




## RESEARCH ARTICLE OPEN ACCESS

# River Drying Causes Local Losses and Regional Gains in Aquatic Invertebrate Metacommunity Diversity: A Cross-Continental Comparison

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**Received:** 26 September 2024 | **Revised:** 10 December 2024 | **Accepted:** 11 December 2024

**Funding:** D.E.-C. was supported by the 2023 Make Our Planet Great Again (MOPGA) visiting Fellowship. This research was funded by the DRYvER project (Horizon 2020 #869226), the MECODISPER project (CTM2017-89295-P) funded by the Spanish “Ministerio de Ciencia, Innovación y Universidades—Agencia Estatal de Investigación”; and co-funded by the ERDF (European Regional Development Fund). Research in Brazil was funded by the FUNCAP project (N° PS1-0186-00210.01.00/21) of the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico, and in Ecuador by Universidad San Francisco de Quito—USFQ grants (#17074). R.Sa. was funded by the Environment Agency (award SC220011).

**Keywords:** assembly mechanisms | dispersal | drying duration | intermittent river | macroinvertebrate | metacommunity | temporal dynamics

## ABSTRACT

Drying river networks include non-perennial reaches that cease to flow or dry, and drying is becoming more prevalent with ongoing climate change. Biodiversity responses to drying have been explored mostly at local scales in a few regions, such as Europe and North America, limiting our ability to predict future global scenarios of freshwater biodiversity. Locally, drying acts as a strong environmental filter that selects for species with adaptations promoting resistance or resilience to desiccation, thus reducing aquatic  $\alpha$ -diversity. At the river network scale, drying generates complex mosaics of dry and wet habitats, shaping metacommunities driven by both environmental and dispersal processes. By repeatedly resetting community succession, drying can enhance  $\beta$ -diversity in space and time. To investigate the transferability of these concepts across continents, we compiled and analyzed a unique dataset of 43 aquatic invertebrate metacommunities from drying river networks in Europe and South America. In Europe,  $\alpha$ -diversity was consistently lower in non-perennial than perennial reaches, whereas this pattern was not evident in South America. Concomitantly,  $\beta$ -diversity was higher in non-perennial reaches than in perennial ones in Europe but not in South America. In general,  $\beta$ -diversity was predominantly driven by turnover rather than nestedness. Dispersal was

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the main driver of metacommunity dynamics, challenging prevailing views in river science that environmental filtering is the primary process shaping aquatic metacommunities. Lastly,  $\alpha$ -diversity decreased as drying duration increased, but this was not consistent across Europe. Overall, drying had continent-specific effects, suggesting limited transferability of knowledge accumulated from North America and Europe to other biogeographic regions. As climate change intensifies, river drying is increasing, and our results underscore the importance of studying its effects across different regions. The importance of dispersal also suggests that management efforts should seek to enhance connectivity between reaches to effectively monitor, restore and conserve freshwater biodiversity.

## 1 | Introduction

River networks cover <1% of the Earth's surface area but host 10% of all known animal species (Strayer and Dudgeon 2010; Tickner et al. 2020). Despite their ecological significance, they are among the most threatened ecosystems in the world, experiencing the highest rate of biodiversity loss (Reid et al. 2019). Most river networks are drying river networks (DRNs, Datry et al. 2021), which comprise both perennial and non-perennial reaches, the latter recurrently ceasing to flow and/or drying (Price et al. 2021; Messenger et al. 2021; Datry, Boulton, et al. 2023). Drying occurs naturally due to climatic, geologic, and hydrogeologic factors, but is also increasingly driven by human activities such as land use alterations and river damming (Nabih et al. 2021; Tramblay et al. 2021; Zipper et al. 2021). DRNs dominate arid regions and are also common in humid climates (Messenger et al. 2021; Stubbington et al. 2017). As such, DRNs are the norm rather than the exception, calling for paradigm shifts in river science (Allen et al. 2020; Datry, Boulton, et al. 2023).

Although most concepts developed in freshwater sciences have overlooked the significance of drying (Allen et al. 2020; Datry, Boulton, et al. 2023), lateral drying is at the core of the flood pulse concept (FPC) developed for perennial rivers in Neotropical regions (Junk, Bayley, and Sparks 1989). The FPC emphasizes the critical role of alternating wet and dry periods in non-perennial lateral habitats in maintaining ecological balance in river ecosystems, and similarly, wet-dry cycles govern ecosystem dynamics in non-perennial river channels in DRNs (Allen et al. 2020; Datry, Larned, and Tockner 2014). Such cycles can reset ecological processes, promote species adaptations to tolerate and recover from drying, and can sustain biodiversity and nutrient cycling—both in floodplains (Junk, Bayley, and Sparks 1989) and DRNs (Datry, Larned, and Tockner 2014).

The local  $\alpha$ -diversity of aquatic taxonomic groups from microbes to fish, and including invertebrates, declines in response to drying, and is thus generally higher in perennial than non-perennial reaches (Davey and Kelly 2007; Schreckinger et al. 2021; Soria et al. 2017). Overall, aquatic diversity decreases as drying duration increases, due to the loss of species lacking adaptations to resist or recover from drying (Datry, Larned, Fritz, et al. 2014; Crabot, Mondy, et al. 2021). Drying alters in-channel habitats, with conditions ranging from disconnected pools of standing water to completely dry riverbeds (Datry, Bonada, and Heino 2016; Stubbington et al. 2017). Dry riverbeds host only resistant species with desiccation-tolerant life stages, including eggs, larvae, and pupae, while

desiccation-sensitive species may survive in saturated subsurface sediments (Stubbington and Datry 2013; Vander Vorste et al. 2016; DelVecchia et al. 2022). Some species actively migrate to wet refuges, including perennial reaches or pools, while others passively inhabit these refuges; both can recolonize DRNs upon wetting (Arscott et al. 2010; Magoulick and Kobza 2003; Stubbington 2012). In contrast, because drying creates a habitat mosaic inhabited by variable communities at different successional stages (Datry, Pella, et al. 2016), the contribution of non-perennial reaches to regional spatial and temporal  $\beta$ -diversity can be high (Larned et al. 2010; Rodríguez-Lozano et al. 2023). However, high context dependence in biodiversity patterns has been reported (e.g., Gauthier et al. 2020), calling for large-scale approaches to better understand the underlying patterns and drivers of biodiversity organization in DRNs (Crabot, Mondy, et al. 2021; Stubbington, Sarremejane, and Datry 2019; Vander Vorste et al. 2021).

Quantifying  $\beta$ -diversity and its components can advance understanding of the processes underlying regional-scale metacommunity organization (Gauthier et al. 2020; Gianuca et al. 2024). DRN communities often exhibit nestedness-driven compositional changes along drying gradients, suggesting that communities in non-perennial reaches are taxonomic subsets of those in perennial reaches (Datry, Larned, Fritz, et al. 2014; Vander Vorste et al. 2021). In a few cases, drying can cause community turnover if it selects for specialist taxa with resistance or resilience strategies (Chanut et al. 2023; Rogosch and Olden 2019). Upon wetting, colonization by species with strong dispersal abilities can reduce community dissimilarities (Larned et al. 2010), although drying can be detected months after wetting (Datry, Larned, Fritz, et al. 2014; Gauthier et al. 2020). These dynamics result in complex metacommunity patterns, reflecting a combination of limited dispersal (e.g., by aquatic obligates), local extinctions driven by biotic interactions (e.g., predation), and environmental selection following drying (Bogan and Lytle 2007; Larned et al. 2010; Leigh and Datry 2017). Environmental filtering is considered the primary driver of assembly processes in rivers and streams (Brown and Swan 2010; Grönroos et al. 2013; Heino et al. 2015), but dispersal can be the main mechanism in DRNs (Datry, Bonada, and Heino 2016; de Campos et al. 2019; Gauthier et al. 2020). However, several factors can influence metacommunity processes in DRNs, such as fragmentation by anthropogenic barriers (Gauthier et al. 2021), the antecedent landscape-scale extent of river drying (Crabot, Polášek, et al. 2021; Sarremejane et al. 2021), and the evolution of diverse life-history strategies across regions (Tonkin et al. 2017). Current management strategies focus on local-scale actions such as biomonitoring and implementation of environmental

flows (Cid et al. 2020; Gianuca et al. 2024; Messenger et al. 2023), limiting their benefits for ecosystem protection. Characterizing the role of dispersal processes that shape the assembly of DRN metacommunities could inform regional-scale management strategies that better support river ecosystems as they adapt to global change.

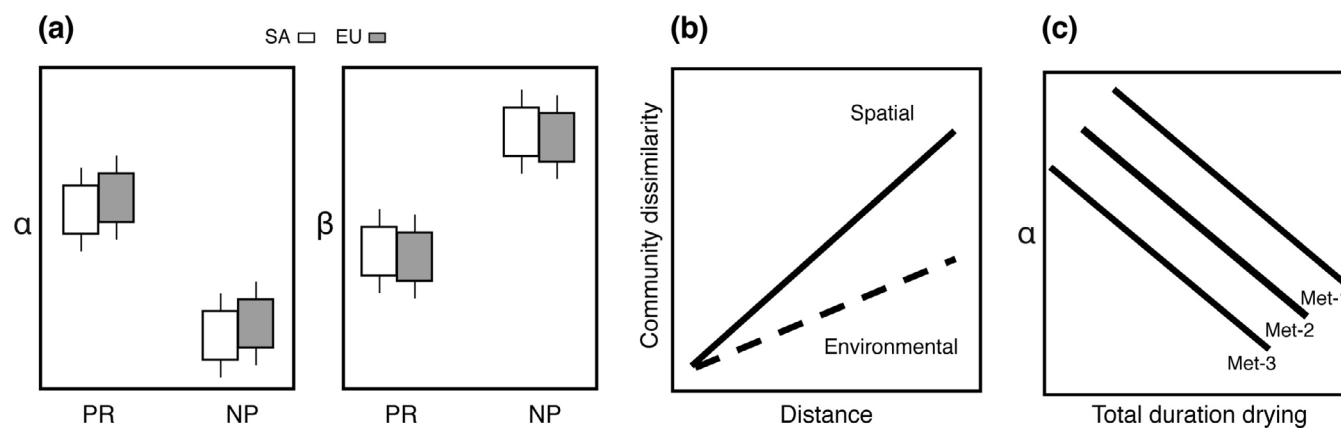
The biological responses to drying have mostly been studied in North America (Crabot, Mondy, et al. 2021; Soria et al. 2017), Europe (Datry, Larned, Fritz, et al. 2014; Stubbington et al. 2022), and Oceania (Arscott et al. 2010; Shanafield et al. 2024) and are increasing in South America (Datry, Melo, et al. 2016; Valente-Neto et al. 2020; Oliveira et al. 2024). Substantial knowledge of DRN metacommunity ecology has emerged from Europe over the last two decades, following the publication of seminal papers (Bonada, Rieradevall, and Prat 2007; Larned et al. 2010; Datry, Larned, and Tockner 2014), which sparked interest in DRNs. Despite significant progress, the absence of insights from South America remains apparent in comprehensive syntheses (Datry, Bonada, and Boulton 2017) and global studies (Datry, Larned, Fritz, et al. 2014; Soria et al. 2017; Vander Vorste et al. 2021). The growing body of research in both Europe and South America presents an opportunity to compare these regions, whose distinct evolutionary histories (Cortés-Guzmán et al. 2024; Hoorn et al. 2010), biodiversity (Balian et al. 2007) and climatic variability (Sayre et al. 2020), may lead to contrasting ecological responses to drying. For example, in South America  $\alpha$ - and  $\beta$ -diversity may not vary between perennial and non-perennial reaches (Datry, Moya, et al. 2016), diversity may remain stable during drying periods (Carvalho, Farias, and Medeiros 2013), and, in some cases,  $\alpha$ -diversity can increase during drying periods (Rocha, Medeiros, and Andrade 2012). Amid global climate change, such comparisons reveal how diverse ecosystems respond to drying under changing conditions, helping to guide conservation strategies that mitigate biodiversity loss and ecosystem degradation.

In this study, the effects of drying on local and regional biodiversity were compared in DRNs in Europe and South America, to assess the generalizability and transferability of reported diversity patterns. Data from 43 DRN metacommunities were used to test three hypotheses: H1: Drying decreases  $\alpha$ - and increases  $\beta$ -diversity in both regions (Figure 1a). H2: Dispersal is more important than environmental filtering in shaping metacommunities (Figure 1b). H3: The magnitude of decreases in  $\alpha$ -diversity is comparable across DRNs as the duration of drying increases (Figure 1c).

## 2 | Materials and Methods

### 2.1 | Metacommunity Datasets

Aquatic invertebrate metacommunity datasets from Europe and South America were identified and compiled. Selection was based on four criteria. First, metacommunities included at least three local communities across DRN catchments < 1000 km<sup>2</sup> to align with the dispersal abilities of invertebrate taxa and ensure comparability across continents. Second, drying was the main source of environmental variation, and sampled rivers were minimally or least impacted with moderate to high water quality. Third, for each metacommunity, each reach was sampled at least once before and once after drying to capture the local effects of the drying on metacommunity dynamics. Fourth, sampling methods were quantitative or semi-quantitative (Chiasson 2009; Everall et al. 2017; Funnell et al. 2020). Nine datasets were compiled, spanning 12 countries, 41 rivers, 43 metacommunities, and 2505 samples from 696 unique reaches and 249 sampling campaigns (Table 1, Table S1, Figure 2, Appendix S1). Communities were sampled between 2004 and 2022 and covered a wide environmental gradient across both continents, ranging from first-order gravel-bed headwater streams to fifth-order sand-bed rivers. DRN catchment areas ranged between 13 and 1076 km<sup>2</sup>. Datasets included 3–8 environmental variables from stream



**FIGURE 1** | Hypothesized diversity patterns for metacommunities in South America (SA) and Europe (EU): (a) Differences in  $\alpha$ - and  $\beta$ -diversity metrics between perennial (PR) and non-perennial (NP) reaches. (b) The influence of environmental factors and dispersal on community composition; the solid line represents the relationship between community dissimilarity and spatial distance, indicating a structured spatial pattern due to variable dispersal rates; the dashed line represents the relationship between community dissimilarity and environmental distance, indicating a random influence of environmental factors on community composition. (c) The relationship between  $\alpha$ -diversity and drying duration; lines represent different metacommunities, showing comparable decreases as taxa are lost as drying duration increases.

**TABLE 1** | The compiled data, indicating the number of metacommunities, reaches and sampling dates for each country and dataset. Dataset 1 encompasses metacommunities from nine countries. Appendix S1 and Table S1 provide full details of the individual datasets and sampling methods.

Continent	Country	Dataset	# Metacom.	Reaches	# Sampling dates	Climate
SA	Bolivia	1	1	22	6	Temperate
SA	Bolivia	2	2	80	1	Temperate, tropical
SA	Brazil	1	1	13	6	Semiarid
SA	Brazil	3	1	20	6	Tropical semiarid
SA	Ecuador	1	1	20	6	Tropical
EU	Croatia	1	1	15	6	Mediterranean
EU	Czech Republic	1	1	20	6	Continental humid
EU	Finland	1	1	21	6	Cold temperate
EU	France	1	1	20	6	Temperate
EU	France	4	11	65	6	Mediterranean, continental, alpine
EU	France	5	10	222	2	Temperate
EU	Hungary	1	1	25	6	Continental
EU	Italy	6	1	6	2	Mediterranean
EU	Spain	1	1	26	6	Mediterranean
EU	Spain	7	2	30	4	Mediterranean
EU	Switzerland	8	1	30	3	Alpine
EU	United Kingdom	9	6	61	4	Temperate

velocity, wetted width, maximum depth, temperature, pH, conductivity, dissolved oxygen and discharge.

## 2.2 | Drying Metrics

Reaches were classified as perennial (PR, no drying) or non-perennial (NP, experiencing  $\geq 1$  drying event per sampling period) (Datry, Larned, Fritz, et al. 2014; Messenger et al. 2021). Classifications were based solely on visual observations during and between sampling dates for 19 metacommunities (Araújo et al., unpublished; Datry et al. 2021; Sefton et al. 2019) and in combination with previous knowledge for three metacommunities (Datry, Melo, et al. 2016; Paillex et al. 2020), with water level and temperature data for 23 European metacommunities (Crabot et al. 2020; Gauthier et al. 2020; Pineda-Morante et al. 2022) and with Sentinel 2-satellite images for one metacommunity in Italy (Cavallo et al. 2022).

For a subset of 27 European metacommunities representing 62% of the dataset, drying duration was quantified as the total number of drying days (TotDur) using loggers and/or hydrological modeling. TotDur ranged from 40 to 400 days (average 74.93) over sampling periods of 106–580 days. Water state data loggers and water presence sensors were used in 11 metacommunities from France (Crabot et al. 2020) and one in Switzerland (Chanut et al. 2023), while hybrid hydrological modeling was developed for six metacommunities across Croatia, Czech Republic, France, Finland, Hungary and Spain (Mimeau et al. 2024). Temperature data loggers were used for two metacommunities

in Spain (Pineda-Morante et al. 2022), monthly visual observations were used in six UK metacommunities and satellite images were used for one metacommunity of Italy.

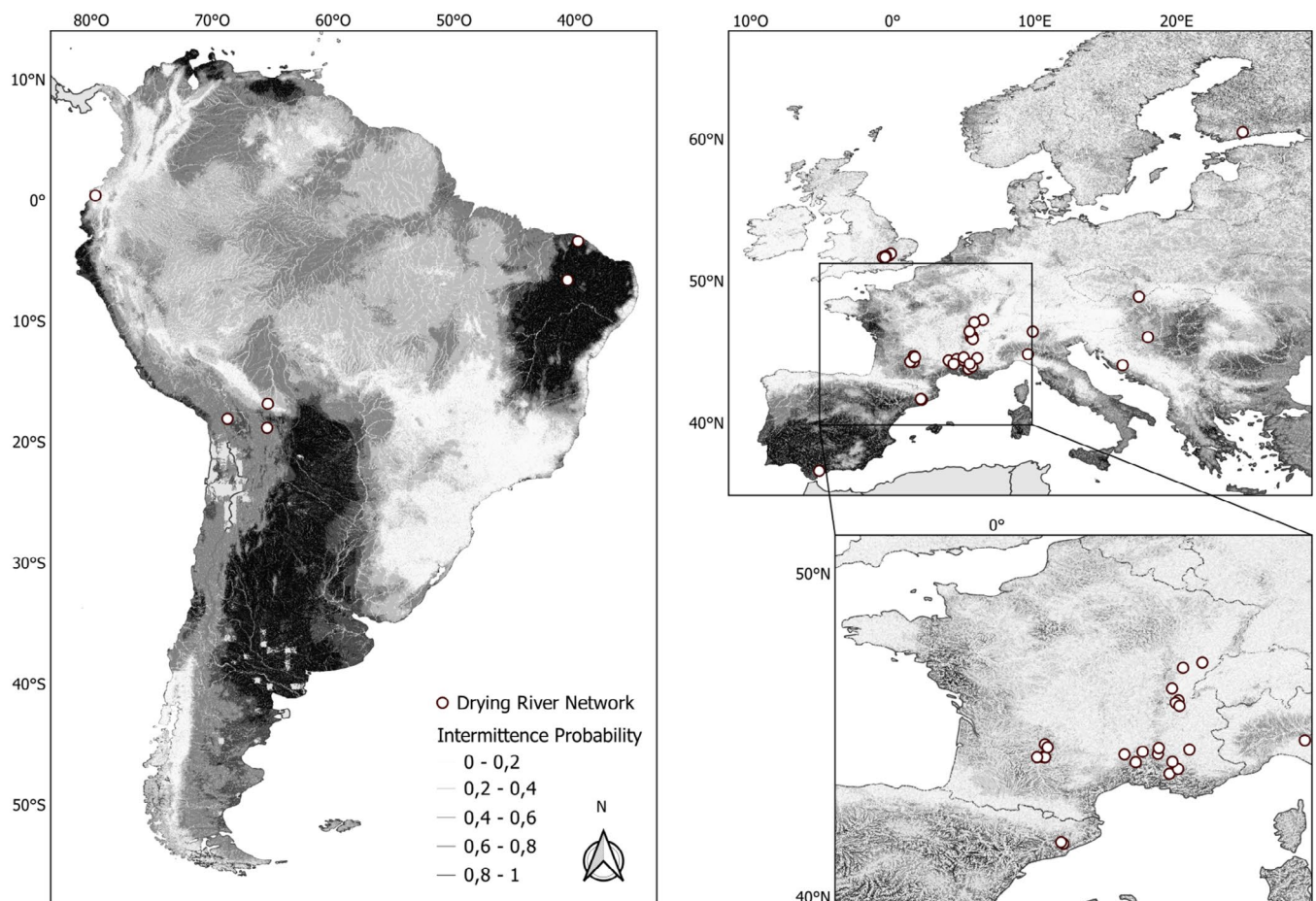
## 2.3 | Invertebrate Sampling and Identification

Some metacommunities were sampled before, during, and after drying, while others were sampled multiple times both before and after drying (Table S1, Appendix S1). Due to the scarcity of DRN metacommunity data from South America, we also included data for two metacommunities in Bolivia that were sampled only once. Surber, Hess, and kick-net (with a 250- to 500- $\mu\text{m}$  mesh) methods were used to collect 51%, 28%, and 19% of metacommunities, respectively. In terms of habitats sampled, 14 metacommunities (33%) were sampled from multiple habitats in proportion to their occurrence, and 29 metacommunities (67%) were sampled from riffles. Twenty-seven metacommunities (63%) were represented by composite samples, and 16 (37%) by single samples from one riffle (Table S1, Appendix S1). The taxonomic resolution varied among datasets. Invertebrates were identified to family level for all six metacommunities from South America and one from Europe and to genus level for all other European metacommunities.

## 2.4 | Data Analysis

To test H1 and H2, the metacommunity datasets were harmonized to the most common level of identification (i.e., family level)





**FIGURE 2** | Distribution of the analyzed metacommunities (circles), overlaid on the distribution of drying river networks (DRNs), based on Messenger et al. (2021). Metacommunities are summarized in Table 1. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

by removing taxa classified at a higher rank (Appendix S2). Taxa in genus-level datasets were assigned to their respective families. Although family-level analysis could reduce detection of fine-scale responses to drying, it removed the potential bias from datasets with different taxonomic resolution (Jones 2008). Previous family-level studies have detected spatial and temporal patterns in community diversity and composition (Beketov et al. 2009; Bevilacqua et al. 2018; Heino and Soininen 2007), including in DRNs (e.g., Datry, Larned, Fritz, et al. 2014; Vander Vorste et al. 2021). For H3, which required quantification of drying event duration, the subset of 23 European metacommunities was harmonized at the genus level by removing taxa classified at a higher rank (Appendix S3).

#### 2.4.1 | $\alpha$ - and $\beta$ -Diversity Responses to Drying

To test H1,  $\alpha$ -diversity was assessed using taxonomic richness, estimated for each reach on each sampling date.  $\beta$ -diversity was quantified using the presence-absence-based Jaccard dissimilarity index and its turnover and nestedness components (Baselga 2010; Legendre 2014). Two aspects of  $\beta$ -diversity were calculated for each metacommunity: spatial  $\beta$ -diversity, reflecting differences in community composition among reaches on each sampling date, and temporal  $\beta$ -diversity, measuring differences in composition across all dates within each reach.

Linear models were fitted to analyze the effect of drying on metacommunities between continents.  $\alpha$ - and  $\beta$ -diversity metrics were used as response variables, with reach type (NP vs. PR) as the explanatory variable and continent (South America vs. Europe) as a covariate. Analysis of covariance (ANCOVA) was conducted to examine these relationships. An interaction term between reach type and continent was included to assess whether the effects of drying varied by continent and reach type. Null models were generated by fitting a linear model with only the intercept (i.e., a model with no predictors) for comparison with the full models. Model validation was performed using likelihood ratio tests (LRT) against null models. Normality and homoscedasticity of residuals were assessed for each model through visual inspection of plots of residuals against fitted values.

#### 2.4.2 | Determinants of Regional Community Composition

To test H2, Mantel tests (Legendre and Legendre 2012), which provide a correlation coefficient between distance matrices, were used to analyze relationships between community dissimilarity and both environmental factors and spatial distances for the whole dataset. First, dissimilarity matrices were constructed

using the Bray-Curtis index based on log-transformed, family-level abundance data for each sampling campaign, using the *vegan* package (Oksanen et al. 2022). Second, environmental (ENVI) distance matrices, based on environmental variables for each metacommunity, were constructed using Euclidean distances after variable normalization (mean = 0; SD = 1, Cañedo-Argüelles et al. 2015). Third, two spatial distance matrices were generated between pairwise combinations of reaches for each DRN: one used overland (OVER) distances derived from GPS coordinates of each reach, calculated using the *geodist* package (Padgham, Summer, and Karney 2020); the other used watercourse distances (WACO), calculated as the distances between reaches following the river network (Datry, Moya, et al. 2016; Gauthier et al. 2020). WACOs were calculated using the *riverdist* package (Tyers 2024) or generated via least-cost path analysis in ArcGIS 2.9.1 (Environmental Systems Research Institute, CA, USA). Both OVER and WACO matrices were calculated for each campaign. Using both overland and watercourse distances recognizes that aquatic invertebrates use aquatic and/or aerial dispersal modes (Cañedo-Argüelles et al. 2015; Elliott 2003), thus aligning with metacommunity theory, which emphasizes the importance of considering multiple dispersal pathways (Grainger and Gilbert 2016). Nineteen campaigns were excluded from analysis because dry in-channel conditions prevented sampling of at least three reaches, thus preventing correlation analysis. In total, 230 Mantel tests were performed between community dissimilarity and the distance matrices (OVER, WACO, and ENVI). When significant correlations were found between the community dissimilarity and spatial distance matrices, partial Mantel tests were performed controlling for the effect of ENVI (Datry, Moya, et al. 2016). When the community dissimilarity and ENVI matrices were correlated, the Moran spectral randomization procedure was performed to correct for spatial autocorrelation (Crabot et al. 2019). To assess if the frequency of significant relationships between community dissimilarity and each distance matrix was more frequent than expected by chance, a chi-square test was used to compare the proportion of significant relationships for each distance matrix against the total. To assess if correlation coefficients differ between the distance matrices, a Kruskal-Wallis test was used to compare the values of the coefficients.

#### 2.4.3 | Quantitative Relationships Between Biological Diversity and Drying

To test H3, linear mixed-effect models were built with the *lme4* package (Bates et al. 2015) to characterize diversity-drying relationships based on 23 European genus-level metacommunities, for which TotDur data was available. Fourteen metacommunities from France (10) and the UK (4) lacked TotDur, hence were excluded from the analysis. To test whether the effect of drying on  $\alpha$ -diversity differed between metacommunities, three nested mixed-effect models with different levels of complexity were compared. All models included  $\alpha$ -diversity as the response variable and metacommunity identity as a random intercept. A null model included only the random intercept for metacommunity identity without any fixed effect. A second (average) model incorporated TotDur as a fixed effect across all metacommunities. A third (metacommunity-specific) model included TotDur as a

fixed effect and allowed its effect to vary among metacommunities by incorporating TotDur as a random slope within the random effect structure (Bolker et al. 2009). The statistical significance of fixed and random effects in the best-fitting models was assessed using LRT by comparing models with and without each effect (Bolker et al. 2009). The most parsimonious models were identified as those with the lowest Akaike's information criterion (AIC) values. Individual linear regressions were used to analyze how much individual metacommunities contributed to the models. Although invertebrates from the alpine metacommunity (Switzerland) were identified at the family level, they were aggregated to the genus-based dataset to evaluate the three models. The results remained consistent regardless of whether this metacommunity was included.

### 3 | Results

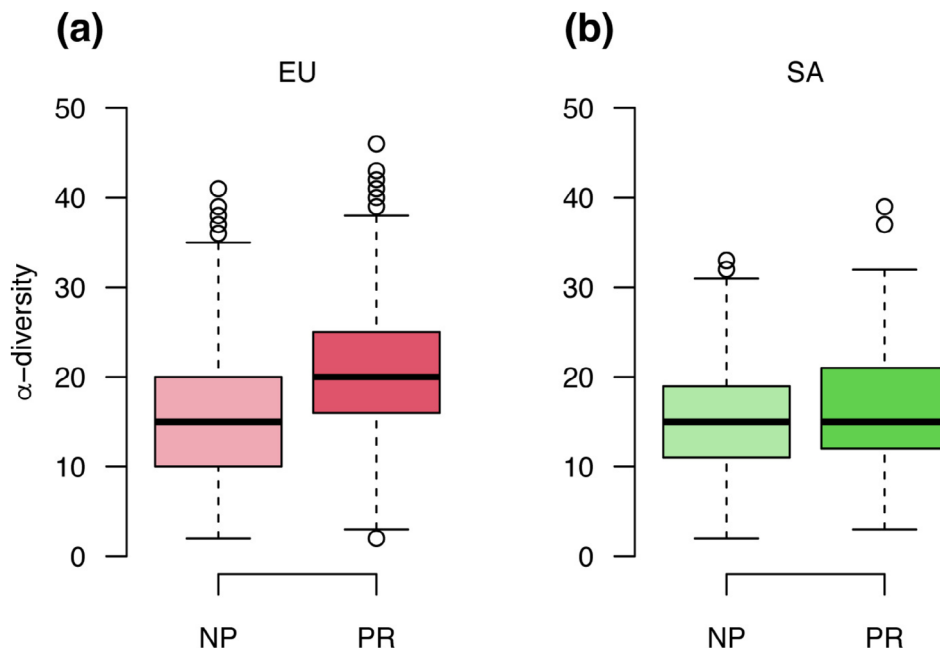
The European dataset comprised 1154 PR and 939 NP invertebrate community samples, while the South American dataset comprised 243 PR and 205 NP samples. The combined metacommunity dataset comprised 3,625,859 individuals from 215 families. On average,  $\alpha$ -diversity was  $17.64 \pm 7.61$  (range 4–52) families per sample.  $\alpha$ -diversity was higher in Europe compared to South America ( $18.2 \pm 7.56$  compared to  $14.9 \pm 7.24$  taxa per sample; Table S2). Spatial and temporal  $\beta$ -diversity were higher in South America ( $0.83 \pm 0.06$ ;  $0.72 \pm 0.11$ ) than in Europe ( $0.64 \pm 0.18$ ;  $0.65 \pm 0.12$ ) (Figure S1A–D). The European genus-level dataset consisted of 2,027,024 individuals from 414 invertebrate genera, representing 60% of the original dataset. The  $\alpha$ -diversity across the genus-level dataset was  $19.48 \pm 8.83$  (range 2–57) genera per sample.

#### 3.1 | $\alpha$ - and $\beta$ -Diversity Responses at Local and Regional Scales

There was an interaction between reach type and continent for  $\alpha$ -diversity, which was lower in NP than PR in Europe but not South America (Figure 3, Table 2). There were no interactions between reach type and continent for spatial  $\beta$ -diversity (Figure 4a) or its turnover or nestedness components (Figure 5a,b). However, the interaction effect for nestedness approached significance (Table 2), potentially suggesting a stronger difference in nestedness between NP and PR reaches in South America. Spatial  $\beta$ -diversity was similar in NP and PR reaches on both continents. Interactions for temporal  $\beta$ -diversity and its turnover component were detected (Table 2, Figures 4b and 5c). Temporal  $\beta$ -diversity was comparable in NP and PR reaches in South America, while it was higher in NP reaches compared to PR reaches in Europe (Table 2). Temporal nestedness was higher in NP reaches than in PR reaches in Europe but not in South America (Figure 5d).

#### 3.2 | Dispersal and Environmental Gradients Shaping Community Composition

Spatial distances, encompassing both overland (OVER) and watercourse (WACO) distances, influenced community



**FIGURE 3** |  $\alpha$ -diversity of communities in perennial (PR) and non-perennial (NP) reaches across (a) Europe and (b) South America.

composition on both continents (Table 3, Table S3). OVER influenced community composition in 50% (3 of 6) of metacommunities in South America and 71% (23 of 37) in Europe, while WACO influenced 66% (4 of 6) of metacommunities in South America and 62% (23 of 37) in Europe. Environmental (ENVI) distance influenced community composition in 33% (2 of 6) of metacommunities in South America and 30% (11 of 37) in Europe.

OVER influenced community composition in approximately 25% (6 of 24) and 22% (46 of 206) of sampling campaigns in South America and Europe, respectively. WACO influenced composition in 29% (7 of 24) and 26% (54 of 206) of campaigns in South America and Europe, respectively. ENVI-influenced composition was in 17% (4 of 24) and 11% (23 of 206) of campaigns in South America and Europe, respectively. Spatial distances were correlated with community dissimilarity more frequently than ENVI distances (chi-squared test:  $\chi^2=19.076$ ,  $df=2$ ,  $p<0.001$ ) (Figure 6a); however, correlation coefficients were comparable for ENVI, OVER, and WACO distances (Kruskal-Wallis  $\chi^2=0.228$ ,  $df=2$ ,  $p=0.892$ ) (Figure 6b).

### 3.3 | $\alpha$ -Diversity and Drying Duration in Europe

The metacommunity-specific model, which incorporated TotDur as a random slope within the random effect structure, best explained the response of  $\alpha$ -diversity to increasing drying duration (LRT:  $\chi^2=427.44$ ,  $df=2$ ,  $p<0.001$ ). This model revealed that, while  $\alpha$ -diversity generally decreased with increasing drying duration (estimate =  $-0.026$ ,  $SE=0.005$ ,  $t=-5.243$ ,  $p<0.001$ ), the response to drying duration differed across metacommunities. On average, one genus was lost for every 36-day increase in drying duration (Figure 7a). Specifically,  $\alpha$ -diversity decreased in 17 metacommunities, showed no response in five, and increased in one (Figure 7b, Figure S2).

## 4 | Discussion

Our results suggest limited transferability of knowledge related to the effects of drying on river metacommunities from Europe to South America.  $\alpha$ - and  $\beta$ -diversity responded differently to drying on the two continents, and some variation was also detected across European DRNs. Our results also support the theory that dispersal may be more important than environmental filtering in shaping DRN metacommunities. As DRNs increase in space and time (Datry, Truchy, et al. 2023; Zipper et al. 2021), the metacommunity framework provides a robust template for understanding assembly processes in DRNs. By establishing the transferability of the effects of drying across climatic and biogeographic regions, such as Europe and South America, our results offer powerful insights that could improve river ecosystem management under climate change.

### 4.1 | River Drying Decreases $\alpha$ -Diversity in Europe but Has a Weaker Impact in South America

Contrary to hypothesis H1,  $\alpha$ -diversity was significantly lower in non-perennial than perennial reaches in European but not South American DRNs. Broad-scale studies of aquatic invertebrates across North America, Europe, and Oceania have consistently found that  $\alpha$ -diversity is lower in non-perennial than in perennial reaches (Datry, Larned, Fritz, et al. 2014; Soria et al. 2017; Vander Vorste et al. 2021) and that increasing aridity exacerbates these patterns (Vander Vorste et al. 2021). For example, Datry, Larned, Fritz, et al. (2014) showed that  $\alpha$ -diversity steadily decreased as drying increased (1 family lost every 10% increase in flow intermittence) in 14 DRN across Europe, North America, and New Zealand. The more modest decline in South America could reflect the greater occurrence of adaptations conferring resistance to drying. For example, desiccation-resistant invertebrates significantly aid community

**TABLE 2** | Results of ANCOVA testing the interaction of  $\alpha$ -diversity, spatial  $\beta$ -diversity, and temporal  $\beta$ -diversity in perennial (PR) and non-perennial (NP) reaches in Europe (EU) and South America (SA). Jaccard dissimilarity (total  $\beta$ -diversity) and its components were calculated using presence-absence data.

Response variable	Source of variation	Estimate	SE	t-value	p
$\alpha$ -diversity	Intercept	15.327	0.225	67.845	<0.001
	Reach type (PR)	5.394	0.303	17.759	<0.001
	Continent (SA)	-0.109	0.562	-0.195	0.845
	PR $\times$ SA	-4.359	0.744	-5.857	<0.001
Spatial $\beta$ -diversity–turnover	Intercept	0.529	0.015	34.310	<0.001
	Reach type (PR)	0.030	0.020	1.475	0.140
	Continent (SA)	0.157	0.043	3.601	<0.001
	PR $\times$ SA	0.024	0.064	0.378	0.705
Spatial $\beta$ -diversity–nestedness	Intercept	0.120	0.006	19.609	<0.001
	Reach type (PR)	-0.028	0.008	-3.293	<0.001
	Continent (SA)	0.042	0.018	2.310	0.021
	PR $\times$ SA	-0.051	0.027	-1.893	0.059
Total spatial $\beta$ -diversity	Intercept	0.641	0.013	48.929	<0.001
	Reach type (PR)	0.001	0.018	0.095	0.924
	Continent (SA)	0.199	0.039	5.101	<0.001
	PR $\times$ SA	-0.027	0.057	-0.469	0.639
Temporal $\beta$ -diversity–turnover	Intercept	0.554	0.010	53.267	<0.001
	Reach type (PR)	-0.043	0.013	-3.184	0.001
	Continent (SA)	-0.020	0.025	-0.822	0.411
	PR $\times$ SA	0.089	0.037	2.403	0.016
Temporal $\beta$ -diversity–nestedness	Intercept	0.140	0.006	21.159	<0.001
	Reach type (PR)	-0.026	0.008	-3.089	0.002
	Continent (SA)	0.040	0.016	2.457	0.014
	PR $\times$ SA	0.016	0.023	0.700	0.484
Total temporal $\beta$ -diversity	Intercept	0.689	0.008	85.323	<0.001
	Reach type (PR)	-0.069	0.010	-6.600	<0.001
	Continent (SA)	0.019	0.020	0.971	0.331
	PR $\times$ SA	0.105	0.029	3.640	<0.001

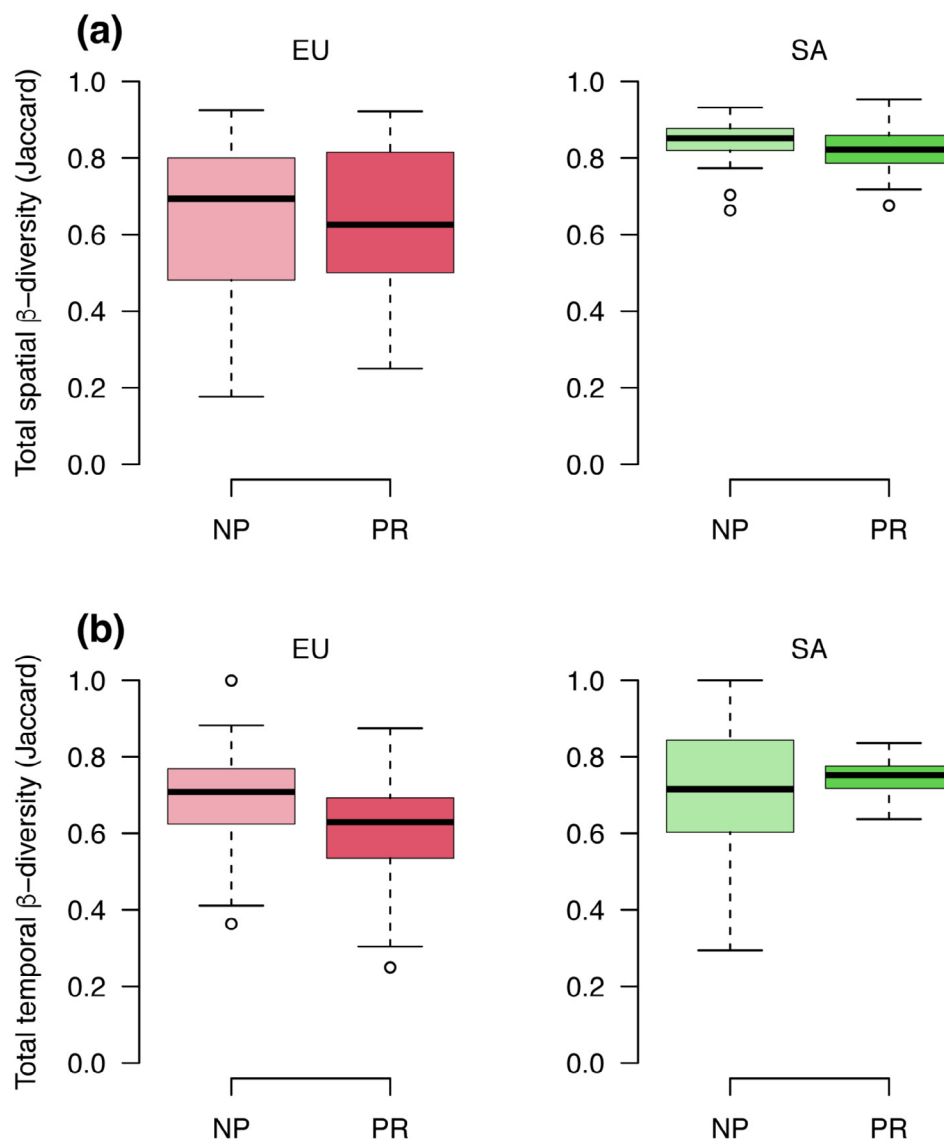
Abbreviation: SE, standard error.

recovery in arid Bolivia, indicating adaptation to regional drying regimes (Datry, Vander Vorste, et al. 2017). Similarly, invertebrate communities inhabiting bromeliads subject to experimental drying in French Guiana recovered post-drying due to resistance traits (Bonhomme et al. 2021). Taxa within the orders Coleoptera, Diptera, Ephemeroptera, Hemiptera, Odonata, and Plecoptera, all present in the South American dataset, can be diverse during drying periods in South American DRNs (Echeverría-Sáenz et al. 2022; Nolte, De Oliveira, and Stur 1997; Rocha, Medeiros, and Andrade 2012). Specifically, Caenidae mayflies and Chironomidae true flies were abundant in non-perennial reaches in this study, reflecting their ability to persist

in habitats characterized by periodic drying, as also observed previously (Nolte, De Oliveira, and Stur 1997; Rocha, Medeiros, and Andrade 2012).

Weak responses to river drying from South American DRNs could also reflect life-history traits conferring resilience to environmental dynamism ecosystems, as South American DRNs can experience frequent, predictable flooding and drying regimes (Junk, Bayley, and Sparks 1989; Lytle and Poff 2004). As such, their regional species pools can be co-adapted to multiple environmental disturbance types. For example, in braided rivers, many invertebrates tolerate drying due to adaptations



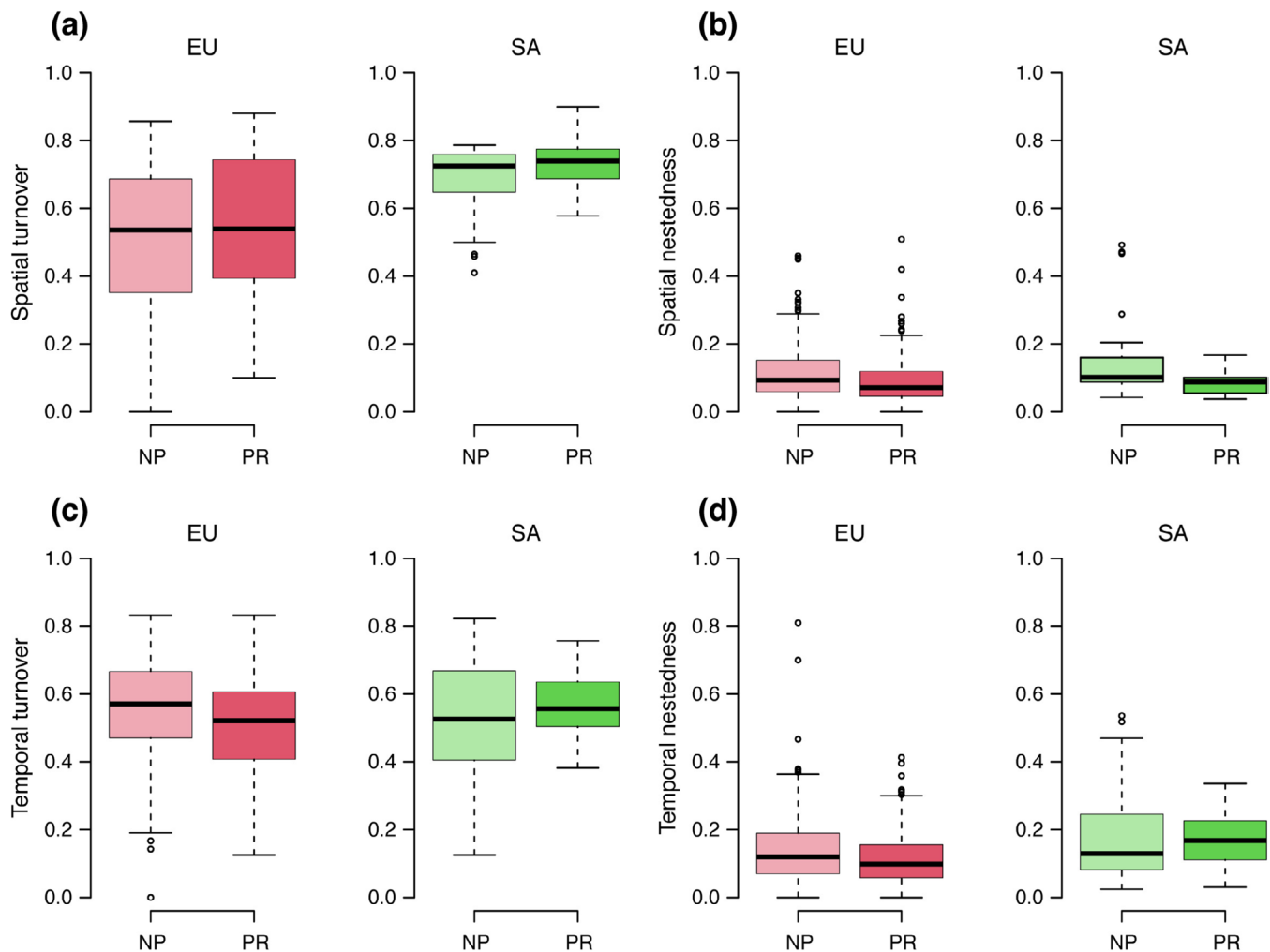


**FIGURE 4** | Spatial (a) and temporal (b)  $\beta$ -diversity (based on Jaccard dissimilarity) of communities in perennial (PR) and non-perennial (NP) reaches in Europe and South America.

that also promote persistence despite flooding and scouring, including dispersal, fecundity, size, and voltinism traits (Vander Vorste et al. 2016). Also, anatomical traits of equatorial forest invertebrates, such as greater body mass and cuticle content (i.e., an exoskeleton layer composed of chitin, proteins, and oils), may confer resistance to drying by reducing water loss (Céréghino et al. 2020). Multivoltinism, which is more common at lower latitudes (Bonada and Dolédec 2018; Corbet, Suhling, and Soendgerath 2006; Jackson and Sweeney 1995), could also promote dispersal, even in unstable conditions, enabling species to complete a life cycle despite drying. For example, in the southeastern Brazilian Cerrado, communities dominated by multivoltine taxa do not decline in similarity as the spatial distance between them increases (Saito et al. 2015). Therefore, the weak response of  $\alpha$ -diversity to drying in South America could reflect a resilient community with both generalist traits and resistance adaptations, enabling persistence and rapid recovery after disturbance (Maltchik and Medeiros 2006; Ríos-Pulgarín et al. 2016; Tonkin et al. 2017).

#### 4.2 | $\beta$ -Diversity Increases With Drying in Time, Not Space

Spatial and temporal  $\beta$ -diversity were higher in South American than in European DRNs, probably due to a combination of higher taxonomic richness and steeper altitude gradients, contributing to greater environmental variability in South America (He et al. 2024). Partially supporting H1, temporal  $\beta$ -diversity was higher in non-perennial reaches, but only in Europe. Higher temporal  $\beta$ -diversity in non-perennial reaches agrees with previous findings that  $\beta$ -diversity increases with drying in temperate regions, generating spatial asynchrony in community composition across DRNs (Crabot et al. 2020; Crabot, Polášek, et al. 2021; Gianuca et al. 2024; Vander Vorste et al. 2021). The higher temporal  $\beta$ -diversity observed in non-perennial reaches is likely the result of extinction-colonization dynamics, where different hydrological phases support different local communities (Crabot et al. 2020; Datry, Larned, Fritz, et al. 2014; Gianuca et al. 2024). Echoing recent findings from southwestern France



**FIGURE 5** | Spatial (a–b) and temporal (c–d)  $\beta$ -diversity components: Turnover (a–c) and nestedness (b–d) of communities in perennial (PR) and non-perennial (NP) reaches in Europe and South America.

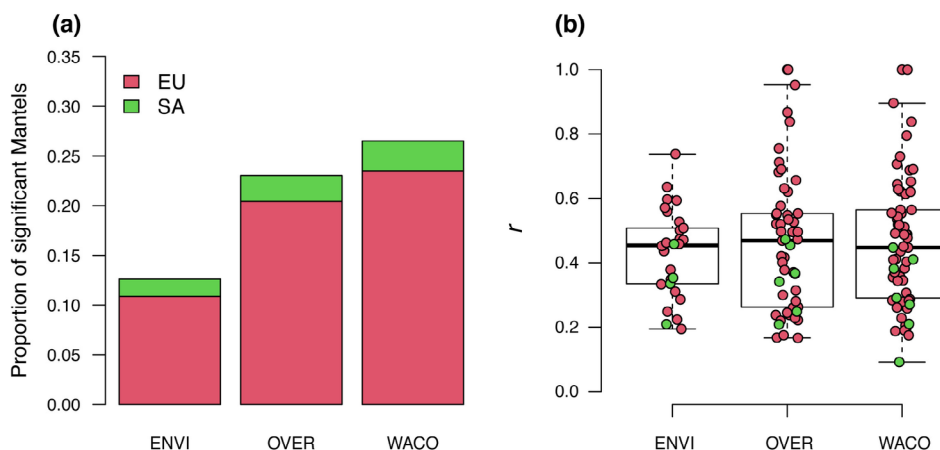
(Gianuca et al. 2024), greater spatial synchrony and thus reduced temporal  $\beta$ -diversity in perennial reaches could be due to similar processes driving metacommunities and to synchronized life-history traits of their inhabitant species (Gianuca et al. 2024). The lack of differences between perennial and non-perennial reaches in South American DRNs may reflect the weak effect of drying on local communities (see H1). Likely, the regional species pool is adapted to dynamic flow regimes, with generalists that quickly recolonize previously dry sites and specialists that tolerate desiccation (Bunting et al. 2021; Crabot et al. 2020; Sarremejane et al. 2020).

Most spatial and temporal  $\beta$ -diversity reflected turnover on both continents, regardless of reach type. This result contrasts with the previous finding that nestedness is generally the main component of spatial (Crabot et al. 2020; Datry, Larned, Fritz, et al. 2014) and temporal  $\beta$ -diversity in DRNs (Crabot, Polásek, et al. 2021; Vander Vorste et al. 2021), notably for strictly aquatic assemblages. Spatial nestedness dominated  $\beta$ -diversity in non-perennial reaches of 14 DRNs (Datry, Larned, Fritz, et al. 2014), where local communities in reaches with lower  $\alpha$ -diversity were subsets of those in reaches with higher diversity. However, how  $\beta$ -diversity varies with drying across DRNs and the drivers underlying this variation remain unclear. For example, temporal turnover can dominate non-perennial

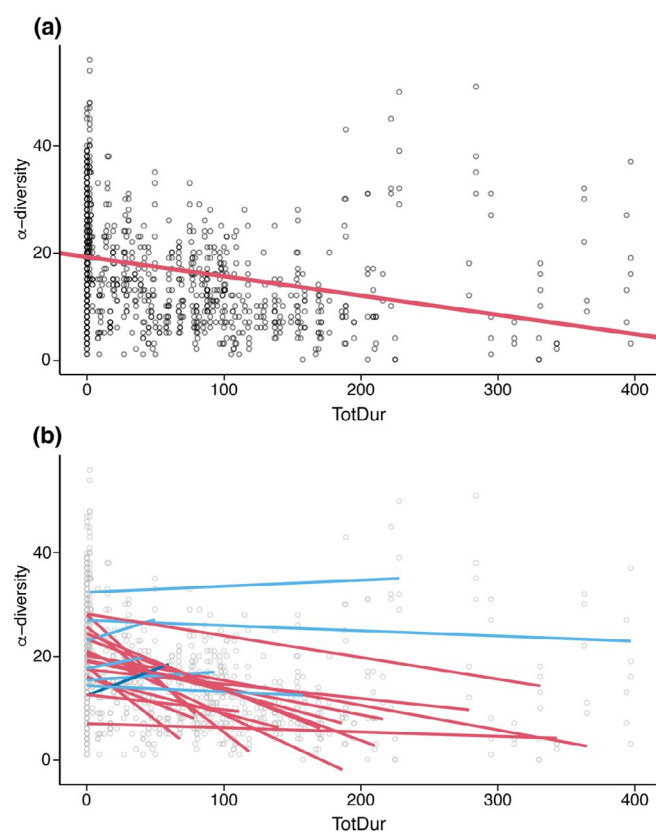
**TABLE 3** | Number of metacommunities (and sampling campaigns) with significant relationships between community dissimilarity and environmental (ENVI), overland (OVER), and/or watercourse (WACO) distances.

	ENVI	OVER	WACO	Total
South America	2 (4)	3 (6)	4 (7)	6 (24)
Europe	11 (23)	23 (46)	23 (54)	37 (206)
All	13	26	27	43

communities upon wetting (Crabot, Polásek, et al. 2021), probably reflecting recolonization dynamics from refuges (Datry, Larned, Fritz, et al. 2014; Sarremejane et al. 2020). The contributions of turnover and nestedness to  $\beta$ -diversity can also vary spatially among non-perennial reaches (Viza et al. 2024) and through time, depending on dispersal type. Specifically, turnover is primarily associated with aerial dispersers, while nestedness is more related to strict aquatic dispersers (Crabot et al. 2020). During the first stages of wetting,  $\beta$ -diversity may increase through its turnover component when species recolonize through dispersal, including mass effects, which can lead to community homogenization (Pařil et al. 2019; Sarremejane, Mykrá, et al. 2017; Schenková et al. 2022).



**FIGURE 6** | (a) Proportion of significant Mantel tests between community dissimilarity and environmental (ENVI), overland (OVER), and watercourse (WACO) distance. (b) Correlation coefficients ( $r$ ) from significant Mantel tests between community dissimilarity and the distance matrices (ENVI, OVER, and WACO).



**FIGURE 7** | Relationships between  $\alpha$ -diversity (taxonomic richness) and drying duration (TotDur, total number of drying days). (a) Overall  $\alpha$ -diversity of 23 metacommunities. (b)  $\alpha$ -diversity response by metacommunity: Decreasing (pink), non-decreasing (light blue), and increasing (dark blue).

### 4.3 | Dispersal Is a Key Mechanism of Metacommunity Organization

As predicted by hypothesis H2, dispersal was a key process explaining metacommunity organization in DRNs, adding a layer of complexity to the current paradigm that environmental filtering—driven by biotic and abiotic interactions—is dominant

in river ecosystems (Cottenie 2005; Brown and Swan 2010; Grönroos et al. 2013; Heino et al. 2015). The influence of dispersal on metacommunity processes suggests that dispersal rates vary due to differences in distances between localities (Heino et al. 2015; Tonkin et al. 2014). Shifting habitat mosaics of lotic and lentic conditions due to drying can create variable environmental filters across space that, when coupled with variable dispersal processes (Datry, Bonada, and Heino 2016), structure metacommunity organization over spatial distances. This enhanced role of dispersal in invertebrate metacommunity organization is supported by research in DRNs in both South America (Datry, Melo, et al. 2016; Datry, Moya, et al. 2016; de Campos et al. 2019) and Europe (Gauthier et al. 2020, 2021; Pineda-Morante et al. 2022; Sarremejane, Cañedo-Argüelles, et al. 2017), suggesting dispersal as a predominant mechanism in metacommunity organization, at least in DRNs, at a global scale. Given the importance of dispersal in metacommunity organization of highly dynamic ecosystems such as DRNs, a more integrated approach is needed to study the interplay between dispersal and environmental filtering across varying climatic conditions, as well as its implications for biodiversity management.

For 37% of DRNs, dispersal was not the primary driver of metacommunity organization, and in five of these DRNs, neither was environmental filtering (based on the lack of relationships between  $\beta$ -diversity and environmental distances), indicating the prevalence of stochastic over deterministic metacommunity processes (Saito et al. 2021). Dispersal seemed to be more influential before (rather than during or after) drying, as 48%–49% of significant relationships between community dissimilarity and overland and watercourse distances occurred before drying. This suggests that drying can alter dispersal by reducing connectivity among reaches and that some species were moving to refuges as DRNs contracted. Contrary to Gauthier et al. (2020), the role of dispersal was not higher upon wetting, despite this hydrological phase being when most species recolonize previously dry reaches (Bogan et al. 2017). Several factors could explain these results. First, DRN metacommunities are characterized by high temporal variability, which could obscure the detection of consistent dispersal patterns or their role in metacommunity organization

(Cañedo-Argüelles et al. 2020; Crabot et al. 2020; Sarremejane, Cañedo-Argüelles, et al. 2017). Similarly, variability in key hydrological periods, such as the flowing phase duration prior to sampling, may have masked the role of dispersal upon wetting. In addition, high flows upon wetting could have caused mass effects to homogenize communities, preventing the detection of spatial metacommunity patterns (Padial et al. 2012; Wilson and McTammany 2016). High connectivity between communities can promote mass effects where the constant influx of individuals stabilizes communities and masks the influence of hydrological disturbances (Huttunen et al. 2017). In North American drylands, communities of strong fliers are homogeneous, with no landscape factors affecting their distribution due to the absence of dispersal restrictions (Cañedo-Argüelles et al. 2015). Lastly, specific spatial features of each DRN, such as topography (Cañedo-Argüelles et al. 2015), anthropogenic structures (Gauthier et al. 2021), or localized drying (Crabot et al. 2020), could have affected metacommunity processes by enhancing or reducing the role of dispersal. Differences in sampling design, methods and timing which are inherent to meta-analyses (Soria et al. 2017), and large-scale comparisons of metacommunity dynamics in DRNs could benefit from coordinated distributed experiments (Yahdjian et al. 2021).

#### 4.4 | Drying Duration Is a Primary Driver of $\alpha$ -Diversity Across European DRNs

Contrary to hypothesis H3,  $\alpha$ -diversity declined with increasing drying duration across most European DRNs (17, 74%), but did not decrease in six DRNs, possibly for reasons similar to those discussed for South American DRNs. The decrease in  $\alpha$ -diversity aligns with previous broad-scale studies that found congruent diversity declines with increasing drying duration across regions with different spatial arrangements of perennial and non-perennial reaches (Datry et al. 2014), as taxa lacking adaptations for resistance or resilience to drying were lost. Equally, the lack of effect of drying on the  $\alpha$ -diversity of five metacommunities has also been reported previously, notably in Europe (Leigh and Datry 2017; Stubbington, Sarremejane, and Datry 2019). For instance, despite prolonged drying over 3 weeks,  $\alpha$ -diversity remained unchanged in three DRNs in oceanic and Mediterranean-climate regions (Stubbington, Sarremejane, and Datry 2019). Notably, all six DRNs in which  $\alpha$ -diversity did not decrease with increasing drying duration were in a Mediterranean climate. Moreover, while they were sampled at different times after wetting, this variation in timing may have contributed to the observed patterns, but it does not fully explain the lack of  $\alpha$ -diversity decline. As discussed for H1, the lack of effects of drying on  $\alpha$ -diversity may reflect factors including local contexts, drying regimes, adaptations of the regional species pool, and the time between flow resuming and sampling. These factors influence invertebrate communities in Mediterranean regions, where life-history traits enable many taxa to tolerate or recover from disturbances (Bonada, Dolédec, and Statzner 2007; Bonada, Rieradevall, and Prat 2007). In a context of increasing river drying including shifts from perennial to intermittent flow (Datry, Boulton, et al. 2023), these results indicate predictable loss of freshwater biodiversity, which could have cascading effects on ecosystem functions.

#### 4.5 | Caveats, Future Directions, and Implications

Limitations of the datasets compiled for this study include the uneven distribution of DRNs across continents, with only 14% of the metacommunities located in South America, where only family-level identifications were conducted. This disparity may have affected our findings, although we adjusted for differences in sample size by controlling for covariates (Huitema 2011). Furthermore, previous family-level studies have quantified the effects of drying on invertebrate biodiversity (Chanut et al. 2023; Datry, Larned, Fritz, et al. 2014; Vander Vorste et al. 2021). Additionally, the environmental conditions (Sayre et al. 2020), biodiversity (Abell et al. 2008), and hydrological regimes (Siddiqui et al. 2021) of South American rivers may have been underrepresented in our analysis. Although metacommunities were sampled from five freshwater ecoregions, this limitation could affect the applicability of our conclusions to other biogeographic regions. Future studies should place greater focus on increasing DRN metacommunity-designed sampling in South America to enhance understanding of diversity responses to drying. Finally, future large-scale studies could incorporate additional spatial deterministic factors in metacommunity organization, such as topographic distance (Cañedo-Argüelles et al. 2015), which may be particularly relevant in South American regions with strong elevational gradients. For example, the significant environmental variation in tropical montane rivers is known to influence habitat heterogeneity and macroinvertebrate diversity (Encalada et al. 2019; Jacobsen, Schultz, and Encalada 1997).

The variable diversity patterns in DRNs across continents highlight the complexity of ecological dynamics under environmental variability, with diversity shifts occurring at broad spatial scales. This calls for further DRN research in different biogeographic regions, particularly across poorly studied regions (e.g., in Africa, Asia). At a regional scale, drying-induced changes in community composition underscore the importance of incorporating both spatial and temporal  $\beta$ -diversity, and their components, into conservation planning (Cid et al. 2022). This approach provides insights into the drivers underlying DRN biodiversity patterns and could help develop effective strategies to manage the dynamics of species turnover and nestedness across space and time. Specifically, recognition of the role of dispersal in metacommunity organization has important implications for the conservation, monitoring, and restoration of DRNs (Cid et al. 2020). In particular, conservation strategies should prioritize maintaining and enhancing connectivity between habitats, particularly in dynamic ecosystems subject to frequent drying and flooding periods (Datry, Boulton, et al. 2023). Management plans should aim to preserve or restore hydrological and terrestrial connectivity, facilitating the movement of both aquatic and aerial dispersers across reaches, even during drying periods, to promote metacommunity resilience to hydrological fluctuations.

#### Author Contributions

**Daniel Escobar-Camacho:** conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing – original draft, writing – review and editing. **Julie Crabot:** data curation, formal analysis, methodology, writing – review and editing. **Rachel Stubbington:** methodology, writing



– review and editing. **Judy England**: data curation, writing – review and editing. **Romain Sarremejane**: data curation, writing – review and editing. **Núria Bonada**: data curation, funding acquisition, investigation, writing – review and editing. **José María Fernández-Calero**: data curation, investigation, writing – review and editing. **Miguel Cañedo-Argüelles**: data curation, funding acquisition, investigation, resources, writing – review and editing. **Carla Ferreira Rezende**: data curation, investigation, resources, writing – review and editing. **Pierre Chanut**: data curation, writing – review and editing. **Zoltán Csabai**: data curation, investigation, resources, writing – review and editing. **Andrea C. Encalada**: funding acquisition, investigation, resources, writing – review and editing. **Alex Laini**: data curation, investigation, writing – review and editing. **Heikki Mykrä**: data curation, resources, writing – review and editing. **Nabor Moya**: investigation, resources, writing – review and editing. **Petr Pařil**: data curation, investigation, resources, writing – review and editing. **Daniela Rosero-López**: data curation, investigation, writing – review and editing. **Thibault Datry**: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, software, supervision, validation, writing – original draft, writing – review and editing.

### Acknowledgments

We thank Maxence Forcellini, Bertrand Launay, Mailys Gauthier, Jéssica Camilla da Silva Vieira de Araújo, Christopher T. Robinson, Gemma Burgazzi, Barbora Loskotová, Marko Miliša, Maria Soria, Pau Fortuño, Raúl Acosta, Guillermo Quevedo-Ortiz, Marek Poláček, Nieves López-Rodríguez, Martí Piñero-Fernández, Dolores Vinyoles, Arnold Móra, Bálint Pernecker, Bernadett Boóz, Dorottya Hárságyi, József Balázs Berta, Zsuzsanna Pap, Anita Szloboda, and Éva Horváth-Tihanyi for collecting and sharing invertebrate abundance data. We thank Naiara López-Rojo for help with spatial distance calculations, Maxime Logez for help with the calculation of diversity metrics, and Hervé Pella for help with the map figure. D.E.-C. was supported by MOPGA 2023 Visiting Fellowship. This research was funded by the DRYvER project (Horizon 2020 #869226), the MECODISPER project (CTM2017-89295-P) funded by the Spanish “Ministerio de Ciencia, Innovación y Universidades—Agencia Estatal de Investigación”; and co-funded by the ERDF (European Regional Development Fund). Research in Brazil was funded by the FUNCAP project (N° PS1-0186-00210.01.00/21) of the Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico, and in Ecuador by Universidad San Francisco de Quito—USFQ grants (#17074). R.Sa. was funded by the Environment Agency (award SC220011).

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data supporting the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.n5tb2rc5w> and <https://doi.org/10.5061/dryad.hqzkh1bn>; in Zenodo at <https://doi.org/10.5281/zenodo.3569563>; and in Recherche Data Gouv at <https://doi.org/10.57745/RS8266>. Sentinel 2-satellite images data were obtained from the Sentinel Hub at <https://apps.sentinel-hub.com/eo-browser/>.

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### Supporting Information

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