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Natural Disturbances and Connectivity Drive Seasonal Taxonomic and Trait Patterns of Aquatic Macroinvertebrate Communities Across Europe

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ABSTRACT

Aim: Understanding the joint influence of natural disturbance regime, connectivity and biogeography on the seasonal variation of community structure.

Location: Drying river networks (DRN) in Europe.

Time Period: Present.

Major Taxa Studied: Aquatic macroinvertebrates.

Methods: We analyse the taxonomic and trait structure of 638 macroinvertebrate communities sampled across 125 reaches with perennial and intermittent streamflow, surveyed in six DRNs across Europe, up to six times over 1 year.

Results: Richness and trait diversity of macroinvertebrate communities decreased with increasing drying frequency, but increased with spatio-temporal connectivity in reaches with long drying events. Communities experiencing frequent drying events had higher relative abundance of taxa with a long lifecycle and drying resistance traits. Communities experiencing long drying events compensated by high spatio-temporal connectivity, and had more taxa with high fecundity and high dispersal ability. Taxa richness peaked in summer but that pattern was more prominent when drying frequency was high. Trait diversity decreased throughout the year, showing increasing abiotic stress as the year progressed. Communities changed from communities of mobile, fecund, short-lived taxa in spring and autumn to communities of long-lived taxa in summer. However, when drying

frequency increased, autumn communities shifted towards communities of long-lived taxa. Macroinvertebrate community trait structure changed across Europe. It opposed communities from Mediterranean and/or upland DRNs (with more fecund and mobile taxa) to lowland DRNs (with more long-lived taxa).

Main Conclusions: Frequency and duration of drying events and spatio-temporal connectivity drive divergent macroinvertebrate community structures, suggesting the presence of an ecological threshold that explains the variability of disturbed ecosystems across broad spatial scales. These factors also influence seasonal variations, with macroinvertebrate communities shaped by distinct trait-filtering processes throughout the year based on drying frequency. Ultimately, spatio-temporal connectivity plays a crucial role in sustaining species richness and trait diversity in reaches experiencing intense drying.

1 | Introduction

Global change is profoundly altering natural disturbance regimes and seasonal climatic variability, with dramatic effects on biological communities (Harris et al. 2018; Heino et al. 2009). Natural disturbances—recurring events that cause sudden population mortality (Jentsch and White 2019; Miller et al. 2011) modify abiotic conditions, altering niche processes and disrupting habitat connectivity, which influences dispersal (Jacquet et al. 2022). Seasonal variability causes temporal fluctuations in environmental conditions, affecting species' life cycles and interactions (Mellard et al. 2019; Pau et al. 2011). Integrating these factors in the analysis of communities and understanding how they vary across biogeographical regions is essential to accurately forecast biodiversity responses to climate change (Holyoak et al. 2020; Tonkin et al. 2017).

Drying river networks (DRNs) provide an ideal system for studying these ecological processes. Representing a significant portion of global river systems, DRNs are crucial to maintaining biodiversity and ecosystem functions but face growing threats from global change (Messager et al. 2021). Intermittent reaches within DRNs experience drying events (i.e., flow cessation and resumption), which fragment networks and reduce hydrological connectivity, creating a shifting mosaic of wet and dry patches (Cañedo-Argüelles et al. 2015; Cunillera-Montcusí et al. 2023). Consequently, DRN communities are shaped by both stochastic and deterministic processes.

If stochastic processes prevail, meta-community theory (Leibold et al. 2004) predicts that intermittent reaches tend to host species-poor, randomly assembled communities due to local extinctions during drying events and stochastic recolonisation upon flow resumption (Pineda-Morante et al. 2022; Sarremejane, Mykrä, et al. 2017). Loss of hydrological connectivity exacerbates these effects by limiting dispersal, promoting ecological drift and reducing community richness (Carrara et al. 2014; Jacquet et al. 2022). Conversely, if deterministic processes prevail, drying and connectivity regimes will drive differences in macroinvertebrate trait structure, that is, mean trait values and trait diversity (Crabot, Polášek, et al. 2021; Gauthier et al. 2021). Some taxa have adapted to drying events by evolving resistance or resilience traits, and they are expected to be in higher proportion in intermittent reaches. For instance, macroinvertebrates, may endure dry phases through diapause or resistant life stages (e.g., eggs, cocoons). Based on community trait assembly theory (HilleRisLambers et al. 2012; Spasojevic et al. 2014), drying events should filter macroinvertebrate species with adequate resistance traits, thus decreasing community trait diversity. However, macroinvertebrates may also exhibit resilience traits (e.g., high dispersal ability, high fecundity or short generation times) that allow for rapid recolonisation once flow resumes (Datry et al. 2016; Sarremejane, Cañedo-Argüelles, et al. 2017). Well-connected intermittent reaches should support both resilience and resistance-adapted taxa, resulting in higher trait diversity compared to isolated intermittent reaches (Chester and Robson 2011).

Knowledge gaps remain regarding how DRN macroinvertebrate communities assemble across different drying regimes and biogeographical regions (but see Crabot, Mondy, et al. 2021; Vander Vorste et al. 2021). Community assembly may vary across intermittence regimes according to the frequency and duration of drying events. These variations are driven by climatic factors—such as the prolonged and frequent drying events characteristic of Mediterranean climates (Bonada et al. 2007; Tonkin et al. 2017)—or by geomorphological differences (Foulquier et al. 2024; Vander Vorste et al. 2021). However, the distinct effects of the frequency versus duration of drying events on the taxonomic and trait structure of macroinvertebrate communities across large spatial scales remain unexplored. Additionally, evolutionary legacies may influence community structure across DRNs, as Mediterranean taxa have experienced river intermittence since at least the last glaciation, whereas temperate taxa have only recently faced similar conditions. Mediterranean macroinvertebrate taxa had more time to evolve traits to cope with extended summer drying and high flow periods in spring/autumn. Thus, communities from Mediterranean DRNs likely support a higher number of taxa with resilience or resistance strategies compared to communities from temperate DRNs (Belmar et al. 2019; Bonada et al. 2007).

Further research is needed to understand how seasonal variations shape freshwater macroinvertebrate communities, particularly regarding trait structure shifts (Woods et al. 2022). General ecological expectations beyond freshwater communities suggest that, in intermediate latitudes, taxonomic and trait diversity peaks in summer as temperatures become favourable, with abiotic filtering dominating in late winter/early spring (Mellard et al. 2019; Pau et al. 2011). However, DRNs may deviate from these patterns. Even without complete drying, summer low flows can cause abiotic stress due to elevated temperatures and low oxygen levels (Bonada et al. 2020). Consequently, macroinvertebrate communities in intermittent reaches may display lower trait diversity during the summer because of a stronger abiotic filtering, as higher abiotic stress selects for similar resistance traits (Spasojevic et al. 2014; Stubbington et al. 2017).

Additionally, many macroinvertebrates adjust to seasonal hydrological changes via short, multivoltine life cycles, often peaking in early summer before intermittent reaches dry (Strachan et al. 2015).

Despite substantial research on DRN macroinvertebrate communities, existing studies often have limited spatial and temporal scope and rarely examine the combined effects of intermittence, connectivity and seasonality across biogeographical regions. To address these gaps, we sampled macroinvertebrate communities up to six times over 1 year across 125 reaches in six DRNs across Europe. This extensive dataset allowed us to explore how drying regimes—particularly drying frequency, duration and spatiotemporal connectivity—influence seasonal variations in macroinvertebrate taxonomic and trait structures across Europe. Our study aims to identify both general and context-specific drivers of community assembly in DRNs.

Specifically, we test four hypotheses:

1. Macroinvertebrate communities in reaches with a high frequency and/or duration of drying events will have lower individual density, taxa richness and trait diversity due to the filtering of taxa without traits to tolerate drying (Sarremejane, Mykrä, et al. 2017; Spasojevic et al. 2014).
2. Macroinvertebrate communities in reaches with a high frequency and/or duration of drying events but with greater connectivity to the broader river network will exhibit higher density, taxa richness and trait diversity, with greater representation of taxa with strong dispersal capabilities, compared to similarly drying but less connected reaches (Datry et al. 2016; Jacquet et al. 2022; Pineda-Morante et al. 2022).
3. Frequency and duration of drying events will drive the seasonal variation of macroinvertebrate communities (Hershkovitz and Gasith 2013; Sarremejane, Cañedo-Argüelles, et al. 2017): frequently drying reaches will show lower diversity than perennial reaches due to abiotic filtering in summer.
4. Mediterranean DRN communities, due to a longer history of river intermittence, will have a higher relative abundance of taxa with resilience and resistance traits than temperate DRN communities (Bonada et al. 2007).

2 | Methods

2.1 | Data

2.1.1 | Sites and Sampling Strategy

This study is part of the project DRYvER (Securing biodiversity, functional integrity and ecosystem services in DRYing riVER networks [DRYvER, Datry et al. 2021). Research was conducted across six European DRNs, spanning longitudes from −5.328 to 24.656 and latitudes from 36.430 to 60.481. Study sites covered five climatic zones (Figure 1): Mediterranean (Spain, Croatia), Continental humid (Czechia), Cold temperate (Finland),

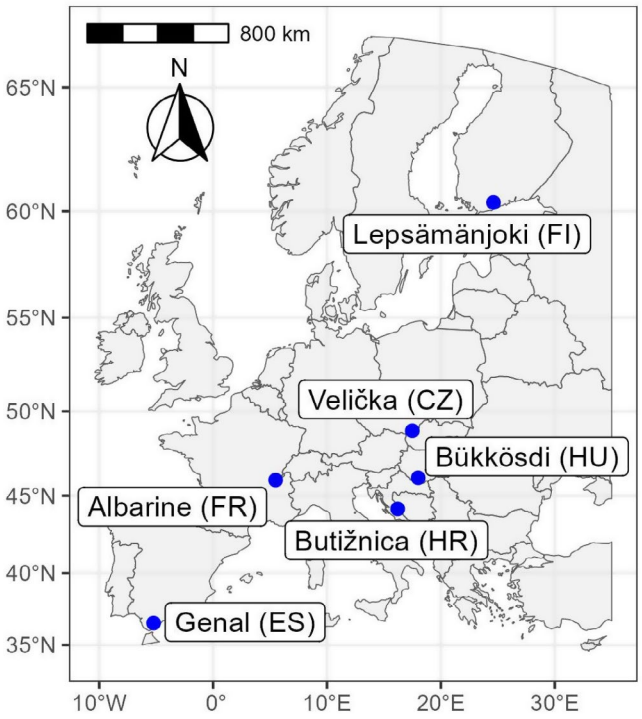

FIGURE 1 | Location of the six drying river networks in Croatia (HR), Czechia (CZ), Finland (FI), France (FR), Hungary (HU) and Spain (ES).

Pre-alpine (France) and Continental (Hungary). Four DRNs were situated in upland areas: Croatia (range of elevation: 220–1289 m), Czechia (170–534 m), France (219–1000 m) and Spain (11–1087 m). The others were in comparatively lowland areas: Finland (30–103 m) and Hungary (104–343 m). The latter were characterised by lower pH, oxygen concentration and particle size, with higher substrate embeddedness (see Figures S1–S4).

Each DRN included 15–26 reaches selected to represent the entire network, incorporating both main streams and tributaries. Reaches were chosen to ensure a balance of perennial and intermittent sites based on expert knowledge from scientific teams monitoring each DRN. Flow intermittence was quantified using a hybrid modelling approach that integrated multiple data sources (e.g., water level measurements, citizen science applications) to capture drying patterns beyond the initial classification (Mimeau et al. 2024). Reaches with significant anthropogenic hydromorphological alterations (e.g., channelisation, proximity to dams) were excluded to focus on natural drying events. Each sampling reach consisted of a river segment at least 50 m long and 20 times the maximum wetted width (measured during the first sampling campaign and held constant thereafter). This ensured the inclusion of multiple geomorphic units (e.g., riffles, pools) representative of the site.

2.1.2 | Hydrological Data

Using the modelling work of Mimeau et al. (2024) and its source data (see Appendix A), we estimated three descriptors of intermittence for each community:

- Frequency of drying events calculated as the number of drying events in the 5 years preceding community sampling.
- Duration of drying events was calculated as the average duration across all drying events in the 5 years preceding community sampling.
- Spatio-temporal river connectivity in the 30 days preceding each sampling campaign was estimated using the framework proposed in Cunillera-Montcusí et al. (2023): we quantified connectivity as the relative number of neighbouring reaches that each site was connected to within a 30-day period. Thus, spatio-temporal connectivity ranged between 0 (i.e., no connection to its potential neighbours in 30 days) and 1 (i.e., connected to all its potential neighbours in 30 days).

The distributions of frequency and duration of drying events were right-skewed, so we apply a square-root transformation to their values for all analyses. In the Supporting Information, we assessed the variation of spatio-temporal connectivity, frequency and duration of drying events across drying river networks and reach types (intermittent vs. perennial) as well as the variation of connectivity across the year (Figures S5, and S6).

2.1.3 | Community Data

Macroinvertebrates were sampled every 2 months in each DRN between January 2021 and February 2022 for a total of six sampled dates per DRN. Macroinvertebrates were not sampled when the reach was completely dry at the time of sampling. The samples were identified as often as possible to genus level, and we excluded terrestrial taxa from the analysis. Details about the sampling and identification process are available in the Supporting Information.

2.1.4 | Trait Data

To evaluate macroinvertebrate community trait structure, we combined two overlapping genus-level trait databases (Sarremejane et al. 2020; Tachet et al. 2010). We selected life-history traits and known resistance and resilience traits based on Stubbington et al. (2017): five were continuous (maximum body size, longevity, lifelong fecundity, drift, number of reproductive cycles per year) and two were categorical (dispersal mode—passive aquatic dispersal, active aquatic dispersal, passive aerial dispersal, active aquatic dispersal; and resistance forms—eggs; cocoons; diapause/dormancy; none). To visualise trait variation among taxa, we grouped taxa into four groups representing contrasted biological traits, as often used in aquatic ecology: EPT (Ephemeroptera, Plecoptera, Trichoptera—112 taxa), OCH (Odonata, Coleoptera, Hemiptera—75 taxa), OI (Other insects, here grouping mainly Diptera and Megaloptera—31 taxa) and finally NI (Non-Insects, including among others Mollusca, Crustacea and Annelida—72 taxa).

In total, across 636 community samples, we sorted and identified over 1.35 million aquatic macroinvertebrate individuals belonging to 290 taxa (240 at the genus level, 45 at the family and 6 at a higher taxonomic level). For trait-based analyses, we analysed 634 community samples containing a total of 1.3×10^6 individuals classified in 265 taxa with sufficient trait data (see Supporting Information for details about the trait database construction).

2.2 | Data Analysis

2.2.1 | Community Statistics

We analysed total density (as total number of individuals), taxa richness, average trait structure and trait diversity for each macroinvertebrate community. For abundance-based metrics (except total density), individual counts in the site by taxa matrix were log-transformed [$\log(x+1)$]. This transformation was necessary due to the disproportionately high local densities of certain taxa (e.g., *Gammarus* individuals reaching up to 30,000 per sample), which could otherwise skew abundance-weighted metrics.

To assess community structure in a multi-trait space, we employed a multivariate approach. First, we performed a correspondence analysis (CA) on the taxa relative abundance matrix. Next, we conducted a principal component analysis (PCA) on the trait matrix. Continuous traits—maximum body size, longevity, lifelong fecundity, drift, and number of reproductive cycles per year—were directly included. Dispersal and resistance traits, coded as fuzzy variables with four modalities each, were treated as independent traits in the PCA, with each modality weighted at 0.25 to ensure equal weighting of the original traits. We then integrated both analyses using co-inertia analysis (Dray et al. 2003), allowing us to visualise community samples, taxa and traits within a shared multivariate space (Figure 2).

To quantify the average multi-trait structure of communities, we extracted community scores from the first two axes of the co-inertia analysis, which explained 66% of the co-inertia between traits and communities (Moretti and Legg 2009). For each continuous trait and each modality of fuzzy-coded traits, we calculated the abundance-weighted mean within each community sample. Supporting Information provides associated results.

We measured multi-trait community diversity using Rao's quadratic entropy. To incorporate both continuous and fuzzy-coded traits, we used Gower's distance. Null trait diversity distributions were generated by permuting the columns (taxa) in the site-by-taxa abundance matrix. We then computed standardised effect sizes (SES) to assess deviations of observed trait metrics from random expectations. SES values were calculated as the difference between the observed metric and the mean of the null distribution, divided by the standard deviation of the null distribution. A negative SES value indicates that the metric is lower than expected, suggesting that species share similar traits selected by abiotic filtering. A positive SES indicates a higher-than-expected metric, implying niche differentiation driven by biotic interactions. An SES close to 0 suggests a random trait distribution, implying that stochastic processes (e.g., colonisation

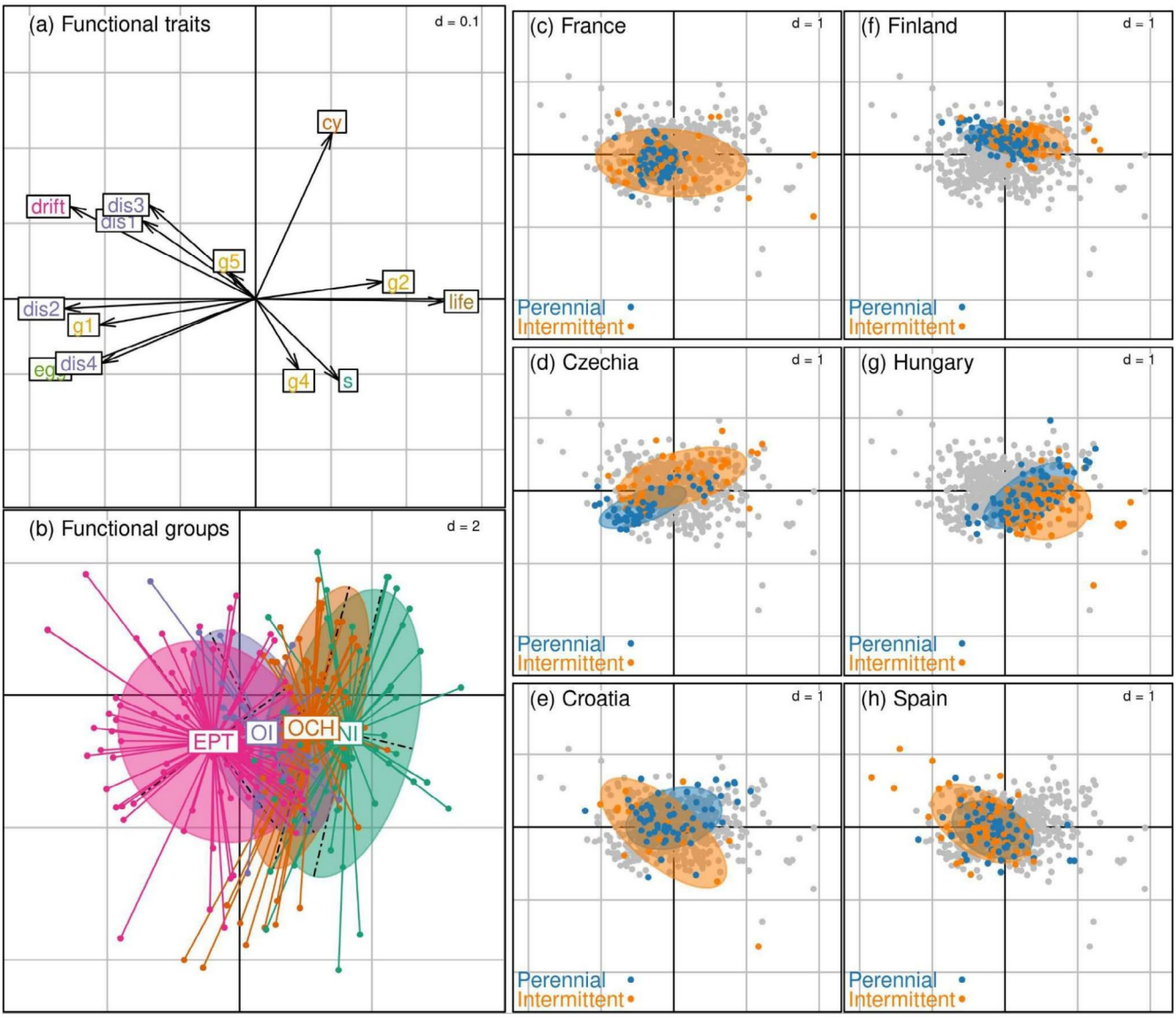

FIGURE 2 | Overview of the trait structure of macroinvertebrate communities. All sub-panels represent the scores of communities, macroinvertebrate taxa and traits along the first two axes of the co-inertia analysis on community and trait data. (a) Scores of traits. The font colour refers to each of the traits: the number of reproductive cycle (orange, 'cy'), dispersal mode (purple: 'dis1'—passive aquatic; 'dis2'—active aquatic; 'dis3'—passive aerial; 'dis4'—active aerial), drift frequency (pink; 'drift'); lifelong fecundity (green; 'egg'); resistance form (yellow; 'g1'—Eggs, statoblasts, gemmules; 'g2'—Cocoons; 'g4'—Dormancy; 'g5'—None); adult life span (brown; 'life'); body size (blue, 's'). (b) Scores of taxa grouped by taxonomic groups: EPT (pink) groups Ephemeroptera, Plecoptera and Trichoptera; OCH (orange) groups Odonata, Coleoptera and Hemiptera; OI (blue) groups other insect clades (i.e., Diptera and Megaloptera taxa); NI (green) groups all non-insect clades. (c–h) Positions of sampled reach communities. In all subpanels, communities across all DRNs and sampling campaigns are displayed. In each subpanel, we highlighted the communities associated with each DRN in blue (perennial reach communities) and orange (intermittent reach communities), communities from other DRNs are in grey.

and extinction) dominate community assembly (Spasojevic et al. 2014).

2.2.2 | Macroinvertebrate Community Structure Modelling

Using linear mixed models, we related community statistics at each reach (the two co-inertia axes, taxa richness and trait diversity SES) to multiple predictors:

- Spatio-temporal connectivity of the community within the river network during the 30 days prior to sampling.
- Frequency and average duration of drying events in the 5 years before sampling.
- Number of days after 01-01-2021 as a degree 2 polynomial covariate to model the temporal variation of communities over approximately 1 year. The variable was standardised.
- The identity of the drying river network to account for biogeographical effects among DRNs.
- Interaction terms between drying metrics and connectivity or day of the year to assess how intermittence interacts with spatio-temporal connectivity to shape community structure and how it may change the seasonal variation of

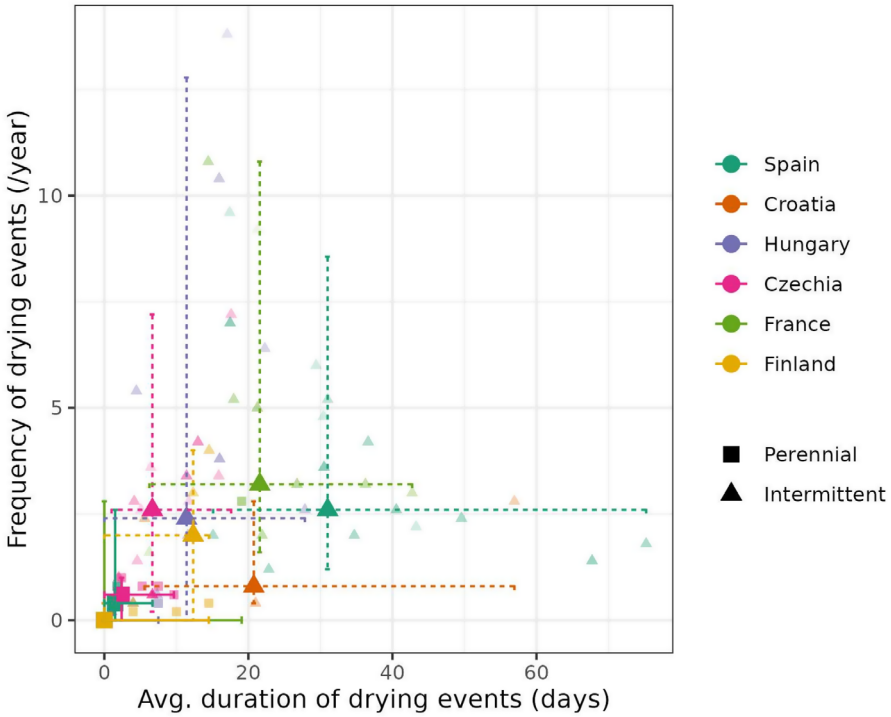

FIGURE 3 | Frequency and duration of drying events (calculated on a time window of 5 years). Small transparent points are the data points. Coloured triangles and squares represent the average frequency and duration of drying events for perennial and intermittent reaches in each DRN. Confidence intervals around large data points represent the 95% quantile interval of each category (solid for perennial, dashed for intermittent). Median values of each category (large, full points) were used to generate Figures 4 and 5.

communities. Interaction terms between connectivity and day of the year did not return significant patterns and thus were not included.

- A reach-level random effect to account for repeated sampling at the same reach and to account for spatial variation in environmental conditions among reaches (see Supporting Information).

For each community metric, we evaluated all the possible linear mixed models including all or a subset of terms, up to eight fixed effect terms using the function 'dredge' from R-package 'MuMIn'. Models were ranked according to corrected Akaike information criterion (AICc). We retained the single model with the smallest AICc as the 'best' model, computed its marginal and conditional R^2 (Nakagawa and Schielzeth 2013) to access the variance explained, respectively, by fixed effects only and both fixed and random effects.

Visualising those modelled relationships is complex due to the non-linear effect of time of sampling and the multiple interaction terms. To facilitate result interpretation, we computed the median levels of duration and frequency of drying events across intermittent reaches in each drying river network (Figure 3). In Figures 4 and 5, we displayed the predicted values of community metrics in each DRN and for those DRN-specific intermittent drying regimes and for values of duration and frequency of drying events equal to 0 ('perennial regime'). To visualise the predicted values of community metrics along continuous gradients of duration and frequency of drying events, refer to Figures S15 and S16.

We ran a sensitivity analysis on the effect of the time windows chosen to compute the frequency and duration of drying events (60 days, 90 days, 1 year, 2 years, 5 years and 10 years). It showed that, for a time window at least equal to 1 year, the models have similar high explanatory power (see Figure S3).

To better interpret multi-trait diversity patterns, we ran a similar analysis on single-trait community weighted means (Tables S4–S6).

All analyses were conducted using R version 4.3.1 (R Core Team 2024) using the packages: 'ade4' (Dray and Dufour 2007), 'gawdis' (de Bello et al. 2021), 'hillR' (Li 2018), 'lme4' (Bates et al. 2014) and 'MuMIn' (Bartoń 2012).

3 | Results

3.1 | Overview of Macroinvertebrate Community Trait Structure

The primary axis of the co-inertia analysis (49% of total co-inertia) between macroinvertebrate community and trait turnover was underpinned by a fecundity–longevity–dispersal trade-off continuum (Figures 2a and S13; Table S3). Taxa with more positive scores tend to display a long-lived adult phase (score = 0.25), lower fecundity (−0.24), higher body size (0.11), were overall less mobile (all dispersal traits have negative scores) and were more likely to exhibit a cocoon resistance form (0.17). Taxa with negative scores tend to display opposite trait features

as well as an egg-based resistance form (−0.2). They were often EPT taxa and other insect taxa (OI).

The second axis (17% of total inertia) separated taxa according to their reproductive strategy and some aspects of dispersal and resistance. Taxa with negative scores tend to have a single reproductive cycle per year (score = 0.21), have a large body size (0.11) and exhibit a dormancy resistance form (−0.09). Taxa with positive scores tend to have opposite trait features, as well as a higher probability of drifting (0.13) and having a passive aerial or aquatic dispersal mode (0.11 and 0.12 respectively). This axis was unrelated to the EPT/OCH/OI/NI classification (Figure 2b) but was more related to trait differences among macroinvertebrate orders (see Figure S13).

Macroinvertebrate community scores along the first two axes depended on their associated DRN and intermittence regime (Figure 2c-h, Table S3). Communities from perennial reaches had a less variable position along the first two co-inertia axes than communities from intermittent reaches (ratio of variance of the first axis = 0.46, p-value < 0.001; second axis = 0.55, p-value < 0.001). This variability was due to a DRN-dependent position of intermittent versus perennial reaches communities (Figure 2, Table S3). The trait diversity of community samples was overall high, with 88% of SES values above 0 (median value of 0.97).

3.2 | Drivers of Macroinvertebrate Community Structure

Linear models linking community metrics to duration and frequency of drying events, spatio-temporal connectivity, seasonality and biogeography explained a moderate proportion of the variance of community metrics (marginal R^2 between 0.20 and 0.33, Table 1). Linear models of macroinvertebrate community weighted means for all single traits displayed a similar performance with a marginal R^2 ranging from 0.24 to 0.38 (Tables S4–S6); except for the 'number of reproductive cycles' (marginal $R^2 = 0.08$). Accounting for random effects (i.e., site effects), the explained conditional variance was much higher and ranged from 0.52 to 0.76 indicating that much of the variation of community metrics among sites remained unexplained by the fixed effects of our models and may be attributed to local environmental contexts.

3.2.1 | Effect of Flow Intermittence on Macroinvertebrate Community Structure

Frequency of drying events had a moderate impact on most community metrics (Table 1). The total density of individuals and taxa richness decreased with frequent drying events. The score of community samples along the first and the second co-inertia axes increased with the frequency of drying events, indicating a higher relative abundance of taxa, reduced dispersal ability and/or multi-voltinism (Figure 4; Tables 1 and S4). This was confirmed by single trait analyses that detailed that this shift was due to a decreased relative abundance of taxa with a high score of aquatic dispersal ability (active/passive) or active aerial ability in frequently drying reaches (Table S5). Macroinvertebrate taxa were also less likely to exhibit an egg-based resistance form and more likely to exhibit a cocoon-based resistance form (Table S6).

Duration of drying events decreased trait diversity (Table 1). It also decreased scores along the second co-inertia axis, indicating a lower relative abundance of taxa with multi-voltinism. It further had some effects on individual resistance traits. In communities from reaches with a high duration of drying events, macroinvertebrate taxa were more likely to have a dormancy-based resistance form ($p < 0.001$) and less likely to have no resistance form ($p = 0.018$).

Spatio-temporal connectivity increased the total density of individuals and the trait diversity of communities. It decreased the score of community samples along the first co-inertia axis, indicating a higher proportion of fecund, short-lived taxa with a strong dispersal ability (Tables 1, S4, and S5). It had significant interaction effects with the frequency or duration of drying events (Table 1, Figure 4). The negative impact of the frequency of drying events on total density was compensated when the reach was highly connected to other reaches. The negative impact of the duration of drying events on richness and trait diversity was compensated when the reach was highly connected to other reaches. There was a marginal interaction effect between the duration of drying events and connectivity for the first axis of co-inertia analysis ($p = 0.067$, Table 1, Figure 4) indicating that highly connected communities with long duration of drying events had a higher relative abundance of taxa with high fecundity, low longevity and lower dispersal ability (Figure 1). This was confirmed by single-trait analyses that also detailed that this shift was due to an increased relative abundance of taxa with a strong drift ability ($p = 0.001$).

3.2.2 | Seasonal Variation of Macroinvertebrate Community Structure

Macroinvertebrate community structure varied significantly throughout the year and that variation depended on the frequency and duration of drying events. Total density of individuals peaked in summer. Trait diversity mostly decreased throughout the year after a slight peak in late spring (Table 1, Figure 5). Richness did not vary significantly throughout the year in reaches that experienced no drying events. However, when drying events occurred, richness had a bell-shaped relationship with a peak of richness in summer.

There was a significant interaction between the frequency of drying events and time of sampling for scores along the first axis of the co-inertia analysis. It showed that when drying events were infrequent, the relative abundance of less mobile, low fecundity and long-lived taxa of macroinvertebrate communities peaked in summer (Tables 1 and S4; Figure 5). In contrast, when drying events were frequent, communities shifted more linearly from fecund, short-lived and mobile taxa in spring to low fecundity, long-lived and less mobile taxa in late summer/autumn. That pattern was due to the decreasing relative abundance of taxa with passive and active aquatic dispersal throughout the year (Table S4).

TABLE 1 | Summary of the linear mixed models between community metrics and intermittency, seasonal and connectivity factors.

	Total density (log ind/m²)		Richness		1st Co-inertia axis		2nd Co-inertia axis		Func. diversity	
Predictors	**Estimates**	***p***	**Estimates**	***p***	**Estimates**	***p***	**Estimates**	***p***	**Estimates**	***p***
(Intercept)	7.62	**<0.001**	25.17	**<0.001**	0.05	0.660	0.15	**0.011**	1.03	**<0.001**
DRN [Czechia]	0.66	**0.008**	4.63	0.058	−0.13	0.348	−0.16	**0.034**	−0.26	0.200
DRN [Finland]	0.00	0.996	0.05	0.982	0.20	0.142	0.05	0.486	−0.31	0.111
DRN [France]	−0.10	0.678	6.45	**0.008**	−0.06	0.669	−0.21	**0.004**	0.35	0.080
DRN [Hungary]	0.70	**0.002**	1.76	0.447	0.46	**0.001**	−0.28	**<0.001**	−0.35	0.064
DRN [Spain]	−0.66	**0.007**	6.48	**0.007**	−0.28	**0.041**	−0.04	0.622	0.45	**0.022**
Drying dur.			−0.52	0.320	−0.01	0.679	−0.04	**0.020**	−0.15	**0.004**
Drying freq.	−0.58	**<0.001**	−4.46	**<0.001**	0.11	0.101	0.10	**0.009**	0.11	0.371
Connect.	0.40	**0.045**	1.64	0.213	−0.15	**0.013**	0.05	0.088	0.27	**0.011**
Connect.:Drying dur.			0.97	**0.042**	−0.04	0.067			0.24	**<0.001**
Connect.:Drying freq.	0.48	**0.004**							−0.60	**<0.001**
Day	0.27	**<0.001**	0.51	0.146	0.07	**0.001**			−0.05	0.059
Day:Drying dur.					0.02	**0.003**				
Day:Drying freq.					−0.08	**<0.001**				
Day²	−0.28	**<0.001**	−0.02	0.954	−0.05	**0.012**	−0.07	**<0.001**	−0.04	0.110
Day²:Drying dur.			−0.31	**0.003**			0.02	**<0.001**		
Day²:Drying freq.					0.04	**0.021**	−0.06	**<0.001**		
Random effects										
σ^2	0.96		37.82		0.07		0.04		0.25	
τ_{00}	0.27_{site}		37.67_{site}		0.14_{site}		0.03_{site}		0.25_{site}	
ICC	0.22		0.50		0.67		0.49		0.51	
N	125_{site}		125_{site}		125_{site}		125_{site}		125_{site}	
Observations	632		636		634		634		634	
Marginal R^2/Conditional R^2	0.325/0.473		0.210/0.604		0.272/0.762		0.241/0.610		0.206/0.608	

Note: The default modality of the DRN factor refers to the Croatian DRN. Day refers to 'day of the year'; 'Connect.' to spatio-temporal connectivity; 'Drying dur.' to duration of drying events; 'Drying freq.' to frequency of drying events. *P*-values inferior to 0.05 are in bold.

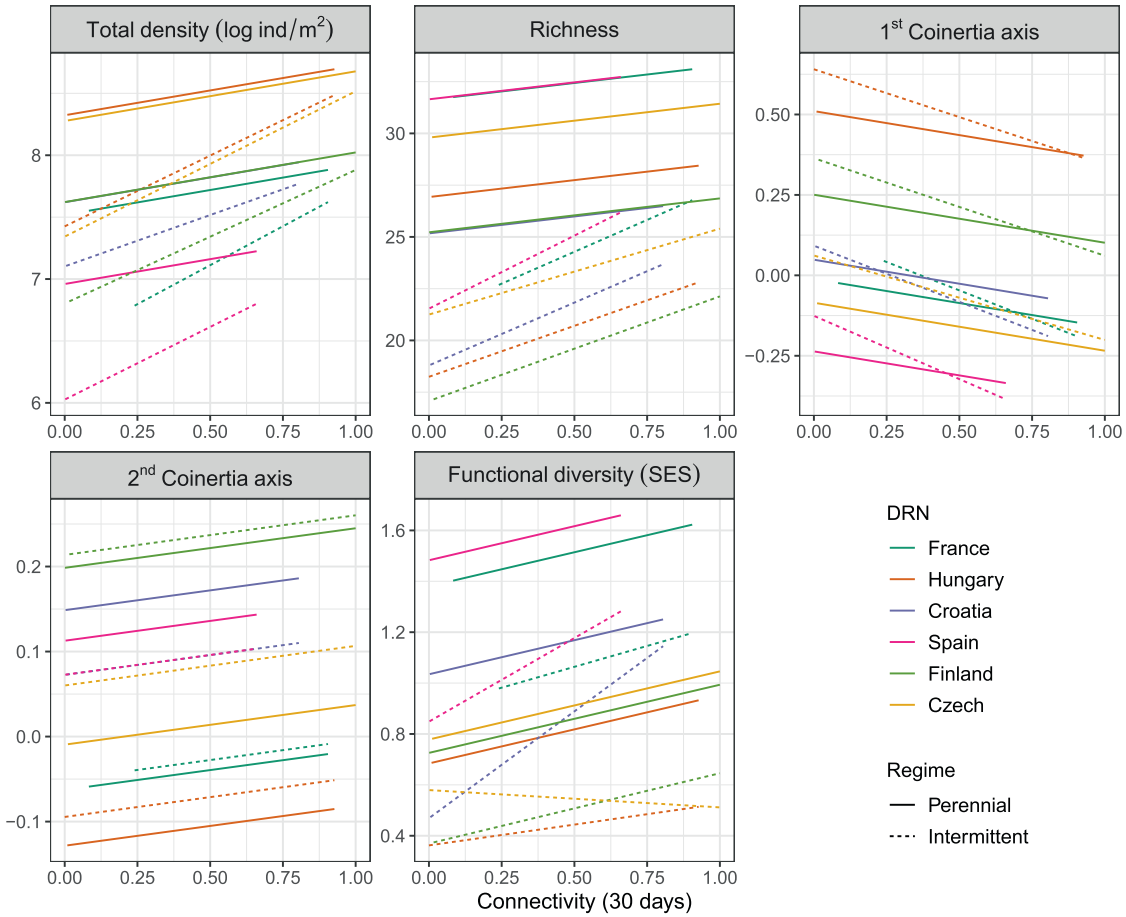

FIGURE 4 | Predicted effect of spatio-temporal connectivity on community structure in 'perennial' (no drying) and according to the median drying regime of intermittent communities in each DRN. The graphics display the effect of the spatio-temporal connectivity in the 30 days prior to sampling on community structure. To visualise the interaction effects of spatio-temporal connectivity, drying predictors and DRN, we displayed the predicted relationships between community metrics and spatio-temporal connectivity for 'perennial' reaches (drying frequency and average duration of drying events equal to 0) and for the median levels of duration and frequency of drying events of 'intermittent' reaches specific to each drying river network (Figure 3). The day of sampling was fixed at 191.6 (average sampling day). Community structure is described by the total density of individuals (log-transformed), community richness, the two first axes of the co-inertia analysis describing the main trait turnover between communities and the standard effect size of trait diversity.

Communities sampled in summer also had higher scores along the second co-inertia axis indicating, notably, a higher relative abundance of taxa with multiple reproductive cycles and small body sizes (Table S3). This pattern was stronger in communities experiencing frequent drying events and less so in communities experiencing long drying events (Table 1).

3.2.3 | Variation of Macroinvertebrate Community Structure Across DRNs

After accounting for differences in duration and frequency of drying events and connectivity, there was a remaining, significant effect of DRN on macroinvertebrate community structure.

Macroinvertebrate communities from the Hungarian DRN had a higher density of individuals ($p < 0.001$). Community samples also had a higher score on the first co-inertia axis, indicating a higher relative abundance of long-lived and less mobile taxa (Tables 1 and S3), in particular for passive/active aquatic dispersal and passive aerial dispersal (Table S4). They also had a more negative score along the second co-inertia axis (Figure 2, Table 1). This was due to a higher relative abundance of macroinvertebrate taxa with a large body size and a low probability of drifting (Table S3). In contrast, communities from the Spanish DRN had a higher taxa richness ($p = 0.002$), a higher trait diversity ($p = 0.022$) and a lower score along the first co-inertia axis ($p = 0.046$). This was due to a higher relative abundance of taxa with a short lifespan and a stronger aerial passive or active ability (Tables S3 and S4).

The Spanish and Hungarian DRN macroinvertebrate communities both displayed a lower relative abundance of taxa with no resistance in comparison to other DRNs (Table S5). However, the dominant resistance strategy differed: macroinvertebrate taxa with an egg-resistant form were more abundant in the Spanish DRN, while taxa with a cocoon-based or dormancy-based resistance form were more abundant in the Hungarian DRN (Table S5).

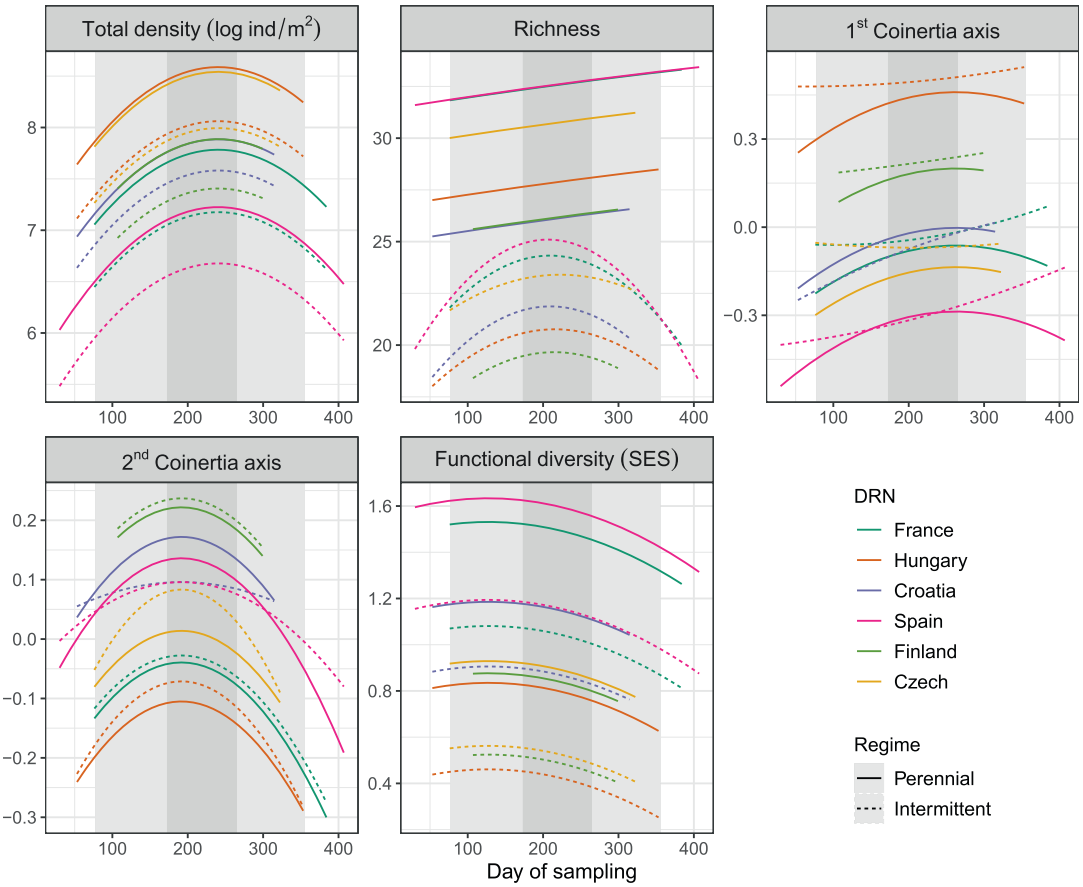

FIGURE 5 | Predicted seasonal variation of community structure in 'perennial' (no drying) and according to the median drying regime of intermittent communities in each DRN. The graphics display the marginal effect of the day of sampling for 'perennial' reaches (drying frequency and average duration of drying events equal to 0) and for the median levels of duration and frequency of drying events of 'intermittent' reaches specific to each drying river network (Figure 3). The spatio-temporal connectivity was fixed at 0.5. Community structure is described by the total density of individuals (log-transformed), community richness, the two first axes of the co-inertia analysis describing the main trait turnover between communities, and the standard effect size of trait diversity. Background areas indicate winter (white), spring and fall (light grey) and summer (grey) according to solstices and equinoxes dates.

4 | Discussion

Macroinvertebrate communities in drying river networks (DRNs) exhibit high variability in taxonomic and trait structures across seasons and biogeographical regions (Figure 2). Our study of six European DRN shows that those variations are structured by a continuum of macroinvertebrate life-history strategies, ranging from fecund, short-lived taxa to less fecund, long-lived taxa. This 'fast-to-slow' life-history continuum (Stott et al. 2024) partially trade-off with dispersal and resistance traits (Schmera et al. 2022). Notably, communities experiencing frequent drying events displayed a 'slow' trait structure, while those exposed to prolonged drying exhibited a 'fast' trait structure (Crabot, Polášek, et al. 2021). In contrast, reaches with no or infrequent drying had more homogeneous community structures (Figure 2). This suggests complex relationships between the modalities of river drying regimes and the strategies displayed by macroinvertebrate to cope with them. These findings provide valuable insights into how disturbances and dispersal dynamics interact with species traits to shape the seasonal variation of community structure across different environmental contexts (Holyoak et al. 2020; Spasojevic et al. 2014; Tonkin et al. 2017).

4.1 | Divergent Effects of the Frequency and Duration of Drying Events

Our results indicate that flow intermittence shapes the trait structure of macroinvertebrate communities and selects for taxa that exhibit specific traits to cope with drying. Consistent with previous studies (Arias-Real et al. 2021; Pineda-Morante et al. 2022), frequent drying events resulted in lower densities, taxa richness and trait diversity, reflecting strong abiotic filtering (Figure 4). More puzzling, frequent versus long drying events lead to divergent community trait structure. Frequent drying events selected for taxa on the 'slow' end of the pace of life continuum while longer drying events—when combined with high spatio-temporal connectivity—selected for taxa on the 'fast' end of this continuum with strong dispersal abilities.

Limited research has explicitly compared the effects of frequency versus duration of drying events on DRN metacommunities (Crabot et al. 2020). However, analogous theoretical studies on plant communities (Miller et al. 2011) suggest that intense disturbances favour fecund species, while frequent,

low-intensity but frequent disturbances favour competitive species. Transposed to drying river networks, this may explain why long drying events select for taxa on the 'fast' taxa but frequent, yet short, drying events select for 'slow' taxa.

During frequent but short drying events, the riverbed may retain refugia in the hyporheic zone, allowing taxa with adequate resistance traits to persist (Viza et al. 2023). However, long drying events likely shift community composition beyond a critical threshold (Aspin et al. 2019), favouring recolonisation-based resilience strategies. This may explain inconsistencies in experimental rewetting studies (Datry et al. 2012; Folch de la Iglesia et al. 2020) and the dominance of macroinvertebrate taxa with resilience strategies in Mediterranean and semi-arid climates, where drying events are longer (Giam et al. 2017; Pineda-Morante et al. 2022).

4.2 | Connectivity Mitigates the Effects of Drying Events

Our study shows that spatio-temporal connectivity enhances total density, richness and trait diversity and mitigates the negative effects of frequent and/or long drying events, supporting theoretical predictions (Jacquet et al. 2022; Journiac et al. 2025). A key question is whether these dispersal-driven patterns align with stochastic or deterministic metacommunity dynamics (Carrara et al. 2014; Spasojevic et al. 2014). Our study provides a complex answer. On the one hand, connectivity increased the total density of individuals, taxa richness and trait diversity (Table 1), suggesting that it enhances stochasticity by introducing poorly adapted taxa into communities (Spasojevic et al. 2014). This could relate to mass effects, where high connectivity promotes dispersal, leading to taxa being present in suboptimal habitat through immigration from optimal habitats (Heino et al. 2015). Given the highly unbalanced topology of river networks (Suzuki and Economo 2021), this leads to variations in community structure within networks that are solely due to differences in connectivity rather than differences in local environments or species traits. On the other hand, increased connectivity was associated with a higher relative abundance of fecund, short-lived species with high dispersal ability in reaches experiencing long drying events (Figure 4). This supports the idea that meta-community dynamics in DRNs are also trait-based, suggesting that patch dynamics drive assembly, with good dispersers thriving in intermittent reaches if they are connected to perennial ones (Cañedo-Argüelles et al. 2015; Sarremejane, Mykrä, et al. 2017).

Furthermore, spatio-temporal connectivity increased the relative abundance of macroinvertebrate taxa with an egg-based resistant form in reaches with high frequency and/or duration of drying events. Those taxa also tend to exhibit resilience strategies (Figure 2). Thus, the idea that connectivity does favour resilient strategies over resistance strategies in intermittent reaches was not as clear-cut as hypothesised (Fournier et al. 2023). This suggests that some taxa integrate both strategies, coordinating resilience and resistance across their life cycle.

4.3 | Influence of Drying Events on the Seasonal Variation of Macroinvertebrate Communities

Seasonal variations in biological communities are often driven by temperature-dependent growth leading to higher diversity in summer (Mellard et al. 2019; Pau et al. 2011). Our study shows that this pattern is more pronounced in reaches experiencing frequent drying events (Figure 5). This is likely due to a stronger seasonal turnover in reaches experiencing drying (see Figures 5, S6–S11; Table S2). This is a common feature of intermittent reaches and more widely of disturbed communities (Crabot et al. 2020).

Our work shows that this seasonal variation of communities is determined by macroinvertebrate traits. Contrary to general expectations, regardless of drying, trait diversity decreased throughout the year, suggesting that compared to spring communities, summer communities are structured by increased abiotic stress (e.g., lower oxygen and higher temperatures, Figure S2) selecting for less stress-sensitive taxa (Arias-Real et al. 2021; Verdonschot et al. 2015). Despite this common pattern, macroinvertebrate communities experiencing drying had different seasonal trait variations from non-drying reaches. While non-drying reaches were dominated by fast-growing taxa in spring and autumn, slow-growing taxa prevailed in summer, consistent with patterns observed in other ecosystems (e.g., Doležal et al. 2019). Multi-voltism and small body size were key traits in active summer taxa (Figure 5), likely driven by high temperatures (Bonacina et al. 2023).

However, this seasonal variation differed in reaches with long drying events, where taxa with strong aquatic dispersal abilities declined throughout the year (Table S5) that modified the multi-trait variation of communities (Figure 5). This suggests that aquatic dispersers (e.g., Gammarus) primarily use intermittent communities in spring but not in autumn; likely because they did not yet have the time to recolonise after drying events in summer compared to aerial dispersers (Fernández-Calero et al. 2024; Pařil et al. 2019). While we did not find significant interactions between connectivity and the seasonal variation of communities (Table S2), seasonal variability in connectivity has previously been reported to alter invertebrate assembly in Mediterranean rivers (e.g., Pineda-Morante et al. 2022; Sarremejane, Cañedo-Argüelles, et al. 2017). Future studies should further test the impact of varying connectivity on the seasonal dynamics of aquatic dispersers across climates. Overall, these findings highlight the importance of reproductive and dispersal traits beyond the fast–slow life-history continuum in structuring disturbed communities (Stott et al. 2024).

4.4 | Differences in Community Assembly Across Europe

Beyond drying regime and connectivity dynamics, macroinvertebrate community assembly varied across European DRNs. Mediterranean communities of the Spanish DRN exhibited higher taxa richness and a higher relative abundance of taxa with resilience strategies (lower scores on the first co-inertia

axis). This supports our hypothesis that a longer history of river intermittence in Mediterranean DRNs has fostered a more diverse pool of taxa capable of tolerating drying events (Bonada et al. 2007). However, this effect was obscured by prominent differences among communities from lowland versus upland DRNs. This suggests that the environmental context of each DRN was also important (Moss 2009). Lowland river networks (Hungary and Finland), characterised by slow flow velocity and small particle size in the riverbed (Figure S2), harboured distinct community structures with more taxa with slow life-history traits and a lower relative abundance of macroinvertebrate taxa with strong dispersal abilities. In contrast, macroinvertebrate communities from upland DRNs (Spain, France, Croatia, and Czechia) contained more taxa with fast life-history traits (fecund and short-lived) and resilience strategies (strong dispersal ability).

Additionally, our study reveals key factors influencing the relative abundance of taxa with resistance strategies across river networks. Despite their contrasting environmental conditions, Spanish and Hungarian DRNs both exhibited a low relative abundance of macroinvertebrate taxa lacking resistance strategies (Table S5). This suggests that optimal resistance strategies vary based on macroinvertebrate life-history traits and local environmental conditions, in particular regarding riverbed substrata (Moss 2009, Figure S1). For instance, egg-based resistance may benefit fast-growing, resilient species in upland or Mediterranean rivers with coarse substrata, while cocoon- or dormancy-based strategies may be better suited for slow-growing species in lowland rivers with fine sediments (Bogan et al. 2017; Chester and Robson 2011).

5 | Conclusion

Our study answers recent calls to better assess the joint influence of natural disturbances and connectivity on the seasonal variations of meta-communities (Holyoak et al. 2020; Tonkin et al. 2017). Three key findings emerge:

First, different facets of natural disturbance regime, here in terms of duration and frequency, select for different ecological strategies and lead to divergent community structure. We also highlight the critical importance of connectivity in those disturbed communities and for taxa with resilience strategies. As future climate and increased anthropic pressures on water resources will likely disrupt river network intermittence and connectivity dynamics (Döll and Schmied 2012): incorporating measures that promote natural flows (e.g., through dam removal or avoiding wastewater releases in intermittent streams) into conservation planning may be essential to preserve river connectivity dynamics and ensure community recovery after drying (Erös et al. 2011).

Second, trait-based assembly processes lead to divergent seasonal variations between non-disturbed and disturbed communities. As global change is expected to disrupt climate seasonal patterns, understanding how species traits shape temporal dynamics is crucial.

Finally, biogeographical and environmental contexts are associated with taxa with different life-history and resistant traits. Recognising these contingencies may enhance our understanding of how different ecological strategies are selected in DRNs and may further call for differentiated river management strategies according to the local regional context.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and R-scripts underlying this study are accessible on https://figshare.com/s/8824ca412357d71ec569 (doi: 10.6084/m9.figshare.27165927).

References

Arias-Real, R., C. Gutiérrez-Cánovas, M. Menéndez, V. Granados, and I. Muñoz. 2021. "Diversity Mediates the Responses of Invertebrate Density to Duration and Frequency of Rivers' Annual Drying Regime." *Oikos* 130, no. 12: 2148–2160. https://doi.org/10.1111/oik.08718.

Aspin, T. W. H., K. Hart, K. Khamis, et al. 2019. "Drought Intensification Alters the Composition, Body Size, and Trophic Structure of Invertebrate Assemblages in a Stream Mesocosm Experiment." *Freshwater Biology* 64, no. 4: 750–760. https://doi.org/10.1111/fwb.13259.

Bartoń, K. 2012. "MuMIn: Multi-Model Inference." *R Package Version* 1, no. 2. http://www.idg.pl/mirrors/CRAN/web/packages/MuMIn/.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. *Fitting Linear Mixed-Effects Models Using lme4*. arXiv. http://arxiv.org/abs/1406.5823.

Belmar, O., D. Bruno, S. Guareschi, A. Mellado-Díaz, A. Millán, and J. Velasco. 2019. "Functional Responses of Aquatic Macroinvertebrates to Flow Regulation Are Shaped by Natural Flow Intermittence in Mediterranean Streams." *Freshwater Biology* 64, no. 5: 1064–1077. https://doi.org/10.1111/fwb.13289.

Bogan, M. T., E. T. Chester, T. Datry, et al. 2017. "Resistance, Resilience, and Community Recovery in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams*, 349–376. Elsevier.

Bonacina, L., F. Fasano, V. Mezzanotte, and R. Fornaroli. 2023. "Effects of Water Temperature on Freshwater Macroinvertebrates: A Systematic Review." *Biological Reviews* 98, no. 1: 191–221. https://doi.org/10.1111/brv.12903.

Bonada, N., M. Cañedo-Argüelles, F. Gallart, et al. 2020. "Conservation and Management of Isolated Pools in Temporary Rivers." *Water* 12, no. 10: 2870. https://doi.org/10.3390/w12102870.

Bonada, N., S. Dolédec, and B. Statzner. 2007. "Taxonomic and Biological Trait Differences of Stream Macroinvertebrate Communities Between Mediterranean and Temperate Regions: Implications for Future Climatic Scenarios." *Global Change Biology* 13, no. 8: 1658–1671. https://doi.org/10.1111/j.1365-2486.2007.01375.x.

Cañedo-Argüelles, M., K. S. Boersma, M. T. Bogan, et al. 2015. "Dispersal Strength Determines Meta-Community Structure in a Dendritic Riverine Network." *Journal of Biogeography* 42, no. 4: 778–790. https://doi.org/10.1111/jbi.12457.

Carrara, F., A. Rinaldo, A. Giometto, and F. Altermatt. 2014. "Complex Interaction of Dendritic Connectivity and Hierarchical Patch Size on Biodiversity in River-Like Landscapes." *American Naturalist* 183, no. 1: 13–25. https://doi.org/10.1086/674009.

Chester, E. T., and B. J. Robson. 2011. "Drought Refuges, Spatial Scale and Recolonisation by Invertebrates in Non-Perennial Streams: Drought Refuges and Recolonisation in Streams." *Freshwater Biology* 56, no. 10: 2094–2104. https://doi.org/10.1111/j.1365-2427.2011.02644.x.

Crabot, J., J. Heino, B. Launay, and T. Datry. 2020. "Drying Determines the Temporal Dynamics of Stream Invertebrate Structural and Functional Beta Diversity." *Ecography* 43, no. 4: 620–635. https://doi.org/10.1111/ecog.04835.

Crabot, J., C. P. Mondy, P. Usseglio-Polatera, et al. 2021. "A Global Perspective on the Functional Responses of Stream Communities to Flow Intermittence." *Ecography* 44, no. 10: 1511–1523. https://doi.org/10.1111/ecog.05697.

Crabot, J., M. Polášek, B. Launay, P. Pařil, and T. Datry. 2021. "Drying in Newly Intermittent Rivers Leads to Higher Variability of Invertebrate Communities." *Freshwater Biology* 66, no. 4: 730–744. https://doi.org/10.1111/fwb.13673.

Cunillera-Montcusí, D., J. M. Fernández-Calero, S. Pölsterl, et al. 2023. "Navigating Through Space and Time: A Methodological Approach to Quantify Spatiotemporal Connectivity Using Stream Flow Data as a Case Study." *Methods in Ecology and Evolution* 14, no. 7: 1780–1795. https://doi.org/10.1111/2041-210X.14105.

Datry, T., D. Allen, R. Argelich, et al. 2021. "Securing Biodiversity, Functional Integrity, and Ecosystem Services in Drying River Networks (DRYvER)." *Research Ideas and Outcomes* 7: e77750. https://doi.org/10.3897/rio.7.e77750.

Datry, T., N. Bonada, and J. Heino. 2016. "Towards Understanding the Organisation of Metacommunities in Highly Dynamic Ecological Systems." *Oikos* 125, no. 2: 149–159. https://doi.org/10.1111/oik.02922.

Datry, T., R. Corti, and M. Philippe. 2012. "Spatial and Temporal Aquatic–Terrestrial Transitions in the Temporary Albarine River, France: Responses of Invertebrates to Experimental Rewetting." *Freshwater Biology* 57, no. 4: 716–727. https://doi.org/10.1111/j.1365-2427.2012.02737.x.

de Bello, F., Z. Botta-Dukát, J. Lepš, and P. Fibich. 2021. "Towards a More Balanced Combination of Multiple Traits When Computing Functional Differences Between Species." *Methods in Ecology and Evolution* 12, no. 3: 443–448. https://doi.org/10.1111/2041-210X.13537.

Doležal, J., V. Lanta, O. Mudrák, and J. Lepš. 2019. "Seasonality Promotes Grassland Diversity: Interactions With Mowing, Fertilization and Removal of Dominant Species." *Journal of Ecology* 107, no. 1: 203–215. https://doi.org/10.1111/1365-2745.13007.

Döll, P., and H. M. Schmied. 2012. "How Is the Impact of Climate Change on River Flow Regimes Related to the Impact on Mean Annual Runoff? A Global-Scale Analysis." *Environmental Research Letters* 7, no. 1: 014037. https://doi.org/10.1088/1748-9326/7/1/014037.

Dray, S., D. Chessel, and J. Thioulouse. 2003. "Co-Inertia Analysis and the Linking of Ecological Data Tables." *Ecology* 84, no. 11: 3078–3089. https://doi.org/10.1890/03-0178.

Dray, S., and A. B. Dufour. 2007. "The ade4 Package: Implementing the Duality Diagram for Ecologists." *Journal of Statistical Software* 22, no. 4: 1–20. https://doi.org/10.18637/jss.v022.i04.

Erös, T., D. Schmera, and R. S. Schick. 2011. "Network Thinking in Riverscape Conservation—A Graph-Based Approach." *Biological Conservation* 144, no. 1: 184–192.

Fernández-Calero, J. M., D. Cunillera-Montcusí, V. Hermoso, et al. 2024. "Integrating Spatiotemporal Hydrological Connectivity Into Conservation Planning to Protect Temporary Rivers." *Aquatic Conservation: Marine and Freshwater Ecosystems* 34, no. 3: e4139. https://doi.org/10.1002/aqc.4139.

Folch de la Iglesia, G., N. Bonada, and M. Cañedo-Argüelles. 2020. *Time to Leave or to Stay: Responses of Aquatic Invertebrates to Flow Intermittence*. University of Barcelona. http://www.ub.edu/fem/docs/treballs/TFM%20Guillem%20Folch%20de%20la%20Iglesia.pdf.

Foulquier, A., T. Datry, R. Corti, et al. 2024. "Unravelling Large-Scale Patterns and Drivers of Biodiversity in Dry Rivers." *Nature Communications* 15, no. 1: 7233. https://doi.org/10.1038/s41467-024-50873-1.

Fournier, R. J., G. de Mendoza, R. Sarremejane, and A. Ruhi. 2023. "Isolation Controls Reestablishment Mechanisms and Post-Drying Community Structure in an Intermittent Stream." *Ecology* 104, no. 2: e3911. https://doi.org/10.1002/ecy.3911.

Gauthier, M., G. L. Goff, B. Launay, C. J. Douady, and T. Datry. 2021. "Dispersal Limitation by Structures Is More Important Than Intermittent Drying Effects for Metacommunity Dynamics in a Highly Fragmented River Network." *Freshwater Science* 40, no. 2: 302–315. https://doi.org/10.1086/714376.

Giam, X., W. Chen, T. A. Schriever, et al. 2017. "Hydrology Drives Seasonal Variation in Dryland Stream Macroinvertebrate Communities." *Aquatic Sciences* 79, no. 3: 705–717. https://doi.org/10.1007/s00027-017-0530-7.

Harris, R. M. B., L. J. Beaumont, T. R. Vance, et al. 2018. "Biological Responses to the Press and Pulse of Climate Trends and Extreme Events." *Nature Climate Change* 8, no. 7: 579–587. https://doi.org/10.1038/s41558-018-0187-9.

Heino, J., A. S. Melo, T. Siqueira, J. Soininen, S. Valanko, and L. M. Bini. 2015. "Metacommunity Organisation, Spatial Extent and Dispersal in Aquatic Systems: Patterns, Processes and Prospects." *Freshwater Biology* 60, no. 5: 845–869. https://doi.org/10.1111/fwb.12533.

Heino, J., R. Virkkala, and H. Toivonen. 2009. "Climate Change and Freshwater Biodiversity: Detected Patterns, Future Trends and Adaptations in Northern Regions." *Biological Reviews* 84, no. 1: 39–54. https://doi.org/10.1111/j.1469-185X.2008.00060.x.

Hershkovitz, Y., and A. Gasith. 2013. "Resistance, Resilience, and Community Dynamics in Mediterranean-Climate Streams." *Hydrobiologia* 719, no. 1: 59–75. https://doi.org/10.1007/s10750-012-1387-3.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. "Rethinking Community Assembly Through the Lens of Coexistence Theory." *Annual Review of Ecology, Evolution, and Systematics* 43, no. 1: 227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411.

Holyoak, M., T. Caspi, and L. W. Redosh. 2020. "Integrating Disturbance, Seasonality, Multi-Year Temporal Dynamics, and Dormancy Into the

Dynamics and Conservation of Metacommunities." *Frontiers in Ecology and Evolution* 8: 571130. https://doi.org/10.3389/fevo.2020.571130.

Jacquet, C., F. Munoz, N. Bonada, T. Datry, J. Heino, and F. Jabot. 2022. "Disturbance-Driven Alteration of Patch Connectivity Determines Local Biodiversity Recovery Within Metacommunities." *Ecography* 2022, no. 12: e06199. https://doi.org/10.1111/ecog.06199.

Jentsch, A., and P. White. 2019. "A Theory of Pulse Dynamics and Disturbance in Ecology." *Ecology* 100, no. 7: e02734. https://doi.org/10.1002/ecy.2734.

Journiac, L., F. Munoz, F. Jabot, et al. 2025. "Exploring the Spatio-Temporal Dynamics of Disturbed Metacommunities: A Mechanistic Modeling Approach to Species Resistance and Resilience Strategies in Drying River Networks." *Ecological Modelling* 506: 111136. https://doi.org/10.1016/j.ecolmodel.2025.111136.

Leibold, M. A., M. Holyoak, N. Mouquet, et al. 2004. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7, no. 7: 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x.

Li, D. 2018. "hillR: Taxonomic, Functional, and Phylogenetic Diversity and Similarity Through Hill Numbers." *Journal of Open Source Software* 3, no. 31: 1041. https://doi.org/10.21105/joss.01041.

Mellard, J. P., P. Audoye, and M. Loreau. 2019. "Seasonal Patterns in Species Diversity Across Biomes." *Ecology* 100, no. 4: e02627. https://doi.org/10.1002/ecy.2627.

Messager, M. L., B. Lehner, C. Cockburn, et al. 2021. "Global Prevalence of Non-Perennial Rivers and Streams." *Nature* 594, no. 7863: 391–397. https://doi.org/10.1038/s41586-021-03565-5.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. "How Frequency and Intensity Shape Diversity–Disturbance Relationships." *Proceedings of the National Academy of Sciences* 108, no. 14: 5643–5648. https://doi.org/10.1073/pnas.1018594108.

Mimeau, L., A. Künne, F. Branger, S. Kralisch, A. Devers, and J.-P. Vidal. 2024. "Flow Intermittence Prediction Using a Hybrid Hydrological Modelling Approach: Influence of Observed Intermittence Data on the Training of a Random Forest Model." *Hydrology and Earth System Sciences* 28, no. 4: 851–871. https://doi.org/10.5194/hess-28-851-2024.

Moretti, M., and C. Legg. 2009. "Combining Plant and Animal Traits to Assess Community Functional Responses to Disturbance." *Ecography* 32, no. 2: 299–309. https://doi.org/10.1111/j.1600-0587.2008.05524.x.

Moss, B. R. 2009. *Ecology of Fresh Waters: Man and Medium, Past to Future*. John Wiley & Sons. https://books.google.com/books?hl=fr&lr=&id=lfZH-xA3BVUC&oi=fnd&pg=PR7&dq=Brian+moss&ots=mttXbz17y8&sig=DsOxM4gAYtjYXe5G4TR_fkrZwQc.

Nakagawa, S., and H. Schielzeth. 2013. "A General and Simple Method for Obtaining R2 From Generalized Linear Mixed-Effects Models." *Methods in Ecology and Evolution* 4, no. 2: 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Pařil, P., C. Leigh, M. Polášek, et al. 2019. "Short-Term Streambed Drying Events Alter Amphipod Population Structure in a Central European Stream." *Fundamental and Applied Limnology* 193, no. 1: 51–64. https://doi.org/10.1127/fal/2019/1164.

Pau, S., E. M. Wolkovich, B. I. Cook, et al. 2011. "Predicting Phenology by Integrating Ecology, Evolution and Climate Science." *Global Change Biology* 17, no. 12: 3633–3643. https://doi.org/10.1111/j.1365-2486.2011.02515.x.

Pineda-Morante, D., J. M. Fernández-Calero, S. Pölsterl, D. Cunillera-Montcusí, N. Bonada, and M. Cañedo-Argüelles. 2022. "Local Hydrological Conditions and Spatial Connectivity Shape Invertebrate Communities After Rewetting in Temporary Rivers." *Hydrobiologia* 849, no. 6: 1511–1530. https://doi.org/10.1007/s10750-022-04799-8.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Sarremejane, R., M. Cañedo-Argüelles, N. Prat, H. Mykrä, T. Muotka, and N. Bonada. 2017. "Do Metacommunities Vary Through Time? Intermittent Rivers as Model Systems." *Journal of Biogeography* 44, no. 12: 2752–2763. https://doi.org/10.1111/jbi.13077.

Sarremejane, R., N. Cid, R. Stubbington, et al. 2020. "DISPERSE, a Trait Database to Assess the Dispersal Potential of European Aquatic Macroinvertebrates." *Scientific Data* 7, no. 1: 386. https://doi.org/10.1038/s41597-020-00732-7.

Sarremejane, R., H. Mykrä, N. Bonada, J. Aroviita, and T. Muotka. 2017. "Habitat Connectivity and Dispersal Ability Drive the Assembly Mechanisms of Macroinvertebrate Communities in River Networks." *Freshwater Biology* 62, no. 6: 1073–1082. https://doi.org/10.1111/fwb.12926.

Schmera, D., J. Heino, and J. Podani. 2022. "Characterising Functional Strategies and Trait Space of Freshwater Macroinvertebrates." *Scientific Reports* 12, no. 1: 12283. https://doi.org/10.1038/s41598-022-16472-0.

Spasojevic, M. J., S. Copeland, and K. N. Suding. 2014. "Using Functional Diversity Patterns to Explore Metacommunity Dynamics: A Framework for Understanding Local and Regional Influences on Community Structure." *Ecography* 37, no. 10: 939–949. https://doi.org/10.1111/ecog.00711.

Stott, I., R. Salguero-Gómez, O. R. Jones, et al. 2024. "Life Histories Are Not Just Fast or Slow." *Trends in Ecology & Evolution* 39, no. 9: 830–840. https://doi.org/10.1016/j.tree.2024.06.001.

Strachan, S. R., E. T. Chester, and B. J. Robson. 2015. "Freshwater Invertebrate Life History Strategies for Surviving Desiccation." *Springer Science Reviews* 3, no. 1: 57–75. https://doi.org/10.1007/s40362-015-0031-9.

Stubbington, R., M. T. Bogan, N. Bonada, et al. 2017. "The Biota of Intermittent Rivers and Ephemeral Streams: Aquatic Invertebrates." In *Intermittent Rivers and Ephemeral Streams*, 217–243. Elsevier.

Suzuki, Y., and E. P. Economo. 2021. "From Species Sorting to Mass Effects: Spatial Network Structure Mediates the Shift Between Metacommunity Archetypes." *Ecography* 44, no. 5: 715–726. https://doi.org/10.1111/ecog.05453.

Tachet, H., P. Richoux, M. Bournaud, and P. Usseglio-Polatera. 2010. *Invertébrés D'eau Douce—Systématique, Biologie, Écologie*. CNRS Éditions. https://www.cnrseditions.fr/catalogue/ecologie-environnement-sciences-de-la-terre/invertebres-d-eau-douce-henri-tachet/.

Tonkin, J. D., M. T. Bogan, N. Bonada, B. Rios-Touma, and D. A. Lytle. 2017. "Seasonality and Predictability Shape Temporal Species Diversity." *Ecology* 98, no. 5: 1201–1216. https://doi.org/10.1002/ecy.1761.

Vander Vorste, R., R. Stubbington, V. Acuña, et al. 2021. "Climatic Aridity Increases Temporal Nestedness of Invertebrate Communities in Naturally Drying Rivers." *Ecography* 44, no. 6: 860–869. https://doi.org/10.1111/ecog.05349.

Verdonschot, R. C. M., A. M. Van Oosten-Siedlecka, C. J. F. Ter Braak, and P. F. M. Verdonschot. 2015. "Macroinvertebrate Survival During Cessation of Flow and Streambed Drying in a Lowland Stream." *Freshwater Biology* 60, no. 2: 282–296. https://doi.org/10.1111/fwb.12479.

Viza, A., R. Arias-Real, M. Menéndez, and I. Muñoz. 2023. "The Role of Seedbanks and Hyporheic Refuges in Supporting Benthic Invertebrate Community Resistance and Resilience to Dry Phases." *Aquatic Sciences* 86, no. 1: 16. https://doi.org/10.1007/s00027-023-01034-x.

Woods, T., A. Kaz, and X. Giam. 2022. "Phenology in Freshwaters: A Review and Recommendations for Future Research." *Ecography* 2022, no. 6: e05564. https://doi.org/10.1111/ecog.05564.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Appendix A

Data Sources

Mimeau, L., A. Künne, A. Devers, F. Branger, S. Kralisch, and J.-P. Vidal. 2025. "Hydrological Reconstruction (1960–2021) of the Albarine DRN (France)." *Recherche Data Gouv, V1*. https://doi.org/10.57745/VTRRQL.

Mimeau, L., A. Künne, A. Devers, F. Branger, S. Kralisch, and J.-P. Vidal. 2025. "Hydrological Reconstruction (1960–2021) of the Bükkösdi DRN (Hungary)." *Recherche Data Gouv, V1*. https://doi.org/10.57745/SLQKXX.

Mimeau, L., A. Künne, A. Devers, F. Branger, S. Kralisch, and J.-P. Vidal. 2025. "Hydrological Reconstruction (1960–2021) of the Butiznica DRN (Croatia)." *Recherche Data Gouv, V1*. https://doi.org/10.57745/1XGAMX.

Mimeau, L., A. Künne, A. Devers, F. Branger, S. Kralisch, and J.-P. Vidal. 2025. "Hydrological Reconstruction (1960–2021) of the Genal DRN (Spain)." *Recherche Data Gouv, V1*. https://doi.org/10.57745/VXBMAF.

Mimeau, L., A. Künne, A. Devers, F. Branger, S. Kralisch, and J.-P. Vidal. 2025. "Hydrological Reconstruction (1960–2021) of the Lepsämänjoki DRN (Finland)." *Recherche Data Gouv, V1*. https://doi.org/10.57745/EJG7KJ.

Mimeau, L., A. Künne, A. Devers, F. Branger, S. Kralisch, and J.-P. Vidal. 2025. "Hydrological Reconstruction (1960–2021) of the Velicka DRN (Czechia)." *Recherche Data Gouv, V1*. https://doi.org/10.57745/QFNFPN.