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Hydroseasonal and spatial drivers of macroinvertebrate communities in Mediterranean intermittent rivers: the Upper Loukkos Basin (northwestern Morocco)

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SUMMARY

Macroinvertebrate communities in the Upper Loukkos basin (northern Morocco) exhibited marked spatio-temporal variability across contrasting hydrological phases, reflecting the dynamic nature of Mediterranean intermittent systems. Sampling at 18 sites, comprising both protected and impacted reaches, during post-flood and post-drought periods (2014–2015), revealed a total of 102 species. Assemblage composition changed across seasons and sites, largely driven by hydroseasonal dynamics, habitat connectivity, and environmental gradients. Chorological patterns showed a clear predominance of taxa associated with Mediterranean biogeographical affinities, with endemic species accounting for 25% of the assemblage. Protected headwater sites supported higher diversity and a greater proportion of specialist taxa, particularly under post-drought conditions, highlighting their role in maintaining community structure under hydrological variability. Some groups, notably Coleoptera, persisted under low-flow conditions, demonstrating both resistance and recolonisation capacity. Community structure was primarily shaped by interacting environmental and seasonal filters, with a noticeable decline in sensitive lotic taxa, especially during dry periods. Multivariate analyses showed a diffuse community structure across sites and seasons, reflecting the combined effects of hydroseasonal dynamics and environmental gradients on biotic assemblages. Our results indicate that the Upper Loukkos basin acts as a micro-reserve interface, where geographic position, historical context, and topographic complexity contribute to the maintenance of regionally distinctive biodiversity within the western Mediterranean. This highlights the need to integrate multi-scale environmental drivers into biomonitoring frameworks, particularly in intermittent systems where community dynamics remain closely constrained by hydrological variability and where disturbance-sensitive taxa appear especially vulnerable.

INTRODUCTION

Freshwater biodiversity is increasingly affected by the combined effects of anthropogenic pressures and natural environmental variability (Byun et al. 2019; Saffarinia et al. 2022). Land-use change and associated human activities lead to habitat fragmentation, aquatic ecosystem degradation, and increased pollutant inputs (Krynak et al. 2018; Castro-López et al. 2019). These disturbances modify the structure of macroinvertebrate assemblages by favouring tolerant taxa, while sensitive ones decline, resulting in a reduction of ecological complexity (Alcaraz-Hernández et al. 2024; Bae and Kim 2025).

Conservation strategies often rely on spatial protection measures (Chape et al. 2005). Protected areas constitute key tools for biodiversity conservation, but their design has largely focused on terrestrial vertebrates, with freshwater ecosystems remaining poorly represented (Rondinini et al. 2011; Carrizo et al. 2017). As a result, many high-value aquatic habitats remain outside protected networks, limiting their effectiveness for freshwater conservation (Sánchez-Fernández et al. 2004; Nogueira et al. 2021).

The effectiveness of these strategies is constrained by the dynamics of Mediterranean rivers (Acuña et al. 2014; Stubbington et al. 2019). These systems are characterized by marked seasonal variability, alternating between flood events and drought periods that transform flowing sections into isolated pools (Gasith and Resh 1999). Flow intermittence strongly influences the structure of benthic communities through the reduction of habitat connectivity and the deterioration of environmental conditions.

Macroinvertebrate assemblage composition integrates the cumulative effects of environmental stressors and is widely used as an indicator of ecological condition (Allan 2004). Biological traits such as physiology, dispersal ability, and life-history strategies mediate species responses to environmental changes. Macroinvertebrate assemblages therefore provide a relevant diagnostic of ecological status, reflecting the combined influence of environmental pressures. Their high endemism further emphasizes their importance in Mediterranean ecosystems (Sánchez-Fernández et al. 2004; Buschke et al. 2014).

Northern Morocco, particularly the Rif region, lies within the western Mediterranean

biodiversity hotspot and represents an important center of freshwater diversity (Dakki 1997; Laouina 2006). Its position at the interface between Atlantic, Mediterranean, and African influences, combined with a complex topography, supports a rich and diversified aquatic fauna, with endemism reinforced by isolation and intermittent flow regimes (Errochdi et al. 2014). This area acts as a biogeographical crossroads, favouring the coexistence of taxa with diverse chorological affinities.

Within the Betic–Rif system, habitat heterogeneity and historical isolation have contributed to the high diversity and endemism observed in macroinvertebrate communities (Bonada et al. 2008; Benamar et al. 2021). Intermittent flow regimes and fragmented headwaters further enhance specialization, making these systems important reservoirs of unique taxa, but also particularly vulnerable to environmental change and anthropogenic pressures (Bennas et al. 2009; Guellaf et al. 2025).

In North Africa, Mediterranean intermittent rivers face increasing management challenges under growing aridification and land-use pressure (Slimani et al. 2022; Belhaj et al. 2023). Despite their high biodiversity, these systems remain poorly studied compared to European regions, which limits the development of appropriate assessment frameworks (Sánchez-Fernández et al. 2008; Guellaf and Kettani 2025). Conventional approaches, often designed for perennial rivers, fail to capture the ecological dynamics associated with flow intermittence and seasonal variability (Datry et al. 2017; Stubbington et al. 2019).

Situated within the Intercontinental Mediterranean Biosphere Reserve, the Loukkos basin illustrates the contrast between relatively preserved upstream areas and increasingly impacted downstream sections. Headwater reaches still maintain relatively well-preserved habitats and support diverse macroinvertebrate communities, whereas lowland sections are increasingly affected by agricultural, urban, and industrial activities.

Although Morocco has expanded its protected areas, with national conservation targets aiming to reach 30% coverage by 2030 (Dasgupta et al., 2025), freshwater conservation priorities remain insufficiently integrated (Belhaj et al., 2024). Consequently, many high-value sites remain outside the network, while some protected reaches do not necessarily reflect high ecological value (Bonada et

al. 2008; Guellaf et al. 2025). The recent extension of Bouhachem Natural Park provides an opportunity to compare macroinvertebrate assemblages between protected and impacted areas. Improving ecological assessments is therefore needed to evaluate whether protected areas effectively act as refugia for freshwater biodiversity.

To address these gaps, we tested three main hypotheses: (i) that protected reaches within the Upper Loukkos basin function as biodiversity refugia, supporting a higher proportion of specialist and sensitive taxa; (ii) that variation in macroinvertebrate community composition is driven by the combined influence of spatial and seasonal dynamics, together with local habitat heterogeneity; and (iii) that anthropogenic pressures combine with

low-flow conditions to favour tolerant taxa at the expense of lotic-sensitive groups.

MATERIALS AND METHODS

Study area

The study area is located in the upper part of the Loukkos basin in northern Morocco, within the central Rif domain and upstream of the Oued El Makhazine reservoir (Fig. 1). This headwater zone extends across Chefchaouen, Larache and Ouazzane provinces, while its headwaters originate at around 1,300 m altitude on Jbel Khesana (western Rif), forming a transition between mountainous areas and downstream alluvial plains (Slimani 2018; Hrouir 2023).

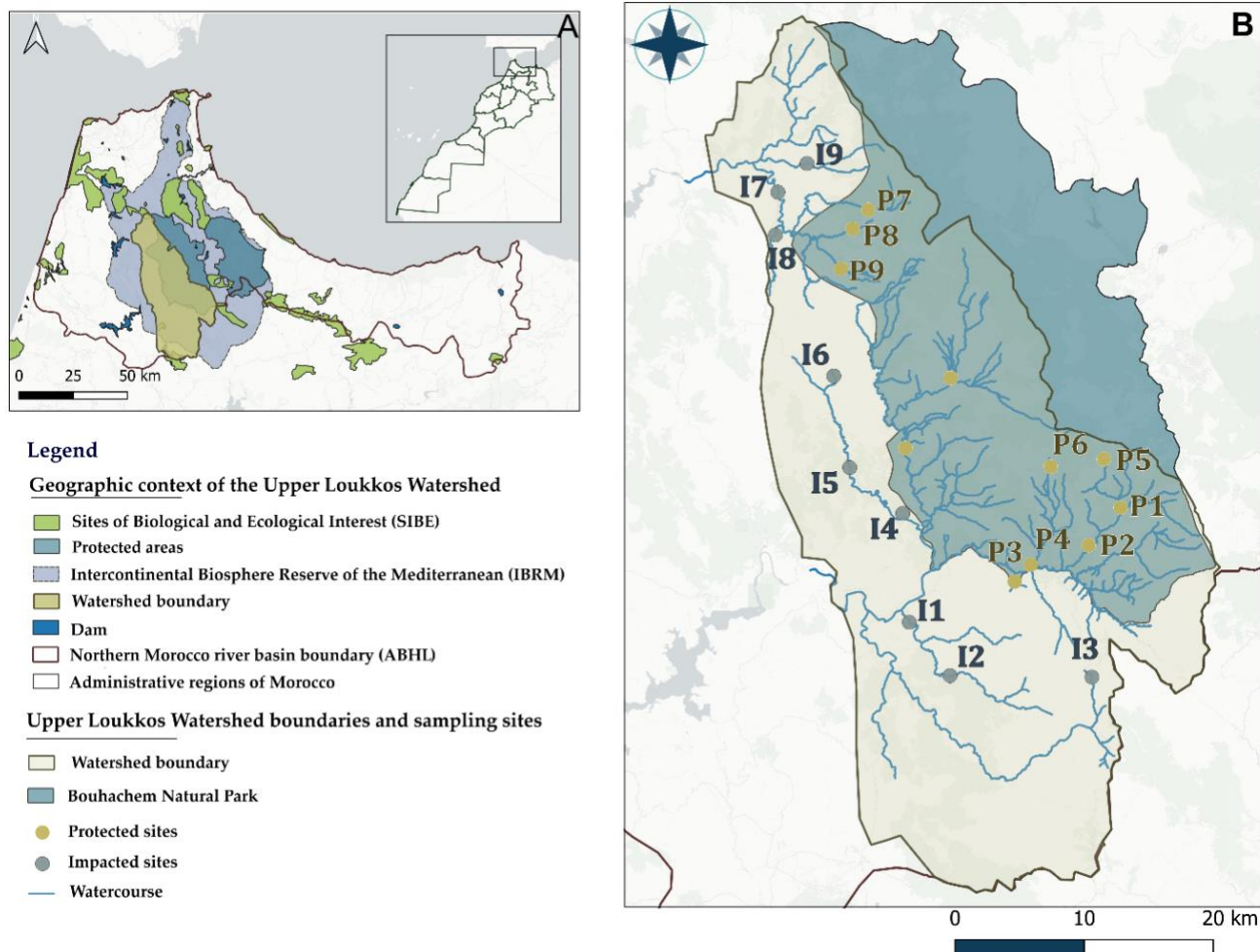


Figure 1. Location of the Upper Loukkos Watershed showing (A) geographic context and (B) the distribution of the sampling sites.

The regional climate is Mediterranean, influenced by both Atlantic inputs and local topographic conditions. Rainfall ranges from 700 to 1,000 mm per year, with most precipitation occurring between autumn and early spring, whereas summers remain dry and relatively warm. Mean seasonal temperatures range from mild winter conditions (~11 °C) to warmer summer values (~25 °C), contributing to marked seasonal hydrological variability (Salhi et al. 2019).

The study area is dominated by a pluvial regime showing high interannual variability. Flow dynamics are characterized by rapid responses to rainfall events, generating episodic floods, while extended dry periods lead to pronounced low flows or temporary stream intermittence. Geomorphologically, steep slopes, narrow valleys, and erosion-prone substrates further enhance these hydrological constraints (Agharroud et al. 2023).

Land cover reflects this environmental gradient. Intensive agriculture dominates the lower basin, whereas the Upper Loukkos Basin areas remain occupied by matorral vegetation and cork oak

(*Quercus suber*) formations. These landscapes support grazing and small-scale farming activities, particularly olive cultivation (Guellaf & Hammoudi 2015; Ballouche et al. 2024).

From an ecological perspective, the area retains a high conservation value. Its northern part overlaps with the Bouhachem Natural Park, and it also includes several Sites of Biological and Ecological Interest (SIBE), including Bellouta, Brikcha and Souk El Hed. Together, these zones form part of the Intercontinental Mediterranean Biosphere Reserve, emphasizing the role of this basin as a biogeographical interface (Guellaf & Hammoudi 2015).

A total of 18 sites were selected, including 9 located within protected areas: sites P1–P4 situated within the newly established boundaries and sites P5–P9 within the former boundaries of Bouhachem Natural Park. The remaining 9 sites, coded I1–I9, are located in impacted areas. Sampling was conducted during spring and autumn 2014 and repeated during the same seasons in 2015 (Table 1).

Table 1. Main characteristics and anthropogenic pressures recorded at the sampling sites in the Upper Loukkos Basin.

Code	Station	Altitude	Latitude	Longitude	Anthropogenic pressures
P1	O.S.B.Saada	220	34.98264	-5.50751	*
P2	O.Mlilah	198	34.94939	-5.46608	*
P3	O.Quob	110	34.94622	-5.35252	*
P4	O.Loukous	140	35.06108	-5.51339	*
P5	O.Harakate	740	35.09193	-5.56163	*
P6	O.Yema Souna	684	35.15768	-5.57430	*
P7	O.Stah	766	35.28912	-5.62578	
P8	O.Khandeq louastiya	804	35.25426	-5.62762	
P9	O.Khandeq Lihoudi	792	35.30423	-5.59103	
I1	O.S.Mghar	81	35.06666	-5.32836	**
I2	O.Loukous 2	110	35.03498	-5.35729	*
I3	O.Bouhassan	31	35.01398	-5.42087	***
I4	O.Boukrouch	124	35.02567	-5.40642	**
I5	O.Maadan	170	35.09716	-5.32448	**
I6	O.Ansar	122	35.09717	-5.34472	***
I7	O.Sgher	200	35.27339	-5.54507	***
I8	O.Azoumagh	202	35.26149	-5.55761	**
I9	O.S.Mchich	208	35.23058	-5.56672	*

* low, ** moderate, *** high anthropogenic pressures

Macroinvertebrate sampling and identification

Sampling focused on two ecologically relevant hydrological phases. The post-flood phase (spring) corresponded to the period following winter floods, which are typically intense in the Upper Loukkos Basin and often lead to marked changes in benthic

assemblages, frequently limiting the establishment of macroinvertebrate communities reflecting local habitat and environmental conditions. In contrast, the post-drought phase (autumn) followed the dry summer period, during which several reaches experienced severe flow reduction, complete drying,

or fragmentation into isolated pools, making sampling difficult or locally impossible. These two periods were therefore selected because they represent transitional but comparatively stable phases following hydrological extremes, allowing a better assessment of natural community responses to local environmental conditions. Hydrological conditions nevertheless varied among sites according to local topography, flow permanence, and habitat connectivity.

Macroinvertebrate assemblages were collected using a hand net (frame size: 25 × 25 cm; mesh size: 500 µm) by kicking and sweeping across all available microhabitats. Sampling duration varied from 30 to 60 minutes per site, depending on local habitat complexity and diversity. Each microhabitat was swept for a minimum of 3 minutes, with an overall effort of approximately 10–15 minutes devoted to each habitat type. Sampling within each habitat type continued until repeated sweeps no longer yielded new taxa. The collected material was immediately fixed in 96% ethanol in the field and subsequently transported to the laboratory for further processing. Before analysis, samples were carefully rinsed and cleared of coarse debris such as stones, plant fragments, and sediments. Sorting was carried out under a binocular microscope, allowing the separation of macroinvertebrates from the remaining material. The study focused on EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) and OCH taxa (Odonata, Coleoptera, and Hemiptera), which are commonly used as ecological indicators in Mediterranean freshwater ecosystems. Taxonomic identification relied on Tachet et al. (2002), with most individuals identified to the family level. When possible, species-level identification was achieved with the assistance of taxonomic specialists from the Laboratory of Ecology, Systematics and Biodiversity Conservation.

Occurrence data, together with site coordinates, are available as Supplementary material and in the GBIF with DOI: 10.15468/a66x3r.

Environmental analysis and habitat indices

Water quality was assessed through a combination of in situ measurements and laboratory analyses. Temperature (Temp, °C), pH, electrical conductivity (EC, µS cm⁻¹) and dissolved oxygen (DO, mg L⁻¹) were recorded at each station using a calibrated multiparameter probe (EUTECH CyberScan PCD

650), directly immersed in the main flow to reflect ambient environmental conditions.

Water samples were collected simultaneously, stored in appropriate containers, and transported to the Loukkos Hydraulic Basin Agency laboratory (ABHL, Tetouan). Analyses included chloride (Cl⁻), nitrate (NO₃⁻), sulfate (SO₄²⁻), total suspended solids (TSS), biochemical oxygen demand (BOD₅), and chemical oxygen demand (COD), all expressed in mg L⁻¹. Procedures followed standard protocols described by Rodier et al. (2009).

Habitat conditions were evaluated using two complementary indices. The Riparian Quality Index (QBR) (Munné et al. 1998) was used to characterize riparian vegetation structure and integrity, while the Fluvial Habitat Index (IHF) (Pardo et al. 2002) was applied to assess in-stream habitat heterogeneity.

Data analysis

All analyses were performed in R (version 4.5.2; R Core Team 2025). We first explored assemblage structure through total richness, abundance, and the distribution of major taxonomic groups across sampling periods and site categories.

To test these differences, we used a permutational multivariate analysis of variance (PERMANOVA; *adonis2* function from the *vegan* package; Oksanen et al. 2025). The model included status (protected vs impacted sites), season (spring vs autumn), and year (2014 vs 2015), along with a nested structure (station within status) and crossed terms (status × season, status × year), to assess the relative influence of spatial and temporal drivers on community structure.

We also examined contrasts between protected and impacted sites using Jaccard dissimilarity. Indicator taxa were identified using the *IndVal* approach (De Cáceres & Legendre 2009), which combines the specificity and fidelity of taxa within predefined groups. The statistical significance of indicator values was tested using Monte Carlo permutation procedures (999 permutations).

To isolate the overall effect of site status independently of temporal variability and nested spatial structure, a simplified PERMANOVA model was subsequently conducted using Jaccard dissimilarity. This complementary approach allowed us to evaluate whether differences between protected and impacted sites persisted when controlling for seasonal and local-scale heterogeneity.

Significance was assessed using 999 permutations. The homogeneity of multivariate dispersion was evaluated using PERMDISP (betadisper function from the vegan package, Oksanen et al. 2025) to test for differences in within-group variability. Differences in community composition among sites were visualized using non-metric multidimensional scaling (NMDS) to complement PERMANOVA results and to provide a graphical representation of compositional patterns.

Relationships between macroinvertebrate assemblages and environmental variables were analysed using redundancy analysis (RDA). Species data were Hellinger-transformed beforehand, while environmental variables were standardized to avoid scale effects. Collinearity among environmental variables was first examined through variance inflation factors (VIF) derived from the RDA model, and predictors showing excessive redundancy were removed before running the final ordination. Model significance was then evaluated using Monte Carlo permutation tests (999 permutations), considering both canonical axes and individual explanatory variables. Throughout the analysis, differences were considered significant at $p < 0.05$.

RESULTS

Taxonomic composition

Across the four sampling campaigns, a total of 1,779 macroinvertebrate individuals were collected, spanning 30 families, 62 genera, and 102 species (Supplementary Data 1; GBIF dataset: 10.15468/a66x3r). The assemblage was unevenly structured. A limited number of taxa contributed to total abundance. Among them, *Baetis rhodani* (Pictet, 1843) clearly dominated (202 individuals), whereas *Deronectes fairmairei* (Leprieur, 1876) and *Hydroporus discretus* (Fairmaire & Brisout, 1859) followed with lower but still notable counts (122 individuals each). In terms of species richness, Dytiscidae represented the most diverse family, accounting for 19 species.

Only a small subset of species persisted across all sampling periods. Nine taxa were consistently recorded, forming a relatively stable core assemblage. Beyond this group, species composition varied between post-drought and post-flood periods. Spring 2015 showed the highest richness and abundance (64 species; 965 individuals). In contrast, autumn 2014 was

characterized by a more restricted assemblage (34 species; 197 individuals).

Taxonomic and biogeographical composition

In terms of geographic distribution, Mediterranean species clearly prevailed (64%), although a substantial proportion of taxa belonged to wider distribution ranges (36%). Within the Mediterranean pool, contributions were uneven. West Mediterranean elements were the most represented (18%), followed by Holo-Mediterranean (12%) and Atlanto-Mediterranean taxa (9%).

Endemism patterns were dominated by Ibero-Maghrebian species, which represented the highest proportion (16%), while Maghrebien (5%) and strictly Moroccan taxa (4%) remained more restricted. Some species, such as *Choroterpes volubilis* (Thomas & Vitte, 1988), *Ecdyonurus ifranensis* (Vitte & Thomas, 1988), *Isoperla kir* (Fochetti & Vinçon, 1993), and *Siphonoperla lepineyi* (Navás, 1935), were exclusively confined to Morocco (Fig. 2).

Clear differences emerged between site categories. Protected stations supported a higher overall richness (82 taxa; mean of 21.7 species per site), whereas impacted reaches hosted lower richness values (63 taxa; mean of 14.6). This contrast was also reflected in the distribution of exclusive taxa. Forty taxa were recorded only in protected sites, compared to 21 restricted to impacted ones. At the site scale, variability remained high. Oued Stah (P7) exhibited the highest richness (33 species), whereas Oued Maadan (I5) showed the lowest richness (9 species) (Fig. 3). Moreover, protected sites supported a greater number of endemic species (21 taxa), whereas impacted sites hosted a comparatively reduced endemic pool (14 taxa).

Spatio-seasonal variation in community structure

Taxonomic richness varied across stations and sampling periods (Fig. 4). Richness was higher during the post-flood period (spring) than during the post-drought period (autumn). Mean richness reached 9.44 taxa in spring 2014 but declined to 3.16 taxa in autumn 2014. Temporal dynamics differed between years. Seasonal contrasts were less pronounced in 2015, with average richness values of 7.05 taxa in spring and 4.61 taxa in autumn.

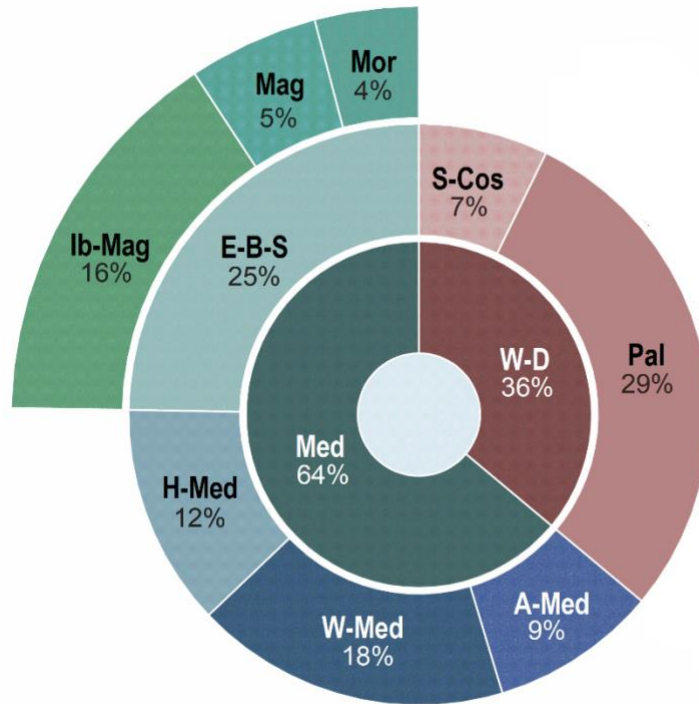


Figure 2. Main chorological categories of macroinvertebrate species recorded in the Upper Loukkos Basin. Abbreviations: W-D, wide distribution; Pal, Palearctic; S-Cos, subcosmopolitan; Med, Mediterranean; A-Med, Atlanto-Mediterranean; W-Med, West Mediterranean; H-Med, Holo-Mediterranean; E-B-S, endemic in the broadest sense; Ib-Mag, Ibero-Maghrebian; Mag, Maghrebien; Mo, Moroccan.

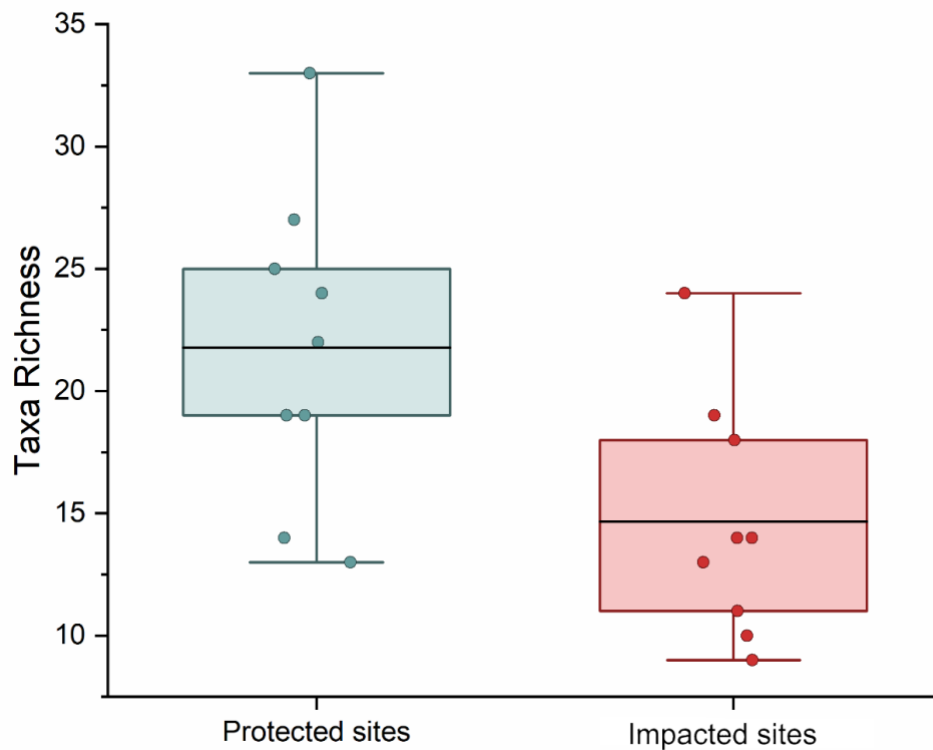


Figure 3. Variation in taxonomic richness across sampling sites, highlighting contrasts between protected and impacted areas.

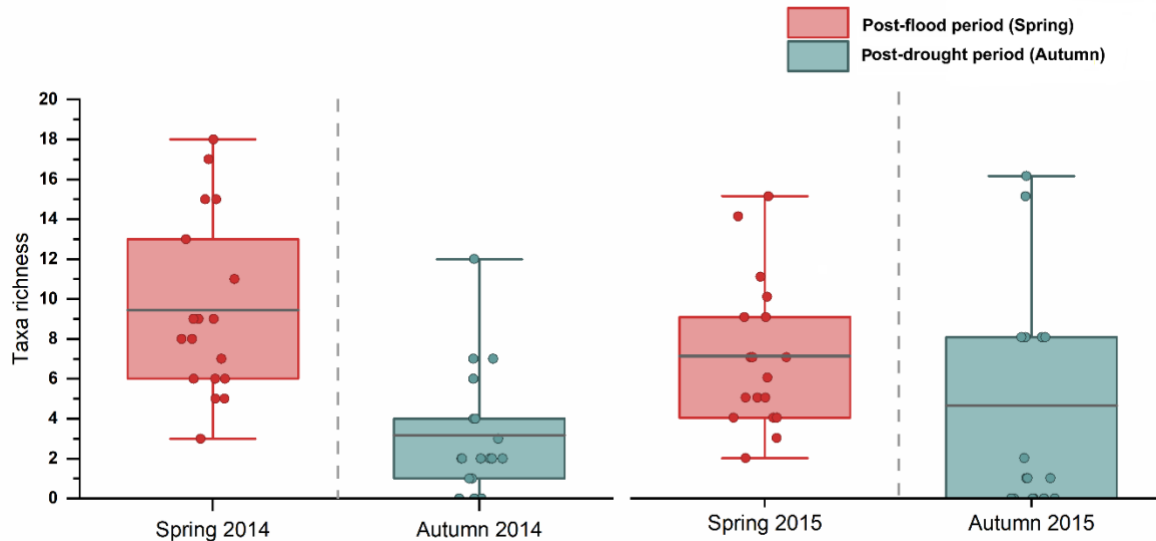


Figure 4. Seasonal variation in taxa richness during spring and autumn across the two sampling years (2014 and 2015).

Table 2. Indicator value (IndVal) and associated significance level (p) for macroinvertebrate taxa between protected and impacted sites.

Protected sites			Impacted sites		
Species	IndVal	p-value	Species	IndVal	p-value
<i>Graptodytes varius</i> (Aubé, 1836)	0.561	0.008	-		
<i>Hydraena allomorpha</i> Fresneda & Lagar, 1991	0.539	0.003			
<i>Rhyacophila munda</i> McLachlan, 1862	0.475	0.009			
<i>Hydropsyche pellucidula</i> (Curtis, 1834)	0.472	0.033			
<i>Hydroporus obsoletus</i> Aubé, 1836	0.440	0.026			
<i>Stictonectes optatus</i> (Seidlitz, 1887)	0.440	0.026			

IndVal > 0.5 = a very strong indicator

Table 3. Summary of PERMANOVA (adonis) results for macroinvertebrate abundance.

Source of variation	Df	Sum of Squares	R ²	F	p-value	Significance
Status	1	0.834	0.032	2.211	0.003	*
Season	1	0.448	0.017	1.187	0.194	ns
Year	1	0.812	0.031	2.152	0.002	*
Status × Station	16	8.138	0.313	1.349	0.001	**
Status × Season	1	0.322	0.012	0.853	0.715	ns
Status × Year	1	0.406	0.016	1.077	0.319	ns
Residual	40	15.082	0.579			
Total	61	26.040	1.000			

** p < 0.001, * p < 0.01, ns p ≥ 0.05; Df = degrees of freedom

Differences in species composition and habitat types

Indicator species analysis identified a small set of taxa significantly associated with protected sites (p < 0.05). Six species met the selection criteria, several of which showed relatively high indicator values,

particularly *Graptodytes varius* (Aubé, 1836) (IndVal = 0.561), *Hydraena allomorpha* (Fresneda & Lagar, 1991) (IndVal = 0.539), and *Rhyacophila munda* (McLachlan, 1862) (IndVal = 0.475), indicating a strong association with less disturbed conditions. No taxa were identified as indicators of impacted sites (Table 2).

To assess the influence of spatial and temporal factors on community composition, a PERMANOVA (adonis2) based on Jaccard distance revealed a significant effect of site status ($R^2 = 0.032$, $p = 0.003$), indicating weak but statistically significant differences between impacted and protected sites. Year also showed a significant effect ($R^2 = 0.031$, $p = 0.002$), suggesting interannual variability in community structure (Table 3).

However, the largest proportion of variance was explained by the nested factor station within status ($R^2 = 0.313$, $p = 0.001$), highlighting that local-scale spatial heterogeneity was the dominant driver of community structure, far exceeding the effect of site status.

To assess the overall effect of site status independently of other structuring factors, a simplified PERMANOVA model was applied to sampling sites using taxa richness summed across the four seasons (Table 4). Jaccard dissimilarity also revealed a significant difference in species composition between protected and impacted sites ($F = 1.70$, $R^2 = 0.096$, $p = 0.029$). However, the magnitude of this effect remained limited. A large proportion of taxa was shared between site categories, indicating an important overlap in species composition rather than clearly distinct assemblages. Moreover, no significant differences in multivariate dispersion were detected between groups (PERMDISP, $p > 0.05$).

Table 4. Results of Jaccard-based analysis comparing species composition between protected and impacted sites.

Source	Df	Sum of Squares	R ²	F	p-value
Type	1	0.5701	0.0959	1.6981	0.029 *
Residual	16	5.3717	0.9041		
Total	17	5.9419	1.0000		

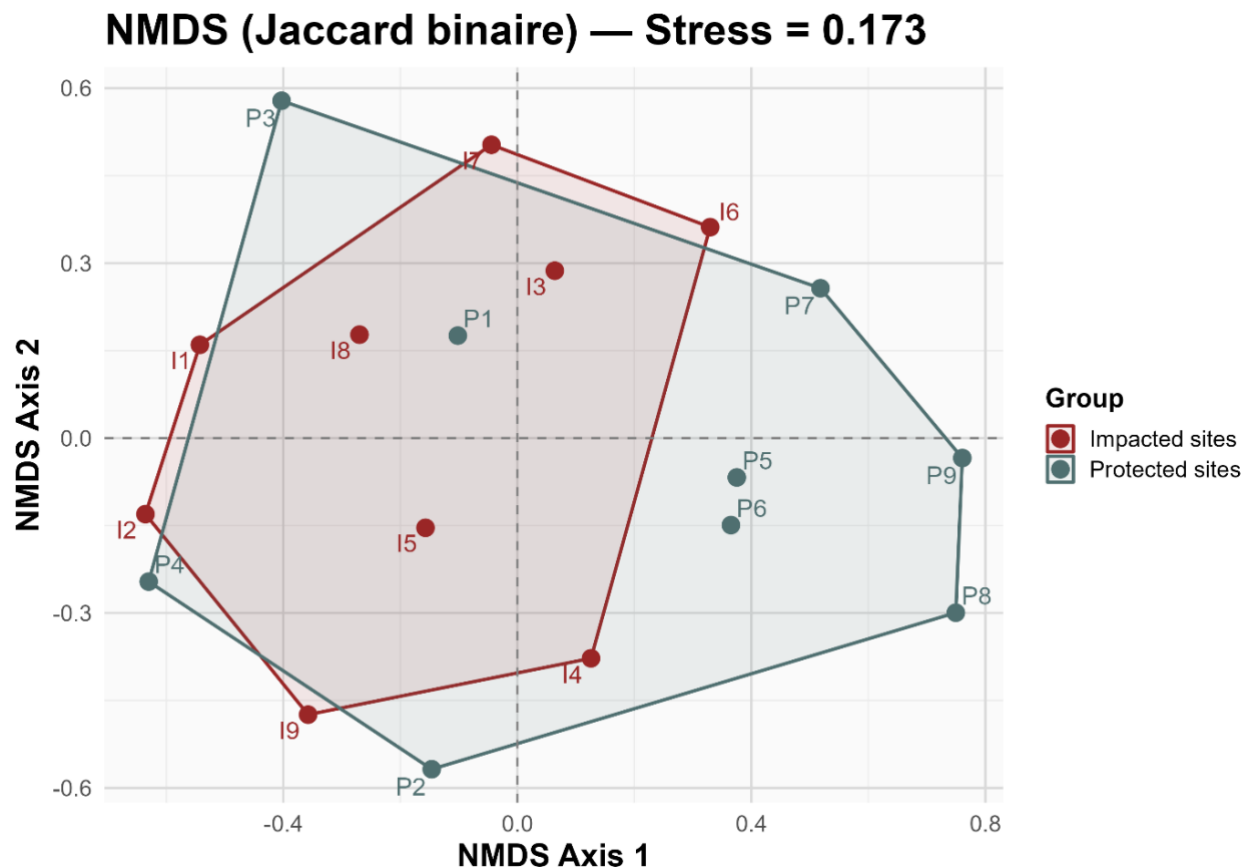


Figure 5. NMDS ordination of macroinvertebrate community composition based on Bray–Curtis dissimilarity.

Table 5. Summary of physical and chemical parameters measured at protected and impacted sites (mean $\pm$ SD).

Parameter	Unit	Protected sites	Impacted sites
Temperature	°C	17.2 $\pm$ 1.99	21.2 $\pm$ 1.58
pH	-	7.84 $\pm$ 0.163	7.92 $\pm$ 0.131
Electrical conductivity	$\mu\text{S}\cdot\text{cm}^{-1}$	556 $\pm$ 642	865 $\pm$ 283
Chloride (Cl^-)	$\text{mg}\cdot\text{L}^{-1}$	202 $\pm$ 306	211 $\pm$ 168
Nitrate (NO_3^-)	$\text{mg}\cdot\text{L}^{-1}$	1.88 $\pm$ 1.50	1.48 $\pm$ 0.601
Sulfate (SO_4^{2-})	$\text{mg}\cdot\text{L}^{-1}$	81.7 $\pm$ 53.3	115 $\pm$ 33.1
Dissolved oxygen (DO)	$\text{mg}\cdot\text{L}^{-1}$	4.64 $\pm$ 0.408	3.95 $\pm$ 0.646
Biochemical oxygen demand (BOD_5)	$\text{mg}\cdot\text{L}^{-1}$	18.8 $\pm$ 3.33	20.2 $\pm$ 3.08
Chemical oxygen demand (COD)	$\text{mg}\cdot\text{L}^{-1}$	39.6 $\pm$ 6.49	42.0 $\pm$ 5.69
Total suspended solids (TSS)	$\text{mg}\cdot\text{L}^{-1}$	58.7 $\pm$ 10.4	64.6 $\pm$ 10.5
Habitat Fluvial Index (IHF)	-	63.7 $\pm$ 4.02	57.3 $\pm$ 3.45
Riparian Quality Index (QBR)	-	56.8 $\pm$ 35.8	31.7 $\pm$ 15.2

Ordination analysis provided additional nuance. The NMDS solution (stress = 0.173) indicated a moderate fit of the ordination (Fig. 5). Rather than forming clearly separated clusters, samples were arranged along a gradient. Protected and impacted sites largely overlapped, although some internal structure was observed. A subset of protected sites (P7–P9) tended to be positioned toward the positive side of the first axis, whereas impacted sites were more dispersed across the ordination space. This broader dispersion may reflect a combination of environmental filtering and stochastic processes under disturbed conditions.

Environmental drivers of assemblage composition

Environmental variables showed considerable spatial variability. Water temperature ranged from 15.05°C to 22.9°C, with higher values generally observed at impacted sites. pH remained slightly alkaline across all stations. Electrical conductivity varied widely from 46.18 $\mu\text{S}\cdot\text{cm}^{-1}$ (O. Yema Souna, P6) to 2012 $\mu\text{S}\cdot\text{cm}^{-1}$ (O. Mlilah, P2), indicating strong differences in mineralization (Table 5).

Chloride concentrations ranged from 32.66 $\text{mg}\cdot\text{L}^{-1}$ (O. Khandeq louastiya, P8) to 988 $\text{mg}\cdot\text{L}^{-1}$ (O. Mlilah, P2), while nitrates varied between 0.455 $\text{mg}\cdot\text{L}^{-1}$ (O. Khandeq louastiya, P8) and 5.24 $\text{mg}\cdot\text{L}^{-1}$ (O. Harakate, P5). Sulfates ranged from 30.74 $\text{mg}\cdot\text{L}^{-1}$ (O. Stah, P7) to 186.3 $\text{mg}\cdot\text{L}^{-1}$ (O. Sgher, I7). Dissolved oxygen values were low overall, ranging from 3.4 $\text{mg}\cdot\text{L}^{-1}$ (O. Sgher, I7) to 5.39 $\text{mg}\cdot\text{L}^{-1}$ (O. Stah, P7).

Organic pollution indicators showed higher values at impacted sites, with BOD_5 ranging from 14.9 $\text{mg}\cdot\text{L}^{-1}$ (O. Mlilah, P2) to 24.3 $\text{mg}\cdot\text{L}^{-1}$ (O. Sgher, I7), and COD from 32.5 $\text{mg}\cdot\text{L}^{-1}$ (O. Mlilah, P2) to 49.7 $\text{mg}\cdot\text{L}^{-1}$ (O. Sgher, I7). TSS ranged from 47.4 to 77.42 $\text{mg}\cdot\text{L}^{-1}$. Habitat quality indices were higher at protected sites, with IHF reaching 69.75 (O. Stah, P7) and QBR 112.2 (O. Stah, P7), but dropping to 52.7 (O. Azoumagh, I8) and 17 (O. S. Mchich, I9) at impacted sites.

The RDA explained a substantial proportion of the variation in community composition (37.9%), and the overall model was significant ($F = 1.29$, $p = 0.029$). The first two axes accounted for 23.6% and 14.3% of the constrained variance, respectively (Fig. 6).

Along the first axis, a clear shift was observed. Protected sites (particularly P5–P9) were associated with higher values of IHF, QBR scores, and dissolved oxygen. In contrast, impacted sites tended to be positioned closer to the centre or on the negative side of the axis, where conductivity and ionic concentrations were higher.

The second axis represented a gradient related to organic enrichment. Higher scores were associated with increased COD, BOD_5 , suspended solids, and nitrate concentrations, whereas lower values corresponded to better habitat conditions. Several variables, including temperature, chloride, nitrate, and IHF, were identified as significant, although their effects were not independent and were attributable to combined environmental influences.

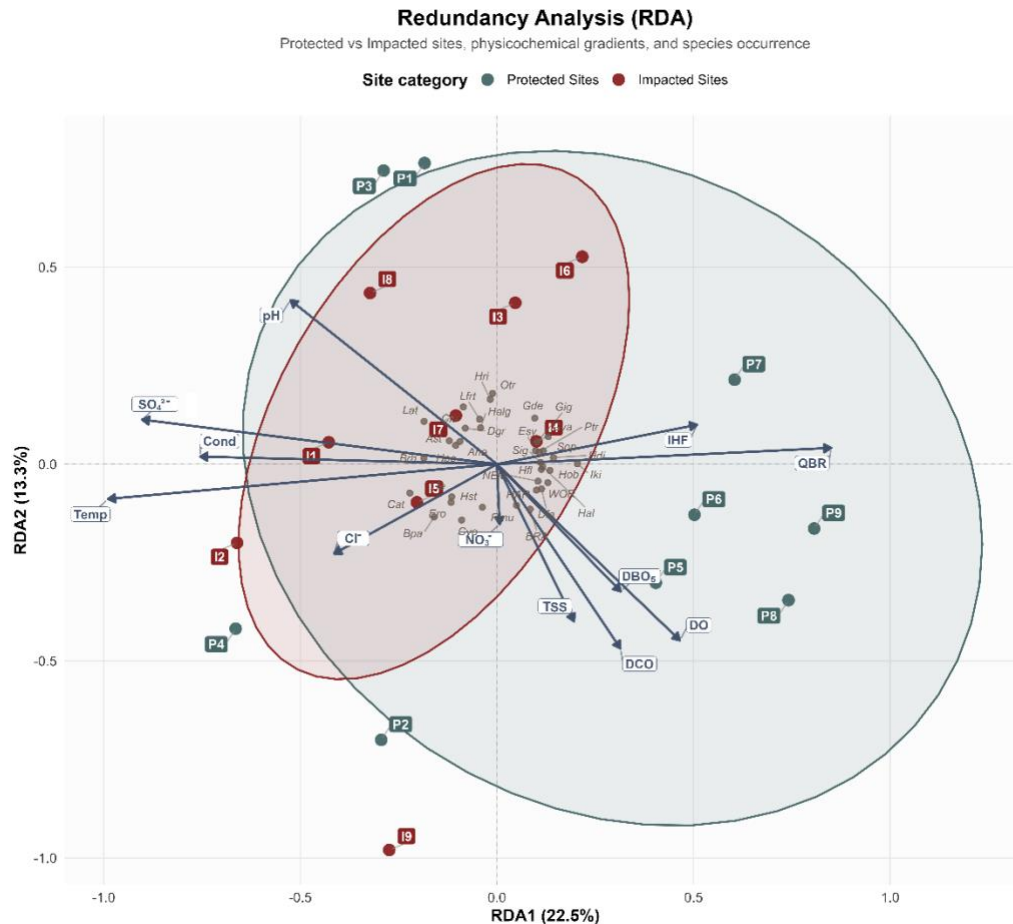


Figure 6. Redundancy analysis (RDA) showing relationships between macroinvertebrate communities and environmental variables. Protected and impacted sites are represented by different points and ellipses, grey dots indicate species distribution within the ordination space, and arrows represent the direction and relative influence of environmental variables on community composition.

DISCUSSION

Our study shows that macroinvertebrate assemblages in the Upper Loukkos Basin are structured by the combined effects of spatial and seasonal dynamics, with anthropogenically impacted streams favoring widespread and tolerant taxa compared to protected areas, where more sensitive assemblages were better maintained. Overall, the three hypotheses were supported. Macroinvertebrate assemblages appear to be shaped by interactions between hydroseasonal and local environmental filters, while protection status remains important, particularly for sensitive taxa.

The observed decrease in EPT (Ephemeroptera, Plecoptera, Trichoptera) richness, paired with a concomitant expansion of the OCH (Odonata, Coleoptera, Heteroptera), reflects this temporal reorganisation of assemblages. This pattern suggests a shift from taxa with high oxygen demand

and limited resistance traits to assemblages dominated by more tolerant and flexible organisms.

Some lotic taxa were able to persist under reduced flow conditions, suggesting a certain tolerance to environmental constraints. This may explain the continued presence of *Baetis rhodani* despite hydrological stress. Its recurrent dominance is consistent with previous studies describing this species as resistant under variable flow conditions (Guellaf et al. 2021a; Grgić et al. 2022; El Alami et al. 2022; El Yaagoubi et al. 2025; Ergović et al. 2025; Rimcheska et al. 2026).

During spring, taxonomic richness was higher, likely reflecting habitat heterogeneity and recolonisation following flow recovery (Ergović et al. 2025). While flow recovery played a key role, life-history traits also appeared influential, as many taxa seem to exploit this relatively stable and favourable period (Belmar et al. 2013; Grgić et al. 2022). This

was particularly evident in their contrasting responses: sensitive taxa were more closely associated with flowing and protected sites, as reported in Mediterranean freshwaters (Belmar et al. 2013; Theodoropoulos et al. 2015; Lobera et al. 2019).

Coleoptera, on the other hand, maintained relatively stable richness and abundance. Dytiscidae, the most diverse family, showed a pattern similar to that observed in other intermittent systems (Picazo et al. 2010; Theodoropoulos et al. 2015; Ergović et al. 2025). This stability appears to reflect both dispersal ability and physiological tolerance, thereby reinforcing their relevance as indicators of biodiversity in intermittent freshwater ecosystems (Guareschi et al. 2012).

Environmental gradients also contributed to structuring assemblages. Sites within the former limits of Bouhachem (P5–P8), located in the upper mountainous area of the Oued El Makhazine sub-basin, supported higher richness and more diverse assemblages under relatively stable conditions, typical of Mediterranean mountain streams. These areas may function as local refugia, allowing the persistence of sensitive taxa. In contrast, recently integrated protected sites (P1–P4) and impacted sites were associated with higher conductivity, organic enrichment, and a dominance of tolerant taxa, consistent with the environmental gradients identified in the RDA analysis.

Indicator species significantly associated with protected sites included Coleoptera such as *Graptodytes varius* and *Hydraena allomorpha*, which have been recognized in the Ibero-Maghrebian region as typical of well-preserved mountain freshwater streams (Millán et al. 2014; Benamar, 2015; Touaylia, 2017; Guellaf et al. 2021b). Similarly, indicator Trichoptera species such as *Rhyacophila munda* and *Hydropsyche pellucidula* are widely reported as characteristic of high-quality lotic habitats (Muñoz 2003; Bonada et al. 2008; El Bazi et al. 2017; Guellaf et al. 2021a). However, the limited number of indicator taxa may suggest that differentiation between site categories remains moderate, with impacted sites being dominated by tolerant and generalist taxa.

Differences between protected and impacted sites were noticeable but not absolute. NMDS analyses showed substantial overlap between assemblages, consistent with the relatively low effect size detected by PERMANOVA, indicating that

compositional differences remain limited despite statistical significance. Beyond the significant differences observed between protected and impacted sites, the dominant contribution of the nested factor (station within status), together with the low number of indicator taxa, supports the idea that community structure is shaped by interacting environmental filters acting across spatial and temporal scales, rather than being determined by protection status alone. This highlights the importance of multi-scale environmental filtering processes in intermittent systems, where spatial protection alone may not be sufficient to preserve freshwater biodiversity.

Similar overlaps across contrasting hydrological regimes and land-use contexts have been widely reported (Theodoropoulos et al. 2015; Nogueira et al. 2021; Giusto et al. 2026), reflecting consistent biogeographic responses to hydrological instability and environmental constraints.

In this context, interpretation remains limited by strong environmental variability and hydroseasonal dynamics (Bonada et al. 2007; Theodoropoulos et al. 2015). The intensity of floods and droughts further shapes assemblage patterns, particularly in winter and summer, which led us to focus sampling on post-flood and post-drought periods (Garcia-Roger et al. 2011). At this stage, relying solely on taxonomic patterns appears insufficient. Functional traits, connectivity, and multi-level interactions should be considered to better understand system responses to environmental change (Piano et al. 2020).

The predominance of western, Atlanto-Mediterranean, and especially Ibero-Maghrebian species reflects the biogeographical importance of the Rif region within the western Mediterranean basin (Médail and Quézel 1997; Bonada et al. 2008). The Betico-Rifan massif, acting as a historical connection between southern Iberia and northern Morocco, has favoured faunal exchange while maintaining endemic lineages. Within this context, the Upper Loukkos watershed, located in the Intercontinental Mediterranean Biosphere Reserve (IBRM), illustrates this biogeographical setting through the occurrence of regionally distinctive assemblages.

The results obtained suggest that conservation strategies based solely on spatial protection may be somewhat limited without considering hydrological dynamics and local

environmental conditions (Touaylia 2017). The expansion of protected areas should therefore be coupled with a careful evaluation of candidate sites. Moreover, conservation at the basin scale remains crucial, as protected areas may not fully guarantee the persistence of refugia or endemic taxa (Piano et al. 2020).

Treating rivers as hydrologically connected continua rather than isolated aquatic patches embedded within a terrestrial matrix is therefore fundamental, since the ecological stability of intermittent Mediterranean rivers depends on preserving exchanges among headwaters, refuge habitats, and downstream reaches (Nogueira et al. 2021). Under recurrent droughts, flow contractions, and increasing land-use pressures, the disruption of this continuity may progressively reduce the capacity of sensitive assemblages to persist, recolonize, and recover across highly variable hydrological conditions (Theodoropoulos et al. 2015).

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AUTHOR CONTRIBUTIONS

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