

1 **How freshwater biomonitoring tools vary sub-seasonally reflects temporary river flow regimes.**

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3 **Running head:** Biomonitoring tool responses to temporary river flow regimes

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25 **Abstract**

26 Characterizing temporary river ecosystem responses to flow regimes is vital for conserving their biodiversity  
27 and the suite of services provided to society. However, freshwater biomonitoring tools rarely reflect  
28 community responses to hydrological variations or flow cessation events, and those available have not been  
29 widely tested within temporary rivers. This study examines two invertebrate biomonitoring tools  
30 characterizing community responses to different flow-related properties: the ‘Drought Effect of Habitat Loss  
31 on Invertebrates’ (DEHLI) and ‘Lotic-invertebrate Index for Flow Evaluation’ (LIFE), which respectively  
32 reflect community responses to habitat and hydraulic properties associated with changing flow conditions.  
33 Sub-seasonal (monthly) variations of LIFE and DEHLI were explored within two groundwater-fed intermittent  
34 rivers, one dries sporadically (a flashy, karstic hydrology - TR1) and the other dries seasonally (a highly  
35 buffered flow regime - TR2). Biomonitoring tools were highly sensitive to channel drying and also responded  
36 to reduced discharges in permanently flowing reaches. Biomonitoring tools captured ecological recovery  
37 patterns in TR1 following a supra-seasonal drought. Some unexpected results were observed in TR2 where  
38 LIFE and DEHLI indicated relatively high-flow conditions despite low discharges being observed during some  
39 summer months. This probably reflected macrophyte encroachment which benefitted certain invertebrates (e.g.  
40 marginal-dwelling taxa) and highlights the importance of considering instream habitat conditions when  
41 interpreting flow regime influences on biomonitoring tools. Although LIFE and DEHLI were positively  
42 correlated, the latter responded more clearly to drying events, highlighting that communities respond strongly  
43 to the disconnection of instream habitats as flows recede. The results highlighted short-term ecological  
44 responses to hydrological variations and the value in adopting sub-seasonal sampling strategies within  
45 temporary rivers. Findings from this study indicate the importance of establishing flow response guilds which  
46 group taxa that respond comparably to flow cessation events. Such information could be adopted within  
47 biomonitoring practices to better characterize temporary river ecosystem responses to hydrological variations.

## 48 **Introduction**

49 Temporary rivers are broadly defined as lotic environments that periodically experience flow cessation  
50 events and potentially the partial or complete loss of surface waters (Datry *et al.*, 2017). Temporary  
51 rivers occur in various forms worldwide as a result of both natural (e.g. climate and geology) and  
52 anthropogenic (e.g. water resource management operations) controls. Temporary rivers are estimated  
53 to comprise at least 50% of the global river network and are projected to become more widespread  
54 through future climatic change and societal water demands (Datry *et al.*, 2014; 2017). In recent years,  
55 a growing body of research has illustrated the high biodiversity supported by transitions between  
56 flowing, ponded and dry conditions (Meyer *et al.*, 2007; Steward *et al.*, 2011; Hill and Milner, 2018),  
57 as well as the suite of ecosystem services provided by temporary rivers (Steward *et al.*, 2012; Datry *et*  
58 *al.*, 2018; Stubbington *et al.*, 2018b). Despite this, temporary rivers have historically received limited  
59 research attention compared to their perennial counterparts (Leigh *et al.*, 2016) and there remains a lack  
60 of evidence indicating reliable ways of characterizing ecological responses to flow regime variations in  
61 temporary rivers.

62 A lack of ecological and hydrological evidence available globally constrains the ability to effectively  
63 manage river flow regimes capable of supporting healthy riverine ecosystems (Poff *et al.*, 2010; Chen  
64 and Olden, 2018). As such, there is a growing need to derive robust and spatially transferrable  
65 relationships between flow regime properties and ecological responses which can inform how water  
66 resources could be balanced to support societal and riverine ecosystem demands (Chen and Olden,  
67 2018). Flow response guilds, defined as groups of taxa which respond to water availability and fluvial  
68 disturbance in similar ways (Lytle *et al.* 2017), have been found to reliably characterize ecological  
69 responses to hydrological controls (Lytle *et al.*, 2017; White *et al.*, 2017; Chen and Olden, 2018).  
70 Despite this, flow response guilds have rarely been incorporated into biomonitoring practices, which  
71 predominantly focus on the sensitivity of taxa to water quality parameters (Carter *et al.*, 2006; Bonada  
72 *et al.*, 2006; Birk *et al.*, 2012). This significantly hinders the management and conservation of riverine  
73 ecosystems where the water quality of riverine environments may not pose the limiting stressor to

74 aquatic ecosystems, which are instead constrained by other anthropogenic pressures (e.g. flow  
75 alterations – Matthaei *et al.*, 2010; White *et al.*, 2017).

76 Within the United Kingdom (UK), two biomonitoring tools exist which characterize different flow  
77 response guilds of aquatic invertebrate communities: the ‘Lotic-invertebrate Index for Flow Evaluation’  
78 (LIFE; Extence *et al.*, 1999) and ‘Drought Effect of Habitat Loss on Invertebrates’ (DEHLI; Chadd *et*  
79 *al.*, 2017). LIFE characterizes the preferences of invertebrate taxa to flow velocities and has been  
80 historically utilized by UK regulatory bodies (principally the Environment Agency – the environmental  
81 regulator of England) to guide water abstraction licencing and track the ecological effects of droughts  
82 (Monk *et al.*, 2006; Klaar *et al.*, 2014). LIFE is calculated by assigning taxa to one of six flow response  
83 guilds incorporating ‘rapid’ flow conditions to ‘dry or drought impacted’ environments (Extence *et al.*,  
84 1999). However, LIFE scores have been found to respond inconsistently to flow cessation events  
85 (Chadd *et al.*, 2017), particularly when flow velocity preferences of individual taxa may not reflect the  
86 hydraulic conditions present during drying events (Wilding *et al.*, 2018). DEHLI was developed to  
87 address this issue by assigning invertebrate taxa into one of six flow-habitat groups (flow response  
88 guilds) typically lost sequentially during flow cessation and drying events based on their ecological  
89 preferences (building on the conceptual models and research of Boulton, 2003 and Boulton and Lake,  
90 2008 - Chadd *et al.*, 2017). However, thus far LIFE or DEHLI have not been widely tested in temporary  
91 rivers and it remains unclear how these biomonitoring tools respond to flow cessation events (but see  
92 Chadd *et al.*, 2017; Wilding *et al.*, 2018).

93 Studies examining the ecological structure and functioning of temporary rivers, as well as  
94 biomonitoring tools specifically, have typically adopted seasonally targeted sampling programmes (e.g.  
95 García-Roger *et al* 2011; Cid *et al.*, 2016; Garcia *et al.*, 2018; Wilding *et al.*, 2018). However, such  
96 sampling strategies may not adequately capture temporal trajectories of ecological change occurring  
97 within or between different seasons, such as the rapid recolonization of taxa and biological  
98 transformations occurring following the resumption of flowing conditions (e.g. Ledger and Hildrew,  
99 2001; Bogan *et al.*, 2015; Leigh *et al.*, 2019) or multiple flow cessation events occurring intra-annually  
100 (e.g. Stubbington *et al.*, 2016; Hill and Milner, 2018). As such, ecological responses and changes to

101 biomonitoring tool scores associated with flow regime variations in temporary rivers may not be  
102 adequately captured by traditional seasonal sampling strategies. Thus, studies examining short-term  
103 ecological responses to hydrological variations, and flow cessation events specifically, are needed in  
104 temporary rivers to facilitate a more detailed understanding of ecosystem responses to changing flow  
105 regime conditions and the implications this has for biomonitoring programmes. However, examples of  
106 sub-seasonal sampling campaigns within temporary rivers are limited globally (rare examples include  
107 Davey and Kelly, 2007; Storey and Quinn, 2008; Arscott *et al.*, 2010; Stubbington *et al.*, 2016; Hill and  
108 Milner, 2018) and are even less common for biomonitoring tools (but see Chadd *et al.*, 2017). To  
109 address this research gap, this study examines how invertebrate biomonitoring tool scores vary sub-  
110 seasonally and how this corresponds with community temporal transformations and flow regime  
111 variations within two temporary rivers.

## 112 **Materials and methods**

### 113 *Study area*

114 The sub-seasonal (monthly) variations of biomonitoring tools (LIFE and DEHLI) were explored using  
115 two case study temporary rivers in the UK and compared to invertebrate community temporal  
116 trajectories and hydrological variations. Invertebrate samples were collected at monthly intervals over  
117 a c. 1-year period in each case study: the River Lathkill, Derbyshire (December 2011 and November  
118 2012), and the South Winterbourne, Dorset (June 1974 and July 1975; see Fig. 1). The drying patterns  
119 within the R. Lathkill and South Winterbourne differ markedly and ecological data was collected during  
120 hydrologically dissimilar time periods (see below). As a result, the case studies provide independent  
121 opportunities to examine the sensitivity of biomonitoring tools (LIFE and DEHLI) to changes in aquatic  
122 invertebrate communities associated with varying river flow conditions and drying events.

### 123 *River Lathkill*

124 The River Lathkill (and its tributary Cales Dale) was sampled monthly between December 2011 and  
125 November 2012 (except October 2012) from 10 sampling locations (Fig. 1a). In total, 96 samples were  
126 collected, 26 of which were collected from 3 sites that dried during the study period (the remaining 7

127 flowed continuously during the study period). The environmental characteristics of the study sites and  
128 the hydrological conditions within the R. Lathkill prior to and during the sampling period have been  
129 detailed elsewhere (Stubbington *et al.*, 2016) and are summarised here. The R. Lathkill rises from a  
130 carboniferous limestone outcrop and the karstic nature of the underlying bedrock facilitates rapid  
131 hydrological responses to individual rainfall events. The fast draining of the underlying aquifer often  
132 results in low groundwater levels following periods of low rainfall which causes channel drying along  
133 different sections of the R. Lathkill. This is further exacerbated by subterranean anthropogenic drainage  
134 networks constructed to transfer water away from historic lead mines, which reduces the water table  
135 below its natural level (Wood *et al.*, 2005; Ford and Rieuwerts, 2007). Land use across the catchment  
136 during the study period was (and remains) predominantly low intensity grazing on unimproved  
137 grassland (Stubbington *et al.*, 2016). The headwater sites (A-C) typically remain dry for *c.*>6 months  
138 annually, while all other sites (D-J, Fig. 1a) flow for longer periods (some of which dry every summer  
139 and others dry only during extreme droughts – see Wood *et al.*, 2005; Stubbington *et al.*, 2016 for  
140 further site information). The study period coincided with a significant supra-seasonal drought which  
141 affected large parts of central England between December 2010-April 2012 (see Parry *et al.*, 2013). The  
142 extended drought period caused all study sites to dry for the majority of 2011, until significant winter  
143 rainfall triggered the resumption of flowing conditions across all sampling sites during winter 2011-  
144 2012. The presence/absence of flow was recorded at *c.* monthly intervals during the study period (Fig.  
145 2a), although staff (rangers) within the National Nature Reserve and a water level recorder (maintained  
146 by Prof John Gunn, University of Birmingham, UK) also provide regular measurements on the  
147 hydrological conditions along the study reaches (Fig. 2b). Such information highlighted that only sites  
148 A-C experienced drying events on three separate occasions for *c.* 28, 39 and 46 days in mid-March,  
149 mid-May and early-August (2012), respectively (although Site C did not dry during March – Fig. 2a;  
150 Stubbington *et al.*, 2016). Atypical heavy rainfall and high discharges occurred at several points during  
151 the sampling period (Fig. 2b).

152 Invertebrates were collected using three-minute kick samples (using a pond net with a 1 mm mesh), with  
153 sampling effort being divided equally between the mesohabitats present. Specimens were preserved in

154 the field using 4% formaldehyde solution prior to processing and identification in the laboratory.  
155 Invertebrate taxa were identified to the lowest practical taxonomic resolution, which was predominantly  
156 species level; although Leuctridae, Baetidae, Sphaeriidae, Gerridae, Dytiscidae, Gyrinidae, Planariidae,  
157 Zonitiidae and various Dipterans were resolved to family level, while Oligochaeta, Tricladida (non-  
158 Planariidae) and Collembola were recorded as such.

#### 159 *South Winterbourne*

160 Monthly invertebrate community samples were collected from 12 locations along the South  
161 Winterbourne (Fig. 1b) between June 1974 and July 1975, whereby the total extent of flowing and dry  
162 reaches was recorded upon each sampling event (Fig. 2a). In total, 152 samples were collected, 58 of  
163 which were collected from 5 sites that dried during the study period. The South Winterbourne is  
164 predominantly underlain by a chalk ( $\text{CaCO}_3$ ) lithology and drying occurs along the river in response to  
165 seasonal fluctuations in the water table (Sear *et al.*, 1999). In contrast to the limestone underlying the  
166 R. Lathkill (see above), the chalk provides a highly buffered hydrological response to rainfall events  
167 (Sear *et al.*, 1999). Landuse across the South Winterbourne is predominantly a mixture of arable  
168 agriculture and grassland (NRFA, 2019b), and this has changed minimally across the catchment since  
169 the study period (Jon Bass, *Personal observation*). The South Winterbourne exhibits a seasonally  
170 variable flow regime, with peak discharges typically occurring between late winter and early spring,  
171 before declining over the summer and autumn months (Casey and Ladle, 1976; Armitage and Bass,  
172 2013). Temporary sites along the South Winterbourne dried in summer-autumn 1974 (Watkinson *et al.*,  
173 1994 – Figs. 2c and 2d), typical of flow cessation events experienced inter-annually along the river and  
174 other headwater chalk streams (Armitage and Bass, 2013). The South Winterbourne is one of few rivers  
175 regionally which dry within the mid-reaches (most others dry longitudinally downstream from the  
176 headwaters – White *et al.*, 2018), which occurs due to inflowing springs and flow augmentation schemes  
177 operated in the headwaters by the regional water company (Watkinson *et al.*, 1994; Armitage and Bass,  
178 2013; Fig. 1b). High nutrient levels within the South Winterbourne (typical of chalk streams regionally  
179 – White *et al.*, 2018) resulted in a diverse macrophyte community (including *Ranunculus* sp., *Callitriche*

180 sp., *Rorippa* sp., *Apium/Berula* sp.) being recorded along the length of the South Winterbourne during  
181 the study period (Watkinson et al., 1994).

182 Invertebrates were collected *via* three-minute kick samples (as above), with an additional 1-minute hand  
183 search being performed on bed features difficult to disturb via kicking (e.g. larger substrates; Murray-  
184 Bligh, 1999, ISO, 2012). Invertebrate taxa were identified to the lowest practical taxonomic resolution,  
185 which was predominantly species level; although certain Diptera and Coleoptera were recorded at  
186 family-level, along with Libellulidae, Notonectidae, Corixidae, Lepidostomatidae Limnephilidae and  
187 Leptoceridae, while Oligochaeta, Ostracoda and Cladocera were identified as such. Invertebrate data  
188 from the South Winterbourne was recorded in a presence-absence format.

### 189 *Biological information*

190 In total, four presence-absence matrices (two from each temporary river case study) were examined,  
191 with abundance data from the R. Lathkill being transformed to presence-absence to enable direct  
192 comparisons with the recording of taxa from the South Winterbourne. For both the R. Lathkill and  
193 South Winterbourne, community compositions containing taxa resolved to the lowest practical  
194 resolution (respective to each study) was examined ('species-level' dataset). In addition, all taxa  
195 comprising each case study were aggregated to 'family-level' (except for those identified to a coarser  
196 resolution which were retained in their original format), with both species- and family-level datasets  
197 being explored to examine the temporal variations of invertebrate communities at different taxonomic  
198 resolutions. The 'Lotic-invertebrate Index for Flow Evaluation' (LIFE - Extence *et al.*, 1999) score was  
199 calculated for all samples from both case studies at family- (Family LIFE) and species-level (Species  
200 LIFE). For calculating the 'Drought Effect of Habitat Loss on Invertebrates' (DEHLI) index, taxa  
201 recorded within the species-level dataset were harmonized with the taxonomic resolution required for  
202 calculating DEHLI, which predominantly utilizes family-level data but with some/ genus-level  
203 classifications (Chadd *et al.*, 2017). Lower biomonitoring tool scores indicate changing hydraulic  
204 (Family LIFE and Species LIFE) and habitat conditions (DEHLI) as flow velocities and water levels  
205 (and associated stages of habitat connectivity) are reduced, respectively.



206 *Data analyses*

207 All statistical analyses reported herein were performed in R studio (operated within R version 3.3.1; R  
208 Development Core Team, 2014). Multivariate differences in invertebrate community compositions  
209 between monthly sampling periods for both case studies were tested *via* a ‘Permutational Analysis of  
210 Variance’ (PERMANOVA) using the ‘*adonis*’ function in the Vegan package (Oksanen *et al.*, 2017).  
211 Pairwise PERMANOVA was used to test how communities differed between successive months.  
212 ‘Principal Coordinate Analysis’ (PCoA) plots were constructed using a Sorenson dissimilarity index to  
213 visualize community differences between months and were performed using the ‘*cmdscale*’ function in  
214 Vegan. The correlation between PCoA axis scores and each of the three biomonitoring tools, as well as  
215 between each paired combination of biomonitoring tools, were tested *via* the ‘*cor.test*’ function, with a  
216 Pearson’s correlation coefficient being utilized.

217 Temporal variations of biomonitoring tools were visualized separately for sites which dried and flowed  
218 continuously across the duration of each temporary river case study (it should be noted that individual  
219 sites are not defined as ‘temporary’ or ‘perennial’ to avoid differences in classification and  
220 nomenclature established in previous studies – see Stubbington *et al.*, 2016). In total, six Generalized  
221 Additive Mixed-Effect Models (GAMMs) were utilized to examine how each biomonitoring tool varied  
222 spatially and temporally within each case study (i.e. a separate GAMM for each biomonitoring tool  
223 within each case study). All GAMMs were fitted using the ‘*gam*’ function in the mgcv package  
224 (Wood, 2017). Each biomonitoring tool (response) was modelled as a smooth function of both time and  
225 the distance from the downstream perennial source (km) of each river, which were fitted using cubic  
226 splines. Study site was specified as a random effect within all models to reflect the fact that community  
227 compositions from individual sites may be correlated over time (Mathers *et al.*, 2016). This was  
228 determined as the optimal random effect structure in all instances, with pairwise comparisons between  
229 each GAMM and a respective model exhibiting the same formula, but without a random effect (also  
230 using the *gam* function) revealing that the former possessed ‘Akaike Information Criterion’ (AIC)  
231 values at least 2 units lower in all instances (Burnham and Anderson, 2002). GAMM outputs were  
232 visualized using the ‘*persp*’ function in the plotrix package (Lemon *et al.*, 2018).

## 233 **Results**

### 234 *Temporal and spatial variations in community compositions*

#### 235 *River Lathkill*

236 PERMANOVA highlighted that the invertebrate community compositions exhibited highly significant  
237 differences ( $p\text{-value} \leq 0.001$ ) between monthly sampling periods (Family:  $r^2 = 0.31$ ,  $F = 3.84$ ; Species:  
238  $r^2 = 0.32$ ,  $F = 3.91$ ) in the R. Lathkill. Pairwise PERMANOVA testing for differences in invertebrate  
239 community compositions between successive months indicated significant changes between February  
240 and March (Family:  $r^2 = 0.13$ ,  $F = 2.31$ ,  $p\text{-value} = 0.039$ ; Species:  $r^2 = 0.16$ ,  $F = 2.77$ ;  $p\text{-value} = 0.003$ );  
241 August and September (Family:  $r^2 = 0.28$ ,  $F = 5.51$ ,  $p\text{-value} = 0.002$ ; Species:  $r^2 = 0.25$ ,  $F = 4.61$ ;  $p\text{-}$   
242  $value = 0.001$ ) and September and November (Family:  $r^2 = 0.20$ ,  $F = 3.57$ ,  $p\text{-value} = 0.027$ ). Principal  
243 Coordinate Analysis (PCoA) highlighted clear shifts in invertebrate communities between successive  
244 months moving from left to right along axis 1 (explaining 25.07-31.40% of the overall variance)  
245 associated with increasing time lapses since the last drying event (and shifts from right to left occurring  
246 after drying events in March, May and August; see Fig. 3a). Invertebrate communities inhabiting sites  
247 that dried during the study period displayed lower PCoA axis 1 scores, while the sites that flowed  
248 continuously exhibited higher axis 1 scores (see Supplementary Material, Appendix A, Fig. A1). PCoA  
249 also indicated an increase in axis 2 scores (explaining 17.50-19.82% of the overall variance) throughout  
250 the study period in the R. Lathkill. Highly significant ( $p\text{-value} \leq 0.001$ ) positive correlations were  
251 observed between PCoA axis 1 scores (for both family- and species-level ordinations) versus DEHLI,  
252 Family LIFE and Species LIFE scores, while only DEHLI exhibited a significant (low, negative)  
253 correlation with axis 2 scores (Table 1).

#### 254 *South Winterbourne*

255 Within the South Winterbourne, PERMANOVA indicated highly significant differences ( $p\text{-values} \leq$   
256  $0.001$ ) between monthly averaged community compositions (Family:  $r^2 = 0.20$ ,  $F = 2.62$ ; Species:  $r^2 =$   
257  $0.18$ ,  $F = 2.30$ ), although this exhibited a slightly lower explanatory power compared to models from  
258 the R. Lathkill. Pairwise PERMANOVA highlighted that no community centroids differed significantly

259 between successive months on the South Winterbourne. PCoA indicated that the summer and autumn  
260 months of 1974 were characterised by high axis 1 scores (explaining 21.30-25.07% of the overall  
261 statistical variance), although no clear trends were evident in axis 2 scores (explaining 13.08 -14.15%  
262 of the overall statistical variance; Fig. 3b). A large shift from right to left along axis 1 occurred between  
263 September and October, and community centroids displayed lower and higher axis 1 and 2 scores  
264 thereafter, respectively (Fig. 3b). PCoA indicated no clear distinction between invertebrate community  
265 compositions inhabiting sites which dried and those which flowed continuously along the South  
266 Winterbourne (see Supplementary Material, Appendix A, Fig. A2). Highly significant ( $p\text{-value} \leq 0.001$ )  
267 positive correlations were recorded between PCoA axis 1 values (for both family- and species-level  
268 ordinations) versus DEHLI, Family LIFE and Species LIFE scores from the South Winterbourne (Table  
269 1).

## 270 *Temporal and spatial variations in biomonitoring tools*

### 271 *River Lathkill*

272 For the R. Lathkill, correlations between each pairwise combination of biomonitoring indices were all  
273 highly significant ( $p\text{-value} < 0.001$ ) and highlighted that DEHLI versus Family LIFE ( $r = 0.80$ ,  $t = 13.21$ )  
274 and Family LIFE versus Species LIFE ( $r = 0.84$ ,  $t = 14.77$ ) exhibited strong positive correlations, while  
275 DEHLI versus Species LIFE displayed a moderate-strong positive correlation ( $r = 0.66$ ,  $t = 8.62$ ).  
276 Biomonitoring tool values generally increased within reaches that flowed continuously between winter  
277 2011-2012 and summer 2012, before declining between June and July 2012 and displaying temporally  
278 stable values thereafter (Fig. 4a; see Supplementary Material, Appendix A, Fig. A3). Biomonitoring  
279 scores were consistently lower at sites which dried compared those which flowed continuously,  
280 although DEHLI scores displayed more pronounced differences compared to Family LIFE and Species  
281 LIFE (Fig. 4a). In addition, biomonitoring tools (most notably DEHLI) displayed more marked changes  
282 between successive months at sites which dried relative to continuously flowing reaches (Fig. 4a). This  
283 was particularly evident for March 2012, when all biomonitoring tools displayed a large increase at one  
284 site which dried (the other two headwater sites were completely dry at this time – see Fig. 1a) compared  
285 to the preceding month (see Fig. 4a and Supplementary Material, Appendix A, Fig. A3). Sites which

286 dried along the R. Lathkill yielded DEHLI scores that declined substantially between April and May  
287 2012 (but only one of the three sites which dried in the R. Lathkill was sampled in May 2-days before  
288 the site dried) and between September and November 2012 (see Fig. 4a and Supplementary Material,  
289 Appendix A, Figs. A3a-c). GAMM outputs indicated significant temporal and spatial variations  
290 (indicated by the distance from the perennial source) for each biomonitoring tool on the R. Lathkill  
291 (Table 2). GAMM outputs highlighted that DEHLI scores from the R. Lathkill sharply increased until  
292 spring 2012 and were less variable towards the end of the study period, with values being consistently  
293 highest in the mid-reaches (Fig. 5a).

#### 294 *South Winterbourne*

295 Within the South Winterbourne, highly significant ( $p$ -values  $<0.001$ ), strong positive correlations  
296 occurred between all biomonitoring tools (DEHLI versus Family LIFE -  $r = 0.77$ ,  $t = 14.97$ ; DEHLI  
297 versus Species LIFE -  $r = 0.73$ ,  $t = 13.11$ ; Family LIFE versus Species LIFE -  $r = 0.83$ ,  $t = 18.43$ ).  
298 Biomonitoring tools displayed a general decrease between June 1974 and October 1974, and  
299 subsequently increased until winter 1975 (Fig. 4b and see Supplementary Material, Appendix A, Figs  
300 A3c-e). Family LIFE and Species LIFE were less temporally variable compared to DEHLI (Fig. 4b and  
301 see Supplementary Material, Appendix A, Fig. A3f). Samples from sites which dried along the South  
302 Winterbourne consistently yielded lower and more temporally variable biomonitoring tool values  
303 compared to sites which flowed continuously (Fig 4b and see Supplementary Material, Appendix A,  
304 Figs. A3d-f). Some of the highest biomonitoring tool scores obtained from sites which dried occurred  
305 in June 1974 (*c.* 2-months prior to channel drying) and January 1975 (*c.* 3-months after channel drying;  
306 Fig 4b and Supplementary Material, Appendix A, Figs. A3d-f). DEHLI exhibited highly significant  
307 temporal and spatial trends within the South Winterbourne during the study period (Table 2), with  
308 DEHLI values notably declining during autumn-winter 1974 and displaying the lowest values within  
309 the mid-reaches which dried (Fig. 5b). Although the amount of statistical variation explained by  
310 GAMMs was lower for all biomonitoring tools within the South Winterbourne compared to the R.  
311 Lathkill (Table 2).

#### 312 **Discussion**

313 *Invertebrate community temporal trajectories and correlations with biomonitoring tools*

314 This study provides novel evidence examining how independent biomonitoring tools characterizing  
315 invertebrate community responses to different flow-related properties vary in response to hydrological  
316 disturbances (channel drying and flow resumption events). Specifically, DEHLI and LIFE (Family and  
317 Species taxonomic resolutions) were explored to respectively characterize community responses to  
318 flow-habitat and hydraulic properties associated with changing hydrological conditions in two  
319 temporary river environments. These biomonitoring tools characterize how invertebrate communities  
320 are proportionally represented by different groups of taxa classified by their responses to different flow  
321 conditions (i.e. ‘flow response guilds’ – *sensu* Lytle *et al.* 2017).

322 The results of this study demonstrate that biomonitoring tools (DEHLI, Family LIFE and Species LIFE)  
323 captured the primary forms of community variability (PCoA axis 1 scores) occurring in both temporary  
324 rivers. This supports evidence highlighting that biomonitoring tools incorporating information on flow-  
325 response guilds can reliably capture temporal trajectories of biotic community change (Vaughan and  
326 Ormerod, 2012) and their responses to flow regime variations (Chen and Olden, 2018). This is  
327 reinforced by all biomonitoring tools examined in this study displaying lower scores (indicating more  
328 hydrologically stressed environments) in reaches that dried compared to those which flowed  
329 continuously during the study period. However, it should be noted that previous research has  
330 highlighted that other biomonitoring tools characterizing alternative ecological preferences and  
331 tolerances (e.g. water quality indicators) display strong differences between temporary and perennial  
332 river systems due to the strong deleterious effect that channel drying events can have on aquatic  
333 communities (Morais *et al.*, 2004; Wilding *et al.*, 2018). This suggests care should be exercised when  
334 interpreting biomonitoring tools in isolation and that multiple metrics characterizing ecological  
335 responses to different environmental pressures should be explored where possible (Clews and Ormerod,  
336 2009; Chadd *et al.*, 2017).

337 Within the R. Lathkill, three headwater sites (of the ten sampled) dried on multiple occasions for *c.* 28-  
338 46 days during the study period (Stubbington *et al.*, 2016). The temporal variability of invertebrate  
339 communities and biomonitoring tools in the R. Lathkill largely reflected these changes in hydrological

340 conditions. This was most evident in the early stages of the study period, which followed a major supra-  
341 seasonal drought that caused all study sites to dry for *c.* nine-months in 2011 (Stubbington *et al.*, 2016).  
342 Shifts in community compositions associated with increasing antecedent flow durations reflected the  
343 (re)colonization of taxa dependent on an extended period of continuous flow, suggesting that ecological  
344 recovery took place rapidly during the early stages of the study period. The reduction or partial reversal  
345 of ecological recovery in the months following drying events (April, June and September 2012) is in  
346 keeping with the limited number of studies that have employed high frequency sampling strategies to  
347 examine community responses to multiple drying events occurring intra-annually (e.g. Davey and  
348 Kelly, 2007; Storey and Quinn, 2008; Arscott *et al.*, 2010; Stubbington *et al.*, 2016; Hill and Milner,  
349 2018). Such findings are critical for understanding the resistance and resilience of riverine ecosystems  
350 to multiple flow cessation and drying events (Davey and Kelly, 2007; Ledger *et al.*, 2012), which is  
351 becoming ever pressing given that such conditions are projected to become more frequent in the future  
352 within lotic environments (Wanders *et al.*, 2015).

353 In the South Winterbourne, five sites (of the twelve sampled) located in the mid-reaches of the study  
354 area dried on one occasion for *c.* one-five months during the summer-autumn 1974 (although one site  
355 also dried in July 1975). Temporal variations in invertebrate communities within the South  
356 Winterbourne were not as pronounced as those observed in the R. Lathkill, which probably reflects a  
357 greater resistance/resilience of communities to a typical seasonal drying event (Magalhaes *et al.*, 2007;  
358 Bogan *et al.*, 2015) and the presence of upstream perennial sources which allowed invertebrates to  
359 rapidly recolonize downstream temporary reaches after flows resumed (Storey and Quinn, 2008; Bogan  
360 *et al.*, 2017).

### 361 *Temporal variations in biomonitoring tools*

362 This study identified strong sub-seasonal (monthly) variations in biomonitoring tools associated with  
363 the cessation and resumption of flowing conditions in both case studies. Ecological responses to flow  
364 cessation events in riverine environments are often tested through seasonal sampling programmes  
365 and/or a space-for-time substitution designs (e.g. control versus impact; Leigh *et al.*, 2019). Such study  
366 designs and biomonitoring practices may overlook ecological transformations occurring over time

367 within riverine ecosystems as species are gained or lost, the biotic interactions that stem from this and  
368 ecological tolerances to environmental conditions changing over time (Murdock *et al.*, 2012; Bogan *et*  
369 *al.*, 2015; Leigh *et al.*, 2019). This study reinforces the value of adopting sub-seasonal sampling  
370 strategies within temporary rivers in order to understand ecological responses to the cessation and  
371 resumption of flows at time scales in keeping with the temporal dynamics of ecosystem responses.

372 In the R. Lathkill, all three biomonitoring tools examined displayed temporal patterns broadly congruent  
373 with the temporal transformations of invertebrate communities observed during the study period (see  
374 above). This was most evident where biomonitoring tools increased consistently between December  
375 2011 (when flows had recently resumed after a severe supra-seasonal drought) and May 2012,  
376 illustrating clear patterns of recolonization and ecological recovery in the R. Lathkill outlined above.

377 Increases in DEHLI, Family LIFE and Species LIFE scores during this time reflects the colonization of  
378 taxa with preferences for high-flow conditions ('early colonists' herein) following the supra-seasonal  
379 drought (e.g. *Wormaldia* sp. - Philopotomidae, Order: Trichoptera; Rhyacophilidae, Order: Trichoptera;  
380 see Supplementary Material, Appendix A, Fig. A4). Biomonitoring tools identified signs of ecological  
381 recovery occurring within the mid-reaches of the R. Lathkill, which probably reflects the following two  
382 mechanisms. First, early colonists probably resided within the seedbank (life stages that remain viable  
383 in the sediments of the riverbed - Tronstad *et al.*, 2005) when the R. Lathkill dried during 2011.

384 Although Stubbington *et al* (2016) did not record any early colonists utilizing the seedbank across the  
385 R. Lathkill during the same study period, it is possible that the thermal or photic cues required for these  
386 aquatic insects were not fulfilled (Nordlie and Arthur, 1981) as the authors did not rehydrate the  
387 sediments during winter months (when recolonization occurred in the R. Lathkill after the supra-  
388 seasonal drought). Second, it is likely that some early colonists sought refuge in adjacent caves and  
389 'soughs' (abandoned, subterranean channels historically constructed to drain water from lead mines -  
390 Ford and Rieuwerts, 2007) when the R. Lathkill headwaters dried. These subsurface environments have  
391 been found to support extensive aquatic invertebrate communities (Wood *et al.*, 2002). Such patterns  
392 illustrate the importance of proximal aquatic refuges during drought conditions in facilitating  
393 subsequent ecological recovery patterns (Bogan and Boersma, 2012; Hill and Milner, 2018).

394 In the South Winterbourne, biomonitoring tools responded in synchrony with hydrological variability  
395 for most of the study period (Winter 1974 – Summer 1975), with higher DEHLI, Family LIFE and  
396 Species LIFE scores indicating invertebrate communities adapted to higher flow conditions and the  
397 habitat and hydraulic conditions associated with this (Extence *et al.*, 1999; Chadd *et al.*, 2017).  
398 However, biomonitoring tool scores were notably higher during the early stages of the study period  
399 (Summer 1974), despite seasonally low discharges occurring at this time. This suggests that habitat  
400 conditions within the South Winterbourne during this low-flow period were suitable for torrenticoles  
401 and rheophilic taxa (DEHLI and LIFE), as well as taxa inhabiting marginal regions of the river channel  
402 (DEHLI). Various drought tolerant macrophyte species (e.g. *Rorippa nasturtium-aquaticum*, *Berula*  
403 *erectua*, *Apium nodiflorum* and *Oenanthe crocata* – see Westwood *et al.*, 2006) are typically most  
404 abundant during the summer months in the South Winterbourne (Casey and Ladle, 1976; Armitage and  
405 Bass, 2013). Furthermore, surveys conducted during the study period indicated the presence of a diverse  
406 macrophyte community across the South Winterbourne during the study period (Watkinson *et al.*,  
407 1994). The marginal encroachment of vegetation probably created habitats suitable for torrenticoles and  
408 rheophilic taxa (through high flow velocities created between stands - Ladle *et al.*, 1972; White *et al.*,  
409 2019), as well as species typically associated with streamside vegetation. This habitat complexity  
410 associated with macrophytes almost certainly helped maintain high DEHLI, Family LIFE and Species  
411 LIFE scores recorded during summer 1974. Comparable findings have been reported previously by  
412 Dunbar *et al.* (2010), who found that Species LIFE scores responded unexpectedly to hydrological  
413 controls within channelized river reaches, with a lack of refugia resulting in lower LIFE scores despite  
414 conveying faster flow velocities. Such findings highlight the need for further research to examine how  
415 habitat conditions (and specifically macrophyte assemblages) modify how hydrological controls shape  
416 flow response guilds and biomonitoring tools derived from this.

#### 417 *Incorporating flow response guilds within biomonitoring practices*

418 There remains a pressing need to understand and model how temporary river ecosystems respond to  
419 flow regime variability, including transitions between flowing, ponded and dry conditions, in order to  
420 conserve their biodiversity and the suite of services they provide to society. This study highlighted that



421 biomonitoring tools summarizing different flow response guilds could be more widely incorporated to  
422 guide the conservation of temporary river environments (Stubbington *et al.*, 2018). To date, flow  
423 response guilds have not been widely utilized for examining ecological responses to the cessation and  
424 resumption of flowing conditions. Stromberg and Merritt (2016) provide an alternative approach to this  
425 by characterizing the ecological guilds of riparian plant communities based on functional typologies  
426 associated with ephemeral, intermittent and perennial river systems. Such approaches could potentially  
427 be used for characterizing biotic communities inhabiting temporary rivers as the functional properties  
428 of biota do not have the biogeographic constraints of taxonomic approaches (White *et al.*, 2017, Poff,  
429 2018). This study also highlights that establishing flow response guilds which incorporate the sensitivity  
430 of multiple species (which are prevalent across large spatial scales - e.g. nation-wide assessments) to  
431 flow cessation events provide a reliable means of deriving ecological associations with flow  
432 intermittency.

433 There are few global examples of biomonitoring tools which incorporate information from flow  
434 response guilds beyond the UK (a rare example being the ‘Canadian Ecological Flow Index’ - Armanini  
435 *et al.*, 2011). As such, this study provides a unique insight into how different biomonitoring tools  
436 established to detect ecological responses to different flow properties perform under extreme  
437 hydrological conditions (i.e. channel drying). DEHLI, Family LIFE and Species LIFE were all  
438 positively correlated in this research, highlighting the broad associations between hydraulic conditions  
439 (LIFE) and flow-habitat groupings (DEHLI) lost during flow cessation events (Chadd *et al.*, 2017). This  
440 also suggests that invertebrate community responses to hydrological variability, including flow  
441 cessation events, can be detected at both family- and species-level taxonomic resolutions (but see Monk  
442 *et al.*, 2012). However, DEHLI displayed stronger temporal variations compared to Family LIFE and  
443 Species LIFE in both case studies and broadly tracked hydrological conditions, most notably within  
444 temporary reaches. This provides further evidence highlighting that riverine ecosystems display a  
445 stepped response to flow cessation events as key habitats become disconnected within the channel,  
446 rather than instream communities responding to a linear continuum of reduced flow velocities (Boulton,  
447 2003; Bogan *et al.*, 2015; Chadd *et al.*, 2017; Aspin *et al.*, 2019a; 2019b).

448 The findings of this research provide valuable insights to help inform future research and management  
449 objectives aiming to establish and utilize biomonitoring tools capable of characterizing temporary river  
450 ecosystems responses to flow regime variations. Our results suggest that such efforts should target  
451 establishing flow response guilds which characterize biotic communities based on their ecological  
452 preferences associated with habitats typically available (or lost) at different water levels and flow  
453 magnitudes. With temporary rivers likely to become more prevalent due to future climatic change and  
454 increasing societal water demands, this study informs the ever growing need to test, develop and refine  
455 biomonitoring tools capable of quantifying ecological responses to temporary river flow regimes.

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#### 463 **Data availability statement**

464 Part of the data (from the River Lathkill) underpinning this research are available from the authors upon  
465 request. Other data supporting the findings of this study (from the South Winterbourne) are available  
466 from the Environment Agency. Restrictions apply to the availability of these data, which were used  
467 under license for this study. Data are available from the authors with the permission of the Environment  
468 Agency (enquiries@environment-agency.gov.uk).

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473 **References**

- 474 Armitage, P.D. and Bass, J. (2013). Long-term resilience and shortterm vulnerability of South  
475 Winterbourne macroinvertebrates. *Proceedings of the Dorset Natural History and Archaeological*  
476 *Society, 134*, pp.43-55.
- 477 Arscott, D.B., Larned, S., Scarsbrook, M.R. and Lambert, P. (2010). Aquatic invertebrate community  
478 structure along an intermittence gradient: Selwyn River, New Zealand. *Journal of the North American*  
479 *Benthological Society, 29(2)*, pp.530-545.
- 480 Arthington, A.H., Bernardo, J.M. and Ilhéu, M. (2014). Temporary rivers: linking ecohydrology,  
481 ecological quality and reconciliation ecology. *River Research and Applications, 30(10)*, pp.1209-1215.
- 482 Aspin, T.W., Khamis, K., Matthews, T.J., Milner, A.M., O'callaghan, M.J., Trimmer, M., Woodward,  
483 G. and Ledger, M.E. (2019a). Extreme drought pushes stream invertebrate communities over functional  
484 thresholds. *Global change biology, 25(1)*, pp.230-244.
- 485 Aspin, T.W., Hart, K., Khamis, K., Milner, A.M., O'Callaghan, M.J., Trimmer, M., Wang, Z., Williams,  
486 G.M., Woodward, G. and Ledger, M.E. (2019b). Drought intensification alters the composition, body  
487 size, and trophic structure of invertebrate assemblages in a stream mesocosm experiment. *Freshwater*  
488 *Biology, 64*. pp. 750–760
- 489 Bass, J., Armitage, P.D and Pretty, J. L (2014). Severe drought and exceptional summer flooding:  
490 consequences for the south winterborne macroinvertebrates. *Proceedings of the Dorset Natural History*  
491 *and Archaeological Society, 135*, pp.43-55.
- 492 Bickerton, M., Petts, G., Armitage, P. and Castella, E. (1993). Assessing the ecological effects of  
493 groundwater abstraction on chalk streams: three examples from eastern England. *Regulated Rivers:*  
494 *Research & Management, 8(1-2)*, pp.121-134.
- 495 Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., Solimini, A., Van De Bund, W.,  
496 Zampoukas, N. and Hering, D. (2012). Three hundred ways to assess Europe's surface waters: an almost  
497 complete overview of biological methods to implement the Water Framework Directive. *Ecological*  
498 *Indicators, 18*, pp.31-41.

499 Bogan, M.T. and Boersma, K.S. (2012). Aerial dispersal of aquatic invertebrates along and away from  
500 arid-land streams. *Freshwater Science*, 31(4), pp.1131-1144.

501 Bogan, M.T., Boersma, K.S. and Lytle, D.A. (2015). Resistance and resilience of invertebrate  
502 communities to seasonal and suprasedasonal drought in arid-land headwater streams. *Freshwater*  
503 *Biology*, 60(12), pp.2547-2558.

504 Bogan, M.T., Chester, E.T., Datry, T., Murphy, A.L., Robson, B.J., Ruhi, A., Stubbington, R. and  
505 Whitney, J.E. (2017). Resistance, Resilience, and Community Recovery in Intermittent Rivers and  
506 Ephemeral Streams. In: Datry, T., Bonada, N., Boulton, A.J. (Eds.), *Intermittent Rivers and Ephemeral*  
507 *Streams: Ecology and Management*. Elsevier, Netherlands, pp. 349–376.

508 Bonada, N., Prat, N., Resh, V.H. and Statzner, B. (2006). Developments in aquatic insect biomonitoring:  
509 a comparative analysis of recent approaches. *Annual Review of Entomology.*, 51, pp.495-523.

510 Boulton, A.J. (2003). Parallels and contrasts in the effects of drought on stream macroinvertebrate  
511 assemblages. *Freshwater Biology*, 48(7), pp.1173-1185.

512 Boulton, A. J. and Lake. P. S. (2008) Effects of drought on stream insects and its ecological  
513 consequences. Pages 81–102 in Lancaster. J and Briers. R (eds). *Aquatic insects: challenges to*  
514 *populations*. CABI Publishing, Wallingford, UK.

515 Carter, J.L., Resh, V.H., Rosenberg, D.M., Reynoldson, T.B., Ziglio, G., Siligardi, M. and Flaim, G.  
516 (2006). Biomonitoring in North American rivers: a comparison of methods used for benthic  
517 macroinvertebrates in Canada and the United States. *Biological monitoring of rivers: applications and*  
518 *perspectives*, pp. 203-228.

519 Casey, H. and Ladle, M. (1976). Chemistry and biology of the South Winterbourne, Dorset, England.  
520 *Freshwater Biology*, 6(1), pp.1-12.

521 Chen, W. and Olden, J.D. (2018). Evaluating transferability of flow–ecology relationships across space,  
522 time and taxonomy. *Freshwater Biology*, 63(8), pp.817-830.

523 Cid, N., Verkaik, I., García-Roger, E.M., Rieradevall, M., Bonada, N., Sánchez-Montoya, M.M.,  
524 Gómez, R., Suárez, M.L., Vidal-Abarca, M.R., Demartini, D. and Buffagni, A. (2016). A biological  
525 tool to assess flow connectivity in reference temporary streams from the Mediterranean Basin. *Science*  
526 *of the Total Environment*, 540, pp.178-190.

527 Crichton, M.I., Fisher, D. and Woiwod, I.P. (1978). Life histories and distribution of British  
528 Trichoptera, excluding Limnephilidae and Hydroptilidae, based on the Rothamsted Insect Survey.  
529 *Ecography*, 1(1), pp.31-45.

530 Davey, A.J. and Kelly, D.J. (2007). Fish community responses to drying disturbances in an intermittent  
531 stream: a landscape perspective. *Freshwater Biology*, 52(9), pp.1719-1733.

532 Datry, T., Bonada, N., Boulton, A.J. (2017). General introduction. In: Datry, T., Bonada, N., Boulton,  
533 A.J. (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management*. Elsevier,  
534 Netherlands, pp. 1–16.

535 Datry, T., Boulton, A.J., Bonada, N., Fritz, K., Leigh, C., Sauquet, E., Tockner, K., Hugueny, B. and  
536 Dahm, C.N. (2018). Flow intermittence and ecosystem services in rivers of the Anthropocene. *Journal*  
537 *of applied ecology*, 55(1), pp.353-364.

538 Datry, T., Larned, S.T. and Tockner, K. (2014). Intermittent rivers: a challenge for freshwater ecology.  
539 *BioScience*, 64(3), pp.229-235.

540 Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman,  
541 R.J., Prieur-Richard, A.H., Soto, D., Stiassny, M.L. and Sullivan, C.A. (2006). Freshwater biodiversity:  
542 importance, threats, status and conservation challenges. *Biological reviews*, 81(2), pp.163-182.

543 Dunbar, M.J., Pedersen, M.L., Cadman, D.A.N., Extence, C., Waddingham, J., Chadd, R. and Larsen,  
544 S.E. (2010). River discharge and local-scale physical habitat influence macroinvertebrate LIFE scores.  
545 *Freshwater Biology*, 55(1), pp.226-242.

546 Elliott, J.M. (2003). A comparative study of the dispersal of 10 species of stream invertebrates.  
547 *Freshwater biology*, 48(9), pp.1652-1668.

548 Extence, C.A. (1981). The effect of drought on benthic invertebrate communities in a lowland river.  
549 *Hydrobiologia*, 83(2), pp.217-224.

550 Extence, C.A., Balbi, D.M. and Chadd, R.P. (1999). River flow indexing using British benthic  
551 macroinvertebrates: a framework for setting hydroecological objectives. *Regulated Rivers: Research &*  
552 *Management*, 15(6), pp.545-574.

553 Ford, T.D. and Rieuwerts, J. (2007). Lead miners' soughs in Derbyshire. *Geology Today*, 23(2), pp.57-  
554 62.

555 Fritz, K.M. and Dodds, W.K. (2004). Resistance and resilience of macroinvertebrate assemblages to  
556 drying and flood in a tallgrass prairie stream system. *Hydrobiologia*, 527(1), pp.99-112.

557 Garcia, C., Gibbins, C.N., Pardo, I. and Batalla, R.J. (2017). Long term flow change threatens  
558 invertebrate diversity in temporary streams: evidence from an island. *Science of the Total Environment*,  
559 580, pp.1453-1459.

560 García-Roger, E.M., del Mar Sánchez-Montoya, M., Gómez, R., Suárez, M.L., Vidal-Abarca, M.R.,  
561 Latron, J., Rieradevall, M. and Prat, N. (2011). Do seasonal changes in habitat features influence aquatic  
562 macroinvertebrate assemblages in perennial versus temporary Mediterranean streams? *Aquatic*  
563 *sciences*, 73(4), pp.567-579.

564 Hearne, J.W. and Armitage, P.D. (1993). Implications of the annual macrophyte growth cycle on habitat  
565 in rivers. *Regulated Rivers: Research & Management*, 8(4), pp.313-322.

566 Hill, M.J. and Milner, V.S. (2018). Ponding in intermittent streams: A refuge for lotic taxa and a habitat  
567 for newly colonising taxa?. *Science of the Total Environment*, 628, pp.1308-1316.

568 ISO (2012). Water Quality – Guidelines for the Selection of Sampling Methods and Devices for  
569 Benthic Macroinvertebrates in Fresh Waters.

570 Klaar, M.J., Dunbar, M.J., Warren, M. and Soley, R. (2014). Developing hydroecological models to  
571 inform environmental flow standards: a case study from England. *Wiley Interdisciplinary Reviews:*  
572 *Water*, 1(2), pp.207-217.

573 Ladle, M., Bass, J.A.B. and Jenkins, W.R. (1972). Studies on production and food consumption by the  
574 larval Simuliidae (Diptera) of a chalk stream. *Hydrobiologia*, 39(3), pp.429-448.

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

578 Ledger, M.E. and Hildrew, A.G. (2001). Recolonization by the benthos of an acid stream following a  
579 drought. *Archiv für Hydrobiologie*, pp.1-17.

580 Leigh, C., Aspin, T.W.H, Matthews., T.J., Rolls., R.J., Ledger, M.E. (2019) Drought alters the  
581 functional stability of stream invertebrate communities through time. *Journal of Biogeography*. 00. pp.  
582 1– 13.

583 Leigh, C., Boulton, A.J., Courtwright, J.L., Fritz, K., May, C.L., Walker, R.H. and Datry, T. (2016).  
584 Ecological research and management of intermittent rivers: an historical review and future directions.  
585 *Freshwater Biology*, 61(8), pp.1181-1199.

586 Lemon, J., Bolker, B., Oom, S., Klein, E., Rowlingson, B., Wickham, H., Tyagi, A., Eterradosi, O.,  
587 Grothendieck, G., Toews, M., Kane, M., Turner, R., Witthoft, C., Stander, J., Petzoldt, T., Duursma,  
588 R., Biancotto, E., Levy, O., Dutang, C., Solymos, P., Engelmann, R., Hecker, M., Steinbeck, F.,  
589 Borchers, H., Singmann, H., Toal, T., Ogle, D., Baral, D and Groempin. U (2018) Package ‘plotrix’ –  
590 Various plotting functions. Version 3.7-4. Retrieved from [https://cran.r-](https://cran.r-project.org/web/packages/plotrix/plotrix.pdf)  
591 [project.org/web/packages/plotrix/plotrix.pdf](https://cran.r-project.org/web/packages/plotrix/plotrix.pdf). [Accessed 21/01/2019].

592 Lytle, D. A., Merritt, D. M., Tonkin, J. D., Olden, J. D., and Reynolds, L. V. (2017). Linking river flow  
593 regimes to riparian plant guilds: a community-wide modeling approach. *Ecological Applications*, 27(4),  
594 1338–1350.

595 Magalhaes, M.F., Beja, P., Schlosser, I.J. and Collares-Pereira, M.J (2007). Effects of multi-year  
596 droughts on fish assemblages of seasonally drying Mediterranean streams. *Freshwater Biology*, 52(8),  
597 pp.1494-1510.

598 Mathers, K.L., Chadd, R.P., Dunbar, M.J., Extence, C.A., Reeds, J., Rice, S.P. and Wood, P.J. (2016).  
599 The long-term effects of invasive signal crayfish (*Pacifastacus leniusculus*) on instream  
600 macroinvertebrate communities. *Science of the Total Environment*, 556, pp.207-218.

601 Matthaei, C.D., Piggott, J.J. and Townsend, C.R. (2010). Multiple stressors in agricultural streams:  
602 interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied*  
603 *Ecology*, 47(3), pp.639-649.

604 Marjoribanks, T.I., Hardy, R.J., Lane, S.N. and Parsons, D.R. (2017). Does the canopy mixing layer  
605 model apply to highly flexible aquatic vegetation? Insights from numerical modelling. *Environmental*  
606 *Fluid Mechanics*, 17(2), pp.277-301.

607 Meyer, J.L., Strayer, D.L., Wallace, J.B., Eggert, S.L., Helfman, G.S. and Leonard, N.E. (2007). The  
608 contribution of headwater streams to biodiversity in river networks<sup>1</sup>. *JAWRA Journal of the American*  
609 *Water Resources Association*, 43(1), pp.86-103.

610 Monk, W.A., Wood, P.J., Hannah, D.M., Extence, C.A., Chadd, R.P. and Dunbar, M.J. (2012). How  
611 does macroinvertebrate taxonomic resolution influence ecohydrological relationships in riverine  
612 ecosystems. *Ecohydrology*, 5(1), pp.36-45.

613 Monk, W.A., Wood, P.J., Hannah, D.M., Wilson, D.A., Extence, C.A. and Chadd, R.P. (2006). Flow  
614 variability and macroinvertebrate community response within riverine systems. *River Research and*  
615 *Applications*, 22(5), pp.595-615.

616 Morais, M., Pinto, P., Guilherme, P., Rosado, J. and Antunes, I. (2004). Assessment of temporary  
617 streams: the robustness of metric and multimetric indices under different hydrological conditions.  
618 *Hydrobiologia*, 516, pp. 229-249.

619 Murray-Bligh, J., 1999. Procedures for Collecting and Analysing Macroinvertebrate Samples- BT001.  
620 The Environment Agency, Bristol, pp. 1–176.

621 National River Flow Archive (2019a). 44004 - Frome at Dorchester Total, National River Flow  
622 Archive, Centre for Ecology and Hydrology. Retrieved from <http://nrfa.ceh.ac.uk> (Accessed  
623 20/01/2019).

624 National River Flow Archive (2019b). 44008 - South Winterbourne at Winterbourne Steepleton,  
625 National River Flow Archive, Centre for Ecology and Hydrology. Retrieved from <http://nrfa.ceh.ac.uk>  
626 (Accessed 20/01/2019).

627 Nordlie, K.J. and Arthur, J.W. (1981). Effect of elevated water temperature on insect emergence in  
628 outdoor experimental channels. *Environmental Pollution Series A, Ecological and Biological*, 25(1),  
629 pp.53-65.

630 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L.,  
631 Solymos, P., Stevens, M. H. M., Szoecs, E., Wagner, H. (2017). Community ecology package. Version  
632 2.4.1. Retrieved from <https://cran.r-project.org/web/packages/vegan/vegan.pdf>. [Accessed  
633 12/02/2017].

634 Parry, S., Marsh, T. and Kendon, M. (2013) 2012: from drought to floods in England and Wales.  
635 *Weather*, 68(10), pp.268-274.



636 Petersen, I., Winterbottom, J.H., Orton, S., Friberg, N., Hildrew, A.G., Spiers, D.C. and Gurney, W.S.C.  
637 (1999). Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream,  
638 UK. *Freshwater Biology*, 42(3), pp.401-416.

639 Poff, N.L. (2018). Beyond the natural flow regime? Broadening the hydro-ecological foundation to  
640 meet environmental flows challenges in a non-stationary world. *Freshwater biology*, 63(8), pp.1011-  
641 1021.

642 Poff, N.L., Richter, B.D., Arthington, A.H., Bunn, S.E., Naiman, R.J., Kendy, E., Acreman, M., Apse,  
643 C., Bledsoe, B.P., Freeman, M.C. and Henriksen, J. (2010). The ecological limits of hydrologic  
644 alteration (ELOHA): a new framework for developing regional environmental flow standards.  
645 *Freshwater Biology*, 55(1), pp.147-170.

646 R Development Core Team (2014). R: A language and environment for statistical  
647 computing. Vienna, Austria: R Foundation for Statistical Computing.

648 Sear, D.A., Armitage, P.D. and Dawson, F.H. (1999). Groundwater dominated rivers. *Hydrological*  
649 *processes*, 13(3), pp.255-276.

650 Steward, A.L., Marshall, J.C., Sheldon, F., Harch, B., Choy, S., Bunn, S.E. and Tockner, K. (2011).  
651 Terrestrial invertebrates of dry river beds are not simply subsets of riparian assemblages. *Aquatic*  
652 *Sciences*, 73(4), p.551.

653 Steward, A.L., von Schiller, D., Tockner, K., Marshall, J.C. and Bunn, S.E. (2012). When the river runs  
654 dry: human and ecological values of dry riverbeds. *Frontiers in Ecology and the Environment*, 10(4),  
655 pp.202-209.

656 Storey, R.G. and Quinn, J.M. (2008). Composition and temporal changes in macroinvertebrate  
657 communities of intermittent streams in Hawke's Bay, New Zealand. *New Zealand Journal of Marine*  
658 *and Freshwater Research*, 42(1), pp.109-125.

659 Stromberg, J.C. and Merritt, D.M. (2016). Riparian plant guilds of ephemeral, intermittent and perennial  
660 rivers. *Freshwater Biology*, 61(8), pp.1259-1275.

661 Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., Munné, A., Pařil, P., Peřić, V.,  
662 Tziortzis, I. and Verdonschot, R.C. (2018a). Biomonitoring of intermittent rivers and ephemeral streams

663 in Europe: current practice and priorities to enhance ecological status assessments. *Science of the total*  
664 *environment*, 618, pp.1096-1113.

665 Stubbington, R., England, J., Acreman, M., Wood, P.J., Westwood, C., Boon, P., Jorda-Capdevila, D.  
666 (2018b). The natural capital of temporary rivers: characterising the value of dynamic aquatic-terrestrial  
667 habitats. Valuing Nature Natural Capital Synthesis Report VNP12. Valuing Nature Programme,  
668 Valuing Nature Programme, pp. 52.

669 Stubbington, R., England, J., Wood, P.J. and Sefton, C.E. (2017). Temporary streams in temperate  
670 zones: recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *Wiley*  
671 *Interdisciplinary Reviews: Water*, 4(4), e1223.

672 Stubbington, R., Gunn, J., Little, S., Worrall, T.P. and Wood, P.J. (2016). Macroinvertebrate seedbank  
673 composition in relation to antecedent duration of drying and multiple wet-dry cycles in a temporary  
674 stream. *Freshwater Biology*, 61(8), pp.1293-1307.

675 Stubbington, R., Paillex, A., England, J., Barthès, A., Bouchez, A., Rimet, F., Sánchez-Montoya, M.M.,  
676 Westwood, C.G. and Datry, T. (2019). A comparison of biotic groups as dry-phase indicators of  
677 ecological quality in intermittent rivers and ephemeral streams. *Ecological indicators*, 97, pp.165-174.

678 Tachet, H., Bournaud, M., Richoux, P., and Usseglio-Polatera, P. (2010) *Invertébrés d'eau douce:*  
679 *systématique, biologie, écologie*. Paris: CNRS Editions.

680 Theodoropoulos, C., Papadaki, C., Vardakas, L., Dimitriou, E., Kalogianni, E. and Skoulikidis, N.  
681 (2019). Conceptualization and pilot application of a model-based environmental flow assessment  
682 adapted for intermittent rivers. *Aquatic Sciences*, 81(1). pp. 1-17.

683 Tronstad, L.M., Tronstad, B.P. and Benke, A.C. (2005). Invertebrate seedbanks: rehydration of soil  
684 from an unregulated river floodplain in the south-eastern US. *Freshwater Biology*, 50(4), pp.646-655.

685 Vander Vorste, R., Malard, F. and Datry, T. (2016). Is drift the primary process promoting the resilience  
686 of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river.  
687 *Freshwater Biology*, 61(8), pp.1276-1292.

688 Vaughan, I.P. and Ormerod, S.J. (2012). Large-scale, long-term trends in British river  
689 macroinvertebrates. *Global Change Biology*, 18(7), pp.2184-2194.

690 Wanders, N., Wada, Y. and Van Lanen, H.A.J. (2015). Global hydrological droughts in the 21st century  
691 under a changing hydrological regime. *Earth System Dynamics*, 6(1), pp.1-15.

692 Watkinson, J., Cooling, D. and Green, G. P (1994) A biological study of the South Winterbourne, Dorset  
693 in 1974-1978. Environment Agency report.

694 Westwood, C.G., Teeuw, R.M., Wade, P.M., Holmes, N.T.H. and Guyard, P. (2006). Influences of  
695 environmental conditions on macrophyte communities in drought-affected headwater streams. *River*  
696 *Research and Applications*, 22(6), pp.703-726.

697 Wharton, G., Cotton, J.A., Wotton, R.S., Bass, J.A., Heppell, C.M., Trimmer, M., Sanders, I.A. and  
698 Warren, L.L. (2006). Macrophytes and suspension-feeding invertebrates modify flows and fine  
699 sediments in the Frome and Piddle catchments, Dorset (UK). *Journal of Hydrology*, 330(1-2), pp.171-  
700 184.

701 White, J.C., Hannah, D.M., House, A., Beatson, S.J., Martin, A. and Wood, P.J. (2017).  
702 Macroinvertebrate responses to flow and stream temperature variability across regulated and non-  
703 regulated rivers. *Ecohydrology*, 10(1), e1773.

704 White, J.C., House, A., Punchard, N., Hannah, D.M., Wilding, N.A. and Wood, P.J. (2018).  
705 Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects  
706 across intermittent and perennial headwater streams. *Science of the Total Environment*, 610, pp.1514-  
707 1526.

708 White, J.C., Krajenbrink, H.J., Hill, M.J., Hannah, D.M., House, A. and Wood, P.J. (2019). Habitat-  
709 specific invertebrate responses to hydrological variability, anthropogenic flow alterations, and  
710 hydraulic conditions. *Freshwater Biology*, 64, pp. 555–576.

711 Wilding, N.A., White, J.C., Chadd, R.P., House, A. and Wood, P.J. (2018). The influence of flow  
712 permanence and drying pattern on macroinvertebrate biomonitoring tools used in the assessment of  
713 riverine ecosystems. *Ecological Indicators*, 85, pp.548-555.

714 Wright, J.F. and Symes, K.L. (1999). A nine-year study of the macroinvertebrate fauna of a chalk  
715 stream. *Hydrological Processes*, 13(3), pp.371-385.

716 Wood, P. J., Gunn, J and Perkins, J. (2002) The impact of pollution on aquatic invertebrates within a  
717 subterranean ecosystem - out of sight out of mind. *Archiv für Hydrobiologie*, 155(2), pp.223-227.

718 Wood, P.J., Gunn, J., Smith, H. and Abas-Kutty, A. (2005). Flow permanence and macroinvertebrate  
719 community diversity within groundwater dominated headwater streams and springs. *Hydrobiologia*,  
720 545(1), pp.55-64.

721 Wood, S. (2019) Package MGCV - Mixed GAM Computation Vehicle with Automatic Smoothness  
722 Estimation. Retrieved from <https://cran.r-project.org/web/packages/mgcv/mgcv.pdf>. [Accessed  
723 21/01/2019].

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727 **Table 1** – Pearson r correlation tests between Principal Coordinate Analysis (PCoA) axis scores and different biomonitoring tools tested. Stars indicate the degree of significance:728 NS = non-significant; \* =  $p \leq 0.05$ ; \*\* =  $p \leq 0.01$ ; \*\*\* =  $p \leq 0.001$ .

Watercourse	Biomonitoring tool	Family ordination						Species ordination					
		PCOA1			PCOA2			PCOA1			PCOA2		
		R	T	<i>p-value</i>	R	T	<i>p-value</i>	r	t	<i>p-value</i>	R	t	<i>p-value</i>
Lathkill	DEHLI	0.72	10.17	<0.001***	-0.31	-3.18	0.002**	0.72	10.03	<0.001***	-0.31	-3.21	0.002**
	Family LIFE	0.80	13.11	<0.001***	0.05	0.45	0.653 <sup>NS</sup>	0.81	13.39	<0.001***	0.02	0.22	0.827 <sup>NS</sup>
	Species LIFE	0.67	8.85	<0.001***	-0.02	-0.16	0.877 <sup>NS</sup>	0.66	8.60	<0.001***	-0.07	-0.65	0.515 <sup>NS</sup>
South Winterbourne	DEHLI	0.62	9.60	<0.001***	0.37	4.86	<0.001***	0.60	9.17	<0.001***	0.16	1.99	0.049*
	Family LIFE	0.51	7.18	<0.001***	0.16	1.97	0.051 <sup>NS</sup>	0.52	7.51	<0.001***	-0.12	-1.56	0.122 <sup>NS</sup>
	Species LIFE	0.73	13.14	<0.001***	0.19	2.31	0.022*	0.73	13.03	<0.001***	0.05	0.63	0.530 <sup>NS</sup>

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**Table 2**– Generalized Additive Mixed-effect Model (GAMM) outputs examining the responses of biomonitoring tools to temporal controls and distance from the perennial source. Stars indicate the degree of significance: NS = non-significant; \* =  $p \leq 0.05$ ; \*\* =  $p \leq 0.01$ ; \*\*\* =  $p \leq 0.001$ .

Watercourse	Biomonitoring tool	Model $r^2$	Time		Distance from perennial source (km)	
			F	<i>p-value</i>	F	<i>p-value</i>
Lathkill	DEHLI	0.43	4.80	<0.001***	0.93	0.009*
	Family LIFE	0.54	4.94	<0.001***	2.04	<0.001***
	Species LIFE	0.44	1.59	0.002**	2.15	<0.001***
South Winterbourne	DEHLI	0.39	3.04	<0.001***	1.93	<0.001***
	Family LIFE	0.18	4.82	<0.001***	0.27	0.129(NS)
	Species LIFE	0.39	6.03	<0.001***	0.92	0.014*

756 **Figures**

757 **Fig. 1** - The location of the two temporary watercourses explored and the study sites therein. a) The River Lathkill  
758 (Derbyshire) and b) the South Winterbourne (Dorset). Triangles indicate sites which dried during the study period,  
759 circles denote those which flowed continuously and squares denote local settlements.

760 **Fig. 2** – Hydrological conditions along the River Lathkill (a and b) and South Winterbourne (c and d) during each  
761 respective study period. a) and c) Matrices showing when sites were flowing (grey) or dry (black) for each sampling  
762 site (please refer to Fig. 1 for sampling site locations). b) and d) Hydrographs highlighting changes in discharge over  
763 time. Note: In d), the black line depicts observed discharges from the South Winterbourne (NRFA, 2019b); while the  
764 grey line represents modelled discharges based on a highly significant linear regression ( $r^2 = 0.74$ ,  $F = 17604$ ,  $p\text{-value} \leq$   
765  $0.001$ ) with discharge time series from a nearby chalk river (NRFA, 2019a) over a 30-year period.

766 **Fig. 3** – Principal Coordinate Analysis (PCoA) plot highlighting average community compositional differences between  
767 monthly sampling periods in the a) River Lathkill and b) South Winterbourne.

768 **Fig 4** – Temporal variations in biomonitoring tools (mean  $\pm$  2 standard errors) within each case study – a) River Lathkill  
769 and b) South Winterbourne. Black = Family LIFE and grey = DEHLI (Species LIFE was excluded for aesthetic purposes  
770 due to the high degree of congruency of Family LIFE, but see Supplementary Material, Appendix A). It should be noted  
771 that the terms ‘temporary’ or ‘perennial’ to avoid differences in classification and nomenclature of study sites established  
772 in previous studies.

773 **Fig. 5** – Generalized Additive Mixed-Effect Model (GAMM) outputs highlighting temporal and spatial trajectories of  
774 DEHLI scores within each case study. a) Lathkill and b) South Winterbourne. Low to high DEHLI scores are indicated  
775 by a gradient ranging from white to black.

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Fig. 1

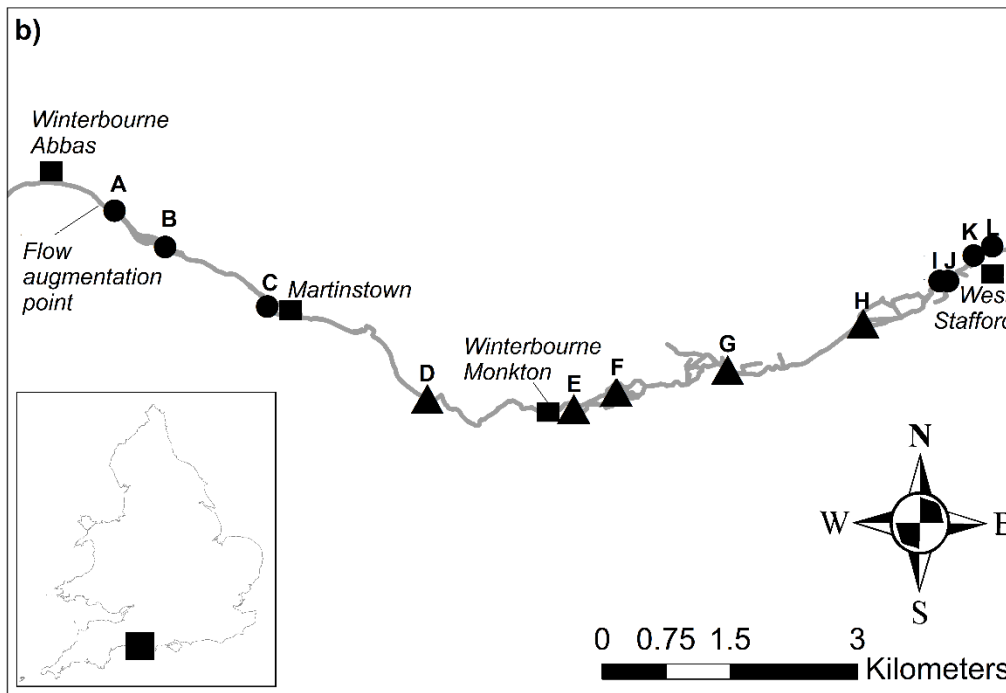
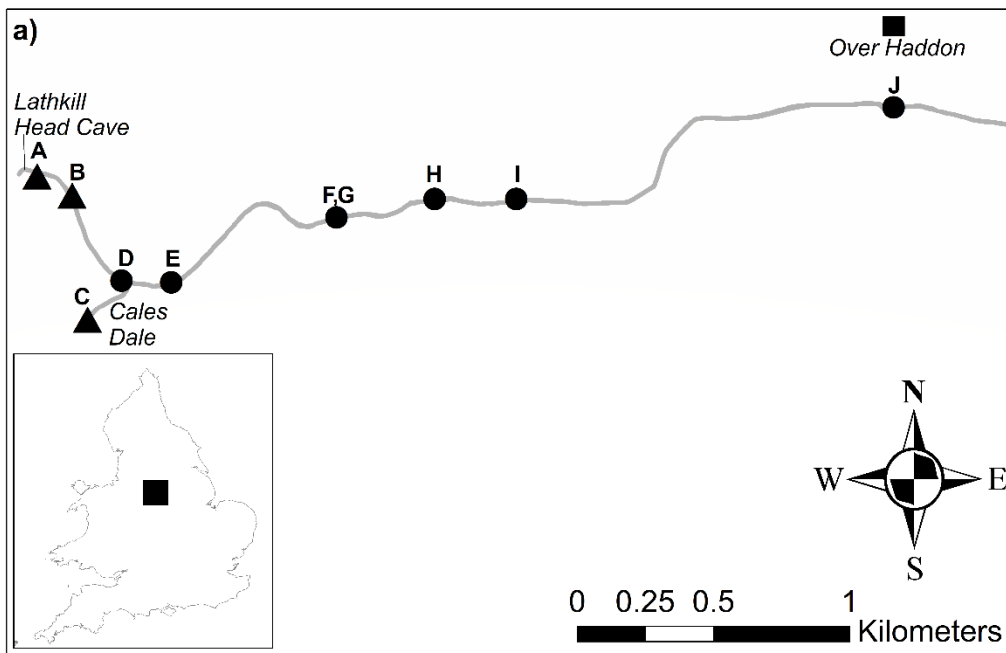
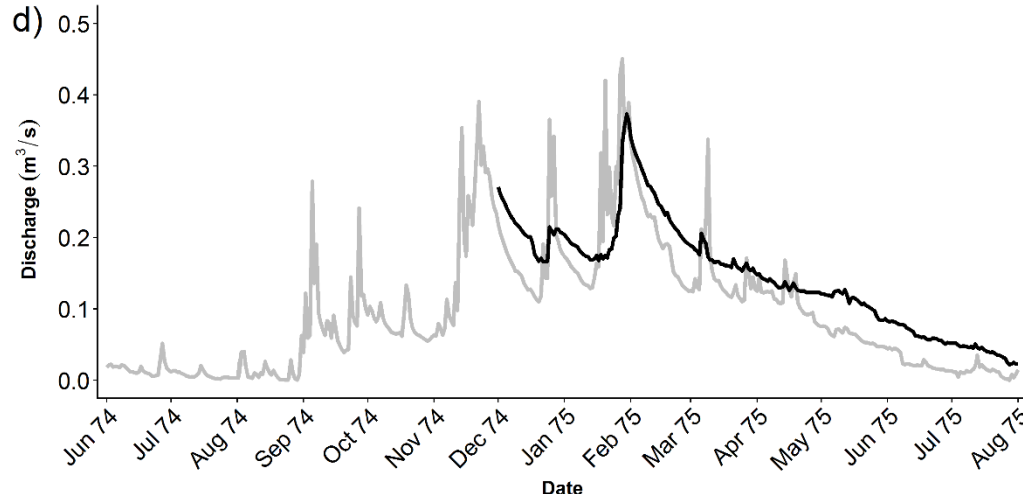
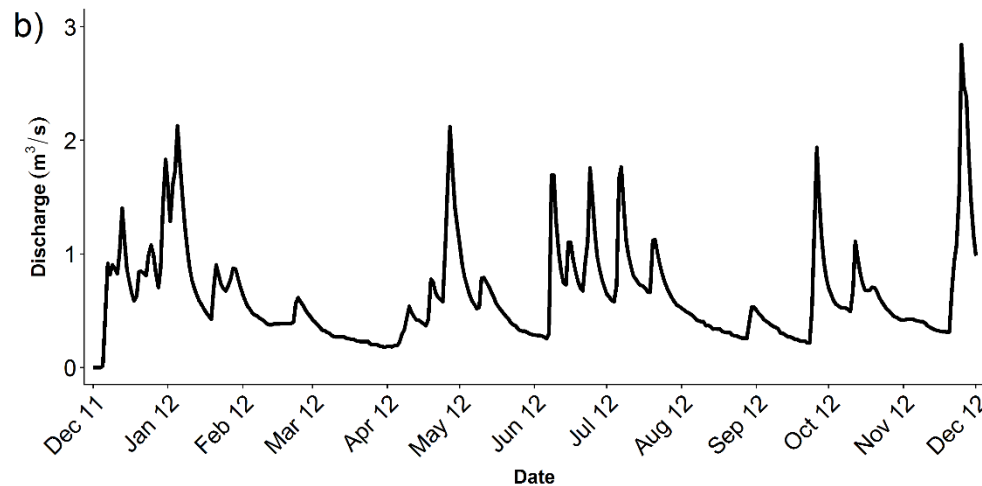
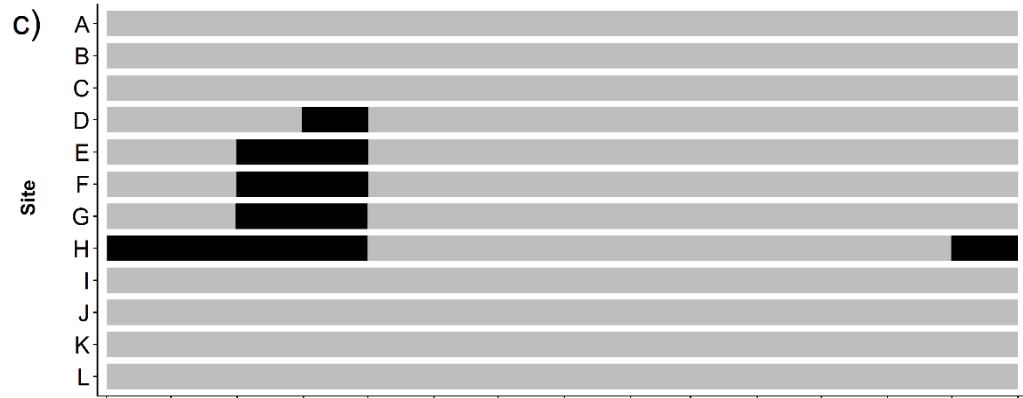
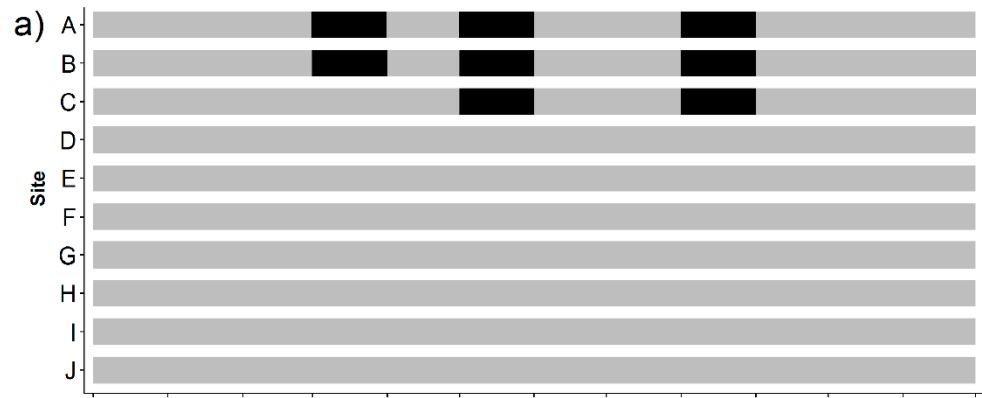
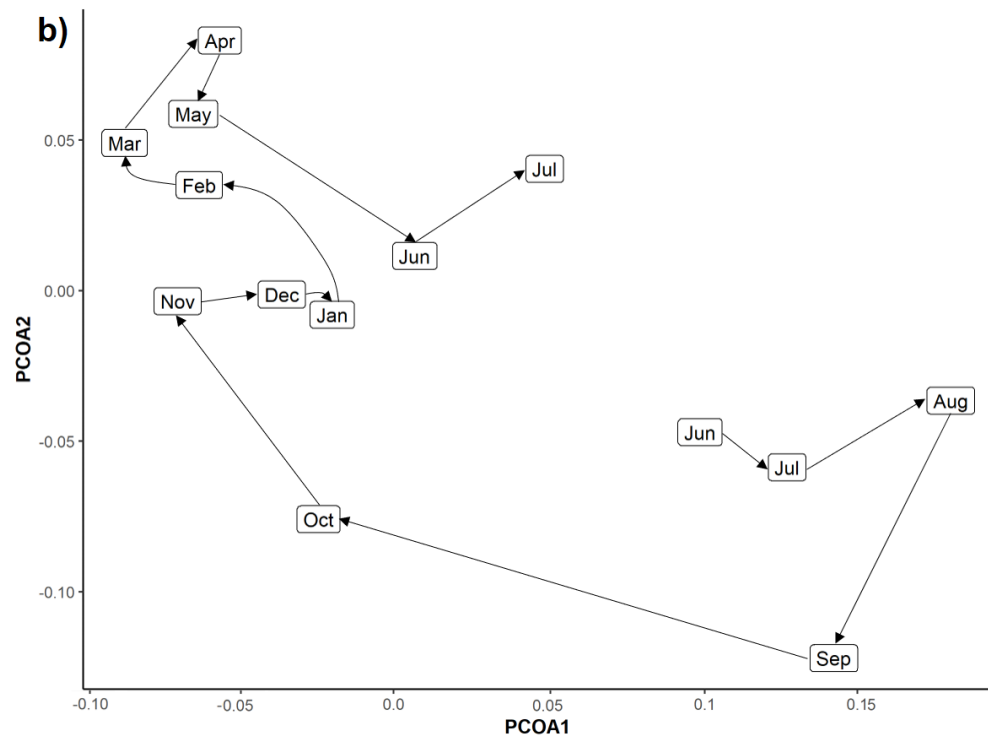
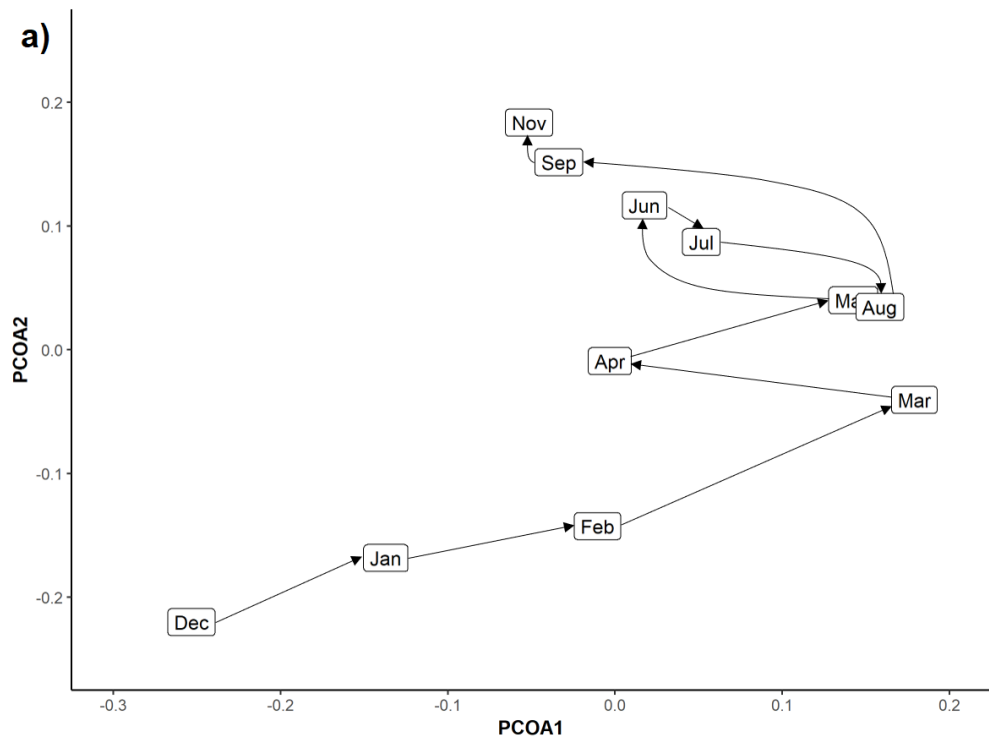




Fig. 2





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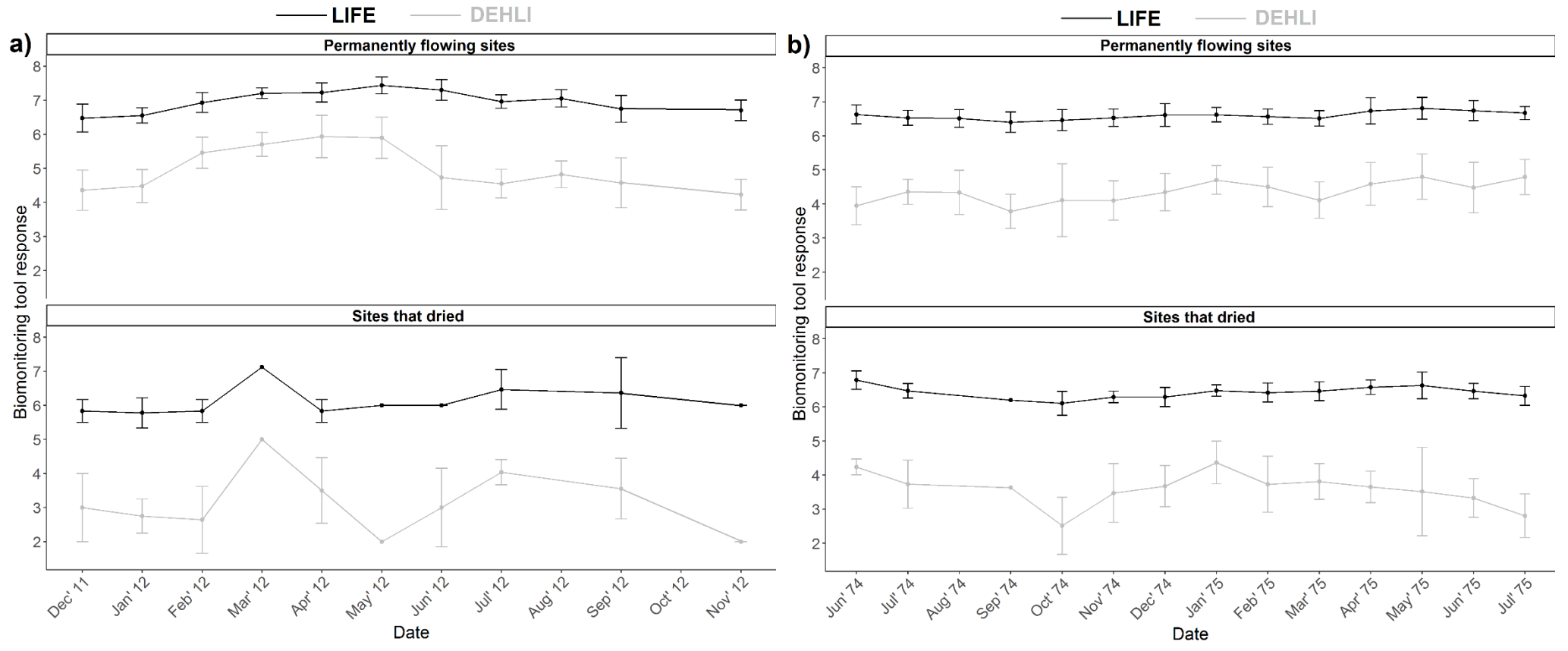
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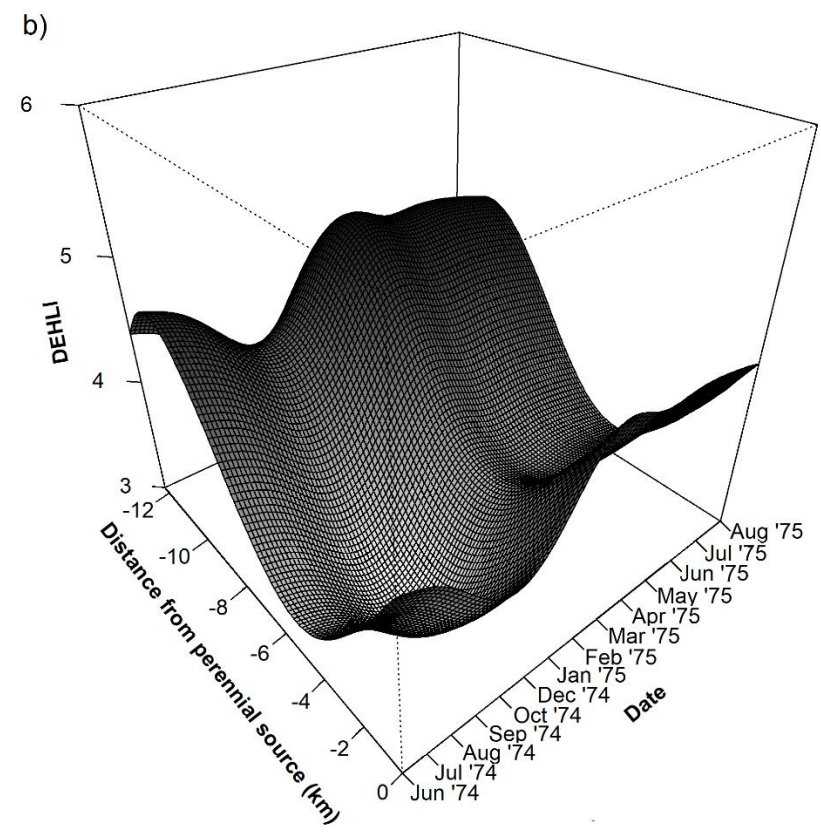
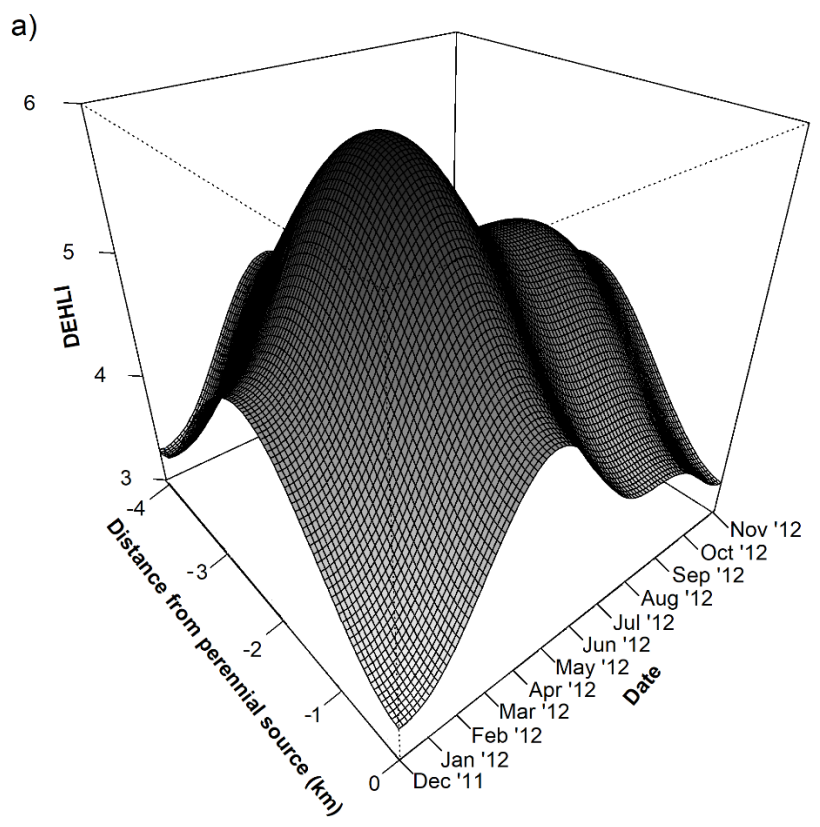
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Fig. 4



800 Fig. 5

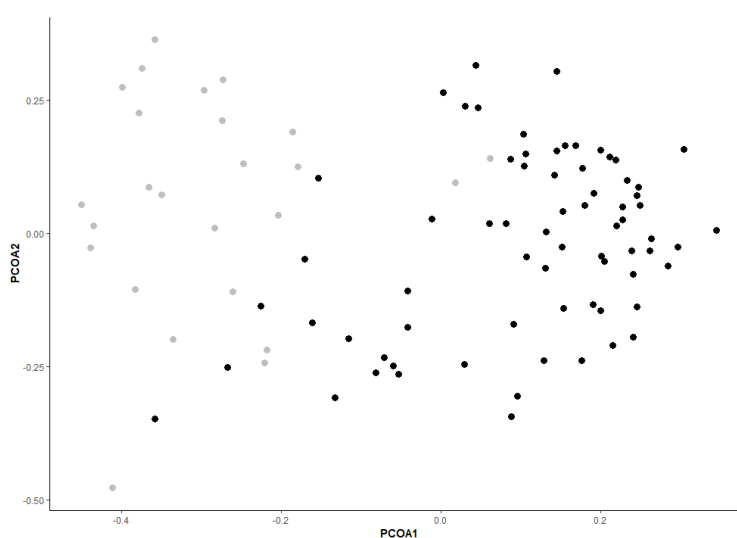


803 **Appendix A**

804 The following appendix displays additional ecological findings within this study using both multivariate and univariate  
805 statistical techniques to assess how invertebrate communities, individual taxa and biomonitoring tools vary spatially and  
806 temporally within the River Lathkill and South Winterbourne (the two case studies examined in this study). The three  
807 biomonitoring tools are ‘Lotic-invertebrate Index for Flow Evaluation’ (LIFE - at both family- and species-level  
808 taxonomic resolutions) and ‘Drought Effect of Habitat Loss on Invertebrates’ (DEHLI - the reader is referred to the  
809 main text for further details on the case studies and the biomonitoring tools).

810 *Multivariate analyses*

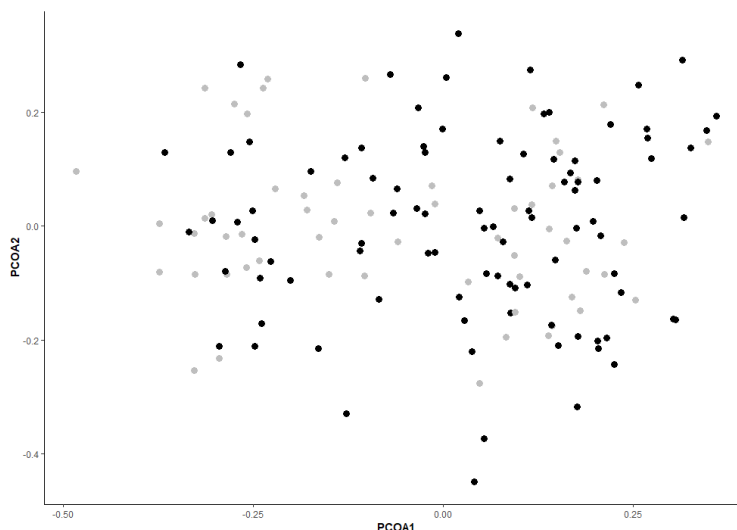
811 Spatial differences in invertebrate community compositions were examined along each of the two temporary  
812 watercourses, whereby sampling sites were categorised into one of two ‘flow permanence’ groups based on whether  
813 they flowed continuously throughout the study period (perennial) or exhibited a drying event (temporary).  
814 ‘Permutational Analysis of Variance’ (PERMANOVA) and ‘Principal Coordinate Analysis’ (PCoA – the reader is  
815 referred to the main text for further details on techniques undertaken to perform this analyses) were used to test and  
816 visualize community differences between flow permanence groups. Within the R. Lathkill, average community  
817 compositions differed significantly ( $p$ -values  $\leq 0.001$ ) between flow permanence groups (Family:  $r^2 = 0.20$ ,  $F = 24.13$ ;  
818 Species:  $r^2 = 0.20$ ,  $F = 24.13$ ). PCoA plots highlighted that temporary and perennial sites typically exhibited low and  
819 high PCoA axis 1 scores (explaining 31.4% of the overall ecological variance), respectively (Fig. A1).



820

821 **Fig. A1** – Principal Coordinates Analysis (PCoA) plot highlighting average community compositional differences  
822 between temporary (grey) and perennial (black) in the River Lathkill case study.

823 Within the South Winterbourne, average community compositions differed significantly ( $p$ -values  $\leq 0.001$ ) between  
824 flow permanence groups, although exhibited a much weaker statistical power compared to the R. Lathkill (Family:  $r^2 =$   
825 0.04,  $F = 5.73$ ; Species:  $r^2 = 0.03$ ,  $F = 4.79$ ). PCoA highlighted a large degree of overlap between invertebrate  
826 multivariate compositions exhibited between temporary and perennial sites (Fig. A2).



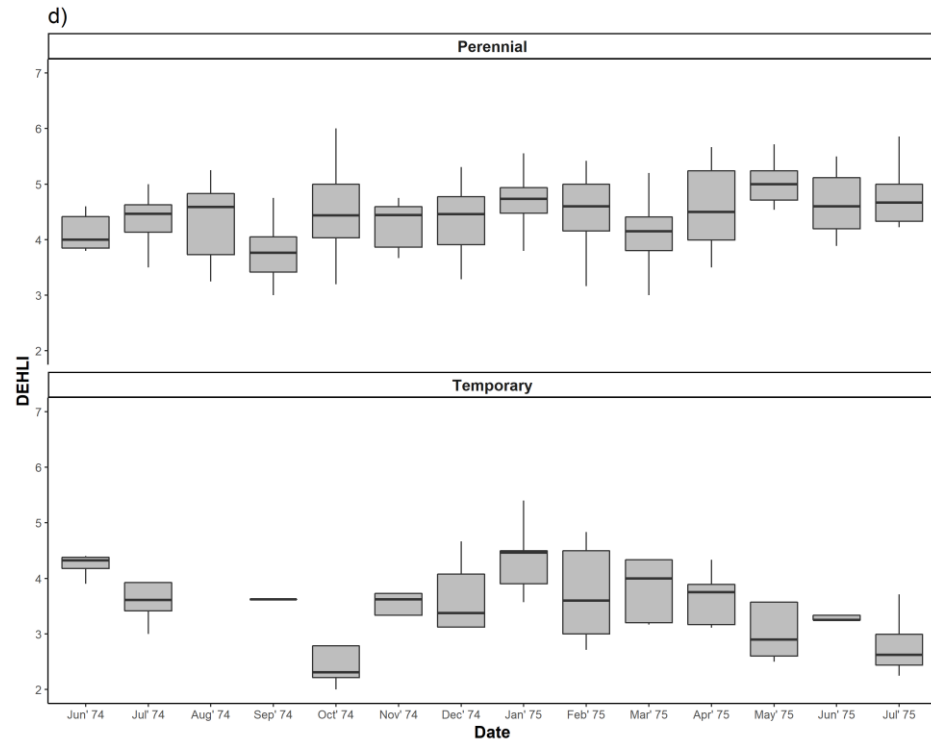
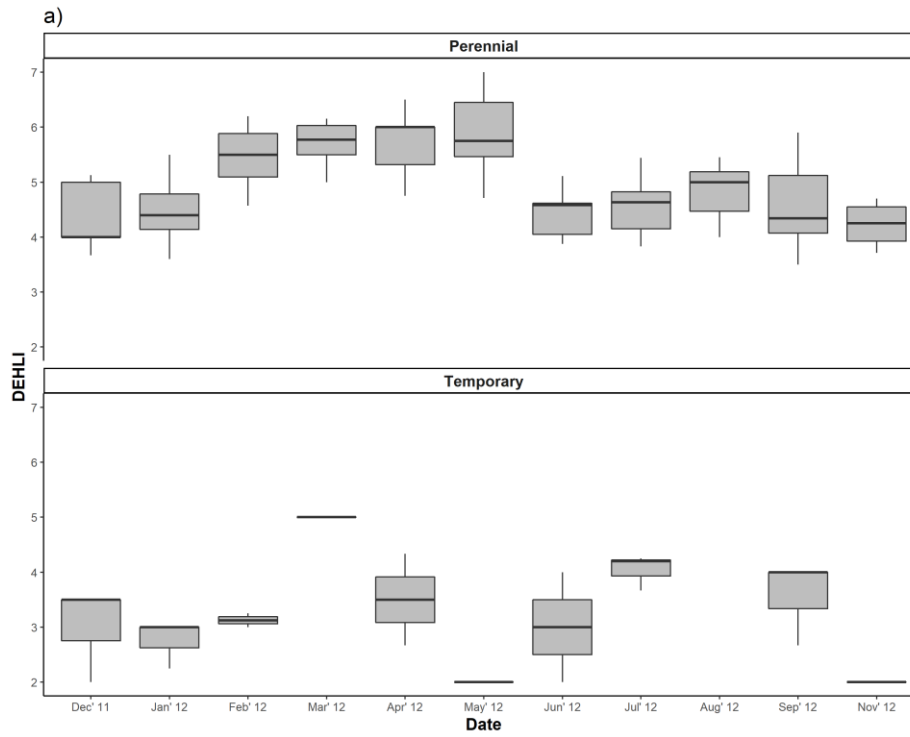
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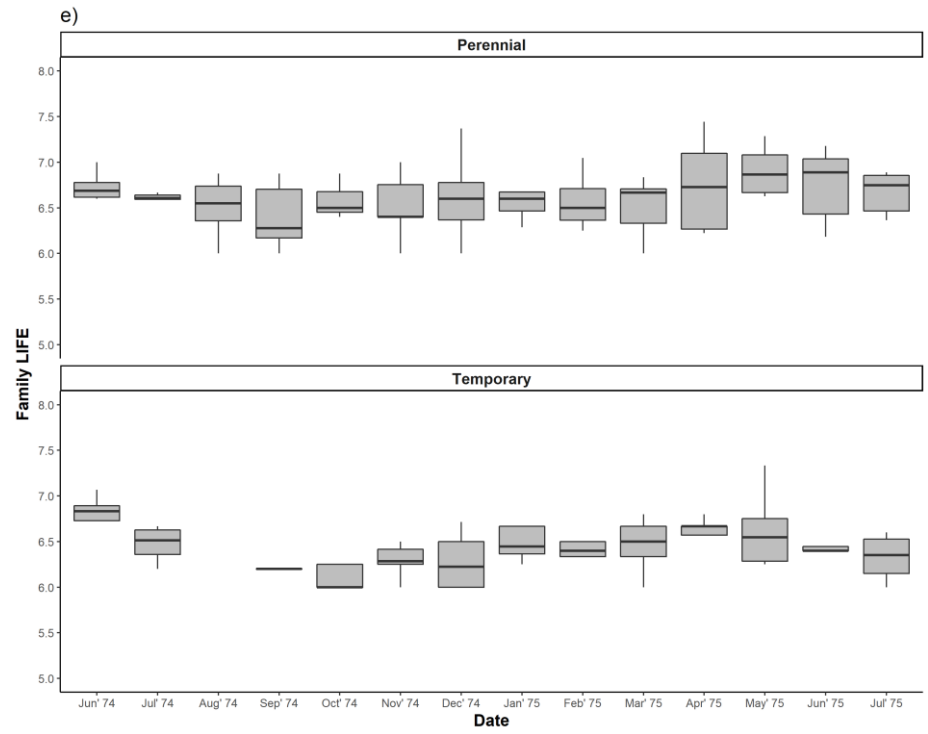
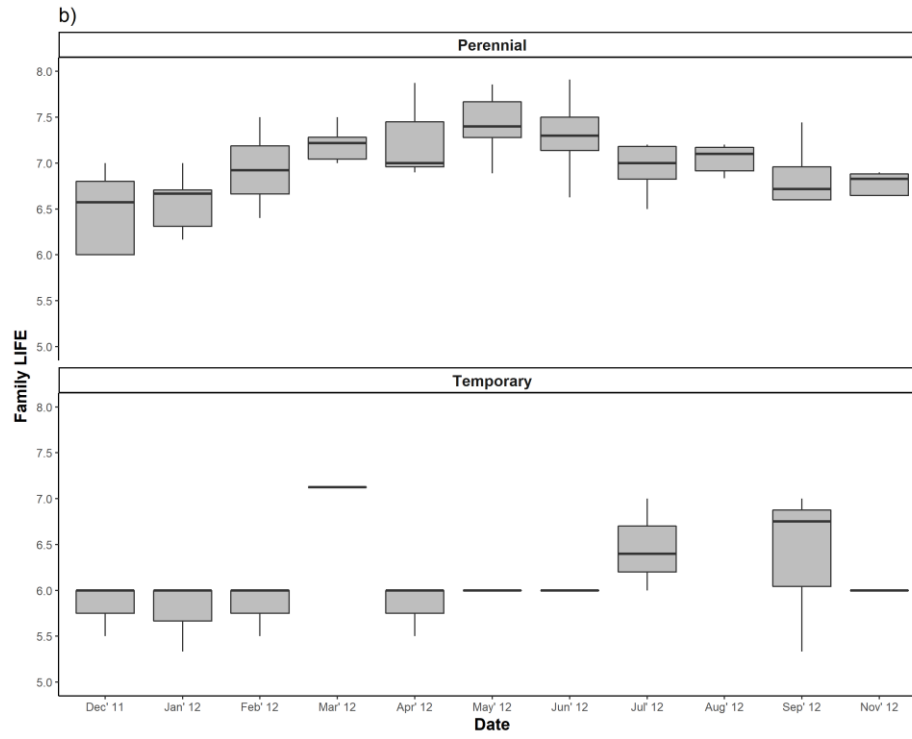
828 **Fig. A2** – Principal Coordinates Analysis (PCoA) plot highlighting average community compositional differences  
829 between temporary (grey) and perennial (black) in the South Winterbourne case study.

### 830 *Univariate analyses*

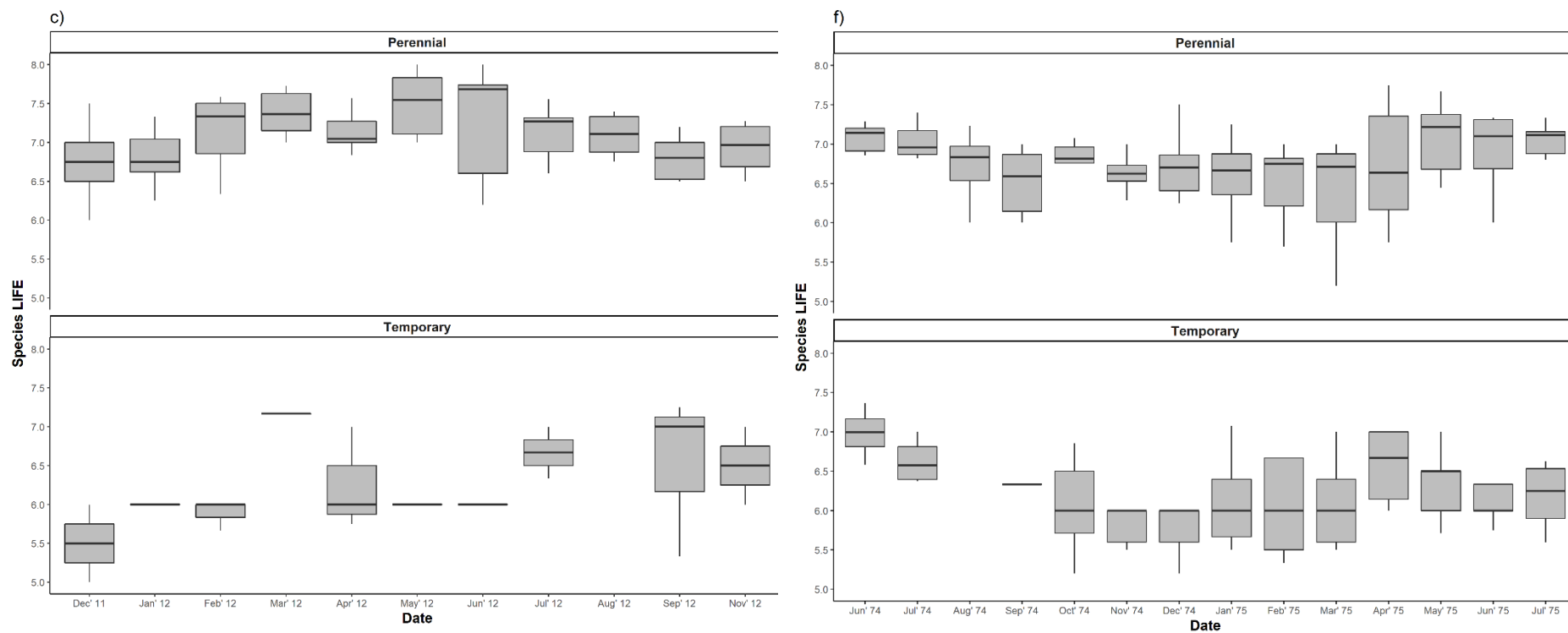
831 In the R. Lathkill, all biomonitoring tools within perennial sites displayed an increase in values from the beginning of  
832 the study period (December, 2011) until May, 2012 and stabilized (albeit with a slight negative trend) thereafter; while  
833 responses in temporary sites fluctuated more widely in accordance with hydrological conditions (e.g. drying events in  
834 March and May, 2012 – see the main text for further discussion). In the R. Lathkill, DEHLI (Fig. A3a) and Family LIFE  
835 (Fig. A3b) displayed a greater degree of temporal heterogeneity compared to Species LIFE (Fig. A3c).

836 In the South Winterbourne, there was a general decrease in biomonitoring tool values between June, 1974 and autumn,  
837 1974, with values increasing thereafter until winter 1975; this pattern was more accentuated within temporary sites (Figs  
838 A3d-e). The remainder of the study period witnessed more stable biomonitoring index values, although DEHLI was  
839 more temporally variable (Fig. A3d) compared to Family (Fig. A3e) and Species LIFE (Fig. A3f).









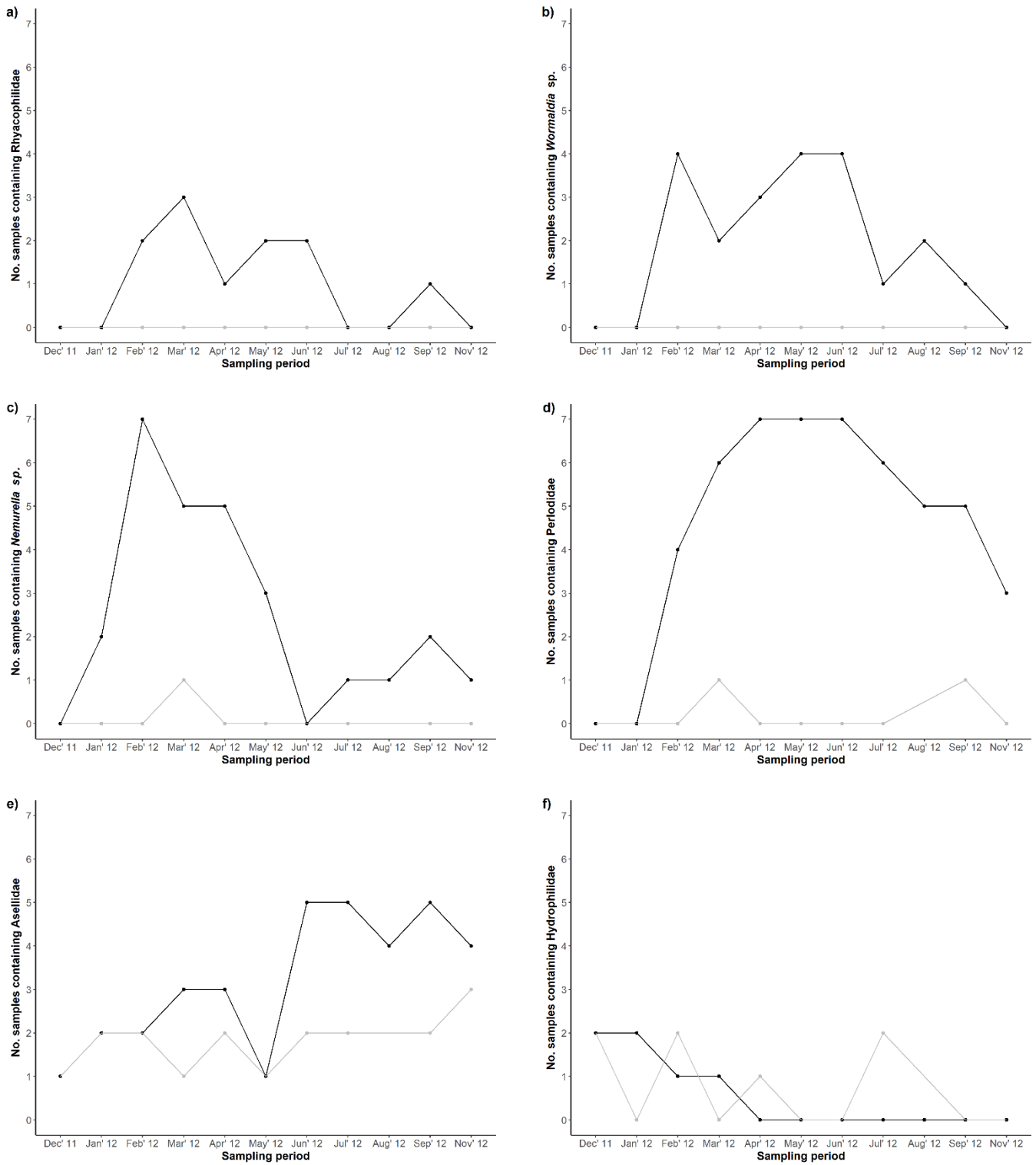
840 **Fig. A3** – Boxplots highlighting differences in biomonitoring index values between monthly sampling periods from the Lathkill (a, b and c) and South  
 841 Winterbourne (d, e and f) case studies. a) and d) DEHLI; b) and e) Family LIFE and c) and f) Species LIFE. Boxes show the 25th, 50th and 75th percentiles,  
 842 whiskers indicate the minimum and maximum values within 1.5 times of the interquartile range (for aesthetical purposes, outliers beyond this limit have been  
 843 removed).

844 Herein, the temporal variation of taxa individual taxa are described and reported at the taxonomic resolution specified  
845 within the DEHLI calculation (i.e. primarily family-level, but with some genus-level classifications) in order to provide  
846 some context on the underlying taxonomic responses underpinning variations in biomonitoring tools.

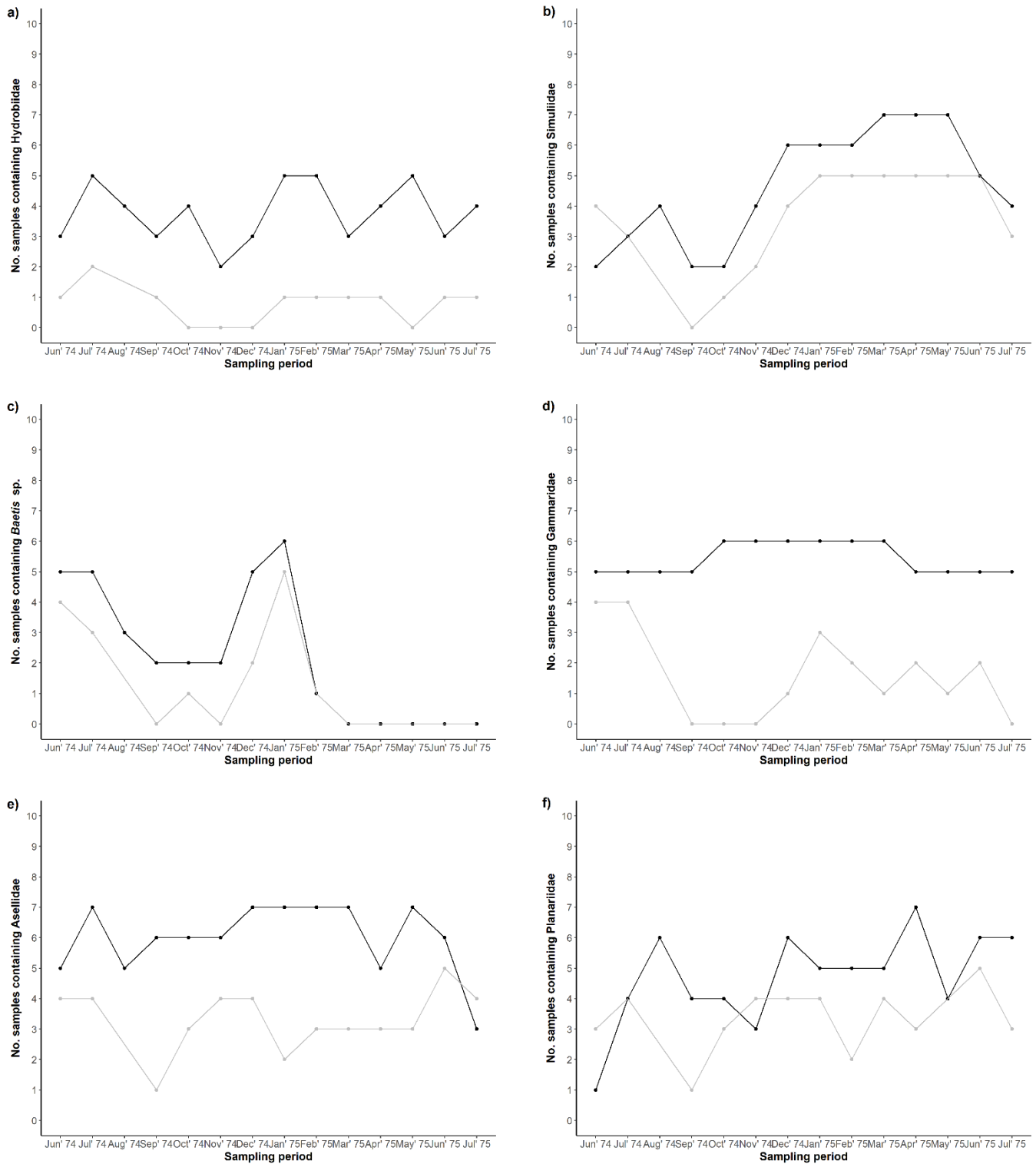
847 Within the R. Lathkill, certain torrenticoles (e.g. Rhyacophilidae – which contained three species representatives within  
848 the *Rhyacophila* genus – Order: Trichoptera and *Wormaldia* sp., Order: Trichoptera) began to establish across perennial  
849 reaches between February-June, 2012 (Figs. A4a-b). Other rheophilic taxa (e.g. *Nemurella* sp., Order: Plecoptera;  
850 Perlodidae – which contained one species representative, *Isoperla grammatica* – Order: Plecoptera) displayed similar  
851 temporal trends at the beginning of the study period, but with a greater degree of success inhabiting larger sections of  
852 the R. Lathkill). Alternatively, certain taxa tolerant of dry conditions (e.g. Asellidae, Order: Isopoda; Hydrophilidae,  
853 Order: Coleoptera) were sampled from both temporary and perennial sections even from the beginning over the study  
854 period (Figs. A4e-f), after a major supra-seasonal drought occurred.

855 Within the South Winterbourne, certain taxa typically associated with inhabiting macrophyte communities (e.g.  
856 Hydrobiidae - which contained one species representative, *Potamopyrgus antipodarum*, Order: Gastropoda and  
857 Simuliidae, Order: Diptera) were sampled from both temporary and perennial reaches during summer, 1974, before  
858 declining in the succeeding autumn. It should be noted that within the DEHLI calculation, Simuliidae is recorded as  
859 being sensitive to the loss of longitudinal flow connectivity (rather than latitudinal connectivity associated with marginal  
860 macrophytes, like Hydrobiidae – Chadd *et al.*, 2017), but has been widely associated with different macrophytes,  
861 including the marginal macrophyte *Rorippa aquaticum*, which inhabited temporary reaches of the South Winterbourne  
862 during the study period. Subsequently, these taxa associated with macrophytes increased across the winter months of  
863 1974-1975 (Figs. A5a-b). Other rheophilic taxa (e.g. *Baetis* sp., Order: Ephemeroptera; Gammaridae – which contained  
864 one species representative, *Gammarus pulex* – Order: Amphipoda) displayed similar temporal trends to taxa associated  
865 with macrophytes, although exhibited strong declines across spring and summer, 1975 (although *G. pulex* were sampled  
866 consistently from perennial reaches throughout the study period - Figs. A5c-d). Specialist taxa tolerant of dry conditions  
867 (e.g. Asellidae, Order: Isopoda; Planariidae, Order: Tricladida) were sampled from both perennial and temporary  
868 sections of the South Winterbourne at the beginning of the study period, although these taxa were more consistently  
869 sampled in the former until winter 1974-1975, but declined in temporary reaches across autumn, 1974 before resurging  
870 in the succeeding winter months (Figs. A5e-f).

871



872 **Fig. A4** - Number of samples containing specific taxa each month within perennial (black) and temporary (grey) reaches  
 873 in the River Lathkill. a) Rhyacophilidae; b) *Wormaldia* sp.; c) *Nemurella* sp.; d) Perlodidae; e) Asellidae and f)  
 874 Hydrophilidae.



875 **Fig. A5** – Number of samples containing specific taxa each month within perennial (black) and temporary (grey) reaches  
 876 in the South Winterbourne. a) Hydrobiidae; b) Simuliidae; c) *Baetis* sp.; d) Gammaridae; e) Asellidae and f) Planariidae.

877 **References**

878 Chadd, R. P., England, J. A., Constable, D., Dunbar, M. J., Extence, C. A., Leeming, D. J. and Wood, P. J. (2017). An  
 879 index to track the ecological effects of drought development and recovery on riverine invertebrate communities.  
 880 *Ecological Indicators*, 82. 344–356.