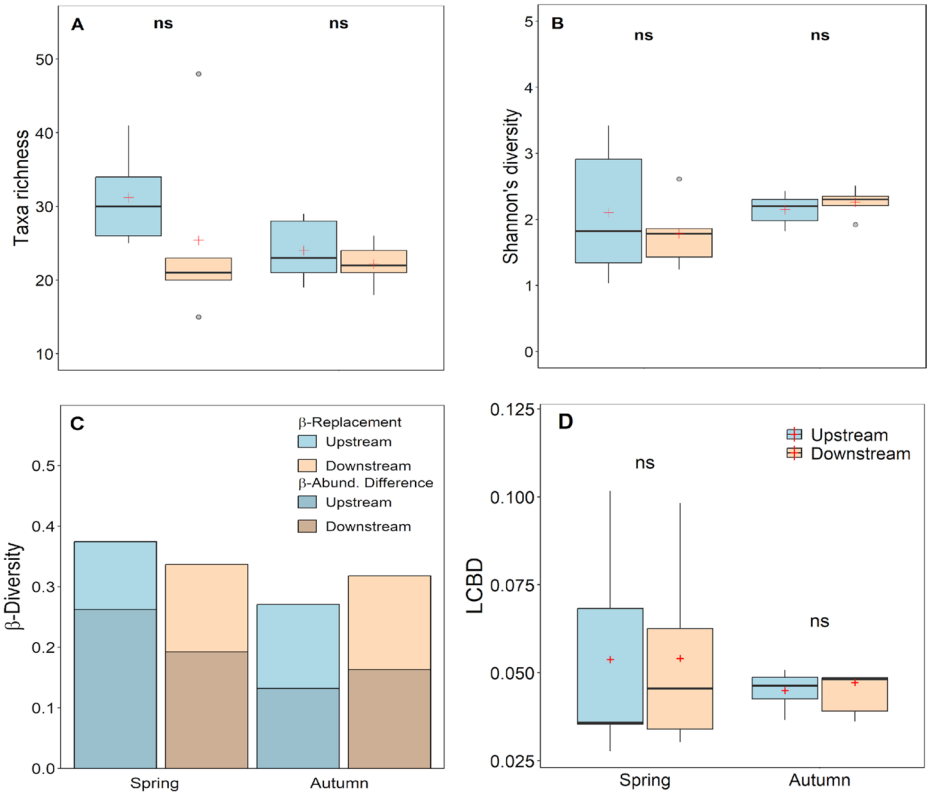

Fig. 5 Local (α) taxonomic richness (**A**) and Shannon's diversity (**B**), interlocal β-diversity (**C**), distinguishing between species replacement (β-Repl) and abundance difference (Ab-Diff), and the local contribution to β-diversity (LCBD) (**D**) ($n = 5$ streams) during spring and autumn seasons comparing upstream and downstream sites. Box represents median and the interquartile range (25–75%), whiskers are the range, crosses are the mean and dots are outliers. Different symbols (ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$) indicate levels of significance based on the Wilcoxon signed-rank test for paired samples

Almost all mean values of the 14 biotic indices measured were higher in upstream than in downstream reaches across the two sampling seasons. Effect sizes were generally small to medium, although some indices showed stronger differences between reaches (Table S2). The IBMWP index is officially recommended in the Iberian Peninsula for evaluating the ecological quality of rivers, with well-defined reference conditions and quality classes for the region's different stream types (BOE 2015). Our streams fit the R-T11 type (Siliceous Mediterranean mountain rivers), and their mean IBMWP values did not differ between upstream and downstream reaches (Table S2), showing only small effect sizes in both spring and autumn (g = -0.28 and −0.36, respectively), and falling within the "good" quality class (ranging from 158 to 96) (Fig. 7A). Only some spring samples from upstream-reference reaches, and one downstream-impacted site reached the "very good" quality class (Fig. 7A). In spring, three qualitative — IASPT, ICM11a (Fig. 7B and C), and EPT — and two quantitative indices — ICM7 (Fig. 7D) and ICM10 — were signifi-

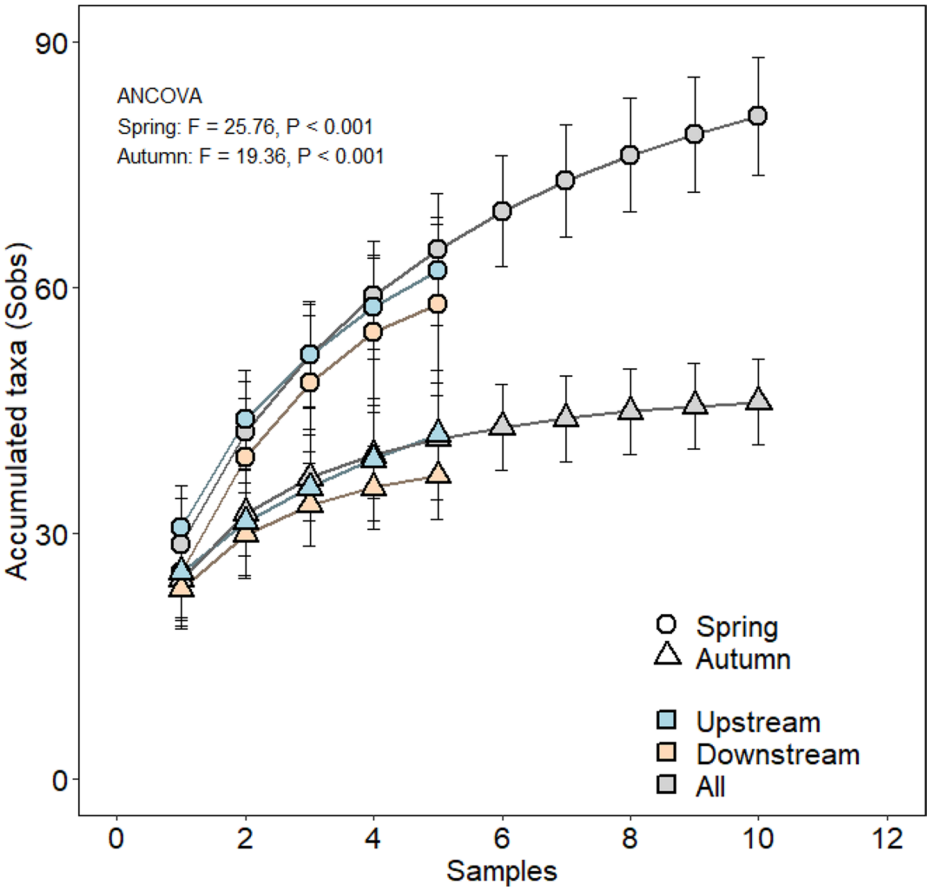

Fig. 6 Curves of accumulated taxa (rarefaction curves) ($n = 5$ streams) during spring and autumn, comparing upstream and downstream reaches, and all sites pooled ($n = 10$ streams), in each season. The results of the ANCOVA (F and p value) comparing types of reach are also shown

cantly higher in upstream reaches, despite generally small effect sizes (Table S2). The Log Sel EPTCD index showed only marginally significant higher values in upstream sites but a large effect size (g = -0.91). In autumn, Log Sel ETD and Log Sel EPTD presented large effect sizes (g = -0.87 and −0.88, respectively), although only the former index exhibited a statistically significant higher value upstream (Table S2).

The Non-Metric Multidimensional Scaling ordination (NMDS; Figure S4) of macroinvertebrate samples yielded a stress value of 0.14, which is acceptable (values < 0.2). The NMDS plot showed a clear separation between samples collected in different seasons (autumn to the right, spring to the left), indicating significantly distinct community structure between the two periods (ANOSIM, $R = 0.58$, $p < 0.001$). However, community composition was not significantly different between upstream and downstream reaches, independently of the sampling season: spring (ANOSIM, R = -0.16, $p = 0.86$) or autumn (ANOSIM, R = -0.20, $p = 0.96$). Community composition did not differ among reach types when samples from both seasons were pooled (ANOSIM, R = -0.08, $p = 0.93$).

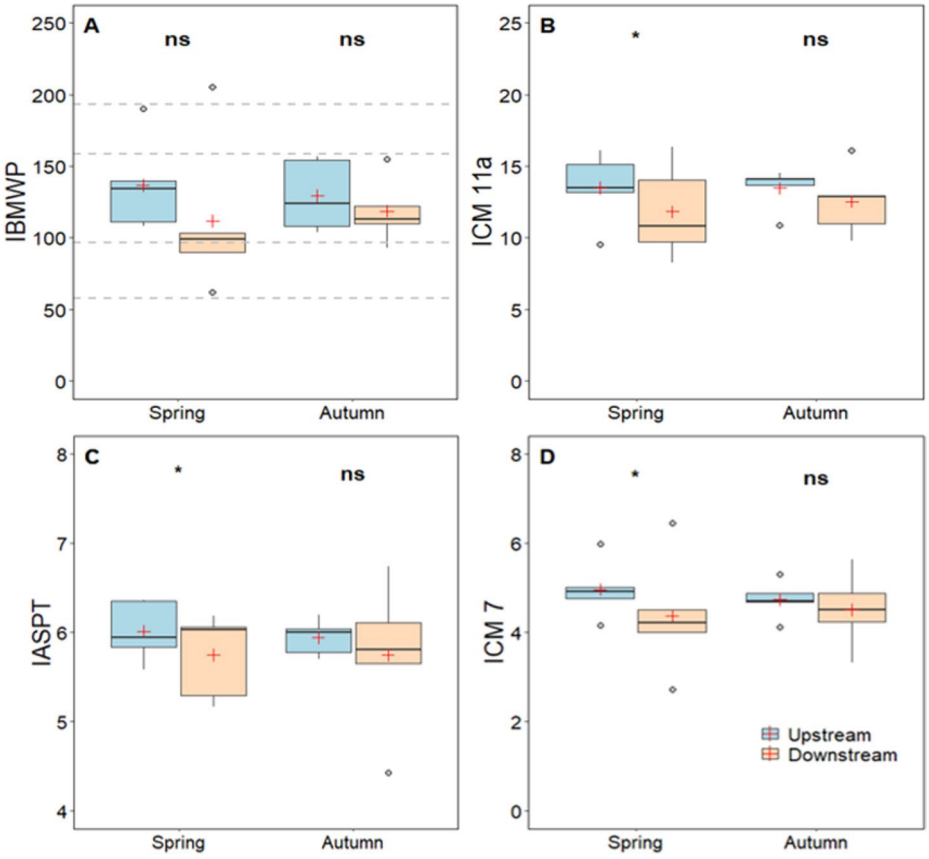

Fig. 7 Scores of four biotic indices—the single metrics IBMWP (**A**) and IASPT (**C**) and the multimetrics ICM 11a (**B**) and ICM7 (**D**)—comparing upstream and downstream reaches ($n = 5$ streams) during spring and autumn. Dotted lines represent the reference value (193), and the thresholds between quality classes: excellent/good = 158.3; good/moderate = 96.5; and moderate/poor = 57.9. Box represents median and the interquartile range (25–75%), whiskers are the range, crosses are the mean and dots are outliers. Different symbols (ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$) indicate levels of significance based on the Wilcoxon signed-rank test for paired samples

4 Discussion

Quantifying how flow reduction impacts biodiversity is crucial for sustainable stream management amid growing human water demands and climate-driven scarcity. This represents a particularly pressing issue in the Mediterranean basin (Papadaki et al. 2020), a biodiversity and climate change hotspot (Arroyo et al. 2022). The ecological effects of traditional irrigation on aquatic biodiversity in this region remain largely unexplored, raising concerns as agricultural expansion increasingly alters mountain habitats of high conservation value (Yao et al. 2017). Empirical evidence increasingly suggests that water management and environmental background strongly shape how ecosystems react to hydrological changes. Understanding these interactions is essential for advancing ecological science and meeting EU environmental policy requirements (Martín-Ortega et al. 2011).

4.1 Effects of Flow Reduction on Streamwater Physicochemical Characteristics

Estimated streamflow reductions downstream of *careo*-irrigation ditches during the study year exceeded ≈ 50% (most frequently between 76 and 98%). These values can be considered relatively elevated based on previous studies (Poff and Zimmerman 2010; Rhoades et al. 2025), suggesting limited implementation of scientifically tailored environmental flows. Our results identified careo-irrigation diversion as the dominant factor associated with the flow loss. Flow reductions persisted year-round rather than just during spring melt, the traditional usage period (Martos-Rosillo et al. 2019). This pattern suggests intensified system use driven by rising agricultural and urban demands amidst regional aridification (Beguería et al. 2025). Despite heavy diversion, impacted reaches maintained continuous—though minimal—surface flow. This critical persistence for downstream biodiversity (see below) reflects a combination of structural leakage and groundwater contributions. First, seepage returns from traditional leaky weirs and ditches, and fractured or poorly sealed concrete-lined channels (e.g., in Cáñar, Mecina, and Laroles). Second, our continuous water-temperature records indicate downstream groundwater effluents to the impacted reaches. These inputs align with the pervasive discharge from weathered hard-rock aquifers documented in Sierra Nevada (Cabello et al. 2026a; Zakaluk et al. 2024).

Despite sharp flow reductions, water chemistry remained stable, and significant contamination was unlikely given the pristine catchments. Temperature differences, though statistically significant, were biologically negligible (< 1 °C). Therefore, as typical for small impoundment structures (Mbaka and Wanjiru Mwaniki 2015), downstream shifts in community metrics depends primarily on physical habitat alterations — specifically, reduced flow diversity and increased sedimentation (Dewson et al. 2007b; González and Elosegi 2021; Mollá et al. 2017).

4.2 Effects of Flow Reduction on Macroinvertebrate Density and Abundance

Flow reduction led to a substantial decline in macroinvertebrate density in downstream-impacted reaches, with a 3.5-fold decrease in spring, supporting our first hypothesis (H1a). Reported density responses to partial flow abstraction are highly variable, ranging from decreases (Aspin et al. 2019; Dewson et al. 2007a; Vallefuoco et al. 2022) to no significant change (González and Elosegi 2021) and even increases (Dewson et al. 2007a; Rhoades et al. 2025). This variability largely reflects differences in the duration of reduced-flow exposure among studies (González and Elosegi 2021). Short-term flow reductions lead to macroinvertebrate crowding within the remaining wetted areas, whereas prolonged flow reduction can cause density declines due to drift as habitat conditions deteriorate further (Dewson et al. 2007b; González and Elosegi 2021).

The prolonged duration of flow reduction in our study provides a mechanistic explanation for the observed declines in density and abundance. Reduced-flow conditions persisted for at least 1 year, resulting in a major contraction of the wetted area (63–85% reduction in wetted channel width). Consequently, lower densities and habitat contraction slashed macroinvertebrate abundance per reach length to one-tenth of reference values. This decline in benthic abundance, along with concomitant reductions in insect drift (Rhoades et al. 2025) and emergence (Richardson et al. 2010), likely results in severe food shortages for trout and riparian insectivorous predators.

4.3 Effects of Flow Reduction on Local Diversity and Ecological Quality

While severe flow reductions typically decrease macroinvertebrate richness (Aspin et al. 2019; González and Elosegi 2021), our findings suggest less pronounced declines, partially challenging our initial hypotheses (H1b, H2). We observed a decreasing trend in the impacted reaches—particularly for taxonomic richness of the collector FFG in spring. Several non-mutually exclusive mechanisms may explain this pattern. First, because most organisms were identified at family or genus level, species-level turnover may have remained undetected. Given the long history of flow diversion in these streams, such turnover would be expected to have already occurred if driven by chronic flow reduction. In addition, the absence of a sharp drop in local diversity, despite severe flow reductions, might be notably attributed to the maintenance of hydrological connectivity in the impacted reaches, probably due to the two concurrent processes mentioned above: (i) the leaky nature of weirs and ditches, and (ii) the slightly gaining condition (groundwater inflows) of the impacted reaches. Increased habitat connectivity has been shown to enhance local species richness (Rolls et al. 2018). During our study period, the minimal upstream hydrological connectivity likely prevented downstream reaches from being reduced to isolated pools. In these, macroinvertebrates become confined and cut off from drift, intensifying predation and often leading to prey population collapse (Aspin et al. 2019). Consequently, it seems that severe impacts on macroinvertebrate local richness would fundamentally arise if these biotic stressors—and/or severely worsened abiotic conditions—began to operate. Neither of these circumstances was observed in our study.

Although hydrological connectivity is critical, groundwater subsidies per se may mitigate local diversity declines in impacted reaches. In alpine streams, meltwater imposes severe abiotic stress—such as low temperatures, high suspended solids, and substrate instability—which constrains benthic communities (Brown et al. 2007). Conversely, moderate groundwater upwelling often enhances macroinvertebrate abundance and taxonomic richness (Khamis et al. 2016). In unglaciated systems like the Sierra Nevada, cryospheric melt is less severe than in glacier-fed streams; however, spring flow peaks may still depress local diversity in reference reaches relative to impacted ones.

Nevertheless, flow reductions had a clear negative impact on ecologically important components of the community, partially supporting H2. In particular, the decline in certain taxonomic groups — Ephemeroptera, Plecoptera, and Trichoptera (EPT) — and collector FFG richness suggests that functional and ecological changes may precede detectable reductions in overall taxonomic diversity. Families in these orders significantly drive single metrics (IASPT and EPT) and multimetric (ICM11a, ICM7, and ICM10) index performance, accounting for 40–60% of total scores of the multimetric ones. They are highly vulnerable to multiple stressors, including hydrological disturbances and habitat loss (Walsh 2006). Conversely, the single-metric IBMWP index—the regulatory standard for Iberian Mediterranean river biomonitoring—failed to differentiate between reference and impacted reaches, with both averaging ‘good’ ecological quality. These findings suggest that monitoring flow-diversion impacts in mountain streams requires supplementing the IBMWP with EPT-driven metrics to enhance diagnostic sensitivity.

4.4 Effects of Flow Reduction on Interlocal and Regional Diversities

While the impact of flow reductions on β-diversity are largely unaddressed, habitat homogenization and environmental stress are widely recognized to promote taxonomic and functional homogenization (Liu et al. 2022). Contrary to H3, we did not detect a significant decline in β-diversity associated with flow reduction, even though groundwater contribution was detected downstream. Alpine stream-reaches characterized by high contributions of meltwater—although poorer in species than groundwater-fed streams—often contribute with higher β-diversity because of their specialist endemic fauna (Khamis et al. 2016). Herein, however, low natural abiotic stress in upstream-reference reaches, along with limitations in taxonomic resolution, may explain the lack of β-diversity differences between reach types. Community ordination results support this interpretation, showing no apparent differences between reach types.

Flow reduction had contrasting effects across spatial scales, with no significant effects on local (α) and interlocal (β) diversity, but a substantial decline in regional taxonomic richness (γ-diversity). Although differences in local richness were small and non-significant, their cumulative effect reduced γ-diversity. In headwater streams, regional and local species richness are often positively related, indicating unsaturated local communities primarily structured by abiotic factors, such as hydrological disturbance (Heino et al. 2003). Accordingly, the moderate negative effects of flow reduction on local taxonomic richness appear to be amplified at the regional scale.

5 Conclusions

Infrastructure-scale 'inefficiencies' (e.g., leaky weirs and unlined ditches), inherent to this traditional irrigation system (Martos-Rosillo et al. 2019; Cabello et al. 2026b), is essential to maintain hydrological connectivity and mitigate downstream biodiversity loss, particularly in reaches lacking groundwater upwelling. However, this minimal yet constant connectivity does not entirely prevent ecological degradation, as evidenced by reduced benthic macroinvertebrate density and lower biotic index scores in flow-impacted reaches.

The recent water policy paradigm has prioritized efficiency in water diversion and conveyance at the infrastructure scale, a shift evidenced here in some concrete-lined canals. Reversing this trend is urgent to halt the advance of river degradation. Despite ample evidence of the "irrigation efficiency paradox" (Grafton et al. 2018) and the growing global discourse on the need for adaptive water management (Pahl-Wostl 2007), its institutional adoption in biodiversity-rich mountain regions remains extremely slow (Sanchis-Ibor et al. 2024). Overcoming this inertia requires urgent and intensified collaboration among scientists, water managers, and local users.

Our results also emphasize the need to maximize stream reaches under natural or ecologically compatible flow regimes (e.g. environmental flows; Tonkin et al. 2014; Ramos et al. 2017, 2018), as local biodiversity losses can turn into substantial regional declines.

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Data Availability Data supporting this study are provided in the Supporting Information.

Declarations

Conflicts of Interest The authors declare no conflicts of interest.

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