

Extra terrestrials

Aspin, Thomas; Khamis, Kieran; Matthews, Tom; Williams, Gavin; Windsor, Fredric M; Woodward, Guy; Ledger, Mark

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1 Extra terrestrials: drought creates niche space for rare invertebrates in a large-
2 scale and long-term field experiment

3

4 Thomas W.H. Aspin^{1,2*}, Kieran Khamis¹, Thomas J. Matthews^{1,3,4}, Gavin M.D. Williams¹, Fredric M.
5 Windsor⁵, Guy Woodward⁶, Mark E. Ledger¹

6 ¹School of Geography, Earth and Environmental Sciences, University of Birmingham, UK

7 ²Environment Agency, Bristol, UK

8 ³Birmingham Institute of Forest Research, University of Birmingham, Birmingham, B15 2TT, UK.

9 ⁴CE3C – Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group /
10 CHANGE – Global Change and Sustainability Institute and Universidade dos Açores – Faculty of
11 Agricultural Sciences and Environment, PT-9700-042, Angra do Heroísmo, Açores, Portugal.

12 ⁵School of Biosciences, Cardiff University, UK

13 ⁶Georgina Mace Centre for the Living Planet, Department of Life Sciences, Imperial College London,
14 Silwood Park, Ascot, Berkshire, UK SL5 7PY

15 *Email: twhaspin@gmail.com ORCID ID: 0000-0003-1599-1532

16 **Keywords:** biodiversity, community assembly, drying, invertebrates, mesocosm experiment, stream
17 drought

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19

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21

22 **Abstract**

23 Freshwater habitats are drying more frequently and for longer under the combined pressures of
24 climate change and overabstraction. Unsurprisingly, many aquatic species decline or become locally
25 extinct as their benthic habitat is lost during stream droughts, but less is known about the potential
26 ‘winners’– those terrestrial species that may exploit emerging niches in drying riverbeds. In
27 particular, we do not know how these transient ecotones will respond as droughts become more
28 extreme in the future. To find out we used a large-scale, long-term mesocosm experiment spanning
29 a wide gradient of drought intensity, from permanent flows to full streambed dewatering, and
30 analysed terrestrial invertebrate community assembly after one year. Droughts that caused stream
31 fragmentation gave rise to the most diverse terrestrial invertebrate assemblages, including 10
32 species with UK conservation designations, and high species turnover between experimental
33 channels. Droughts that caused streambed dewatering produced lower terrestrial invertebrate
34 richness, suggesting that the persistence of instream pools may benefit these taxa as well as aquatic
35 biota. Particularly intense droughts may therefore yield relatively few ‘winners’ among either
36 aquatic or terrestrial species, indicating that the threat to riverine biodiversity from future drought
37 intensification could be more pervasive than widely acknowledged.

38

39 **1. Background**

40 Climate change and overabstraction of water are leading to increased occurrence of droughts in
41 rivers and streams [1]. As wetted habitat shrinks, aquatic invertebrate species are lost [2], and the
42 reciprocal expansion of dry streambed leads to an increase in terrestrial invertebrate biodiversity [3].
43 However, these initial terrestrial species gains may be reversed as a drought further intensifies, as
44 riverbeds become inhospitable and relict aquatic resources are exhausted [3]. Our currently limited
45 understanding of these dynamics relies on observational data from seasonally dry streams, so we

46 know little of how terrestrial invertebrate communities might develop during the extreme,
47 prolonged droughts set to become increasingly common [4].

48

49 In theory, particularly intense drying should expose species to harsher environmental conditions and
50 more severe food resource shortages, thus eroding terrestrial biodiversity, consistent with the
51 intermediate disturbance hypothesis [5]. Conversely, an increase in alpha diversity would be
52 predicted by the species–area relationship as more terrestrial habitat becomes available [6], and
53 would additionally be expected as plant succession creates greater niche space for invertebrates. It
54 is also unclear how the trajectory of terrestrial community development may vary in space during
55 prolonged drying, hampering our ability to predict the impacts of droughts on biodiversity patterns
56 among reaches (i.e., beta diversity). Beta diversity may increase as different reaches follow different
57 successional trajectories, or decline as complex wetland community types are replaced by a more
58 uniform, dry channel. As future drought intensification gives rise to novel river- and reach-specific
59 drying regimes, evidence of how terrestrial alpha and beta diversity respond will increasingly be
60 required to inform adaptive river management and conservation.

61

62 Experiments are needed to expose ecological communities to these possible future conditions [7] in
63 isolation from the confounding environmental gradients that beset field survey data [8]. We
64 therefore simulated year-long (i.e., suprasedasonal) droughts of varying intensity using artificial
65 stream channels (mesocosms), and characterised the terrestrial invertebrate assemblages that
66 developed. Drought treatments ranged from flowing streams retaining connectivity among riffles
67 and pools, through to the disconnection of these habitats and, ultimately, to complete streambed
68 drying. We analysed differences in invertebrate alpha and beta diversity between these treatments,
69 thus exploring the potential impacts of drought intensification on terrestrial community assembly at
70 local and network scales.

71

72 **2. Methods**

73 **(a) Drought experiment and data collection**

74 We used outdoor mesocosms to replicate conditions in perennial headwater streams, in Hampshire,
75 UK [further details given in 8]. Of the 21 channels in the experiment, we used 18 for this study, with
76 the remainder unable to be assigned to a particular treatment as their riffle habitat was partially but
77 not fully submerged. All channels had gravel beds with riffle-pool sequences (four per channel),
78 analogous to their natural counterparts. The channels were fed by borehole water and seeded with
79 a “common garden” of water crowfoot (*Ranunculus penicillatus* subsp. *pseudofluitans*), algae, and
80 aquatic invertebrates from the adjacent chalk stream. Following six months of aquatic community
81 establishment under ambient flow, we left three channels as controls and adjusted flows across the
82 remainder to create a gradient of drought intensity. This gradient spanned three characteristic
83 habitat states [2]: (i) flowing channels, with no dry substratum (connected [CON]; n = six channels);
84 (ii) fragmented channels, with approximately 50 % dry substratum and isolation of pool habitats
85 (fragmented [FRAG]; nine channels); and (iii) dewatered streambeds, with 95-99% dry substratum
86 (dry [DRY]; three channels). These treatments were designed to capture a broad spectrum of
87 hydrological states, from stable flows through to the harsh, patchy conditions, including prolonged
88 ponding and drying, associated with suprasedasonal drought [9,10].

89

90 After one year of drought, channels from each treatment had developed plant communities
91 representative of the major hydrological classification groups of ephemeral chalk stream
92 macrophytes [10], driven by wind dispersal of seeds (see supplementary material, Figure S1). There
93 was a shift from fully aquatic taxa such as water crowfoot and water parsnip (*Berula erecta*) in
94 connected streams to emergent (e.g. watercress; *Nasturtium officinale*) and wetland species (e.g.

95 reed canary grass; *Phalaris arundinacea*) in fragmented channels. The riffle habitats of fragmented
96 channels had largely terrestrialsed and so these channels also supported many of the non-aquatic
97 herbs that dominated dry streams, such as willowherbs (*Epilobium* spp.), mayweed
98 (*Tripleurospermum inodorum*) and nettle (*Urtica urens*). As plant growth is a key driver of terrestrial
99 invertebrate diversity in riverine environments [11], we estimated the total volume of terrestrial
100 vegetation in each channel. The percentage cover of plants was estimated across the top three
101 riffles and three pools per channel at the end of the experiment. The volume (m^3) of each plant
102 taxon was calculated from its areal coverage (m^2) multiplied by plant stand height (m). We then
103 sampled terrestrial invertebrates through exhaustive (i.e. until no further individuals could be found)
104 sweep netting and hand searching [see 12] of one randomly selected riffle-pool pair ($1.5 m^2$) to yield
105 a single invertebrate sample for each channel. Invertebrates were collected from dry gravels,
106 emergent and terrestrial plants and, in connected channels, from emergent fronds of water
107 crowfoot. Invertebrate specimens were identified to species wherever possible, with aphids
108 (Aphidae), chalcid wasps (Chalcidoidea), springtails (Collembola), vinegar flies (Drosophilidae) and
109 non-biting midges (Chironomidae) identified to family level.

110

111 **(b) Statistical analyses**

112 All analyses were conducted in R (version 4.2.2) [13,14]. We quantified differences in invertebrate
113 community composition between treatments using non-metric multidimensional scaling (NMDS) and
114 then tested for significant differences in alpha diversity. To account for the underlying influence of
115 relative abundance on species detection success (and thus diversity estimation), we equalised
116 samples by adjusting for sample coverage, which allows for fairer comparisons of diversity estimates
117 drawn from communities with greater or lesser proportions of rare species [see 15]. We compared
118 samples at 90% coverage (i.e. the level of sample completeness giving a 10% probability that the
119 next recorded individual will belong to a previously undetected species), dropping a single sample

120 from all further analyses as it exhibited a particularly low coverage value (60%), and was therefore
121 not deemed to be representative of the community in the (connected) channel from which it was
122 collected. We then calculated alpha diversity as Hill-Shannon diversity to afford similar sensitivity to
123 rare and common species and retain intuitive scaling behaviour (i.e. proportional to changes in
124 richness [15]). We compared Hill-Shannon diversities using a Kruskal-Wallis one-way analysis of
125 variance to account for different numbers of replicates per group. Following rejection of the null
126 hypothesis (no significant difference between treatments), we conducted Conover-Imam tests to
127 determine which treatments differed significantly in alpha diversity, controlling for the false
128 discovery rate using the Benjamini-Hochberg procedure [16].

129

130 Beta diversity, interpreted here as the dissimilarity in species composition among the communities
131 of two (i.e. pairwise dissimilarity) or more (i.e. multiple site dissimilarity) channels [17], was
132 calculated and decomposed into turnover (species replacement) and nestedness-resultant (species
133 gain/loss; hereafter NRD) components using the partitioning methods of Baselga [18]. Under this
134 framework, total beta diversity is calculated as Sørensen dissimilarity (β_{sor}), turnover as Simpson
135 dissimilarity (β_{sim}) and NRD as the difference between these ($\beta_{sor} - \beta_{sim} = \beta_{nes}$). High turnover would
136 imply the presence of many species unique to certain channels; whereas high NRD would signify (i) a
137 nesting of species-poor assemblages within richer ones, and thus (ii) greater overlap in species'
138 identities among channels [18].

139

140 We calculated (1) pairwise measures of beta diversity (β_{sor} , β_{sim} and β_{nes}), to analyse turnover and
141 NRD between the pooled communities of each of the three treatments; and (2) multiple site
142 dissimilarity (β_{SOR} , β_{SIM} and β_{NES}) to compare the communities of all channels within each treatment
143 [18]. As each treatment contained a different number of channels, with a minimum of three (dry),
144 we accounted for a sampling effort effect by conducting analyses on random subsets of three

145 channels. We calculated beta diversity for 100 combinations of paired treatment subsample pools
146 (pairwise measures) and for 100 combinations of treatment-specific subsamples (multiple site
147 measures). The final results were obtained by taking the mean and 95% confidence intervals of these
148 100 repeats.

149

150 **3. Results**

151 We recorded 166 terrestrial invertebrate taxa, 158 of which were found in fragmented and dry
152 streams, and 131 of which were unique to these channels (full taxa list in supplementary material,
153 Table S1). Taxa from connected channels were predominantly dipterans with an aquatic larval phase
154 (but collected in their adult form so considered here as terrestrial invertebrates; e.g., non-biting
155 midges, shore flies (Ephydriidae) and dagger flies (Empididae)), while dry channels were associated
156 with numerous species of arachnid and hymenopteran (Figure 1). Assemblages in fragmented
157 channels were not simply intermediate combinations of those found in the other treatments but
158 were instead diverse and distinct, comprising beetles, true bugs, dipterans and arachnids (Figure 1),
159 reflecting high terrestrial plant coverage (see supplementary material, Figure S2). These channels
160 harboured nine nationally scarce species (i.e. those with species quality scores (SQS) of 4 in Pantheon
161 (<https://pantheon.brc.ac.uk/lexicon/sqs>)) while a further species of conservation note, the UK
162 Biodiversity Action Plan (BAP) moth *Scotopteryx chenopodiata*, was recorded in both fragmented
163 and dry channels. Hill-Shannon diversity differed between treatments (Kruskal-Wallis $\chi^2(2) = 13.2$, p
164 $= 0.001$), being significantly greater in fragmented channels (mean = 21 ± 4) than in both connected
165 (5 ± 3 ; Conover-Imam $t(12) = 7.91$, $p < 0.001$) and dry streams (11 ± 2 ; $t(10) = 3.97$, $p = 0.001$). The
166 latter also contained significantly richer communities than connected channels ($t(6) = 2.42$, $p =$
167 0.015).

168

169 Communities of connected channels differed substantially from those of both fragmented ($\beta_{\text{SOR}} =$
170 0.73) and dry ($\beta_{\text{SOR}} = 0.66$) streams. This was driven primarily by NRD ($\beta_{\text{NES}} = 0.41$) and turnover ($\beta_{\text{SIM}} =$
171 0.49) respectively (Figure 2, top panel). Fragmented and dry channel communities were relatively
172 similar to each other ($\beta_{\text{SOR}} = 0.53$), with turnover the dominant component ($\beta_{\text{SIM}} = 0.32$). There were
173 also large differences among channels within each treatment (connected $\beta_{\text{SOR}} = 0.63$; fragmented
174 $\beta_{\text{SOR}} = 0.64$; dry $\beta_{\text{SOR}} = 0.65$; Figure 2, bottom panel). Connected channel communities differed from
175 one another due to both turnover ($\beta_{\text{SIM}} = 0.30$) and NRD ($\beta_{\text{NES}} = 0.33$), whereas differences among
176 fragmented and to a slightly lesser extent dry channel communities were largely attributable to
177 turnover ($\beta_{\text{SIM}} = 0.60$ and 0.54 respectively).

178

179 **4. Discussion**

180 This study has shown that streams exposed to suprasedasonal drying can support diverse and distinct
181 terrestrial invertebrate communities and provide refuges for rare species. However, dry streambeds
182 did not support the most diverse or notable species assemblages, demonstrating that the
183 persistence of instream pools through droughts, which are crucial for aquatic biota [19], could also
184 be invaluable for terrestrial fauna. We therefore present rare experimental evidence that future
185 drought intensification could threaten terrestrial as well as aquatic biodiversity across impacted
186 riverscapes.

187

188 Some differences in invertebrate community composition were apparent between our channels and
189 that typical of riparian habitats and seasonally dry streams. Notable early riparian colonists of dry
190 streambeds, such as ground beetles (Carabidae) [11], were absent from our samples, but the
191 widespread presence of other common inhabitants of riparian zones, such as rove beetles
192 (Staphylinidae) and money spiders (Linyphiidae), suggests that this is unlikely to reflect the lack of

193 riparian habitat in the mesocosms. It could instead point towards a key difference between the
194 effects of seasonal drying and prolonged drought on terrestrial species composition, with
195 adaptations that allow rapid colonisation of newly dry streambeds, such as inundation tolerance and
196 strong flight among some carabids [11,20], becoming significantly less advantageous over longer dry
197 periods. Further studies of prolonged stream droughts are needed to explore this.

198

199 The absence of some seasonally dry streambed specialists did not prevent the emergence of high
200 species diversity in fragmented channels, which partly reflected a prevalence of phytophagous
201 insects including leaf beetles (Chrysomelidae), mirid bugs (Miridae) and weevils (Curculionidae),
202 consistent with high plant coverage. Several of the nationally scarce species we recorded have close
203 associations with specific plants, such as *Gymnetron veronicae* with speedwells (*Veronica* spp.) and
204 *Drupenatus nasturtii* with cresses (*Nasturtium* spp.). As riparian plants close to a stream can differ
205 markedly from those further away, reflecting differences in subsurface moisture and humidity [11],
206 so those of fragmented streams would also seem to vary analogously between the centre of an
207 exposed riffle and its margins. Pool and riffle interfaces were colonised by wetland plants (e.g., *V.*
208 *anagallis-aquatica*), contrasting with the more terrestrial species (e.g., *T. inodorum* and *U. urens*)
209 found in drier gravels. In fragmented streams, as in riparian zones, this patchiness would appear to
210 produce high invertebrate richness due to the niche space afforded to monophagous taxa (see
211 supplementary material, Figure S3).

212

213 Patchiness and host specificity could be strong drivers of the high species turnover we observed
214 between different fragmented and dry channels, which arose despite their close spatial proximity
215 (see supplementary material, Figure S4). This contrasted with the high nestedness observed
216 between connected channels, which itself could reflect differences in the timing of insect emergence
217 between streams. In fragmented channels turnover appeared to be driven partly by shifts in habitat

218 availability between treatments (e.g. semi-aquatic beetles present in fragmented but not dry
219 channels) but to a greater extent by patch dynamics, with fragmentation generating discrete areas
220 of streambed with different successional trajectories. For instance, while some fragmented pools
221 were dominated by emergent plants (e.g. *V. anagallis-aquatica*, *N. officinale*), others retained a
222 sizeable coverage of *R. penicillatus* in varying growth forms (see supplementary material, Figure S5).
223 Supraseasonal drought may therefore produce high terrestrial biodiversity among fragmented and
224 dry reaches at the stream network (i.e. metacommunity) scale, a pattern that contrasts with the loss
225 of beta diversity widely observed among insect communities in response to climate and land-use
226 change [21].

227

228 Our study provides rare experimental evidence of a mechanistic relationship between drought
229 intensity and riverine terrestrial biodiversity. Its findings suggest that drying stream channels can
230 provide important habitat for rare and threatened species, a particularly notable observation amid
231 growing concerns over the impacts of natural habitat loss and other pressures on terrestrial insect
232 populations [22]. The difference in alpha diversity between fragmented and dry streams reported
233 here nonetheless highlights the importance of drought-resilient surface water refuges in adaptive
234 river management and conservation.

235

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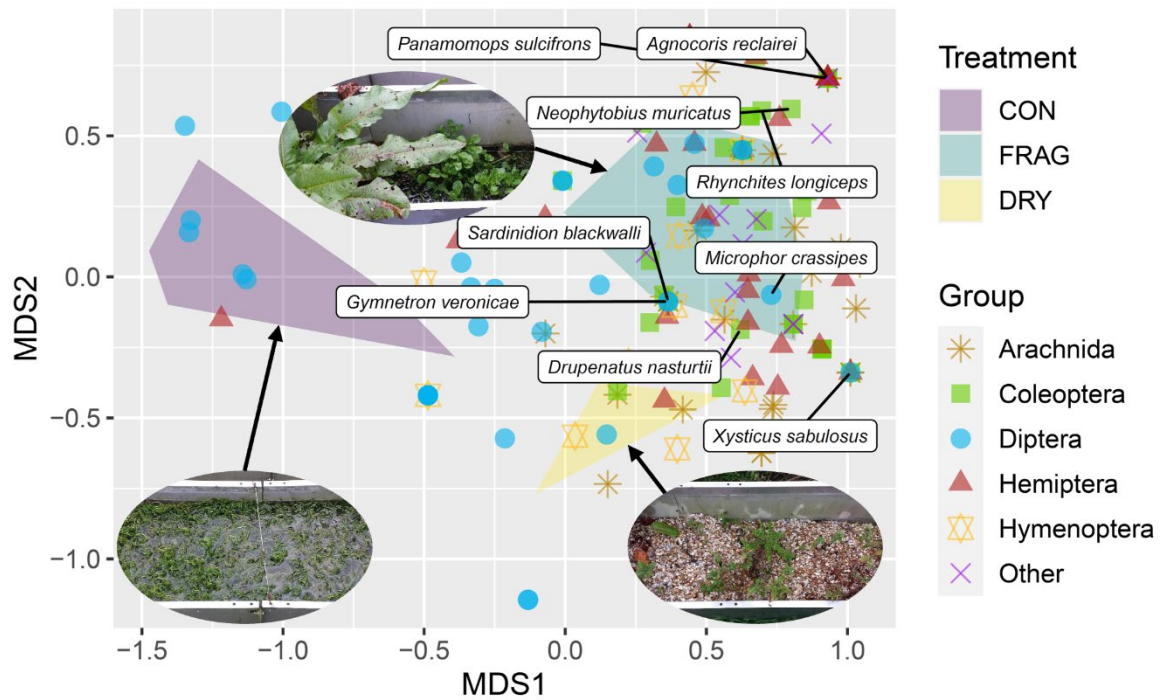
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285

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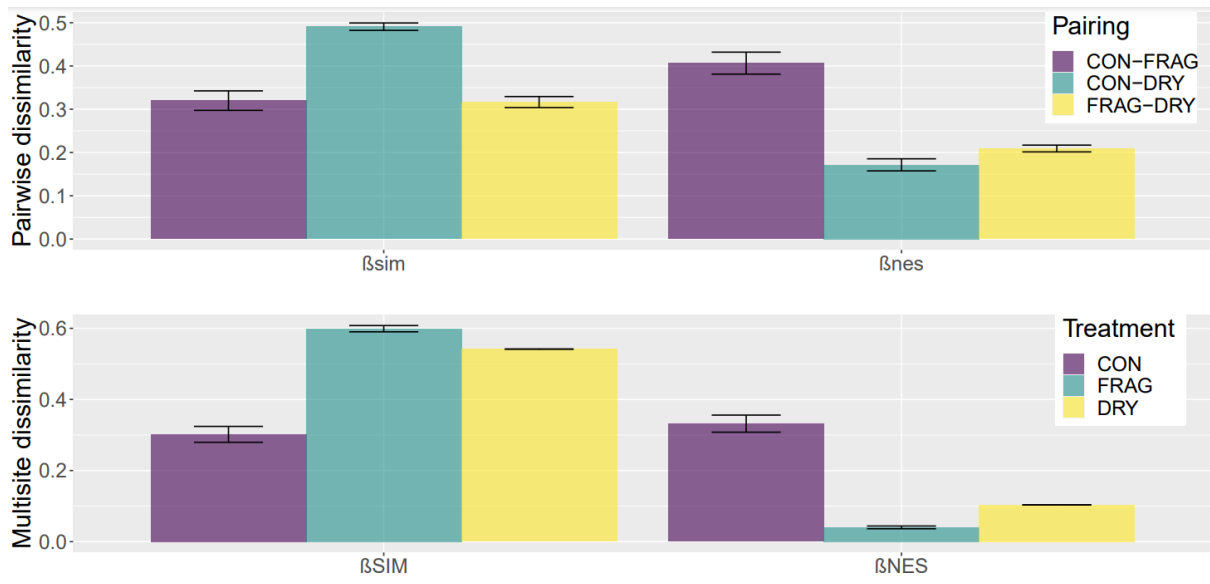
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293

294 **Figure 1** Non-metric multidimensional scaling output (stress = 0.1) illustrating differences in
 295 assemblage composition between treatments, with species scores displayed by taxonomic order.
 296 Shaded polygons are the minimum convex hulls that encompass all the channels in each treatment
 297 and photos depict an example channel from each treatment (clockwise from bottom left: connected,
 298 fragmented and dry). Labelled species are those designated nationally scarce in the UK.

299



300

301

Figure 2 Pairwise Sørensen dissimilarities between the pooled communities of connected,

302

fragmented and dry treatments, partitioned into turnover (β_{sim}) and nestedness-resultant (β_{nes})

303

components (top) and multiple site dissimilarities among channels within each treatment (bottom).

304

Error bars in both panels display 95% CI.