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

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

## 1. Background

Climate change and overabstraction of water are leading to increased occurrence of droughts in rivers and streams [1]. As wetted habitat shrinks, aquatic invertebrate species are lost [2], and the reciprocal expansion of dry streambed leads to an increase in terrestrial invertebrate biodiversity [3]. However, these initial terrestrial species gains may be reversed as a drought further intensifies, as riverbeds become inhospitable and relict aquatic resources are exhausted [3]. Our currently limited understanding of these dynamics relies on observational data from seasonally dry streams, so we know little of how terrestrial invertebrate communities might develop during the extreme, prolonged droughts set to become increasingly common [4].

In theory, particularly intense drying should expose species to harsher environmental conditions and more severe food resource shortages, thus eroding terrestrial biodiversity, consistent with the intermediate disturbance hypothesis [5]. Conversely, an increase in alpha diversity would be predicted

64 by the species–area relationship as more terrestrial habitat  
 65 becomes available [6], and would additionally be expected  
 66 as plant succession creates greater niche space for invert-  
 67 ebrates. It is also unclear how the trajectory of terrestrial  
 68 community development may vary in space during pro-  
 69 longed drying, hampering our ability to predict the impacts  
 70 of droughts on biodiversity patterns among reaches (i.e.  
 71 beta diversity). Beta diversity may increase as different  
 72 reaches follow different successional trajectories, or decline  
 73 as complex wetland community types are replaced by a  
 74 more uniform, dry channel. As future drought intensification  
 75 gives rise to novel river- and reach-specific drying regimes,  
 76 evidence of how terrestrial alpha and beta diversity respond  
 77 will increasingly be required to inform adaptive river  
 78 management and conservation.

79 Experiments are needed to expose ecological commu-  
 80 nities to these possible future conditions [7] in isolation  
 81 from the confounding environmental gradients that beset  
 82 field survey data [8]. We therefore simulated year-long (i.e.  
 83 suprasedonal) droughts of varying intensity using artificial  
 84 stream channels (mesocosms), and characterized the terres-  
 85 trial invertebrate assemblages that developed. Drought  
 86 treatments ranged from flowing streams retaining connec-  
 87 tivity among riffles and pools, through to the disconnection  
 88 of these habitats and, ultimately, to complete streambed  
 89 drying. We analysed differences in invertebrate alpha and  
 90 beta diversity between these treatments, thus exploring the  
 91 potential impacts of drought intensification on terrestrial  
 92 community assembly at local and network scales.

## 95 2. Methods

### 96 (a) Drought experiment and data collection

97 We used outdoor mesocosms to replicate conditions in perennial  
 98 headwater streams, in Hampshire, UK [further details given in  
 99 8]. Of the 21 channels in the experiment, we used 18 for this  
 100 study, with the remainder unable to be assigned to a particular  
 101 treatment as their riffle habitat was partially but not fully sub-  
 102 merged. All channels had gravel beds with riffle-pool sequences  
 103 (four per channel), analogous to their natural counterparts. The  
 104 channels were fed by borehole water and seeded with a  
 105 ‘common garden’ of water crowfoot (*Ranunculus penicillatus*  
 106 subsp. *pseudofluitans*), algae and aquatic invertebrates from the  
 107 adjacent chalk stream. Following six months of aquatic commu-  
 108 nity establishment under ambient flow, we left three channels as  
 109 controls and adjusted flows across the remainder to create a gradi-  
 110 ent of drought intensity. This gradient spanned three characteristic  
 111 habitat states [2]: (i) flowing channels, with no dry substratum  
 112 (connected;  $n = \text{six channels}$ ); (ii) fragmented channels, with  
 113 approximately 50% dry substratum and isolation of pool habitats  
 114 (fragmented [FRAG]; nine channels); and (iii) dewatered stream-  
 115 beds, with 95–99% dry substratum (dry [DRY]; three channels).  
 116 These treatments were designed to capture a broad spectrum of  
 117 hydrological states, from stable flows through to the harsh,  
 118 patchy conditions, including prolonged ponding and drying,  
 119 associated with suprasedonal drought [9,10].

120 After one year of drought, channels from each treatment had  
 121 developed plant communities representative of the major hydro-  
 122 logical classification groups of ephemeral chalk stream  
 123 macrophytes [10], driven by wind dispersal of seeds (see elec-  
 124 tronic supplementary material, figure S1). There was a shift  
 125 from fully aquatic taxa such as water crowfoot and water parsnip  
 126 (*Berula erecta*) in connected streams to emergent (e.g. watercress;  
*Nasturtium officinale*) and wetland species (e.g. reed canary grass;

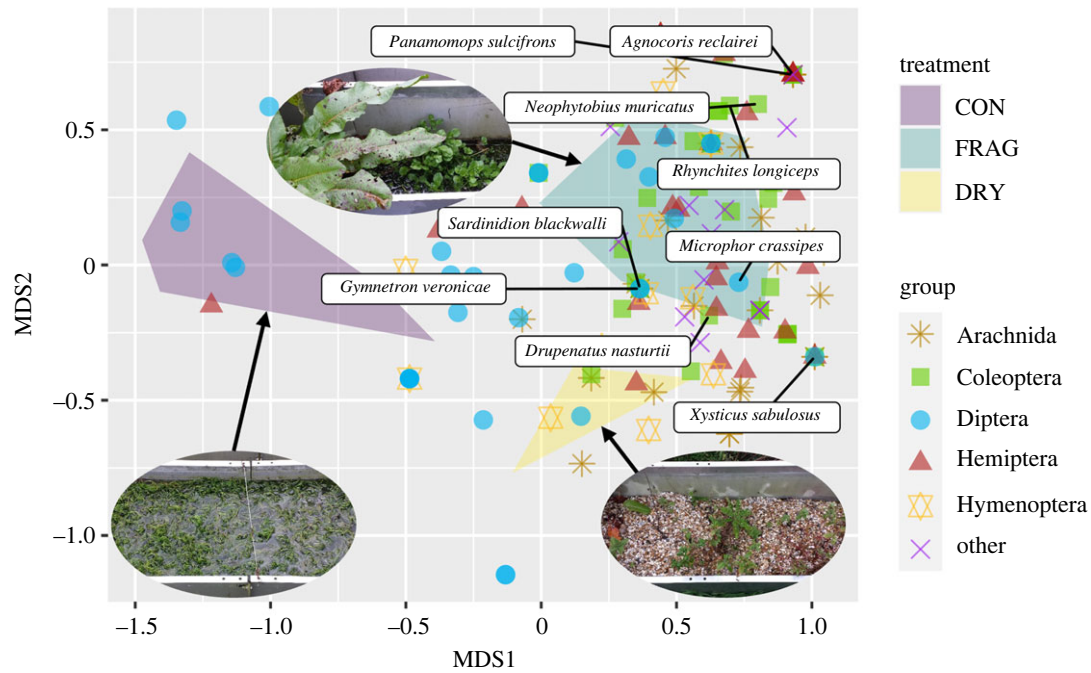
*Phalaris arundinacea*) in fragmented channels. The riffle habitats  
 of fragmented channels had largely terrestrialised and so these  
 channels also supported many of the non-aquatic herbs that  
 dominated dry streams, such as willowherbs (*Epilobium* spp.),  
 mayweed (*Tripleurospermum inodorum*)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

### 100 (b) Statistical analyses

101 All analyses were conducted in R (v. 4.2.2) [13,14]. We quantified  
 102 differences in invertebrate community composition between  
 103 treatments using non-metric multidimensional scaling (NMDS)  
 104 and then tested for significant differences in alpha diversity. To  
 105 account for the underlying influence of relative abundance on  
 106 species detection success (and thus diversity estimation), we  
 107 equalized samples by adjusting for sample coverage, which  
 108 allows for fairer comparisons of diversity estimates drawn from  
 109 communities with greater or lesser proportions of rare species  
 110 [15]. We compared samples at 90% coverage (i.e. the level of  
 111 sample completeness giving a 10% probability that the next  
 112 recorded individual will belong to a previously undetected  
 113 species), dropping a single sample from all further analyses as  
 114 it exhibited a particularly low coverage value (60%), and was  
 115 therefore not deemed to be representative of the community in  
 116 the (connected) channel from which it was collected. We then  
 117 calculated alpha diversity as Hill-Shannon diversity to afford  
 118 similar sensitivity to rare and common species and retain intu-  
 119 itive scaling behaviour (i.e. proportional to changes in richness  
 120 [15]). We compared Hill-Shannon diversities using a Kruskal-  
 121 Wallis one-way analysis of variance to account for different num-  
 122 bers of replicates per group. Following rejection of the null  
 123 hypothesis (no significant difference between treatments), we  
 124 conducted Conover-Imam tests to determine which treatments  
 125 differed significantly in alpha diversity, controlling for the false  
 126 discovery rate using the Benjamini-Hochberg procedure [16].

Beta diversity, interpreted here as the dissimilarity in species  
 composition among the communities of two (i.e. pairwise dis-  
 similarity) or more (i.e. multiple site dissimilarity) channels  
 [17], was calculated and decomposed into turnover (species  
 replacement) and nestedness-resultant (species gain/loss; here-  
 after NRD) components using the partitioning methods of  
 Baselga [18]. Under this framework, total beta diversity is calcu-  
 lated as Sorensen dissimilarity ( $\beta_{\text{SOR}}$ ), turnover as Simpson  
 dissimilarity ( $\beta_{\text{SIM}}$ ) and NRD as the difference between these  
 ( $\beta_{\text{SOR}} - \beta_{\text{SIM}} = \beta_{\text{NES}}$ ). High turnover would imply the presence of  
 many species unique to certain channels; whereas high NRD  
 would signify (i) a nesting of species-poor assemblages within  
 richer ones, and thus (ii) greater overlap in species’ identities  
 among channels [18].

We calculated (1) pairwise measures of beta diversity ( $\beta_{\text{SOR}}$ ,  
 $\beta_{\text{SIM}}$  and  $\beta_{\text{NES}}$ ), to analyse turnover and NRD between the



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

pooled communities of each of the three treatments; and (2) multiple site dissimilarity ( $\beta_{\text{SOR}}$ ,  $\beta_{\text{SIM}}$  and  $\beta_{\text{NES}}$ ) to compare the communities of all channels within each treatment [18]. As each treatment contained a different number of channels, with a minimum of three (dry), we accounted for a sampling effort effect by conducting analyses on random subsets of three channels. We calculated beta diversity for 100 combinations of paired treatment subsample pools (pairwise measures) and for 100 combinations of treatment-specific subsamples (multiple site measures). The final results were obtained by taking the mean and 95% confidence intervals of these 100 repeats.

### 3. Results

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

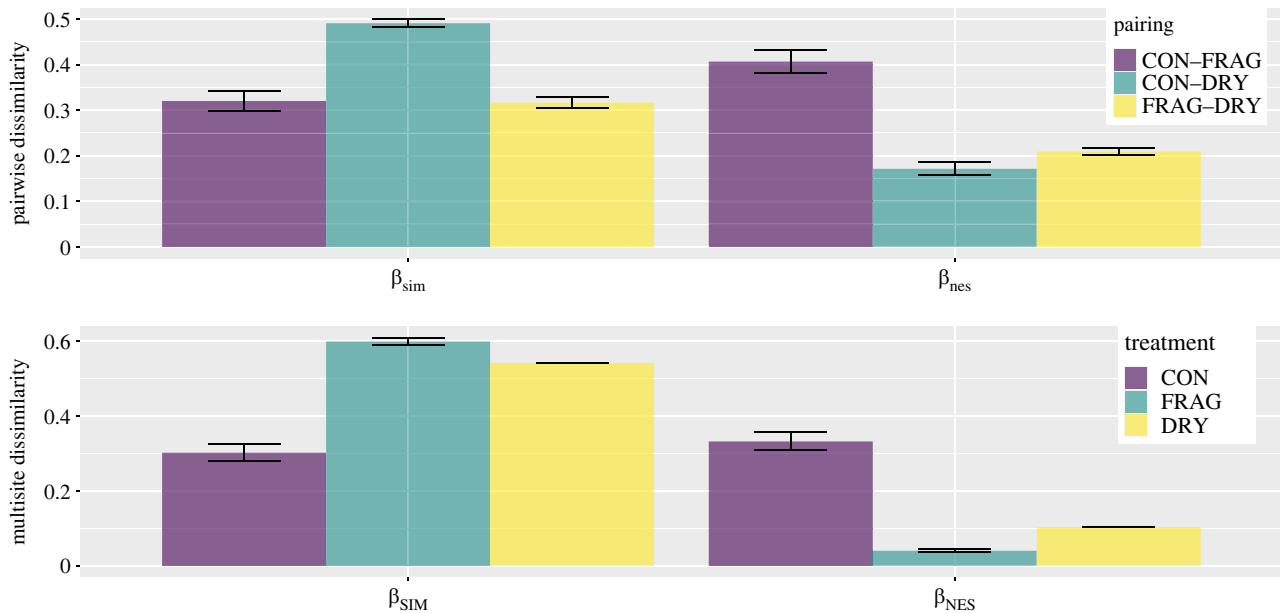
$t_{12} = 7.91$ ,  $p < 0.001$ ) and dry streams ( $11 \pm 2$ ;  $t_{10} = 3.97$ ,  $p = 0.001$ ). The latter also contained significantly richer communities than connected channels ( $t_6 = 2.42$ ,  $p = 0.015$ ).

Communities of connected channels differed substantially from those of both fragmented ( $\beta_{\text{SOR}} = 0.73$ ) and dry ( $\beta_{\text{SOR}} = 0.66$ ) streams. This was driven primarily by NRD ( $\beta_{\text{NES}} = 0.41$ ) and turnover ( $\beta_{\text{SIM}} = 0.49$ ) respectively (figure 2a). Fragmented and dry channel communities were relatively similar to each other ( $\beta_{\text{SOR}} = 0.53$ ), with turnover the dominant component ( $\beta_{\text{SIM}} = 0.32$ ). There were also large differences among channels within each treatment (connected  $\beta_{\text{SOR}} = 0.63$ ; fragmented  $\beta_{\text{SOR}} = 0.64$ ; dry  $\beta_{\text{SOR}} = 0.65$ ; figure 1b). Connected channel communities differed from one another due to both turnover ( $\beta_{\text{SIM}} = 0.30$ ) and NRD ( $\beta_{\text{NES}} = 0.33$ ), whereas differences among fragmented and to a slightly lesser extent dry channel communities were largely attributable to turnover ( $\beta_{\text{SIM}} = 0.60$  and  $0.54$ , respectively).

### 4. Discussion

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

Some differences in invertebrate community composition were apparent between our channels and that typical of riparian habitats and seasonally dry streams. Notable early riparian colonists of dry streambeds, such as ground beetles (Carabidae) [11], were absent from our samples, but the



**Figure 2.** Pairwise Sorensen dissimilarities between the pooled communities of connected, fragmented and dry treatments, partitioned into turnover ( $\beta_{sim}$ ) and nestedness-resultant ( $\beta_{nes}$ ) components (top) and multiple site dissimilarities among channels within each treatment (bottom). Error bars in both panels display + 95% CI.

widespread presence of other common inhabitants of riparian zones, such as rove beetles (Staphylinidae) and money spiders (Linyphiidae), suggests that this is unlikely to reflect the lack of riparian habitat in the mesocosms. It could instead point towards a key difference between the effects of seasonal drying and prolonged drought on terrestrial species composition, with adaptations that allow rapid colonisation of newly dry streambeds, such as inundation tolerance and strong flight among some carabids [11,20], becoming significantly less advantageous over longer dry periods. Further studies of prolonged stream droughts are needed to explore this.

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

Patchiness and host specificity could be strong drivers of the high species turnover we observed between different fragmented and dry channels, which arose despite their close spatial proximity (see electronic supplementary material, figure S4). This contrasted with the high nestedness observed between connected channels, which itself could reflect

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

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

**Ethics.** This work did not require ethical approval from a human subject or animal welfare committee.

**Data accessibility.** Data and code are available via Zenodo at <https://zenodo.org/record/8156532> [14]

The data are provided in electronic supplementary material [23].

**Declaration of AI use.** We have not used AI-assisted technologies in creating this article.

**Authors' contributions.** T.A.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; K.K.: conceptualization, data curation, formal analysis, investigation,

methodology, supervision, writing—review and editing; T.M.: data curation, formal analysis, methodology, supervision, writing—review and editing; G.W.: data curation, methodology, project administration, resources, writing—review and editing; F.W.: data curation, resources, writing—review and editing; G.W.: conceptualization, funding acquisition, project administration, writing—review and editing; M.L.: conceptualization, funding acquisition, investigation, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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