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Climatic aridity increases temporal nestedness of invertebrate communities in naturally drying rivers

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Climate change is altering the water cycle globally, increasing the frequency and magnitude of floods and droughts. An outstanding question is whether biodiversity responses to hydrological disturbance depend on background climatic context – and if so, which contexts increase vulnerability to disturbance. Answering this question requires comparison of organismal responses across environmental gradients. However, opportunities to track disturbed communities against an undisturbed baseline remain rare. Here we gathered a global dataset capturing responses of aquatic invertebrate communities to river drying, which includes 112 sites spanning a gradient of climatic aridity. We measured the effects of river drying on taxonomic richness and temporal β-diversity (turnover and nestedness components). We also measured the relative abundance of aquatic invertebrates with strategies that confer resilience (or resistance) to drying. Contrary to our expectations, we found that taxonomic richness recovered from drying similarly across the aridity gradient. The turnover component of β-diversity (i.e. species replacements over time) largely accounted for differences in community composition before versus after drying. However, increasing aridity was associated with greater nestedness-driven compositional changes at intermittent sites – that is, after drying communities became subsets of those before drying. These results show that climatic context can explain variation in community responses to the same hydrological disturbance (drying), and suggest that increased aridity will constrain biodiversity responses at regional scales. Further consideration of the climatic context in hydroecological research may help improve predictions of the local impacts of hydrological disturbance by identifying climate regions where communities are more (or less) sensitive to extremes, including river drying events.

Keywords: beta diversity, drought, macroinvertebrates, nestedness, resilience, resistance, turnover

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Introduction

Disturbance events such as droughts, floods, fires and hurricanes structure biological communities at local to regional scales (Hutchinson 1961, Chesson 2000, Woodward et al. 2016, Tonkin et al. 2017). Disturbance causes displacement or mortality of individuals – opening space and creating new opportunities for individuals to establish (Sousa 1984). Post-disturbance states can be difficult to predict because the rates and trajectories of community recovery are often context dependent (Franklin et al. 2016, Leigh et al. 2016, Datry et al. 2017). For example, climate (mean annual temperature and precipitation) can influence forest recovery rates following disturbance (Anderson-Teixeira et al. 2013), and affect the mechanical vulnerability of coral reefs to hydrodynamic action via shifts in species dominance (Madin et al. 2008). Similarly, riverine communities exposed to drying may recover quickly, but only if they are dominated by organisms with adaptations conferring resistance or resilience to drying (i.e. ability to withstand conditions locally or to recolonize after persisting elsewhere) (Vander Vorste et al. 2016, Bogan et al. 2017). Climate could influence community responses to disturbance, for instance by selecting for resilience and resistance strategies related to dispersal in space versus 'in time' (Buoro and Carlson 2014). However, global studies comparing community responses across climate types to the same disturbance are rare (Seidl et al. 2020). While the issue of climate-dependent biodiversity responses to disturbance is relevant to many ecosystems, it is particularly timely in the context of river drying, as overallocation of water resources and climatic droughts continue to induce flow regime shifts.

The effects of disturbance on biological communities are often assessed by quantifying changes in α-diversity (Seidl et al. 2020), because some but not all species may be tolerant to the stressor, decreasing α-diversity (Sousa 1984, McCabe and Gotelli 2000). In turn, this environmental filtering may elicit nested community patterns across a metacommunity, with a core of tolerant species being widespread but most species being sensitive and only found at undisturbed, species-rich sites (Ruhí et al. 2015). However, β-diversity, a multivariate measure of compositional dissimilarity across a set of local communities, can shed light on the mechanisms that allow communities to reassemble after disturbance. The fundamental niche may or may not influence assembly, and species may or may not be dispersal limited (Larsen et al. 2018). Higher β-diversity in regions with more variable disturbance regimes (Sagar et al. 2003, Tonkin et al. 2017) suggest that communities tend to differentiate with disturbance (Socolar et al. 2016). Temporal β-diversity, or local compositional change across time, could provide mechanistic insight into how communities change, especially in dynamic ecosystems (Baselga et al. 2015, Ruhí et al. 2017, Tonkin et al. 2017). However, this approach remains underused – likely due to the scarcity of studies with repeated measures at sites over time (i.e. longitudinal studies).

Intermittent streams are ecosystems that periodically undergo flow cessation, often including partial or complete loss of surface water. Although they are most prevalent in dry climates, they occur around the globe (Datry et al. 2014). The dry phase of intermittent rivers represents a disturbance to aquatic organisms, as it subjects them to physiological challenges (gas exchange, thermal stress, desiccation), high predation pressure, reduced habitat availability and hydrological connectivity (Lake 2003, Leigh et al. 2016). Importantly, at evolutionary time scales, regional climate and predictable disturbances such as seasonal drying may have shaped organismal adaptations (Lytle and Poff 2004, Tonkin et al. 2017). For example, climate gradients are associated with variation in physiological, morphological and life-history traits of riverine biota (Thuiller et al. 2004, Bonada et al. 2007, Datry et al. 2017). Thus, at ecological timescales communities in arid regions should be less affected by river drying, both in terms of taxonomic richness and community composition. Communities in arid regions experiencing drying should have higher proportions of taxa with active and dormant desiccation-resistant forms (Bogan et al. 2017). In contrast, communities in streams from more humid climates may experience greater change following river drying because these communities should have higher taxa richness (i.e. more taxa to lose). Community composition in humid regions may have a lower proportion of taxa with desiccation resistance and thus comprised of taxa relying on active dispersal (e.g. flying and swimming from neighboring sites; Bohonak and Jenkins 2003, Datry et al. 2017). Local environmental factors, such as drying duration, may influence community composition by acting as filters of the regional taxonomic pool (Chase 2007, Datry 2012). Considering climate is a global determinant of species richness (Hawkins et al. 2003), and influences the selection of resilience versus resistance strategists (Buoro and Carlson 2014), we propose that it may also explain variation in how communities respond to river drying. Notably, drying may affect composition via community turnover, i.e. species identities changing despite species richness remaining stable; or via nestedness, i.e. species being subset determined by the environmental filter, creating an association between changes in temporal β-diversity and α-diversity.

In this study, we asked how climate context mediates the effects of river drying on stream biodiversity. To this end, we compiled studies that used a before–after–control–impact (BACI)-like design on invertebrate communities. We tested the relationships between taxonomic richness, trait richness and climatic aridity across sites to explore the patterns that may underpin community responses to drying (objective 1). We predicted that 1a) the richness of resistance and resilience traits would be positively correlated with taxonomic richness and 1b) climate aridity would be negatively correlated with taxonomic richness at both perennial and intermittent sites. We then focused on changes in taxonomic richness, the relative abundance of resistant and resilient taxa, and temporal β-diversity as a result of drying, by comparing intermittent sites to perennial sites across a gradient of aridity (objective 2). We specifically focused on the interaction between

the effects of river drying and climatic aridity. We predicted that climatic aridity would: 2a) decrease the magnitude of reductions in taxonomic richness, 2b) increase the relative abundance of resistant taxa following drying, 2c) decrease temporal β-diversity associated with drying and 2d) increase the nestedness component of temporal β-diversity, because communities will be comprised mainly of taxa with resistance to arid conditions, including river drying. Given that the duration of drying influences community composition, we also predicted that 2e) increasing drying duration would amplify the effects of drying on both taxonomic richness and temporal β-diversity regardless of climatic aridity.

Methods

Global dataset of invertebrate communities

We assembled 13 aquatic invertebrate community datasets from seven countries worldwide (Table 1, Fig. 1, Supporting information). Our dataset contained 224 samples collected from 112 stream sites, which were classified as either intermittent (n = 67) or perennial (n = 45; Table 1, Fig. 1). Stream sites covered a wide environmental gradient from first-order, headwater streams to larger gravel-bed, braided rivers. Samples were collected from sites that ranged from pristine conditions to mildly affected by anthropogenic pressures (primarily agriculture); however, in all cases flow intermittence was the main source of disturbance or stress affecting invertebrate communities. Datasets included samples collected on two occasions from at least one intermittent (*INT*) and one perennial site (*PER*): before and after a drying event occurred at *INT* sites, with visits at *PER* sites acting as control baselines (i.e. an experimental design akin to BACI; further details described in Supporting information). Visits took place when streams were flowing (i.e. before flow cessation, and after flow resumption). The timing and duration of river drying events was estimated using a combination of temperature data loggers, discharge gauging stations, modeling and expert opinion. Invertebrate samples were collected at 2–6 sampling stations (4 ± 1.6, mean ± SD) within a defined site using standardized and consistent sampling methods that targeted the entire invertebrate community (Surber, Hess and kick-net samplers; 250–500 µm mesh size). When samples representing multiple habitats were not composited in the field (i.e. within-site replicates; 8 of 13 datasets), we aggregated samples within each site to create comparable composite samples. Taxonomy across datasets was homogenized to genus level, and we excluded taxa identified to family or higher taxonomic levels (Supporting information). As a consequence, we included 545 066 individuals (mean ± SD = 71 ± 31%, range = 22–97% of individuals from original datasets) comprising 402 taxa (mean ± SD = 73 ± 19%, range = 53–91% of taxa from original datasets; Supporting information). Although this conservative filtering process likely decreased our ability to detect patterns in the data, it reduced the potential effects that uncontrolled variation in taxonomic resolution could have on the detected patterns.

Invertebrate traits

We characterized invertebrate taxa using traits conferring resistance or resilience to drying, following Datry et al. (2014). Resistance traits comprised the following: presence of desiccation-resistant dormancy forms; body armoring that limits water loss; and respiration systems that allow breathing air (e.g. plastron/spiracles) (Bogan et al. 2017). Resilience traits comprised the following: high aerial adult female dispersal; strong adult flying ability; propensity to disperse via drift; and strong swimming ability (Bogan et al. 2017). We did not consider voltinism because information for this trait was incomplete (64% of taxa), and highly redundant with the selected traits representing resilience strategies. All traits were assigned at the family level or coarser, to make trait states and categories (e.g. thresholds) comparable across several trait databases, following Datry et al. (2014) (Supporting

Table 1. Details of the sites considered in this study. Country, aridity index, number of intermittent and perennial sites and samples, drying duration and mean number of taxa for each of the datasets are shown. Full details about individual datasets and sampling methods are described in Supporting information.

		No. of sites (no. of samples)		Drying duration (days)	Mean no. of taxa observed (Chao estimate)	
Country	Aridity index	Intermittent	Perennial	Mean (range)	Intermittent	Perennial
Australia	1.15–1.28	2 (4)	1 (2)	139 (67–211)	14 (30)	7 (16)
France	0.37–0.63	7 (14)	5 (10)	62 (12–132)	13 (31)	18 (36)
Lebanon	0.73	1 (2)	1 (2)	60 (NA)	12 (33)	12 (16)
New Zealand	0.75	6 (12)	5 (10)	90 (NA)	21 (21)	25 (25)
New Zealand	0.68	10 (20)	4 (8)	273 (243–291)	12 (12)	25 (25)
New Zealand	0.01–1.46	16 (32)	6 (12)	83 (0–189)	25 (29)	29 (34)
Spain	0.56	1 (2)	1 (2)	90 (NA)	16 (16)	19 (19)
Spain	0.58–0.88	3 (6)	3 (6)	130 (104–160)	43 (52)	47 (53)
United Kingdom	0.58	1 (2)	1 (2)	21 (NA)	24 (30)	18 (38)
United Kingdom	0.58	2 (4)	2 (4)	190 (180–200)	10 (11)	12 (15)
United States	1.25	3 (6)	4 (8)	360 (270–540)	10 (10)	44 (44)
United States	0.79–0.95	7 (14)	7 (14)	24 (15–60)	31 (33)	29 (36)
United States	0.18–1.28	8 (16)	5 (10)	86 (30–120)	15 (30)	14 (34)

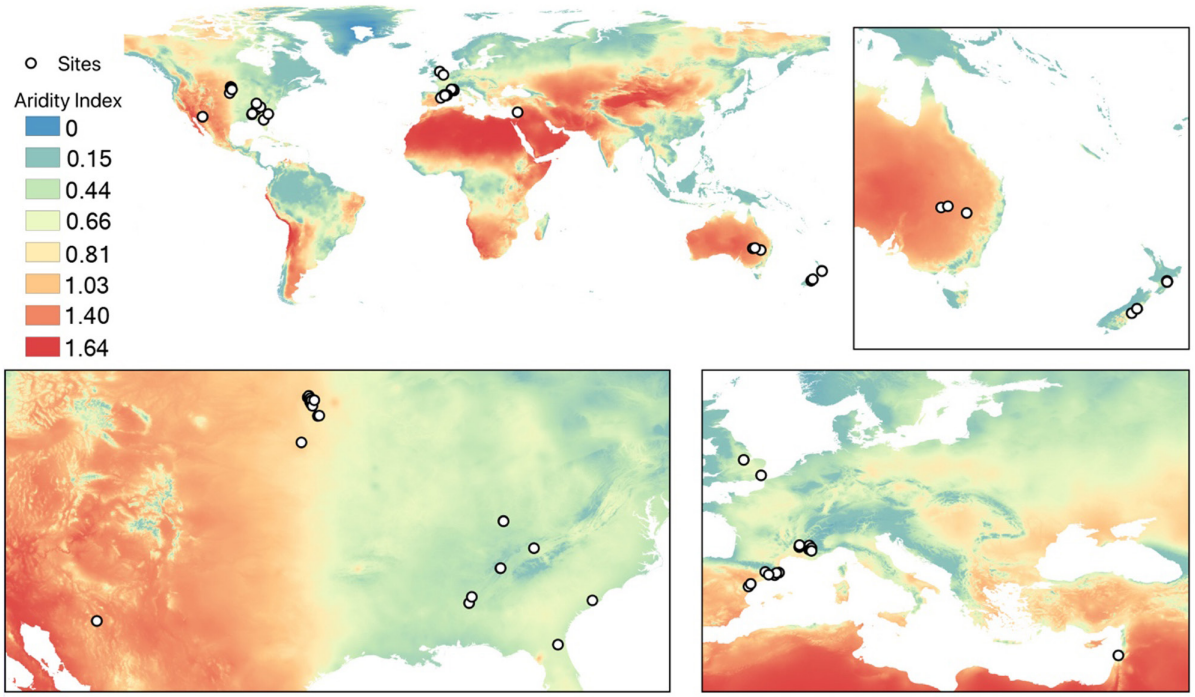


Figure 1. Climatic aridity across the study sites (n = 112). Aridity is defined as the ratio between mean annual precipitation and mean annual potential evapotranspiration, using the WorldClim global dataset (Hijmans et al. 2005) (Methods for details).

information). Although assigning traits at the family level rather than species level can reduce the accuracy of trait information, family-level assignment of traits has proven sufficient to detect community responses to drying in a variety of intermittent river systems (Bonada et al. 2006, Chessman 2009, Datry et al. 2014). Only taxa with complete trait information were used for trait analysis, comprising 83 out of 114 families and 92 ± 10% of individuals. Taxa excluded from trait analysis are provided in Supporting information.

Regional-scale environmental covariates

We chose climatic aridity (hereafter, aridity) as a proxy for climatic harshness because this continuous metric represents a ratio between precipitation and potential evapotranspiration, and can thus be mechanistically linked to the severity of drying stress at a particular site. We used mean aridity index (AI) from the 1950 to 2000 period at 30 arc second spatial resolution, available from the Consortium for Spatial Information's Global-Potential Evapotranspiration and Global Aridity Index dataset (Zomer et al. 2008; <www.cgiar-csi.org>). Aridity was calculated based on the WorldClim global climate data (Hijmans et al. 2005), following: AI = MAP/MAET, where: MAP = mean annual precipitation, and MAET = mean annual potential evapotranspiration. To improve interpretability of this index, we subtracted AI from 1 so that more arid sites had higher AI values. AI values ranged from humid to semi-arid (range = 0.21–1.46), indicating a broad gradient of aridity along which to explore invertebrate community responses to river drying.

Data analysis

General relationships between taxonomic and trait richness versus aridity

Taxonomic richness was estimated for each sample following Chao et al. (2014), which allows for rigorous comparisons of taxa richness when abundances differ between samples. Trait richness was defined as the total number of traits conferring either resistance or resilience to drying within the invertebrate community. For each site, we combined before and after samples. We then tested for relationships between taxonomic and trait richness, and between each richness metric and aridity using linear mixed-effects models (LMM; Bolker et al. 2009). LMM used flow regime (categorical; *INT*, *PER*), time (categorical; before, after) and aridity index (continuous; range 0.21–1.46) as fixed-effect terms, and included dataset as a random intercept to account for potential dataset-specific variability in taxonomic richness. A linear model was used to test the significance of the univariate relationship between taxonomic richness and climatic aridity for each flow regime separately. Taxonomic richness was log transformed because we expected it to have a saturating relationship with trait richness.

Changes in taxonomic richness and the relative abundance of resistant and resilient taxa

At each site, we tested the effects of river drying, aridity and drying duration on changes in taxonomic richness and on the relative abundance of resistant and resilient taxa before and after drying at each site. Taxa were considered either resistant, resilient or both if they had at least one of the traits

mentioned above. We fitted LMM using flow regime, aridity and drying duration (21–360 days) as fixed-effect terms, and dataset as a random intercept. We log-transformed taxa richness to meet model assumptions.

Temporal β-diversity across the aridity gradient

We measured temporal β-diversity in *INT* and *PER* sites to quantify compositional changes associated with drying. Temporal β-diversity was defined as the pairwise dissimilarity of communities between before and after samples within each site. We first calculated total dissimilarity, and then partitioned its turnover and nestedness-resultant components. Whereas turnover captures compositional change driven by species replacements, nestedness-resultant dissimilarity reflects changes in composition that arise from gains and losses of taxa (i.e. richness gradients). We used the Sørensen dissimilarity index with presence/absence data, using the function beta.pair. To test the effects of aridity on temporal β-diversity we used LMM (as in the previous section) also including flow regime and drying duration as fixed effects. We visually assessed compositional changes using Bray–Curtis dissimilarity in a non-metric multidimensional scaling (NMDS) ordination and tested the effects of flow regime and time of sampling (before versus after drying) on compositional changes using a non-parametric multivariate test (PERMANOVA).

All data analyses and visualizations were done in R (ver. 4.0.1, <www.r-project.org>), using the packages iNEXT (Hsieh et al. 2016), lme4 (Bates et al. 2014), betapart (Baselga 2010), vegan (Oksanen et al. 2007) and ggplot2 (Wickham 2009).

Results

General relationships between taxonomic richness, trait richness and aridity

Local taxonomic richness at sites across the global dataset was 20 ± 5 taxa per sample (mean ± SD), and ranged between 4 and 52 taxa per sample. Mean invertebrate abundance was 2901 ± 1938 individuals per sample, and ranged between 7 and 25 611 individuals per sample.

We found a positive, steep relationship between the richness of taxa in a given community and the richness of traits conferring resilience or resistance to drying (prediction 1a). This relationship did not differ between perennial (*PER*) and intermittent (*INT*) sites (LMM, Table 2, Fig. 2a). Taxa richness was higher at *PER* sites compared to *INT* sites, and differences in taxa richness between *INT* and *PER* sites increased with aridity (LMM, Table 2, Fig. 2b). Taxonomic richness at *INT* sites decreased with increasing aridity (linear model, slope = 0.50, t = 2.14, p = 0.036), however, richness at *PER* sites was not correlated with aridity (linear model, slope = −0.26, t = −0.88, p = 0.387; prediction 1b).

Changes in taxonomic richness and relative abundance of resistant and resilient taxa

Contrary to our prediction, changes in taxonomic richness before versus after drying were not associated with flow regime, aridity or their interaction (LMM, Table 2; prediction 2a). Drying duration did not have any significant

Table 2. Results of the linear mixed-effect models testing general relationships between aquatic invertebrate trait richness, taxonomic richness and changes in richness or relative abundance of resistant and resilient taxa, and a set of community and environmental covariates: aridity, flow regime, drying duration and the interaction between flow regime and aridity (*FR* × *AI*) (SE = standard error, df = degrees of freedom).

Response variable	Source of variation	Estimate	SE	df	t-value	p
Trait richness	Intercept	2.38	0.84	48	2.82	0.007
	Flow regime (*FR*)	1.70	1.27	96	1.34	0.184
	Taxonomic richness (*TR*)	1.66	0.27	50	6.21	< 0.001
	FR × *TR*	−0.47	0.39	94	−1.22	0.225
Taxonomic richness	Intercept	2.76	0.31	22	8.83	< 0.001
	Flow regime (*FR*)	0.79	0.29	92	2.75	0.007
	Aridity index (*AI*)	0.41	0.38	21	1.09	0.290
	FR × *AI*	−0.71	0.33	92	−2.13	0.036
Change in taxonomic richness	Intercept	0.19	7.17	26	0.03	0.979
	Flow regime (*FR*)	−6.81	7.10	95	−0.96	0.340
	Aridity index (*AI*)	−3.25	7.72	17	−0.42	0.680
	Drying duration	0.00	0.02	93	0.27	0.785
	FR × *AI*	12.07	7.36	92	1.64	0.105
Change in relative abundance of resistant taxa	Intercept	0.09	0.10	33	0.84	0.405
	Flow regime (*FR*)	0.00	0.11	106	−0.02	0.984
	Aridity index (*AI*)	−0.09	0.11	20	−0.82	0.423
	Drying duration	0.00	0.00	80	−0.21	0.837
	FR × *AI*	0.06	0.12	103	0.54	0.588
Change in relative abundance of resilient taxa	Intercept	0.02	0.10	37	0.15	0.879
	Flow regime (*FR*)	0.04	0.10	105	0.41	0.685
	Aridity index (*AI*)	−0.03	0.11	24	−0.31	0.760
	Drying duration	0.00	0.00	98	−0.82	0.416
	FR × *AI*	−0.05	0.11	102	−0.50	0.621

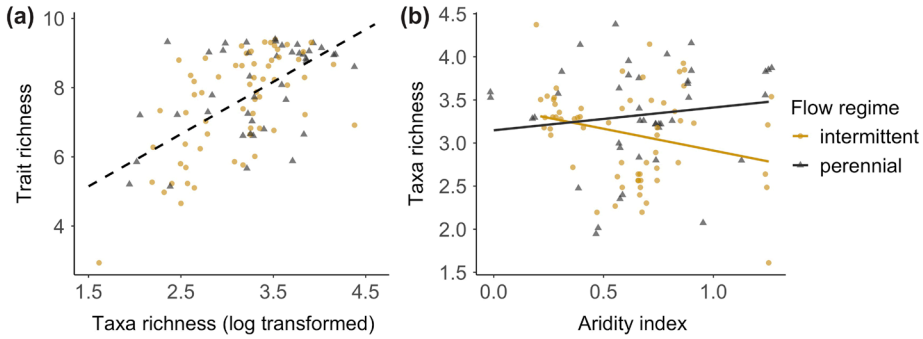


Figure 2. Relationship between aquatic invertebrate: (a) taxa richness (Chao estimate; log transformed) and trait richness; and (b) aridity and taxa richness (Chao estimate), in streams with perennial and intermittent flow regimes. The dashed line indicates a significant linear relationship ($p < 0.05$) between taxa richness and trait richness; solid lines indicates relationships between the aridity index and taxa richness for each flow regime.

effect of taxonomic richness, suggesting that any variation was independent of river drying (LMM, Table 2, Fig. 3a). Functional analysis of the community using resistance and resilience trais supported the results: changes in the relative abundance of taxa with resistance or resilient traits were not related to drying duration, flow regime, aridity or the interaction between flow regime and aridity (Table 2, Fig. 3b–c; prediction 2b). Both *INT* and *PER* sites presented a wide range of changes in taxonomic richness and in the relative abundance of resistant and resilient taxa (Fig. 3). However,

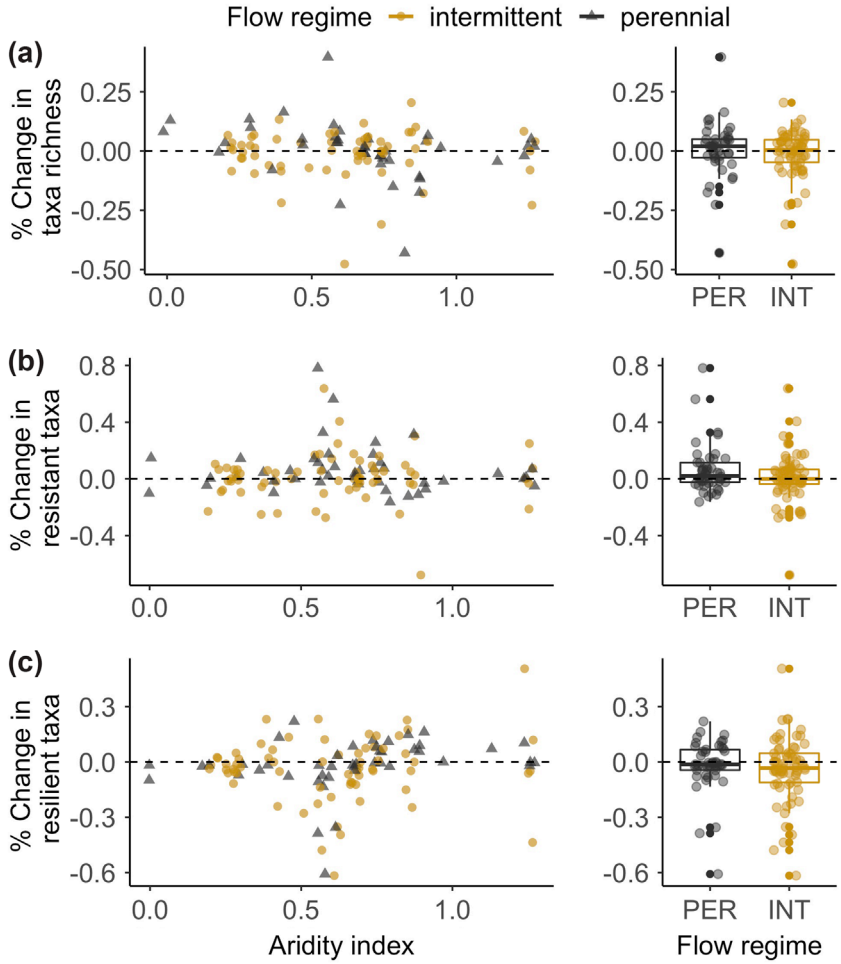


Figure 3. Change (%) in aquatic invertebrate (a) taxonomic richness, and (b–c) the relative abundance of resistant taxa and resilient taxa, before versus after drying at intermittent sites, across the aridity gradient (left); and between intermittent (*INT*) and perennial (*PER*) sites (right). Solid horizontal lines represent median values for each flow regime.

the median across all sites was very close to zero, suggesting no net change, at either site type (Fig. 3b–c).

Temporal β-diversity across the aridity gradient

Contrary to our prediction, temporal β-diversity and community dissimilarity, were not affected by flow regime, aridity or their interaction (Table 3, Fig. 4a; prediction 2c). Partitioned total β-diversity (0.44 ± 0.22%) was driven to a greater extent by turnover (32 ± 23%) than by nestedness (12 ± 15%), whereas the relative contributions of nestedness was higher at *INT* relative to *PER* sites (Fig. 4b). The relative contribution of nestedness increased in intermittent sites across the aridity gradient, while decreasing at perennial sites (Fig. 4b; prediction 2d). This significant interaction (Table 3) indicates that environmental filtering was likely stronger at more arid sites – but only if those sites were intermittent. Drying duration did not have a significant effect on temporal β-diversity (Table 3; prediction 2e). A closer examination of variation in community composition within each study confirmed that although communities often differed between perennial and intermittent sites, time (i.e. variation in composition before versus after drying) was rarely significant, either by itself or interacting with flow regime (Supporting information).

Discussion

The effects of river drying on aquatic biodiversity have been studied for decades (Williams 1996, Lake 2003), but local responses are often deemed variable and highly context dependent (Leigh et al. 2016, Datry et al. 2017, Stubbington et al. 2019). Although understanding context dependencies would represent an important advance, research on this topic is challenging because it requires spatial replication across broad environmental gradients. Here we studied temporal responses of aquatic invertebrates to river drying across a gradient of aridity. We did not confirm our predictions that aridity would dampen reductions in richness and temporal β-diversity, increase the representation of resilient and resistant taxa, or that duration would amplify the effects of drying. However, we found that although intermittent and perennial sites had similar temporal β-diversity levels, changes in community composition at intermittent sites reflected more nestedness – and the importance of that component increased with aridity at intermittent but not perennial sites. This finding suggests that local river drying may represent a stronger environmental filter in arid contexts, challenging the notion that drying will have less impact on intermittent stream communities in arid regions because their taxa are adapted to intermittence.

Changes in environmental conditions over time can increase temporal β-diversity (Tonkin et al. 2017). If species are not adapted to the new conditions, they may migrate and/or become locally extinct; conversely, new species may colonize from the regional pool if dispersal allows – in either case, β-diversity increases (Heino et al. 2015). Early colonizers can differ across sites, with such differences persisting over time (thus keeping β-diversity high) via priority effects (Chase 2007). Previous studies suggested that partitioning β-diversity into its turnover and nestedness components may provide insights into the controls on community composition, such as spatially heterogenous disturbance versus environmental gradients (Legendre 2014, Lamy et al. 2015). In our case, aridity did not influence total β-diversity, but did increase the contribution of nestedness to β-diversity (at the expense of the replacement component, hence the lack of net change). This result suggests that climatic aridity is a large-scale environmental filter that alters the response of communities to local-scale disturbance (Poff et al. 1997, Bonada et al. 2007), even if total β-diversity remains unaffected. Differences in the importance of nestedness between intermittent and perennial streams (regardless of aridity) indicate that river drying filters the regional species pool (in agreement with Datry et al. 2014, Soria et al. 2017). Here we further show that such filtering leads to post-drying communities being more nested within pre-drying communities – particularly in arid climates. In turn, the higher contributions of turnover (three times greater, on average, than the nestedness component) likely reflected 'time-sharing' among taxa that fluctuate with changing hydrological conditions (e.g. wetter or drier periods of the year; Bogan and Lytle 2007, Tonkin et al. 2017). In this vein, Bogan and Lytle (2007) found time-sharing among two distinct taxonomic groups following seasonal shifts in flow and water temperature. These coexistence mechanisms may allow community-level parameters (e.g. richness) to remain relatively stable despite drying.

Table 3. Results of the linear mixed-effect model testing for the effects of flow regime, aridity index and drying duration on the temporal β-diversity of aquatic invertebrate communities (SE = standard error, df = degrees of freedom).

Response	Source of variation	Estimate	SE	df	t-value	p
Total β-diversity	Intercept	0.56	0.13	49	4.41	< 0.001
	Flow regime (*FR*)	−0.11	0.09	98	−1.19	0.236
	Aridity index (*AI*)	−0.11	0.14	58	−0.76	0.453
	Drying duration	0.00	0.00	100	0.92	0.363
	FI × *AI*	0.08	0.09	97	0.88	0.379
Nestedness	Intercept	0.49	0.16	34	3.08	0.004
	Flow regime (*FR*)	0.50	0.17	105	2.93	0.004
	Aridity index (*AI*)	0.22	0.17	21	1.32	0.202
	Drying duration	0.00	0.00	88	0.53	0.596
	FR × *AI*	−0.56	0.18	103	−3.14	0.002

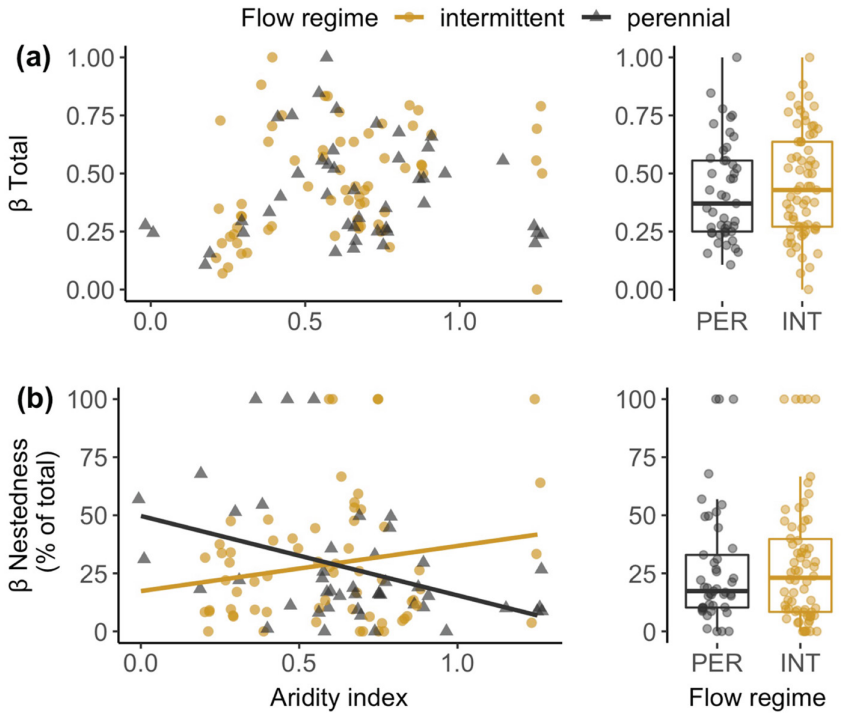


Figure 4. (a) Total temporal β-diversity, and (b) the relative contributions of nestedness-driven changes (i.e. species gains and losses) of aquatic invertebrates across the aridity gradient (left), and between intermittent (*INT*) and perennial (*PER*) sites (right). Solid horizontal lines represent median values for each flow regime.

The overall weak and variable responses to drying detected by this study underscore the strong capacity of aquatic invertebrate communities to bounce back within short timescales (i.e. resilience) and thus difficulties in quantifying the effects of natural disturbances (Leigh et al. 2016, Vander Vorste et al. 2016). The ability to detect impacts of river drying on taxonomic richness and composition can also be influenced by other factors, some unrelated to flow (Bêche et al. 2006, Korhonen et al. 2010, Batzer 2013). For example, remnant pools, hyporheic zones and upstream perennial waters that persist during the dry phase are sometimes sinks with high mortality but at other times support survival and may be an important source of colonists driving post-drying community recovery (Vander Vorste et al. 2020a). Fast recovery may, in turn, reduce the detectability of changes in community composition after flow resumption (Boersma et al. 2014). The finding that neither resistance or resilience strategies became dominant after river drying likely indicates that both strategies are important (as in Leigh et al. 2016). Incorporating the full ensemble of traits, including those related to trophic and habitat preferences, may help anticipate ecosystem-level responses to drying (Bogan and Lytle 2007, Leigh et al. 2019). More research using field experiments and outdoor mesocosms (Leigh et al. 2019) may also help uncover fine-scale determinants of community change, and thus integrate spatial context across hierarchical scales (Poff et al. 1997). Increasing consistency in experimental designs, and promoting designs that offer strong inference (e.g. BACI) across environmental gradients, would reduce site-level variation in communities, and would help understand context dependencies in community re-assembly. Evidence from other freshwater ecosystems (Power et al. 2008, Datry et al. 2017) indicates that responses to disturbance can depend not only on spatial but also on temporal context, e.g. whether the year in which the disturbance occurs is wet or dry, or how the community had assembled up to that point. Temporal dependencies were not considered here, but could be natural extensions of this research.

In summary, we found that aridity did not influence temporal changes in taxa richness or in the relative abundance of taxa with resistance and/or resilience traits, but temporal nestedness increased in naturally intermittent rivers as climatic aridity increased. This suggests that harsher environmental conditions associated with global change may further reduce biodiversity at these sites even if they are already intermittent. More broadly, our results illustrate the need to consider climatic context when studying ecological responses to stress and disturbance in dynamic river systems, as also demonstrated by research in terrestrial and marine environments (Madin et al. 2008, Anderson-Teixeira et al. 2013). As human overallocation of freshwater resources interacts with climate change to cause more frequent and widespread drying (Prudhomme et al. 2014), we need to anticipate how biodiversity will respond to novel drying disturbance across a range of climatic contexts. In systems in which river drying creates a novel disturbance regime, climate context may influence drying-induced compositional and functional changes in communities (Sarremejane et al. 2020). However, our

results suggest that climate context is unlikely to buffer the effects of drying on taxa richness.

Data availability statement

Data available from the Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.12493991> (Vander Vorste et al. 2020b).

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