

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 (CaCO₃) 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 ‘*gamm*’ 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 *gamm* 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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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 ^{NS}	0.81	13.39	<0.001***	0.02	0.22	0.827 ^{NS}
	Species LIFE	0.67	8.85	<0.001***	-0.02	-0.16	0.877 ^{NS}	0.66	8.60	<0.001***	-0.07	-0.65	0.515 ^{NS}
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 ^{NS}	0.52	7.51	<0.001***	-0.12	-1.56	0.122 ^{NS}
	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 ^{NS}

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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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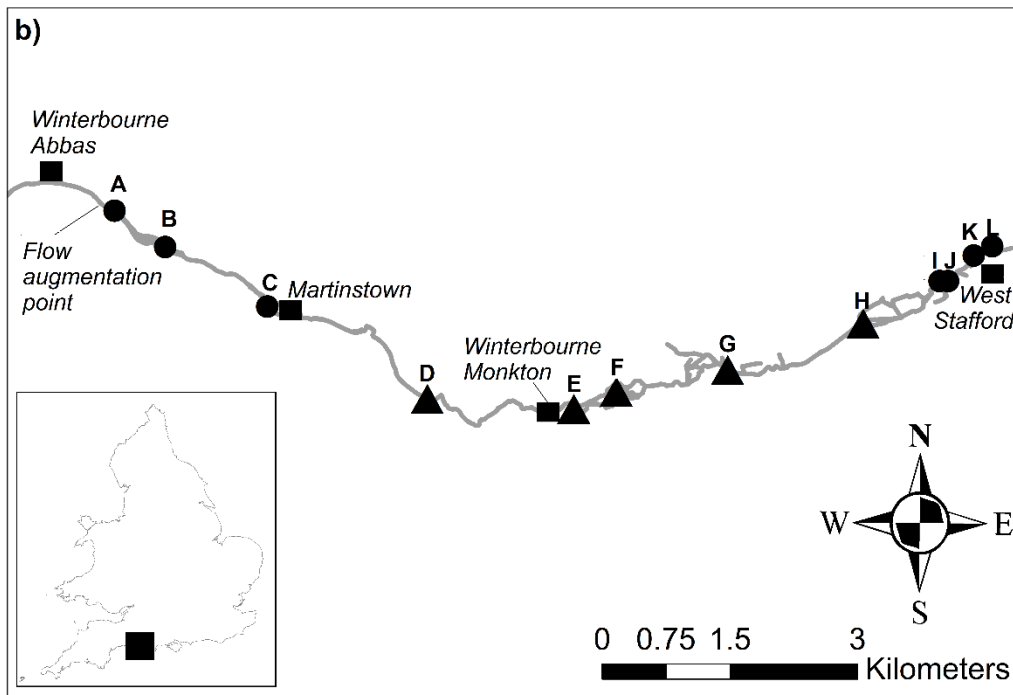
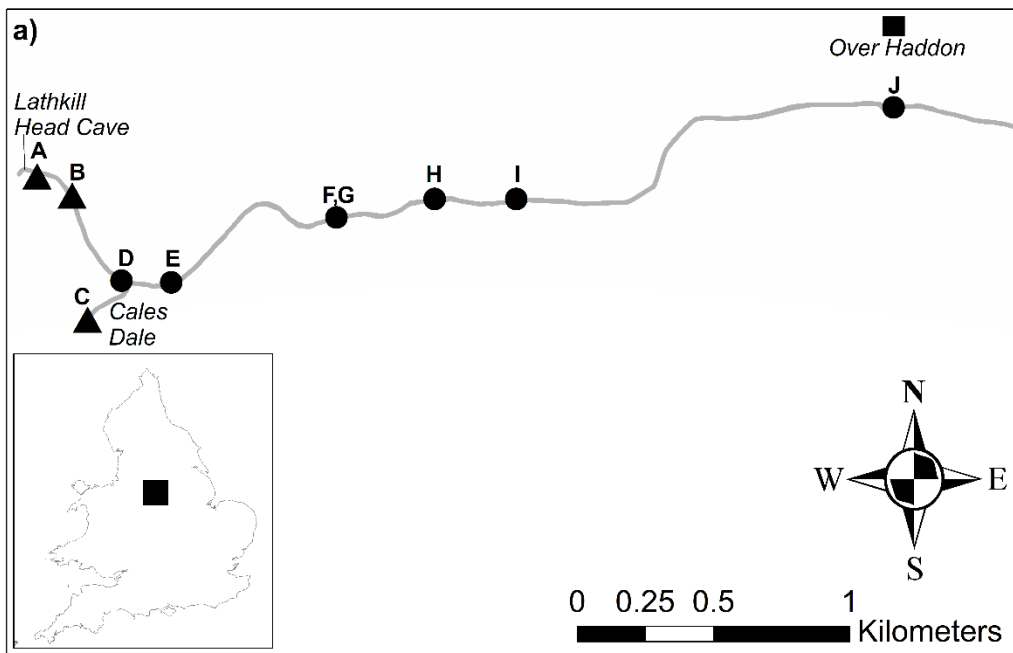
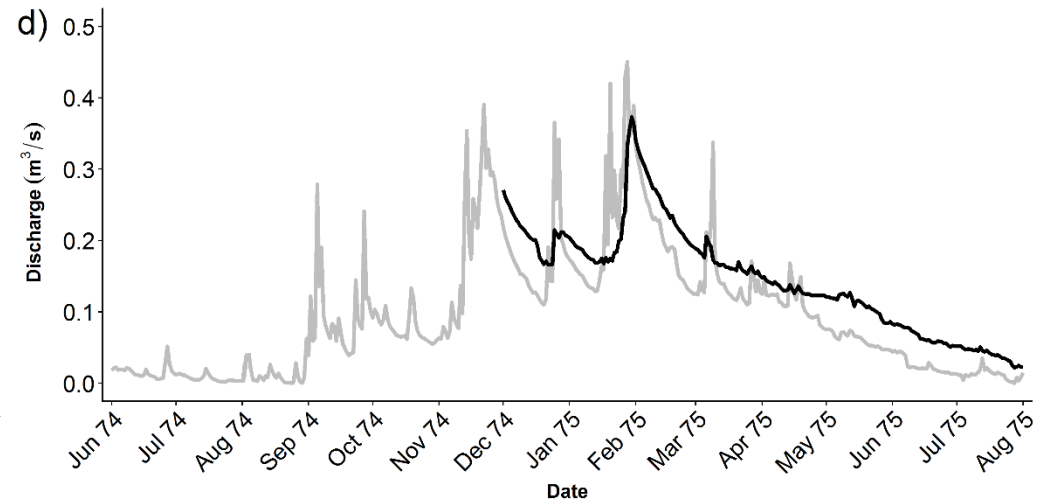
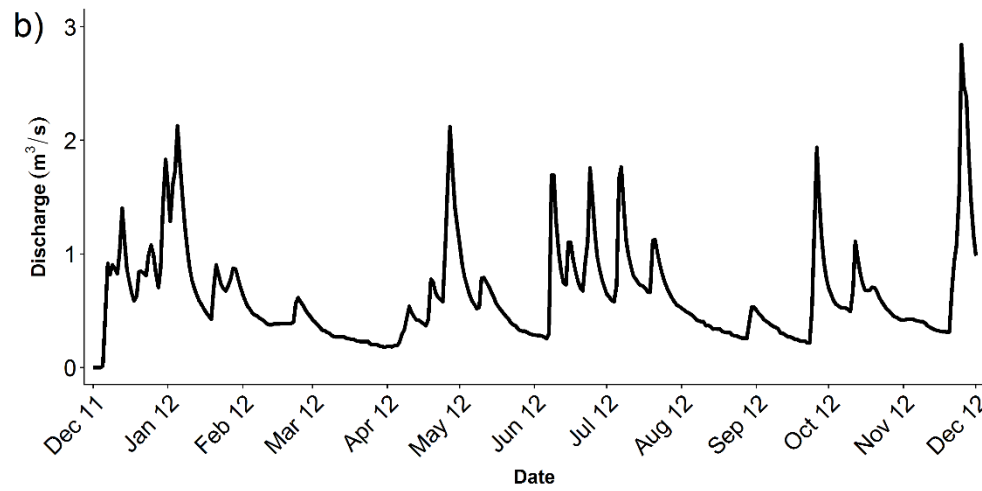
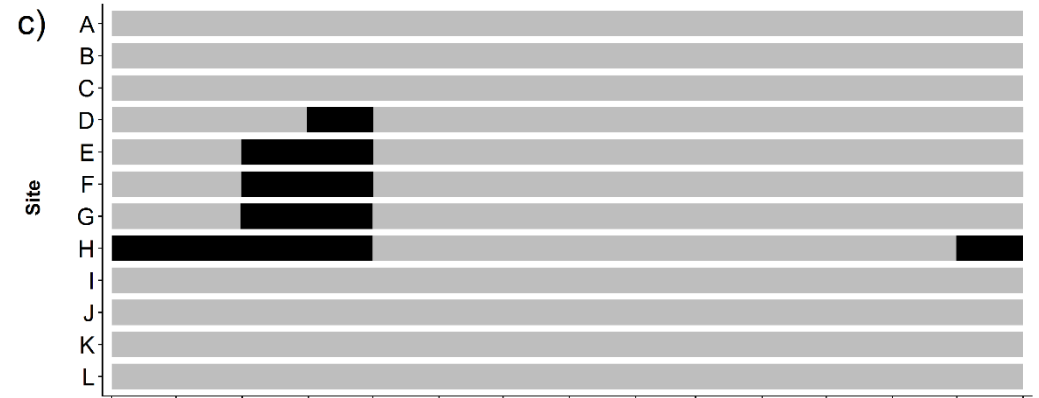
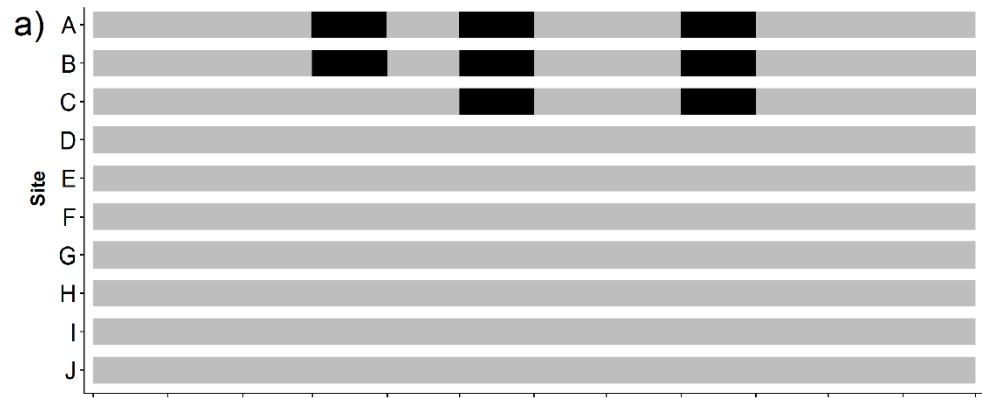
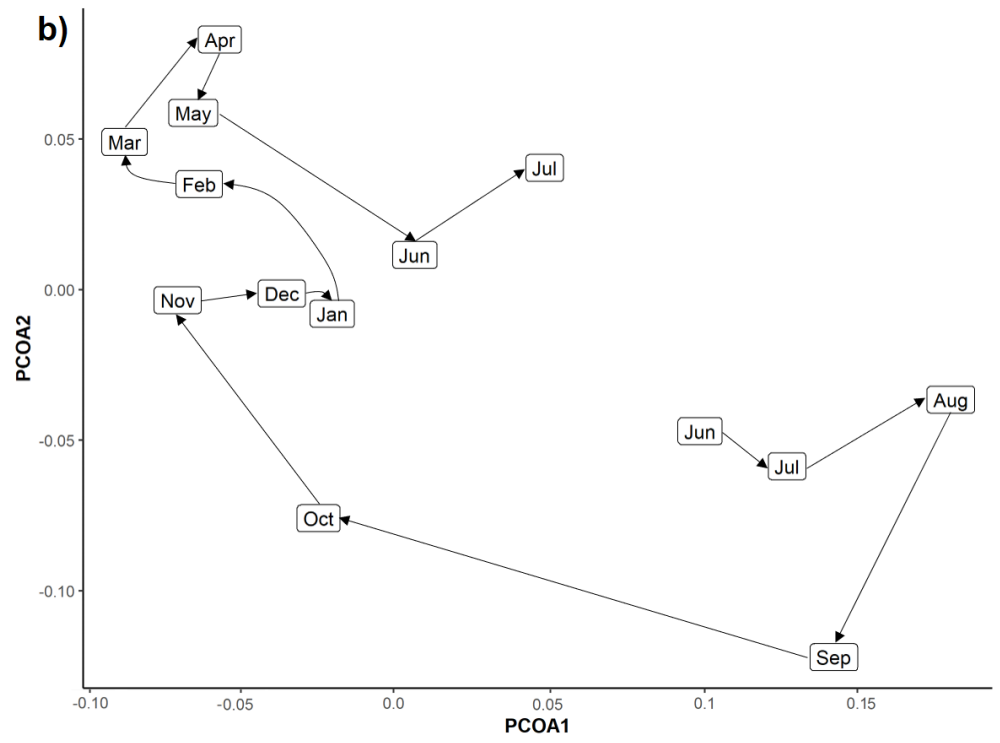
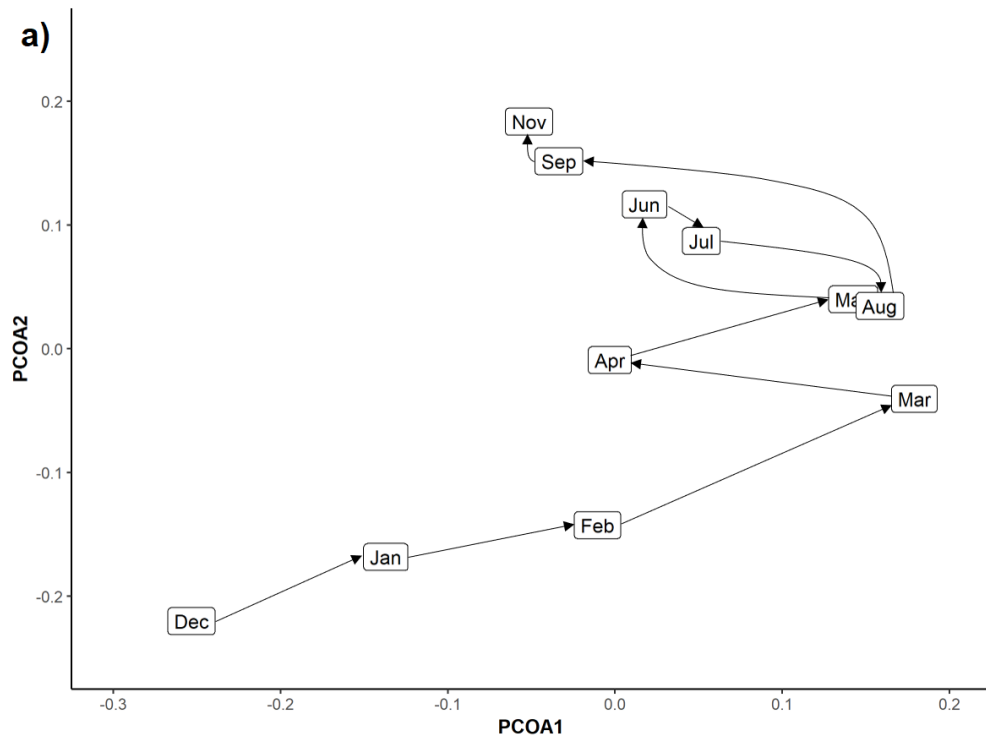


Fig. 2





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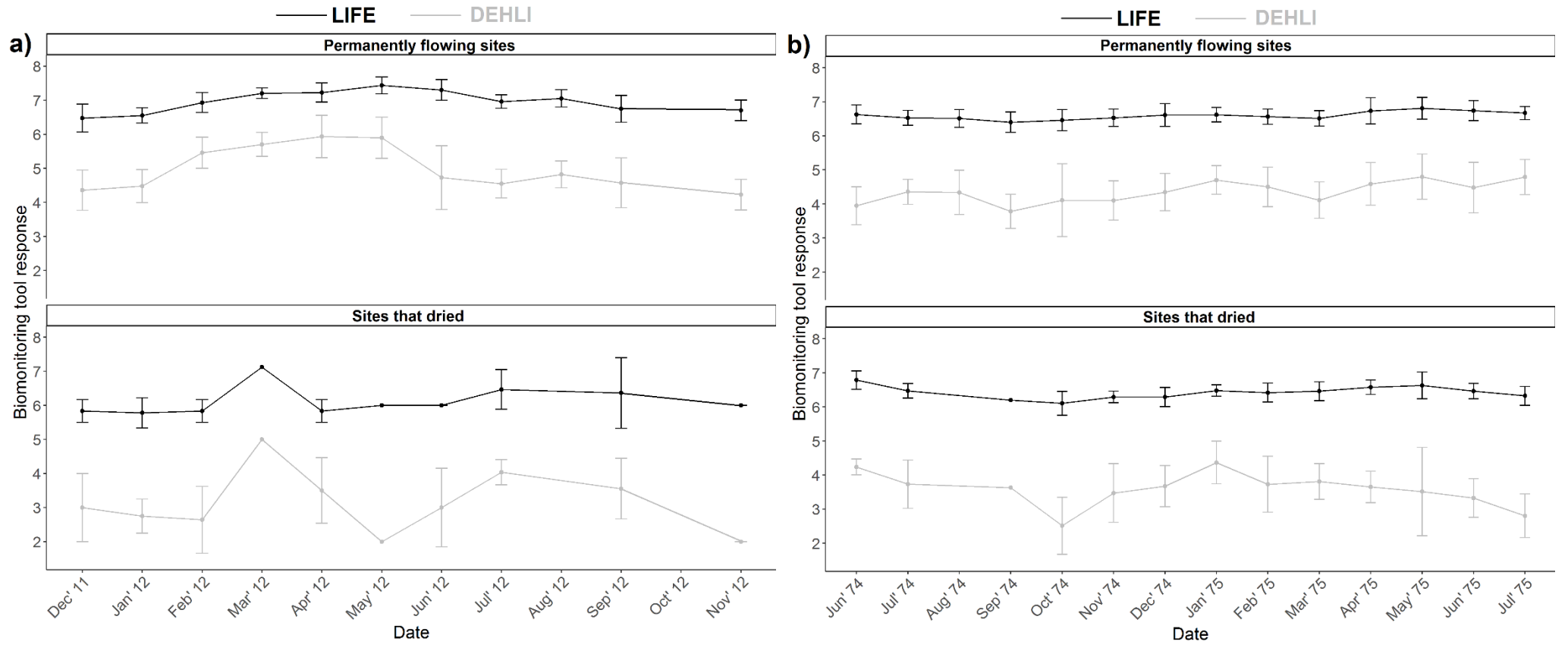
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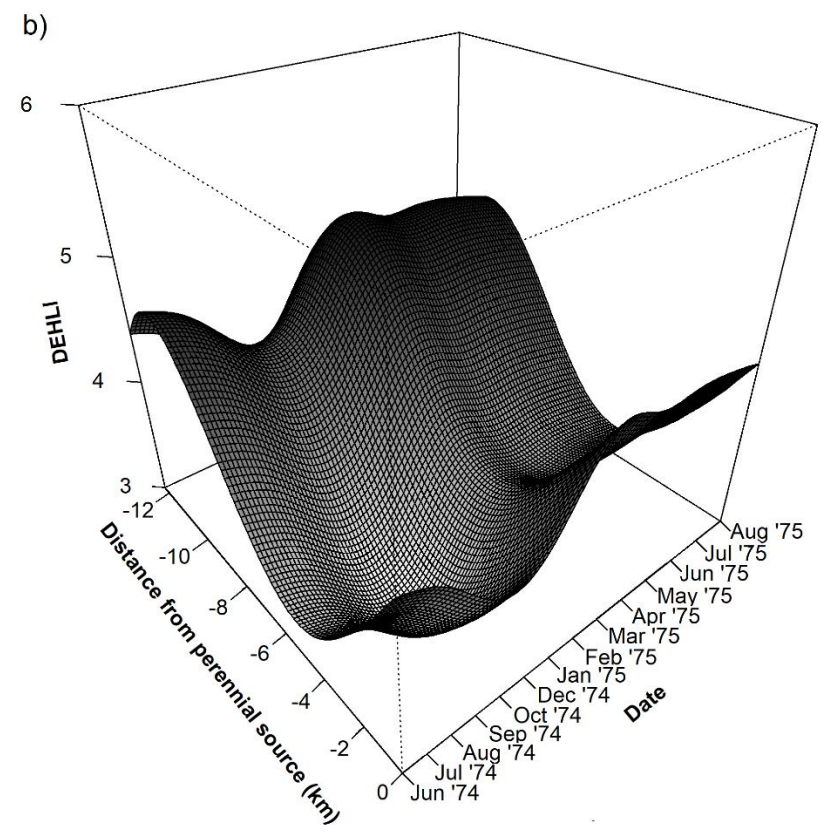
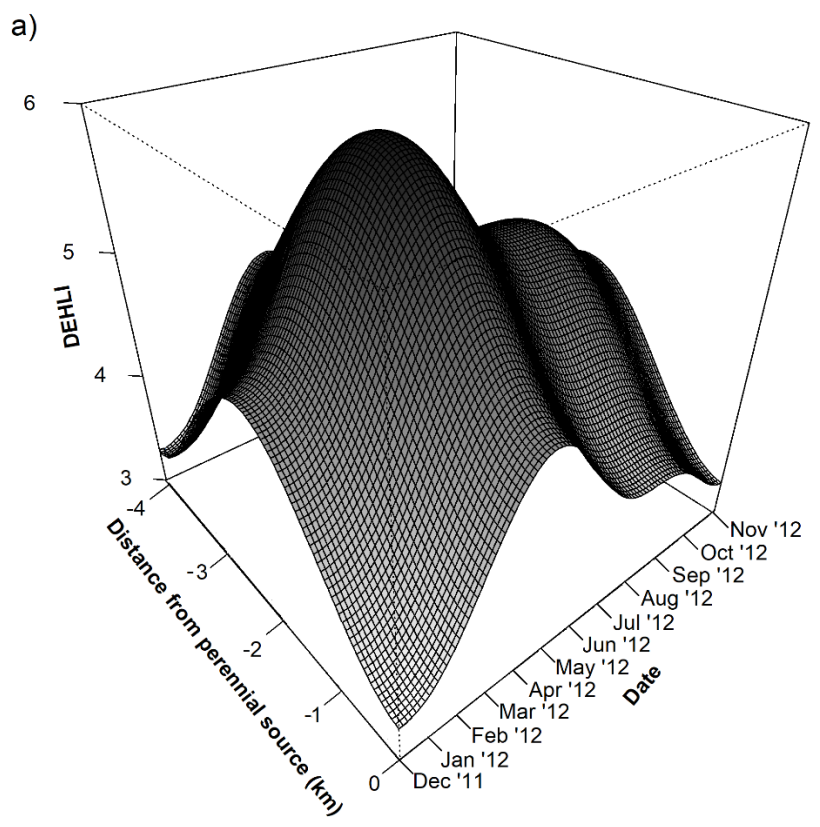
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Fig. 4



800 Fig. 5

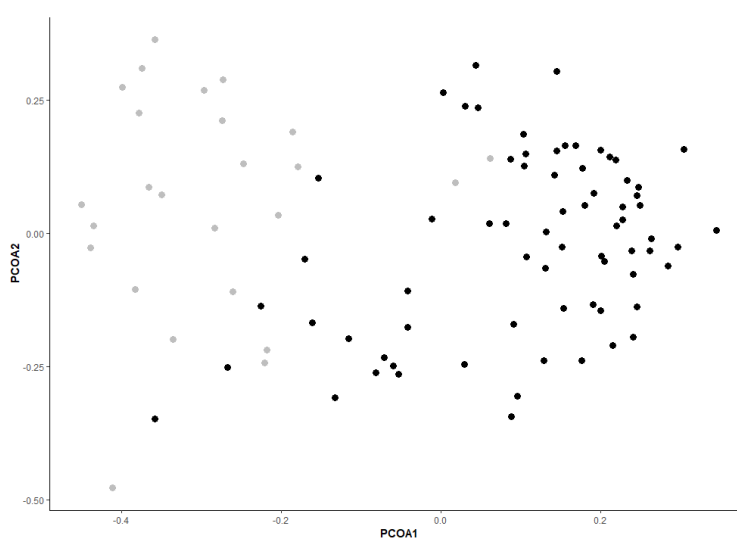


803 **Appendix A**

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*

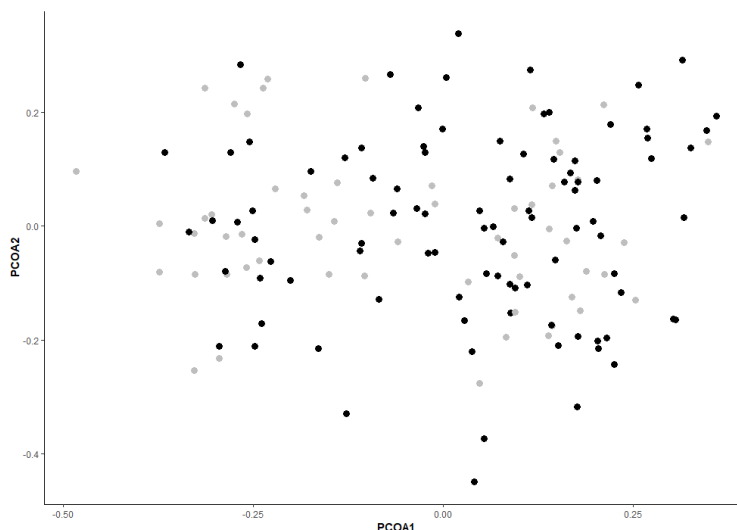
811 Spatial differences in invertebrate community compositions were examined along each of the two temporary
812 watercourses, whereby sampling sites were categorised into one of two ‘flow permanence’ groups based on whether
813 they flowed continuously throughout the study period (perennial) or exhibited 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 ($p\text{-values} \leq 0.001$) 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 ≤ 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).



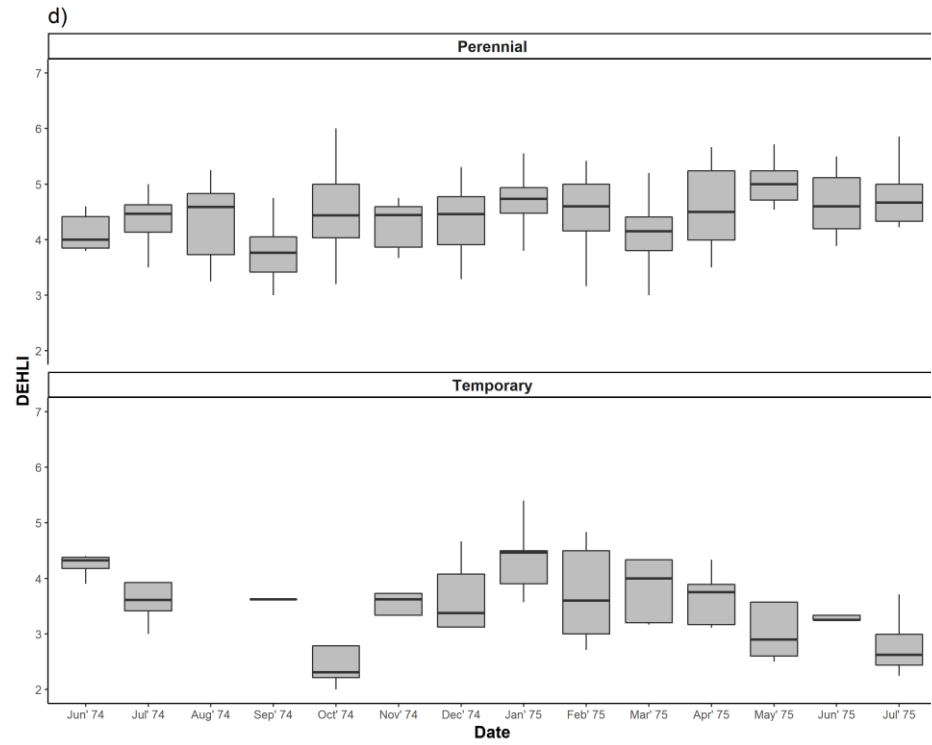
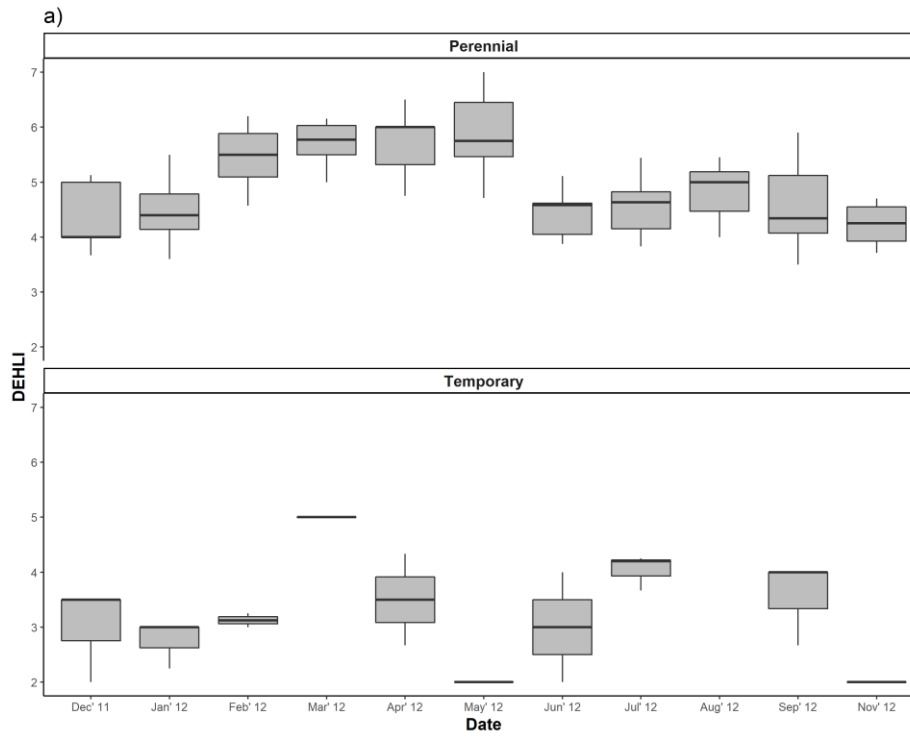
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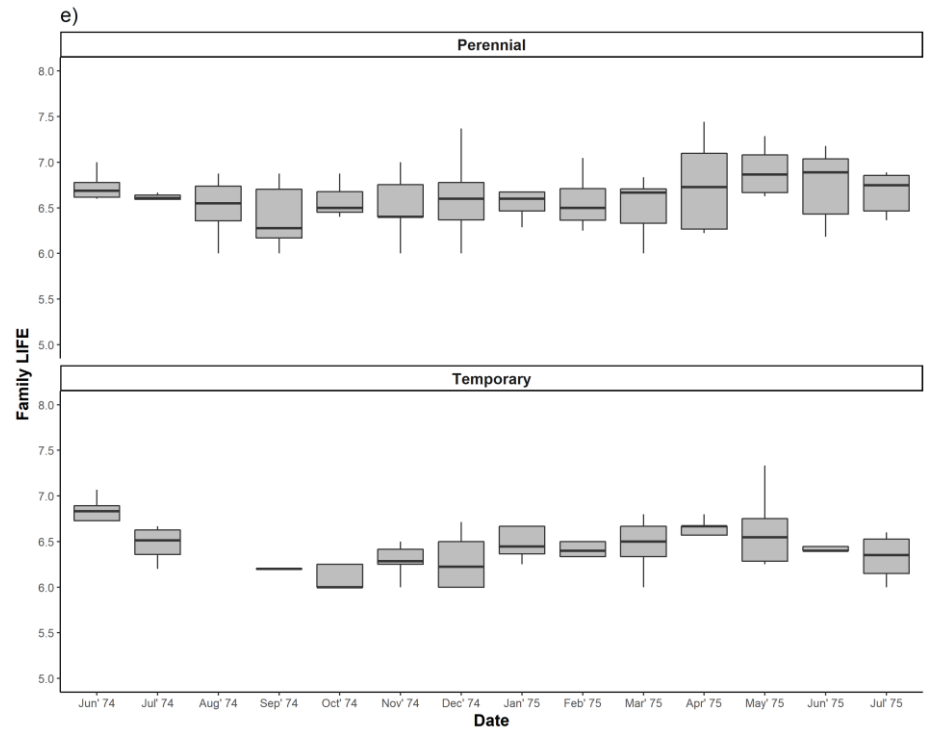
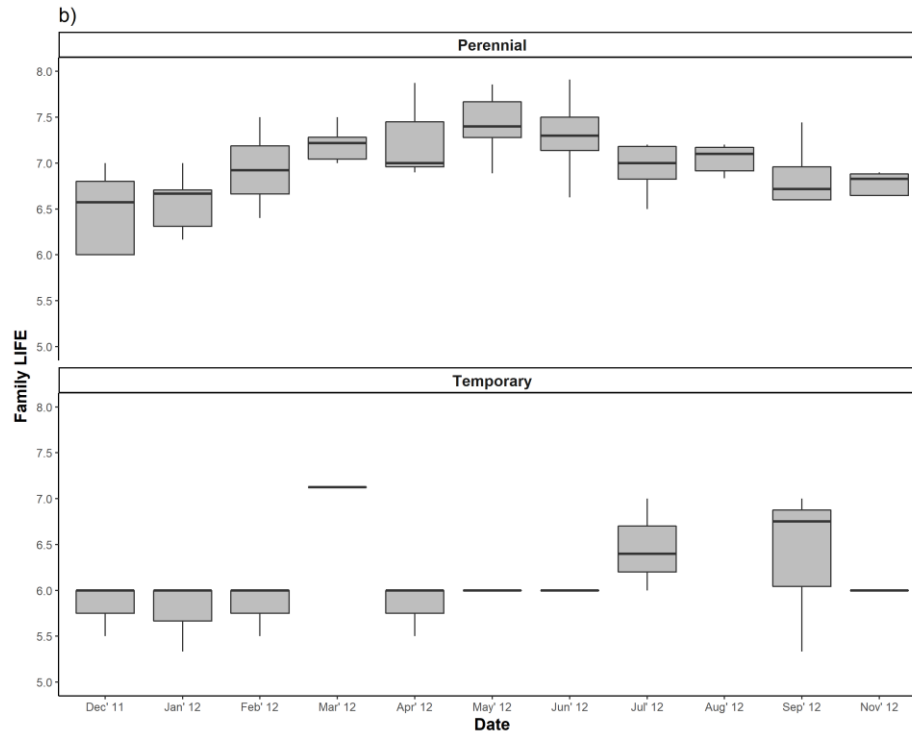
828 **Fig. A2** – Principal Coordinates Analysis (PCoA) plot highlighting average community compositional differences
829 between temporary (grey) and perennial (black) in the South Winterbourne case study.

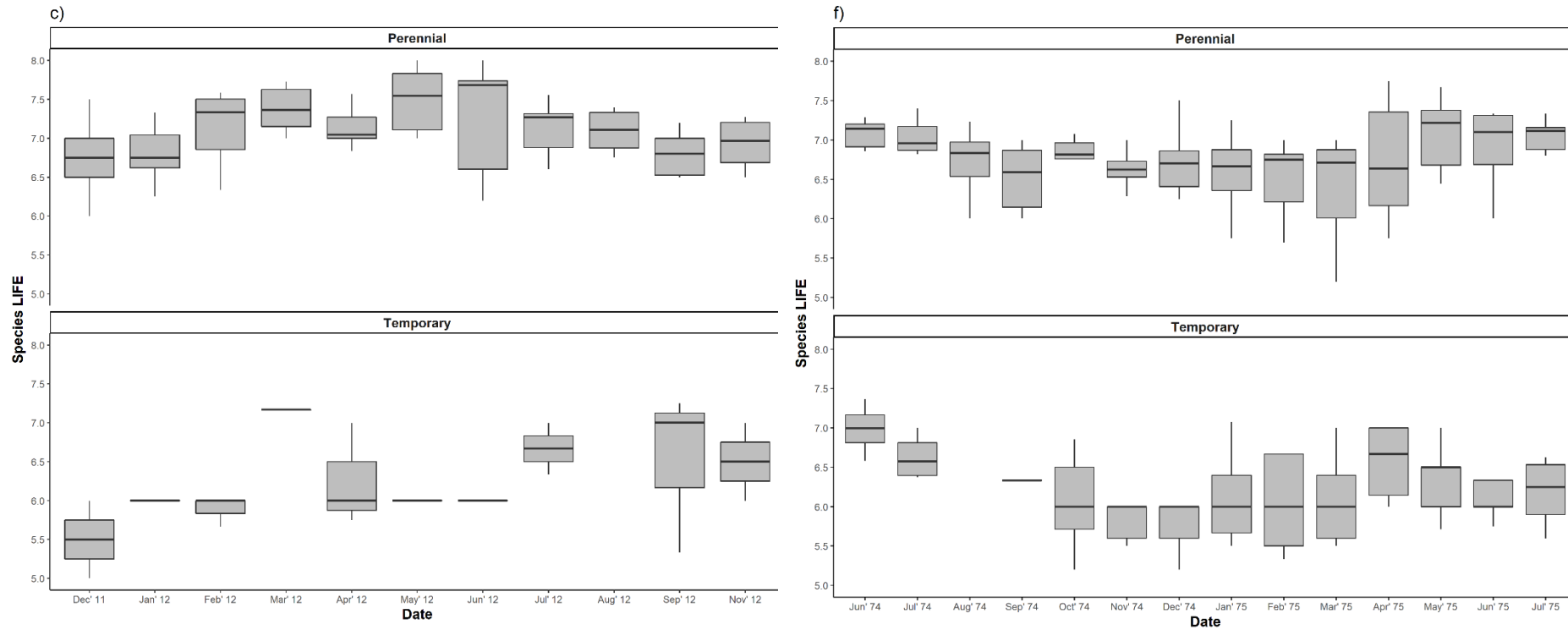
830 *Univariate analyses*

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).







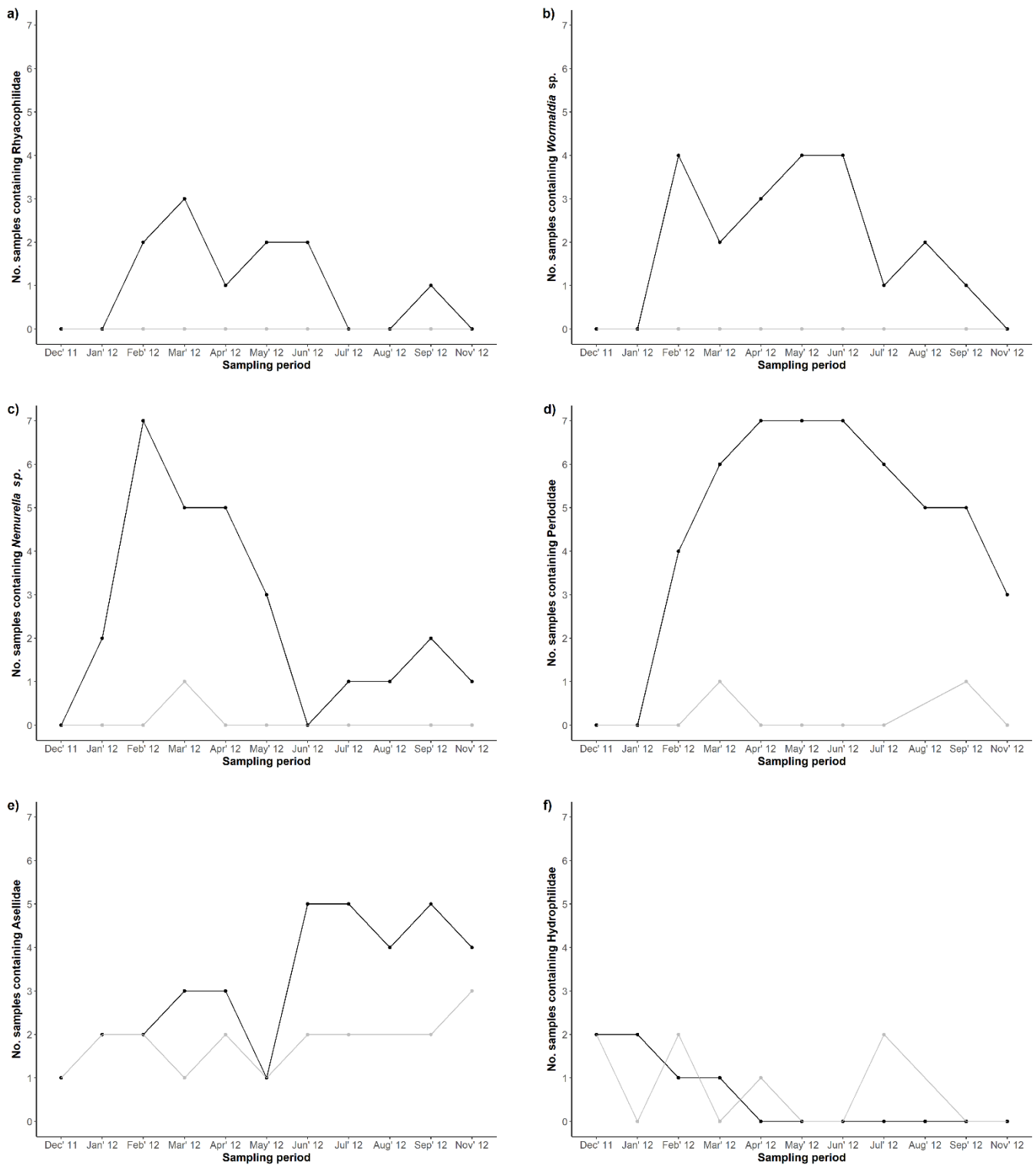
840 **Fig. A3** – Boxplots highlighting differences in biomonitoring index values between monthly sampling periods from the Lathkill (a, b and c) and South
 841 Winterbourne (d, e and f) case studies. a) and d) DEHLI; b) and e) Family LIFE and c) and f) Species LIFE. Boxes show the 25th, 50th and 75th 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.

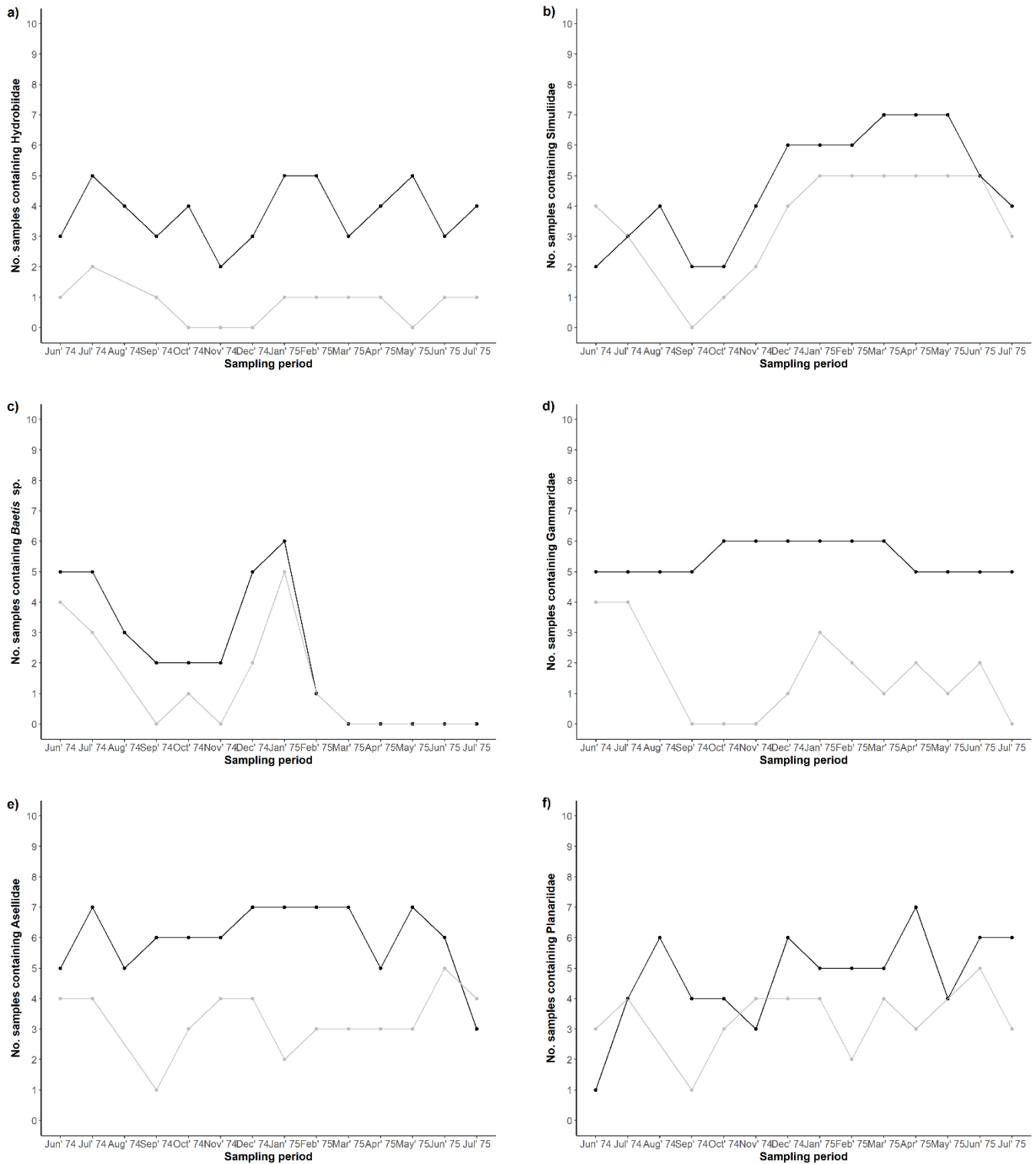
847 Within the R. Lathkill, certain torrenticoles (e.g. Rhyacophilidae – which contained three species representatives within
848 the *Rhyacophila* genus – Order: Trichoptera and *Wormaldia* sp., Order: Trichoptera) began to establish across perennial
849 reaches between February-June, 2012 (Figs. A4a-b). 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**

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