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Drought alters the functional stability of stream invertebrate communities through time

Running title: Temporal betadiversity and disturbance

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31

32 **Abstract**

33 *Aim.* In fresh waters, most biogeographical understanding of how extreme events such as drought
34 modify biodiversity and ecosystem functioning derives from static, spatial comparisons of ecological
35 communities, between intact and disturbed sites or along stress gradients. Impacts of drought on
36 the development of ecological communities over time remain poorly resolved, with information on
37 parallel trends in community structure and function particularly scarce. In theory, drought could
38 progressively eliminate both species and functional traits, rendering communities increasingly
39 taxonomically and functionally nested subsets of their pre-existing counterparts. Alternatively,
40 drought could create new niche opportunities, producing a continuous turnover of species and
41 traits, or simply constrain natural community succession.

42 *Location.* Dorset, UK

43 *Taxon.* Aquatic invertebrates

44 *Methods.* We studied temporal changes in community structure and function in artificial streams
45 over two years, comparing drought (frequent drying) with control (constant flow) conditions.
46 Temporal beta-diversity was partitioned into turnover and nestedness components, calculated using
47 both presence-absence and abundance data, and analysed using time-lag and null modelling
48 approaches.

Results. Community development was comparable taxonomically under control and drought conditions, driven primarily by temporal turnover of species. Under control conditions, corresponding trends in functional composition were not apparent, and species turnover was characterised by the progressive replacement of some species by others of equivalent abundance. By contrast, species turnover in disturbed communities was accompanied by both functional turnover and greater loss of individuals, indicating that new colonists were not equivalent, either functionally or numerically, to those they replaced. Furthermore, functional dissimilarities between timepoints were greatest under drought, and more similar in magnitude to taxonomic dissimilarities, implying that drying reduced the stability and redundancy of functional attributes.

Main conclusion. A shift to drier climate could disrupt the natural development of stream community structure, and undermine functional stability, at local and biogeographical scales, with potentially significant consequences for ecosystem services provisioning in fresh waters.

Keywords

Aquatic invertebrates, climate change, community development, disturbance, drought, functional traits, nestedness, streams and rivers, temporal beta diversity, turnover

Introduction

Predicting the consequences of changing climate and hydrological regimes is essential for effective preservation and restoration of biodiversity and related ecosystem services, such as nutrient cycling and water filtration (Cadotte, Carscadden, & Mirotnick, 2011; Hooper et al., 2012). Yet our ability to protect ecosystems is limited by an overwhelming focus on taxonomic diversity and its surrogates, such as species richness, rather than their functional components, such as the feeding or behavioural traits that underpin certain services (Cadotte et al., 2011; Jarzyna & Jetz, 2016a). Despite our limited understanding of the links among biodiversity, functional traits and ecosystem

service provisioning (Hevia et al., 2017), it has become apparent that changes in taxonomic diversity do not necessarily mirror shifts in functional diversity (i.e. the functional differences among species in a community), with the latter usually providing a better indication of ecosystem functioning and stability (Villéger, Grenouillet, & Brosse, 2014; Gagic et al., 2015). Moreover, because species composition varies considerably more than functional composition (i.e. the total functional volume among biogeographic regions, a functional approach to environmental change research is likely to yield more globally relevant insights into the ecological impacts of climate disturbances (McGill, Enquist, Weiher, & Westoby, 2006; Hobbs, Higgs & Harris, 2009).

As the global climate warms, droughts are predicted to intensify in regions of every inhabited continent (Prudhomme et al., 2014; Trenberth et al., 2014; IPCC, 2014), with potentially severe consequences for ecosystem functioning. In running waters, drought reduces streamflow and habitat availability and can increase mortality of biota (Lake, 2003; Lancaster & Ledger, 2015). Biotic homogenisation, a time-dependent process of species loss and/or gain (Olden, Poff, Douglas, Douglas, & Fausch, 2004), is expected to ensue as local communities become increasingly dominated by drought-adapted species via environmental filtering (Rahel, 2002; Chase, 2007; Leigh & Datry, 2017). Although biotic homogenisation is a temporal process, biogeographical research testing effects of drought and other disturbances focusses on spatial comparisons (but see e.g. Socolar, Gilroy, Kunin, & Edwards, 2016; Sarremejane et al., 2017, Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). How protracted drying events alter stream community composition through time remains unclear (Leigh, Bonada et al., 2016; Leigh, Boulton et al., 2016; Ruhí, Datry, & Sabo, 2017), with information on parallel temporal changes in both community structure and function lacking.

Streams are naturally dynamic ecosystems in which the taxonomic composition of communities changes through time due to both ecological drift (Hubbell, 2001; Chase, 2007) and variation in

environmental conditions (Palmer & Poff, 1997). Ecological theory suggests that temporal species turnover is a prerequisite for community persistence (Darwin, 1859; Magurran et al., 2018) and despite taxonomic changes, functional attributes and relative species' abundances within communities may remain largely stable due to the generally high level of functional redundancy among species, particularly in streams (Villéger, Grenouillet & Brosse, 2013). In the face of drought, however, communities may be functionally vulnerable (Aspin et al., 2018), with *K*-selected traits such as large body size and long lifespan progressively eroded from the species pool, and abundance distributions increasingly skewed towards a small number of tolerant taxa with high abundance (Ledger, Harris, Armitage & Milner, 2012). As a stream drought progresses we might therefore expect homogenisation of both taxonomic and functional composition through time, as species and their traits are progressively filtered out, creating temporal nestedness, where future communities are subsets of past communities. Alternatively, if drying disturbances create niche space for opportunistic species from the regional pool, temporal turnover (i.e. replacement through time) of species and traits may be the dominant pattern, even where drought-induced filtering reduces overall species richness (Leigh, Bonada et al., 2016).

Experiments are regarded increasingly as a key biogeographical research tool (Alexander, Diez, Hart, & Levine, 2016; Pearse et al., 2018). While the theoretical concepts outlined above have application at biogeographical scales, an experimental approach is first necessary to rigorously test the effects of drought on temporal beta diversity (a measure of the difference in community composition between times at the same location; Matthews, Sadler, Carvalho, Nunes & Borges, 2018) without the confounding effect of environmental gradients that undermine field studies and most meta-analyses. Here, we examine partitioned temporal beta diversity calculated using presence-absence data and abundance data from a two-year stream mesocosm experiment, in which habitat was subjected to either continuous flow or repeated episodes of stream drying, to test how drought as a

disturbance influences temporal changes in the structure and function of aquatic invertebrate communities. Although other studies have assessed 'temporal changes' in both taxonomic and functional beta diversity of freshwater ecosystems undergoing environmental alteration, these typically compare spatial beta diversity between time periods (e.g. Cheng et al., 2014; Villéger et al., 2014). Our study examines temporal beta diversity explicitly in stream ecosystems; our data span multiple endpoints enabling evaluation of compositional changes within individual communities over a time series. Additionally, our study assesses both taxonomic and functional composition for multiple beta diversity components, including total temporal beta-diversity, temporal turnover and temporal nestedness-resultant dissimilarity (cf. Jarzyna & Jetz, 2016b, which analyses turnover alone). Testing the theoretical concepts outlined above, we asked the following questions:

- 1) Does drought alter the magnitude and/or direction of temporal change in the taxonomic composition of stream communities, due to either the temporal turnover or temporal nestedness of species and/or individuals?
- 2) Does drought alter the magnitude and/or direction of temporal change in the functional composition of stream communities, due to either the temporal turnover or temporal nestedness of traits?
- 3) Is the observed temporal change in taxonomic and/or functional composition non-random?

Material and methods

Experimental design

A flow manipulation experiment was conducted between March 2000 and February 2002 in eight outdoor stream channels (12 m length x 0.3 m width) adjacent to and fed by a lowland chalk stream in Dorset, southern UK (50°40'48" N, 2° 11' 06" W), a region known for its biodiverse aquatic invertebrate species pool (Wright et al., 1984). The experimental design is detailed extensively elsewhere; briefly, all channels were subject to a common period of community establishment (two

months for both aquatic invertebrates and plants; Ledger, Harris, Armitage, & Milner, 2008; Ledger et al., 2009) commencing March 2000, when flow was routed into the channels from the same source stream (Harris, Armitage, Milner, & Ledger, 2007). Taxa colonised both aerially and by aquatic drift. Thereafter, treatments were applied, with four channels receiving constant flow ('undisturbed control') and four channels subjected to six days of dewatering per month ('drought treatment') until the experiment ended. Assessment of the biota present in the channels prior to implementation of the drought treatment confirmed that the mesocosms were not only highly replicable but also realistic, representing 90% of the aquatic invertebrate taxa resident in the source stream (Harris, Armitage, Milner, & Ledger, 2007; Ledger, Harris, Armitage, & Milner, 2009). The taxa in these channels can thus be considered as a single (meta)community, which was then separated into a 'drought' community comprising the four 'drought treatment' channels and a 'control' community comprising the four 'control' channels (akin to four habitat patches in the source stream under either drought or non-drought conditions). During dewatering, surface flows ceased and exposed substrata dried at natural ambient rates, leaving a few small remnant pools at various intervals along the drought-treatment channels. This drying pattern and duration falls within the range of conditions observed in southern UK chalk streams during suprasedational drought, which has been associated with frequent, patchy channel drying at timescales ranging from days to months (Ledger et al., 2008; Kendon, Marsh, & Parry, 2013).

Invertebrate data

Benthic macroinvertebrates were sampled monthly from June 2000 to February 2002, comprising 20 sampling occasions (endpoints). Each month, one Surber sample (0.025 m², 300 µm mesh size) was collected from randomly selected locations within the upper, middle and lower section of each channel immediately before each dewatering event, with data derived from these three samples later combined. Animals sorted from the samples were identified to the lowest practicable

taxonomic unit (usually species and referred to as such hereafter). To reliably assess temporal variation in beta-diversity we aggregated data from each channel replicate within a treatment (i.e. for the four controls and for the four drought-disturbed channels) on each sampling occasion, generating a time series for community structure (i.e. $n = 2$ treatments $\times$ 20 endpoints). One hundred and twenty species were identified in total over the course of the experiment. Eighty-nine fuzzy-coded functional trait categories describing the ecological preferences and life history traits of European aquatic invertebrates were assigned to the 114 species for which trait information was available (Usseglio-Polatera, Bournaud, Richoux, & Tachet, 2000; Appendix S1, Table S1). Rare species were retained due to their recognised functional importance in a wide range of ecosystems (Leitão et al., 2016) and sensitivity to environmental disturbances (Marchant, 2002).

Data analysis

Dissimilarity partitioning

We followed the pairwise taxonomic beta diversity partitioning method of Baselga (2010) and analogous partitioning method for functional beta diversity developed by Villéger et al. (2013), implemented within the 'betapart' package in R (Baselga, Orme, Villéger, De Bortoli, & Leprieur, 2018). This first calculates overall temporal beta diversity as (i) the total compositional variation between pairs of assemblages, as measured by the Sørensen dissimilarity index (β_{sor}), with assemblage pairs here being the species occurrence lists from any two endpoints for either the drought treatment or control. β_{sor} is then partitioned into components of (ii) temporal turnover (as measured by the Simpson dissimilarity index, β_{sim}) and (iii) temporal nestedness-resultant dissimilarity (β_{sne} , calculated as the difference between β_{sor} and β_{sim}). We calculated these dissimilarity measures using presence-absence data.

For taxonomic composition, the pairwise beta diversity indices β_{sor} , β_{sim} and β_{sne} use information on the number of species shared between two assemblages and the number unique to each. For functional composition, the pairwise beta diversity indices β_{sor} , β_{sim} and β_{sne} use information on the volume of multivariate trait space shared by two assemblages and the volume unique to each. Multivariate trait space was generated following Cornwell, Schilck, & Ackerly (2006), Villéger, Mason, & Mouillot (2008) and Pavoine, Vallet, Dufour, Gachet, & Daniel (2009) using the species by traits matrix to calculate functional dissimilarities using the Gower distance, followed by a principal coordinates analysis (PCoA) to generate a reduced number of independent, synthetic traits (Villéger et al. 2013). As a satisfactory trade-off between information quality, computational time and trait-space interpretability (Maire, Grenouillet, Brosse, & Villéger, 2015), we retained the first four axes (Table S2; globally summarising 35.5% of the trait variance), the maximum number of trait dimensions recommended by Baselga et al. (2018). These PCoA axes represent the multivariate trait space of the assemblage analysed.

PCoA1 correlated positively with traits of larger maximum body sizes (2-8 cm), longer life cycle duration (> 1 y), spiracle respiration, predator feeding habit, and negatively with shorter life-cycle duration (≤ 1 y), passive dispersal and scraper feeding habit; PCoA2 correlated positively with smaller body size (1-2 cm), nymph life stage, predatory feeding habit and larger inorganic substrate sizes ($\geq$ pebbles), and negatively with flying locomotion; PCoA3 correlated positively with multivoltinism and deposit feeding habit, and negatively with longer life cycle duration (> 1 y) and adult life stage; PCoA4 correlated positively with reproduction by clutches and negatively with gill respiration (Spearman correlation coefficients $> |0.5|$; Table S3). Assemblages of invertebrates were projected onto the multivariate trait space, with the synthetic trait values of the species present in any one sample defining the vertices of a convex hull that summarised the functional composition of each community (Figure S1).

Shifts in species' abundances in the absence of taxonomic extinctions or colonisations can have significant implications for community functioning (e.g. Säterberg, Sellman, & Ebenman, 2013), and thus we extended our approach to incorporate abundance-based measures of temporal community dissimilarity. We used the Baselga (2013) family of measures, which incorporates (i) the Bray-Curtis dissimilarity index (d_{BC}) as an abundance-based extension of β_{sor} . d_{BC} can be decomposed into its two constituent drivers, namely (i) balanced variation in abundances (d_{BC-bal}), where species turnover between communities entails no change in overall abundance (i.e. individuals of some species are replaced by the same number of individuals of other species); and (ii) abundance gradients (d_{BC-gra}), the abundance-based counterpart to β_{sne} , where individuals are lost between communities (Baselga, 2013).

The above steps resulted in nine temporal dissimilarity variables (taxonomic presence-absence based $T\beta_{sor}$, $T\beta_{sim}$ and $T\beta_{sne}$, functional $F\beta_{sor}$, $F\beta_{sim}$ and $F\beta_{sne}$ and abundance-based d_{BC} , d_{BC-bal} and d_{BC-gra}) for each pairwise comparison of assemblages sampled through time (i.e. endpoint 1 vs 2, 1 vs 3, ..., 1 vs 20, 2 vs 3, ..., 2 vs 20, ..., 18 vs 19, 18 vs 20, 19 vs 20). These were replicated for both the drought treatment (190 pairs) and control (190 pairs), yielding 3420 beta-diversity values in total (Table S4).

Time-lag analysis

We used time-lag correlation analyses to explore temporal patterns of directional change in taxonomic and functional beta diversity and abundance-based dissimilarity. We plotted each dissimilarity measure ($T\beta_{sor}$, $T\beta_{sim}$, ... d_{BC-gra} , for both the control and drought treatment) against the time lag between samples, which ranged from 1 to 19. For example, the control $T\beta_{sor}$ value derived from the pairwise comparison of taxonomic composition at endpoint 1 vs 2 would have a

time lag of 1, and for endpoint 4 vs 9 would have a time lag of 5. We first square rooted all time lags to minimise the probability that a small number of values at larger time lags would bias the analysis (following Collins, 2000). As our pairwise observations were not independent, we then used Mantel permutation tests to calculate Pearson correlations (Baselga, 2010), allowing us to detect significant trends in structural and/or functional composition through time. This analysis tests for directional change in assemblage composition by producing a measure of community persistence unbiased by seasonality or timing of individual disturbance events (Collins, 2000).

To detect significant differences in the magnitude and direction of each dissimilarity measure between control and drought treatments, we bootstrapped intercepts and slopes from ordinary linear regression models (following Baselga, 2010). For each combination of treatment and dissimilarity measure (e.g. control T β sor) we obtained a frequency distribution of 1000 intercepts and slopes, and then compared the distributions of corresponding measures between treatments to test the significance of an intercept, or slope, being larger for one treatment than the other. We also compared the intercepts and slopes of taxonomic and functional measures within each treatment (e.g. control T β sor vs control F β sor, drought T β sor vs drought F β sor) to provide insights on the impact of drought on functional redundancy.

Null modelling

To test whether the observed temporal changes in taxonomic and functional composition (the beta diversity values) were non-random, i.e. significantly different to the temporal changes in composition due to stochastic variation alone, we used a null modelling procedure. For taxonomic beta diversity, we used a fixed-fixed null model that constrained marginal row and column totals (Ulrich & Gotelli, 2007). For both the 20 control and drought treatment samples we created a presence-absence matrix whereby rows represented samples and columns represented species.

These presence-absence matrices were randomised using the fixed-fixed model, implemented using the quasi-swap algorithm. We generated 1000 random matrices and calculated standardised effect sizes (z-scores) using the observed $T\beta_{sor}$ value and the mean and the standard deviation of the null model $T\beta_{sor}$ values, and an associated p -value (see Matthews, Cottee-Jones, & Whittaker, 2015; Table S4). Significant z-scores ($p < 0.05$) indicate that the temporal change between time periods is non-random (i.e. significantly more or less than expected by chance) and the observed change can thus be attributed to deterministic factors, such as drought. We focused only on $T\beta_{sor}$ because using a fixed-fixed null model results in the same absolute value of z-score for $T\beta_{sor}$, $T\beta_{sim}$ and $T\beta_{sne}$.

For functional temporal beta diversity, we randomly shuffled the species names in the species-trait matrix (see Bishop, Robertson, van Rensburg, & Parr, 2015) and then re-calculated $F\beta_{sor}$, $F\beta_{sim}$ and, $F\beta_{sne}$, as unlike for the taxonomic null model approach, this produces a unique set of z-score values for each component. The functional null model approach ensures that the total functional space is kept constant, but the particular set of traits for each species is randomised. Using the aforementioned approach, we calculated z-scores and associated p -values for each value (Table S4). The computer power required to run such analyses greatly exceeded that of the taxonomic beta-diversity analyses. We therefore simulated 200 randomised values (100 using the control samples and 100 using the drought samples) each for $F\beta_{sor}$, $F\beta_{sim}$ and $F\beta_{sne}$, using the first three trait axes (using four would require > 400 h of computation time on a multi-core processor). After calculating the z-scores for the taxonomic and functional beta-diversity values, we conducted Mantel permutation tests to calculate Pearson correlations, as applied to the original beta-diversity values, to detect if there were also significant trends through time in the z-scores for each component. The null modelling analyses were performed using the presence-absence data only.

We used R (Version 3.4.4, R Core Team, 2018) for all analyses, and the packages ‘ade4’ (Dray, Dufour, & Thioulouse, 2017), ‘betapart’ (Baselga et al., 2018), ‘boot’ (Canty & Ripley, 2017), ‘picante’ (Kembel et al., 2016), ‘CommEcol’ (Melo, 2016) and ‘vegan’ (Oksanen et al., 2017).

Results

Q1: Does drought alter the magnitude and/or direction of temporal change in the taxonomic composition of stream communities, due to either the temporal turnover or temporal nestedness of species and/or individuals?

Total taxonomic temporal beta diversity ($T\beta_{sor}$) increased significantly with the extent of the time lag between samples in both the control and drought treatment (Figure 1; Table 1), signifying progressive change in community structure over time. The significant positive trends detected across all time lags provided evidence of increasing taxonomic beta diversity as time between samples increased, above and beyond any seasonality, which was apparent at time lags of 9-12 months (3.0-3.5 on the square root scale), when sample pairs were from the same season and had more similar compositions (i.e. lower beta diversity values). There was no significant difference between control and drought in intercepts or slopes (Table 1). $T\beta_{sor}$ trends were primarily driven by temporal species turnover, which increased significantly with time lag between samples in both the control and drought treatment, while there was no significant trend in $T\beta_{sne}$ in either treatment (Figure 1, Table 1). Temporal taxonomic beta diversity trends under drought thus closely mirrored those observed in the absence of disturbance (i.e. drought had no discernible impact on either the magnitude or direction of temporal change in stream community structure).

In the control, we observed a significant progressive change in abundance-based community composition (d_{BC}) over time, driven by balanced variation in abundances (d_{BC-bal} ; Figure 2; Table 2).

Under drought there were no significant trends in either d_{BC} or d_{BC-bal} , and slopes were significantly lower than in the control (Table 2). There were contrasting distinctions in d_{BC-gra} , with the slope significantly greater under drought, and no significant difference in intercepts (Table 2). In the absence of drought, we therefore observed a strong pattern of progressive turnover of species of equivalent abundances. This pattern was disrupted in the drought treatment, with the trend in (abundance-based) community composition both weaker and more attributable to the loss of individuals between endpoints.

Q2: Does drought alter the magnitude and/or direction of temporal change in the functional composition of stream communities, due to either the temporal turnover or temporal nestedness of traits?

We detected a significant trend in one facet of temporal functional beta diversity across the control and drought treatments, namely $F\beta_{sim}$ under drought (Figure 3; Table 1). Functional changes between endpoints were also generally greater under drought, as indicated by a significantly higher $F\beta_{sor}$ intercept (than in the control) and no significant difference between $F\beta_{sor}$ control and drought slopes (Table 1). This reduced functional stability (i.e. changes in the multivariate trait space through time) under drought was driven by significantly increased nestedness of traits at short time lags ($F\beta_{sne}$ drought intercept greater than its control counterpart), and increasingly by trait turnover at longer lags ($F\beta_{sim}$ drought slope greater than its control counterpart; Table 1). Drought therefore altered both the magnitude (increase) and the direction (emergence of significant trait turnover) of temporal change in functional composition.

$T\beta_{sor}$ slopes were significantly steeper than $F\beta_{sor}$ slopes in both control (0.016 vs -0.005, $p = 0.002$) and drought (0.024 vs -0.003, $p < 0.001$) treatments, suggesting that the functional impacts of

changes in taxonomic composition were muted by redundancy of traits among species. Comparisons of intercepts revealed that, in the absence of drought, pairwise taxonomic dissimilarities were significantly greater than functional dissimilarities across all time lags ($T\beta_{sor} = 0.271$, $F\beta_{sor} = 0.171$, $p < 0.001$). However, under drought, intercepts were not significantly different ($T\beta_{sor} = 0.299$, $F\beta_{sor} = 0.267$, $p = 0.109$), indicating that drying led to greater similarity in the magnitude of taxonomic and functional shifts between samples (i.e. functional redundancy was lower under drought, particularly at short time lags).

Q3: Is the observed temporal change in taxonomic and/or functional composition non-random?

There was a greater proportion of significantly non-random ($p < 0.05$), total taxonomic temporal-beta-diversity ($T\beta_{sor}$) z-scores in the control (0.23) than under drought conditions (0.13), whereas the opposite occurred for total functional temporal-beta-diversity ($F\beta_{sor}$) z-scores (i.e. greater proportion of significantly non-random scores under drought, 0.25, than control, 0.08; Table 3). The former pattern was also observed for $F\beta_{sim}$ z-scores (control = 0.17; drought = 0.02), whereas the latter pattern was also observed for $F\beta_{sne}$ z-scores (drought = 0.25; control = 0.01; Table 3). The null model results thus supported time-lag analyses on the observed beta-diversity values, providing evidence of both reduced functional stability under drought (i.e. the higher proportion of significant $F\beta_{sor}$ z-scores, indicating that there was greater non-random temporal change in functional composition under repeated drying than constant flow) and reduced redundancy under drought. Differences in functional redundancy can be seen by comparing the relative proportions of significantly non-random $T\beta_{sor}$ and $F\beta_{sor}$ z-scores; in controls, the proportion was higher for $T\beta_{sor}$ (0.23) than $F\beta_{sor}$ (0.08), but this was reversed under drought (0.13 vs 0.25, respectively; Table 3). This reversal indicates that frequent drying increases the amount of non-random temporal change in functional composition relative to that in taxonomic composition. Furthermore, $T\beta_{sor}$ z-scores increased significantly with the extent of the time lag between samples in both the control and

drought treatment (Table 3), mirroring the results based on the observed beta-diversity values. Although the positive trend in the observed $F\beta_{sim}$ values was marginally significant ($p = 0.070$) when based on z-scores, the significant $F\beta_{sim}$ z-scores were consistently positive (Table 3) indicating that the observed turnover in functional composition was significantly greater than expected by chance.

Discussion

Drought alters the magnitude and direction of temporal change in the composition of stream communities

Our findings revealed a marked absence of drought impacts on taxonomic beta diversity trends, which concealed pervasive impacts on functional compositional change through time, highlighting the importance of looking beyond species' identities (Jarzyna & Jetz, 2016a). Our findings suggest that while the high levels of functional redundancy inherent in stream invertebrate communities (Boersma, Bogan, Henrichs, & Lytle, 2014) may partially buffer against variation driven by species turnover, redundancy may be lower in the face of severe, frequent drying, and additionally that absolute functional stability may be reduced. Our null modelling results indicate that this functional instability might primarily manifest itself through loss of trait combinations over short intervals, rather than the ensuing replacement at longer time lags. Disturbances due to suprasedasonal (i.e. extreme) drought could thus lead to unforeseen changes or transience in the functional attributes of aquatic communities and their ecosystem services.

Both species sorting (niche) and mass effects (dispersal-based) models predict that relative abundances of species should change predictably through time where environmental conditions change, but remain relatively constant otherwise (Chase et al., 2005). The trends in abundance-based dissimilarities we observed are thus broadly consistent with ecological theory. Previous

analyses on the mesocosm data showed that densities of amphipods, isopods, mayflies and caddisflies declined over the course of the experiment, contrasting with increasing densities of gastropods, bivalves and oligochaetes (Ledger et al., 2012). Our abundance-based beta diversity results suggest that the progressive emergence of the latter group of taxa directly compensated for the decline in the former (at least in terms of numbers), driving the strong trend in balanced variation in abundance (d_{BC-bal}) we observed through time. This process of natural community development, reflecting predictable evolution of environmental conditions (e.g. sand and fine sediment accumulation among gravel and macrophytes; Ledger et al. (2012)) was not replicated under drought. In drying streams, habitat structure remained relatively static, with repeated disturbances constraining the natural physical processes driving habitat and thus community change. Under these conditions loss or gain of individuals (d_{BC-gra}) between endpoints was more prevalent, with drought-sensitive mayflies, caddisflies and beetles replaced by either scarcer drought specialists (e.g. Ceratopogonidae, Limoniidae) or more abundant generalists (e.g. Orthocladiinae, Tanytarsini), as observed by Ledger et al. (2012). Our study therefore demonstrates that completely different mechanisms of community succession, reflecting completely different environmental conditions, can give rise to highly similar patterns of species turnover ($T\beta_{sim}$) and thus compositional change ($T\beta_{sor}$). This underlines the importance of incorporating abundance data when studying community responses to disturbance over time, allowing us to detect changes over and above the natural temporal turnover of species inherent in even relatively stable environments (Magurran et al., 2018).

Drivers of temporal beta diversity trends

In addition to the habitat change detected by Ledger et al. (2012), temporal species turnover in the control was likely associated with the seasonality of species that naturally occurs in undisturbed perennial streams within the study region (Wright, 1992). By contrast, species turnover under

drought appeared to be driven by severe environmental filtering, with opportunistic species possessing traits such as multivoltinism, asynchronous life cycles and habitat preference for still waters colonising niche space vacated by drought-sensitive taxa (Bonada, Rieradevall, & Prat, 2007; Robson, Chester, & Austin, 2011). New colonists to the drought treatment that replaced lost species such as the beetle *Hydroporinae* (Dytiscidae, Figure S1) and caddisfly *R. dorsalis* (Rhyacophilidae, Figure S1) included the caddisflies *Holocentropus* sp. (Polycentropodidae; Figure S1) and *C. dissimilis* (Leptoceridae), and the true flies *Gonomyia* sp., *Pilaria* sp. (Limoniidae) and *O. trilineata* (Stratiomyidae). These new colonists possess active aerial life stages, preferences for slow-flowing or stagnant waters, short life cycles (typically <1 year), production of clutches of offspring, and small body sizes (<2 cm maximum potential size), contrasting with the lost species' traits of larger body sizes (>2-4 cm) and longer life-cycle durations (>1 year; Usseglio-Polatera et al., 2000). Typically greater dispersal abilities and shorter life cycles within drought-disturbed communities could explain the greater transience of functional attributes (i.e. higher $F\beta_{sor}$) apparent in drying streams, reflecting the periodic colonisation and short-lived occupation of niches by opportunistic species.

This transience was primarily driven by high $F\beta_{sne}$ values at short timescales, indicating that new colonists in disturbed habitats possessed subsets of the functional strategies of the species they replaced. However, under drought functional turnover became relatively more significant at longer time lags, a pattern consistent with the distinct trait profiles that may enable adaptation of respective taxa to opposing ends of extreme disturbance gradients (Aspin et al., 2018). Functional turnover thus appeared to be the only component of functional beta diversity in either treatment that was not 'reset' by seasonal trends in community composition, as evident in the $F\beta_{sor}$ values, which declined at time lags of 9-12 months. Our results therefore provide evidence that extreme disturbances such as suprasedonal drought could disrupt natural seasonality in functional composition (Sarremejane et al., 2017), driven by the progressive shifting of trait space over time.

Such shifts are likely to be associated with declining biomass stocks because the replacement of larger, *K*-selected taxa by smaller *r*-strategists, capable of reaching greater densities, cannot offset drying-driven mortality across the community (Ledger, Brown, Edwards, Milner, & Woodward, 2011; 2013). However, null models of functional turnover revealed patterns that were not significantly different to random expectation, potentially reflecting the small (patch) scale of our study system. At larger spatial scales, as the size and thus functional diversity of the species pool increase, we might expect the relative influence of stochastic community assembly processes to fade (Spasojevic, Catano, LaManna & Myers, 2018), which would potentially allow more significant functional turnover patterns to emerge (reflecting greater niche selection), a result which may also occur if more variation in the original traits were to be captured by the PCoA axes.

Reduced stability of functional attributes under drought appeared to erode functional redundancy, with functional shifts between endpoints more commensurate with taxonomic changes compared to the control. Previous studies suggest that inherently high levels of functional redundancy in stream communities promote some resistance to perturbation by stream drying, buffering against changes to ecosystem functioning (Boersma et al., 2014; Schriever et al., 2015). We likewise found evidence of functional redundancy, but our results highlight the important caveat that it may be weakened in the face of frequent drying. A dependence of functional redundancy on drought duration and/or predictability appears to be a commonality among stream invertebrate communities (Stubbington et al., 2017; Aspin et al., 2018), but ours is the first study to reveal potential implications for community stability over time. Intuitively, we might expect redundancy of traits to decline as selection for highly tolerant lentic taxa and drought specialists occurs (Boulton & Lake, 2008), as such taxa will be, by definition, functionally distinct from the species they replace. Progressive colonisation of disturbed streams by specialists through the course of the experiment thus provides a convincing explanation for the significant temporal trend in functional turnover we detected.

468

469 *Conclusions*

470 Temporal analysis of community composition is essential for understanding and predicting outcomes
471 of future changes to disturbance regimes and the subsequent effects on ecosystem functioning
472 (Dornelas et al., 2014). While our study draws conclusions from a mesocosm experiment, which
473 controls the range of conditions present in the ecosystem it mimics, our findings are robust and
474 applicable to natural running waters. Large mesocosm channels were used to sustain complex
475 communities similar to those of natural chalk streams, and drying stress was applied outdoors under
476 semi-natural conditions (Harris et al., 2007; Ledger et al., 2009). The longevity of our experiment was
477 realistic relative to past suprasedational droughts in the region and beyond, and to those projected in
478 the future (Parry, Hannaford, Lloyd-Hughes, & Prudhomme, 2012; Roudier et al., 2016), capturing
479 both inter- and intra-generational responses to drought stress. Many rivers are experiencing channel
480 drying for the first time in recorded history, due to unprecedented drought and escalating water
481 demands (Gleick, 2003; Döll & Schmied, 2012). With freshwater biodiversity in crisis, at local,
482 regional and global scales (Bálint et al., 2011; Dudgeon et al., 2006; Vörösmarty et al., 2010),
483 experimental assessments of biodiversity responses to predicted environmental change are vital
484 (Leigh, Boulton et al., 2016). Biodiversity is intimately linked with ecosystem functioning and
485 services, such as clean drinking water and predictable food supply (Cardinale et al., 2013).
486 Understanding how drought and other disturbances alter biodiversity through time, both
487 taxonomically and functionally, is vital for scenario prediction and formulation of management
488 strategies applicable within and across biogeographic regions, for example by guiding the protection
489 or creation of aquatic refuges to sustain functionally rare or unique species (Robson et al., 2011).
490 This is particularly salient given that suprasedational drought may increase the transience of
491 functional attributes, with uncertain but potentially significant consequences for ecosystem service
492 provisioning.

Tables

Table 1: Pearson (r) correlations and their p -values from Mantel tests, examining the pairwise dissimilarities in the taxonomic (T β sor, T β sim, T β sne) and functional (F β sor, F β sim, F β sne) composition of invertebrate communities as a function of the time lag between samples under both control (C) and drought (D) conditions, shown along with p -values associated with tests comparing either slopes or intercepts (from bootstrapping of linear model coefficients) between control and drought conditions. Bold typeface indicates significant correlations or differences ($p < 0.05$).

	Component	r	p	Intercept	p (C vs D intercept)	Slope	p (C vs D slope)
C	T β sor	0.20	0.018	0.271	0.085	0.016	0.130
D	T β sor	0.31	<0.001	0.299		0.024	
C	T β sim	0.24	0.004	0.187	0.021	0.021	0.329
D	T β sim	0.18	0.017	0.233		0.017	
C	T β sne	0.06	0.292	0.084	0.151	-0.005	0.041
D	T β sne	0.09	0.148	0.066		0.007	
C	F β sor	-0.06	0.279	0.171	<0.001	-0.005	0.428
D	F β sor	-0.03	0.453	0.267		-0.003	
C	F β sim	-0.01	0.472	0.073	0.259	-0.001	0.012
D	F β sim	0.18	0.015	0.083		0.013	
C	F β sne	-0.05	0.341	0.098	0.001	-0.004	0.135
D	F β sne	-0.11	0.087	0.185		-0.016	

Table 2: Pearson (r) correlations and their p -values from Mantel tests, examining the pairwise dissimilarities in the abundance-based community composition (d_{BC} , d_{BC-bal} , d_{BC-gra}) of invertebrate communities as a function of the time lag between samples under both control (C) and drought (D) conditions, shown along with p -values associated with tests comparing either slopes or intercepts (from bootstrapping of linear model coefficients) between control and drought conditions. Bold typeface indicates significant correlations or differences ($p < 0.05$).

	Component	r	p	Intercept	p (C vs D intercept)	Slope	p (C vs D slope)
C	d_{BC}	0.47	<0.001	0.362	<0.001	0.081	<0.001
D	d_{BC}	0.11	0.079	0.531		0.022	
C	d_{BC-bal}	0.60	<0.001	0.109	<0.001	0.104	<0.001
D	d_{BC-bal}	-0.04	0.338	0.286		-0.007	
C	d_{BC-gra}	-0.15	0.011	0.253	0.454	-0.024	<0.001
D	d_{BC-gra}	-0.12	0.066	0.245		0.029	

Table 3: Null modelling results. The proportion of z-scores for each temporal beta diversity component (T β sor, F β sor, F β sim, F β sne) under control (C) vs drought (D) conditions that were significantly non-random ($p < 0.05$) together with Pearson (r) correlations and their p -values from Mantel tests examining the pairwise dissimilarities as a function of the time lag between samples under control (C) and drought (D) conditions. Bold typeface indicates the greater of the two proportions (control vs drought) for each component.

Component	Proportion of all z-scores (C vs D)	Proportion of positive z-scores (C vs D)	Control r (p)	Drought r (p)
T β sor	0.23 vs 0.13	0.13 vs 0.08	0.30 (0.002)	0.33 (< 0.001)
F β sor	0.08 vs 0.25	0.08 vs 0.25	-0.09 (0.174)	-0.10 (0.146)
F β sim	0.17 vs 0.2	0.17 vs 0.2	-0.003 (0.499)	0.12 (0.070)
F β sne	0.01 vs 0.25	0.01 vs 0.25	-0.13 (0.033)	-0.11 (0.104)

521 **Figure 1** Pairwise dissimilarities in the taxonomic composition of invertebrate communities as a
522 function of the time lag between samples under both control (blue) and drought (orange)
523 conditions. Total compositional change (β_{sor}) is shown along with its constituent components
524 turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}). Time lags were square-root
525 transformed ($\sqrt{\text{time lag}}$) to reduce the impact of the small number of values at longer lags
526 (Collins, 2000). Pearson (r) correlations and their p -values are from Mantel tests, and slopes and 95%
527 confidence intervals from bootstrapping of linear model coefficients.

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532 **Figure 2** Pairwise abundance-based dissimilarities in the taxonomic composition of invertebrate
533 communities as a function of the time lag between samples under both control (blue) and drought
534 (orange) conditions. Total abundance-based dissimilarity (d_{BC}) is shown along with its constituent
535 components balanced variation in abundance (d_{BC-bal}) and abundance gradients (d_{BC-gra}). For further
536 details see Figure 1.

537

538

539

Figure 3 Pairwise dissimilarities in the functional composition of invertebrate communities as a function of the time lag between samples under both control (blue) and drought (orange) conditions. Total compositional change (β_{sor}) is shown along with its constituent components turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}). For further details see Figure 1.

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759 **Biosketch**

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Author contributions: C.L. and M.E.L. conceived the idea, which was further developed by all authors. M.E.L. provided the original invertebrate density and trait data. C.L., T.W.H.A, and T.M.M. performed the analyses. C.L. and T.W.H.A. led the writing with substantial contributions from all authors.

Supporting information

Appendix S1: Aquatic invertebrate communities

One hundred and twenty species were identified in total over the course of the experiment. Trait information was lacking for six of the 120 species (the baetid mayflies *Alainites muticus*, *Labiobaetis atrebatinus*, *Nigrobaetis niger*, and *Procloeon pennulatum*, dytiscid beetle *Potamonectes depressus elegans* and oligochaete *Glossoscolecidae* spp.), and these six species were excluded from all subsequent analyses (taxonomic and functional). Of the remaining 114 species, which consisted of flatworms (4%), molluscs (10%), annelid worms (6%), crustaceans (3%) and insects (77%, primarily beetles, caddisflies, mayflies and true flies), 109 were present at some time over the course of the experiment in samples from the control and 94 from the drought treatment (Table S1), at densities ranging from 3665 to 32160 ind. m⁻² in the control and from 3373 to 35370 ind. m⁻² in the drought treatment. Twenty species were present only in the control (the platyhelminth *Dugesia tigrina*, molluscs *Acroloxus lacustris*, *Bithynia leachii*, *Bithynia tentaculata*, *Sphaerium* sp., beetles *Haliphus haliphus* sp., *Oulimnius troglodytes*, *Oulimnius tuberculatus*, *Hydraena riparia*, *Hydroporinae* spp., caddisflies *Drusus annulatus*, *Mystacides azurea*, *Oecetis testacea*, *Lype* sp., *Rhyacophila dorsalis*, mayflies *Caenis horaria*, *Caenis rivulorum*, *Ecdyonurus* sp., damselfly *Calopteryx splendens*, and true fly *Limonia* sp.) whereas only five were unique to the drought treatment (the caddisflies *Ceraclea dissimilis*, *Holocentropus* sp., and true flies *Gonomyia* sp., *Oxycera trilineata*, *Pilaria* sp.).

Table S1: Benthic macroinvertebrates present in (1) or absent from (0) the control (C) and drought-treatment (D) community sampled from June 2000 to February 2002 (data are pooled across all endpoints).

Table S2: Benthic macroinvertebrates and their corresponding synthetic trait (PCoA axis) values.

Table S3: Spearman correlation (*r* coefficient) between each functional trait and each synthetic trait (PCoA axis).

Table S4: Pairwise dissimilarity measures for control and drought-treatment communities for: taxonomic (T) and functional (F) total compositional change (β_{sor}) and its constituent components, turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}); abundance-based taxonomic compositional change (dBC) and its constituent components, balanced variation in abundances (dBC-bal) and abundance gradients (dBC-gra); and null-model z-scores for $T\beta_{sor}$, $F\beta_{sor}$, $F\beta_{sim}$ and $F\beta_{sne}$ along with their associated p-values.

Figure S1: Multivariate trait space defined by the first four axes of principal coordinates analysis (PCoA) generated from the species by fuzzy-coded traits matrix and the species present in the control only (light blue triangles), drought treatment only (dark orange diamonds), or both communities (dark blue inverted triangles) across all samples combined (note: temporal beta diversity values analysed in this paper were calculated from every possible pairwise comparison of samples). Circled symbols show species present in the control only that fall outside the drought-treatment community trait space (*Hydroporinae* and *Rhyacophila dorsalis*) and species present in the drought treatment only that fall outside the control community trait space (*Holocentropus* sp.).