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Local and regional drivers influence how aquatic community diversity, resistance and resilience vary in response to drying

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Disturbance events govern how the biodiversity of ecological communities varies in both space and time. In freshwater ecosystems, there is evidence that local and regional-scale drivers interact to influence ecological responses to drying disturbances. However, most research provides temporal snapshots at the local scale, whereas few studies encompass a gradient of drying severity spanning multiple years. Using a dataset of rare spatiotemporal extent and detail, we demonstrate how independent and interacting local and regional-scale factors drive shifts in the α and β diversities of communities in dynamic river ecosystems. We examined aquatic invertebrate assemblage responses to hydrological variability (as characterized by monthly observations of instream conditions) at 30 sites over a 12-year period encompassing typical years and two severe drought disturbances. Sites varied in their disturbance regimes and hydrological connectivity at both local (i.e. site-specific) and regional (i.e. river catchment) scales. Whereas α diversity was mainly influenced by local factors including flow permanence and the temporal extent of ponded and dry conditions, both temporal and spatial β diversities also responded to regional-scale metrics such as the spatial extent of flow and hydrological connectivity. We observed stronger local negative responses for taxa with lower capacities to tolerate drying (i.e. resistance) and/or to recover after flow resumes (i.e. resilience), whereas taxa with functional traits promoting resilience made an increasing contribution to spatial β diversity as hydrological connectivity declined. As droughts increase in extent and severity across global regions, our findings highlight the functional basis of taxonomic responses to disturbance and connectivity, and thus advance understanding of how drying disturbances shape biodiversity in river networks. Our identification of the role of regional hydrological factors could inform catchment-scale management strategies that support ecosystem resilience in a context of global change.

Keywords: alpha diversity, beta diversity, drought, gamma diversity, intermittence, intermittent rivers

Introduction

Ecosystems experience considerable natural variability in environmental conditions, including disturbance events that influence the organization of biodiversity in space and time (Pickett et al. 1989). Climate change and other anthropogenic pressures are interacting to alter disturbance regimes, including an increase in unpredictable, extreme events (Prudhomme et al. 2014) that disrupt ecosystems and threaten their ecological communities (Dudgeon et al. 2006, Reid et al. 2019). Rivers are dynamic ecosystems which experience natural hydrological variability, including flow cessation and drying in temporary rivers (Datry et al. 2014a). Predicted increases in drought disturbances (Prudhomme et al. 2014, Spinoni et al. 2018) are set to increase the extent of these instream conditions in temporary rivers and to cause drying in historically perennial systems (Döll and Schmied 2012, Hill et al. 2019), which may have profound effects on riverine communities (Leigh and Datry 2017).

Ecological community responses to environmental change can be characterized by local α diversity (e.g. taxonomic richness), spatial β diversity (variability in composition among sites) and temporal β diversity (site-specific compositional variability among times), which collectively influence regional γ diversity (Tuomisto 2010). Experimental research has shown how biodiversity changes along controlled gradients of drought and drying intensity, revealing the functional basis of taxon-specific responses (Aspin et al. 2018, 2019). In contrast, few field studies have explored biotic responses to natural hydrological variability along a spatial gradient of drying severity or considered timescales long enough to encompass droughts with different characteristics (Wood and Armitage 2004, Mathers et al. 2019); even fewer characterize river-scale responses over long periods (Sarremejane et al. 2018).

Locally, the composition, α diversity and temporal β diversity of local communities typically respond to disturbance frequency, magnitude, duration and predictability (Lepori and Malmqvist 2009, Leigh and Datry 2017, Aspin et al. 2018). In non-perennial waters, α diversity typically declines as drying intensities increase due to the loss of desiccation-sensitive organisms (Datry et al. 2014b, Soria et al. 2017), a pattern which can also limit regional γ diversity in networks dominated by temporary waterbodies (Daniel et al. 2019, Piano et al. 2019). However, species at sites that dry frequently may have traits conferring the ability to tolerate a disturbance (resistance) and/or to recover afterwards (resilience; Lytle 2001, Bogan et al. 2017) and drying may therefore cause greater decreases in α diversity at sites that rarely dry (Wood and Armitage 2004, Hill et al. 2019). Compositional changes concurrent with declines in local taxonomic richness may cause temporal β diversity to increase with drying duration (Crabot et al. 2020). However, temporal changes may be lower at sites experiencing predictable drying events (Boulton and Lake 1992), due to the persistence of adapted species (Gasith and Resh 1999).

At regional scales, spatial β diversity may increase with disturbance extent if catchment-wide habitat heterogeneity increases (Rolls et al. 2016, Schriever and Lytle 2016), if reduced hydrological connectivity limits homogenization by mass effects (Heino et al. 2015, Sarremejane et al. 2018), and/or if communities reassemble along divergent trajectories after a disturbance ends (Didham et al. 2005, Datry et al. 2016). In addition, low richness at disturbed sites enhances differences among communities (Chase and Myers 2011). Alternatively, spatial β diversity can decline if extended dry phases homogenize communities through convergent niche selection (Chase 2007, Stubbington et al. 2019). Alpha diversity and community temporal stability may also decrease with increasing disturbance extent, if drying reduces catchment-wide colonist sources, thus reducing stabilizing mass effects (Zelnik et al. 2018). Gamma diversity may also decrease with disturbance extent if its regional-scale effects are homogeneous, filtering out sensitive species at multiple localities and thus increasing regional extinction risks (Chase 2007, Starzomski and Srivastava 2007).

Hydrological connectivity influences spatial β diversity (Cañedo-Argüelles et al. 2015, Sarremejane et al. 2017a) and biotic responses to disturbances thus vary among sites with different levels of connectivity (Vanschoenwinkel et al. 2013, Tornwall et al. 2017). Dispersal by resilient taxa from undisturbed communities facilitates rapid recovery and subsequent community stability at well-connected sites (Carrara et al. 2012, Shackelford et al. 2017), such as those near to perennial sections (Chester and Robson 2011, Bogan and Boersma 2012). Colonization by mobile aquatic invertebrates may occur from upstream and downstream reaches through drift and active migration, respectively (Eveleens et al. 2019, Pařil et al. 2019), and by overland aerial dispersal (Bogan et al. 2015, Cañedo-Argüelles et al. 2015). In contrast, isolated communities typically have lower α diversity and higher spatial (Altermatt et al. 2013, Sarremejane et al. 2017b) and temporal (Huttunen et al. 2017) β diversity. Drying reduces hydrological connectivity between disturbed sites and colonist sources, with community recovery reflecting interactions between connectivity and the dispersal capacity of potential colonists (Tonkin et al. 2014, Cañedo-Argüelles et al. 2015). However, how connectivity and drying-related changes in habitat conditions interact to influence biodiversity patterns remains unclear.

We examined aquatic invertebrate communities at 30 sites across seven streams over a 12-year period encompassing typical years in which temporary sites experienced seasonal drying, and drought years (i.e. 2005–2007 and 2011–2012; Marsh et al. 2007, Kendon et al. 2013) during which typically perennial sites also dried and temporary sites experienced unusually long dry phases. Recognizing that biodiversity patterns observed at one scale can be determined by factors operating at other scales (Rolls et al. 2017, Chase et al. 2019, Altermatt et al. 2020), we analyzed how α diversity, spatial and temporal β diversity and γ diversity respond to drying events, in relation to local and catchment-scale drivers.

Our first hypothesis (H1) was that α diversity declines as local drying severity increases, especially at sites that rarely dry, and then increases after flow resumes, with the rate of increase accelerated by hydrological connectivity. Second, we hypothesized (H2) that temporal β diversity increases with drying severity, and that these changes are mediated by both site-specific flow permanence regimes and regional-scale hydrological connectivity and catchment-scale disturbance extent. Our third hypothesis (H3) was that spatial β diversity increases with catchment-scale disturbance extent and disturbance-mediated habitat heterogeneity and then decreases after flow resumes, with greater changes occurring at sites with lower connectivity and lower flow permanence. Our fourth hypothesis (H4) was that γ diversity decreases with catchment-scale disturbance extent. We explored the taxon-specific responses underpinning observed patterns, and related these responses to traits promoting resistance and/or resilience to drying.

Methods

Study area

The study area includes seven groundwater-fed, temperate-zone headwater streams, each draining a 35–175 km² catchment underlain by Cretaceous chalk in southern England, UK (Fig. 1). The catchments are dominated by arable, pastoral and urban land uses and all sites had high water quality based on nitrate concentrations, good to high quality based on dissolved oxygen, and moderate to high phosphate-based quality during the study period (Sarremejane et al. 2019). River discharge typically peaks in late winter (February–March), then declines until late summer/autumn, when drying may occur at temporary sites. The spatial extent and timing of dry phases varies among years depending on antecedent precipitation and thus groundwater levels (Sefton et al. 2019).

Invertebrate samples

Our dataset comprised 311 invertebrate samples collected from 30 sites in spring (March–May) between 2006 and 2017 (mean ± SD = 10.4 ± 1.3 samples site^{-1}). Drying prevented sampling of some sites in some years, particularly in 2006 (Fig. 2). Samples were collected using a 3-min kick/sweep technique supplemented by a 1-min hand search and including all habitats in proportion to their occurrence. Most invertebrates were identified to species or genus, with a few exceptions identified to a higher taxonomic level (Supplementary material Appendix 1 Table A1).
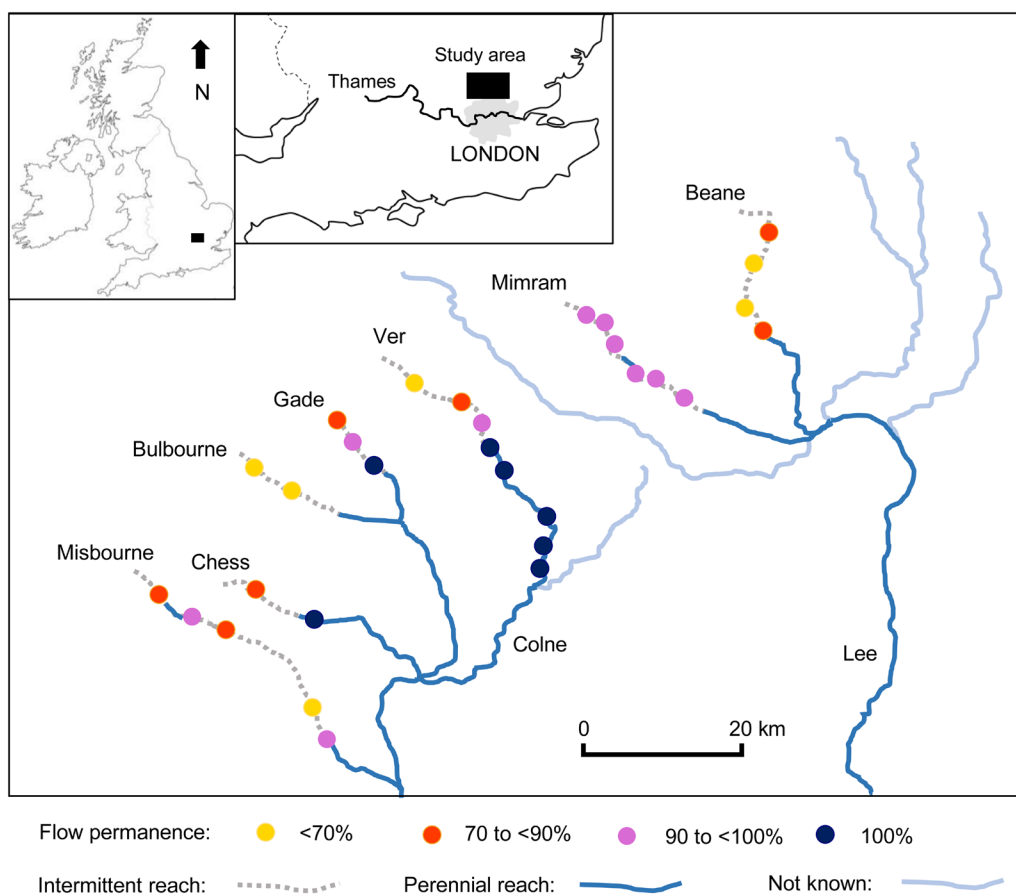

Figure 1. Thirty sampling sites across seven streams, indicating sites with perennial and different non-perennial flow regimes as described by the % of flowing months (TotalFlow) between 2004 and 2018.
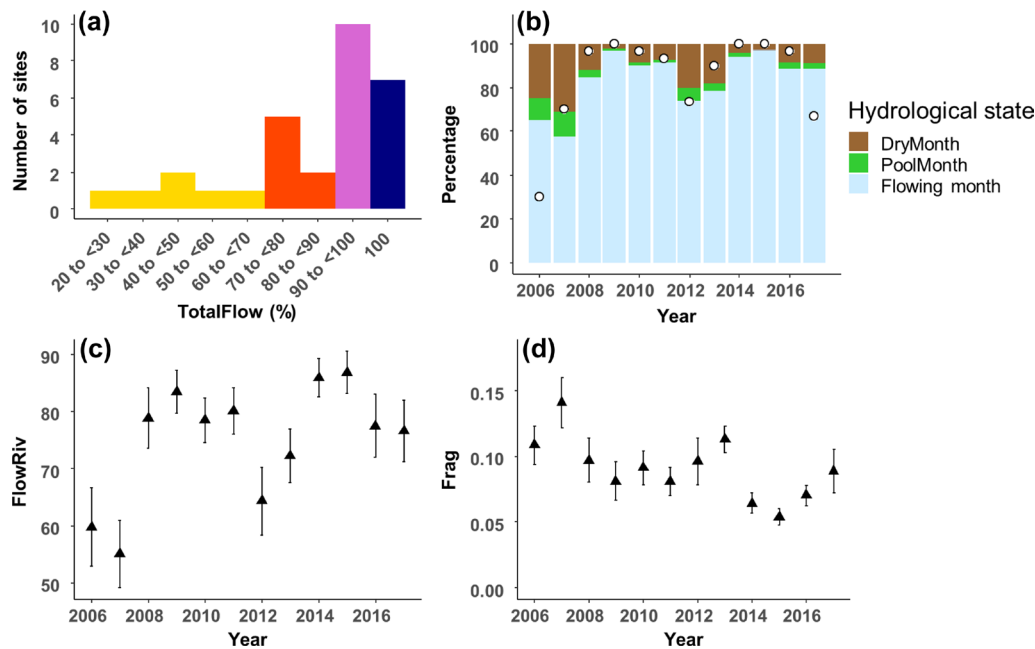
Figure 2. Hydrological conditions across the 30 sampling sites: (a) site-specific % of flowing months (TotalFlow) over the study period; (b) all-site mean % flowing, ponded (PoolMonth) and dry (DryMonth) months in the year preceding sample collection; (c) mean ± SE of the % extent of flowing reaches (FlowRiv) in the preceding year; and (d) mean ± SE fragmentation (Frag) in the preceding year. White circles in (b) indicate the percentage of sites sampled in each year.

Hydrological state observations

Monthly observations of hydrological states (flowing, ponded, dry) were made over 14 years from March 2004 to November 2018, in 18–32 reaches per river. Flowing, ponded and dry states include low to flood flows, isolated and connected pools, and wet and dry bed conditions, respectively (Sefton et al. 2019). Dry and ponded states constitute no-flow conditions. On average, 5.9 ± 1.9% of observations were missing (i.e. approx. 9 months site^{-1}), with absences often limited to 1–2 consecutive months. Reaches in which states were observed were matched with invertebrate sampling sites: 24 were co-located, two were < 800 m apart within a perennial section, and four were < 500 m apart and experience comparable states.

Local and regional-scale hydrological state metrics

We calculated two site-specific and three sample-specific hydrological state metrics to represent local no-flow (ponded + dry) conditions (Supplementary material Appendix 1 Table A2, Fig. A1). Both site-specific metrics were calculated using the 14-year hydrological state dataset. First, the total percentage of flowing months (TotalFlow) is the number of flowing months divided by the total number of months in which observations were made, and indicates the long-term flow permanence of the site. Second, the six-month seasonality (i.e. predictability) of the no-flow phase (Pred) was calculated as per Gallart et al. (2012).

The three sample-specific metrics characterize hydrological conditions in the period preceding sampling. The proportion of months with dry (DryMonth) and ponded (PoolMonth) conditions collectively quantify the occurrence of no-flow conditions in the 12-month period ending in the February prior to sample collection (hereafter, the preceding year), a duration of particular importance in driving aquatic invertebrate community responses to hydrological variability (Leigh and Datry 2017). DryMonth and PoolMonth indicate the severity of no-flow conditions, with dry conditions being more severe than ponded conditions for most aquatic organisms. The third sample-specific metric is the number of months since the most recent no-flow observation (MonthSince) and describes the number of consecutive months with observations of flow preceding sample collection. Samples from sites which did not experience no-flow conditions during the study period were given an arbitrary value of 156 MonthSince (i.e. maximum MonthSince + 1).

Three metrics were calculated to describe 'regional' no-flow conditions at the individual river catchment scale, because at the temporal scale of our study, invertebrate community responses are likely to be influenced more by hydrologically connected reaches than by those on adjacent streams (Heino et al. 2004). The relative spatial extent of flowing (and thus no-flow) reaches in each river catchment (FlowRiv) is the mean monthly percentage of flowing reaches in the sampled river in the preceding year. Second, the regional-scale heterogeneity of hydrological habitats in the preceding year was quantified using mean fragmentation (Frag): the number of

changes between flow, ponded and dry states as a proportion of the number of reach boundaries (sensu Sefton et al. 2019). Where Frag = 1, the state in each reach differed from that in both adjacent reaches, and where Frag = 0, only one state was observed in all reaches. Third, the distance to the closest perennial reach (DistPer) was calculated for each site, as a measure of connectivity to potential colonist sources (Fig. 1).

Resistance and resilience scoring

We used nine traits relating to life cycles, morphology, physiology and behaviour (Table 1) to determine taxon-specific resistance and/or resilience to drying conditions, sourced from Tachet et al. (2010) and Sarremejane et al. (2020a). A fuzzy-coding approach was used to assign traits to taxa at genus level, with affinities for each trait modality standardized as percentage affinities within a trait. Twenty-two infrequent (i.e. occurring in < 0.5% of samples) taxa with incomplete trait information and all taxa identified to above family level were omitted. For taxa identified to family, we assigned a mean calculated using the traits of all genera in the family.

Each trait modality was weighted between 0 and 4, with higher weights given to modalities promoting resilience and/or resistance to drying (Table 1, Sarremejane et al. 2017b). We then calculated total resistance and resilience (hereafter, Res) scores for each taxon as the sum of the trait affinities within each modality multiplied by the corresponding weights. We ranked taxa by Res then used the ranked list to create high (top 25%), low (bottom 25%) and intermediate (middle 50%) Res groups (Supplementary material Appendix 1 Table A1).

Data analysis

Diversity metrics

Diversity metrics were calculated for the whole community and for each Res group using presence–absence data. We calculated α diversity as the sum of taxa (i.e. taxonomic richness) in each sample. We used the Sørensen dissimilarity index to describe β diversity. Spatial β diversity was determined for each sample as the distance of the community from the multidimensional space centroid of all sampled communities in a given year, which indicates how much each community deviated from the 'average' regional community in that year. Similarly, temporal β diversity was calculated as the distance of a community to the centroid of all samples from a site, indicating its deviation from other temporal replicates from that site. To control for variability in the number of sites sampled in each year, γ diversity was calculated as the mean number of taxa across nine samples (the lowest number collected in an individual year [2006]) randomly selected (×1000) in each year across all rivers.

We used a null model approach to simulate random communities and to control for the effect of differences in α diversity on β diversity (Chase and Myers 2011). Null models were generated separately for spatial and temporal β diversities using a quasiswap algorithm, which swaps the community matrix while maintaining row sums (i.e. α diversity) and column frequencies (i.e. taxon frequencies; Miklós and Podani 2004). For spatial β diversity, we used separate null models for each year, to avoid confounding factors related to interannual variability in the regional species pool (Sarremejane et al. 2018). Similarly, we built site-specific null

Table 1. Traits, trait modalities and weights used to calculate the resistance and resilience scores. References indicate sources of evidence supporting the suggestion that trait modalities promoted resistance and/or resilience.

Trait	Modality	Weight	References
Maximum size	< 0.5 cm	4	Bonada et al. 2007 Aspin et al. 2019
Life cycle duration	< 1 year	4	Bogan et al. 2015 Sarremejane et al. 2017a
Potential number of reproductive cycles per year	> 1	4	Bonada et al. 2007 Sarremejane et al. 2017a
Reproductive behaviour	Egg clutches in vegetation	2	Bonada et al. 2007
	Egg clutches, terrestrial	4	
	Asexual	4	
Resistance forms	Any resistance form (egg, cocoon, housing against desiccation, dormancy and diapause)	4	Bonada et al. 2007 Aspin et al. 2019
Respiration	Spiracle	4	Bonada et al. 2007
	Hydrostatic vesicle	4	Sarremejane et al. 2017a
Mobility	Capacity to fly	2	Bonada et al. 2007
	Capacity to move into interstitial spaces	4	
Dispersal strategy	Aquatic passive	2	Sarremejane et al. 2017a
	Aquatic active	2	
	Aerial passive	2	
	Aerial active	4	
Wing length	Small (< 1 cm)	1	Arribas et al. 2012
	Medium (1–2 cm)	2	Bogan et al. 2015
	Large (> 2 cm)	4	

models for temporal β diversity, to avoid confounding spatial factors (Huttunen et al. 2017).

For each randomly generated community matrix ($n = 499$ site^{-1} and year^{-1}), we calculated pairwise Sørensen dissimilarities and determined each community distance to the year (spatial β diversity) or site (temporal β diversity) centroid (Dis-null). Dis-null values were compared to the observed distance to the centroid for each sample using deviations from the null model (Dis-dev). Dis-dev values express the difference between the observed distances to the centroid and the mean of the 499 Dis-null values divided by their SD. Positive and negative Dis-dev values indicate communities that were more or less dissimilar to other communities (i.e. farther from their group centroid) than expected at random, respectively, with values around 0 ± 1.8 indicating that community dissimilarity was as expected at random.

Modelling invertebrate diversity responses
Separate models were built for the whole community and each Res group to assess if diversity responses differed depending on taxon-specific resistance/resilience strategies. We built generalized linear mixed-effects models (GLMM) using a Poisson distribution and a log link function, to assess the response of α diversity to the hydrological state metrics and their interactions (H1). We used linear mixed-effect models (LMM) to assess the responses of temporal and spatial β diversity (as Dis-dev) to each hydrological metric and to metric interactions (H2–3). We used linear models (LM) to assess the response of γ diversity to the mean annual FlowRiv across all streams (H4).

We used variance inflation factor (VIF) analysis to assess multicollinearity among hydrological state metrics, and sequentially removed those with the highest VIF until all had a VIF < 3 (Zuur et al. 2010). On this basis, Pred was excluded, leaving four local-scale metrics (TotalFlow, DryMonth, PoolMonth, MonthSince) and all three regional-scale metrics (FlowRiv, Frag, DistPer). Six two-way interaction terms were selected based on hypotheses 1–4 to assess if responses to local and regional hydrological metrics differed among sites with different flow permanence regimes (TotalFlow) and connectivity (DistPer; Supplementary material Appendix 1 Table A3). To account for the non-independence of samples from individual sites and streams, we included site ($n = 30$) nested within stream ($n = 7$) as random factors in each GLMM and LMM. Each hydrological metric was centred around its mean and scaled (i.e. divided by its SD).

We used a model-averaging approach to calculate parameter estimates and confidence intervals (CI) for each model. We calculated Akaike information criteria (AIC) to examine model performance and averaged parameter estimates and CI of all models with an ΔAIC < 4 from the model with the lowest AIC (Anderson 2008). The relative number of times a variable or interaction term was selected in the averaged models was used to evaluate its importance, with variables selected in > 50% of the averaged models considered important. We also verified that initial GLMM models were not overdispersed, i.e. had a Pearson χ^2 ratio < 1.2 (Payne et al. 2018).

We used R ver. 3.5.0 (<www.r-project.org>) for all analyses, including the packages vegan (Oksanen et al. 2019) for null model analyses, nlme (Pinheiro et al. 2019), lme4 (Bates et al. 2015) and MuMIn (Bartoń 2019) for model building and averaging, and usdm (Naimi et al. 2014) for VIF analyses.

Results

Hydrological conditions

Of the 30 sites, seven were perennial and 23 non-perennial, with six, seven and ten non-perennial sites flowing for < 70%, > 70–< 90% and 90–< 100% of months, respectively (Fig. 1, 2a). The distance from non-perennial sites to the nearest perennial site (DistPer) varied between 0.1 km and 20.2 km. The mean no-flow period (DryMonth + PoolMonth) exceeded four months in the years preceding 2006 and 2007 invertebrate sample collection and exceeded two months prior to 2012 and 2013, with dry conditions usually dominating (Fig. 2b). No-flow conditions covered > 40% of the surveyed river length in the years preceding 2006 and 2007 and > 20% before 2012 and 2013 sampling (Fig. 2c) with correspondingly high hydrological habitat heterogeneity (as Frag; Fig. 2d). Mean MonthSince was lowest (34 ± 13 months) in 2007, when all non-perennial sites experienced a no-flow event in the preceding two years, and was highest (81 ± 14 months) in 2017.

Community diversity responses to hydrological state metrics

A total of 188 taxa were recorded, of which 140 taxa occurred in > 3 samples (Supplementary material Appendix 1 Table A1).

Alpha diversity increased with long-term flow permanence (i.e. TotalFlow; Fig. 3a, 4a) and decreased with PoolMonth and DryMonth (Fig. 3a, 4b), which were the most selected variables in the best models (Supplementary material Appendix 1 Table A4). DryMonth had three times the effect of PoolMonth on α diversity (Fig. 3a), suggesting that drying had a stronger effect than ponding. Contrary to H1, the interaction between TotalFlow and DryMonth had no significant effect on α diversity: parameter estimate CI strongly overlapped with 0, indicating that the response of α diversity was comparable at sites with different flow permanence regimes. The interaction between connectivity (DistPer) and post-drying flowing duration (MonthSince) was also non-significant, suggesting that flowing duration had comparable random effects on α diversity at sites with contrasting connectivity (Fig. 3a).

As hypothesized (H2), temporal β diversity (as Dis-dev) marginally increased with DryMonth (as indicated by slight overlap between CI and 0) and decreased with the regional extent of flowing conditions (i.e. FlowRiv; Fig. 3b), suggesting that communities became less temporally variable than
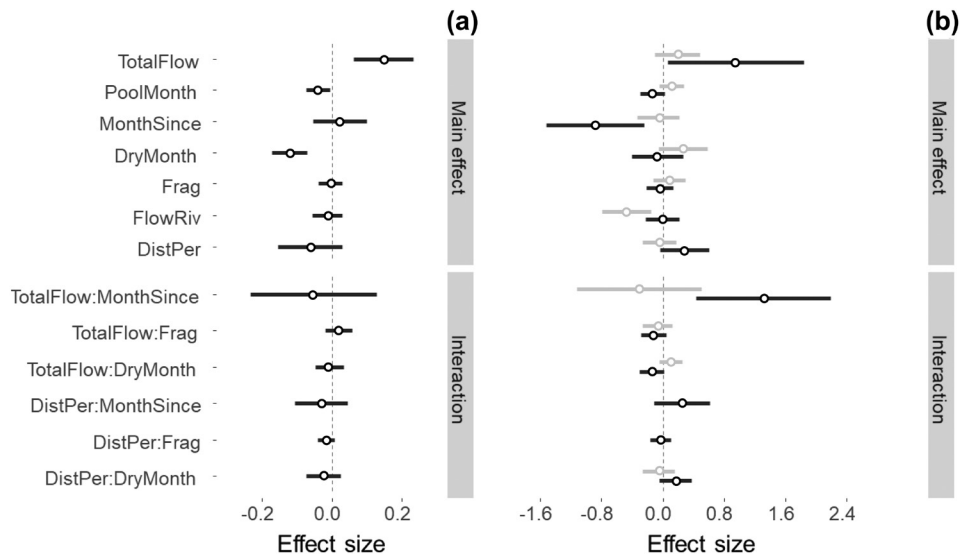
Figure 3. Model averaging results for (a) α diversity (GLMM) and (b) temporal (grey) and spatial (black) β diversities (LMM). White dots and horizontal lines represent average effect sizes and confidence intervals for each variable and their interactions. Metrics and abbreviations are described in the text.

expected at random as flowing conditions in the preceding year increased. Contrary to H2, interactions between TotalFlow or DistPer and DryMonth had no significant effect on temporal β diversity, indicating that temporal variability in community composition was comparable at sites with different connectivity levels and flow permanence regimes (Fig. 3b).

Spatial β diversity (as Dis-dev) increased with TotalFlow, increased marginally with DistPer, and as predicted (H3), decreased as flowing durations increased (MonthSince; Fig. 3b). Contrary to H3, spatial β diversity did not change with FlowRiv or Frag. A positive interaction between TotalFlow and MonthSince was also selected in most of the top models (Supplementary material Appendix 1 Table A4): whereas community composition at sites with higher TotalFlow varied little with MonthSince, communities at sites with lower TotalFlow became more similar than expected at random as MonthSince increased (Fig. 4c), suggesting that communities homogenized over time only at non-perennial sites.

Contrary to H4, γ diversity was unrelated to FlowRiv (LM: p = 0.89).

Diversity responses of resistance/resilience groups

There were 35, 84 and 47 taxa in the high, intermediate and low Res groups, respectively. The high Res group was dominated by Diptera (31%), Heteroptera (29%) and Coleoptera (20%) and included many infrequently recorded taxa (34%), each of which occurred in < 3 samples. The intermediate Res group was dominated by Trichoptera (39%), Coleoptera (20%) and Gastropoda (12%), and the low Res group by Gastropoda (27%), Hirudinea (21%) and Trichoptera (21%). The most common taxa were the true flies *Simulium* sp. and Empididae in high Res; the true fly family Chironomidae, the pea mussel *Pisidium* sp., the mayfly *Baetis rhodani* and

the caddisfly *Limnephilus lunatus* in intermediate Res; and *Gammarus* sp., the flatworm *Polycelis* sp. and the snail *Radix balthica* in low Res (Supplementary material Appendix 1 Table A1).

The α diversity of the high Res group marginally decreased with FlowRiv and increased with MonthSince (Fig. 5a). Low and intermediate Res α diversity increased with TotalFlow and decreased with DryMonth, with the effect of DryMonth being stronger for the low Res group (Fig. 5a). The negative effect of DryMonth on intermediate Res α diversity became stronger as DistPer increased, as suggested by a marginal interaction: as the extent of drying increased, taxa richness decreased more strongly at sites farther from perennial reaches (Fig. 6a).

The temporal β diversity of all Res groups decreased with increasing FlowRiv (Fig. 5b): all groups contributed to the overall community response. Intermediate Res temporal β diversity also increased with DryMonth, and a marginal interaction with TotalFlow reflected a stronger increase at sites with higher flow permanence (Fig. 5b): assemblages became more variable than expected at random with DryMonth at sites that rarely dry (Fig. 6b).

The spatial β diversity of intermediate and low Res groups was best explained by an interaction between TotalFlow and MonthSince, following a similar pattern to the whole community (Fig. 3b, 4c). Frag was the most selected predictor in low Res spatial β diversity models (Supplementary material Appendix 1 Fig. A2), with spatial variability among assemblages decreasing as river-scale hydrological habitat heterogeneity increased. Frag had a marginally greater effect on low Res spatial β diversity at sites with high TotalFlow (Fig. 5c), suggesting that community homogenization increased with flow permanence (Fig. 6c). The spatial β diversity of the high Res group increased with DistPer (Fig. 5c), suggesting that these
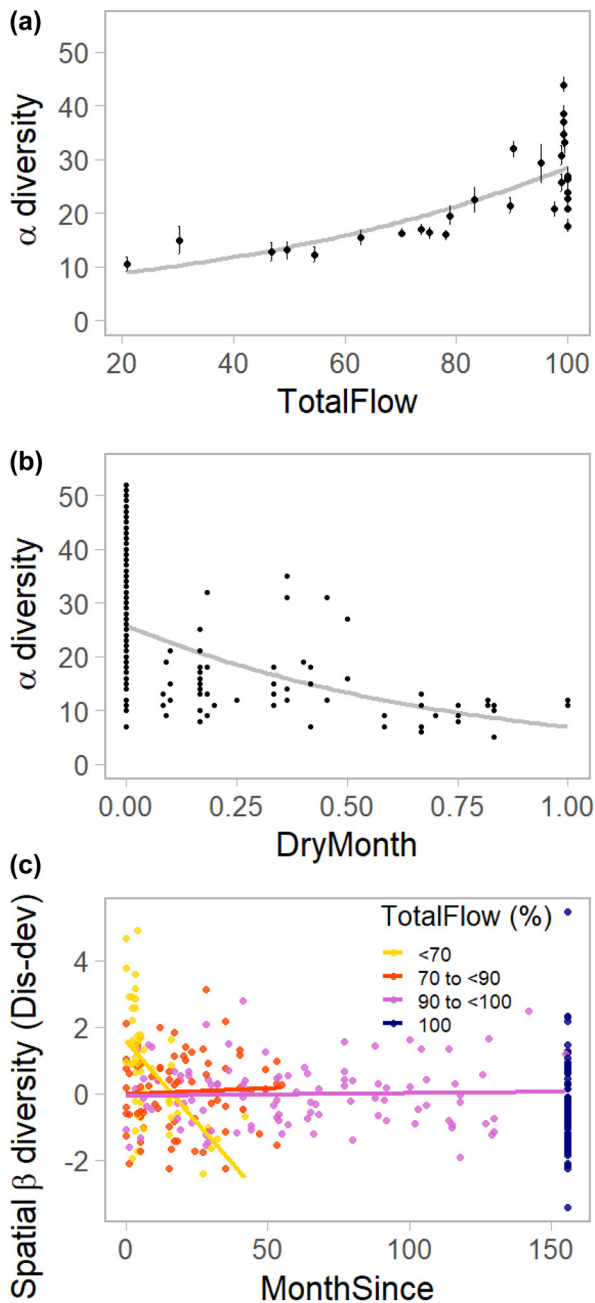
Figure 4. Relationship between: (a) TotalFlow and mean ± SE α diversity per site and (b) DryMonth and α diversity per sample; and (c) the response of spatial β diversity to MonthSince at sites with different % of flowing months (TotalFlow). Lines in (a) and (b) were fitted using a generalized linear model with a Poisson distribution, and in (c) using a linear model to visualize interactions. Metrics and abbreviations are described in the text.

assemblages became more dissimilar than expected at random with increasing distance from perennial reaches. DistPer interacted with MonthSince (Fig. 6d) and DryMonth, indicating that increases in high Res community spatial β diversity with MonthSince and DryMonth were more pronounced at sites farther from perennial reaches.

The γ diversity of all Res groups was unrelated to FlowRiv (LM: all $p > 0.20$): regional diversity did not respond to the spatial extent of flowing reaches.

Discussion

Our study of aquatic invertebrate communities across 30 sites on seven streams demonstrates how local and regional-scale disturbance characteristics and connectivity levels act individually and collectively to influence α, spatial β and temporal β diversities – but not γ diversity. We identified both contrasting and comparable responses to drying disturbances between taxa with different resistance/resilience strategies, highlighting the functional basis underpinning community structural responses. Our 12-year study period spanned typical years and two droughts, thus encompassing variability in the responses of riverine habitats and communities to conditions including seasonal and extreme disturbances. Enabled by high-resolution network-scale hydrological information, this study is one of the first to show that disturbance events operate at multiple spatial scales to affect freshwater biodiversity.

Local disturbance characteristics drive α diversity

Supporting H1, α diversity (i.e. taxonomic richness) increased with local flow permanence, measured as TotalFlow, and decreased with the prevalence of both ponded (PoolMonth) and dry (DryMonth) conditions in the year preceding sample collection. The negative relationship between flow intermittence and the α diversity of aquatic communities is well-established (Datry et al. 2014b, Leigh and Datry 2017, Stubbington et al. 2019). Our long-term monthly observations of instream conditions advance understanding of this relationship, by distinguishing between responses to partial (PoolMonth) and complete drying (DryMonth).

Although flow cessation typically increases physiological stress for aquatic taxa due to declining water quality (Bogan et al. 2017), many organisms can persist for extended periods in ponded habitats (Verdonschot et al. 2015). Surface water loss thus represents a far greater physiological stress for desiccation-sensitive aquatic organisms (Boulton 2003, Chadd et al. 2017). Accordingly, α diversity decreased more strongly with DryMonth than PoolMonth, and declined more sharply with DryMonth for taxa with low resistance and/or resilience capacities (low Res) than for the intermediate Res group. For example, *Gammarus* amphipods, which dominated the low Res group, die within days of exposure to air (Stubbington et al. 2009, Poznańska et al. 2013), and recover relatively slowly where – as in our study streams – an absence of perennial headwaters limits recolonization by drift (Pařil et al. 2019). In contrast, the α diversity of highly resistant and/or resilient taxa did not respond to the temporal extent of drying, with true bugs and beetles (i.e. 49% of the high Res group) including many taxa that can escape drying and recolonize quickly as flying adults (Bogan et al. 2017).
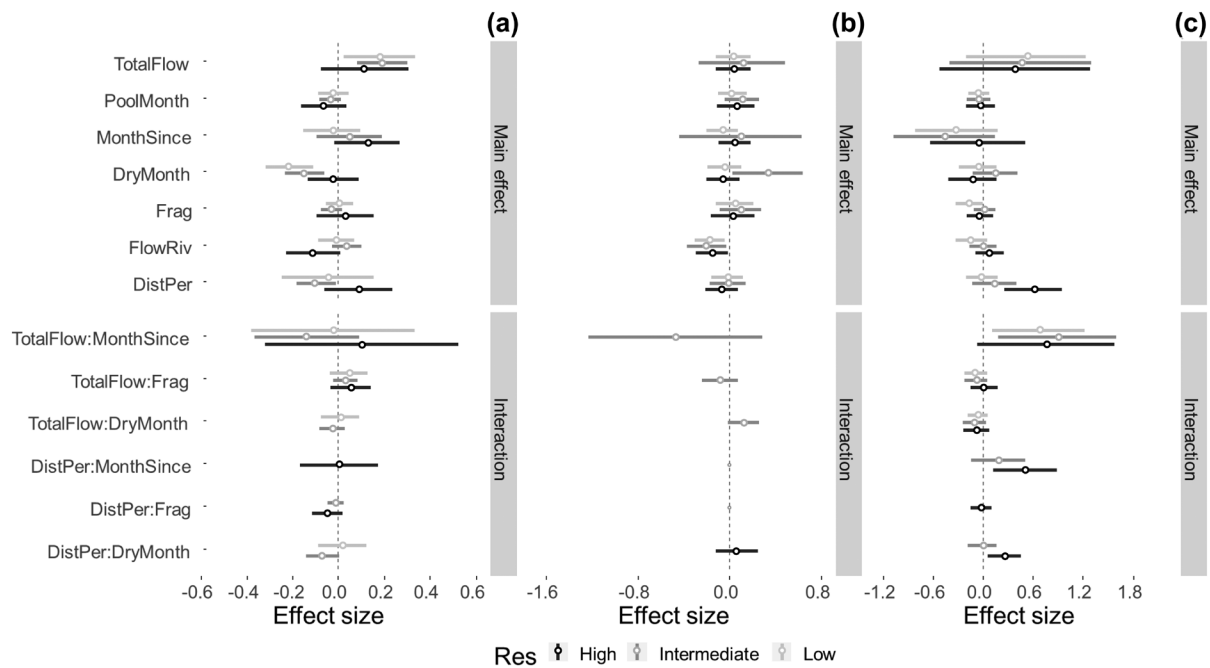
Figure 5. Model averaging results for (a) α diversity and (b) temporal and (c) spatial β diversities for the low (light grey), intermediate (dark grey) and high (black) resistance/resilience (Res) groups. White dots and horizontal lines represent average effect sizes and confidence intervals for each variable and their interactions. Metrics and abbreviations are described in the text.

We found no evidence that α diversity declines more strongly with increasing drying severity at sites with higher flow permanence. This finding contrasts with research attributing greater reductions at rarely disturbed sites to their support of sensitive species and thus higher pre-disturbance taxonomic richness (Tornés and Ruhí 2013, Hill et al. 2019). Comparable decreases in α diversity across sites with contrasting flow permanence may indicate that a limited range of species in the regional pool have adaptations promoting resistance and/or resilience to drying. Although Sarremejane et al. (2019) showed that some semi-terrestrial and lentic taxa inhabited the most temporary sites in our study area, the opportunistic lotic generalists that numerically dominated communities at non-perennial sites may respond similarly to drying across streams with contrasting flow permanence regimes.

How local diversity responds to disturbance may also reflect hydrological connectivity, with mass effects enabling dispersal to compensate for individual losses at highly connected sites, therefore limiting regional extinctions (Altermatt et al. 2011, Vanschoenwinkel et al. 2013). Accordingly, we found that the α diversity of the intermediate Res group decreased with increasing distance to perennial reaches (DistPer), and that the effect of DryMonth, although marginal, was higher at hydrologically isolated sites. The local diversity of taxa with intermediate resistance and/or resilience capacities may be particularly sensitive to interactions between environmental sorting mechanisms and dispersal limitation (Cañedo-Argüelles et al. 2015). In comparison, high Res taxa can persist despite high disturbance intensities or recolonize

despite low connectivity, and low Res taxa diversity is mainly driven by disturbance intensity and their limited dispersal is punctuated by stochastic events even at well-connected sites which dry rarely (Vanschoenwinkel et al. 2013).

Our prediction that α diversity increases over time after flow resumes was based on studies indicating that communities take months to years to recover after a drying disturbance (Ladle and Bass 1981, Wood and Petts 1999), especially as hydrological isolation increases (Resh 1992, Bogan et al. 2015). However, taxonomic richness did not change between years as flowing durations increased. This stability suggests that after a dry phase ends, local changes in diversity are either random (Shackelford et al. 2017) or result from factors other than disturbance regime and connectivity, such as local refuge availability (Chester and Robson 2011, Stubbington et al. 2019).

Temporal β diversity is enhanced by disturbance extent

Supporting H2, temporal β diversity marginally increased with DryMonth, with a reduced occurrence of dry conditions indicating relative hydrological habitat stability, which promotes community stability (Mykrä et al. 2011, Crabot et al. 2020). This increase was independent of changes in α diversity: temporal variability in community composition reflected turnover (i.e. taxa replacements) rather than nestedness (i.e. taxa gains/losses; Baselga 2010). The intermediate Res group drove these changes, its temporal β diversity increasing with the occurrence of drying more strongly at sites that rarely dry,
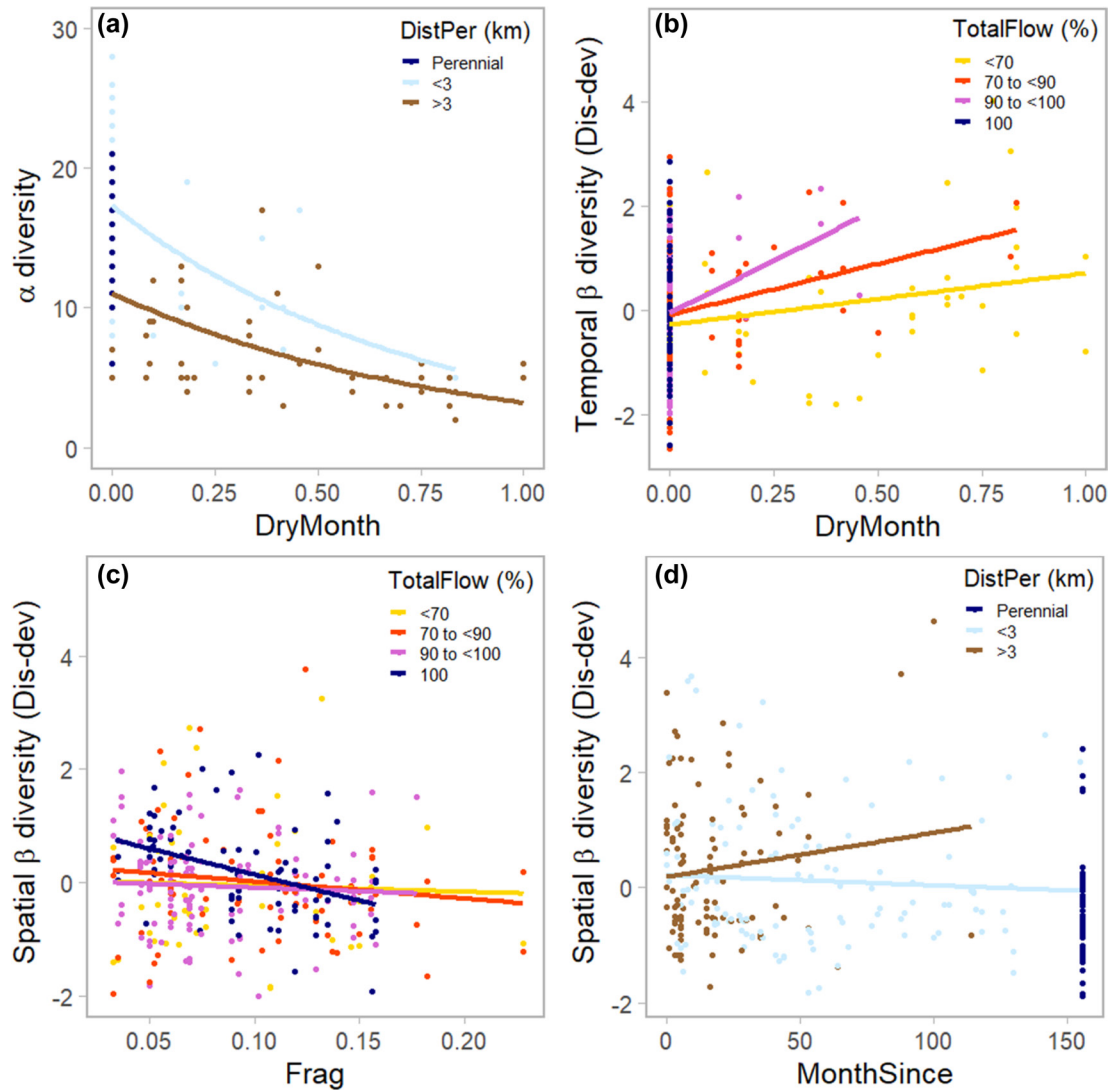
Figure 6. Relationships between the diversity of assemblages with contrasting resistance and/or resilience (Res) to drying and hydrological state metrics: interactions between (a) intermediate Res α diversity and DryMonth among sites with different DistPer, (b) intermediate Res temporal β diversity and DryMonth at sites with different TotalFlow, (c) low Res spatial β diversity and Frag at sites with different TotalFlow, and (d) high Res spatial β diversity and MonthSince at sites with different DistPer. Lines in (a) were fitted separately for each DistPer/TotalFlow group using a generalized linear model with a Poisson distribution, and in (a–c) using a linear model to visualize interactions. Metrics and abbreviations are described in the text.

which could be due to the replacement of lotic species (e.g. *Agapetus* sp., *Baetis rhodani* and *Hydropsyche angustipennis*) by lentic specialists (e.g. *Crangonyx pseudogracilis*, *Gyraulus albus* and *Planorbis* sp.). Stronger compositional changes may occur at such near-perennial sites if much of the community is replaced as drying intensity increases or if different taxa recolonize immediately after flow resumes (Leigh et al. 2019). However, at the most temporary sites, temporal β diversity changed less predictably, probably because the persistence and post-disturbance recovery of intermediate Res taxa was stochastic and variable (Sarremejane et al. 2017a).

The regional extent of flowing reaches (FlowRiv) also influenced temporal β diversity, with communities varying more among years as FlowRiv decreased. Temporal β diversity was thus driven by the catchment-wide extent of colonist sources (as FlowRiv) rather than their spatial organization (as Frag). Disturbances with larger spatial extents can decrease ecosystem stability by limiting dispersal from undisturbed habitats and hence preventing mass effects (Zelnik et al. 2018). The observed effects of FlowRiv may thus reflect changes in colonization processes from surrounding aquatic habitats that support stable communities.

Spatial β diversity reflects post-disturbance recovery

Our third hypothesis predicted that spatial β diversity would decline in response to both spatial and temporal increases in flow. As flowing conditions persist locally and spread

regionally, communities in different localities may converge to similar sets of lotic species, unless other environmental factors and/or connectivity override the filtering effect of continuous flow on community assembly (Sarremejane et al. 2018). Accordingly, spatial β diversity decreased as flowing durations (as MonthSince) increased, particularly at sites with high drying occurrences (as indicated by low TotalFlow), highlighting the rapid recovery of frequently disturbed communities. Extended flowing phases homogenize communities by offering a stable environment that facilitates among-site movements of taxa with both aquatic and aerial dispersal modes (Bogan and Boersma 2012, Heino et al. 2015). During such phases, even sites with lower flow permanence, which typically had lower α diversity, may have been colonized by a comparable set of competitive lotic taxa – including low and intermediate Res group members. For example, *Gammarus* amphipods and *Baetis* mayfly juveniles became increasingly widespread across non-perennial sites in the years following flow resumption (Wood and Armitage 2004, Sarremejane et al. 2019).

The hypothesized increase in spatial β diversity with increasing regional-scale hydrological habitat heterogeneity (as Frag) was not observed (H3). Instead, higher Frag was associated with lower variability among low Res assemblages, especially at sites with greater flow permanence. Hydrological fragmentation may have homogenized communities at the most perennial sites, as similar reduced subsets of lotic species such as *Gammarus* persisted in the remaining flowing habitats (Leigh and Datry 2017).

The spatial β diversity of highly resistant and/or resilient assemblages increased with DistPer. Environmental filters increase in influence with spatial isolation, creating site-specific communities of taxa sorted according to local habitat conditions, and protecting them from the greater dispersal that enables mass effects to homogenize better connected sites (Heino et al. 2015, Sarremejane et al. 2017b). In addition, the ability of highly mobile taxa to track favourable environmental conditions despite isolation (Heino 2013) may have grown stronger over time after flow resumed, increasing compositional distinctness at sites farther from perennial reaches. Alternatively, priority effects may have caused communities to assemble along different trajectories at isolated sites after stochastic initial colonization (Vanschoenwinkel et al. 2013, Daniel et al. 2019), with their distinctness growing stronger over time after flow resumed, as suggested by an interaction between DistPer and MonthSince.

Gamma diversity remains stable despite hydrological variability

Gamma diversity did not respond to increasing disturbance extent, indicating that, even during droughts, sufficient aquatic habitat persisted in our cool, humid study systems to prevent regional extinctions. Regional-scale habitat heterogeneity may have supported a stable regional species pool across years by providing habitats for all taxa (Ward et al. 1999). In our study area, dry and ponded conditions were most extensive during 2006–2007 and 2011–2012, when drought likely created network-scale mosaics of contrasting habitat patches (Datry et al. 2014a, England et al. 2019). Such increases in environmental heterogeneity with increasing disturbance extent may have promoted the colonization of newly created habitats by lentic or semi-aquatic specialists. Although community composition and diversity may change locally with disturbance intensity, regionally asynchronous responses and higher β diversity may have maintained γ diversity (Starzomski and Srivastava 2007, Wilcox et al. 2017).

Conclusion

We observed α, spatial β and temporal β diversity responses driven by regional factors, evidencing the fundamental role of source–sink dynamics in driving community recovery after disturbance. We found contrasting diversity patterns for groups with different resistance and/or resilience capacities, highlighting that taxa with different functional attributes may have contrasting responses to disturbance and connectivity. For the intermediate Res group, α diversity changed along disturbance and connectivity gradients, indicating that patterns were driven by both environmental sorting and dispersal processes. In contrast, the low Res group experienced decreases in both α diversity in response to local factors and in spatial β diversity in response to increasing fragmentation, suggesting environmental filtering as the main driver of this assemblage. Again in contrast, the diversity responses of high Res taxa reflected their capacity to override mass effects and track favourable environmental conditions even at isolated sites. Our findings thus suggest that local-scale whole-community studies may only partially represent the role of disturbance in structuring biodiversity, and that responses may depend on regional factors as well as site-specific disturbance severity, connectivity and taxon-specific resistance and/or resilience capacities. As disturbances become increasingly common in our changing climate, we highlight that community recovery may be compromised where disturbance frequency and/or extent increase, particularly in fragmented landscapes.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.jm63xsj83> (Sarremejane et al. 2020b).

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