

24 **Abstract**

25 The duration, intensity and frequency of hydrological droughts are predicted to increase significantly
26 over the 21st century globally, threatening the long-term stability of lotic communities. In this paper
27 we examine the recovery and recolonization of macroinvertebrate taxa in ephemeral and near
28 perennial reaches of the River Lathkill (UK) after a supra-seasonal drought event. Following flow
29 resumption, species accumulation (recolonization) occurred rapidly over a four-month period, with a
30 steady increase observed thereafter. Taxonomic richness was significantly higher in the section with
31 near perennial flow after the first month of the study (near perennial) than the naturally ephemeral
32 reach. Serial correlation was observed in the near perennial section but not in the upstream ephemeral
33 reach. Serial correlation in the near perennial section may reflect: (1) the ongoing process of recovery
34 or (2) the macroinvertebrate community following a new ecological trajectory. Our results suggest
35 that supra-seasonal droughts may cause initial reductions in lotic diversity during stream desiccation
36 events but may re-set ecological succession and / or temporarily provide new ecological niches,
37 thereby supporting increased taxonomic diversity when the full range of hydrological conditions are
38 considered. Quantifying the recovery of ecological communities following supra-seasonal drought can
39 provide information to help develop ecologically effective conservation and management strategies.

40 **Key words:** aquatic conservation, biodiversity, community composition, disturbance, ephemeral
41 streams, lotic habitat.

42 **Introduction**

43 Global climate models predict that the duration, intensity and frequency of drought events are likely
44 to increase significantly over the 21st century (Prudhomme et al. 2014). Climatic variability combined
45 with increasing abstraction pressures and the construction of artificial impoundments to supply
46 increasing human populations globally, is likely to increase the number of waterbodies that
47 experience channel drying (Larned et al. 2010), extend the duration of drying events in waterbodies
48 that already experience dewatering (Benejam et al. 2010; Rahiz and New 2013; Skoulikidis et al.
49 2017) and lead to significant changes to biological communities, such as the loss of taxa poorly
50 adapted to drying events (Datry et al. 2014).

51

52 Supraseasonal drought is defined here as an extended duration of reduced rainfall and surface water
53 availability over multiple seasons or years (Lake 2011). This differs from seasonal drought which is
54 characterised by seasonal reductions in rainfall and water availability, such as those regularly
55 experienced in semi-arid or Mediterranean ecosystems (Gasith and Resh 1999). Extreme, high
56 magnitude but low frequency supra-seasonal events may significantly increase the spatial and
57 temporal extent of stream drying (Boulton 2003; Wood and Armitage 2004) and in some instances
58 affect historically perennially flowing sites (Stubbington et al. 2015).

59

60 Surface water drying is a primary determinant of aquatic floral and faunal diversity and community
61 structure in intermittent lotic ecosystems (Lake 2003; Stubbington et al. 2011; Aspin et al. 2018), with
62 streambed drying events commonly being associated with reductions in aquatic diversity (Soria et al.
63 2017). Following streambed drying, harsh environmental conditions selectively remove taxa which
64 are dependent on surface flow and good water quality (Wood and Petts 1999; Datry et al. 2013) and
65 may cause an increase in faunal densities and competition as habitat availability is reduced (James et
66 al. 2008). However, recovery of flow and the recolonization of aquatic flora and fauna following
67 channel drying in intermittent streams can be rapid, reflecting the range of traits / adaptations which

68 promote resilience and resistance in temporary waterbodies (Fritz and Dodds 2004; Stubbington and
69 Datry 2013; Vander Vorste et al. 2015; Sarremejane et al. 2017). Resistance can be enhanced due to
70 strong dispersal capacity with taxa being able to migrate from the stream as it dries and rapidly
71 recolonize when flow resumes (Leigh et al. 2016). Resilience can be facilitated by physiological and
72 morphological traits that enable drought survival *in situ* (e.g., short life cycles, desiccation resistant
73 eggs or adult life stages able to persist in moist sediments; Williams 2006; Vander Vorste et al. 2015).
74 Resilience strategies may be strongly influenced by the presence of refuges, such as nearby perennial
75 pools, the hyporheic zone, perennial downstream reaches or patches of moist leaf litter, proximal to
76 intermittent streams (Chester and Robson 2011; Hill and Milner 2018).

77

78 In streams that experience regular or predictable drying, the effect of seasonal drought on aquatic
79 communities may be compared to those of perennially flowing systems (Côté and Darling 2010;
80 Vander Vorste et al. 2015; Chessman 2015). Typically, perennial streams have high ecosystem
81 stability and may be dominated by a limited number of highly abundant flora and fauna (Fisher 1983;
82 Milner et al. 2008). However, supra-seasonal droughts and the subsequent recolonization and
83 recovery period may encourage the development of distinct faunal assemblages (Boulton 2003; Chadd
84 et al. 2017), and may help maintain, and in some instances, enhance habitat and faunal diversity at the
85 landscape scale. Supra-seasonal droughts potentially open new ecological niches for some organisms
86 following the removal or reduction in abundance of numerically dominant and highly competitive
87 taxa or through the disturbance and re-setting of ecological succession trajectories. For example, the
88 gradual drying and ponding of surface water in a river channel as it dries may provide suitable
89 conditions for colonization by a wide range of taxa associated with lentic conditions (Sheldon et al.
90 2010; Hill and Milner 2018).

91

92 While the process of recolonization and recovery following stream drying and drought events within
93 seasonally intermittent waterbodies has been widely studied (Boulton 2003), there is a paucity of
94 research examining aquatic biodiversity following supra-seasonal drought events (Lake 2003). This is

95 particularly apparent in temperate regions due to the difficulties associated with collecting long-term
96 data and predicting the onset and termination of supra-seasonal drought events. In arid landscapes,
97 Bogan et al. (2015) found that robust recovery after a supra-seasonal drought occurred in streams with
98 historically predictable intermittency, with these communities demonstrating both resistance and
99 resilience mechanisms. In the same study, the response of perennial macroinvertebrate communities
100 to supra-seasonal drought differed due to a lack of resistance traits in the pre-drought community;
101 long lived (>1 year) weak dispersing macroinvertebrates were replaced by short lived (<1 year) strong
102 dispersers that were able to rapidly recolonize.

103

104 A supra-seasonal drought in the UK between December 2010 and April 2012 (Parry et al. 2013),
105 which caused channel drying in both historically perennial and ephemeral reaches of the River
106 Lathkill, provided a unique opportunity to examine the response of macroinvertebrate communities to
107 flow recovery. As a result, this is one of the first studies to examine ecological responses to supra-
108 seasonal drought from communities in ephemeral and historically perennial flow sites in temperate
109 regions. This study aimed to characterise the recolonization of aquatic macroinvertebrate communities
110 of naturally ephemeral and near perennial sites (flowing except under extreme drought conditions) in
111 the River Lathkill (UK) following a high magnitude supra-season drought.

112

113 **Materials and Methods**

114 *Study sites*

115 The River Lathkill (Derbyshire, UK) is a groundwater-fed river in the White Peak area of the Peak
116 District National Park. Land-use in the catchment is predominantly low intensity grazing on
117 unimproved grassland (Stubbington et al. 2016). The perennial source originates at Bubble Springs (SK
118 2049 6612, 159m AOD; Figure 1) and the entire catchment of the river above the springs is underlain
119 by Carboniferous limestone.

120

121 A total of 11 sites within two sections upstream of the perennial source (Bubble Springs), based on
122 their historic flow permanence (after Wood et al. 2005), were studied. Naturally ephemeral sites
123 comprised the headwater sites (Sites 1-6; Figure 1) which typically experience surface water drying
124 for at least six-months per-annum, although flows can occur in response to high rainfall events (two to
125 four times per year; Stubbington et al. 2016). Exposed limestone bedrock with boulder to gravel size
126 clasts dominated headwater sites. Finer organic rich sediments with patches of semi-aquatic and
127 terrestrial flora were also present. The second downstream section comprised five near perennial sites;
128 three sites which dry most years for a short period (typically around 2 weeks but up to 2 months)
129 depending on meteorological conditions, and two sites that have dried only once in the last 30 years
130 (Sites 7-11; Figure 1). The substratum at sites with near perennial flow consisted predominately of
131 mixed alluvial deposits (sand to cobble sized angular clasts) with instream vegetation dominated by
132 mosses and liverworts (Stubbington et al. 2011). All study sites were upstream of the confluence
133 between the R. Lathkill and the River Bradford (Figure 1).

134

135 *Hydroclimatic conditions*

136 The 2010-2012 supra-seasonal drought affected large parts of England, particularly southern and
137 midland areas (Parry et al. 2013). By the end of March 2012, 14 of the previous 24 months had
138 recorded <70% of average rainfall across lowland England (10 of those recorded <55% of average
139 rainfall: Marsh et al. 2013). As a result, the channel was dry upstream of the perennial source (Bubble
140 Springs) and both study reaches (ephemeral and near perennial sites) remained dry for the longest
141 duration since the start of monitoring in 1998. After a nine-month dry period, flow resumed in the
142 ephemeral headwaters but dried again in mid-March 2012 for ca. 28 days (Stubbington et al. 2016).
143 The supra-seasonal drought ended abruptly in April 2012 which experienced double the monthly
144 average rainfall (Parry et al. 2013). As a result, surface flow resumed throughout the near perennial
145 reach in April 2012 and the channel experienced flowing conditions throughout the remainder of the
146 study. Overall, 2012 was the wettest year in England since 1910 (Parry et al. 2013). Flow remained
147 ephemeral in the ephemeral reach and streambed drying occurred on three additional occasions; (1)

148 ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May 2012; and (3) ca. 46 days from early
149 August 2012 (Stubbington et al. 2016). Regional monthly mean temperatures for 2012 were within
150 0.5 °C of the long-term average (1961-1990; Met Office 2015).

151

152 *Macroinvertebrate sampling*

153 Aquatic macroinvertebrate samples were collected from 11 sites along the R. Lathkill at monthly
154 intervals where possible (some samples could not be taken during high flow events or dry periods)
155 between December 2011 and September 2012. A total of 138 samples were collected; 72 from the
156 ephemeral and 66 from the near perennial reach (Figure 1b). Two additional macroinvertebrate
157 sampling events were undertaken in November 2012 and February 2013. Samples comprised a three-
158 minute kick sample (using a pond net fitted with 1 mm mesh) divided equally between mesohabitats
159 present. Aquatic macroinvertebrate samples were preserved in the field with 4% formaldehyde
160 solution prior to processing and identification in the laboratory. The majority of macroinvertebrate
161 taxa were identified to species level but Diptera, Leuctridae, Baetidae, Sphaeriidae and Planariidae
162 were resolved to family level and Oligochaeta, Tricladida (non-Planariidae) and Collembola were
163 recorded as such.

164

165 *Statistical analysis*

166 To examine temporal changes in diversity and the relative abundance of individual taxa over time
167 mixed-effects models were fitted to selected taxon and community metrics. Prior to statistical
168 analysis, data were examined to ensure they met the assumptions of statistical tests (e.g., normal
169 distribution). The following taxa; *Asellus aquaticus*, *Gammarus pulex*, *Isoperla grammatica*,
170 *Serratella ignita*, Baetidae and *Perlodes mortoni* were selected for further investigation as they
171 typically occurred in greater abundances and in multiple samples throughout the study period. The
172 month of sample collection and sample sites were fitted as random effects to account for potential
173 spatial and temporal dependence, and month and intermittence (ephemeral and near perennial) were

174 fitted as fixed interacting factors. Taxonomic richness was tested via a Generalised Linear Mixed
175 Effects Model (GLMM) fitted using a Poisson distribution and log link structure via the ‘*glmer*’
176 function in the lme4 package (Bates et al. 2018). Community abundance and abundances of individual
177 taxa were tested via a Linear Mixed Effects Model (LMM) using the ‘*lmer*’ function in the lme4
178 package with the restricted maximum likelihood (REML) estimation function. Abundances were
179 $\log_{10}(x+1)$ transformed to normalise residuals prior to model fitting. Conditional R^2 (proportion of
180 variance explained by the fixed and random factors; r^2_c) values were extracted using
181 ‘*rsquared.glm*’ function in the MuMIn package (Bartoń 2018). To account for the non-linear
182 association of *I. grammatica* with time, a third order polynomial model was fitted. This technique has
183 been shown to reliably model nonlinear associations without model overfitting (Kennen et al. 2014).
184 Species accumulation plots were constructed to examine the rate of recolonization over time for
185 ephemeral and near perennial sites and a linear model fitted to assess the rate of invertebrate
186 colonisation differed over time between ephemeral and near perennial sites. All univariate analyses
187 were conducted using R version 3.2.3 (R Development Core Team 2015).

188

189 Heterogeneity of macroinvertebrate communities between the ephemeral and near perennial reaches
190 was assessed using Analysis of Similarity (ANOSIM) and visualised using Non-metric
191 Multidimensional Scaling (NMDS) ordination plots (using Bray Curtis dissimilarity). To identify
192 changes in community composition among months in ephemeral and near perennial sites, spearman
193 rank correlations (RELATE) and centroid NMDS ordination plots were examined. A monthly
194 similarity matrix (Bray-Curtis) for each site was compared to a linear sequence (the sampling months
195 in this study) to examine if similarity among macroinvertebrate assemblages was higher in adjacent
196 sampling months than in more distant sampling months (*Serial RELATE*; Clarke and Gorley 2006).
197 Distances among centroid matrices were constructed by calculating the averages (e.g., the centroid -
198 the centre-point of all replicates for each month in multi-dimensional space) in the ‘Bray-Curtis
199 space’ of macroinvertebrate compositions from the replicate samples for each month (Anderson et al.
200 2008). Centroid NMDS ordinations were generated using the distance among centroid matrices.

201 Similarity Percentage analysis (SIMPER) was used to determine which species were driving the
202 differences in community composition between ephemeral and near perennial sites. Faunal abundance
203 data was log transformed prior to ANOSIM, NMDS, centroid NMDS, SIMPER and RELATE
204 analysis, which was undertaken in PRIMER V7 (PRIMER-E Ltd, Plymouth, UK).

205

206 **Results**

207 *Spatial macroinvertebrate diversity and variability in community composition in ephemeral and near* 208 *perennial reaches*

209 Following the supra-seasonal drought (2011-2013), a total of 101 taxa were recorded from the
210 ephemeral (total: 65 taxa, mean: 7.1, range: 3-13) and near perennial sites (total: 85 taxa, mean: 14.6,
211 range: 5-25) during the 12 surveys from the 11 sample sites. Of the 101 taxa recorded between 2011-
212 2013, the most widely distributed taxa were: Chironomidae, Tipulidae, Simuliidae, Oligochaeta, *A.*
213 *aquaticus*, *G. pulex* (recorded at all 11 sites) and, Baetidae, *G. truncatula* and *Nemurella picteti*
214 (recorded at 10 sites). The most diverse orders were Trichoptera (23 taxa), Coleoptera (21 taxa),
215 Plecoptera (14 taxa) and Diptera (14 taxa).

216

217 Taxonomic richness (df=9, t=3.905, p=0.004) and total relative abundance (df=9, t=3.615, p=0.006)
218 were significantly higher in near perennial than ephemeral sites (Figure 2). No significant differences
219 in the abundance of *A. aquaticus*, *I. grammatica*, *S. ignita*, Baetidae and *P. mortoni* between near
220 perennial and ephemeral sites were recorded; however, *G. pulex* had significantly greater abundances
221 in near perennial than ephemeral sites (df=9, t=2.425 p=0.038). Significant differences were observed
222 in macroinvertebrate community composition between ephemeral and near perennial sites (ANOSIM
223 $r=0.457$ p=0.01; Figure 3a). The top four macroinvertebrate taxa identified by SIMPER to be driving
224 the differences in macroinvertebrate community composition between ephemeral and near perennial
225 sites were *A. aquaticus* (contributing 6% to the dissimilarity) which were recorded in greater
226 abundances in ephemeral sites and Baetidae (8.4% dissimilarity), Chironomidae (7.3% dissimilarity)

227 and *I. grammatica* (6% dissimilarity) which were recorded in greater abundances from near perennial
228 sites. A total of 16 taxa were unique to ephemeral and 35 taxa to near perennial sites (see
229 Supplementary Material Part 1).

230

231 *Temporal diversity and variability in community composition in ephemeral and near perennial*
232 *reaches*

233 At a regional scale, a steep increase in taxonomic richness was recorded in ephemeral and near
234 perennial sites over the first three months after flow resumed (December 2011 to March 2012), with a
235 more gradual increase in taxa richness in ephemeral and near perennial sites from month 4 (April
236 2012) to the end of the study (Figure 4). Species accumulation was determined to be significantly
237 greater in near perennial sites ($t_{3,23}=2.604$, $p=0.017$), although the rate of colonisation over time did
238 not differ between ephemeral and near perennial sites ($t_{3,23}=0.390$, $p=0.7$; Figure 4). At an alpha scale,
239 both taxonomic richness (GLMM) and total abundance (LMM) were significantly greater ($p<0.001$)
240 in the near perennial sites and demonstrated little variation over time (Figure 2, Table 1). When
241 examining individual reaches, mean taxonomic richness in the ephemeral sites was similar (between
242 5-10 taxa) among all sampling months, whilst in the near perennial sites taxonomic richness was
243 highest 2-3 months after flow resumed (February 2012 and March 2012), but was similar (between
244 10-15 taxa) for the other sampling periods (Figure 2a). Mean macroinvertebrate abundance increased
245 rapidly up to 3-months after flow resumed in near perennial flow sites (March 2012) and subsequently
246 declined gradually thereafter to the end of the survey period (Figure 2b). Similarly, mean abundance
247 increased rapidly up to 3 months after flow resumed in ephemeral sites, but was more variable in the
248 proceeding months, decreasing at month 4 (April 2012 - reflecting spate conditions) and month 6-9
249 (June-September 2012- reflecting the periods of desiccation in ephemeral sites headwaters: Figure
250 2b).

251

252 Abundances of *A. aquaticus* increased monthly in ephemeral and near perennial sites ($p < 0.001$ in both
253 instances; Table 1), reaching their greatest abundance in the final survey month (Feb 2013; Figure 5a)
254 but demonstrated no differences by intermittence ($p > 0.05$; Table 1). *G. pulex* abundances were
255 consistently and significantly greater in near perennial sites than ephemeral sites (Table 1). *G. pulex*
256 abundance was broadly similar over the 12-months after flow resumed in ephemeral sites before
257 rising to a peak in the final sampling month. In near perennial sites, *G. pulex* abundance was stable for
258 5-months after flow resumed (Dec 2011- April 2012) but was markedly reduced during month 6-7
259 (May and June 2012) as flow declined (Figure 5b). *I. grammatica* was more abundant in near
260 perennial sites than ephemeral sites (Table 1) and was initially recorded 4 months after flow resumed
261 in ephemeral sites, and 3 months after flow resumed in near perennial sites (Figure 5c). Abundances
262 of *I. grammatica* peaked 3 months after flow resumed (March 2012) in ephemeral sites and 5 months
263 after flow resumed (May 2012) in near perennial sites. However, its abundance declined throughout
264 the summer months and only increased again 11 months after flow resumed (Nov 2012; Figure 5c). *S.*
265 *ignita* was not recorded from ephemeral sites during the 2011-2013 study and was first sampled in
266 near perennial sites three months after flow resumed (Feb 2012), reaching its greatest abundance 5
267 months after flow resumed (May 2012) and declining thereafter (Figure 5d). In ephemeral and near
268 perennial sites, Baetidae demonstrated highly variable abundances throughout the survey period.
269 Baetidae, first recorded 2 months after flow resumed (Feb 2012) in near perennial sites and three
270 months after flow resumed (March 2012) in ephemeral sites, reached highest abundance 7-8 months
271 after flow resumed in the two study sections (Figure 5e). Temporal changes in Baetidae populations
272 were determined to be significantly different (Table 1) with near perennial abundances increasing at a
273 faster rate compared to ephemeral sites. *P. mortoni* was initially recorded 4 months after flow
274 resumed (April 2012) in ephemeral sites and remained consistent throughout the remainder of the
275 study (Figure 5f). In near perennial sites, *P. mortoni* was first recorded 6 months after flow resumed
276 (June 2012) with abundances increasing rapidly and peaking 8 months after flow resumption (August
277 2012; Figure 5f). Abundances of *P. mortoni* were significantly greater in near perennial sites and
278 varied between sections over time (Table 1). Across ephemeral sites, *A. aquaticus*, *G. pulex*, *I.*
279 *grammatica* and Baetidae all demonstrated a reduction in abundance from the 3rd to 4th month after

280 flow resumed (March 2012 to April 2012), although abundance of *P. mortoni* increased in this period.
281 In addition, *A. aquaticus*, Beatidae, *P. mortoni* and *I. grammatica* demonstrated reduced abundances
282 from the 8th to 9th month after flow resumed (August 2012 to September 2012) in ephemeral sites
283 (Figure 5a, b, c, e, f).

284

285 Spearman's rank correlations comparing the similarity matrices of monthly macroinvertebrate
286 communities were statistically significant for near perennial sites (Table 1) demonstrating a strong
287 serial correlation (Figure 3c). In ephemeral sites, 5 of the 6 sites displayed low and non-significant ρ
288 values demonstrating a weak serial correlation (Table 2) and did not follow serially in the centroid
289 NMDS biplot (Figure 3b – particularly 3-5 months after flow resumed, March-April 2012); only site 3
290 recorded a significant Spearman's rank correlation (Table 2).

291

292 **Discussion**

293 *Macroinvertebrate recolonization of ephemeral and near perennial reaches following a supra-*
294 *seasonal drought*

295 Following the resumption of surface flow after the supra-seasonal drought, we found rapid
296 macroinvertebrate recolonization (species accumulation) on the R. Lathkill with the cumulative
297 number of taxa plateauing after approximately 6 months. Similar findings have been recorded from
298 streams in Georgia, USA and Berkshire, UK (Wright et al. 2004; Churchel and Batzer 2006) where
299 rapid recolonization of streams was observed immediately following the onset of flow after drought,
300 and species accumulation also beginning to plateau after 5 to 6 months.

301

302 Different recolonization processes, however, probably operated in the ephemeral and near perennial
303 sites of the R. Lathkill examined. Ephemeral sites in the headwaters and are hydrologically more
304 isolated from perennial water sources. The lack of lateral or longitudinal connectivity and frequent
305 channel drying in ephemeral sites suggests that resilience strategies may have been an important

306 mechanism for the rapid recolonization in this section of the river. Many taxa have developed
307 adaptations to survive *in-situ* in dry river beds such as producing diapause eggs (e.g., the
308 macroinvertebrate seedbank; Stubbington and Datry, 2013), having short development times (Lytle
309 and Poff 2004; Bogan and Lytle 2011) or persisting in damp leaf patches and sub-surface water in the
310 hyporheic zone (Stubbington et al. 2009a, 2011, although this is not the case for all rivers; Datry
311 2012). In this study, *A. aquaticus* recolonized quickly after flow resumed in the ephemeral sites,
312 potentially surviving the period of flow desiccation as small individuals in damp sediments and
313 organic matter in the hyporheic zone (Leberfinger and Herrmann 2010; Vadher et al. 2017).

314

315 Near perennial flow sites were located between the ephemeral headwaters and the fully perennial river
316 further downstream. The return of lateral and longitudinal aquatic connectivity between the perennial
317 zone and near perennial sites is likely to have been an important factor influencing the recolonization
318 of this section of the river. Previous studies have demonstrated that perennial reaches may act as a
319 refuge for taxa capable of dispersal (Chester and Robson 2011; Bogan et al. 2015), with rapid
320 recolonization after the drought event being possible in this study from the proximal perennial zone
321 via resistant mechanisms (life stages) such as aerial dispersal, or through upstream migration
322 (Williams and Hynes 1976; Verberk et al. 2008; Chester et al. 2015). The coleopteran, *Agabus*
323 *guttatus* was recorded as early as two months after flow resumed in near perennial sites and previous
324 studies have indicated them to be one of the first predators to aerially colonise intermittent reaches
325 (Davy-Bowker et al. 2002; Stubbington et al. 2016). Further, the significantly greater abundances of
326 *G. pulex* in near perennial sites may reflect this species rapid ability to recolonize from perennial
327 reaches downstream (White et al. 2018) and through vertical connectivity with the hyporheic zone
328 (Stubbington et al. 2009) and subterranean caves (Wood et al. 2005). Based on the results of this
329 study, the effective recolonization of biological communities to drought in ephemeral and near
330 perennial reaches is likely to be the result of a combination of resistance and resilience strategies
331 (Bogan et al. 2015).

332

333 The mean number of taxa remained consistent throughout the sampling months in ephemeral sites but
334 a peak in richness was recorded in near perennial sites during February 2012. A significant rainfall
335 event prior to sampling in February 2012 increased the discharge in the R. Lathkill and may have
336 provided connectivity to facilitate upstream migration of taxa from the perennial reaches downstream.
337 The loss of surface flow in ephemeral sites on three separate occasions during the sampling period
338 may explain the reductions in abundance of *A. aquaticus*, *G. pulex*, *P. mortoni*, *I. grammatica* and
339 Baetidae at months 3 and 4, and months 8 and 9, as it is likely many of the taxa were unable to
340 complete their life-cycle and those that did may have had to disperse as flow receded (Dobrin and
341 Giberson 2003).

342

343 Macroinvertebrate communities within ephemeral sites did not display a serial correlation, with
344 adjacent sampling months being heterogeneous. This may be the result of the loss of surface flow on a
345 number of occasions during the study period (March, May and August 2012) continually re-setting
346 succession and re-starting the community recolonisation process (Sponsellor et al. 2010). This
347 suggests that ephemeral stream reaches are in a constant state of resetting of community succession,
348 with recovery and recolonization only partially occurring until they are re-set by the next drying
349 event. In contrast, after the first month of the study, flow was continuous throughout the near
350 perennial section following the supra-seasonal drought and as such macroinvertebrate assemblages in
351 these sites demonstrated serial correlation, with adjacent sampling months being most similar, and the
352 first and last sample recording the greatest heterogeneity in community composition. In perennial
353 rivers, macroinvertebrate assemblages typically follow a seasonal cycle (e.g., successive winter
354 communities record similar community assemblages: Giller and Twomey 1993; Leunda et al. 2009)
355 and therefore, the significant serial correlation recorded in near perennial sites indicates that two
356 possible ecological processes may be occurring in the R. Lathkill: (*i*) recolonization and ecological
357 recovery are ongoing. Despite the rapid recolonization by many taxa, the full recovery of
358 macroinvertebrate communities had not occurred during the study period, as communities from
359 January 2012 and February 2013 were most heterogeneous. This suggests that the ecological effect of

360 the supra-seasonal drought on macroinvertebrate communities was evident for multiple seasons
361 following the event (Churchel and Batzer 2006; Bogan and Lytle 2011), with ecological recovery
362 being a long-term process (Wood and Petts 1999; Churchel and Batzer 2006) that typically takes
363 significantly longer than hydrological recovery; and (ii) the supra-seasonal drought may have reset the
364 ecological trajectory of the macroinvertebrate community which is possibly now heading towards a
365 new ecological equilibrium (Bogan and Lytle 2011), reflecting the high heterogeneity between
366 samples. Supra-seasonal drought may cause macroinvertebrate assemblages to permanently differ
367 from pre-drought assemblages. For example, research by Bogan and Lytle (2011) on intermittent
368 streams in Arizona has shown that supra-seasonal drought can cause regime shifts in invertebrate
369 community composition from long-lived sedentary taxa to smaller short-lived and highly vagile taxa.

370

371 If taken in isolation, supra-seasonal droughts appear to have a negative effect on ecosystems, causing
372 an initial decline in taxonomic diversity during the period of stream desiccation (Lake 2003; Boulton
373 and Lake 2008; Aspin et al. 2019). However, when recolonization is examined over longer timescales,
374 supra-seasonal droughts may actually facilitate the development of environmental conditions to
375 support a higher diversity through; (1) a reduction in competition and predation pressure (supra-
376 seasonal drought removed key predators and dominant taxa such as *G. pulex*); (2) an increase in the
377 availability and number of habitats (environmental niches: Ricklefs & Schlüter, 1993), as succession is
378 re-set and dominant environmental / ecological pressure are reduced and; (3) enabling new taxa (that
379 may be outcompeted in later succession lotic habitats) to utilise the increased spatio-temporal
380 environmental and biotic niches. However, it is unclear whether the macroinvertebrate communities
381 in the R. Lathkill will maintain this high diversity, whether successional processes are ongoing, or if
382 the community will be reset to follow another new ecological trajectory following the next flow
383 cessation event.

384

385 Climate change and the increase in water abstraction from growing human populations is likely to
386 increase the number of rivers that experience drying (Larned et al. 2010), the severity / duration of

387 drying events (Rahiz and New 2013) and could lead to irrevocable changes to biological communities
388 and a loss of taxa that are ill adapted to drying (Datry et al. 2014). Currently, consideration of supra-
389 seasonal drought and management in lotic freshwaters is impeded by the lack of knowledge and
390 information available (Arscott et al. 2010). Future research should be directed towards the long-term
391 monitoring of macroinvertebrate communities before, during and after supra-seasonal droughts to
392 provide the information needed to fully quantify the ecological impacts of these disturbances,
393 understand the mechanisms and strategies macroinvertebrates use to persist / recolonise rivers
394 following an extreme drying event, identify possible regime shifts in intermittent freshwater
395 communities and identify strategies to manage drought impacts. For example, ensuring newly
396 intermittent streams are connected with drought refuge sites may facilitate a rapid recovery post-
397 disturbance (Robson et al. 2011).

398

399

400 *Spatial variability of macroinvertebrate communities between ephemeral and near perennial sites*

401 Taxonomic richness was consistently greater within near perennial sites than the headwater ephemeral
402 sites and significant differences in macroinvertebrate assemblages were observed between the two
403 study sections, following the 2011 supra-seasonal drought. Ephemeral sites were subject to multiple
404 drying events during 2012 and increasing flow intermittence has been shown to significantly reduce
405 taxonomic diversity across most biogeographic regions (Datry et al. 2013). Further, flow desiccation
406 in ephemeral sites (which continually re-sets communities) may remove taxa sensitive to drying,
407 while near perennial sites remained wet throughout the study and recolonization could progress
408 providing variable physicochemical and biological conditions for a wide range of taxa to exploit.
409 Taxonomic richness and community assemblage differences may also be the result of spatial
410 organisation of colonist sources (connectivity). The hydrological isolation of ephemeral sites from the
411 perennial reaches reduces the potential for colonisation (Bogan et al. 2015) while hydrological
412 connectivity to the downstream perennial zone provides near perennial sites with a readily available

413 and diverse source of colonists to enhance taxonomic richness and develop a heterogeneous
414 community composition.

415

416

417 **Conclusion**

418 This study has demonstrated that aquatic macroinvertebrate taxa can rapidly recolonise lotic habitats
419 after supra-seasonal drought episodes. The impact of supra-seasonal drought on macroinvertebrate
420 communities may persist for multiple seasons after the event, as the communities may not have
421 reached the end-point of recovery during the study period. The results of this study also suggest that
422 supra-seasonal droughts may cause some communities to head towards a new ecological equilibrium
423 rather than recover to their pre-disturbance composition; making the assessment of the end point of
424 recovery more difficult. Supra-seasonal droughts may therefore effectively re-set ecological
425 succession and during the initial recovery / recolonisation phase, and provide ecological and
426 environmental space for new taxa to colonise. Quantifying the recolonisation and recovery of
427 biological communities to extreme disturbances such as supra-seasonal drought is vital to provide the
428 information required to ensure the persistence of biodiversity through the implementation of
429 ecologically effective conservation and management strategies.

430

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437

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604 **Tables**

605 Table 1 - Univariate analysis for differences in taxonomic richness, total abundance and abundance of
 606 individual taxon associated with intermittence (ephemeral and near perennial, n=2), month (n =12)
 607 and the interaction of these factors.

608

Metric	Intermittence		Month		Month x Intermittence		R ² c
	Stat value	p value	Stat value	p value	Stat value	p value	
Taxonomic richness	4.34	< 0.001	-0.77	0.443	0.15	0.880	62.56
Abundance	3.80	< 0.001	0.75	0.450	-0.62	0.619	62.11
<i>Baetidae</i>	1.63	0.103	-1.24	0.214	3.56	< 0.001	70.48
<i>Asellus aquaticus</i>	-1.61	0.106	3.40	< 0.001	-0.41	0.682	67.02
<i>Seretella ignita</i>	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>Gammarus pulex</i>	2.50	0.012	1.59	0.110	-0.63	0.530	57.06
<i>Isoperla grammatica</i>	5.04	< 0.001	6.70, -6.52, 6.39	<0.001	-0.564	0.574	42.76
<i>Perlodes mortoni</i>	2.57	0.026	-2.45	0.025	4.79	< 0.001	46.01

609 Table 2 - Spearman's rank correlation coefficients calculated among temporal macroinvertebrate
610 communities (serial RELATE analyses) at each site.

	Site	Spearman's correlation (ρ)
Ephemeral sites	1	0.013
	2	0.255
	3	0.572***
	4	0.079
	5	0.178
	6	0.055
Near perennial sites	7	0.626***
	8	0.593***
	9	0.635***
	10	0.609***
	11	0.539***

*** $p < 0.01$

611

612 **Figure captions**

613 Figure 1 – Location of study river (a) and sampling reach and sites (b): ephemeral sites comprises
614 sites 1- 6 and near perennial comprises sites 7-11.

615 Figure 2 - Number of taxa (a) and \log_{10} macroinvertebrate abundance (b) across the sampling period
616 in ephemeral (E) and near perennial (NP) river reaches on R. Lathkill (UK). *Surface flow was*
617 *maintained in near perennial sites throughout the study period. Flow remained ephemeral in*
618 *ephemeral sites and streambed drying occurred for; (1) ca. 28 days from mid-March 2012, (2) ca. 39*
619 *days from mid-May 2012; and (3) ca. 46 days from early Aug 2012.*

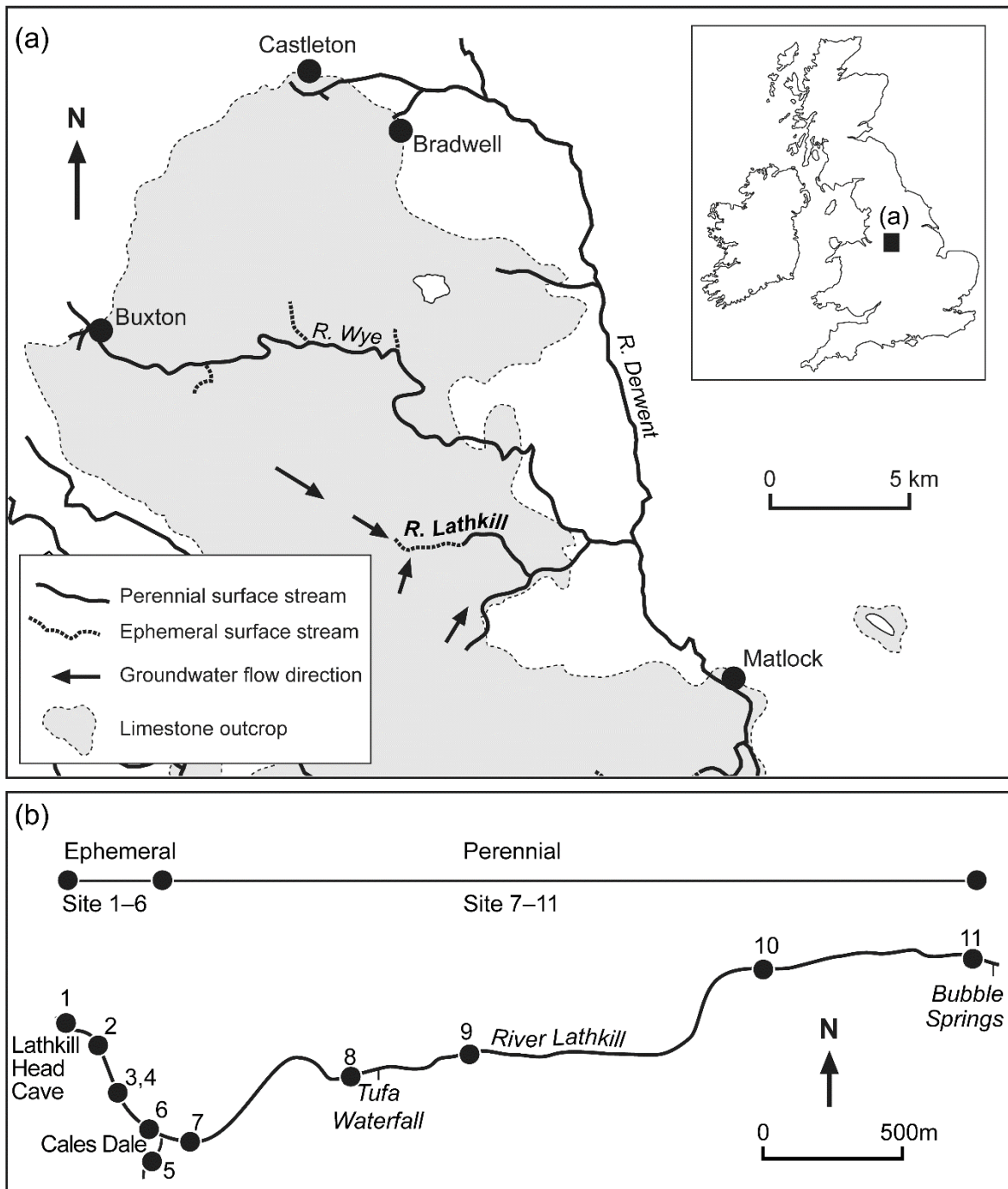
620 Figure 3 – NMDS ordination of macroinvertebrate assemblages from near perennial and ephemeral
621 study sites (a) and; centroid NMDS plots of macroinvertebrate communities from the 12 sampling
622 periods in ephemeral (b) and near perennial sites (c).

623 Figure 4 - Species accumulation plot for the months sampled from the ephemeral and near perennial
624 sites) river reaches on R. Lathkill (UK). *Surface flow was maintained in near perennial sites*
625 *throughout the study period. Flow remained ephemeral in ephemeral sites and streambed drying*
626 *occurred for; (1) ca. 28 days from mid-March 2012, (2) ca. 39 days from mid-May 2012; and (3) ca.*
627 *46 days from early Aug 2012.*

628 Figure 5 - Mean *Asellus aquaticus* (a) *Gammarus pulex* (b) *Isoperla grammatica* (c) *Serratella ignita*
629 (d) Baetidae (e) and *Perlodes mortoni* (f) abundance from each sampling month from ephemeral
630 (ephemeral sites: E) and near perennial (near perennial sites: NP) study sites on the R. Lathkill (UK).
631 *Surface flow was maintained in near perennial sites throughout the study period. Flow remained*
632 *ephemeral in ephemeral sites and streambed drying occurred for; (1) ca. 28 days from mid-March*
633 *2012, (2) ca. 39 days from mid-May 2012; and (3) ca. 46 days from early Aug 2012.*

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635 Figure 1



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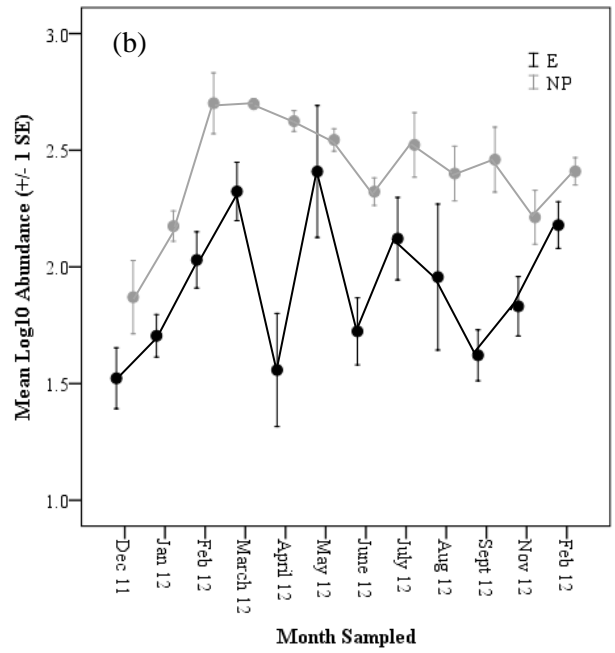
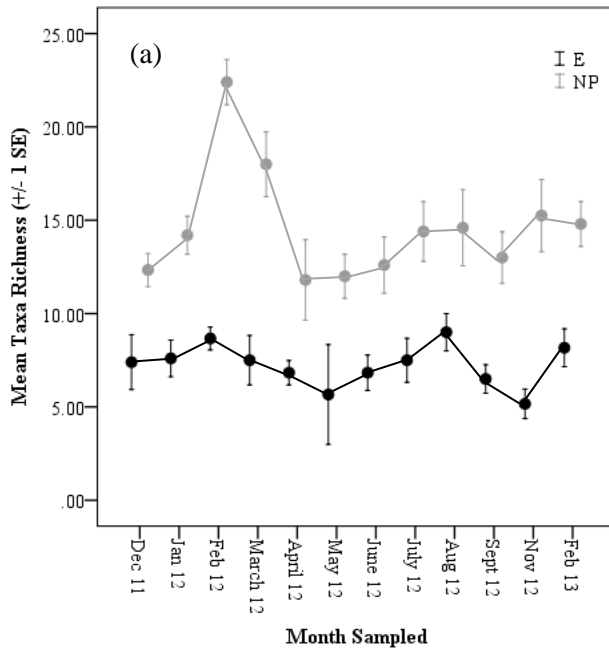
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646 Figure 2

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683 Figure 3

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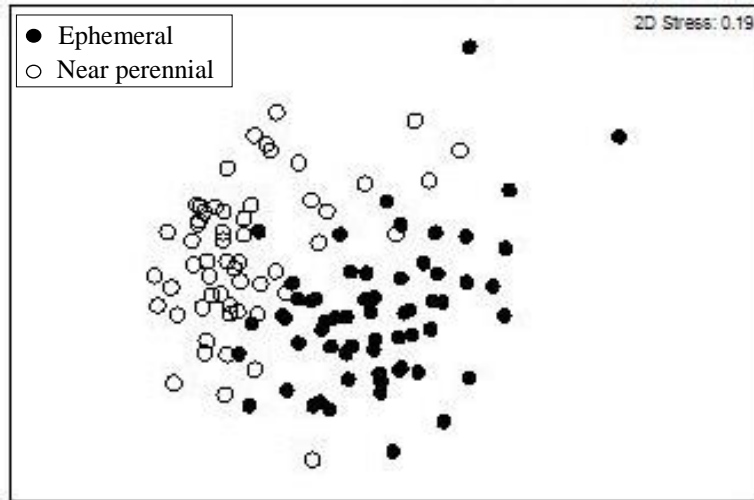
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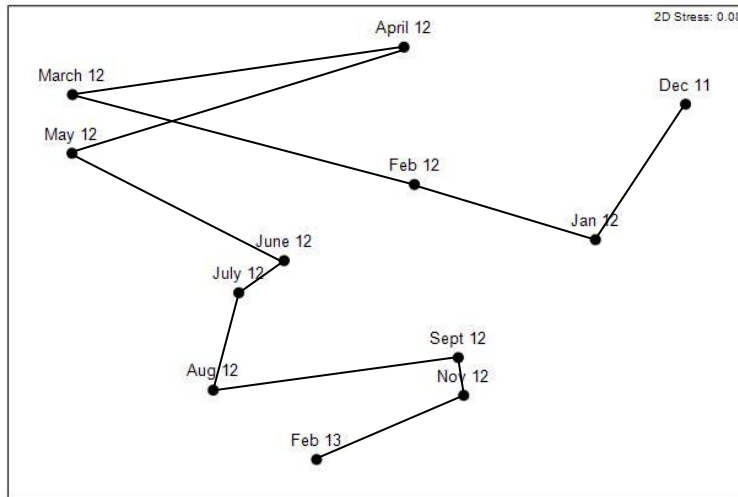
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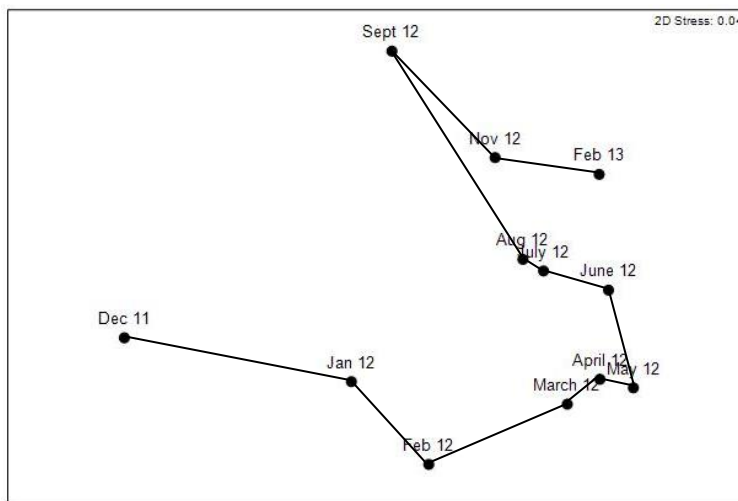
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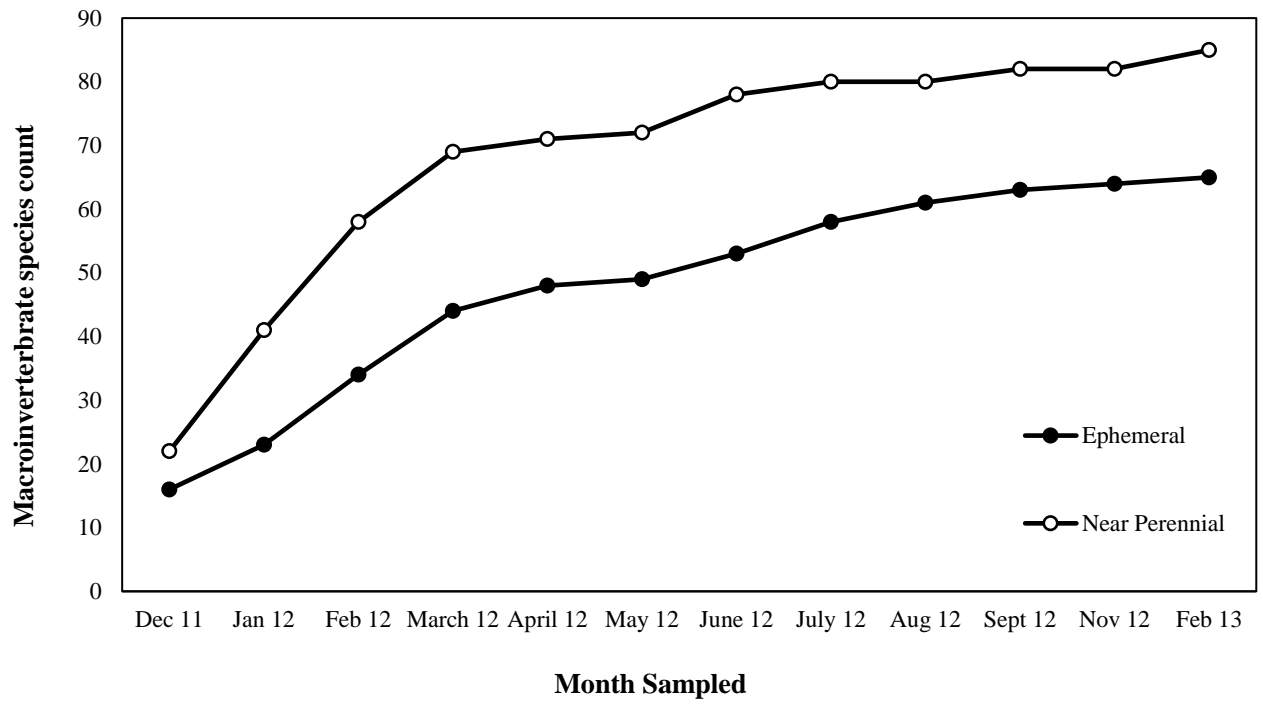
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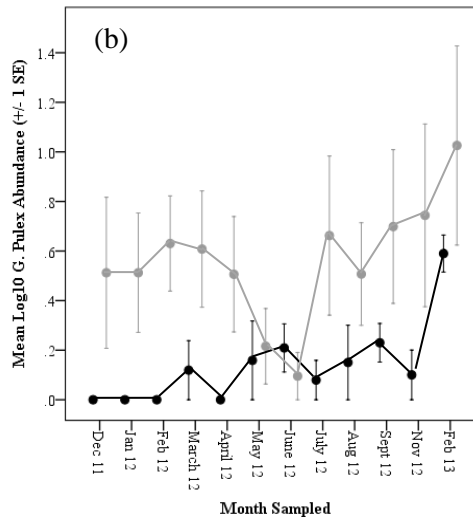
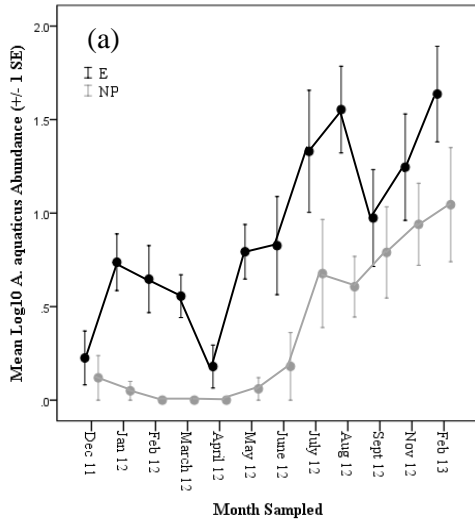
715 Figure 4



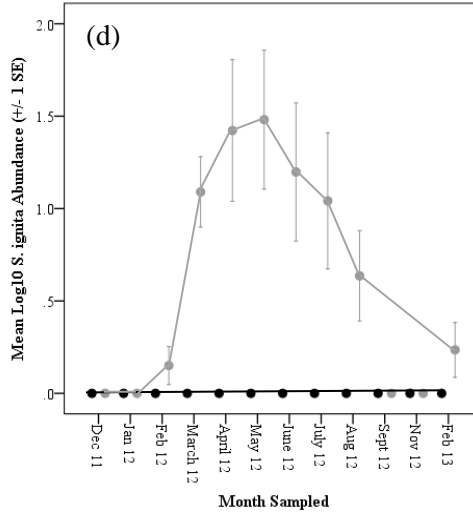
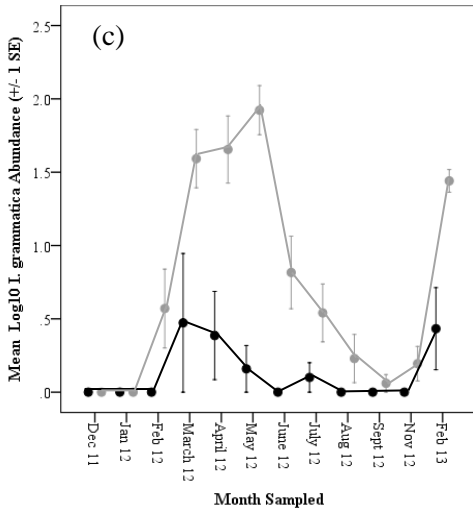
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717 Figure 5

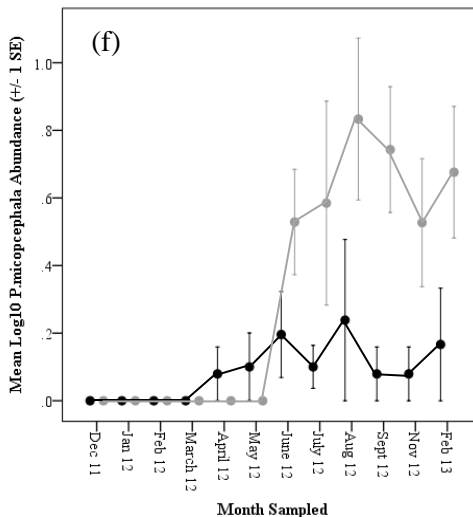
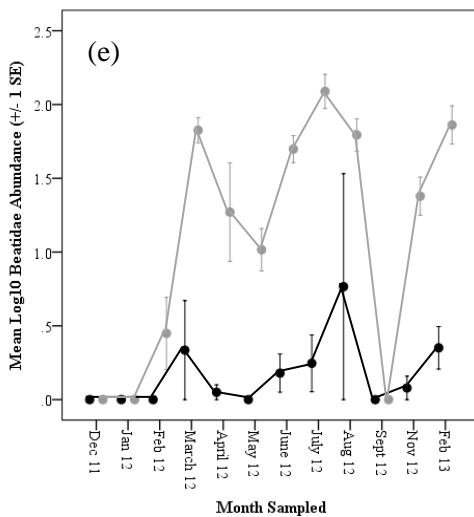
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