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Research

Drying determines the temporal dynamics of stream invertebrate structural and functional beta diversity

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Assembly processes shaping ecological communities can vary over time following variations of environmental conditions at different scales. Such temporal dynamism is exacerbated by climate change and increasing extreme events, and recent evidence suggests that, in turn, community composition and functions can vary substantially. However, empirical relationships between the spatio-temporal dynamics of communities and that extreme events altering ecosystems are poorly investigated. We quantified the temporal dynamics of stream invertebrate communities over two years across 11 river basins prone to drying, covering a large geographical area of France. We tested predictions on the influence of the spatial arrangement and temporal dynamics of drying events across river networks. Combining a high temporal resolution of community description from taxonomic and functional perspectives, we quantified beta diversity over time and space and partitioned them into additive components: replacement of taxa and richness difference. Frequency and duration of drying events were precisely quantified and basins were classified based on the location of the drying events. We found a strong influence of the spatial drying pattern on the dissimilarities of community composition between sites. The high temporal variability of community structure was directly related to the frequency and duration of drying events. This temporal dynamism of communities was also strongly affected by the spatial drying pattern, indicating that fragmentation had a stronger effect on recolonisation processes for upstream-drying basins. Finally, biological traits were unevenly distributed in space and time, suggesting a lack of functional redundancy that could have strong implications for ecosystem functions and services. The high temporal dynamics of communities highlighted in this study challenge the current definition of reference conditions in intermittent rivers, and the community sensitivity to frequency and duration of drying suggest that climate change might lead community dynamics to be increasingly driven by stochastic environmental variability.

Keywords: aquatic invertebrates, beta diversity, fragmentation, functional diversity, metacommunities, temporary rivers



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Introduction

Processes structuring biotic communities can covary over time with variations of environmental conditions at both local (Ricklefs and Schluter 1993) and regional scales (Descamps-Julien and Gonzalez 2005, Auerbach and Poff 2011). While it may be difficult to define spatio-temporal stability for dynamic ecosystems (Azeria and Kolasa 2008, Ricklefs 2008), complex spatial analyses still mostly consider communities at a single snapshot in time or are based on a few sampling occasions (Logue et al. 2011, Heino 2013, Jabot et al. 2018). Failing to consider temporal variations could impair understanding of the mechanisms structuring communities (Erős et al. 2012, Datry et al. 2016, Tonkin et al. 2016), especially with accelerating climate change demanding better understanding of how biotic communities behave in non-stationary environments (Wolkovich et al. 2014, Regos et al. 2018). Measuring and interpreting the spatio-temporal variability of communities is particularly important in dynamic ecosystems, where biotic patterns are driven by severe and often abrupt changes of environmental conditions. For example, wildfire is a crucial process for Mediterranean-type vegetation that controls the plant dynamics (Baeza et al. 2007). Floodplain communities exposed to flood pulses are also driven by intense modifications of the environment with an increase in habitat availability during floods (Franssen et al. 2006, Malard et al. 2006, Chanut et al. 2019) through changes in the channel morphology and a higher connectivity among habitat patches (Thomaz et al. 2007).

Although beta diversity, defined as the extent of change in community composition between localities or occasions (Anderson et al. 2011), can provide valuable insights into the relationship between local and regional patterns of biodiversity and their underlying processes (Socolar et al. 2016, Aspin et al. 2018), it remains poorly quantified in highly dynamic ecosystems, particularly with respect to its temporal dynamics (Datry et al. 2016, Sarremejane et al. 2017a, Leigh et al. 2019). Moreover, the partitioning of beta diversity into two additive components, replacement (taxa replacement between two localities) and richness difference (difference in the number of taxa), can add substantial information on how communities differ (Podani and Schmera 2011, Cardoso et al. 2014). Recent developments in conceptual frameworks allow quantification and interpretation of the temporal dimensions of beta diversity (Ruhí et al. 2017, Jabot et al. 2018, Legendre and Condit 2019), thereby offering promising avenues to understand biodiversity variation in space and time, particularly in highly dynamic ecosystems.

How functional diversity, defined as the variation in the degree of expression of multiple functional traits (Naeem et al. 2012), varies in space and time in highly dynamic ecosystems is still an open question, which prevents a full understanding of how underlying ecosystem processes and functions are affected by severe changes in environmental conditions (Naeem et al. 2012, Matthews et al. 2015, Aspin et al. 2018). Because some functional trait combinations can be expressed

by only one or a few taxa in a local community, quantifying functional beta diversity can provide valuable insights into how biodiversity loss affects ecosystem functioning and, ultimately, the provision of ecosystem services (e.g. traits of plants associated with soil fertility, traits of carabid beetles associated with biocontrol of crop pest, or traits of amphibians associated with nutrient cycling and energy flows, Díaz et al. 2007, Gagic et al. 2015, Riemann et al. 2017). As for taxonomic beta diversity, the decomposition into two additive components can provide important information on how ecosystem functioning varies in time and space by applying similar calculations on trait combinations rather than taxa (Villéger et al. 2013, Cardoso et al. 2014). For example, high functional turnover would indicate, independently from taxa dissimilarities, distinct trait combinations between sites, whereas high functional richness difference would indicate the removal of some traits in response to a disturbance. On the contrary, in the case of functional redundancy (i.e. species fulfill similar functional roles), taxonomic replacement is not associated with a high functional turnover (Rosenfeld 2002). While some links between taxonomic and functional diversity have been explored in some highly dynamic ecosystems (e.g. terrestrial communities exposed to floods or fire-adapted forest, Gerisch 2014, Dell et al. 2019), these have been mostly restricted to static snapshot views of community patterns and, to date, their temporal dynamics have been overlooked.

Intermittent rivers (hereafter IRs), those rivers experiencing natural drying events with flow cessation and loss of surface water, are highly dynamic shifting-habitat mosaics (Larned et al. 2010, Datry et al. 2014, 2016), and therefore represent ideal ecosystems to explore how biotic communities vary in space and time. Recurrent shifts between lotic, lentic and terrestrial phases determine IR community structure and functions locally (Bêche et al. 2006, Bogan and Lytle 2007, Datry et al. 2014). Because community recovery upon rewetting is gradual over time (Larned et al. 2010), such temporal dynamics of drying events, including their frequency and duration, could determine the temporal dynamics of ecological communities in IR ecosystems (Datry et al. 2016, Sarremejane et al. 2017a). Concomitantly, because, in river networks, the unidirectional flow of water drives organism dispersal and material transport from upstream to downstream (Brown and Swan 2010, Liu et al. 2013), any local disturbance can also have different effects on biotic communities depending on their location within river networks (Holyoak et al. 2005, Altermatt et al. 2011, Datry et al. 2016). As such, river networks with contrasting spatial drying patterns could present different spatial dynamics of aquatic communities (Datry et al. 2014). As environmentally harsh systems such as natural IRs contain taxa with traits that promote resistance and resilience to disturbance and consequently present a high functional redundancy (Boersma et al. 2014, Vander Vorste et al. 2016), differences in functional diversity according to the spatial drying pattern could be less pronounced compared to taxonomic trends. Finally, as aerial

dispersal allows some aquatic organisms to overcome the loss of hydrological connectivity (Bogan and Boersma 2012), the patterns above could differ between strict aquatic dispersers and dispersers with an aerial stage.

In this study, we investigated the temporal responses of stream invertebrate communities to flow intermittence across river basins presenting contrasting spatial drying patterns. Using data collected across 11 river basins over two years, we quantified taxonomic and functional beta diversity in space and time to test the following hypotheses.

H1: in downstream-drying basins (DDB), we hypothesised that fast recolonisation of intermittent sites upon rewetting through active and passive drift from upstream perennial sites (Fig. 1a) would lead to a low spatial taxonomic beta diversity at the basin scale (Fig. 1b). In contrast, for upstream-drying basins (UDB), being more isolated, intermittent sites should be more slowly recolonized (Fig. 1a), leading to a high spatial taxonomic beta diversity at the basin scale due to low dispersal rates (Fig. 1b). This contrast in recolonisation pathways should also lead to a higher richness difference in UDB compared to DDB (Fig. 1b). Similar patterns are expected for spatial functional beta diversity but due to functional redundancy, these patterns may be less clear compared to taxonomic beta diversity (Fig. 1c).

H2: we predicted that the frequency of drying should be a strong determinant of temporal beta diversity (Fig. 1d) and that with increased drying frequency, temporal taxonomic beta diversity would increase by frequent resets of natural community successions (Fig. 1e). Such an increase should be mostly driven by replacement, due to species replacement in between drying events (Fig. 1e). No trends related to the frequency of drying events are expected for functional beta diversity because we expected replacement of taxa that are functionally redundant (Fig. 1f). Independently of the frequency, temporal taxonomic beta diversity should increase with increased drying duration (Fig. 1h). Such an increase should be predominantly due to richness difference because as drying duration increases, species pools form ever-smaller subsets of those present prior to drying (Fig. 1h). We expect functional beta diversity to decrease with increasing drying duration because long-drying sites could harbour a small subset of particular traits present across all time points and, thus, little temporal variability in traits (Fig. 1i).

H3: we hypothesised that the above temporal beta diversity patterns would differ according to the spatial drying pattern and, thus, we predicted that the increase in taxonomic beta diversity with frequency and duration of drying events would be higher for DDB compared to UDB (Fig. 1j). We predicted that the decrease in functional beta diversity with duration of drying events would be steeper for UDB compared to DDB because we expect a narrower pool of traits in UDB (Fig. 1k).

For each prediction, we expected highly significant responses by strict aquatic dispersers, as their dispersal is more constrained by loss of hydrological connectivity, whereas organisms with aerial stages might be minimally responsive to changes in the dynamics of drying events.

Methods

Study sites

Eleven river basins were selected on the 90 000 km² wide basin of the Rhone river in south-eastern France (Fig. 2, Table 1). The selection was driven to 1) encompass a diversity of geomorphologic and climatic configurations, 2) encompass different spatio-temporal patterns of flow intermittence, 3) remain within a homogeneous biogeographic context and, 4) remain within fairly pristine conditions (Table 1). River basin areas ranged from 80 to 626 km² (mean \pm SD, 233 ± 156 km²), with the mainstem lengths ranging from 33 to 822 km (343 ± 278) (Table 1). Three basins comprised intermittent reaches in their headwaters, while downstream reaches were perennial reaches (UDB). Eight basins comprised perennial headwaters, while downstream reaches were intermittent (DDB). These patterns were described through seven visits during 2014 and six visits during 2015 and the use of 66 continuous water presence loggers (see below).

For each basin, six sites were evenly distributed along the mainstems, located 1.1–3.8 km apart (2.5 ± 1.3 km) (Fig. 2, Table 1). The sites were located in both permanent and intermittent sections of each basin (Fig. 2, Supplementary material Appendix 1). We made sure that environmental heterogeneity was similar within UDB and within DDB (Supplementary material Appendix 2).

Flow intermittence quantification

Flow intermittence, defined as the periodic loss of surface water, was quantified using water presence loggers consisting of a water state data logger, submersible case, coated cable and water presence sensor (Onset Hobo[®], Intermountain Environmental, Logan, UT; (Vander Vorste et al. 2016, Jensen et al. 2019)). At each site, one logger was installed in riffle heads, which are the first habitats to be altered by drying (Boulton 2003), to monitor the presence or absence of surface water hourly from April 2013 to November 2013 and from June 2014 to December 2014. Additionally, visual observations of flow state (flowing, non-flowing or dry) were made at each site based on a monthly basis from November 2013 to June 2014 and from December 2014 to July 2015.

Stream invertebrate sampling and processing

From October 2013 to June 2014 and from December 2014 to July 2015, each site was sampled on a monthly basis. Stream invertebrates were sampled twice at one riffle head for each site to reduce the effects of small-scale habitat variability and allow comparisons within and between river basins (Arcott et al. 2010, Datry 2012, Datry et al. 2014, Vander Vorste et al. 2016). Samples were collected using a Hess sampler (40 cm diameter; 1250 cm² surface area; 250 μ m mesh size). In total, this represented 1274 samples:

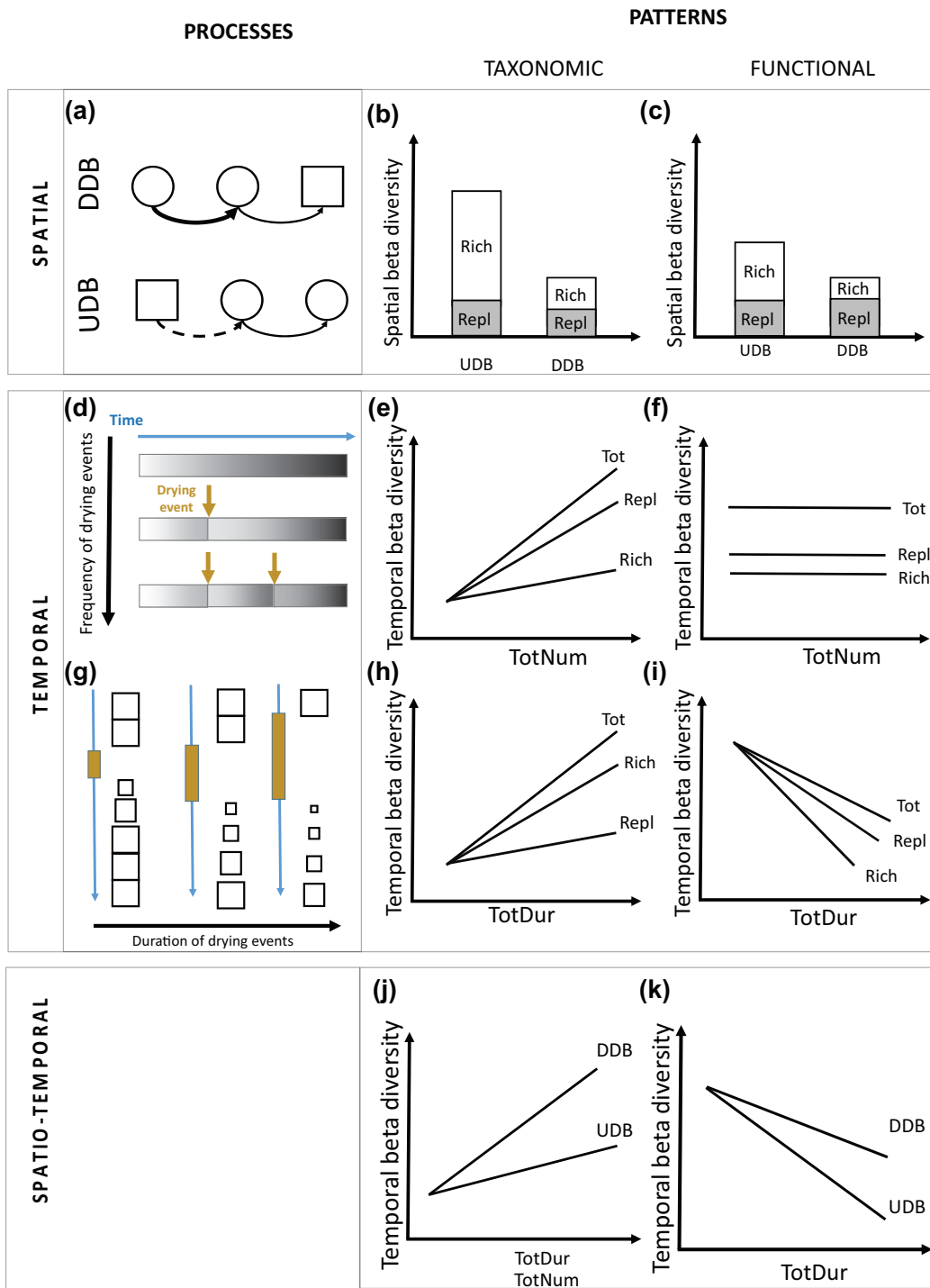


Figure 1. Hypothetical processes occurring in the biological communities of intermittent rivers in space and time, and corresponding expected patterns. In space: (a) representation of three sites (circle for perennial and square for intermittent), strength of dispersal for aquatic dispersers suggested with arrows (for clarity only downstream dispersal is shown), DDB is above and UDB is below. This should lead to the pattern of average beta diversity pattern presented for taxonomy (b) and traits (c) for each type of spatial drying with their relative replacement (Repl) and richness difference (Rich) components. In time: representation of the taxonomic successional trajectory on one site over time according to the frequency of drying events, the color representing a given taxonomic composition in the expected ecological suggestion with no drying (d) and expected pattern of temporal beta diversity with its two components for taxonomic (e) and functional (f) features, representation of the community recovery according to the duration of drying event (g) and expected pattern of temporal beta diversity for taxonomic (h) and functional (i) features. When combining space and time: expected pattern of temporal beta diversity according to the spatial drying pattern for taxonomic (j) and traits (k) features.

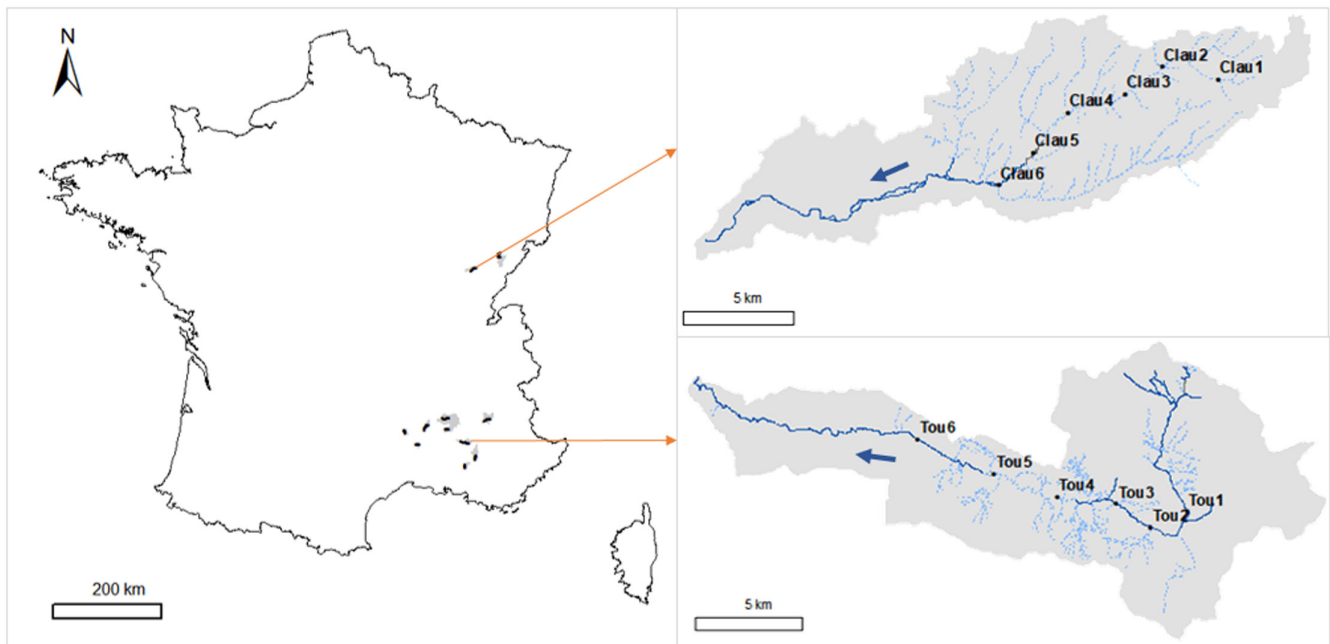


Figure 2. Map of the 11 basins in France (left) and zoom on two basins (right) with the Clauge on top as an example of UDB and the Toulourenc on the bottom as an example of DDB. Dark blue lines represent perennial reaches and light blue dashed lines intermittent reaches, blue arrows indicate flow direction.

2 samples/reach \times 6 reaches/basin \times 11 basins \times 12 sampling dates, with 310 samples not being collected as sites were dry during the visits. Samples were preserved in 96% ethanol, counted and identified to the lowest practical taxonomic level. For the list of taxa identified, see Supplementary material Appendix 5. To test for the variability among samples on each riffle head, tests were conducted on samples separately (Supplementary material Appendix 8) and showed the consistency of the results.

Trait composition analyses

To describe the trait composition of stream invertebrate communities, 39 categories of 8 biological traits were used (Tachet et al. 2010, see selected traits in Supplementary

material Appendix 3A). We only considered biological traits that may be related to drying (i.e. lifespan, resistance forms, Datry et al. 2014), and no ecological traits were used in our analyses (Aspin et al. 2018). Information from Schmidt-Kloiber and Hering (2015) was used to complete information for taxa missing from Tachet et al. (2010). These traits characterise life-cycle features, resilience and resistance features, physiology, morphology, reproduction and feeding behavior. Within the database, each taxon was coded according to its affinity to each category of a trait using a fuzzy-coding approach (Chevenet et al. 1994). The affinity of each genus to each category was coded from 0, for no affinity, to 3 for the strongest affinity, except for feeding and locomotion categories coded from 0 to 5. From the 231 taxa analyzed,

Table 1. Catchment area, mean river length, percentage of drying length of the mainstem, mean distance between the reaches, surveyed elevation and biogeographical region (EEA 2017) across the 11 river basins experiencing upstream- or downstream-drying.

Drying pattern	River	Catchment area (km ²)	River length (km)	% drying length of mainstem	Distance between reaches (km)	Elevation (m)	Biogeographical region
Upstream	Clauge	145	178	37	1.8	241	Continental
	Ibie	154	427	82	3.8	188	Mediterranean
	Séguisous	88	36	42	2.5	266	Mediterranean
Downstream	Aigue Brun	87	67	15	1.1	248	Mediterranean
	Audeux	389	33	47	3.2	385	Continental
	Calavon	240	283	36	2.1	433	Mediterranean
	Cèze	80	156	15	2.5	402	Mediterranean
	Lez	275	618	10	1.6	198	Mediterranean
	Petit Buëch	307	793	8	2.8	875	Mediterranean/Alpine
	Roubion	626	822	10	3.1	187	Mediterranean
Toulourenc	174	367	14	3.2	501	Mediterranean	

trait information for seven taxa (mostly crustaceans) was unavailable and these taxa were omitted. Trait modalities and values are provided in Supplementary material Appendix 3B. Aerial dispersers were separated from strict aquatic dispersers based on traits in Tachet et al. (2010) to form two subsets of the original dataset, and this classification was confirmed by Bertrand Launay, an expert on invertebrate biology.

Data analysis

For each reach, the duration of drying events (TotDur) in days and the number of drying events (TotNum) were quantified from the water state logger data and 12 visual observations.

To analyse the spatial variation of community composition, spatial beta diversity (pairwise differences of composition between sampling sites for each sampling date) was calculated for both taxonomic and functional diversity. For taxonomic beta diversity, the presence–absence Jaccard index was calculated for each basin and partitioned into its two additive components ‘replacement’ and ‘richness difference’ (Podani and Schmera 2011, Legendre 2014). To calculate functional beta diversity matrix, we first computed taxon-by-taxon Gower distances from the trait matrix and, second, we generated a dendrogram using hierarchical clustering analysis on these distances with the unweighted pair group method with arithmetic mean (Cardoso et al. 2014). Then, functional beta diversity was calculated and partitioned for each basin based on the site-by-taxon matrix and the dendrogram using the R function ‘beta’ of package ‘BAT’ (Cardoso et al. 2014). Pairwise beta diversity measures between sites were averaged for each river basin for each sampling date. For a given sampling date, when less than four sites were sampled (the others being dry), spatial beta diversity was not computed. There were 3 UDB with on average 9 (± 3) sampling dates (25 beta diversity measures in total) and 8 DDB with on average 10 (± 2) sampling dates (80 beta diversity measures in total).

To analyse the temporal variation of community composition, temporal beta diversity (pairwise differences of composition between sampling dates for each sampling site) was calculated for each site and partitioned into its two additive components ‘replacement’ and ‘richness difference’ using the same functions as described above for spatial taxonomic and functional diversity. Pairwise beta diversity measures between sampling dates were averaged on each site, there were 18 sites in UDB and 48 sites in DDB.

As several approaches are used in the literature to assess functional redundancy (Lozanovska et al. 2018), we carried out two different types of analyses. First, it was assessed with the ‘SYNCSA’ package as the difference between species diversity and Rao’s quadratic entropy based on their functional dissimilarity (de Bello et al. 2007, Debastiani and Pillar 2012), for each basin separately and for the entire dataset. With this definition, maximal value of functional redundancy is equal to species diversity which can vary across samples, thus we

divided this number by species diversity, so functional redundancy scales from 0 (no redundancy) to 1 (full redundancy). Values were compared between spatial drying patterns with Kruskal–Wallis tests. Then, functional redundancy was also assessed by fitting a hyperbolic curve of functional richness against taxonomic richness from the entire dataset with the form $y = ex/(d+x)$ where e is the asymptotic limit of the curve and d is the half-saturation constant. This allowed us to see if functional trait saturation was reached for a high species richness (Schriever et al. 2015), as the concept of functional redundancy relies on the saturation of functionally similar species in a community (Rosenfeld 2002).

To test the hypothesis H1, mixed-effect models were used on spatial taxonomic and functional beta diversity and on their respective replacement and richness difference components using function ‘lmer’ of the lme4 package. Each full model included the sampling date as random effect and the spatial drying pattern as fixed effect (UDB or DDB). There were six full models: for spatial taxonomic beta diversity, taxonomic replacement, taxa richness difference, for spatial functional beta diversity, functional replacement and functional richness difference. To test the significance of the effect of the spatial drying pattern, each of these six full models was compared with a likelihood ratio test to a null model with a random intercept and sampling date as random effect. This was computed for the entire dataset and separately for aerial and strict aquatic dispersers, as loss of aquatic connectivity may differently affect communities if they are able to disperse overland or not; hence, there were 18 tests in total for this section.

To test the hypotheses H2 and H3 we modelled temporal taxonomic beta diversity, taxonomic replacement, taxonomic richness difference and temporal functional beta diversity, functional replacement and functional richness difference with nested mixed-effect models that progressively increased in complexity. The first model was the null model with rivers as the only random effect. To test H2, we built separate models including TotNum and TotDur as fixed factors. To test H3, we added the spatial drying pattern without interaction then with interaction to H2 models, allowing the effect of TotNum (respectively TotDur) to vary according to the spatial drying pattern. In total, there were four models to test for the effect of TotNum (null model, H2 model, H3 model without and with interaction) and four models to test for the effect of TotDur. In each model, river was a random effect. The significance of each model was tested by a comparison with the reduced version of the model with a likelihood ratio test (the fourth model with the third, the third model with the second, etc.). Each model was first fitted for the entire dataset and, then, separately for subsets of the aerial dispersers and strict aquatic dispersers. In total, there were 36 tests for H2 (3 datasets \times 6 community variables \times 2 quantitative drying events variables \times 1 likelihood test) and 72 tests for H3 (3 datasets \times 6 community variables \times 2 quantitative drying events variables \times 2 likelihood tests with and without interaction).

Table 2. Mean values, standard deviation, maximum and minimum values of number (TotNum) and duration (TotDur) of drying events in the selected river basins (all, downstream and upstream-drying basins). DDB=downstream-drying basin, UDB=upstream-drying basin. Degree of freedom is equal to one for each likelihood test presented in this table.

		All	DDB	UDB
TotNum	Mean	15	15	16
	SD	13	14	8
	Max	50	50	33
	Min	2	2	4
TotDur	Mean	114	93	156
	SD	79	71	69
	Max	300	300	235
	Min	11	11	36

Results

Quantification of drying events features

Overall, mean TotNum was 15 ± 13 with no significant difference between DDB and UDB (F-value=6.7, $p=0.201$, Table 2). Mean TotDur was 114 ± 79 d, with slightly lower duration for DDB (93 ± 71 d) than UDB (156 ± 69 , F-value=5.9, $p=0.021^*$) (Table 2).

Invertebrate communities

In total, 267 645 organisms were collected, belonging to 232 taxa. There were on average 26 (± 9) taxa, and 768 (± 841) individuals per reach. The top three most abundant taxa were Orthocladiinae, Simuliidae and *Baetis*, representing 25, 13 and 11%, respectively, of all individuals per reach on average (Supplementary material Appendix 5).

Functional redundancy

Functional redundancy was, on average, 0.51 considering all reaches and sampling dates, indicating moderated redundancy. Accordingly, the saturation curve of functional richness against taxonomic richness did not reach a plateau

(Supplementary material Appendix 6). However, functional redundancy was slightly lower for DDB compared to UDB (0.50 versus 0.51, Chi-squared=13.5, $p < 0.001^{***}$).

H1: effect of the spatial drying pattern on spatial beta diversity

Spatial taxonomic beta diversity was significantly higher for UDB compared to DDB when considering all taxa and aerial dispersers but not strict aquatic dispersers (Table 3, Fig. 3). There was no difference for the replacement component when considering all taxa and aquatic dispersers. For aerial dispersers, replacement was higher in UDB than DDB (Table 3, Fig. 3). For the three datasets, richness difference was higher in UDB than DDB (Table 3, Fig. 3). On average, across all basins, replacement was higher than richness difference when considering all invertebrates and aerial dispersers (respectively 0.152 versus 0.102, $F=1880$, $p < 0.001^{***}$ and 0.144 versus 0.103, $F=1880$, $p < 0.001^{***}$). For aquatic dispersers, however, replacement was lower than richness difference (0.123 versus 0.151, $F=730.0$, $p < 0.001^{***}$).

Spatial functional beta diversity was significantly higher for UDB compared to DDB for the three datasets (Table 3, Fig. 3). Spatial functional replacement was higher in UDB than DDB when considering all taxa and aerial dispersers but not aquatic dispersers (Table 3, Fig. 3). Spatial functional richness difference was higher for UDB than DDB for all datasets (Table 3, Fig. 3). On average, across all basins, functional replacement was higher than functional richness difference when considering all invertebrates (respectively 0.225 versus 0.186, $F=13.3$, $p < 0.001^{***}$). For aerial and aquatic dispersers separately, however, functional replacement was lower than richness difference (respectively 0.173 versus 0.463, $F=341.8$, $p < 0.001^{***}$ and 0.128 versus 0.659, $F=605.1$, $p < 0.001^{***}$).

Tests on subsets of the dataset to account for a possible confounding effect of differences of environmental heterogeneity showed that differences of spatial beta diversity between UDB and DDB were robust (Supplementary material Appendix 2C).

Table 3. Mixed model results of spatial beta diversity, replacement and richness difference for all organisms, for aerial and strict aquatic dispersers, with sampling date as random effect and drying pattern as fixed effect. DDB=downstream-drying basin, UDB=upstream-drying basin. Degree of freedom is equal to one for each likelihood test presented in this table.

		Taxonomic				Functional			
		F value	p-value	Mean UDB	Mean DDB	F value	p-value	Mean UDB	Mean DDB
Beta diversity	All	12.7	< 0.001***	0.288	0.245	13.7	< 0.001***	0.477	0.391
	Aerial	14.8	< 0.001***	0.284	0.235	31.8	< 0.001***	0.750	0.603
	Aquatic strict	0.8	0.367	0.291	0.269	9.1	0.003**	0.848	0.756
Replacement	All	0.7	0.414	0.158	0.151	7.4	0.006**	0.253	0.217
	Aerial	7.9	0.005**	0.160	0.139	20.9	< 0.001***	0.234	0.156
	Aquatic strict	2.3	0.132	0.112	0.126	0.0	0.892	0.130	0.127
Richness difference	All	7.9	0.005**	0.130	0.094	4.5	0.034*	0.225	0.174
	Aerial	4.3	0.039*	0.124	0.096	4.0	0.045*	0.516	0.448
	Aquatic strict	7.0	0.008**	0.178	0.142	5.0	0.024*	0.719	0.630

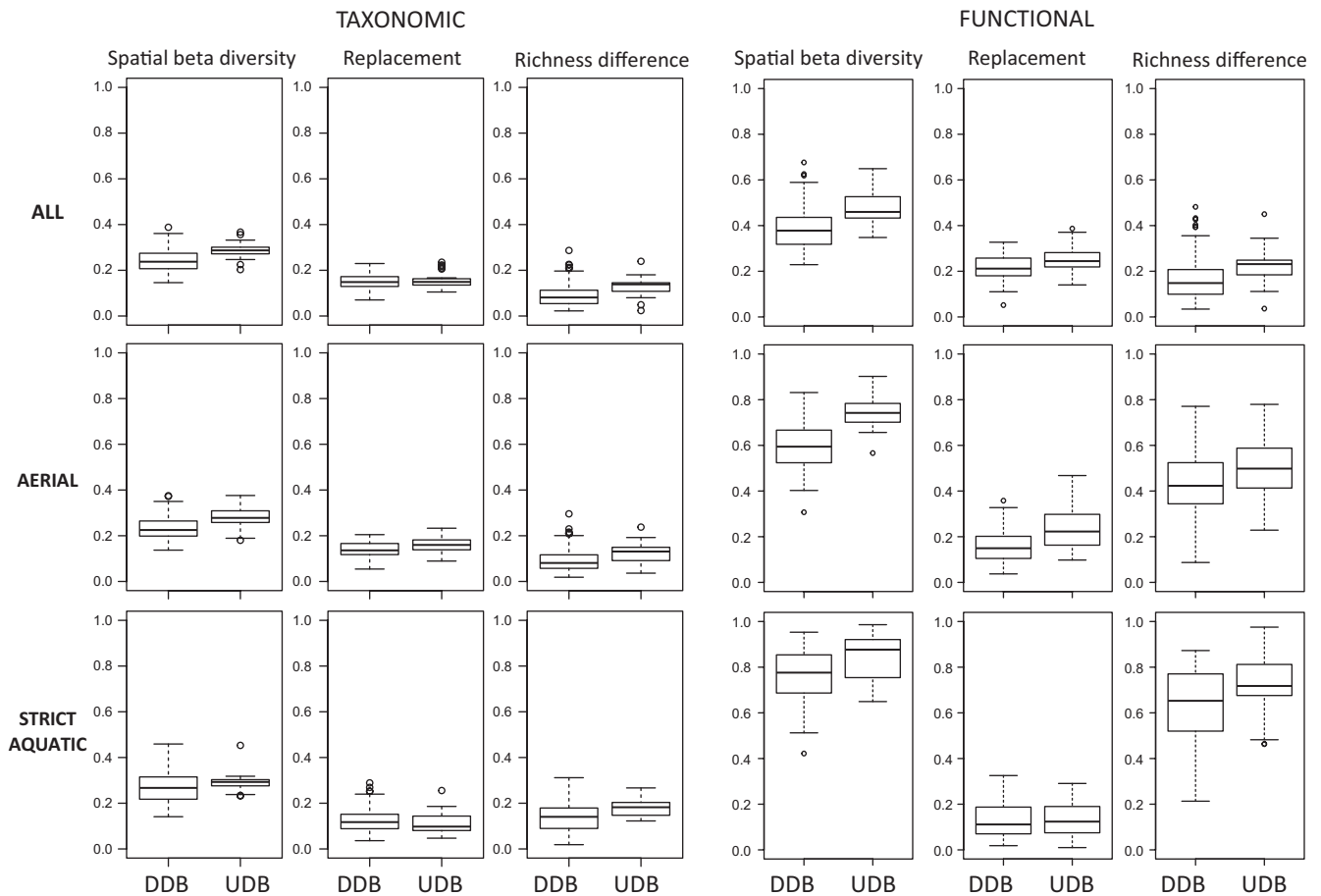


Figure 3. Boxplots of spatial beta diversity, replacement and richness difference for each drying pattern, for all invertebrates, for aerial dispersers only and for strict aquatic dispersers.

H2: effect of the temporal dynamics of drying events on temporal beta diversity

Temporal taxonomic beta diversity increased with TotNum across all datasets (Table 4). When considering all invertebrates and aerial dispersers, temporal taxonomic replacement increased with increasing TotNum, but it did not for aquatic dispersers (Table 4, Fig. 4). Across all datasets, taxonomic richness difference did not vary with increasing TotNum (Table 4). As with taxonomic beta diversity, temporal functional beta diversity increased with increasing TotNum for all datasets (Table 4, Fig. 4). Temporal functional replacement increased with increasing TotNum for the entire dataset and aerial dispersers, but not for aquatic dispersers (Table 4, Fig. 4). Temporal functional richness difference increased with increasing TotNum for all datasets (Table 4, Fig. 4).

Temporal taxonomic beta diversity increased with increasing TotDur when considering all taxa and aquatic dispersers, but not aerial dispersers (Table 4, Fig. 4). For all datasets, taxonomic replacement increased with increasing TotDur but taxa richness difference did not vary (Table 4, Fig. 4). Temporal functional beta diversity increased with increasing TotDur when considering all invertebrates and aquatic

dispersers but not aerial dispersers (Table 4, Fig. 4). For all datasets, temporal functional replacement did not vary with increasing TotDur (Table 4). Temporal functional richness difference increased with increasing TotDur only for aquatic dispersers (Table 4, Fig. 4).

H3: effect of the spatial drying pattern on the temporal patterns of beta diversity

Temporal taxonomic beta diversity increased with increasing TotNum in DDB, whereas it decreased in UDB when considering all invertebrates but not considering aerial and aquatic dispersers separately (Table 5, Fig. 5). For all datasets, there was no interaction effect of TotNum and the spatial drying pattern on taxonomic replacement nor on taxa richness difference (Table 5, Fig. 5).

For all datasets, there was no interaction effect between TotNum and the spatial drying pattern on temporal functional beta diversity, temporal functional replacement and temporal functional richness difference (Table 5).

Temporal taxonomic beta diversity increased with increasing TotDur on DDB, whereas it slightly decreased in UDB when considering all invertebrates and aerial dispersers

Table 4. Results of mixed models of H2 for each dataset: all invertebrates, aerial and strict aquatic dispersers. We modelled taxonomic and functional beta diversity and contribution of their replacement component as a function of TotNum (upper part of the table) or TotDur in days (lower part). Likelihood ratio tests represent the significance of each model compared to the associated null model. River as random effect was significant to very significant for 95% of all models and is not displayed in the table. For clarity, only the sign of the estimate was indicated: it indicates if the number of drying events and their durations had a positive or a negative effect on beta diversity and the contribution of replacement to beta diversity. Degree of freedom is equal to one for each likelihood test presented in this table.

TotNum	Taxonomic		All				Aerial				Aquatic			
			Likelihood ratio test		Likelihood ratio test		Likelihood ratio test		Likelihood ratio test		Likelihood ratio test		Likelihood ratio test	
			Estimate	Chi 2	p-value	Estimate	Chi 2	p-value	Estimate	Chi 2	p-value	Estimate	Chi 2	p-value
		Beta diversity	+	22.0	<0.001***	+	15.7	<0.001***	+	13.4	<0.001***	+	13.4	<0.001***
		Replacement	+	20.4	<0.001***	+	14.1	<0.001***	+	2.4	0.123	+	2.4	0.123
		Richness difference	+	1.0	0.326	+	0.7	0.392	+	0.2	0.691	+	0.2	0.691
	Functional	Beta diversity	+	16.0	<0.001***	+	13.3	<0.001***	+	10.1	0.001**	+	10.1	0.001**
		Replacement	+	3.9	0.049*	+	4.6	0.032**	-	0.8	0.374	-	0.8	0.374
		Richness difference	+	6.8	0.009**	+	5.8	0.019**	+	12.7	<0.001***	+	12.7	<0.001***
	Taxonomic	Beta diversity	+	7.0	0.008**	+	3.8	0.052	+	6.0	0.014*	+	6.0	0.014*
		Replacement	+	10.2	0.001**	+	4.1	0.044*	+	3.9	0.049*	+	3.9	0.049*
		Richness difference	-	0.1	0.773	-	0.0	0.977	-	0.0	0.890	-	0.0	0.890
	Functional	Beta diversity	+	3.4	0.065*	+	2.4	0.123	+	5.5	0.019*	+	5.5	0.019*
		Replacement	+	1.1	0.288	+	0.6	0.438	-	0.7	0.410	-	0.7	0.410
		Richness difference	+	1.1	0.299	+	0.9	0.338	+	4.7	0.031*	+	4.7	0.031*

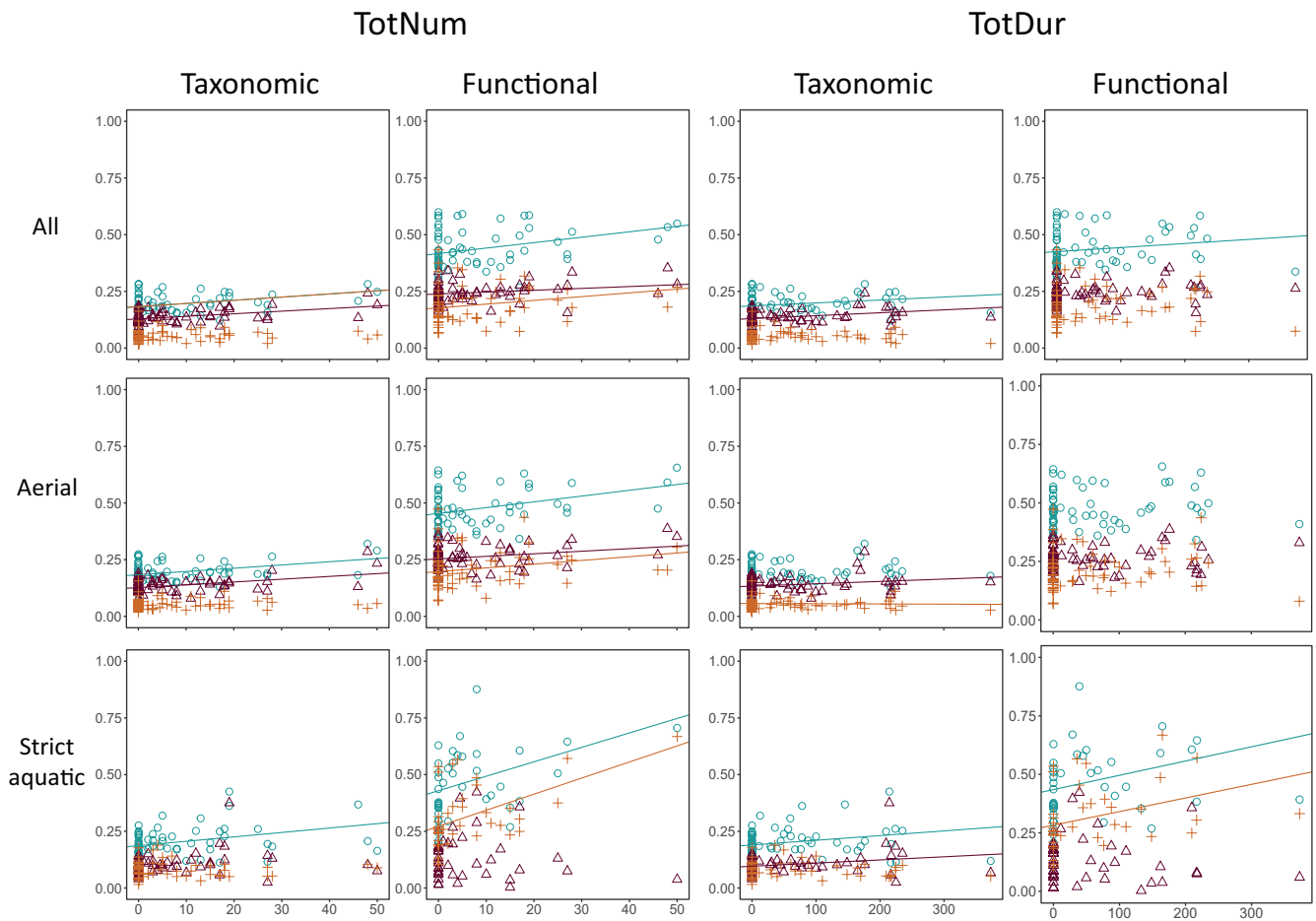


Figure 4. Relationships of taxonomic and functional temporal beta diversity (blue circles and lines) and their relative components replacement (red crosses and lines) and richness difference (orange triangles and lines) with the number of drying events (left) and duration of drying events in days (right) for all invertebrates, for aerial dispersers only and for strict aquatic dispersers. When a significant effect was found for the associated mixed model, a line was plotted with the intercept and slope estimated in the model.

(Table 5, Fig. 5, Supplementary material Appendix 7A). For aquatic dispersers, temporal beta diversity increased faster on DDB than in UDB with increasing TotDur (Table 5, Supplementary material Appendix 7B). For all datasets, there was no interaction effect of TotDur and the spatial drying pattern on temporal taxonomic replacement (Table 5). When considering all invertebrates, taxonomic richness difference decreased with TotDur for UDB, whereas it remained stable for DDB but, for aerial dispersers and aquatic dispersers, there was no interaction effect of the spatial arrangement (Table 5, Fig. 5).

Temporal functional beta diversity increased for DDB, whereas it decreased for UDB when considering all invertebrates (Table 5, Fig. 5). This was also true for aerial dispersers and aquatic dispersers (Table 5, Supplementary material Appendix 7A, 7B). For all datasets, there was no interaction effect of TotDur and the spatial drying pattern on temporal functional replacement (Table 5). For all invertebrates, functional richness difference decreased for UDB, whereas it increased for DDB (Table 5, Fig. 5). For aquatic dispersers, functional richness difference increased faster for DDB than

for UDB (Table 5, Supplementary material Appendix 7B), whereas there was no trend for aerial dispersers (Table 5).

Discussion

Understanding spatio-temporal variations of ecological communities in highly dynamic ecosystems is important in the context of climate change, which increases the frequency and the duration of extreme events (Wolkovich et al. 2014, Regos et al. 2018). Using IRs as model ecosystems, we quantified both taxonomic and functional beta diversity over space and in time, and explored their components ‘replacement’ and ‘richness difference’ to gain understanding on the processes at work. Our results showed that temporal beta diversity and its components varied with both the frequency and the duration of drying events, and these variations were dependent on the location of drying events in river networks. While previous studies dealing with community responses to drying mostly considered snapshots (Aspin et al. 2018) or averaged patterns over time (Leigh et al. 2016) and studies

Table 5. Results of mixed models of H3 for each dataset: all invertebrates, aerial and strict aquatic dispersers; results are displayed as in Table 4. Likelihood ratio tests represent the significance of the model compared to the simpler version of the model. For clarity, only the sign of the estimate was represented: for overall pattern, it indicated if UDB had higher or lower values in average compared to DDB; for interaction, it indicated if the slope for UDB was higher or lower than the slope for DDB. DDB = downstream-drying basin, UDB = upstream-drying basin.

		All						Aerial			Aquatic		
		Likelihood ratio test			Likelihood ratio test			Likelihood ratio test			Likelihood ratio test		
		Estimate	Chi 2	p-value	Estimate	Chi 2	p-value	Estimate	Chi 2	p-value	Estimate	Chi 2	p-value
Taxonomic	Pattern (UDB)	+	0.0	0.849	+	0.3	0.571	+	0.1	0.796			
	Replacement	+	0.8	0.358	+	0.6	0.445	+	1.5	0.214			
	Richness difference	+	0.4	0.551	+	0.0	0.964	+	0.5	0.477			
Functional	Interaction	-	4.0	0.046*	-	2.3	0.133	-	1.9	0.172			
	Ntot x pattern	-	0.3	0.613	-	1.4	0.229	+	0.5	0.462			
	Richness difference	-	3.3	0.070	-	0.4	0.519	-	2.2	0.137			
Taxonomic	Pattern (UDB)	+	0.2	0.640	+	0.5	0.459	+	0.2	0.634			
	Replacement	+	2.1	0.146	+	0.1	0.761	+	1.0	0.322			
	Richness difference	+	0.0	0.915	+	0.3	0.606	+	0.2	0.680			
Taxonomic	Interaction	-	3.3	0.069	-	1.7	0.191	-	0.4	0.504			
	Ntot x pattern	+	0.0	0.904	+	1.8	0.179	+	0.3	0.607			
	Richness difference	-	3.6	0.056	-	0.3	0.582	-	1.4	0.235			
Taxonomic	Pattern (UDB)	+	0.0	0.951	+	0.1	0.734	+	0.3	0.589			
	Replacement	+	0.1	0.703	+	0.2	0.692	+	0.8	0.359			
	Richness difference	+	0.3	0.613	+	0.0	0.911	+	0.4	0.508			
Functional	Interaction	-	11.5	< 0.001***	-	5.4	0.020*	-	9.5	0.002**			
	Dtot x pattern	-	0.2	0.056	-	2.8	0.094	-	0.2	0.655			
	Richness difference	-	4.8	0.028*	-	1.9	0.166	-	3.4	0.065			
Functional	Pattern (UDB)	+	0.1	0.743	+	0.4	0.543	+	0.0	0.896			
	Replacement	+	1.6	0.208	+	0.1	0.782	+	1.4	0.232			
	Richness difference	+	0.0	0.857	+	0.2	0.642	+	0.8	0.378			
Functional	Interaction	-	10.0	0.002**	-	4.9	0.026*	-	9.0	0.003**			
	Dtot x pattern	-	0.0	0.910	-	1.0	0.308	+	0.1	0.784			
	Richness difference	-	9.7	0.002**	-	3.7	0.056	-	8.2	0.004**			

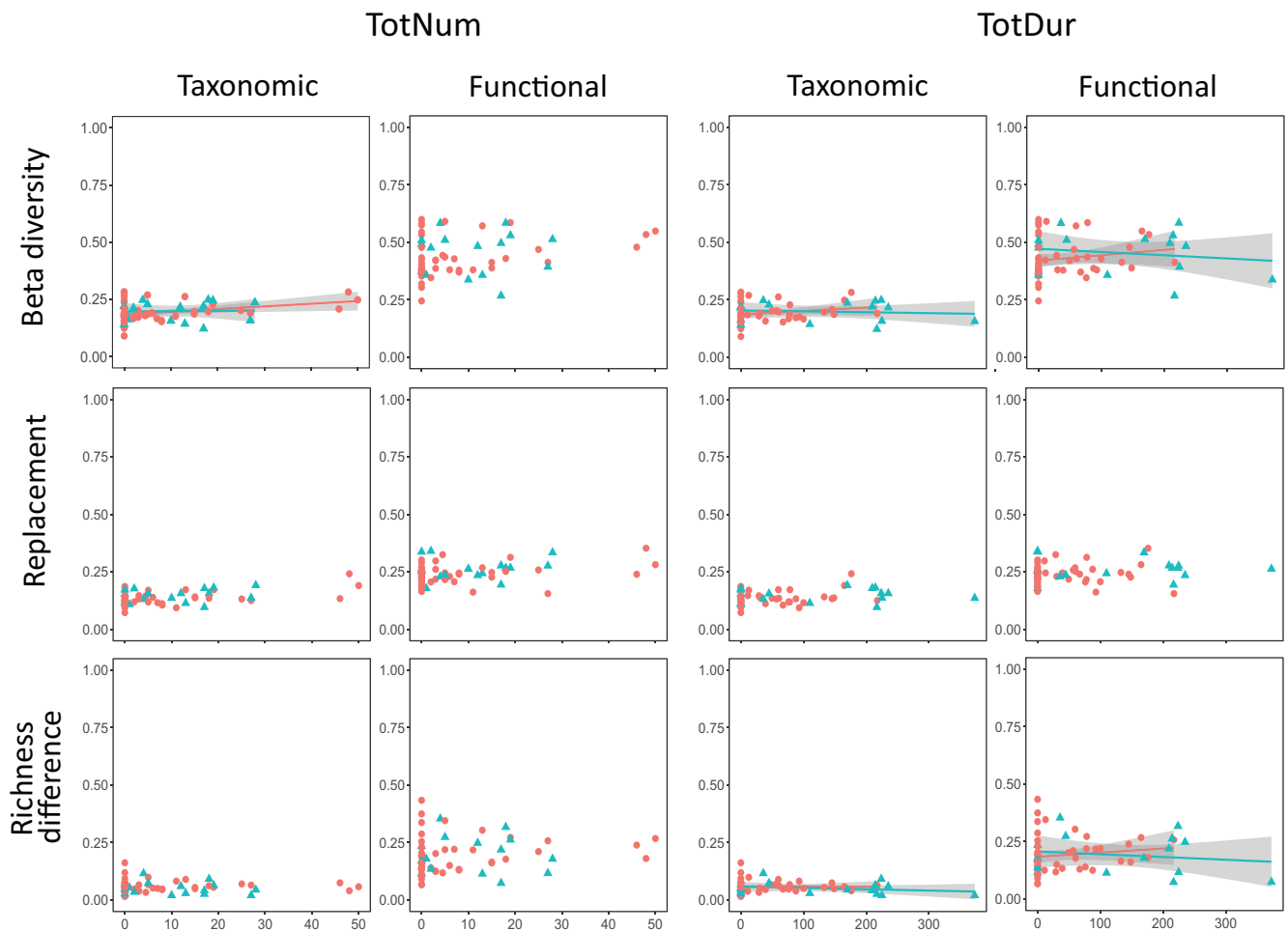


Figure 5. Taxonomic and functional temporal beta diversity and their replacement and richness difference components against number of drying events (left) and duration in days (right) as computed on the entire dataset for both drying patterns: DDB (red) and UDB (blue). When an interaction effect between TotNum or TotDur and the drying pattern was found, lines were plotted with the associated parameter estimates. Grey areas indicate 95% confidence intervals.

with finer temporal resolutions are scarce (but see Leigh et al. 2019), we gained a better understanding of how drying influences biodiversity patterns by including the temporal and spatial dynamics of drying. Our results underline some limits of current biomonitoring methods in IRs and offer refined avenues to better target sites for conservation prioritization.

H1: the spatial drying pattern drives the spatial community structure

We found the spatial drying pattern to influence the spatial distribution of taxa. As expected, higher spatial taxonomic and functional beta diversities were found in UDB compared to DDB, and this was due to higher taxonomic and functional richness differences in UDB. The isolation of headwater intermittent sites and the associated difficulties in recolonisation due to dispersal limitation probably led to a divergence in community composition, mostly through differences in taxa and traits richness between sites in these three river basins. Such patterns detected across our 11 river

basins align with previous findings originating from simulations (Altermatt et al. 2011) and mesocosm experiments (Aspin et al. 2018), and indicate that the spatial location of disturbances in dendritic networks does mediate the responses of communities in space and time. Taxa and traits responding the same way to the spatial drying pattern could also imply that observed dissimilarities between UDB and DDB are due to environmental selection of taxa with particular biological traits rather than stochastic extinction processes. Moderated functional redundancy was found across the dataset and the slightly higher redundancy in UDB compared to DDB might indicate a stronger environmental selection of adapted taxa on these basins, as functional redundancy has previously been attributed to traits selection following environmental harshness (Boersma et al. 2014, Vander Vorste et al. 2016).

There was more spatial taxonomic replacement than spatial taxonomic richness difference for aerial dispersers, but the opposite was found for aquatic dispersers, with such differences being stronger in UDB. This supports the idea that fragmentation represents a higher constraint on dispersal for

aquatic dispersers than for those species with aerial stages (Datry et al. 2014, Cañedo-Argüelles et al. 2015). Whereas aerial dispersers such as Odonata, Coleoptera and some Heteroptera can rapidly colonize and actively select favorable habitats (Bonada et al. 2006, Bogan and Boersma 2012), resulting in ‘replacement’ through species sorting, some extinction–colonisation dynamics might conversely occur for strict aquatic dispersers such as *Abedus herberti* (Phillipsen and Lytle 2013), leading to higher ‘richness difference’. Both groups of dispersers presented a very high spatial functional richness difference, aligning with the taxonomic pattern for aquatic dispersers. This functional richness difference could be related to resistance traits (e.g. respiration through spiracles and diapause) and resilience traits (e.g. multivoltinism) associated with communities exposed to drying (Sarremejane et al. 2017a, Aspin et al. 2018). For aerial dispersers, the high taxonomic replacement combined to a high functional richness difference suggests that the aerial taxa replaced among sites are not functionally equivalent. This suggests that the fragmentation also puts some selective pressure on good dispersers and, consequently, some sites harboured more aerial dispersers with unique biological traits than other sites. This could be due to different flight propensities among aerial dispersers as weak flyers were previously found to be more affected by loss of habitat connectivity (Sarremejane et al. 2017b). In addition, functional richness difference was lower than functional replacement when considering the entire dataset, and this could mean that sites rich in aquatic dispersers with unique traits are replaced by aerial dispersers with unique traits on other sites.

H2: communities are taxonomically and functionally highly variable in response to drying dynamics

As predicted, we found considerable temporal variability of community composition in the 11 studied river basins in response to the temporal dynamics of drying. Both temporal taxonomic and functional beta diversity increased with the frequency and the duration of drying events. This change was mostly driven by an increase of replacement over time for taxonomic beta diversity and an increase of richness difference for functional beta diversity. While such a pattern was recently revealed from Mediterranean IRs and assumed to be driven by the unpredictability of the studied systems (Tonkin et al. 2017), our results indicate this could be a very general response, even in IRs where drying is rather predictable. This pattern could be due to repeated resets of ecological successions over time due to increased drying frequency (Larned et al. 2010, Datry et al. 2016), as suggested by the increased number of taxa replaced over time. Surprisingly, while we expected drying duration to promote taxonomic richness difference between sampling dates (Datry 2012, Cañedo-Argüelles et al. 2015), we rather found an increased replacement. This could be explained by a very fast recolonisation of previously dry sites upon rewetting due to resistance and resilience strategies allowing predictable successional stages, as shown in other systems (Datry et al. 2014), or in

contrast by stochastic recolonisation of intermittent sites (Sarremejane et al. 2017a).

Temporal functional beta diversity components responded differently to drying dynamics than those of taxonomic beta diversity, confirming that functional approaches yield meaningful and complementary information to taxonomic ones. Strong responses of functional beta diversity also contradict our initial hypothesis, which was based on previous reports of high functional redundancy in IRs (Boersma et al. 2014, Schriever et al. 2015, Vander Vorste et al. 2016). Here, we found evidence that functional redundancy was moderate across the 11 river basins considered. Such lack of redundancy could explain why sites with high flow intermittence harbored sets of taxa with unique traits unevenly distributed over time, traits such as aerial passive dispersal and multivoltinism dominating during the rewetting period for instance (Sarremejane et al. 2017a), leading to increased trait richness differences over time. This could also indicate that along the gradient of frequency and duration of drying events, very few key taxa with unique trait profiles were lost but, rather, generalist taxa sensitive to desiccation such as mayflies (Ephemeroptera) and stoneflies (Plecoptera) were gradually disappearing (del Rosario and Resh 2000, Arscott et al. 2010, Datry 2012). More work is needed to shed light on this pattern, which was also found recently from mesocosm experiments manipulating drying (Leigh et al. 2019). For aquatic dispersers, the increase in temporal functional richness difference was not associated with an increase in temporal functional replacement, indicating that their number of traits over time was more altered than those of aerial dispersers by increasing frequency and duration of drying. This could be because the different aquatic dispersers with unique traits might have been observed at the same sampling dates, specialist taxa, such as Psychodidae, Ceratopogonidae and Stratiomyidae, appearing after rewetting of a dry site (Aspin et al. 2018) and generalist taxa dominating a long time after rewetting, leading to low functional replacement over time and high functional richness difference. This would reflect the importance of some specific traits related to resistance to drying, which could promote temporal dispersal between drying phases (Datry et al. 2016). Further work is needed to compare the relative importance of temporal and spatial dispersal in IRs and how they shape community dynamics in river networks.

H3: the spatial drying pattern influences the temporal response of communities to drying

The effect of the spatial drying pattern on community organization has not been previously studied over time but, rather, in a time-averaged condition (Datry et al. 2014). There was virtually no effect of the spatial drying pattern on how temporal beta diversity responded to the frequency of drying. However, several interactions between the spatial drying pattern and the duration of drying were found, indicating that the location of drying events within a river basin does affect the temporal dynamic of communities prone to drying events. When

drying duration increases, there is a higher variation in the number of taxa and traits at different sampling dates in DDB but a lower variation in UDB. This could be explained by a mass-effect recolonisation upon rewetting in DDB through passive and active drift by a set of taxa presenting no or little functional redundancy, as redundancy was slightly higher in DDB. On the contrary, the long drying duration in UDB, associated with the high dispersal limitation, may lead to a very small pool of taxa adapted to persist such long drying or able to recolonize and, finally, show similar traits. When considering aquatic dispersers, the difference in functional richness increased in UDB with the duration of drying. When drying events are long, there may be more aquatic dispersers presenting unique traits in UDB compared to DDB. While working on fish, Henriques-Silva et al. (2019) tested the network position hypothesis, stating that the position of a community in the network determines whether its composition is controlled by local environment or by dispersal processes. As a main conclusion, these authors stressed the context-dependency of this network position effect (Henriques-Silva et al. 2019). Our present work, by characterizing both the spatial and temporal dynamics of drying, indicates how a precise description of the context of disturbance can enhance our understanding of the spatio-temporal organization of communities in river basins.

Implications for community ecology and ecosystem management in dynamic systems

Analyzing beta diversity allowed us to quantify both spatial and temporal variability in community composition and its decomposition into two components allowed us to make assumptions on dispersal limitation and recolonisation processes. Drying induces a very high temporal variability of communities, which varies with the frequency and duration of drying events through an increased number of taxa replaced over time. In the context of increasing extremes due to climate change (Jaeger et al. 2014, Kirtman et al. 2014), our results suggest that community dynamics will become increasingly driven by stochastic variations in the environment. Coupling a taxonomic approach with a functional approach also provided valuable insights, showing that biological traits are unevenly distributed across space and time, especially when there are high dispersal constraints for strict aquatic dispersers. The low functional redundancy, the replacement of taxa and the richness difference of biological functions with increasing drying could generate severe consequences for the resilience of some key ecosystem process (e.g. leaf litter decomposition, growth primary production, ecosystem respiration) at larger spatial and temporal scales (Gounand et al. 2018). We also demonstrated for the first time that the temporal dynamics of communities are strongly related to the location of drying events within river networks, contrary to what was suggested before (Datry et al. 2014). This is because the location of a strong and punctual disturbance in the river network affects recolonisation processes (Altermatt et al. 2011), and this cascades through to the

temporal dynamics of communities. Most likely, the location of drying induces different contribution of metacommunity assembly processes, namely species sorting and dispersal processes (Heino 2013).

These results have strong implications for the management of IRs and other dynamic ecosystems. For example, the high temporal variability challenges the current definition of reference conditions, for which a snapshot of communities cannot represent the high variations they undergo over very short time scales. If river managers continue using such approaches in the biomonitoring of river systems, they should incorporate the temporal variability in the ecological status assessment instead of considering the average community composition. In addition, the high variations in community responses to spatio-temporal dynamics of drying events suggest that a tentative typology of IRs could be built based on the spatial pattern of drying and quantitative hydrological data: upstream-drying represents a strong constraint on dispersal and, therefore, enhancing connectivity should be a key conservation target. In the context of increased extreme events and drying worldwide (Döll and Schmied 2012, Datry et al. 2018), improving our understanding of community composition and functions over time and space in dynamic ecosystems is vital to preserve biodiversity and the ecological functions and services they provide.

Data availability statement

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.hqzbkh1bn>> (Crabot et al. 2019).

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Author contributions – TD initiated the study, TD and BL established the sampling design, BL carried out the sampling and invertebrate processing and JC carried out data analyses. JC, TD and JH co-wrote the manuscript.

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Supplementary material (available online as Appendix ecog-04835 at www.ecography.org/appendix/ecog-04835). Appendix 1–8.