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A comprehensive spatial analysis of invertebrate diversity within intermittent stream networks: Responses to drying and land use

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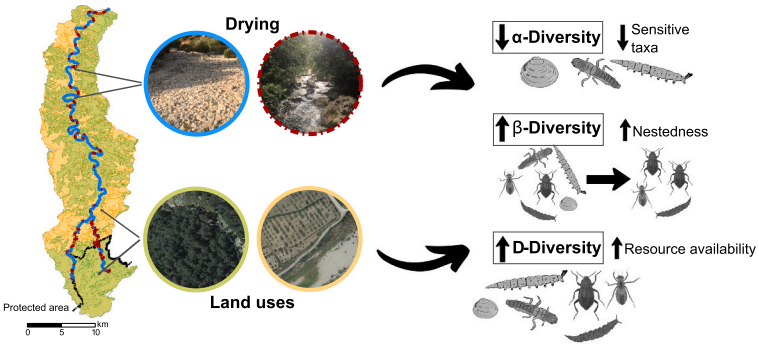
HIGHLIGHTS

- Drying reduces α-diversity, boosts β-diversity, and heightens nestedness.
- Moderate nutrients favour α-diversity and functional richness, not altering β-diversity.
- High habitat heterogeneity supports diverse taxa, including sensitive ones.

GRAPHICAL ABSTRACT



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ABSTRACT

Freshwater ecosystems are highly vulnerable to the impacts of climate change, which affect both diversity and ecosystem functioning. Furthermore, these ecosystems face additional threats from human activities, such as changes in land use, leading to water pollution and habitat degradation. Intermittent streams represent nearly half of all fluvial systems and support a rich diversity adapted to cope with drying. This study examines the impact of drying and different land uses on the taxonomic and functional diversity of aquatic invertebrates in a Mediterranean intermittent stream network. By sampling 16 reaches seasonally, we hypothesised that longer dry-phase duration and agriculture would both reduce α-diversity, with drying dominating impacts on β-diversity over agricultural practices. We anticipated that drying and agriculture would alter species and trait compositions, favouring desiccation-tolerant and generalist taxa. Drying adversely affected the taxonomic and functional α-diversity of aquatic invertebrates, while it positively influenced β-diversity. Land use only affected α-diversity. Specifically, habitat heterogeneity and increased water nutrient levels within the stream network correlated positively with invertebrate diversity. However, the negative effects of drying were less pronounced in upstream forested regions with high habitat heterogeneity compared to downstream areas influenced by agriculture. Our research highlights the importance of preserving natural and forested streams in intermittent networks, particularly in headwater regions, thus facilitating recolonization when flow is restored throughout the stream network.

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1. Introduction

Freshwater systems are among the ecosystems most threatened by human-induced climate change, which affects both freshwater diversity and ecosystem functioning (Parmesan et al., 2023). Consequently, the global distribution and extent of intermittent rivers are changing. Comprising almost 50 % of the global river network, intermittent watercourses are found in all climates, biomes, and continents (Messager et al., 2021). Although natural intermittent streams experience periodic flow interruption, the frequency and intensity of these interruptions have increased in recent decades due to anthropogenic alterations to hydrological regimes and regional water scarcity, increasing the spatial and temporal extension of flow intermittency and intensifying and prolonging dry periods (Datry et al., 2016).

Typically, flow interruption occurs irregularly across an intermittent stream network, creating a spatially and temporally dynamic mosaic of wet and dry sections (Datry et al., 2014). Intermittent streams are common in Mediterranean climates and are characterized by seasonal and predictable dry and wet periods (Bonada and Resh, 2013). Between late spring and early summer, the flow gradually decreases, leading first to the lentification of running waters and then to the formation of isolated pools by flow fragmentation, and depending on the intensity and duration of drying, the total dry-up of the streambed occurs. At the end of summer or in early autumn, rewetting usually occurs quickly due to heavy rainfall events, although it is sometimes re-established more gradually through a decrease in evapotranspiration and an increase in the groundwater level (Costigan et al., 2017).

Natural intermittent stream networks support high diversity and are adapted to cope with a certain level of drying (Bogan et al., 2017). The natural variability of intermittent streams results in temporal and spatial changes in α- and β-diversity across the stream network, as species in these streams exhibit traits such as aerial respiration or aerial dispersal ability, which promote their survival through strategies of either resistance or resilience (Bogan et al., 2017). For instance, at the reach scale, when flow disruption begins, macroinvertebrates characteristic of lentic pools replace lotic taxa through turnover (Bonada et al., 2006). The progression of drying leads to the disappearance of rheophilic and desiccation-sensitive taxa, reflecting a nestedness process (Stubbington et al., 2017) and negatively affecting α-diversity (Arias-Real et al., 2021). At the reach scale, when the water table recedes and the streambed dries, aquatic taxa can persist only in hyporheic refuges or as part of the invertebrate seedbank (Robson et al., 2011). However, increases in the intensity and extension of drying events can compromise the viability of *in situ* survival strategies (Crabot et al., 2021), as well as the persistence of perennial reaches, one of the sources of colonizers, becoming intermittent (Gill et al., 2022).

Intermittent stream networks have been both directly and indirectly impacted by changes in human activities in recent decades (Datry et al., 2018). For instance, the intensification of agriculture strongly influences water quality through the enrichment of water nutrients, particularly inorganic N and P concentrations, as well as pesticide pollution (Carpenter et al., 2011; Liess et al., 2021). Moreover, agricultural intensification leads to habitat destruction and increased water demand, which in turn influences hydrology (Allan, 2004). These factors affect aquatic diversity; experience alterations in their taxa and trait composition (Pallottini et al., 2017). For instance, in areas impacted by agriculture, generalist taxa of aquatic invertebrates typically increase in abundance, leading to reductions in both functional and taxonomic diversity (Lange et al., 2014). However, the specific effect of agriculture on invertebrate composition depends on stressor intensity (Piscart et al., 2009), and agricultural activity can positively influence the abundance or richness of invertebrates (Jähnig et al., 2021; van Klink et al., 2020). However, the impacts of agriculture on intermittent stream communities have been less studied, especially when evaluating entire stream networks and spatial distributions during drying (but see Cid et al., 2022; Datry et al., 2023). Specifically, the invertebrate communities in reaches with a high prevalence of agricultural activities paired with lower discharge, complete disconnection or dry out may be the most adversely affected.

The aim of this study was to analyse the changes in the taxonomic and functional diversities of aquatic invertebrate assemblages across an intermittent stream network under a Mediterranean climate with respect to different degrees of drying intensity and land use. To achieve this goal, we selected 16 sites within the Algars, a small stream network that transitions from forested headwaters to agricultural areas downstream, and collected macroinvertebrate samples seasonally over the course of a hydrological year. Specifically, we hypothesize that (1) sites with longer dry periods or those affected by agriculture, expressed as nutrient water enrichment, will exhibit lower taxonomic and functional α-diversities due to the disappearance of desiccation- or pollution-sensitive taxa; (2) this translates into shifts in the taxa and trait compositions towards desiccation-tolerant life stages and generalist taxa; and (3) temporal changes in β-diversity will be greater in drying sites than in agriculturally impacted reaches owing to desiccation-induced nestedness processes affecting sensitive taxa (Rolls et al., 2023).

2. Materials and methods

2.1. Study area and site selection

This study was conducted in the Algars stream network, which is located in the northeastern part of the Iberian Peninsula. It flows into the Matarranya River, a tributary of the Ebro River (Fig. 1). The stream network encompasses a total catchment area of 405 km^2 and features a 70 km long mainstream. The Algars headwaters comprise two streams, Estrets and Algars, both of which are located mainly in the natural park of Els Ports. The region's climate is typically Mediterranean, characterized by scarce precipitation concentrated in spring and autumn and drier and warmer summers. Extensive agriculture, predominantly olive groves, fruit trees, and vineyards, covers 44.6 % of the catchment area. The natural cover, which includes coniferous forests, bare rocks, sclerophyllous vegetation, and transitional woodlands–shrubs, constitutes 55.3 % of the catchment area. Urban land use is minimal, accounting for <0.45 % of the area (European Environment Agency, 2019). For this study, we selected 16 sites across the catchment: seven on the Estrets stream (headwaters), three on the Algars stream (headwaters), and six on the Algars mainstream after the confluence (Fig. 1). The two last reaches in each headwater stream, A3 and E16, were located outside of the Natural Park. This study spanned a hydrological year, from November 2018 to November 2019, during which the basin received a total of 368.9 mm of cumulative precipitation (Meteorological Service of Catalonia, METEOCAT).

2.2. Macroinvertebrate sampling and trait data collection

We conducted four seasonal samplings at each site and collected macroinvertebrate samples using a 250-μm mesh. At each site and during each sampling occasion, we collected a total of five replicate samples from different lotic and lentic zones using a Surber sampler (quantitative method; Storey et al., 1991), provided that the flow was connected. In cases where disconnected pools occurred in any of the reaches, we collected three-minute kick samples (semi-quantitative method) with a 250-μm net following a standardized multihabitat protocol that represented each habitat in proportion to its occurrence (Jáimez-Cuéllar et al., 2002; Storey et al., 1991).

All invertebrates were identified to the genus level following Tachet et al. (2010), except for Diptera (which were identified to the subfamily or family level), Oligochaeta (identified to the subclass level), Nematoda (identified to the phylum level), and individuals that were too small for accurate identification. Given the use of various sampling methods, and in order to facilitate comparisons between reaches, we pooled the replicates within each site and calculated the relative abundances of all the taxa.

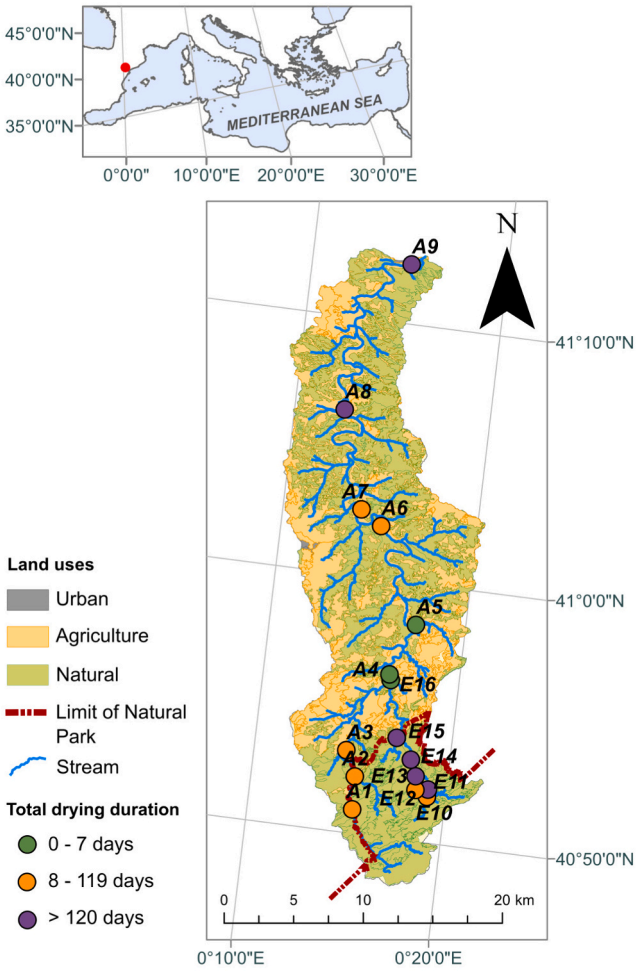

Fig. 1. Location of the Algars stream network in the Mediterranean basin and the site locations (points) inside the stream network. The background of the map is coloured according to land use: grey, urban; orange, agricultural; and green, natural. Points are coloured according to total dry-phase duration during the whole study period: green, permanent (0–5 days); orange, low and medium (6–119 days); and lilac, high (> 120 days).

To explore trait composition, we selected traits related to strategies to cope with both drying (i.e., drying traits) and nutrient-enriched water from two different databases (Múrria et al., 2020; Sarremejane et al., 2020a). The selected traits included maximum body size, life cycle duration, potential number of reproduction cycles per year, reproduction type, resistance forms, respiration type, locomotion, and propensity to drift. All traits were codified using a fuzzy code approach (Chevenet et al., 1994), and category scores were standardized to proportions by setting their sum to 1. Our final trait set included 30 categories belonging to 9 traits (Table S1).

2.3. Stream flow intermittency assessment

To characterize drying, we installed leveloggers (Solinst Levelogger Edge, with a full-scale reading accuracy of 0.05 %) on the streambed at each site to measure the water level and daily streambed temperature variation as an indicator of water presence throughout a hydrological year. To correct the recorded data, we used atmospheric pressure variations obtained from barologgers (Solinst Barologger, full-scale reading accuracy of 0.05 %) installed in the riparian zone of each site (Constantz et al., 2001). We calculated the total number of days without water (DD, dry-phase duration) and the total number of periods without water (DF, drying frequency) during the three months before each sampling occasion at each site (Tables 1 & S2).

2.4. Environmental parameters

During the study period, physical and chemical parameters were seasonally measured at each site (Table 1). At each sampling occasion, a portable probe (YSI Professional Plus Multiparameter Instrument, USA) was used *in situ* at each site to measure electrical conductivity, water temperature, water dissolved oxygen, and pH (±1 μS cm − 1, ± 0.1 °C, ± 0.1 mg L − 1 and ± 0.005 pH, respectively). However, water temperature and oxygen concentration were excluded due to inconsistent collection times affecting daily temperature variation. To characterize the water nutrient concentrations, three water samples were filtered through glass fiber filters (0.7 μm pore size; Whatman GF/F, Germany) into prewashed polyethylene containers, transported to the laboratory and stored at 4 °C in the dark until analysis. Water samples were analysed for soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) (nitrite, nitrate, ammonium) by ionic chromatography (± 2.8 % at 1 ppm; IC5000, DIONEX, USA). However, many samples had SRP concentrations below the detection limit (<0.005 mg/L) of the equipment, hence SRP was not considered in our analysis. Dissolved organic carbon (DOC) was measured using a TOC analyser (TOC-V CSH, Shimadzu Corporation, Japan) (Tables 1 & S2).

To characterize land use, we delineated the sub-basin of each site using a digital elevation model with a resolution of 25 m, computing the flow direction and applying a watershed tool with geospatial processing software (ArcMap 10, ArcGIS, USA). We simplified the categories of land-use cover to urban, natural, and agricultural land uses, adapted from European Environment Agency (2019) (Tables 1 & S2).

Additionally, we used a spherical densitometer (Lemmon, 1956) to calculate the average canopy cover percentage at each site, taking four measurements (upstream, downstream and right and left sides of the site) at three points for each site. The riparian quality and fluvial habitat indices adapted to Mediterranean streams (QBR and IHF, respectively) were calculated at each site and time (Tables 1 & S2) (Munné et al., 1998; Pardo, 2002). The QBR index measures the preservation rate of riparian ecosystems, with scores ranging from 0 to 100. It is calculated by summing the scores of four attributes: total cover of riparian vegetation, structure, complexity and naturality, and the degree of river channel alteration (Munné et al., 2003). The second index, IHF, assesses physical aspects of the riverbed related to habitat heterogeneity, largely dependent on hydrology and the existing substrate. This includes the frequency of rapids, variety in flow velocity and depth, substrate inclusion and sedimentation in pools, and diversity of substrates (Garcia-Burgos et al., 2015). Moreover, we calculated the Iberian Biological Monitoring Working Party (IBMWP) index, a measure of biological quality (Tables 1 & S2). The IBMWP is based on the invertebrate families identified, each assigned a score according to their sensitivity, which ranges from 1 (most tolerant organisms) to 10 (most sensitive organisms) (Alba-Tercedor, 2002; Munné and Prat, 2009).

2.5. Statistical analyses

2.5.1. Environmental exploration and variable selection

We explored the relationships between environmental variables for collinearity using Spearman correlation and bivariate scatter plots and selected variables with correlation coefficients <0.50. Multicollinearity was further assessed using the variance inflation factor (VIF) function of the usdm R package (Naimi et al., 2014), with a threshold set above 4. For subsequent analyses, we selected DD, DOC, and DIN concentrations; water conductivity; and the IHF index, treating the DIN concentration as an indicator of agricultural land use due to its high correlation with this variable (Spearman correlation: 0.70) (Lassaletta et al., 2009). The selected factors demonstrated VIF values ranging from 1.37 to 1.46, a reduction from initial values of 1.77 to 6.10. DIN, DD, and DOC were

Table 1
List of different variables used in this study, classified by explanatory and response variables.

	Type	Metrics	Description
Descriptor	Biological	**IBMWP** (Iberian Biological Monitoring Working Party)	Biological quality index based on invertebrate families presence
Explanatory variables	Environmental	**Water chemistry:** DIN, DOC, SRP	Measured at each seasonal sampling campaign
		Physicochemical: Conductivity, oxygen concentration and saturation, temperature	Measured at each seasonal sampling campaign
		Season: Au, Wi, Sp, Su	Season of sampling campaign
		Canopy cover	Percentage of canopy cover at each reach
		IHF (from *Índice de Habitat Fluvial*, index of fluvial habitat)	IHF, assesses physical aspects of the riverbed related to habitat heterogeneity
		QBR (from *Qualitat del Bosc de Ribera*, index of riparian forest quality)	QBR index measures the preservation rate of riparian ecosystems
		Land cover (%)	Percentages of agricultural, natural and urban land cover at each subbasin of studied reaches
	Hydrology	**DD** (dry-phase duration)	Total duration of dry periods previous to the sampling moment
		DF (drying frequency)	The total number of periods without water
		Hydrological conditions	Hydrological conditions at each sampling campaign (disconnected, connected, dry)
Response variables	Taxonomic α-diversity	**S** (taxonomic richness)	The total number of different taxa present
		H′ (Shannon–Wiener index)	Diversity measure that considers taxa richness and abundance
		EPT (Ephemeroptera–Plecoptera–Trichoptera index)	Proportion of Ephemeroptera, Plecoptera and Trichoptera taxa present
	Functional α-diversity	**FRic** (functional richness)	The minimum hypervolume of functional space occupied by a set of invertebrates
		FRed (functional redundancy)	The degree of functional equivalence among taxa within an ecosystem
	Taxonomic β-diversity	$\mathbf{T\beta D} = \mathbf{T\beta_{Replacement}}$ (species replacement) + $\mathbf{T\beta_{Richness}}$ (richness difference)	Temporal β-diversity was calculated using Sørensen family indices, which were partitioned into species replacement ($\beta_{Replacement}$) and richness difference ($\beta_{Richness}$) components
	Functional β-diversity	$\mathbf{F\beta D} = \mathbf{T\beta_{Replacement}}$ (species replacement) + $\mathbf{T\beta_{Richness}}$ (richness difference)	

square root-transformed to approximate a normal distribution because these variables exhibited a very skewed distribution.

To check for independence of the sites in the stream network, we employed empirical variograms to evaluate the spatial autocorrelation of the selected variables (Calder and Cressie, 2009) using the *GStat* R package (Gräler et al., 2016; Pebesma, 2004). None of the variables exhibited spatial correlation (Fig. S1).

2.5.2. Diversity metrics

For taxonomic α-diversity, we calculated the Shannon–Wiener index (H′), taxonomic richness (S), and Ephemeroptera–Plecoptera–-Trichoptera index (EPT) using the *vegan* R package (Oksanen et al., 2022) (Table 1). For functional α-diversity, functional richness (FRic) and functional redundancy (FRed) were calculated. FRic was determined as the minimum hypervolume of functional space occupied by a set of invertebrates (Villéger et al., 2008). The functional space, encompassing all taxa and traits, was constructed using a Gower dissimilarity trait matrix. This analysis was carried out through a principal coordinates analysis (Múrria et al., 2020) conducted using the *ade4* R package (Dray and Dufour, 2007). FRed was defined as the difference between the Simpson index of taxonomic diversity and Rao's quadratic entropy (de Bello et al., 2007). FRed is the degree of functional equivalence among species within an ecosystem and refers to the situation in which one specific ecological function can be carried out by one or multiple species (Naeem, 2008).

To analyse changes within the community, we calculated temporal taxonomic and functional β-diversity metrics (TβD and FβD, respectively) at each site using Sørensen family indices (Table 1). These were partitioned into species replacement ($\beta_{Replacement}$) and richness difference ($\beta_{Richness}$) components (Cardoso et al., 2014). For the taxonomic data, we employed a presence/absence-based approach using the *adespatial* R package (Dray et al., 2022). For the trait data, we computed the taxon Gower's distance matrix (Gower, 1971) and subsequently generated a dendrogram using hierarchical clustering analysis, which employed Ward's algorithm. The final step of calculating the functional β-diversity was carried out using the "beta" R function of the *BAT* package (Cardoso et al., 2022).

2.5.3. Regressions and models

To analyse the effects of environmental factors and dry-phases on diversity metrics, we constructed linear mixed models (LMMs) using diversity metrics as response and environmental factors and dry-phases and seasons as predictors. Stream reach was used as a random factor. To determine the best-performing LMMs, we employed a top-down approach for model evaluation and selection (Zuur et al., 2009). Model selection was based on the Akaike information criterion (AIC) and residual checks. The variance explained by each selected model was obtained using the 'r.squaredGLMM' function from the *MuMIn* R Package (Bartoń, 2023). Post hoc tests for pairwise season comparisons were conducted using estimated marginal means or least squares means through the 'emmeans' function of the *emmeans* package in R (Lenth, 2023).

To examine the effects of dry-phases and environmental factors on β-diversities and their partitions, we compiled annual environmental data and explored the relationships between them as explained above (Section 2.5.1). We used the square root-transformed DD, the square root-transformed percentage of canopy, and the percentage of agriculture in the reach area to analyse the effects of these variables on all the β-diversity components. We conducted a beta regression with a log link function using the 'betareg' function of the *betareg* R package (Cribari-Neto and Zeileis, 2010). We tested betareg models using the 'lrtest' function of the *lmtest* R package (Zeileis and Hothorn, 2002) and checked the diagnostic plots to assess the residuals.

To test the effects of dry-phase duration and land use on invertebrate community composition, we used generalized linear latent variable models (GLLVMs) in the R package *gllvm* (Niku et al., 2019). Rare taxa (<0.5 % abundance among all individuals and taxa with only one occurrence; Nijboer and Verdonschot, 2004) were excluded from the analysis to avoid convergence problems due to zero inflation, reducing the total number of taxa to 117. We built a GLLVM model with a zero-inflated Poisson distribution, log-link function, and one latent variable that excluded environmental predictors to generate a model-based unconstrained ordination. This approach allowed us to visually represent the similarity of the study plots based on species composition. To control for the effects of environmental factors on species, we included all possible combinations of environmental variables and time as constraining environmental predictors in the GLLVM. Due to the high computational demands of GLLVM, we limited the maximum number of predictors to three, resulting in 217 models ranked according to their second-order Akaike information criterion (AICc). We used likelihood

ratio tests (LRTs) to assess the predictive ability of the two competing models, and we calculated the proportional increase (%) in deviance explained by the best environmentally constrained model. To test for trait–environment interactions, we used fourth-corner models, where multivariate abundance data were regressed as a function of species traits and environmental predictors. Taxa traits were converted into factorial variables (Table S1). Specifically, we tested the interactions of the three most informative functional traits in the best environmentally constrained model, iterating all possible combinations of traits, resulting in 730 models that were ranked as explained before. We confirmed interactions between functional traits and environmental variables when the 95 % confidence intervals (CIs) of each trait–environment coefficient did not overlap zero. We evaluated the significance of the whole model using LRT between nested models with or without trait interactions (Niku et al., 2019).

3. Results

3.1. Characterization of the study sites

In the Algars stream intermittent stream network, drying primarily began in spring, where we observed disconnected flow in two reaches (E15 and A8). This continued into summer with four reaches becoming disconnected and five completely drying up. The number of days without water prior to the sampling campaign (DD) ranged between 21 and 100 days, with the dry phase predominantly occurring in summer (Table S2). However, in reach E11, water flowed only when it rained.

Regarding environmental characterization, the highest values of QBR and IHF, indicative of excellent riparian ecosystem and fluvial habitat status respectively, were observed in the headwaters. The IHF values, however, varied seasonally, displaying the lowest values in summer and in reaches experiencing a dry phase due to the loss of lotic habitats (Table S2). The highest percentage of agricultural catchment was found in the middle reaches, post-confluence (A4, A5, and A6), while the headwater reaches showed the lowest values (Fig. 1; Tables 2 & S2). DIN values also followed this pattern but changed seasonally; specifically, DIN values were higher in winter compared to autumn and spring, but almost all reaches showed the highest values in summer. Water conductivity was higher in autumn than in winter, slightly increasing in summer. However, two downstream reaches that were disconnected in summer (A8 and A9) showed a significant increase in this value (Table S2). The disconnected reaches in summer (A6, A8, A9) also exhibited an increase in DOC with drying. Generally, DOC values were lowest in autumn, with the highest values observed in winter and spring (Table S2).

The IBMWP index also varied seasonally, showing the highest values, which correspond to excellent ecological status, in two headwater reaches in spring (E12 and E14; Table S2). In nutrient-enriched and permanent reaches (A4 and A5) IBMWP values ranged between 69 and 105, almost corresponding to good ecological status. However, intermittent downstream reaches displayed values between 20 and 75, nearly corresponding to poor and deficient ecological status. In reaches where water was absent during the sampling campaign, the IBMWP assigned was 0 (Table S2).

3.2. Taxonomic and functional diversity

We identified a total of 87,645 individuals belonging to 194 distinct taxa, 82 families and 146 genera (Tables S3 and S4). Taxonomic (S) and functional (FRic) richness, as well as taxonomic diversity (H'), were highest in E10, a headwater reach located within the Natural Park ($S = 44 \pm 6$, $H' = 2.92 \pm 0.03$, and $FRic = 0.49 \pm 0.06$; Fig. 2), which experienced a short dry-phase duration of 41 days during summer. These metrics were comparable to those found in A4 ($S = 44 \pm 1$; $H' = 2.41 \pm$

Table 2
Physical, chemical and ecological characteristics of each study site, including the mean of IBMWP, biological index and its ecological meaning; the QBR index, riparian quality index; the mean of IHF, fluvial habitat index; the canopy cover (%); land cover (Agr, agricultural; and Nat, natural); the means of dry-phase duration (DD - total days without surface water in the three months prior to the sampling campaign); and the means of DOC and DIN (mg/L).

Reach	IBMWP	Ecological status (mean)	QBR	IHF	Canopy	Agr	Nat	Conductivity	pH	DD	DOC	DIN
E10	107.75 ± 9.29	Good	95	88 ± 0	59.38	33.41	66.59	318.00 ± 15.74	8.43 ± 0.11	26.50 ± 12.97	22.08 ± 7.22	1.00 ± 0.42
E11	0	Bad	95	34 ± 0	26.56	0	100	NA	NA	100 ± 0.00	NA	NA
E12	73 ± 20.93	Good	80	84 ± 6	25.78	0	100	537.73 ± 42.15	7.86 ± 0.16	9.25 ± 9.25	54.01 ± 18.21	0.22 ± 0.01
E13	57.25 ± 20.32	Poor	60	56.63 ± 19.56	13.54	33.41	66.59	489.27 ± 34.88	8.80 ± 0.28	35.75 ± 21.00	56.22 ± 27.30	0.17 ± 0.07
E14	75.25 ± 27.55	Good	95	53.29 ± 20.65	35.42	33.41	66.59	437.60 ± 58.12	8.63 ± 0.23	32.50 ± 15.34	41.72 ± 20.15	0.19 ± 0.08
E15	36 ± 13.20	Deficient	95	45.27 ± 15.76	26.3	0.21	99.79	371.77 ± 78.79	8.41 ± 0.19	90.75 ± 5.39	2.91 ± NA	0.10 ± 0.04
E16	89 ± 6.04	Good	85	61 ± 0	1.04	33.41	66.59	430.75 ± 25.25	8.77 ± 0.19	1.75 ± 1.75	32.61 ± 11.36	4.29 ± 1.94
A1	61.50 ± 5.24	Poor	95	61 ± 0	7.03	3.1	96.9	372.50 ± 18.05	9.02 ± 0.09	10.25 ± 10.25	29.98 ± 9.91	0.18 ± 0.05
A2	62.25 ± 9.01	Poor	80	73.50 ± 3.00	29.69	3.1	96.9	338.23 ± 30.75	8.95 ± 0.09	6.75 ± 6.75	25.55 ± 8.84	0.11 ± 0.03
A3	84.50 ± 11.61	Good	55	72 ± 0	2.6	3.1	96.9	412.28 ± 35.21	8.89 ± 0.19	13.75 ± 13.75	34.36 ± 10.97	0.57 ± 0.36
A4	98 ± 3.11	Good	55	53 ± 0	0	73.33	26.67	443.53 ± 33.81	8.85 ± 0.10	0	34.93 ± 11.24	5.26 ± 1.29
A5	81 ± 7.36	Good	10	63 ± 0	5.73	57.57	42.41	476.60 ± 42.41	8.70 ± 0.36	0	40.77 ± 13.20	3.77 ± 1.46
A6	53.75 ± 11.24	Poor	20	47.50 ± 5.00	0	57.57	42.41	460.83 ± 70.44	8.68 ± 0.35	16.75 ± 9.78	33.91 ± 15.87	4.57 ± 1.19
A7	38.25 ± 13.46	Deficient	10	67.82 ± 15.76	0	47.79	51.76	456.13 ± 40.53	8.90 ± 0.11	5.25 ± 5.25	32.22 ± 14.92	2.11 ± 1.22
A8	43 ± 10.56	Poor	50	49 ± 3.46	0	47.79	51.76	986.13 ± 473.30	8.78 ± 0.26	32.25 ± 19.80	44.66 ± 21.06	1.52 ± 0.99
A9	34.50 ± 10.72	Deficient	20	68 ± 2.00	4.95	46.73	53.03	1086.85 ± 346.18	8.53 ± 0.42	46.50 ± 25.05	100.97 ± 56.62	3.85 ± 0.0.70

0.27; FRic = 0.46 ± 0.02; Fig. 2), a perennial reach after confluence with a high DIN concentration (Table 2 & Table S2). The EPT was highest in the headwaters (A1 = 0.45 ± 0.05; E10 = 0.38 ± 0.02), which showed varied levels of intermittency. Conversely, S, H′, EPT and FRic were lowest in reaches with prolonged dry-phase durations (E13, E15 and A9) and downstream durations (A7, A8, and A9), with S ranging from 15 ± 5 to 21 ± 0, H′ ranging from 1.20 ± 0.42 to 1.48 ± 0.42, EPT ranging from 0.20 ± 0.08 to 0.29 ± 0.03, and FRic ranging from 0.22 ± 0.08 to 0.27 ± 0.01 (Table S5). The functional redundancy (FRed) was greatest at the headwater sites with short drying periods, with E12 having the highest value (FRed = 0.50 ± 0.01). In contrast, the FRed was lowest in reach E15, which exhibited the longest dry-phase duration (FRed = 0.35 ± 0.01).

The taxonomic and functional β-diversity indices showed the highest values in reaches that completely dried in summer (E13, E14, E15 and A7) (TβD = 0.36–0.41; FβD = 0.58–0.69), followed by reaches with remnant pools, while the lowest values were observed for reach E10 (TβD = 0.19 and FβD = 0.14). Among the 15 analysed reaches, the taxonomic β-replacement component represented >50 % of the TβD in 8 reaches, while the taxonomic β-richness difference dominated in the remaining reaches (Fig. 3a & Table S6), primarily in reaches that were completely dry in summer (E13, E14, E15, and A7). However, in the functional β-partitioning, a clear dominance of the functional β-replacement component was observed, except for the reaches that were completely dry in summer (E13, E14, E15, and A7), where functional β-richness differences also dominated (Fig. 3b & Table S6).

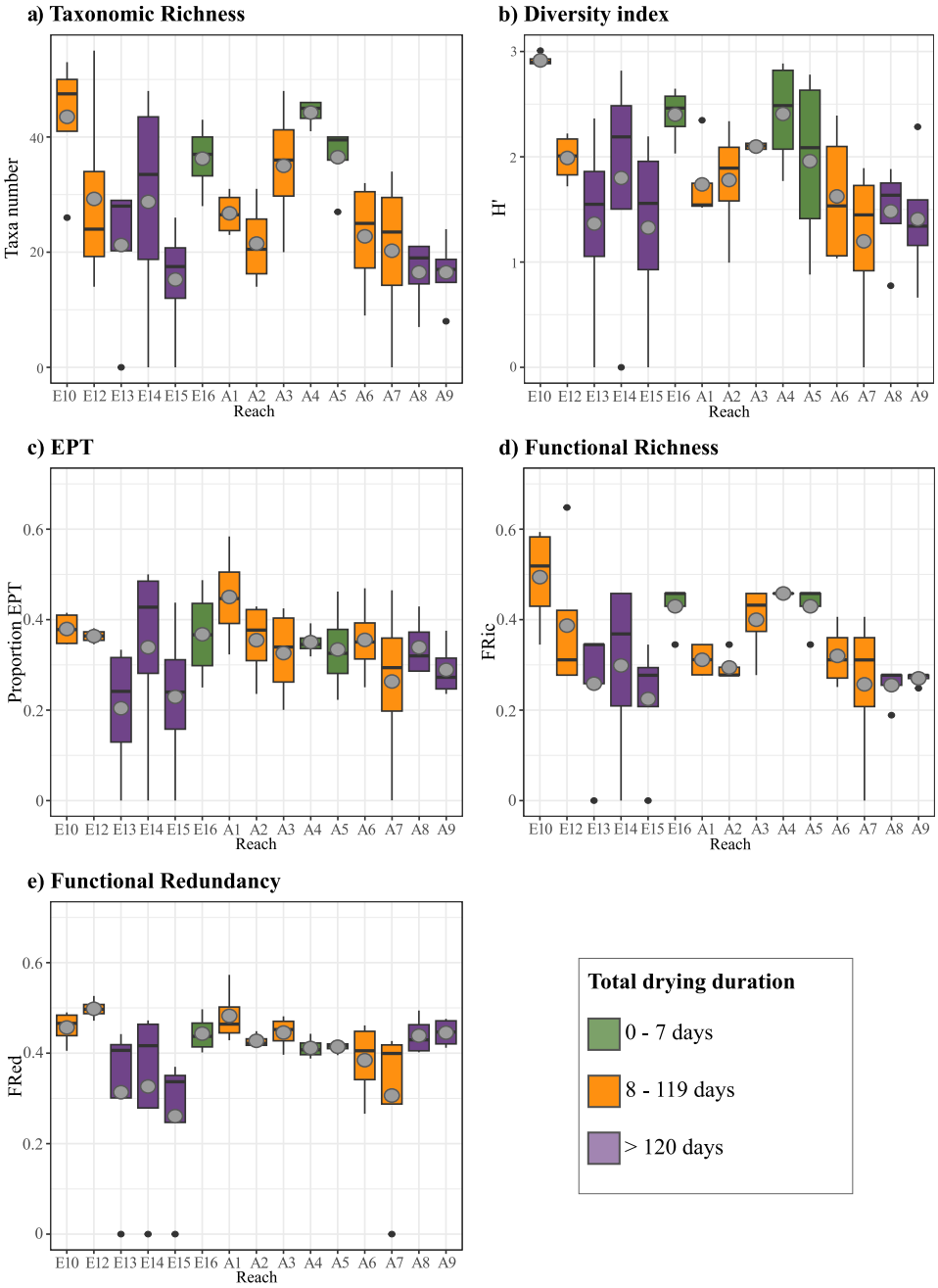

Fig. 2. Boxplots of a) taxonomic richness, b) diversity index, c) EPT, d) functional richness, and e) functional redundancy, categorized by reach. The mean values are represented by grey dots, and the median values are represented by black lines. Points are coloured according to total dry-phase duration (days) during the study period: green, permanent (0–7 days); orange, low and medium (8–119 days); and lilac, high (> 120 days).

3.3. Interplay between diversity metrics and environmental factors

Taxonomic richness and the proportion of EPTs were affected only by the sampling season. Post hoc analysis revealed that the taxonomic richness was lower in the summer season than in the spring ($t(41) = 4.116$, p value = 0.001) and winter ($t(41) = -4.006$, p value = 0.001). The proportion of EPTs was greater in winter than in summer ($t(39) = -4.524$, p value<0.001). Taxonomic diversity and functional richness were positively influenced by IHF and DIN but negatively influenced by dry-phase duration (Table 3). Functional redundancy was associated with conductivity, dry-phase.

duration, IHF, and sampling season and was found to be lowest in summer (autumn: $t(39) = -3.761$, p value = 0.003; winter: $t(39) = -4.934$, p value<0.001; spring: $t(39) = 4.008$, p value = 0.002). The reach (random factor) explained variances ranging from 0.19 to 0.53 (Table 3).

Conversely, dry-phase duration affected both the taxonomic and functional β-diversity indices and their components (Table 4). DD had a positive effect, except for taxonomic β-replacement, which was negatively affected by DD. The difference in functional β-richness was too small for meaningful comparison.

3.4. GLLVM results

The environmentally constrained GLLVMs that were selected included the sampling season, DIN concentration, and dry-phase duration as drivers of invertebrate species composition, collectively explaining 75 % of the covariation in the invertebrate species relative abundances. The ranked point estimates (±95 % CIs) obtained from this model indicated a strong association between the abundance of 55 % of the invertebrate species and at least one of the environmental variables, with sampling season having the greatest impact on a majority of the species (54 %) (Fig. S2). Drying, represented by DD, had a negative effect on the abundance and distribution of 6 % of invertebrate abundances, affecting less the community than sampling season (seven taxa: *Pisidium*, Bivalvia; *Atrichops* and sF. Clinocerinae, both Diptera; *Sialis*, Megaloptera; fam. Libellulidae, Odonata; *Chimarra* and *Holocentropus*, Trichoptera). None of the taxa were associated with the DIN water concentration, which is affecting less invertebrate community (Table S7).

The selected model, which included traits (maximum body size, resistance form, and respiration type), both with and without interactions, did not reveal any significant trait–environment relationships and failed to explain the observed variation in the invertebrate species community composition. Additionally, the inclusion of traits accounted for a smaller proportion of the variation (4 %) than did the environmentally constrained model. Only respiration type was negatively affected by all sampling seasons.

4. Discussion

In this study, we analysed the effects of drying and land use on invertebrate communities throughout a hydrological year in a Mediterranean stream network. We found that drying (represented by dry-phase duration, DD) negatively influenced the taxonomic and functional α-diversities of aquatic invertebrates. However, agricultural practices (represented by dissolved inorganic nitrogen, DIN) positively affected these diversities, partially contradicting our first hypothesis. In addition, we found that habitat heterogeneity positively influenced α-diversity, which was not initially proposed. Specifically, the negative effects of drying were less pronounced in headwater forested regions with high habitat heterogeneity than in downstream areas impacted by agricultural activities. Temporal changes in taxonomic and functional β-diversity were positively affected by drying, whereas no effect was

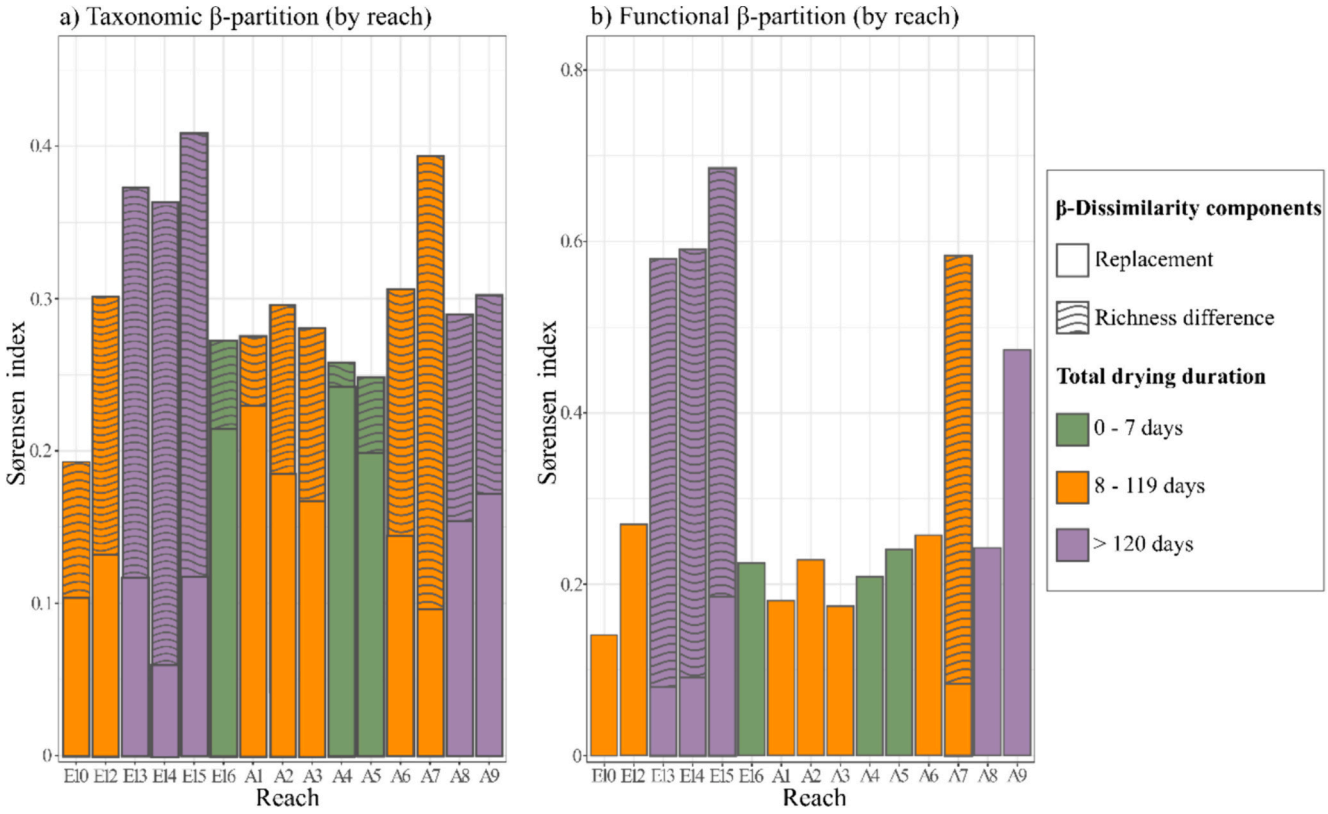

Fig. 3. Barplots of β-diversity categorized by site, including (a) taxonomic and (b) functional aspects. The bars are divided into two β-partitioning components: solid bars represent the replacement component, while the hatched bars depict the difference in richness. The bars are coloured according to total dry-phase duration during the study period: green, permanent (0–7 days); orange, low and medium (8–119 days); and yellow, high (> 120 days).

Table 3
Selected linear mixed models for each α-diversity index. Abbreviations: DD, total dry-phase duration; DIN, dissolved inorganic nitrogen; IHF, fluvial habitat index; canopy, percentage of canopy. Std. Error, standard error; DF, degrees of freedom. R^2 conditional, variance proportion explained by the whole model; R^2 marginal, variance proportion explained by fixed effects.

Index	Variables	Value	Std.Error	DF	*p*-value
S	(Intercept)	26.06	3.40	41	0.000*
	Conductivity	2.28	1.53	41	0.144
	Season.Spring	6.84	3.47	41	0.055
	Season.Summer	−7.46	3.49	41	0.038*
	Season.Winter	6.86	3.49	41	0.056
	R^2 marginal		0.17		
	R^2 conditional		0.57		
H′	(Intercept)	1.83	0.09	42	0.000*
	$\sqrt{DD}$	−0.16	0.09	42	0.03*
	$\sqrt{DIN}$	0.25	0.10	42	0.01*
	IHF	0.34	0.10	42	0.001*
	R^2 marginal		0.26		
	R^2 conditional		0.32		
EPT	(Intercept)		0.33	39	0.000*
	Conductivity		0.03	39	0.05.
	$\sqrt{DIN}$		0.03	39	0.06.
	IHF		0.03	39	0.07.
	Season.Spring		0.01	39	0.754
	Season.Summer		−0.08	39	0.022*
	Season.Winter		0.08	39	0.019*
	R^2 marginal		0.38		
	R^2 conditional		0.52		
FRic	(Intercept)	0.34	0.02	42	0.000*
	$\sqrt{DD}$	−0.03	0.01	42	0.037*
	$\sqrt{DIN}$	0.05	0.01	42	0.003*
	IHF	0.06	0.02	42	0.001*
	R^2 marginal		0.31		
	R^2 conditional		0.34		
FRed	(Intercept)	0.41	0.02	39	0.000*
	$\sqrt{DD}$	−0.03	0.01	39	0.03*
	Conductivity	0.05	0.01	39	<0.01*
	IHF	0.03	0.01	39	0.022*
	Season.Spring	0.02	0.03	39	0.582
	Season.Summer	−0.11	0.03	39	<0.01*
	Season.Winter	0.05	0.03	39	0.032*
	R^2 marginal		0.50		
	R^2 conditional		0.59		

Table 4
Beta regression summary tables. Abbreviations: DD, total dry-phase duration; DIN, dissolved inorganic nitrogen; IHF, fluvial habitat index; canopy, percentage of canopy. Std. Error, standard error; DF, degrees of freedom. Expl. Var., explained variance.

Index	Variables	Estimate	Std.Error	p-value
TβD	(Intercept)	−0.81	0.06	<2e-16***
	$\sqrt{DD}$	0.17	0.07	0.02*
	Agriculture	−0.06	0.07	0.42
	$\sqrt{Canopy}$	−0.1	0.07	0.16
	Phi coefficients (precision model with identity link):			
	(phi)	97.76	35.54	0.006*
	Log-likelihood: 24.89 on 5 Df		**Pseudo R^2:** 0.32	
Tβ-replacement	(Intercept)	−1.74	0.08	<2e-16***
	$\sqrt{DD}$	−0.24	0.1	0.02*
	Agriculture	−0.13	0.1	0.183
	$\sqrt{Canopy}$	−0.17	0.1	0.10.
	Phi coefficients (precision model with identity link):			
	(phi)	84.07	30.65	0.006**
	Log-likelihood: 27.69 on 5 Df		**Pseudo R^2:** 0.44	
Tβ-richness	(Intercept)	−1.75	0.15	<2e-16***
	$\sqrt{DD}$	0.53	0.18	0.003**
	Agriculture	−0.02	0.19	0.92
	$\sqrt{Canopy}$	0.02	0.18	0.93
	Phi coefficients (precision model with identity link):			
	(phi)	22.6	8.28	0.006**
	Log-likelihood: 20.1 on 5 Df		**Pseudo R^2:** 0.46	
FβD	(Intercept)	−1.16	0.1	<2e-16***
	$\sqrt{DD}$	0.27	0.12	0.031*
	Agriculture	0.01	0.13	0.94
	$\sqrt{Canopy}$	−0.12	0.13	0.33
	Phi coefficients (precision model with identity link):			
	(phi)	37.03	13.4	0.01*
	Log-likelihood: 19.17 on 5 Df		**Pseudo R^2:** 0.21	
Fβ-replacement	(Intercept)	−1.16	0.1	<2e-16***
	$\sqrt{DD}$	0.27	0.12	0.031*
	Agriculture	0.01	0.13	0.946
	$\sqrt{Canopy}$	−0.12	0.13	0.33
	Phi coefficients (precision model with identity link):			
	(phi)	37.03	13.4	0.005*
	Log-likelihood: 19.17 on 5 Df		**Pseudo R^2:** 0.21	

found for any land use-related variable. This finding is partially in line with our second hypothesis. Contrary to our third hypothesis, we identified only some taxa negatively affected by drying, whereas no taxa responded to land use.

4.1. Influence of drying and land use on α-diversity in the natural intermittent network

Regarding our first hypothesis, we found a negative relationship between dry-phase duration and both taxonomic and functional α-diversity. Contrary to our expectations, agriculture (expressed as water nutrient enrichment) positively affected these diversities. Furthermore, the fluvial habitat index (IHF) had a positive impact on these variables. The negative effects of dry-phases on invertebrate communities, such as decreases in diversity, reductions in organism numbers, and shifts in functional composition and structure, are well established (Bogan et al., 2013; Lake, 2000; Leigh and Datry, 2017). Our study corroborated that drying negatively influenced taxonomic diversity, functional richness, and functional redundancy. The latter showed an increase in moderate levels of drying (<120 days annually; Table S5), but it did not counterbalance the decline in taxonomic diversity caused by prolonged dry-phase periods (Crabot et al., 2021). In addition, no differences were detected in the number of taxa or in the EPT, which responded to the seasonal trend and predictable drying process, with the lowest EPT occurring during summer, the driest Mediterranean season (Bonada et al., 2007). Overall, aquatic invertebrates inhabiting the Algars stream network should be adapted to cope with both drying and seasonal patterns.

Our results suggested that the negative effects of drying were less pronounced in headwater forested reaches than in downstream areas impacted by agriculture, which may be attributed to the observed positive correlations between both α-diversities and the index of habitat heterogeneity (IHF). The IHF test assesses the relationship between habitat heterogeneity and physical variables and indicates high habitat heterogeneity and quality (Pardo, 2002). Habitat heterogeneity positively influences both taxonomic and functional diversity (Béjar et al., 2020; Milesi et al., 2016). Consequently, habitat heterogeneity can provide refuge areas for various taxa, enabling them to recolonize drying sites once the flow resumes (Dieterich and Anderson, 2000). In addition, habitat heterogeneity at drying sites can provide niches for adapted specialists, which replace taxa limited to less disturbed locations, thus decreasing diversity (Bogan et al., 2013). Furthermore, in Algars, the IHF had Spearman correlations of 0.85 with canopy cover and 0.60 with natural land cover in our study area. Headwater sites located within natural parks maintain natural riparian vegetation and are less impacted by human activities, resulting in enhanced habitat heterogeneity that supports increased invertebrate diversity (Castela et al., 2008; Urban, 2004). Hence, forested headwaters, such as those in Algars, may act as reservoirs for taxa with a range of adaptations to drying conditions (Progar and Moldenke, 2002).

Reaches with permanent flow and high agricultural influence had elevated α-diversity; conversely, intermittent reaches with high agricultural impact had the lowest α-diversity. Agricultural practices contribute to water quality deterioration and habitat destruction (Allan,

2004), but dissolved nutrients can increase the invertebrate density of some taxa (Niyogi et al., 2003), biomass (Rosemond et al., 2002), and species richness (Gruner et al., 2008) at low levels of nutrient water enrichment, as observed in the permanent reaches of Algars. This effect is attributed to the positive impact of increased water nutrient enrichment on aquatic decomposers and the enhanced quality of resources for aquatic invertebrates (Viza et al., 2022), particularly in nutrient-poor waters like the headwaters of Algars, where nutrients can be limiting (Gulis and Suberkropp, 2003). However, excessive levels can depress ecosystem function or specific species components (Clapcott et al., 2012; Wang et al., 2007). Furthermore, low-flow conditions can elevate water temperature, and evaporation can escalate water salinity and specific nutrient concentrations, particularly in the form of reduced solutes such as ammonium (Von Schiller et al., 2011). These conditions are particularly prevalent in open-canopied streams (Gómez et al., 2017), such as the downstream reaches in our study (Table S2). Moreover, during extended drying periods, organic matter and pollutants can accumulate and remain in situ until flow resumes, exposing biota to higher concentrations of contaminants, nutrients, and polluted sediments than under continuous flow conditions (Chiu et al., 2017). These factors can detrimentally impact stream invertebrate communities, especially sensitive taxa such as EPTs (Camargo and Alonso, 2006). Although we did not detect notable effects of land-use variables on EPT, our results suggested a negative impact on diversity due to the interplay between drying and agriculture.

Furthermore, the stream network under study is part of the Ebro basin, where water demand has increased by 57 % in the last 40 years, primarily due to the expansion of irrigated areas – a trend that is expected to continue (Grouillet et al., 2015). Irrigated agriculture impacts the environment not only by altering the flow regime but also by increasing nutrient loads in the water (Oduor et al., 2023). In addition, there is a decreasing trend in annual precipitation in the region, attributable to climate change (Senent-Aparicio et al., 2023), which further exacerbates drought events and, consequently, drying.

4.2. β-diversity driven by drying in the natural IRES network

In line with our second hypothesis, we observed that drying impacted temporal β- diversity, whereas no impact from agriculture was detected. Specifically, a positive correlation between the duration of dry phases and taxonomic β-diversity suggested alterations in the occupied trait space (Crabot et al., 2021). This positive relationship with dry-phase duration was also observed for the taxonomic richness difference component, indicating nestedness (Rolls et al., 2023). This effect likely results from desiccation-sensitive taxa being filtered out by drying conditions (Vander Vorste et al., 2021). For instance, individuals of *Atherix* sp. and *Hydropsyche* sp. were found at flow-connected sites in Algars during spring and summer but not at disconnected sites (Table S3). The negative effect of dry-phases on the taxonomic β-replacement component suggested that flow fragmentation may act as a barrier across the stream network, increasing some spatial differences. Specifically, flow fragmentation creates selective pressures on dispersers, largely due to the loss of habitat connectivity (Crabot et al., 2020). Moreover, our findings suggest that in the absence of drying, species replacement (or turnover) becomes predominant, driven by temporal shifts in community composition (Baselga, 2010; Sarremejane et al., 2020b).

Functional and taxonomic β-diversity, along with their associated components, showed distinct responses to drying, highlighting that functional responses supplement taxonomic information (Crabot et al., 2020). The functional β-diversity exhibited a positive relationship with drying, which was predominantly driven by the β-replacement component. This component constituted the whole functional diversity, except in reaches that experienced complete drying during summer. Considering the selected traits, alterations in functional β-diversity also supported seasonal trait replacement, suggesting that a community of invertebrates is well adapted to the predictable seasonal drying periods typical of Mediterranean climates (Bonada et al., 2007).

4.3. Limited direct impact of drying on taxonomic composition

In addition to our third hypothesis, we did not identify any specific traits or taxa influenced by variables related to land use. However, nutrient water enrichment positively affected several diversity metrics. Conversely, we identified only a few taxa negatively affected by drying. These affected taxa were active dispersers, suggesting their ability to repopulate post disturbance and, in some instances, possibly avoid the dry phase (Bogan et al., 2017). In addition, dispersal mechanisms in small stream networks, such as those in our study area, may lead to partial community homogenization ("mass effect"), especially with flow resumption (Heino et al., 2015). Among the affected taxa, *Atrichops* sp. does not exhibit traits associated with the capacity to face the in situ dry phase (resistance). However, it does possess traits related to avoiding the dry phase in water, such as a short life cycle duration ($\leq$ 1 year), or facilitating recolonization after flow resumes, such as active dispersal (resilience). Other taxa, such as *Sialis* sp. and *Pisidium* sp., exhibit resistance trait forms, such as cocoons against desiccation or diapause, respectively, but also display traits related to resilience to drying, such as active dispersal and multivoltinism, respectively (Bogan et al., 2017). Concerning dietary habits, almost all taxa affected by dry-phase duration were predators. Initially, they may benefit from drying due to prey accumulation in wet refuge areas, such as isolated pools, but are unable to cope with challenges in prolonged dry conditions (McHugh et al., 2015).

5. Conclusions

Our study highlights the more pronounced impact of the duration of dry periods on aquatic invertebrate diversity compared to the effects of different land uses within a natural intermittent stream network. Specifically, our findings suggest that both habitat heterogeneity and a certain level of agriculture in a catchment have positive effects on aquatic diversity. However, only habitat heterogeneity contributes positively to functional redundancy, reflecting more resilient communities in headwaters. This suggests that habitat heterogeneity can buffer the negative impacts of drying —a trend not observed at sites affected by agricultural activities. In conclusion, our research emphasizes the importance of preserving natural and forested streams. With the increasing spatial and temporal extent of drying events, which exacerbate flow intermittency and co-occurr with human-induced stressors, such preservation is essential. It can mitigate the adverse effects of drying and maintain aquatic refuges, ensuring recolonization opportunities once flow resumes across the entire stream network.

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CRediT authorship contribution statement

Aida Viza: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gemma Burgazzi:** Writing – review & editing, Supervision, Formal analysis. **Margarita Menéndez:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Data curation, Conceptualization. **Ralf B. Schäfer:** Writing – review & editing, Supervision, Formal analysis. **Isabel Muñoz:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

Data availability

Data is shared in supplementary material.

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