

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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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 m², 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 (β_{sor}), with
191 assemblage pairs here being the species occurrence lists from any two endpoints for either the
192 drought treatment or control. β_{sor} is then partitioned into components of (ii) temporal turnover (as
193 measured by the Simpson dissimilarity index, β_{sim}) and (iii) temporal nestedness-resultant
194 dissimilarity (β_{sne} , calculated as the difference between β_{sor} and β_{sim}). We calculated these
195 dissimilarity measures using presence-absence data.

196

197 For taxonomic composition, the pairwise beta diversity indices β_{sor} , β_{sim} and β_{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 β_{sor} , β_{sim} and β_{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 (≤ 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 β_{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 β_{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 β 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 β sor vs control F β sor, drought T β sor vs drought F β 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 (Table 2). 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	$T\beta_{sor}$	0.20	0.018	0.271	0.085	0.016	0.130
D	$T\beta_{sor}$	0.31	<0.001	0.299		0.024	
C	$T\beta_{sim}$	0.24	0.004	0.187	0.021	0.021	0.329
D	$T\beta_{sim}$	0.18	0.017	0.233		0.017	
C	$T\beta_{sne}$	0.06	0.292	0.084	0.151	-0.005	0.041
D	$T\beta_{sne}$	0.09	0.148	0.066		0.007	
C	$F\beta_{sor}$	-0.06	0.279	0.171	<0.001	-0.005	0.428
D	$F\beta_{sor}$	-0.03	0.453	0.267		-0.003	
C	$F\beta_{sim}$	-0.01	0.472	0.073	0.259	-0.001	0.012
D	$F\beta_{sim}$	0.18	0.015	0.083		0.013	
C	$F\beta_{sne}$	-0.05	0.341	0.098	0.001	-0.004	0.135
D	$F\beta_{sne}$	-0.11	0.087	0.185		-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}	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	

508

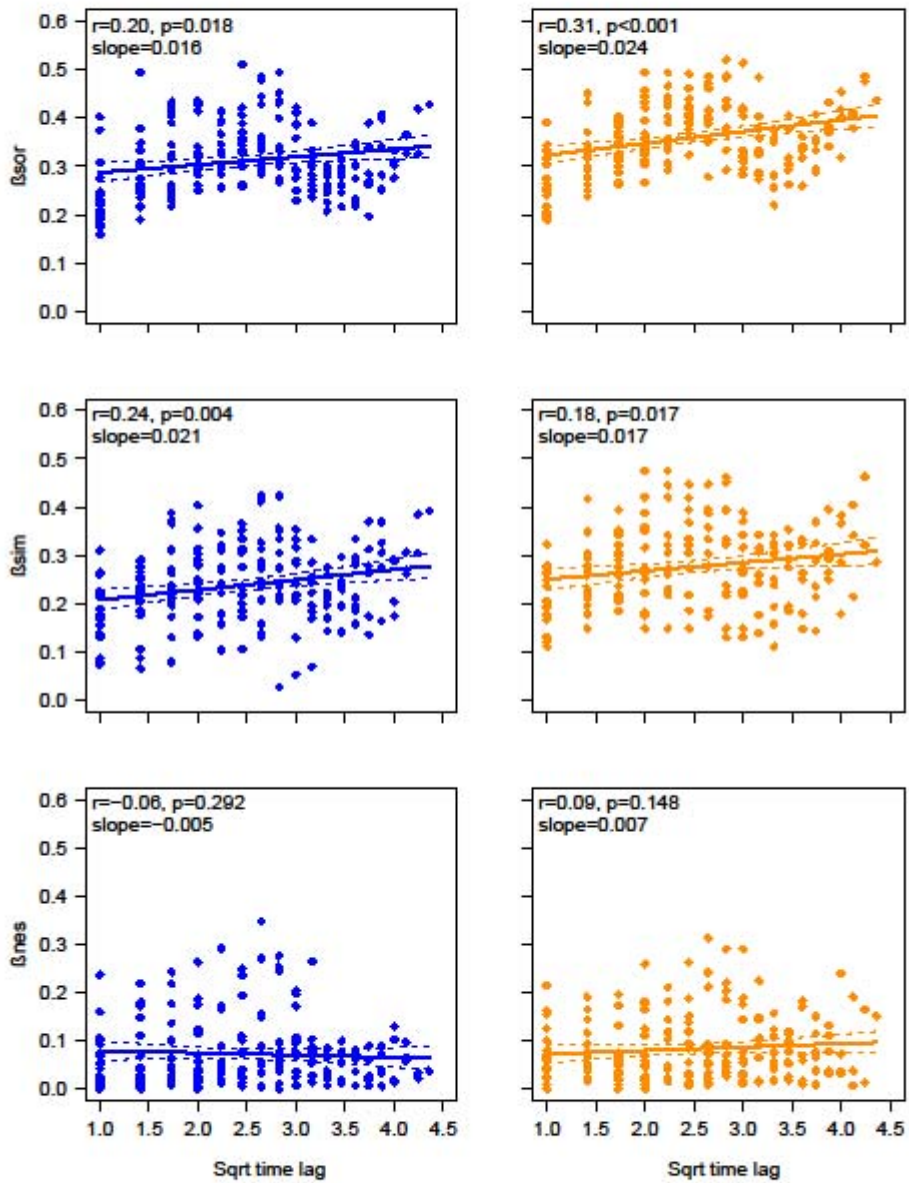
509

510 **Table 3:** Null modelling results. The proportion of z-scores for each temporal beta diversity
 511 component (T β sor, F β sor, F β sim, F β 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.

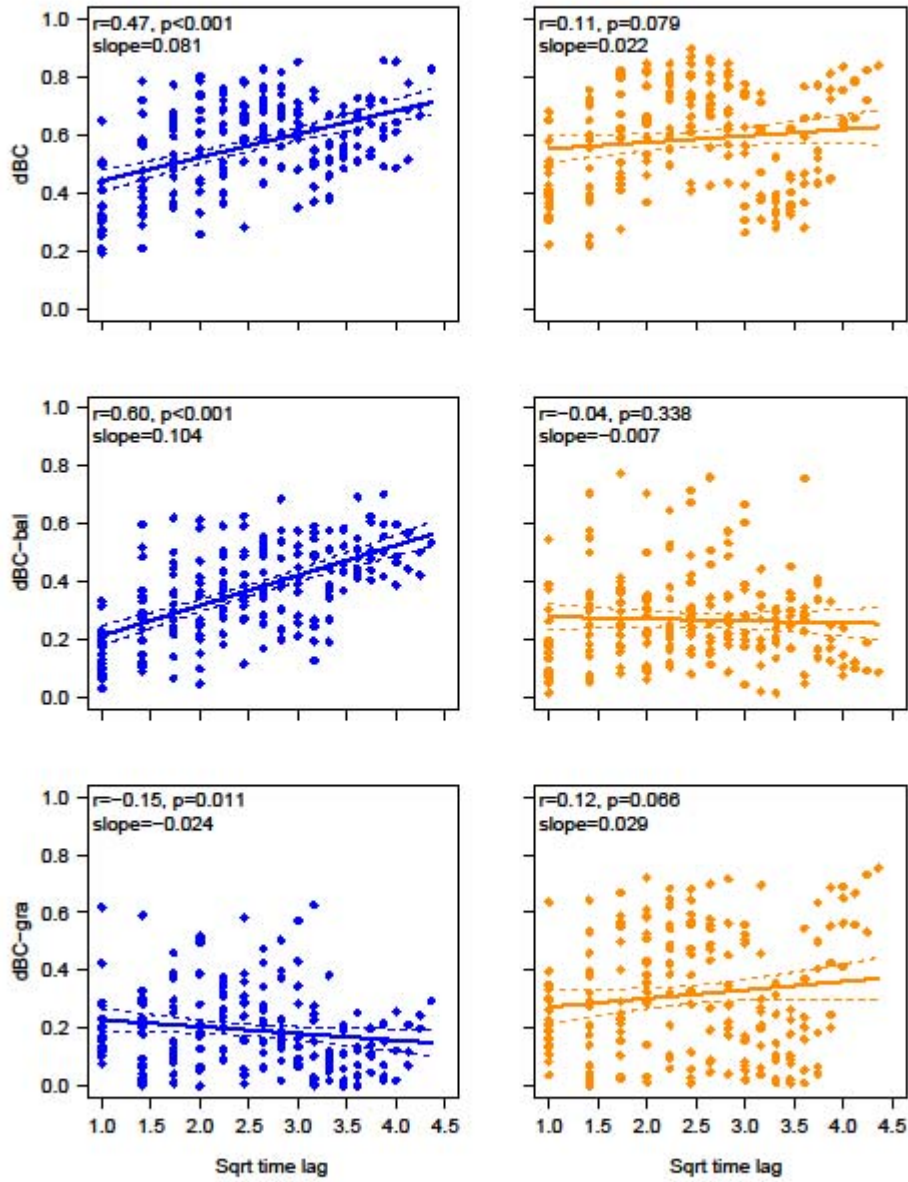
Component	Proportion of all z-scores (C vs D)	Proportion of positive z-scores (C vs D)	Control r (p)	Drought r (p)
T β sor	0.23 vs 0.13	0.13 vs 0.08	0.30 (0.002)	0.33 (< 0.001)
F β sor	0.08 vs 0.25	0.08 vs 0.25	-0.09 (0.174)	-0.10 (0.146)
F β sim	0.17 vs 0.2	0.17 vs 0.2	-0.003 (0.499)	0.12 (0.070)
F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

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 (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.



528

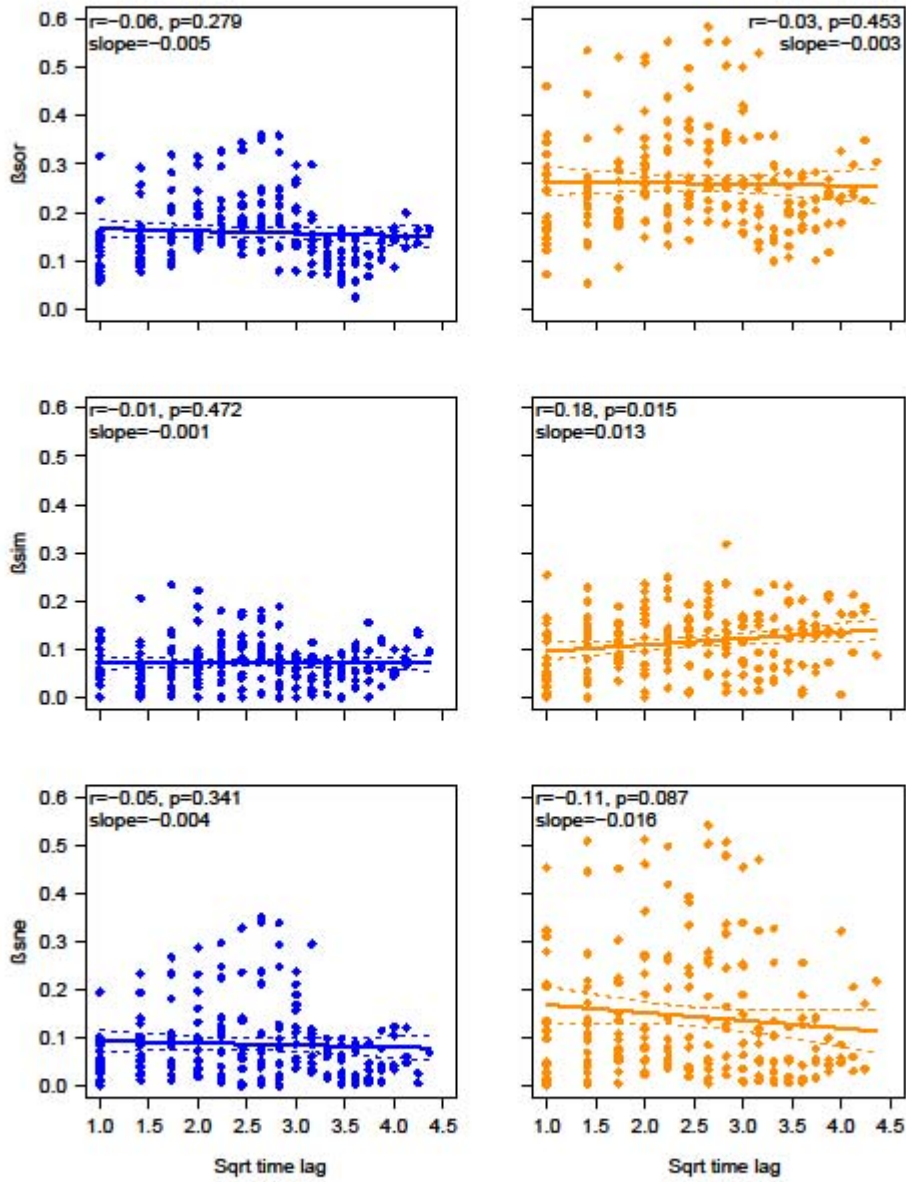
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531

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 (β_{sor}) is shown along with its constituent components
543 turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}). For further details see Figure 1.

544

545 **References**

- 546 Alexander, J. M., Diez, J. M., Hart, S. P. & Levine, J. M. (2016). When climate reshuffles competitors: a
547 call for experimental macroecology. *Trends in Ecology and Evolution*, 31, 831-841.
- 548 Aspin, T. W. H., Matthews, T. J., Khamis, K., Milner, A. M., Wang, Z., O'Callaghan, M. J. & Ledger, M.
549 E. (2018). Drought intensification drives turnover of structure and function in stream
550 invertebrate communities. *Ecography*, 41, 1992-2004.
- 551 Bálint, M., Domisch, S., Engelhardt, C. H. M., Haase, P., Lehrian, S., Sauer, J., ... Nowak, C. (2011).
552 Cryptic biodiversity loss linked to global climate change. *Nature Climate Change*, 1, 313–318.
- 553 Baselga, A. (2010), Partitioning the turnover and nestedness components of beta diversity. *Global*
554 *Ecology and Biogeography*, 19, 134–143.
- 555 Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: balanced
556 changes in abundance vs abundance gradients. *Methods in Ecology and Evolution*, 4, 552–
557 557.
- 558 Baselga, A., Orme, D., Villéger, S., De Bortoli, J., Leprieur, F. (2018). betapart: Partitioning Beta
559 Diversity into Turnover and Nestedness Components. R package version 1.5.0. Retrieved
560 from <https://CRAN.R-project.org/package=betapart>

561 Bishop, T. R., Robertson, M. P., van Rensburg, B. J. & Parr, C. L. (2015). Contrasting species and
562 functional beta diversity in montane ant assemblages. *Journal of Biogeography*, 42, 1776-
563 1786.

564 Boersma, K. S., Bogan, M. T., Henrichs, B. A. & Lytle, D. A. (2014). Invertebrate assemblages of pools
565 in arid-land streams have high functional redundancy and are resistant to severe drying.
566 *Freshwater Biology*, 59, 491–501.

567 Bonada, N., Rieradevall, M. & Prat, N. (2007). Macroinvertebrate community structure and biological
568 traits related to flow permanence in a Mediterranean river network. *Hydrobiologia*, 589, 91-
569 106.

570 Boulton, A. J. & Lake, P. S. (2008). Effects of drought on stream insects and its ecological
571 consequences. In J. Lancaster & R. A. Briers (Eds.), *Aquatic Insects: Challenges to Populations:*
572 *Proceedings of the Royal Entomological Society's 24th Symposium* (pp. 81-102). Wallingford, UK:
573 CAB International.

574 Cadotte, M. W., Carscadden, K. & Mirotnick, N. (2011). Beyond species: functional diversity and
575 the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–
576 1087.

577 Canty, A. & Ripley, B. (2017). Boot: Functions and Datasets for Bootstrapping, Version 1.3-19.
578 Retrieved from <https://cran.r-project.org/web/packages/boot/boot.pdf>

579 Cardinale, B.J., Gross, K., Fritschie, K., Flombaum, P., Fox, J.W., Rixen, C., ... Wilsey, B.J. (2013).
580 Biodiversity simultaneously enhances the production and stability of community biomass,
581 but the effects are independent. *Ecology*, 94, 1697–1707.

582 Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly.
583 *Proceedings of the National Academy of Sciences*, 104, 17430–17434.

584 Chase, J.M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R.D., Holyoak, M., ... Shurin, J.B (2005).
585 Competing theories for competitive metacommunities. In M. Holyoak, M. Leibold & R. D.
586 Holt (Eds.), *Metacommunities: Spatial Dynamics and Ecological Communities* (pp. 335–354).
587 Chicago, IL: University of Chicago Press.

588 Cheng, L., Blanchet, S., Loot, G., Villéger, S., Zhang, T., Lek, S., ... Li, Z. (2014). Temporal changes in the
589 taxonomic and functional diversity of fish communities in shallow Chinese lakes: the effects
590 of river–lake connections and aquaculture. *Aquatic Conservation: Marine and Freshwater
591 Ecosystems*, 24, 23–34.

592 Collins, S. L. (2000). Disturbance frequency and community stability in native tallgrass prairie. *The
593 American Naturalist*, 155, 311–325.

594 Cornwell, W. K., Schilck, D. W. & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex
595 hull volume. *Ecology*, 87, 1465–1471.

596 Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of
597 Favoured Races in the Struggle for Life*. London, UK: John Murray.

598 Döll, P. & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related
599 to the impact on mean annual runoff? A global-scale analysis. *Environmental Research
600 Letters*, 7, 14–37.

601 Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A. E. (2014).
602 Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344, 296-
603 299.

604 Dray, S., Dufour, A. & Thioulouse, J. (2017). ade4: Analysis of Ecological Data- Exploratory and
605 Euclidean Methods in Environmental Sciences, Version 1.7-6. Retrieved from [https://cran.r-
606 project.org/web/packages/ade4/ade4.pdf](https://cran.r-project.org/web/packages/ade4/ade4.pdf)

607 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., ... Sullivan,
608 C.A. (2006). Freshwater biodiversity: importance, threats, status, and conservation
609 challenges. *Biological Reviews*, 81, 163-182.

610 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., ... Tschardtke, T. (2015).
611 Functional identity and diversity of animals predict ecosystem functioning better than species-
612 based indices. *Proceedings of the Royal Society B*, 282, 20142620.

613 Gleick, P. H. (2003). Global freshwater resources: soft-path solutions for the 21st century. *Science*,
614 302, 1524–1528.

615 Harris, R.M., Armitage, P.D., Milner, A.M. & Ledger, M.E. (2007). Replicability of physicochemistry
616 and macroinvertebrate assemblages in stream mesocosms: implications for experimental
617 research. *Freshwater Biology*, 52, 2434–2443.

618 Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., Bello, F. and González, J.A. (2017). Trait-
619 based approaches to analyze links between the drivers of change and ecosystem services:
620 Synthesizing existing evidence and future challenges. *Ecology and Evolution*, 7, 831–844.

621 Hobbs, R. J., Higgs, E. & Harris, J. A. (2009). Novel ecosystems: implications for conservation and
622 restoration. *Trends in Ecology and Evolution*, 24, 599–605.

623 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L., ... O'Connor, M.I.
624 (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change.
625 *Nature*, 486, 105–108.

626 Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ:
627 Jersey Princeton University Press.

628 IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to
629 the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva,
630 Switzerland: IPCC.

631 Jarzyna, M. A. & Jetz, W. (2016a). Detecting the multiple facets of biodiversity. *Trends in Ecology &*
632 *Evolution*, 31, 527–538.

633 Jarzyna, M. A. & Jetz, W. (2016b). A near half-century of temporal change in different facets of avian
634 diversity. *Global Change Biology*, 23, 2999–3011.

635 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C.
636 O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–
637 1464.

638 Kendon, M., Marsh, T. & Parry, S. (2013). The 2010-2012 drought in England and Wales. *Weather* 68,
639 88–95.

640 Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater*
641 *Biology*, 48, 1161–1172.

642 Lancaster, J., Ledger M. E. (2015). Population-level responses of stream macroinvertebrates to drying
643 can be density-independent or density-dependent. *Freshwater Biology*, 60, 2559–2570.

644 Ledger, M. E., Brown, L. E., Edwards, F. K., Milner, A. M. & Woodward, G. (2013). Drought alters the
645 structure and functioning of complex food webs. *Nature Climate Change*, 3, 223–227.

646 Ledger, M. E., Brown, L. E., Edwards, F. K., Milner, A. M. & Woodward, G. (2011). Impact of simulated
647 drought on ecosystem biomass production: an experimental test in stream mesocosms.
648 *Global Change Biology*, 17, 2288–2297.

649 Ledger, M.E., Harris, R.M., Armitage, P.D. & Milner, A.M. (2008). Disturbance frequency influences
650 patch dynamics in stream benthic algal communities. *Oecologia*, 155, 809–819.

651 Ledger, M.E., Harris, R.M., Armitage, P.D. & Milner, A.M. (2009). Realism of model ecosystems: an
652 evaluation of physicochemistry and macroinvertebrate assemblages in artificial streams.
653 *Hydrobiologia*, 617, 91–99.

654 Ledger, M.E., Harris, R.M., Armitage, P.D. & Milner, A.M. (2012). Climate change impacts on
655 community resilience: evidence from a drought disturbance experiment. *Advances in*
656 *Ecological Research*, 46, 211–258.

657 Leigh, C. & Datry, T. (2017). Drying as a primary hydrological determinant of biodiversity in river
658 systems: a broad-scale analysis. *Ecography*, 40, 487–499.

659 Leigh, C., Bonada, N., Boulton, A. J., Hugué, B., Larned, S. T., Vander Vorste, R. & Datry, T. (2016).
660 Invertebrate assemblage responses and the dual roles of resistance and resilience to drying
661 in intermittent rivers. *Aquatic Sciences*, 78, 291–301.

662 Leigh, C., Boulton, A. J., Courtwright, J. L., Fritz, K., May, C. L., Walker, R. H. & Datry, T. (2016).
663 Ecological research and management of intermittent rivers: an historical review and future
664 directions. *Freshwater Biology*, 61, 1181–1199.

665 Leitao, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., ... Mouillot, D. (2016).
666 Rare species contribute disproportionately to the functional structure of species assemblages.
667 *Proceedings of the Royal Society B*, 283, 20160084.

668 Magurran, A. E., Deacon, A. E., Moyes, F., Shimadzu, H., Dornelas, M., Phillip, D. A. T., Ramnarine, I.
669 W. (2018). Divergent biodiversity change within ecosystems. *Proceedings of the National*
670 *Academy of Sciences*, 115, 1843–1847.

671 Maire, E., Grenouillet, G., Brosse, S., Villéger, S. (2015). How many dimensions are needed to
672 accurately assess functional diversity? A pragmatic approach for assessing the quality of
673 functional spaces. *Global Ecology and Biogeography*, 24, 728–740.

674 Marchant, R. (2002). Do rare species have any place in multivariate analysis for bioassessment?
675 *Journal of the North American Benthological Society*, 21, 311–313.

676 Matthews, T. J., Cottee-Jones, H. E. W., & Whittaker, R. J. (2015). Quantifying and interpreting
677 nestedness in habitat islands: a synthetic analysis of multiple datasets. *Diversity and*
678 *Distributions*, 21, 392–404.

679 Matthews, T.J., Sadler, J., Carvalho, R., Nunes, R. and Borges, P.A., 2018. Differential temporal beta-
680 diversity patterns of native and non-native arthropod species in a fragmented native forest
681 landscape. *Ecography*, doi:10.1111/ecog.03812

682 McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from
683 functional traits. *Trends in Ecology & Evolution*, 21, 178–185.

684 Melo, A. S. (2016). CommEcol: Community Ecology Analyses, Version 1.6-4. Retrieved from
685 <https://cran.r-project.org/web/packages/CommEcol/CommEcol.pdf>

686 Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., ... Wagner, H.
687 (2018). vegan: Community Ecology Package. R package version 2.5-2. Retrieved from
688 <https://CRAN.R-project.org/package=vegan>

689 Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E. & Fausch, K. D. (2004). Ecological and
690 evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, 19, 18–
691 24.

692 Palmer, M. A. & Poff, N. L. (1997). The influence of environmental heterogeneity on patterns and
693 processes in streams. *Journal of the North American Benthological Society*, 16, 169–173

694 Parry, S., Hannaford, J., Lloyd-Hughes, B. & Prudhomme, C. (2012). Multi-year droughts in Europe:
695 analysis of development and causes. *Hydrology Resources*, 43, 689–706.

696 Pavoine, S., Vallet, J., Dufour, A. B., Gachet, S. & Daniel, H. (2009). On the challenge of treating
697 various types of variables: application for improving the measurement of functional
698 diversity. *Oikos*, 118, 391–402.

699 Pearse, W. D., Barbosa, A. M., Fritz, S. A., Keith, S. A., Harmon, L. J., Harte, J., ... Davies, T. J. (2018).
700 Building up biogeography: pattern to process. *Journal of Biogeography*,
701 doi:10.1111/jbi.13242

702 Prudhomme, C., Giuntoli, I., Robinson, E.L., Clark, D.B., Arnell, N.W., Dankers, R., ... Hagemann, S.
703 (2014). Hydrological droughts in the 21st century, hotspots and uncertainties from a global
704 multimodel ensemble experiment. *Proceedings of the National Academy of Sciences*, 111,
705 3262–3267.

706 Rahel, F. J. (2002). Homogenization of freshwater faunas. *Annual Review of Ecology and Systematics*,
707 33, 291–315.

708 R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for
709 *Statistical Computing*, Vienna, Austria. Retrieved from <https://www.R-project.org/>

710 Robson, B. J., Chester, E. T. & Austin, C. M. (2011). Why life history information matters: drought
711 refuges and macroinvertebrate persistence in non-perennial streams subject to a drier
712 climate. *Marine and Freshwater Research*, 62, 801–810.

713 Roudier, P., Andersson, J. C., Donnelly, C., Feyen, L., Greuell, W. & Ludwig, F. (2016). Projections of
714 future floods and hydrological droughts in Europe under a + 2° C global warming. *Climatic
715 Change*, 135, 341–355.

716 Ruhí, A., Datry, T. & Sabo, J. L. (2017). Interpreting beta diversity components over time to conserve
717 metacommunities in highly dynamic ecosystems. *Conservation Biology*, 31, 1459–1468.

718 Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T. & Bonada, N. (2017). Do
719 metacommunities vary through time? Intermittent rivers as model systems. *Journal of*
720 *Biogeography*, 44, 2752–2763.

721 Säterberg, T., Sellman, S. & Ebenman, B. (2013). High frequency of functional extinctions in
722 ecological networks. *Nature*, 499, 468–470.

723 Schriever, T.A., Bogan, M.T., Boersma, K.S., Cañedo-Argüelles, M., Jaeger, K.L., Olden, J.D. & Lytle,
724 D.A. (2015). Hydrology shapes taxonomic and functional structure of desert stream
725 invertebrate communities. *Freshwater Science*, 34, 399–409.

726 Socolar, J. B., Gilroy, J. J., Kunin, W. E. & Edwards, D. P. (2016). How should beta-diversity inform
727 biodiversity conservation? *Trends in Ecology & Evolution*, 31, 67–80.

728 Spasojevic, M. J., Catano, C. P., LaManna, J. A. & Myers, J. A. (2018). Integrating species traits into
729 species pools. *Ecology*, 99, 1265-1276.

730 Stubbington, R., Bogan, M.T., Bonada, N., Boulton, A.J., Datry, T., Leigh, C. & Vander Vorste, R.
731 (2017). The biota of intermittent rivers and ephemeral streams: aquatic invertebrates. In T.
732 Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams* (pp. 217–
733 243). London, UK: Elsevier.

734 Tonkin, J.D., Bogan, M.T., Bonada, N., Rios-Touma, B. & Lytle, D.A. (2017). Seasonality and
735 predictability shape temporal species diversity. *Ecology*, 98, 1201–1216.

736 Trenberth, K. E., Dai A., van der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R. & Sheffield, J.
737 (2014). Global warming and changes in drought. *Nature Climate Change*, 4, 17–22.

738 Ulrich, W. & Gotelli, N. J. (2007). Null model analysis of species nestedness patterns. *Ecology*, 88,
739 1824–1831.

740 Usseglio-Polatera, P., Bournaud, M., Richoux, P. & Tachet, H. (2000). Biological and ecological traits
741 of benthic freshwater macroinvertebrates: relationships and definition of groups with similar
742 traits. *Freshwater Biology*, 43, 175–205.

743 Villéger, S., Grenouillet, G. & Brosse, S. (2013). Decomposing functional β -diversity reveals that low
744 functional β -diversity is driven by low functional turnover in European fish assemblages.
745 *Global Ecology and Biogeography*, 22, 671–681.

746 Villéger, S., Grenouillet, G. & Brosse, S. (2014). Functional homogenization exceeds taxonomic
747 homogenization among European fish assemblages. *Global Ecology and Biogeography*, 23,
748 1450–1460.

749 Villéger, S., Mason, N. W. & Mouillot, D. (2008). New multidimensional functional diversity indices
750 for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301.

751 Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., ... Davies, P.M.
752 (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555–561.

753 Wright, J. F. (1992). Spatial and temporal occurrence of invertebrates in a chalk stream, Berkshire,
754 England. *Hydrobiologia*, 248, 11–30.

755 Wright, J. F., Hiley, P. D., Cooling, D. A., Cameron, A. C., Wigham, M. E. & Berrie, A. D. (1984). The
756 invertebrate fauna of a small chalk stream in Berkshire, England, and the effect of
757 intermittent flow. *Archiv für Hydrobiologie*, 99, 176–199.

758

759 **Biosketch**

760 C.L. is a Senior Research Fellow within the Science and Engineering Faculty, Queensland University of
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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⁻² in the control and from 3373 to 35370 ind. m⁻² 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 (β_{sor}) and its constituent components,
799 turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{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.).