

## Drought alters the functional stability of stream invertebrate communities through time

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1 **Drought alters the functional stability of stream invertebrate communities through time**

2 **Running title:** Temporal betadiversity and disturbance

3

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30 Kieran Khamis for advice on functional dissimilarity analysis methods.

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.

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

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

#### 61 **Keywords**

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

64

#### 65 **Introduction**

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

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

81

82 As the global climate warms, droughts are predicted to intensify in regions of every inhabited  
83 continent (Prudhomme et al., 2014; Trenberth et al., 2014; IPCC, 2014), with potentially severe  
84 consequences for ecosystem functioning. In running waters, drought reduces streamflow and  
85 habitat availability and can increase mortality of biota (Lake, 2003; Lancaster & Ledger, 2015). Biotic  
86 homogenisation, a time-dependent process of species loss and/or gain (Olden, Poff, Douglas,  
87 Douglas, & Fausch, 2004), is expected to ensue as local communities become increasingly dominated  
88 by drought-adapted species via environmental filtering (Rahel, 2002; Chase, 2007; Leigh & Datry,  
89 2017). Although biotic homogenisation is a temporal process, biogeographical research testing  
90 effects of drought and other disturbances focusses on spatial comparisons (but see e.g. Socolar,  
91 Gilroy, Kunin, & Edwards, 2016; Sarremejane et al., 2017, Tonkin, Bogan, Bonada, Rios-Touma, &  
92 Lytle, 2017). How protracted drying events alter stream community composition through time  
93 remains unclear (Leigh, Bonada et al., 2016; Leigh, Boulton et al., 2016; Ruhí, Datry, & Sabo, 2017),  
94 with information on parallel temporal changes in both community structure and function lacking.

95

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

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

113

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

123 disturbance influences temporal changes in the structure and function of aquatic invertebrate  
124 communities. Although other studies have assessed ‘temporal changes’ in both taxonomic and  
125 functional beta diversity of freshwater ecosystems undergoing environmental alteration, these  
126 typically compare spatial beta diversity between time periods (e.g. Cheng et al., 2014; Villéger et al.,  
127 2014). Our study examines temporal beta diversity explicitly in stream ecosystems; our data span  
128 multiple endpoints enabling evaluation of compositional changes within individual communities over  
129 a time series. Additionally, our study assesses both taxonomic and functional composition for  
130 multiple beta diversity components, including total temporal beta-diversity, temporal turnover and  
131 temporal nestedness-resultant dissimilarity (cf. Jarzyna & Jetz, 2016b, which analyses turnover  
132 alone). Testing the theoretical concepts outlined above, we asked the following questions:

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

140

## 141 **Material and methods**

### 142 *Experimental design*

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



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

166

#### 167 *Invertebrate data*

168 Benthic macroinvertebrates were sampled monthly from June 2000 to February 2002, comprising 20  
169 sampling occasions (endpoints). Each month, one Surber sample (0.025 m<sup>2</sup>, 300 µm mesh size) was  
170 collected from randomly selected locations within the upper, middle and lower section of each  
171 channel immediately before each dewatering event, with data derived from these three samples  
172 later combined. Animals sorted from the samples were identified to the lowest practicable

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

183

#### 184 *Data analysis*

##### 185 *Dissimilarity partitioning*

186 We followed the pairwise taxonomic beta diversity partitioning method of Baselga (2010) and  
187 analogous partitioning method for functional beta diversity developed by Villéger et al. (2013),  
188 implemented within the 'betapart' package in R (Baselga, Orme, Villéger, De Bortoli, & Leprieur,  
189 2018). This first calculates overall temporal beta diversity as (i) the total compositional variation  
190 between pairs of assemblages, as measured by the Sørensen dissimilarity index ( $\beta_{sor}$ ), with  
191 assemblage pairs here being the species occurrence lists from any two endpoints for either the  
192 drought treatment or control.  $\beta_{sor}$  is then partitioned into components of (ii) temporal turnover (as  
193 measured by the Simpson dissimilarity index,  $\beta_{sim}$ ) and (iii) temporal nestedness-resultant  
194 dissimilarity ( $\beta_{sne}$ , calculated as the difference between  $\beta_{sor}$  and  $\beta_{sim}$ ). We calculated these  
195 dissimilarity measures using presence-absence data.

196

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

210

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

222

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

233

234 The above steps resulted in nine temporal dissimilarity variables (taxonomic presence-absence  
235 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  $d_{BC}$ ,  $d_{BC-bal}$   
236 and  $d_{BC-gra}$ ) for each pairwise comparison of assemblages sampled through time (i.e. endpoint 1 vs 2,  
237 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  
238 the drought treatment (190 pairs) and control (190 pairs), yielding 3420 beta-diversity values in total  
239 (Table S4).

240

#### 241 *Time-lag analysis*

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

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

254

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

264

#### 265 *Null modelling*

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

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

280

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

295

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

299

## 300 **Results**

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

304 Total taxonomic temporal beta diversity ( $T\beta_{sor}$ ) increased significantly with the extent of the time  
305 lag between samples in both the control and drought treatment (Figure 1; Table 1), signifying  
306 progressive change in community structure over time. The significant positive trends detected across  
307 all time lags provided evidence of increasing taxonomic beta diversity as time between samples  
308 increased, above and beyond any seasonality, which was apparent at time lags of 9-12 months (3.0-  
309 3.5 on the square root scale), when sample pairs were from the same season and had more similar  
310 compositions (i.e. lower beta diversity values). There was no significant difference between control  
311 and drought in intercepts or slopes (Table 1).  $T\beta_{sor}$  trends were primarily driven by temporal species  
312 turnover, which increased significantly with time lag between samples in both the control and  
313 drought treatment, while there was no significant trend in  $T\beta_{sne}$  in either treatment (Figure 1, Table  
314 1). Temporal taxonomic beta diversity trends under drought thus closely mirrored those observed in  
315 the absence of disturbance (i.e. drought had no discernible impact on either the magnitude or  
316 direction of temporal change in stream community structure).

317

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

320 Under drought there were no significant trends in either  $d_{BC}$  or  $d_{BC-bal}$ , and slopes were significantly  
321 lower than in the control (Table2). There were contrasting distinctions in  $d_{BC-gra}$ , with the slope  
322 significantly greater under drought, and no significant difference in intercepts (Table 2). In the  
323 absence of drought, we therefore observed a strong pattern of progressive turnover of species of  
324 equivalent abundances. This pattern was disrupted in the drought treatment, with the trend in  
325 (abundance-based) community composition both weaker and more attributable to the loss of  
326 individuals between endpoints.

327

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

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

341

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



344 changes in taxonomic composition were muted by redundancy of traits among species. Comparisons  
345 of intercepts revealed that, in the absence of drought, pairwise taxonomic dissimilarities were  
346 significantly greater than functional dissimilarities across all time lags ( $T\beta_{sor} = 0.271$ ,  $F\beta_{sor} = 0.171$ ,  
347  $p < 0.001$ ). However, under drought, intercepts were not significantly different ( $T\beta_{sor} = 0.299$ ,  $F\beta_{sor}$   
348  $= 0.267$ ,  $p = 0.109$ ), indicating that drying led to greater similarity in the magnitude of taxonomic and  
349 functional shifts between samples (i.e. functional redundancy was lower under drought, particularly  
350 at short time lags).

351

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

353 There was a greater proportion of significantly non-random ( $p < 0.05$ ), total taxonomic temporal-  
354 beta-diversity ( $T\beta_{sor}$ ) z-scores in the control (0.23) than under drought conditions (0.13), whereas  
355 the opposite occurred for total functional temporal-beta-diversity ( $F\beta_{sor}$ ) z-scores (i.e. greater  
356 proportion of significantly non-random scores under drought, 0.25, than control, 0.08; Table 3). The  
357 former pattern was also observed for  $F\beta_{sim}$  z-scores (control = 0.17; drought = 0.02), whereas the  
358 latter pattern was also observed for  $F\beta_{sne}$  z-scores (drought = 0.25; control = 0.01; Table 3). The null  
359 model results thus supported time-lag analyses on the observed beta-diversity values, providing  
360 evidence of both reduced functional stability under drought (i.e. the higher proportion of significant  
361  $F\beta_{sor}$  z-scores, indicating that there was greater non-random temporal change in functional  
362 composition under repeated drying than constant flow) and reduced redundancy under drought.  
363 Differences in functional redundancy can be seen by comparing the relative proportions of  
364 significantly non-random  $T\beta_{sor}$  and  $F\beta_{sor}$  z-scores; in controls, the proportion was higher for  $T\beta_{sor}$   
365 (0.23) than  $F\beta_{sor}$  (0.08), but this was reversed under drought (0.13 vs 0.25, respectively; Table 3).  
366 This reversal indicates that frequent drying increases the amount of non-random temporal change in  
367 functional composition relative to that in taxonomic composition. Furthermore,  $T\beta_{sor}$  z-scores  
368 increased significantly with the extent of the time lag between samples in both the control and

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

373

## 374 **Discussion**

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

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

388

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

393 analyses on the mesocosm data showed that densities of amphipods, isopods, mayflies and  
394 caddisflies declined over the course of the experiment, contrasting with increasing densities of  
395 gastropods, bivalves and oligochaetes (Ledger et al., 2012). Our abundance-based beta diversity  
396 results suggest that the progressive emergence of the latter group of taxa directly compensated for  
397 the decline in the former (at least in terms of numbers), driving the strong trend in balanced  
398 variation in abundance ( $d_{BC-bal}$ ) we observed through time. This process of natural community  
399 development, reflecting predictable evolution of environmental conditions (e.g. sand and fine  
400 sediment accumulation among gravel and macrophytes; Ledger et al. (2012)) was not replicated  
401 under drought. In drying streams, habitat structure remained relatively static, with repeated  
402 disturbances constraining the natural physical processes driving habitat and thus community change.  
403 Under these conditions loss or gain of individuals ( $d_{BC-gra}$ ) between endpoints was more prevalent,  
404 with drought-sensitive mayflies, caddisflies and beetles replaced by either scarcer drought specialists  
405 (e.g. Ceratopogonidae, Limoniidae) or more abundant generalists (e.g. Orthoclaadiinae, Tanytarsini),  
406 as observed by Ledger et al. (2012). Our study therefore demonstrates that completely different  
407 mechanisms of community succession, reflecting completely different environmental conditions, can  
408 give rise to highly similar patterns of species turnover ( $T\beta_{sim}$ ) and thus compositional change  
409 ( $T\beta_{sor}$ ). This underlines the importance of incorporating abundance data when studying community  
410 responses to disturbance over time, allowing us to detect changes over and above the natural  
411 temporal turnover of species inherent in even relatively stable environments (Magurran et al.,  
412 2018).

413

#### 414 *Drivers of temporal beta diversity trends*

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

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

432

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

443 Such shifts are likely to be associated with declining biomass stocks because the replacement of  
444 larger, *K*-selected taxa by smaller *r*-strategists, capable of reaching greater densities, cannot offset  
445 drying-driven mortality across the community (Ledger, Brown, Edwards, Milner, & Woodward, 2011;  
446 2013). However, null models of functional turnover revealed patterns that were not significantly  
447 different to random expectation, potentially reflecting the small (patch) scale of our study system. At  
448 larger spatial scales, as the size and thus functional diversity of the species pool increase, we might  
449 expect the relative influence of stochastic community assembly processes to fade (Spasojevic,  
450 Catano, LaManna & Myers, 2018), which would potentially allow more significant functional  
451 turnover patterns to emerge (reflecting greater niche selection), a result which may also occur if  
452 more variation in the original traits were to be captured by the PCoA axes.

453

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

493 **Tables**

494 **Table 1:** Pearson ( $r$ ) correlations and their  $p$ -values from Mantel tests, examining the pairwise  
 495 dissimilarities in the taxonomic ( $T\beta_{sor}$ ,  $T\beta_{sim}$ ,  $T\beta_{sne}$ ) and functional ( $F\beta_{sor}$ ,  $F\beta_{sim}$ ,  $F\beta_{sne}$ )  
 496 composition of invertebrate communities as a function of the time lag between samples under both  
 497 control (C) and drought (D) conditions, shown along with  $p$ -values associated with tests comparing  
 498 either slopes or intercepts (from bootstrapping of linear model coefficients) between control and  
 499 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	$T\beta_{sor}$	<b>0.20</b>	0.018	0.271	0.085	0.016	0.130
D	$T\beta_{sor}$	<b>0.31</b>	<0.001	0.299		0.024	
C	$T\beta_{sim}$	<b>0.24</b>	0.004	<b>0.187</b>	0.021	0.021	0.329
D	$T\beta_{sim}$	<b>0.18</b>	0.017	<b>0.233</b>		0.017	
C	$T\beta_{sne}$	0.06	0.292	0.084	0.151	<b>-0.005</b>	0.041
D	$T\beta_{sne}$	0.09	0.148	0.066		<b>0.007</b>	
C	$F\beta_{sor}$	-0.06	0.279	<b>0.171</b>	<0.001	-0.005	0.428
D	$F\beta_{sor}$	-0.03	0.453	<b>0.267</b>		-0.003	
C	$F\beta_{sim}$	-0.01	0.472	0.073	0.259	<b>-0.001</b>	0.012
D	$F\beta_{sim}$	<b>0.18</b>	0.015	0.083		<b>0.013</b>	
C	$F\beta_{sne}$	-0.05	0.341	<b>0.098</b>	0.001	-0.004	0.135
D	$F\beta_{sne}$	-0.11	0.087	<b>0.185</b>		-0.016	

500

501

502 **Table 2:** Pearson ( $r$ ) correlations and their  $p$ -values from Mantel tests, examining the pairwise  
 503 dissimilarities in the abundance-based community composition ( $d_{BC}$ ,  $d_{BC-bal}$ ,  $d_{BC-gra}$ ) of invertebrate  
 504 communities as a function of the time lag between samples under both control (C) and drought (D)  
 505 conditions, shown along with  $p$ -values associated with tests comparing either slopes or intercepts  
 506 (from bootstrapping of linear model coefficients) between control and drought conditions. Bold  
 507 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	$d_{BC}$	<b>0.47</b>	<0.001	<b>0.362</b>	<0.001	<b>0.081</b>	<0.001
D	$d_{BC}$	0.11	0.079	<b>0.531</b>		<b>0.022</b>	
C	$d_{BC-bal}$	<b>0.60</b>	<0.001	<b>0.109</b>	<0.001	<b>0.104</b>	<0.001
D	$d_{BC-bal}$	-0.04	0.338	<b>0.286</b>		<b>-0.007</b>	
C	$d_{BC-gra}$	<b>-0.15</b>	0.011	0.253	0.454	<b>-0.024</b>	<0.001
D	$d_{BC-gra}$	-0.12	0.066	0.245		<b>0.029</b>	

508

509

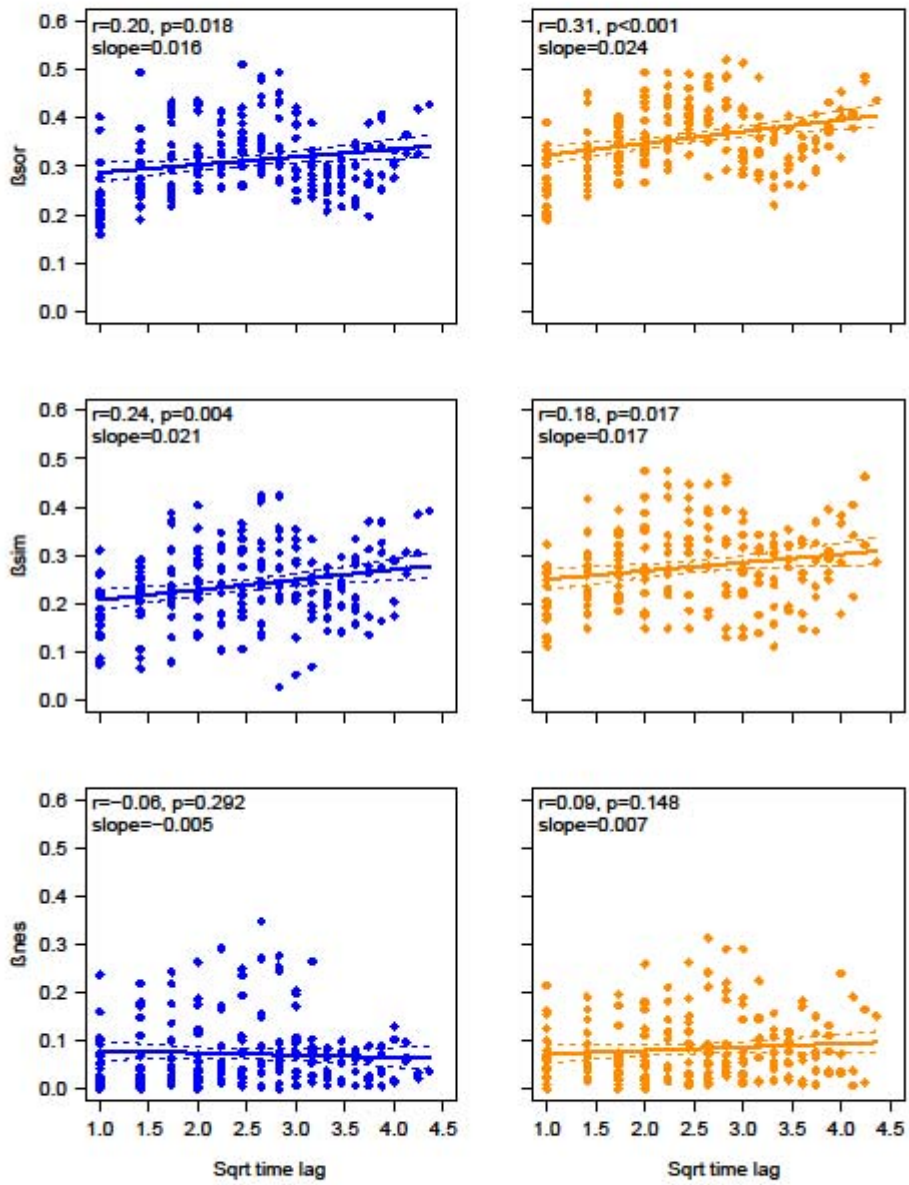


510 **Table 3:** Null modelling results. The proportion of z-scores for each temporal beta diversity  
 511 component (T $\beta$ sor, F $\beta$ sor, F $\beta$ sim, F $\beta$ sne) under control (C) vs drought (D) conditions that were  
 512 significantly non-random ( $p < 0.05$ ) together with Pearson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

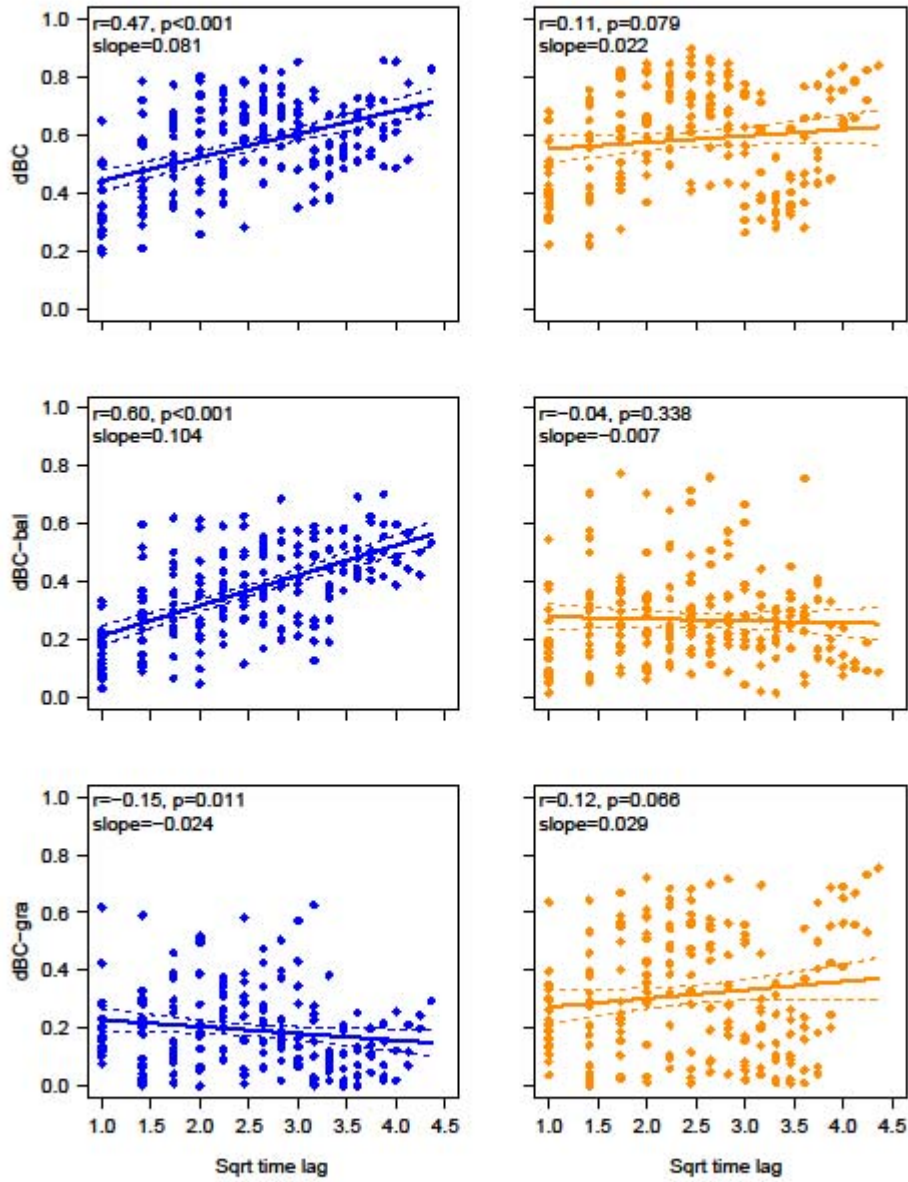
Component	Proportion of all z-scores (C vs D)	Proportion of positive z-scores (C vs D)	Control $r$ ( $p$ )	Drought $r$ ( $p$ )
T $\beta$ sor	<b>0.23</b> vs 0.13	<b>0.13</b> vs 0.08	0.30 (0.002)	0.33 (< 0.001)
F $\beta$ sor	0.08 vs <b>0.25</b>	0.08 vs <b>0.25</b>	-0.09 (0.174)	-0.10 (0.146)
F $\beta$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

516

517



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 ( $\beta_{sor}$ ) is shown along with its constituent components  
524 turnover ( $\beta_{sim}$ ) and nestedness-resultant dissimilarity ( $\beta_{sne}$ ). 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.



528

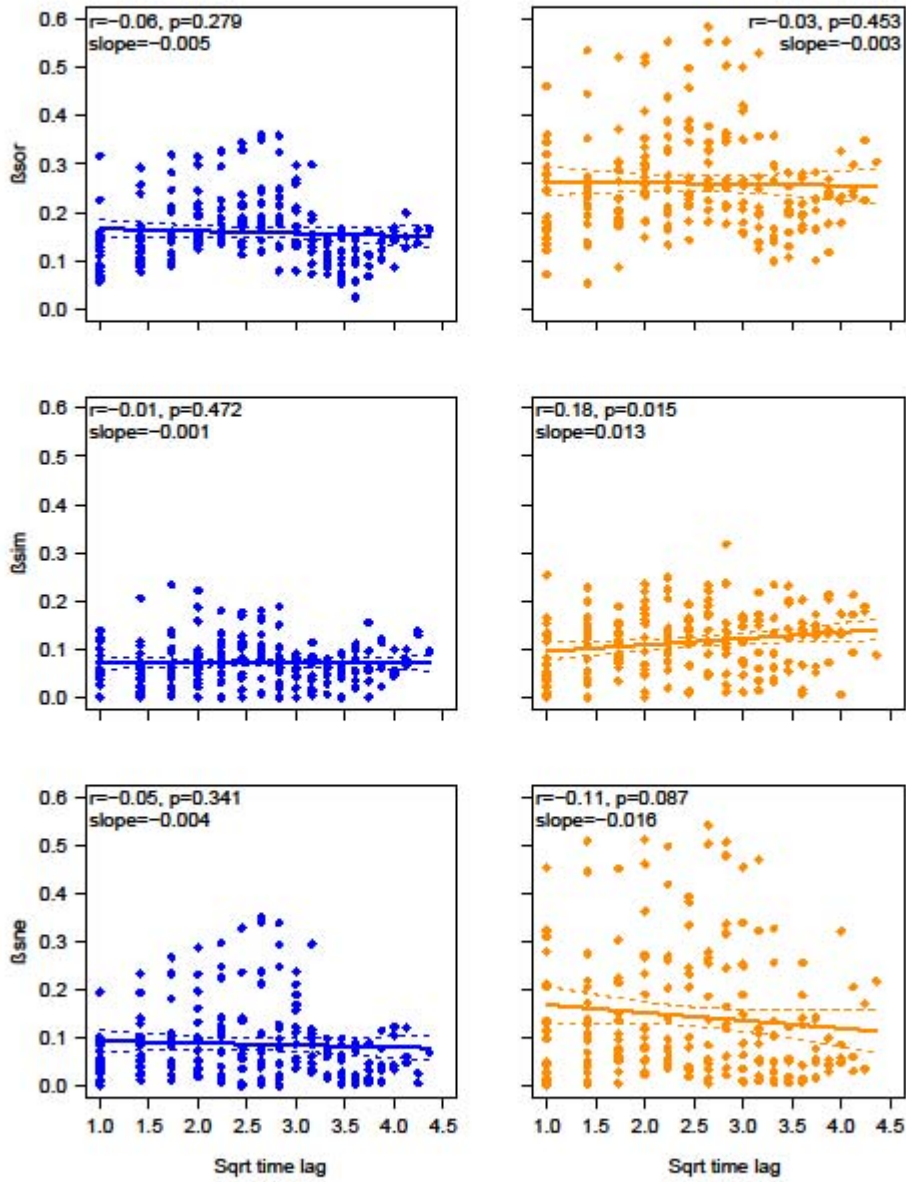
529

530

531

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

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

544

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758

759 **Biosketch**

760 C.L. is a Senior Research Fellow within the Science and Engineering Faculty, Queensland University of  
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767 macroinvertebrates and experimental approaches.

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

772

## 773 **Supporting information**

### 774 ***Appendix S1: Aquatic invertebrate communities***

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

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

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

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

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

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