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Research

Drought intensification drives turnover of structure and function in stream invertebrate communities

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Climatic extremes are becoming more frequent and intense across much of the globe, potentially transforming the biodiversity and functioning of affected ecosystems. In freshwaters, hydrological extremes such as drought can regulate beta diversity, acting as powerful environmental filters to dictate the complement of species and functional traits found at local and landscape scales. New methods that enable beta diversity and its functional equivalent to be partitioned into turnover (replacement of species/functions) and nestedness-resultant (gain/loss of species/functions) components may offer novel insights into the parallel impacts of drought on ecosystem structure and function. Using a series of artificial channels (mesocosms) designed to mimic perennial headwater streams, we experimentally manipulated streamflows to simulate a gradient of drought intensity. We then modelled taxonomic and functional turnover and nestedness of macroinvertebrate communities along this gradient, validating direct gradient approaches (bootstrapping, Mantel tests) against null models of nestedness. Drought intensification produced significant environmental distance decay trends (i.e. communities became increasingly taxonomically and functionally dissimilar the more differentially disturbed by drought they were). Taxonomic distance decay was primarily driven by turnover, while the functional trend reflected a combination of richness differences and turnover at different points along the gradient. Taxonomic and functional distance decay slopes were not significantly different, implying that communities were functionally vulnerable to drying. The increased frequency and intensity of droughts predicted under most climate change scenarios could thus profoundly modify not only the structure of running water invertebrate communities, but also the ecosystem functions they underpin.

Keywords: stream drought, disturbance gradient, beta diversity, functional beta diversity, turnover, nestedness



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Introduction

Current rates of global biodiversity loss are predicted to accelerate as climate change and human disturbances intensify (Bellard et al. 2012, Pimm et al. 2014, Johnson et al. 2017). Empirical biodiversity trends are nonetheless highly complex, and reports of a global biodiversity crisis are seemingly contradictory to observations of stable diversity at more local scales (McGill et al. 2015, Socolar et al. 2016). Reconciling these scale-dependent inconsistencies demands an understanding of beta diversity, commonly defined as the dissimilarity in species' identities between two communities (Anderson et al. 2011). This inter-community dissimilarity unites local species richness (alpha diversity) with the regional species pool (gamma diversity), thus bridging the gap between the scale at which biodiversity data are typically available and that at which conservation decisions are made (Socolar et al. 2016). Despite this, beta diversity remains an understudied facet of biodiversity in the context of environmental disturbance (Hawkins et al. 2015, McGill et al. 2015).

Beta diversity can be partitioned into two components: 1) turnover, which occurs when species are replaced between communities; and 2) nestedness-resultant dissimilarity (hereafter NRD, Table 1), where species loss generates a depauperate community that is a subset of the assemblage

at a richer site (Baselga 2010). NRD is thus used as a surrogate for 'true' nestedness, which is a related but different concept. In the context of our study, the latter describes the ordered composition of presence-absence matrices involving the packing of the matrix into a series of proper subsets (Matthews et al. 2015a), whereas NRD measures the dissimilarity between communities that arises from nestedness (i.e. richness differences, Table 1, Baselga 2012). Recognising the contrasting implications of turnover and NRD for regional diversity patterns, macroecologists are increasingly partitioning beta diversity into its constituent components (Baselga 2010, Bishop et al. 2015). Envisioning a gradient of environmental disturbance, a high degree of turnover between communities would indicate the presence of species unique to disturbed and undisturbed sites. In the absence of stochastic processes generating turnover through random extinctions and/or colonisations (Stegen et al. 2013, Baselga et al. 2015), these species should be specialists adapted to specific parts of the gradient. Conversely, strong NRD would reflect the progressive erosion of species richness with increasing disturbance due to environmental filtering, and the occupation of most or all of the gradient by a number of disturbance-tolerant generalists (Gutiérrez-Cánovas et al. 2013).

Beyond changes to species identity, biodiversity loss can weaken the functional integrity of ecosystems and disrupt

Table 1. Glossary of terms used in the paper.

| Term | Description |
|------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Beta diversity | The dissimilarity in species' identities between sites (Anderson et al. 2011). Can be measured using the Sorensen dissimilarity index (β_{sor} ; Baselga 2010) |
| Turnover | The replacement of some species by others between sites. Can be measured using the Simpson dissimilarity index (β_{sim} ; Baselga 2010) |
| True nestedness | The orderly aggregation of species assemblages that involves a significant propensity for the presence-absence matrix to be packed into a series of proper subsets (Almeida-Neto et al. 2008). Can be measured using the NODF metric (described below) |
| Nestedness-resultant dissimilarity (NRD) | The component of beta diversity attributable to richness differences (Baselga 2012). Can be measured as the difference between β_{sor} and β_{sim} (Baselga 2010) |
| Functional beta diversity | The dissimilarity in functional strategies between sites (Villéger et al. 2013) |
| Functional turnover | The replacement of some functional strategies by others between sites (Villéger et al. 2013) |
| True functional nestedness | A variation on true nestedness that accounts for similarities between species' functional strategies (Melo et al. 2014) |
| Functional NRD | The component of functional beta diversity attributable to functional richness differences (Villéger et al. 2013) |
| Functional redundancy | Where multiple species fulfil similar functional roles, affording communities insurance against species loss (Ricotta et al. 2016) |
| Functional vulnerability | The potential for ecosystem functioning to be eroded by species loss (Mouillot et al. 2014) |
| Functional distinctiveness | A measure of how dissimilar a species' traits are from those of others in the community (Violle et al. 2017) |
| Functional rarity | A measure of ecological rarity incorporating both taxonomic scarcity and functional distinctiveness (Violle et al. 2017) |
| Disturbance predictability | The degree to which a disturbance can be anticipated based on its periodicity and/or correlation with environmental cues (Lytle and Poff 2004) |
| NODF | A nestedness index based on the twin properties of standardized differences in (presence-absence) matrix row and column fills and paired overlap (Almeida-Neto et al. 2008) |
| treeNODF | An extension of the NODF index in which the functional relationships between species, represented by a tree-like object, are taken into account (Melo et al. 2014) |
| Z-score | A method for standardising observed metric values. Calculated using: $(Obs - \mu) / sd$, where Obs is the observed metric value, μ is the mean metric value derived from a null model analysis, and sd is the standard deviation |

the services they provide (Naeem et al. 2012, Lefcheck et al. 2015, Pecl et al. 2017). Traditional taxonomic measures (e.g. richness, abundance) typically provide limited insight into the impacts of disturbance on ecosystem functioning (Mouillot et al. 2013a), which can be better predicted using trait-based estimates of functional diversity (Petchey and Gaston 2006, Gagic et al. 2015, Matthews et al. 2015b). Just as taxonomic beta diversity can be partitioned into two components, so functional beta diversity (the dissimilarity in functional strategies between two communities) can be disaggregated into turnover and NRD components (Table 1, Villéger et al. 2013). High functional turnover along a disturbance gradient would reflect the introduction of novel trait combinations at disturbed sites (Boersma et al. 2016). By contrast, the progressive removal of extreme trait values by environmental filtering would create high true functional nestedness, as disturbed sites would contain only a subset of the functional strategies of undisturbed communities (Villéger et al. 2013). This would also produce high functional NRD, owing to significant differences in functional richness (i.e. the number of traits possessed) between intact and disturbed communities. Analyses of functional dissimilarities can thus reveal the robustness of critical ecosystem functions in the face of species turnover and loss, a property known as functional redundancy (Table 1, Ricotta et al. 2016). Nonetheless, relatively few studies of beta diversity extend their scope beyond taxonomic elements.

In rivers and streams, water availability exerts a primary control on ecosystem structure and function (Datry et al. 2014), with drying disturbances representing a key environmental filter in these systems (Ledger et al. 2012, Leigh and Datry 2017, Woodward et al. 2016). The disruption of natural flow regimes by climate change and human appropriation of water is transforming patterns of running water biodiversity (Poff and Zimmerman 2010, Vörösmarty et al. 2010, Collen et al. 2014, Castello and Macedo 2016), threatening to disrupt the functioning of entire communities (Ledger et al. 2013, Lu et al. 2016, Tonkin et al. 2018). Most insight into the impact of drying on beta diversity comes from studies of intermittence gradients in temporary streams. These have generally reported high true nestedness, as reaches drying for longer periods harbour subsets of the communities in reaches with longer flowing phases (Arcott et al. 2010, Datry 2012). By contrast, temporary streams characterised by exceptionally long dry periods may feature a large number of taxa exclusive to intermittent reaches (Bogan et al. 2013). Under these more extreme conditions, greater requirement for specialist adaptations to drying and greater isolation of disturbed habitats from recolonist sources may drive high species turnover between perennial and intermittent reaches (Datry et al. 2016, Rolls et al. 2016). During the long drying phase, turnover between sites may increase over time as conditions in different reaches increasingly diverge (Piano et al. 2017). However, patterns of community functioning are less well described (Ledger et al. 2013), and we know of no studies that have systematically decomposed both taxonomic and

functional beta diversity trends along a hydrologic disturbance gradient.

We analysed patterns of beta diversity and true nestedness (and their functional equivalents) of macroinvertebrate communities along a gradient of drought intensity. This ranged from flowing control conditions, through isolated pools to drying streambeds, analogous to the reach-scale transitions between perennial flow, fragmentation and complete drying characteristic of temporary streams (Datry et al. 2016), and mimicking those observed in perennial chalk streams during suprasedonal drought (Westwood et al. 2006, Kendon et al. 2013). We simulated the drought gradient using mesocosms, with the aim of exposing biota to levels of environmental stress largely absent from current disturbance regimes but forecast in a warmer climate (Ledger et al. 2012, Kayler et al. 2015). We predicted an environmental distance decay of taxonomic similarity with drought (i.e. treatments with more dissimilar drought intensities have more dissimilar communities, increasing pairwise beta diversity). In light of the turnover patterns observed in temporary streams, we anticipated that this increase in beta diversity would be driven primarily by species turnover, given the duration (suprasedonal) of our experiment and the severe drought conditions in some of the treatments. We thus predicted that the overall set of mesocosm communities would exhibit low NRD and true nestedness. We expected a weaker trend in functional beta diversity, given that invertebrate community responses to drying are often buffered by high functional redundancy (Bêche and Stutzner 2009, Boersma et al. 2014, Schriever et al. 2015). Finally, we predicted NRD to be a more important contributor to functional beta diversity than turnover, as changes in functional richness following stream drying have previously been reported even where species turnover has been prevalent (Boersma et al. 2016).

Material and methods

Study site and experimental design

The experiment was conducted over 18 months (February 2013 – August 2014) at an outdoor mesocosm facility next to a mesotrophic chalk stream (Candover Brook) in the River Itchen catchment, Hampshire, UK (51°10'21"N, 1°18'70"W). Twenty-one stainless steel mesocosms, analogous to perennial, spring-fed headwater streams (each 15 m length × 0.5 m width × 0.5 m depth), were fed to capacity with borehole water, which drained from the channels over outlet weirs. Previous studies have shown that once-through, outdoor mesocosms can adequately replicate the physical, chemical and biological complexity of natural lowland headwater streams (Ledger et al. 2009, Brown et al. 2011). Our mesocosms had clean gravel beds which mimicked the riffle-pool morphologies of lowland chalk streams (three riffles and four pools per channel, each 2 m length). We seeded each channel with macrophytes (predominantly *Ranunculus*

penicillatus), algae and macroinvertebrates, collected from surrounding perennial stream reaches and allowed to establish for six months before drought treatments were implemented. Specifically, benthic algae and microbes were introduced by transferring biofilm-coated cobbles from the adjacent chalk stream. Macrophytes were also transferred from the stream, comprising seven small plants rooted in the gravel substratum of each mesocosm. Macroinvertebrates were kick sampled from benthic habitats in local streams using a pond net (300 μm mesh) and immediately transferred to the mesocosms (10 \times 5 min kick samples per mesocosm).

In August 2013 we adjusted flows into the mesocosms to simulate a range of hydrological, physical and chemical conditions, with treatments assigned to channels on a random basis (Supplementary material Appendix 1 Fig. A1). These conditions described a gradient of declining wetted area (6.5–0.25 m^2), water volume (1.9–0.001 m^3) and flow (2.2–0.001 l s^{-1}) and increasing water temperature variability (6–40°C annual temperature range). Groundwater-dominated chalk stream reaches are characterised by high year-round baseflows (Sear et al. 1999, Garner et al. 2015), but suprasedonal droughts can occur in response to severe dry weather and over-abstraction of groundwater to meet high domestic and agricultural demand (O'Neill and Hughes 2014). For instance, extremely low groundwater levels in southern England in 1989–1992 and 2010–2012 reduced some reaches to isolated pools or dry streambeds for protracted periods (Westwood et al. 2006, Kendon et al. 2013, Folland et al. 2015). Our experiment aimed to mimic these extreme, patchy conditions, which are likely to become increasingly frequent given the reductions in groundwater recharge forecast under climate change (Jackson et al. 2011).

Data collection and processing

After one year (August 2014) we collected four replicate benthic macroinvertebrate surber samples (0.0225 m^2 , mesh size 300 μm) per channel (i.e. one sample per pool). Invertebrates were separated from detritus and identified to the lowest practical taxonomic level (typically species or genus; Supplementary material Appendix 2 Table A1). Data from each of the four pools were combined to describe the overall community of each channel. We recorded water temperature in the fourth pool of each mesocosm at 15 min intervals throughout the experiment (August 2013–August 2014) using Tinytag loggers. Dissolved oxygen (DO) measurements were taken every five min over one 24 h period each month using MiniDOT loggers suspended midway through the water column.

Forty-nine functional traits spanning ten grouping features (sensu Schmera et al. 2015) were assigned at the genus level (Supplementary material Appendix 3 Table A2) using fuzzy-coded trait data published by Tachet et al. (2010) and Serra et al. (2016) for European aquatic invertebrates. In accordance with recommended guidance for calculating functional diversity (Verberk et al. 2013, Schmera et al. 2017), we only considered biological (e.g. body size, lifespan,

respiration mode) and not ecological (i.e. habitat preferences) traits in our analyses. Four taxa with no trait data (*Bagous*, Cecidomyiidae, Cybaeidae and Hydrachnidae) were omitted from all analyses. These taxa collectively accounted for 0.3% of all taxa by abundance. However, taxonomically scarce taxa per se were not excluded, as rare species are disproportionately functionally important in many ecosystems (Mouillot et al. 2013b, Leitão et al. 2016, Toussaint et al. 2016). Since trait values were fuzzy-coded, they were standardised to a range of 0–1 to ensure each grouping feature (e.g. body size, voltinism, diet) was equally weighted.

Statistical analysis

Abiotic variables

We conducted a principal component analysis (PCA, explained variance of first axis = 93.8%) on flow, water volume, wetted area and temperature data, and interpreted the axis one scores as a compound index of drought intensity (DI). These scores were rescaled to vary from 0 (no drought stress) to 1 (severe dewatering). The temperature data described the maximum temperature range recorded during the experiment, as climatic variability may have more profound impacts on physiology and ecology than average conditions (Vázquez et al. 2017).

Channels with low DI (< 0.2) remained longitudinally connected, with minimal loss of wetted area, relatively high flow (0.7–2.3 l s^{-1}), small temperature variations (annual range $< 7.5^\circ\text{C}$) and well oxygenated water (mean diel oxygen minimum $> 9.5 \text{ mg l}^{-1}$; Supplementary material Appendix 1 Fig. A2). Moderate intensity droughts ($0.2 < \text{DI} < 0.7$) fragmented channels into isolated pools (mean 48% loss of wetted area), decreasing flow ($< 0.4 \text{ l s}^{-1}$) and triggering larger temperature fluctuations (annual range 5–29°C, mean 15.7°C) and lower oxygen minima (4.8–10.1 mg l^{-1} , mean 7.3 mg l^{-1}). High intensity droughts ($\text{DI} > 0.7$) were associated with extensive streambed dewatering ($> 95\%$ loss of wetted area), extreme temperature instability (annual range $> 38^\circ\text{C}$) and oxygen minima approaching hypoxia (2.4–5.1 mg l^{-1}).

Calculating functional dissimilarity between taxa

To calculate the functional dissimilarity between taxa, we created a distance matrix from the trait data. As our trait values were fuzzy coded we used Gower's distance and the method outlined in Pavoine et al. (2009). We ran a principal coordinates analysis (PCoA) on this distance matrix to condense the trait data into four independent, synthetic traits (represented by the first four PCoA axes). This number was chosen as four dimensions offer a suitable compromise between functional space quality, parsimony and interpretability (Maire et al. 2015), and here explained 47% of the total variance.

Beta diversity, true nestedness and their functional equivalents

Taxonomic and functional beta diversity were calculated and separated into turnover and NRD components using the parallel partitioning methods developed by Baselga (2010) and

Villéger et al. (2013). Under this framework total pairwise beta diversity is calculated as the Sorensen dissimilarity index (β_{sor}), which accounts for compositional differences between pairs of sites (here mesocosms) caused by both turnover and richness differences. The Simpson dissimilarity index (β_{sim}) is unaffected by absolute richness differences between site pairs, and is thus used as a measure of turnover. The resultant difference ($\beta_{sor} - \beta_{sim}$) yields an estimate of nestedness (NRD; β_{nes}). These metrics were calculated using presence–absence data.

For each mesocosm, the taxa present were plotted in functional space according to their synthetic trait values, and the vertices of a convex hull that described the functional composition of the community were mapped (Cornwell et al. 2006). The degree of convergence between two hulls thus determines the pairwise beta diversity of their communities (Villéger et al. 2013). High beta diversity may result from two hulls occupying distinct parts of the functional space, thus creating high functional turnover. Alternatively, functional beta diversity may be high even if two hulls overlap completely, if a large difference in their respective volumes (i.e. the functional richness of their communities (Villéger et al. 2008)) creates high functional NRD.

As NRD is not a direct measure of true nestedness (Baselga 2012), we validated NRD patterns against the true nestedness of the set of mesocosms, which was calculated using the NODF metric (Table 1, Almeida-Neto et al. 2008) and the maximally packed matrix. To determine if the observed NODF value was significantly different from random expectation, we followed Matthews et al. (2015a) and used a null model procedure in combination with the ‘quasi-swap’ algorithm and 1000 iterations. The ‘quasi-swap’ algorithm randomises the presence–absence values within the matrix whilst keeping marginal totals constant. A Z-score was then calculated using the formula in Matthews et al. (2015a). True functional nestedness was calculated using the treeNODF (by rows) metric (Table 1, Melo et al. 2014) and the procedure in Matthews et al. (2015b). The significance of the observed treeNODF value was determined using a permutation null model (1000 permutations; Matthews et al. 2015b).

Distance decay analysis

We plotted taxonomic and functional β_{sor} , β_{sim} and β_{nes} as a function of the distance along the DI gradient between pairs of mesocosms (21 channels yielding 210 pairwise comparisons for each dissimilarity index). Our pairwise observations violated the assumption of independence required by traditional regression analyses, so we tested for the significance of distance decay trends using Pearson correlations computed by Mantel tests (Baselga 2010). We also tested for significant differences in intercepts and slopes among the dissimilarity indices using a bootstrapping procedure with 1000 resamples. This estimated the significance of an intercept or slope being larger for one index than another (e.g. taxonomic β_{sor} versus functional β_{sor}) by computing

the probability of obtaining the alternative outcome by chance (Baselga 2010).

Analysing trait space occupancy along the drought gradient

Due to the complexity of the trait space (four dimensions) and the significant overlap in functional composition between individual mesocosm communities, we were unable to visually assess changes in trait space occupancy across all channels. We therefore instead pooled the treatments with low DI ($DI < 0.2$) and the treatments with high DI ($DI > 0.7$), and then calculated and plotted the convex hull around all of the taxa within each set of treatments (i.e. low and high DI). That is, we plotted all the taxa present in low DI treatments in trait space and constructed the convex hull, and then did the same for the taxa present in high DI treatments, plotting both in the same space. As we had four synthetic traits (PCoA axes), we did this separately for each unique combination of two traits (i.e. six plots in total). We were then able to assess areas of trait space that were lost or gained due to drought, and used Spearman correlations to relate these to real biological traits.

All analyses were conducted in R (ver. 3.2.4, <www.r-project.org>) using the packages ‘ade4’ (Dray et al. 2017), ‘betapart’ (Baselga et al. 2017), ‘vegan’ (Oksanen et al. 2017), ‘boot’ (Canty and Ripley 2017), ‘picante’ (Kembel et al. 2016) and ‘CommEcol’ (Melo 2016).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.cc8834s> (Aspin et al. 2018).

Results

Community composition

Invertebrate assemblages in the mesocosms were characterised by a high diversity of Diptera (particularly Chironomidae) and Trichoptera which, together with low Plecoptera richness and the presence of several species of Gastropoda, Tricladida, Hirudinea and Coleoptera, indicated close resemblance to typical perennial chalk stream communities (Berrie and Wright 1984, Wright 1984, Ledger et al. 2009, White et al. 2018). There was no clear trend in alpha diversity across the drought gradient, although the most species-poor communities were found at high DI (Supplementary material Appendix 2 Fig. A3a). As drought intensified there was a progressive taxonomic shift from Ephemeroptera, Plecoptera and Trichoptera (EPT) species towards a greater dominance of non-chironomid Diptera (Supplementary material Appendix 2 Fig. A3b–d).

Distance decay analysis: taxonomic dissimilarity

Taxonomic beta diversity (β_{sor}) increased significantly with distance between treatments on the drought gradient

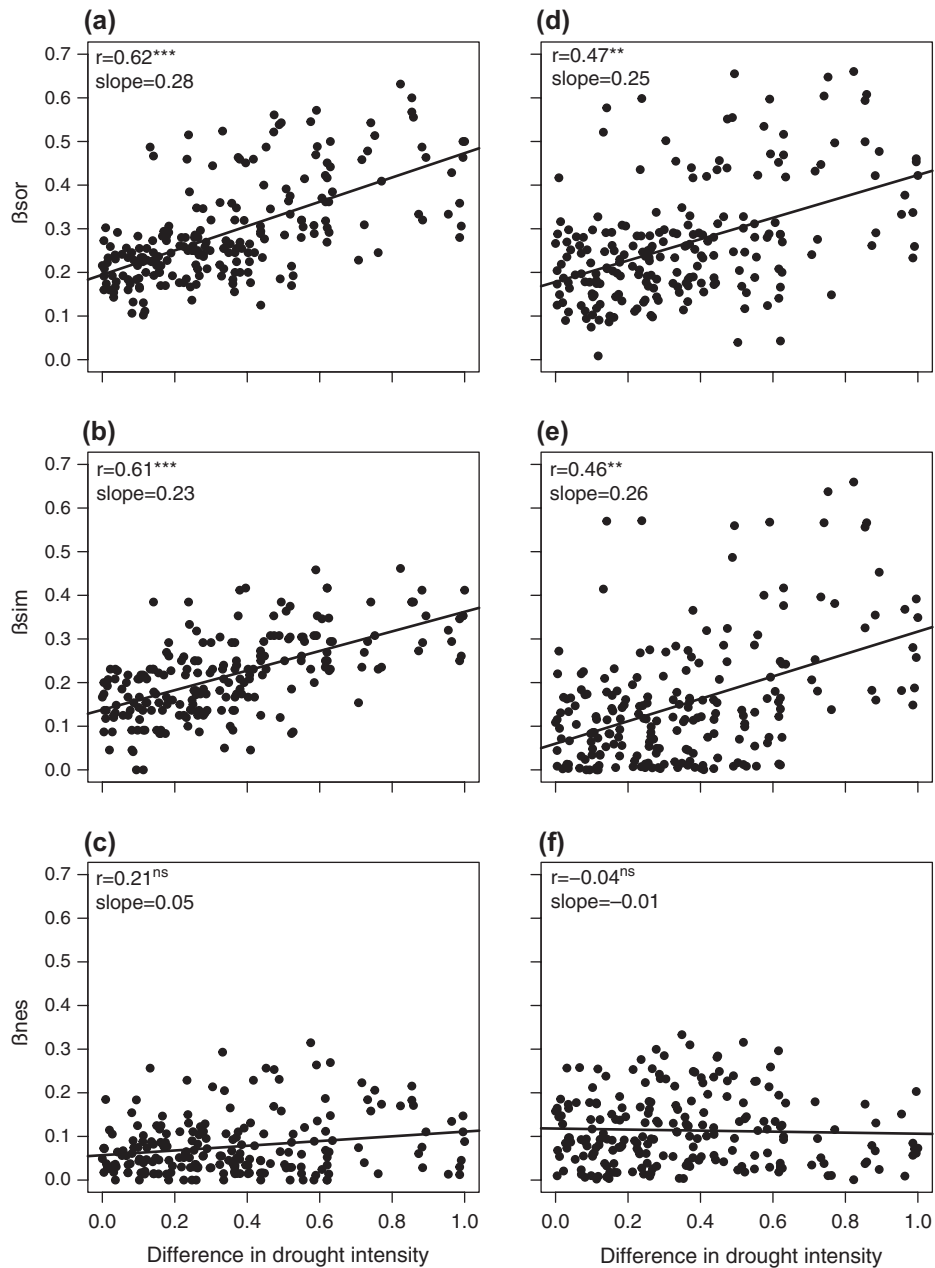


Figure 1. Pairwise dissimilarities in taxonomic (a–c) and functional (d–f) composition of invertebrate communities differentially disturbed by drought. Total beta diversity (β_{sor}) is shown in (a) and (d), turnover (β_{sim}) in (b) and (e) and nestedness-resultant dissimilarity (β_{nes}) in (c) and (f). Pairwise dissimilarities are plotted as a function of the difference in the drought intensity (DI) value between treatments. Pearson (r) correlations and associated p-values were produced by Mantel tests. Significance levels are as follows: $p < 0.001^{***}$; $p < 0.01^{**}$; $p < 0.05^*$; $p > 0.05$ ns.

(Fig. 1a). This was predominantly driven by the turnover component (β_{sim}), which also exhibited a significantly increasing trend (Fig. 1b); whereas there was no significant trend in the NRD component (β_{nes} ; Fig. 1c). Bootstrapping confirmed that taxonomic turnover was greater than NRD along the entire drought gradient, with a significantly higher intercept (0.14 versus 0.06, $p < 0.001$) and slope (0.23 versus 0.05, $p < 0.001$). Analysis of the presence–absence matrix indicated that true nestedness (NODF = 63.30) was

significantly lower than expected by chance (Z-score = -4.23, $p < 0.001$).

Distance decay analysis: functional dissimilarity

A significant distance decay trend was apparent for total functional beta diversity (Fig. 1d), mirroring the trend in taxonomic beta diversity, with no significant difference between slopes (taxonomic β_{sor} slope = 0.28; functional

β sor slope = 0.25, $p = 0.224$). As with taxonomic beta diversity, the functional turnover component increased significantly with DI distance between treatments (Fig. 1e), and again there was no trend in the functional NRD component (Fig. 1f). However, functional turnover was not consistently greater than functional NRD, and instead their relative contributions varied along the drought gradient. At low to moderate distances, functional NRD was typically greater, with a significantly higher intercept than functional turnover (0.12 versus 0.06, $p < 0.001$). As distances between treatments increased, functional turnover became more important, as shown by its significantly higher slope (0.26 versus -0.01 , $p < 0.001$). True functional nestedness (treeNODF = 46.32) was not significantly different than expected by chance (Z -score = 0.73, $p = 0.257$).

Changes in trait space occupancy

The convex hulls of pooled low DI and pooled high DI treatments occupied broadly similar total volumes of trait space (Fig. 2), reflecting the small differences in functional richness (i.e. functional NRD) between low and high DI treatments. Functional dissimilarities were nonetheless evident between the two treatment groups, which both occupied exclusive areas of trait space, signifying a distinct turnover of functional strategies as drought intensified. For example, PCoA axis 4 was negatively correlated with tegument respiration (Spearman correlation coefficient -0.67 ; Supplementary material Appendix 3 Table A3) and substrate attachment (-0.49), and the loss of low axis 4 scores at high DI (Fig. 2 b, d, e) thus represented a decreasing prevalence of these two traits within the community. Specialist predators were also lost as drought intensified, as communities no longer occupied low axis 3 plus intermediate axis 2 scores (Fig. 2f): a macroinvertebrate diet was negatively correlated with axis 3 (-0.74) and was uncorrelated with axis 2.

As DI increased, these traits were replaced by novel functional strategies. For instance, high DI communities occupied new areas of trait space at low axis 3 plus high axis 4 scores (Fig. 2b). This reflected the colonisation of drought-disturbed habitats by active aerial dispersers such as *Culicoides* and *Palpomyia* (Ceratopogonidae): active aerial dispersal was negatively correlated with PCoA axis 3 (-0.22) and positively correlated with axis 4 (0.45). High DI communities also exhibited strategies conferring resistance to drying, involving trait combinations such as spiracle respiration and diapause. These traits were characteristic of taxa such as *Oxycera* (Stratiomyidae), which plotted at low axis 2 plus intermediate axis 1 scores (Fig. 2a): axis 2 was negatively associated with spiracle respiration (-0.72) and diapause (-0.39), while neither trait was strongly correlated with axis 1. Finally, axis 3 was positively correlated with a microphyte diet (0.67) and small body size (0.45), implying that drought led to an increase in the proportion of small grazers in the community (gain of high axis 3 scores; Fig. 2 b, c, f).

Discussion

Understanding the mechanisms that drive taxonomic and functional dissimilarities between unstressed and stressed communities is critical for understanding the ecological impacts of environmental disturbance (Hawkins et al. 2015). Nonetheless, few studies have systematically partitioned both taxonomic and functional beta diversity along a disturbance gradient, and we know of none that have done so in the context of stream drought. Our study found strong distance decay trends, as taxonomic and functional dissimilarity of invertebrate communities increased with the extent of the contrast in drought intensity. These patterns were driven by a continuous turnover of species along the drought gradient, and a combination of NRD and turnover of functional strategies.

In line with our predictions, turnover was the dominant component of taxonomic beta diversity, with NRD low along the entire gradient and true nestedness significantly lower than expected by chance (note that the raw NODF metric value should not be directly interpreted as it is influenced by properties such as matrix fill, Almeida-Neto et al. 2008). One explanation of these patterns is that communities subjected to moderate and high intensity droughts comprised unique assemblages of drought-specialists, rather than impoverished subsets of intact communities. Turnover appeared to be largely driven by the appearance of specialist Diptera, notably Psychodidae, Ceratopogonidae and Stratiomyidae, at moderate and/or high drought intensity. Our findings therefore differ from biodiversity patterns normally observed in temporary streams, where true nestedness is high (Arscott et al. 2010, Datry 2012) and NRD is a significant component of beta diversity along intermittence gradients (Corti and Datry 2016). In temporary streams, dispersal processes are often a strong driver of metacommunity structure, particularly during the flowing phase when habitat connectivity is typically high (Datry et al. 2016, 2017). During suprasedonal drought, harsher environmental filters (drying severity and duration) may override dispersal processes to generate high turnover among reaches (Bogan et al. 2013).

The predictability and frequency of drying disturbances may also have a significant impact on beta diversity patterns. In temporary streams, the drying phase is usually predictable (Table 1), with fragmentation and streambed drying intrinsic features of the natural flow regime. Coping mechanisms should thus be prevalent within the local species pool (Rolls et al. 2016, Stubbington et al. 2017) and may include life cycle or behavioural adaptations with relatively low fitness costs (Lytle and Poff 2004), enabling generalists to persist across a gradient of intermittency. Suprasedonal droughts, as simulated here, are extreme and unpredictable (Lake 2003), filtering out maladapted species to create niche space for drought resistant colonists unable to compete for resources under normal conditions (Fig. 3a–b, d–e). Furthermore, the proximity of our mesocosms to one another (20–80 cm between channels) suggests that suprasedonal drought may

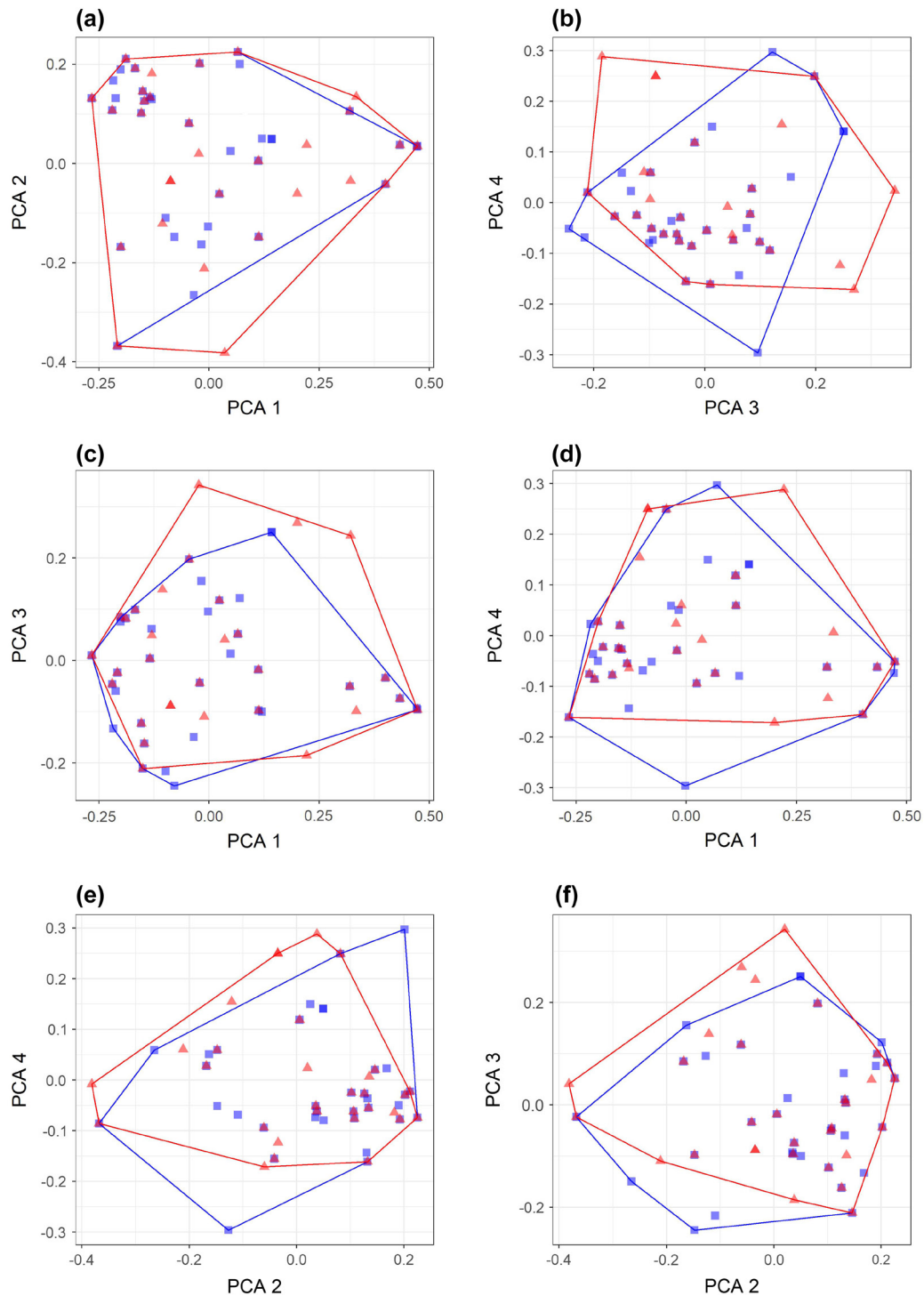


Figure 2. Differences in trait space occupancy between the communities of low intensity (blue) and high intensity (red) drought treatments. Trait space was generated using a principal coordinates analysis (PCoA) of four synthetic traits, based on dissimilarities between the fuzzy-coded trait profiles of macroinvertebrates. To allow changes in trait space occupancy to be assessed visually, the four dimensional trait space was projected onto two dimensions for each unique combination of two synthetic traits (PCoA axes). Taxa present at either low (blue rectangles) or high (red triangles) drought intensity were then plotted according to their synthetic trait values. Finally, convex hulls were fitted around these points using the same colours to describe the functional composition of the communities of low (blue) and high (red) drought intensity.

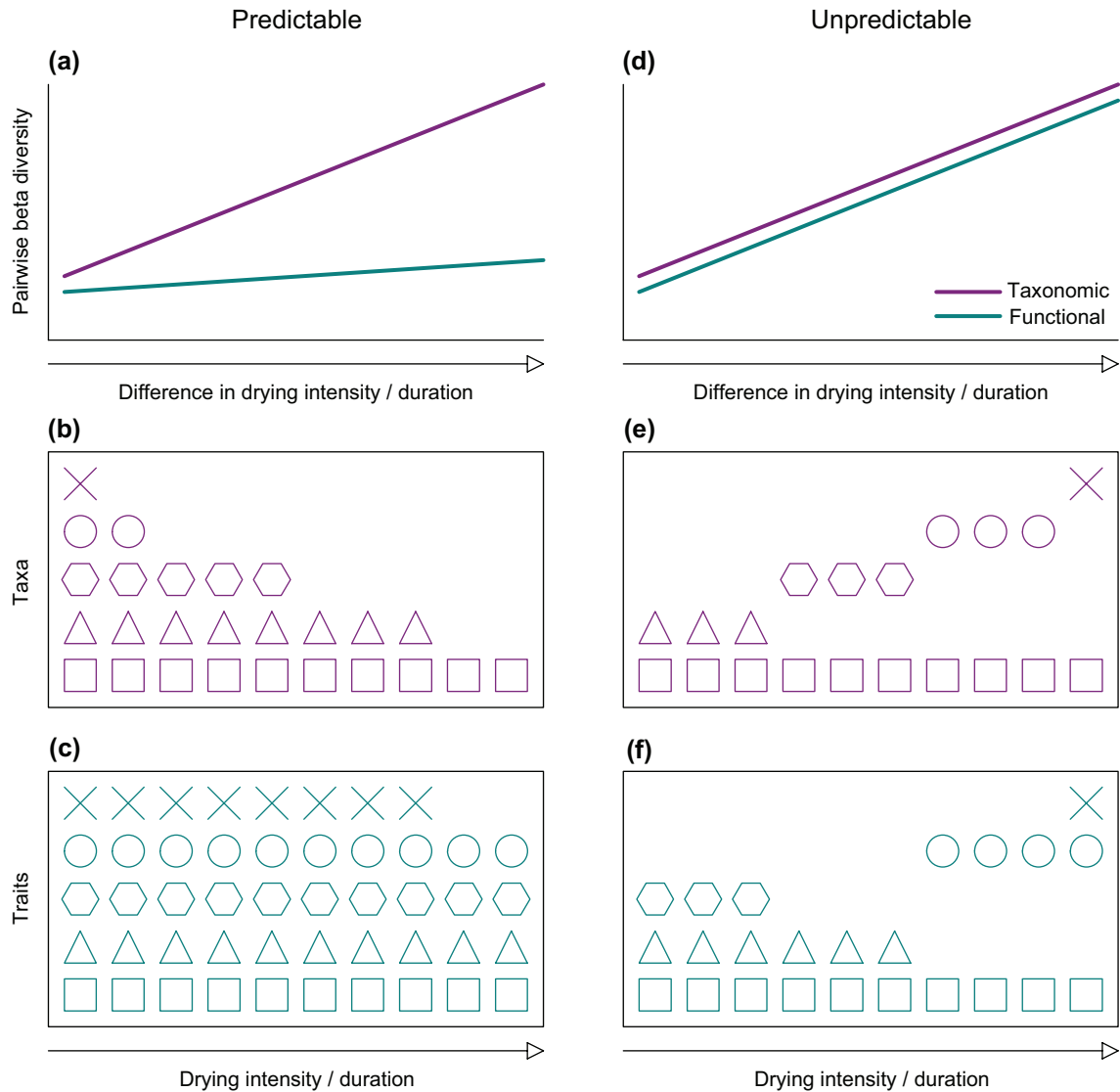


Figure 3. Conceptual differences in beta diversity patterns produced by predictable (a–c) and unpredictable (d–f) drying disturbances, along a gradient of intensity/duration. In (b) and (e) purple shapes denote different taxa and in (c) and (f) green shapes denote different traits recorded along the gradient. For both types of disturbance, communities become increasingly taxonomically dissimilar the more differentially disturbed they are (i.e. taxonomic beta diversity increases; (a), (d)). During predictable disturbances, this is driven by progressive species loss, resulting in nested patterns (b). Unpredictable disturbances produce greater species turnover (e), reflecting colonisation by specialists with adaptations to drying that compromise their competitiveness at lower levels of disturbance. Communities subjected to predictable drying are buffered by high functional redundancy, suppressing functional beta diversity patterns (a) due to significant trait overlap (c). Communities exposed to unpredictable drying are more functionally vulnerable, producing stronger functional beta diversity trends (d), driven by nestedness of traits at moderate levels of disturbance and the appearance of novel strategies as drying further intensifies (f).

drive species turnover even where drought-disturbed habitats are close to perennial refuges (i.e. where the landscape for source–sink dynamics exists). The mesocosms mimicked headwater streams, where recolonisation from upstream refugia is not possible, and high species turnover might thus be expected during drought. Turnover may nonetheless also be prevalent in higher order streams where fragmentation of stream habitat severs in-channel dispersal pathways, and overland routes become the main connections to sources

of recolonists (Cañedo-Argüelles et al. 2015). In mesic systems, where adaptations to extreme drying and habitat fragmentation are low (Ledger et al. 2011), even short overland distances may exceed the dispersal abilities of most taxa.

Functional beta diversity trends closely mirrored taxonomic beta diversity, indicating that species replacement along the gradient was accompanied by changes in the occupied trait space. Supraseasonal drought in perennial streams may therefore have more profound impacts than seasonal

drying in temporary systems, where redundancy of ecological functions has often been reported (Boersma et al. 2014, Schriever et al. 2015, Vander Vorste et al. 2016). It is important to note that we did not find evidence that drought reduces functional diversity, but simply that it may eliminate some of the functional strategies displayed by undisturbed communities. For example, drought eradicated small caddisflies (Glossosomatidae and Hydroptilidae), stripping away trait combinations such as tegument respiration and substrate attachment that were not represented in the species that replaced them. The disappearance of taxa with a specialist macroinvertebrate diet, such as Empididae, triggered a further loss of functional space, indicating that trophic traits were likewise not redundant. The functional vulnerability of stream communities (Table 1) may therefore be high where drying is unpredictable (Fig. 3a, c, d, f). Given that the flow regimes of most rivers and many streams worldwide are artificially regulated, nullifying species' adaptations to natural extremes of flow (Lytle and Poff 2004, Tonkin et al. 2018), many communities may thus be functionally vulnerable to even relatively low intensity droughts. However, currently available trait data for aquatic macroinvertebrates, including those used here, are largely restricted to 'response traits' (sensu Schmera et al. 2017). Better knowledge of traits with direct links to ecosystem functions and services ('effect traits') will be needed to improve our understanding of the impacts of species turnover on ecosystem functioning.

Contrary to our expectations, NRD was not always the dominant driver of functional dissimilarity between treatments, as would be expected in cases where disturbed communities are functionally homogenised (i.e. lower functional richness), which has previously been reported following suprasedonal drought (Boersma et al. 2016). NRD was important at distinguishing between treatments with small differences in drought intensity, implying that some of the trait combinations displayed by slightly and moderately disturbed communities represented generalist strategies that were also viable under moderate and high intensity drought, respectively. For example, tegument respiration was prevalent at both low and moderate DI, and active aerial dispersal at both moderate and high DI. However, functional dissimilarities between communities subjected to low and high intensity droughts were driven by turnover. Severe levels of stress, namely drying of the streambed, thus appeared to demand specialist strategies (involving small body size, spiracle respiration and an ability to diapause) that were uncompetitive in the absence of disturbance (Fig. 3f).

The presence of specialists with novel functional profiles in drought-disturbed habitats has clear relevance to freshwater conservation. The turnover trends reported here contrast with typical patterns associated with human disturbances (e.g. heavy metal pollution, urbanisation). Adaptations to these stressors are not found in nature, thus giving rise to nested communities at disturbed sites that contain few, if any, endemic taxa (Gutiérrez-Cánovas et al. 2013). By comparison, a natural stress gradient (e.g. elevation or latitude) will have been present over evolutionary time,

enabling species to adapt to different parts of the gradient and producing a strong turnover of specialists. Our results suggest that a hybrid stressor such as suprasedonal drought, fundamentally natural but augmented by human influences (e.g. anthropogenic climate change, flow abstractions) may similarly create specialist niches worthy of conservation attention. The species that occupied these niches, including several taxa of Ceratopogonidae, Stratiomyidae and Psychodidae, were found at low abundances and in few samples. These taxa were also typically functionally distinct (Table 1), plotting as outliers in trait space and thus making disproportionately large contributions to functional richness. This combination of taxonomic scarcity and functional distinctiveness is suggestive of high functional rarity (sensu Violle et al. 2017), and by extension conservation value, at the local scale.

To our knowledge, this study is the first to systematically partition taxonomic and functional beta diversity along a gradient of hydrologic disturbance. Our findings suggest that more intense droughts could trigger a turnover of species and functions in perennial stream communities, potentially transforming both the biodiversity of, and ecosystem services provided by, running waters. Aquatic ecology may benefit from more concerted efforts to study beta diversity under the unified partitioning framework used here (Baselga 2010), which to date has largely been restricted to the fields of biogeography and macroecology. This would facilitate more direct comparisons between different systems (e.g. perennial versus temporary streams), stressors (e.g. drying versus warming) and events (e.g. predictable versus unpredictable). Additionally, as extreme events such as drought become more frequent they are increasingly likely to interact with catchment scale pressures, such as land use disturbances (Woodward et al. 2016), the net ecological impacts of which may be non-additive (Jackson et al. 2016). Studies comparing beta diversity patterns along single stressor and multistressor gradients could significantly improve our mechanistic understanding of these complex threats to freshwaters.

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Supplementary material (Appendix Ecog-03711 at <www.ecography.org/appendix/ecog-03711>). Appendix 1–3.