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## The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones

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Review

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3 1 The macroinvertebrate seedbank promotes community persistence in temporary rivers  
4 across climate zones  
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24 Running head line: The invertebrate seedbank of temporary rivers  
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3 17 **SUMMARY**  
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6 19 1. Aquatic macroinvertebrates inhabiting temporary rivers are typically described as  
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8 20 having low resistance to riverbed drying. However, little research has examined the  
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10 21 'seedbank' within dry riverbed sediments, which comprises aquatic life stages that  
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12 22 survive in dewatered sediments and from which active organisms may develop only  
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14 23 after surface water returns.  
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16 24  
17 25 2. We synthesized published and unpublished data from studies that had  
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19 26 experimentally rehydrated sediments collected from dry riverbeds, to establish the  
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21 27 importance of the seedbank in promoting macroinvertebrate community resistance.  
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23 28 Studies from across climate zones were included, to examine seedbank importance in  
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25 29 relation to environmental harshness, and in particular, sediment moisture. We also  
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27 30 assessed the importance of the seedbank relative to alternative habitats promoting  
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29 31 persistence of the flowing river (FR) assemblage. We predicted that the proportion of  
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31 32 the FR assemblage present in rehydrated sediments (RS) would decrease with  
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33 33 environmental harshness, due to conditions within the sediments becoming less  
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35 34 conducive to the survival of biota.  
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37 35  
38 36 3. A negative relationship between the proportion of FR taxa present in RS and  
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40 37 harshness was observed, and this contributed to a reduction in the compositional  
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42 38 similarity of FR and RS assemblages as harshness increased. Significant positive  
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44 39 correlations were identified between sediment moisture content and macroinvertebrate  
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46 40 community metrics (density and taxon richness) in some systems.  
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48 41  
49 42 4. Habitats external to the dry reach, which contribute to community resilience, were  
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51 43 invariably inhabited by a greater number of FR taxa than rehydrated sediments.  
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53 44 However, rehydrated sediments included several FR taxa that were not found in any  
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55 45 other habitats during the dry phase, including families of Coleoptera and Diptera.  
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57 46  
58 47 5. Our results indicate the importance of the seedbank as a resistance mechanism for  
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60 48 temporary river macroinvertebrates. With climate change scenarios predicting an  
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50 49 increase in riverbed drying, maintaining habitats that facilitate the persistence of  
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52 50 instream communities during dry phases is an increasing priority. We identified

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51 strong relationships between sediment moisture and taxon richness, and river  
52 management and rehabilitation activities should therefore aim to retain moisture in  
53 drying sediments, by manipulating parameters such as riparian shading.  
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## 56 Introduction

57 Temporary rivers, which experience seasonal drying of riverbed sediments, are the  
58 dominant type of lotic ecosystem in Mediterranean and arid climates (Gasith & Resh,  
59 1999; Tooth & Nansen, 2011) and are also common in temperate regions (Williams,  
60 1996; Larned *et al.*, 2010). In temporary systems, as well as in typically perennial  
61 rivers, the spatiotemporal extent of riverbed drying may increase during droughts  
62 (Williams, 2006; Sponseller *et al.*, 2010; Bogan & Lytle, 2011). Climate change  
63 scenarios predict an increase in drought frequency and severity in many global  
64 regions (Solomon *et al.*, 2007), with increasing water resource pressures exacerbating  
65 surface water deficits in anthropogenically-influenced systems (Kundzewicz *et al.*,  
66 2008; Vörösmarty *et al.*, 2010). The dry period duration in naturally temporary  
67 systems and the occurrence of drying in typically perennial rivers are therefore both  
68 expected to increase (Solomon *et al.*, 2007; Döll & Schmied, 2012), with  
69 consequences for the persistence of stream communities (Robson, Chester & Austin,  
70 2011).

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72 Macroinvertebrate community responses to drying are considered to be characterised  
73 by low resistance (capacity to withstand drying) and high resilience (capacity to  
74 recover after flow resumes; Stanley *et al.*, 1994; Fritz & Dodds, 2004; Acuña *et al.*,  
75 2005). This means that recolonisation of a rewetted reach is achieved primarily by  
76 individuals originating from external sources, not by emergence of those withstanding  
77 drying in situ. However, this apparently low resistance conflicts with predictions that  
78 communities exposed to regular drying will have adaptive traits, including desiccation  
79 tolerance, to facilitate survival of dry phases (Lytle & Poff, 2004; Diaz, Alonso &  
80 Gutierrez, 2008; Robson *et al.*, 2011).

81  
82 Previous research considering macroinvertebrate survival within sediments extracted  
83 from dry channels has demonstrated that some taxa have active life stages that are  
84 resistant to drying, including dytiscid beetles (Fenoglio, Bo & Bosi, 2006), gastropod  
85 molluscs (Miller, Ponder & Clark, 1999; Lysne & Koetsier, 2006) and larval  
86 trichoptera (Wickson, Chester & Robson, 2012). However, there is increasing  
87 recognition that these active individuals are only one part of an invertebrate  
88 'seedbank' (*sensu* Tronstad, Tronstad & Benke, 2005a; Datry, Corti & Philippe,  
89 2012), which comprises all aquatic life stages that remain viable in dry riverbed

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3 90 sediments. As such, the seedbank includes both active forms and dormant life stages  
4 91 that develop only after rewetting. The importance of seedbanks as a resistance  
5 92 mechanism has previously been recognised in temporary lentic waters including  
6 93 ponds (Kenk, 1949; Williams, 2005), wetlands (Brock *et al.*, 2003; Dietz-Brantley *et*  
7 94 *al.*, 2002) and floodplain habitats (Boulton & Lloyd, 1992; Benigno & Sommer,  
8 95 2008), and in particular for meiofauna (Boulton & Lloyd, 1992; Brock *et al.*, 2003).  
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15 97 Recent sediment rehydration experiments have demonstrated that a substantial  
16 98 proportion of the macroinvertebrate community may also survive in the dry sediments  
17 99 of lotic ecosystems (see Table 1). Many of these published studies have provided  
18 100 system-specific indications of the taxa present in rehydrated sediments, while the  
19 101 wider importance of the seedbank as a mechanism allowing communities to persist in  
20 102 temporary rivers remains unclear (Zwick, 1996). A quantitative synthesis of existing  
21 103 data from across climate zones is required to improve understanding of the  
22 104 contribution the seedbank makes to community persistence in temporary rivers and to  
23 105 identify environmental drivers of seedbank composition. Previous experimental work  
24 106 and field observations have indicated that many taxa show partial but not complete  
25 107 desiccation tolerance (Robson *et al.*, 2011; Wickson *et al.*, 2012; Poznańska *et al.*,  
26 108 2013), indicating that resistance is likely to be related to sediment moisture content.  
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36 110 We synthesized published and unpublished data to determine the importance of the  
37 111 seedbank as a resistance mechanism for macroinvertebrates in temporary rivers.  
38 112 Seedbank 'importance' was defined as the proportion of flowing river (FR) taxa  
39 113 present in the rehydrated sediment (RS) assemblage; this metric acknowledges the  
40 114 influence of the FR assemblage on that present in RS, and also recognises that taxa  
41 115 need only survive at low abundance to contribute to community recovery upon  
42 116 rewetting. Studies from across climate zones were examined to determine how  
43 117 contrasting conditions, in particular environmental harshness (defined as conditions  
44 118 that limit community diversity and abundance; Fritz & Dodds, 2005), influence the  
45 119 role of the seedbank. We hypothesized that the composition of the assemblage  
46 120 surviving in dry sediments would be related to harshness, and in particular to  
47 121 sediment moisture and therefore to the dry period duration, climatic variables and  
48 122 sediment characteristics. We predicted that the proportion of FR taxa in dry sediments  
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58 123 would decrease in relation to harshness, and that this would be observed as a  
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3 124 reduction in taxonomic similarity between FR and RS assemblages as harshness  
4 125 increased. To establish the relative importance of the seedbank as one resistance  
5 126 mechanism within wider survival strategies, we examined the contribution of other  
6 127 habitats to the persistence of FR communities, including other instream areas  
7 128 promoting resistance (e.g. moist surface microhabitats) and instream and external  
8 129 habitats increasing resilience (e.g. the hyporheic zone and local perennial waters,  
9 130 respectively).

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## 17 132 **Methods**

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### 19 134 *The datasets: criteria for inclusion and search parameters*

20 135 Our synthesis examined macroinvertebrate persistence in lotic ecosystems following  
21 136 the loss of free water from the main channel; habitats lateral to the channel (e.g.  
22 137 floodplains) were not included. Flow intermittence occurs along a continuum and we  
23 138 considered it arbitrary to define a cut-off point anywhere along this continuum; rivers  
24 139 with any degree of flow intermittence were therefore eligible for inclusion in our  
25 140 analysis, from ephemeral to near-permanent systems (*sensu* Williams, 2006).

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33 142 For inclusion in our analysis of seedbank importance, a dataset comprising two taxa  
34 143 lists was required: (i) taxa present in sediments extracted from a dry riverbed and  
35 144 experimentally rehydrated; (ii) taxa found within the same system during a period of  
36 145 surface flow either preceding and/or subsequent to the dry phase. 'Dry' sediments  
37 146 were considered as retaining a measured or undetermined amount of moisture but  
38 147 lacking free water. Dry sediments that were not rehydrated prior to examination were  
39 148 excluded, to avoid including deceased individuals in the recorded assemblage.

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47 150 To warrant inclusion, the taxonomic resolution of a study needed to reach a level  
48 151 equivalent to other selected datasets, to facilitate comparison between systems. In  
49 152 practice, this meant Acarina, Oligochaeta and Tricladida were left at the group level  
50 153 stated; Bivalvia, Coleoptera, Diptera and Trichoptera were identified to family level;  
51 154 and Amphipoda, Cnidaria, Ephemeroptera, Gastropoda, Isopoda, Megaloptera,  
52 155 Odonata and Plecoptera were identified to genus. Meiofauna (Copepoda, Cladocera,  
53 156 Nematoda and Ostracoda) were excluded from our analyses as sampling and sample  
54 157 processing methods were not suitable for their retention in many studies. Basic  
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3 158 environmental information was required for each study system, including the climate  
4 159 zone and a qualitative description of sediment characteristics. Details such as  
5 160 sediment grain size distribution, moisture content and organic matter content were  
6 161 desirable but not essential, as such requirements would have excluded most datasets.  
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11 163 To identify relevant datasets, 89 searches incorporating combinations of 22 words or  
12 164 terms (aestivat\*; desiccat\*; dried sediment\*; dry sediment\*; egg bank\*; eggbank\*;  
13 165 emers\*; ephemeral; intermittent; inundat\*; invertebrate; macroinvertebrate; rehydrat\*;  
14 166 re-hydrat\*; rewet\*; river; sediment\*; seed bank\*; seedbank\*; stream; substrat\*;  
15 167 temporary) were performed in the ISI Web of Knowledge database (Thomson Reuters,  
16 168 New York). Seven datasets fulfilling the criteria for inclusion were identified using  
17 169 this process: Boulton (1989), Stanley *et al.* (1994), Paltridge *et al.* (1997), Larned,  
18 170 Datry & Robinson (2007), Stubbington *et al.* (2009), Chester & Robson (2011) and  
19 171 Datry *et al.* (2012). Unpublished data underpinning the published work of Larned *et*  
20 172 *al.* (2007), Stubbington *et al.* (2009) and Datry *et al.* (2012) were used to supplement  
21 173 published results. Stanley *et al.* (1994) did not fully report the composition of the FR  
22 174 assemblage; in place of this, a satisfactory list was compiled from Stanley *et al.* (1994)  
23 175 and other studies conducted within the same system (Boulton *et al.*, 1992; Velasco &  
24 176 Millan, 1998; Sponseller *et al.*, 2010). The FR assemblage relevant to Boulton (1989)  
25 177 was reported by Boulton & Lake (1992). Paltridge *et al.* (1997) identified FR and RS  
26 178 samples using contrasting taxonomic approaches, with FR identification focussing on  
27 179 only three orders; this study was therefore excluded from certain analyses. In addition  
28 180 to the seven published studies, three unpublished datasets were acquired, two from R.  
29 181 Stubbington and one from P. J. Wood (Table 1, Table 2), making a total of 10 datasets.  
30 182 Further information on the aims, study sites, methods and results of the three  
31 183 unpublished studies are provided in Appendix S1 of the Supporting Information.  
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33 185 Five of the 10 datasets fulfilling our basic criteria also investigated the effect of dry  
34 186 period duration on seedbank assemblages. Larned *et al.* (2007) and Datry *et al.* (2012)  
35 187 sampled multiple sites along a spatial gradient of increasing dry period duration.  
36 188 Stanley *et al.* (1994), Stubbington *et al.* (2009) and Stubbington (R. Stubbington,  
37 189 unpublished a) addressed the same question from a temporal perspective by sampling  
38 190 the same sites on repeated occasions during a prolonged dry phase. These five  
39 191 datasets were used to analyse the effect of dry period duration on seedbank  
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3 192 composition, and where data were available (Larned *et al.*, 2007; Datry *et al.*, 2012; R.  
4 193 Stubbington, unpublished a), the effects of sediment moisture were also considered.

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8 195 *Data analysis*

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11 197 *Determination of environmental harshness*

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13 198 To compare environmental conditions across studies, we ranked systems in order of  
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15 199 relative harshness (i.e. conditions limiting survival of aquatic biota), where 1 reflected  
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17 200 a relatively benign environment and 6 indicated the harshest conditions (Table 3).

18 201 Ranks were based on sediment moisture content and were determined using  
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20 202 quantitative measurements and qualitative descriptions, alongside factors influencing  
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22 203 moisture content: dry period duration, climatic variables (temperature, precipitation  
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24 204 inputs) and sediment characteristics (grain size distribution, organic matter content).

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27 206 All studies were conducted in reaches that typically dry annually (Table 1).

28 207 Conditions in Sycamore Creek (Stanley *et al.*, 1994) were considered harshest (6) due  
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30 208 to the effects of extreme high temperatures, virtual absence of precipitation and coarse  
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32 209 sediment composition on sediment moisture retention (Table 1). The semi-arid

33 210 Victoria Range rivers (Chester & Robson, 2011) were also ranked as harsh (5), with  
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35 211 drought conditions reducing average rainfall values (Table 3) and coarse sediments

36 212 exacerbating water loss (Table 1). Of the temperate zone studies, Larned *et al.* (2007)  
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38 213 noted very low mean % sediment moisture; this study was therefore ranked as 4

39 214 (Table 3). Moisture content was not stated by Boulton (1989), but rainfall was similar  
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41 215 to Larned *et al.* (2007), which in combination with higher maximum temperatures is

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43 216 likely to have limited sediment moisture retention; this system was therefore also

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45 217 ranked as 4. Datry *et al.* (2012) recorded moderate moisture content, rainfall and

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47 218 temperatures, earning a rank of 3; in comparison, Stubbington (R. Stubbington,

48 219 unpublished a) noted higher moisture, higher rainfall and lower temperatures, earning

49 220 a rank of 2. Harshness assessment in two other temperate system studies (Stubbington

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51 221 *et al.*, 2009; P. J. Wood, unpublished) was hampered by a lack of sediment moisture

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53 222 data; the climate and sediment moisture retention capacity of these systems were

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55 223 judged as comparable to Stubbington (R. Stubbington, unpublished a) and also

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57 224 assigned a rank of 2. Conditions reported by Stubbington (R. Stubbington,

58 225 unpublished b) were most benign: the rainfall total was high, rain fell on 24/31 days in

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3 226 the dry month, and maximum temperatures (Table 3) were reached only briefly; this  
4 227 study was therefore allocated the lowest harshness rank (1; Table 3). Ranks were  
5 228 verified by researchers who had studied multiple systems (A.J. Boulton and P.J.  
6 229 Wood, pers. comm.).  
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### 231 *Environmental harshness and the importance of seedbank*

12 232 To test our prediction that the proportion of the FR assemblage surviving within dry  
13 233 sediments would decrease as harshness increased, we expressed the number of FR  
14 234 taxa present within the RS of a system as a proportion of FR taxon richness. Sampling  
15 235 effort and timing of FR sample collection varied (pre-drying, during the dry phase  
16 236 and/or post-drying; Table 2) but all studies strived to represent peak FR diversity, thus  
17 237 validating comparison between studies. To avoid over-estimating richness, taxa lists  
18 238 were reduced to the coarsest resolution noted, for example 'Limnephilidae (early  
19 239 instar)' and '*Limnephilus* sp.' were considered one taxon. All terrestrial and semi-  
20 240 aquatic taxa were excluded. These measures resulted in some taxonomic totals  
21 241 differing from previously published values (e.g. Datry *et al.*, 2012) and values stated  
22 242 in the Supporting Information (e.g. Table S2). Proportions were arc-sine square-root  
23 243 transformed then regressed against harshness ranks using linear and non-linear models.  
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35 245 To test the prediction that RS and FR assemblage composition would decrease in  
36 246 similarity as environmental harshness increased, non-metric multidimensional scaling  
37 247 (NMDS) was conducted, producing two-dimensional solutions with ecologically-  
38 248 interpretable solutions (final stress <0.2; Clarke, 1993). For each system, the  
39 249 similarity between RS and FR assemblages was examined using Bray-Curtis distances  
40 250 based on taxonomic richness at the order level, to account for differences in  
41 251 taxonomic resolution between datasets. ANOSIM (analysis of similarity) was used to  
42 252 examine variability in FR and RS samples across harshness ranks using the ANOSIM  
43 253 test statistic  $R$  (range -1 to 1);  $\alpha = 0.05$ . Linear regression analyses were performed to  
44 254 examine relationships between RS-FR similarity values and harshness ranks.  
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### 51 256 *Assemblage response to the dry period duration*

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53 257 To examine trajectories of change in seedbank assemblage composition with  
54 258 increasing dry period duration, NMDS was performed using a Bray-Curtis similarity  
55 259 matrix based on presence-absence data from the five suitable datasets. To explain  
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3 260 patterns observed in the ordination, samples were allocated to one of four dry period  
4 261 durations (0.1-7 d, 8-30 d, 31-63 d, 64-287 d) and taxon richness and  
5 262 macroinvertebrate density (converted to individuals kg<sup>-1</sup> for all studies) calculated.  
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7 263 The significance of temporal change in these community metrics was assessed using  
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9 264 Kruskal-Wallis non-parametric one-way ANOVA tests, with Mann-Whitney U-tests  
10 265 to examine differences between pairs of durations. Abundance data were log-  
11 266 transformed prior to statistical analysis. Linear and non-linear regression analyses  
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13 267 were used to investigate relationships between community metrics and sediment  
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15 268 moisture.  
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#### 20 270 *Seedbank importance relative to other persistence mechanisms*

21 271 To determine the importance of the seedbank relative to other community persistence  
22 272 mechanisms, the occurrence of alternative sources of dry-phase survivors and  
23 273 recolonists was examined. Recolonist sources external to the dry reach comprised  
24 274 upstream and downstream perennial reaches, nearby lentic perennial waters and  
25 275 upwelling groundwater springs; instream recolonist sources included perennial pools  
26 276 and the hyporheic zone; habitats facilitating dry-phase resistance in situ comprised  
27 277 localised microhabitats such as leaf packs, bryophytes and filamentous algae. For all  
28 278 studies, the potential of each source as a persistence mechanism was estimated from  
29 279 its proximity to the dry reach and its spatial extent. Where data were available (eight  
30 280 studies), the number of taxa present in each alternative habitat was calculated and  
31 281 expressed as a proportion of the number of taxa in FR samples, to allow comparison  
32 282 with seedbank importance.  
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43 284 Significance testing and regression analyses were conducted in IBM SPSS Statistics  
44 285 19 (IBM, New York, USA) and NMDS and ANOSIM analyses were performed using  
45 286 PRIMER v6 (Clarke & Gorley, 2006).  
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## 49 288 **Results**

### 50 289 51 290 *Assemblage composition*

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53 291 An overall mean of  $12.1 \pm 2.1$  taxa occurred in the study river systems. Total taxon  
54 292 richness was highest in the temperate Albarine (24 taxa; Datry *et al.*, 2012) and  
55 293 Lerderderg and Werribee Rivers (22 taxa; Boulton, 1989), and lowest in the semi-arid  
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3 294 Victoria Range rivers (3 taxa; Chester & Robson, 2011; Table 4). Chironomidae  
4 295 (Diptera) and Oligochaeta were the most common taxa, occurring in 9 of 10 river  
5 296 systems, while Ceratopogonidae (Diptera) was found in RS in 8 studies. Some orders  
6 297 were represented by a diverse range of families, including Diptera (12 families),  
7 298 Trichoptera (11 families) and Coleoptera (8 families), while Odonata and  
8 299 Megaloptera were both represented by one species in one study (Table 4).  
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15 301 *Seedbank importance in relation to environmental harshness*

16 302 Considering all nine studies (but not Paltridge *et al.*, 1997), a mean of  $32.0 \pm 5.3$  % of  
17 303 FR taxa were present in RS. The proportion of the FR assemblage present in RS was  
18 304 highest in two temperate systems of low to moderate harshness (rank 1-3): the  
19 305 Albarine (54 %; Detry *et al.*, 2012) and upper reaches of the Lathkill (52 %; R.  
20 306 Stubbington, unpublished b; Table 5). In contrast, Chester & Robson (2011) noted  
21 307 only 5 % of the FR assemblage (a single taxon) in the RS of a harsh semi-arid system  
22 308 (rank 5). Other studies recorded 18-42 % of FR taxa in RS, including systems with  
23 309 harshness ranks of 2 (e.g. Stubbington *et al.*, 2009) to 6 (Stanley *et al.*, 1994). Orders  
24 310 commonly present in FR samples but absent from RS included Ephemeroptera,  
25 311 Amphipoda and Hemiptera (Table 5). Regression analysis indicated a moderate linear  
26 312 negative relationship between environmental harshness and the proportion of FR taxa  
27 313 in RS ( $R^2 = 0.339$ ,  $P = 0.100$ ), which became significant when an outlying system  
28 314 (Sycamore Creek, USA; Stanley *et al.*, 1994) was excluded ( $R^2 = 0.647$ ,  $P = 0.016$ ;  
29 315 Fig. 1).  
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41 317 The NMDS ordination distinguished between FR and RS samples (ANOSIM  $R =$   
42 318  $0.125$ ,  $P = 0.034$ ), with samples from individual systems plotting in variable  
43 319 proximity (Fig. 2). Sample pairs from harsher systems (ranks 4-6; Table 3) tended to  
44 320 be more distinct than pairs from more benign environments (ranks 1-3), with  
45 321 similarity between FR and RS assemblages being lowest in the Victoria Range (37.0;  
46 322 Chester & Robson, 2011; rank 5) and highest in the Lathkill upper reaches (78.2; R.  
47 323 Stubbington, unpublished b; rank 1). Regression analysis indicated a linear decline in  
48 324 compositional similarity between FR & RS assemblages as harshness increased ( $R^2 =$   
49 325  $0.774$ ,  $P = 0.002$ ; Fig. 3).  
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58 327 *Assemblage response to the dry period duration*  
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3 328 NMDS indicated that site-specific features were a greater influence on assemblage  
4 329 composition than dry period duration, with individual systems plotting as distinct  
5 330 clusters with minimal overlap (Fig. 4); in particular, samples from arid Sycamore  
6 331 Creek formed a distinct cluster separate from temperate systems. Trajectories of  
7 332 temporal change varied between systems (Fig. 4). In Sycamore Creek (Stanley *et al.*,  
8 333 1994), assemblage composition remained relatively stable over time and was not  
9 334 clearly related to dry period duration (Fig. 4). Assemblage stability was also observed  
10 335 in the Selwyn (Larned *et al.*, 2007), with 1 d samples being more variable in  
11 336 composition than other samples. In contrast, in both the Albarine (Datry *et al.*, 2012)  
12 337 and Lathkill headwaters (R. Stubbington, unpublished a), assemblage composition  
13 338 changed in relation to the dry period duration (Fig. 4).  
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23 340 Considering all five systems, taxon richness decreased steadily and became less  
24 341 variable as the dry period duration increased, from  $9.4 \pm 1.3$  taxa for sediments  
25 342 exposed to 0.1-7 d dry periods, to  $4.7 \pm 0.3$  taxa where the dry period exceeded 64 d  
26 343 (Kruskal-Wallis,  $P = 0.001$ ; Fig. 5a). The reduction in density was sharper, falling  
27 344 from  $101 \pm 18$  individuals to  $49 \pm 7$  individuals between the 0.1-7 d and 8-30 d dry  
28 345 period duration categories (Mann-Whitney U-test,  $P = 0.038$ ; Fig. 5b). After this  
29 346 initial decline, densities remained stable for dry period durations of  $<287$  d (Fig. 5b).  
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36 348 Relationships between dry period duration and taxon richness were system-specific  
37 349 and could be related to sediment moisture content (Fig. 6a). In Sycamore Creek,  
38 350 Stanley *et al.* (1994) recorded a rapid reduction in taxon richness over the 15 d study  
39 351 period, and although moisture data were not collected, the authors emphasized the  
40 352 rapidity with which sediment moisture declined in this arid system. A similar  
41 353 reduction occurred in the temperate Albarine in the first 7 d after drying (Datry *et al.*,  
42 354 2012), the rate of taxon loss then stabilising over the 142 d study period. Excepting a  
43 355 notable outlier for the 0.1 d dry period duration, in which few taxa were recorded  
44 356 despite high moisture content, a strong positive linear relationship was observed  
45 357 between moisture content and taxon richness in the Albarine ( $R^2 = 0.829$ ,  $P < 0.001$ ;  
46 358 Fig. 6a; Datry *et al.*, 2012). In the temperate Lathkill headwaters, taxon richness  
47 359 remained stable (Stubbington *et al.*, 2009) or increased slightly (R. Stubbington,  
48 360 unpublished a) during the dry period; stable sediment moisture content characterised  
49 361 this system, resulting in a positive, linear relationship with the number of taxa present  
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3 362 ( $R^2 = 0.670$ ) which was not significant due to the low number of samples ( $P = 0.181$ ;  
4 363 Fig. 6a). Similar stability in taxon richness was observed in the temperate Selwyn, but  
5 364 no relationship was apparent between the number of taxa and the moisture content in  
6 365 this study ( $R^2 = 0.043$ ; Fig. 6a; Larned *et al.*, 2007).  
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10 366  
11 367 Temporal changes in macroinvertebrate density were similar to patterns described for  
12 368 taxon richness, being positively related to sediment moisture in two of the three  
13 369 temperate systems for which data were available (Fig. 6b). However, while a strong  
14 370 positive linear relationship between moisture content and invertebrate densities was  
15 371 observed on the Selwyn ( $R^2 = 0.538$ ,  $P = 0.001$ ), a moderate linear relationship was  
16 372 observed in the Lathkill headwaters ( $R^2 = 0.376$ ,  $P = 0.387$ ) and no relationship was  
17 373 apparent in the Albarine (Fig. 6b).  
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23 374  
24 375 *Seedbank importance in relation to community resilience*  
25 376 In all eight studies reporting taxa in alternative recolonist sources during the dry  
26 377 period, at least one such habitat contained a greater proportion of FR taxa than RS  
27 378 samples (Table 6). Habitats supporting the greatest proportion of FR taxa were  
28 379 invariably perennial surface waters, namely pools (Boulton, 1989; Chester & Robson,  
29 380 2011), downstream reaches (Stubbington *et al.*, 2009; R. Stubbington, unpublished a,  
30 381 b; P. J. Wood, unpublished) and upstream reaches (Larned *et al.*, 2007; Datry *et al.*,  
31 382 2012). Reference to the raw data indicated that multiple habitats supported the same  
32 383 recolonists; for example all taxa recorded in groundwater springs by Stubbington *et al.*  
33 384 (2009) also occurred in downstream perennial reaches. Some taxa were recorded  
34 385 exclusively in RS samples in four studies: Boulton (1989), Stubbington *et al.* (2009),  
35 386 Stubbington (R. Stubbington, unpublished a) and Wood (P. J. Wood, unpublished).  
36 387 Boulton (1989), for example, found Scirtidae (Coleoptera), Ceratopogonidae,  
37 388 Dolichopodidae, Psychodidae (Diptera), Glacidobidae (Gastropoda) and Calocidae  
38 389 (Trichoptera) in RS and no other habitat sampled during the dry phase, whilst  
39 390 Stubbington *et al.* (2009) recorded Dytiscidae, Hydrophilidae (Coleoptera), Dixidae  
40 391 (Diptera) and *Nemoura cambrica* (Plecoptera, Nemouridae) only in RS.  
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## 54 393 **Discussion**

55 394 Previous research has indicated that macroinvertebrate community persistence in  
56 395 temporary rivers is achieved primarily through resilience mechanisms (Stanley *et al.*,  
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3 1994; Fritz & Dodds, 2004; Acuña *et al.*, 2005; Chester & Robson, 2011), and the  
4 capacity of dry sediments to enhance community resistance has been considered low  
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6 (Boulton & Stanley, 1995; Young, Norris & Sheldon, 2011). Our analysis indicated  
7 398  
8 that survival within dry sediments has previously been underestimated, with a diverse  
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10 macroinvertebrate assemblage including up to 54 % of FR taxa emerging following  
11 400  
12 rehydration of sediments collected across climate zones. Macroinvertebrates survived  
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14 alongside an abundant meiofauna, which was beyond the scope of our analysis; our  
15 402  
16 determination of seedbank importance is therefore likely to remain an underestimate  
17 403  
18 for the entire invertebrate community. The small size of RS sampling areas may also  
19 404  
20 have reduced our richness estimates: riverbed sediments are heterogeneous and  
21 405  
22 consequent spatial variability in assemblage composition (Townsend & Hildrew, 1994)  
23 406  
24 may have excluded some taxa. This is demonstrated, for example, by Chester &  
25 407  
26 Robson's (2011) observation of the FR crayfish *Geocharax* in aestivation chambers  
27 408  
28 constructed beneath cobbles in the dry thalweg, but not in RS.  
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#### 411 *Seedbank importance in relation to environmental harshness*

31 412 We predicted that seedbank importance would decrease with increasing  
32 413  
33 environmental harshness, and that this would be observed as a reduction in similarity  
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35 between FR and RS assemblages as harshness increased. The negative linear  
36 415  
37 relationship observed between harshness and the proportion of FR taxa in RS samples  
38 416  
39 largely supported this prediction, although the high proportion of the FR assemblage  
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41 present in RS from the harshest system (Sycamore Creek, Stanley *et al.*, 1994) was a  
42 418  
43 notable outlier and reflected the presence of high proportion of a taxon-poor FR  
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45 assemblage in RS. The declining proportion of the FR assemblage in RS contributed  
46 420  
47 to these assemblages becoming more distinct as harshness increased.  
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46 422 Moisture content is considered to be a crucial influence on seedbank viability (Stanley  
47 423  
48 *et al.*, 1994; Tronstad *et al.*, 2005a). Moisture is influenced by climate (precipitation,  
49 424  
50 temperature, humidity), shading, sediment characteristics (hydraulic conductivity,  
51 425  
52 grain size distribution, organic matter content) and surface microhabitats that limit  
53 426  
54 evaporation (e.g. leaf packs; Paltridge *et al.*, 2007), as well as the dry period duration.  
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56 Regression analyses confirmed the importance of moisture as a determinant of  
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58 assemblage richness and density in temperate systems, but with some exceptions;  
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60 these are tentatively attributed to a coarse temporal sampling resolution at short dry

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3 430 period durations (Larned *et al.*, 2007) and spatial heterogeneity of invertebrate  
4 431 densities within dry sediments (Datry *et al.*, 2012). Relationships with sediment  
5 432 moisture were stronger for taxon richness than invertebrate densities, with taxa  
6 433 needing only to survive at low densities to facilitate community recovery upon  
7 434 rewetting.

435

#### 436 *Effect of sediment moisture on the seedbank assemblage*

437 For the seedbank to function as a resistance mechanism, inhabitants must survive an  
438 entire dry phase, which may vary from hours to months (Larned *et al.*, 2007).

439 However, invertebrate density and taxon richness were negatively related to sediment  
440 moisture content and consequently experienced pronounced temporal reductions in  
441 both arid and temperate systems that lacked significant dry phase precipitation  
442 (Stanley *et al.*, 1994; Larned *et al.*, 2007; Datry *et al.*, 2012). In such systems,  
443 seedbank importance decreased with dry period duration, due to fewer taxa and  
444 individuals having the physiological traits required to tolerate complete desiccation  
445 (Robson *et al.*, 2011; Wickson *et al.*, 2012; Poznańska *et al.*, 2013). However, a linear  
446 relationship between time and moisture should not be assumed, and where moisture is  
447 maintained by precipitation in conjunction with other variables (e.g. shading, organic-  
448 rich sediments), this is reflected by stable assemblage composition (R. Stubbington,  
449 unpublished a). Stubbington *et al.* (2009) even recorded a temporal increase in  
450 seedbank richness during a year of high rainfall in the temperate Lathkill headwaters,  
451 with terrestrial adult insects potentially adding taxa through oviposition (Towns,  
452 1983).

453

#### 454 *Seedbank importance within wider community persistence strategies*

455 Alternative sources of recolonists, particularly perennial surface waters, supported  
456 more FR taxa than RS. This finding is consistent with reports that temporary river  
457 communities recover primarily through resilience, with recolonists from perennial  
458 upstream reaches (Fritz & Dodds, 2004; Bogan & Lytle, 2007; Corti & Datry, 2012),  
459 instream pools (Boulton, 1989; Chester & Robson, 2011), connected lentic waters  
460 (Paltridge *et al.*, 1997) and aerial recolonists (Carl, 1989; Gagneur & Chaoui-  
461 Boudghane, 1991) contributing to recovery. Downstream perennial reaches may also  
462 be inhabited by many FR taxa (Arscott *et al.*, 2010; R. Stubbington, unpublished a)  
463 and are important recolonist pools for positively rheotaxic taxa (Hughes, 1970; Hultin,



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3 464 1971). In addition, the hyporheic zone may support FR taxa and can therefore  
4 465 contribute to community resilience (Datry, Larned & Scarsbrook, 2007; Datry, 2012;  
5 466 Stubbington, 2012); these saturated sediments form a temporal ecotone that may dry  
6 467 to be inhabited by a desiccation-tolerant seedbank. Complementing these resilience  
7 468 mechanisms, microhabitats promoting community resistance within a dry reach  
8 469 include riparian plant roots (Fritz & Feminella, 2011) and leaf litter (Boulton, 1989;  
9 470 Chester & Robson, 2011; Wickson *et al.*, 2012). Our results, however, suggest that  
10 471 the seedbank is the resistance mechanism supporting the richest assemblage.  
11 472 Recolonist sources may show considerable redundancy (Robson *et al.*, 2011); for  
12 473 example the assemblage in upwelling springs may be a subset of that in downstream  
13 474 perennial reaches (Stubbington *et al.*, 2009). Such redundancy facilitates community  
14 475 persistence: if the viability of one habitat is compromised, others may still function.  
15 476 Redundancy was, however, less pronounced for RS than other recolonist sources, with  
16 477 Diptera, Coleoptera, Trichoptera and Plecoptera taxa being found exclusively in RS  
17 478 (e.g. Boulton, 1989; Stubbington *et al.*, 2009).

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30 480 The seedbank therefore forms a single element in an armoury of community  
31 481 persistence mechanisms. From a landscape perspective, the spatial arrangement of  
32 482 temporary reaches, perennial waters and other sources from which recolonists  
33 483 originate (Lake, 2003) affects the extent to which different habitats function as  
34 484 refuges (Davey & Kelly, 2007). The seedbank may therefore be a particularly  
35 485 important resistance mechanism in certain areas, including headwaters (which lack  
36 486 perennial upstream reaches), reaches several km downstream of perennial water  
37 487 (Paltridge *et al.*, 1997), isolated catchments (with limited aerial recolonisation) and  
38 488 reaches lacking saturated hyporheic sediments (Datry, 2012). The seedbank may also  
39 489 have particular value for certain taxa, including those with low dispersal and  
40 490 recolonisation abilities (Robson *et al.*, 2011) such as insects whose adults are weak  
41 491 fliers (e.g. some Ephemeroptera and Plecoptera genera; Churchel & Batzer, 2006).  
42 492 These taxa must, however, have some physiological tolerance of desiccation to  
43 493 survive in the seedbank (Robson *et al.*, 2011). In addition, our analysis indicated the  
44 494 seedbank as particularly important in certain environments, with the proportion of FR  
45 495 taxa supported by RS being greatest in less harsh systems, typically in temperate  
46 496 climates. Relatively few studies have been conducted in non-temperate climate zones,

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3 497 and further research is therefore required to establish whether the patterns observed in  
4 498 our study were typical.

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8 500 *Recreating inundation: current practice and future challenges.*

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10 501 Rewetting of a dry reach represents a short phase of high biological activity following  
11 502 a longer period of quiescence, or a 'hot moment' (McClain *et al.*, 2003), in which  
12 503 many taxa simultaneously start to develop (Larned *et al.*, 2007). Once the  
13 504 fundamental criterion of free water has been met, other secondary variables influence  
14 505 development, including temperature (Newell & Minshall, 1978; Zwick, 1996) and  
15 506 chemical signals (Jensen, Carlson & Barnard, 1999; Evans & Dennehy, 2005).

16 507 Conditions of experimental rehydration must therefore adequately represent field  
17 508 conditions, but to date, studies have differed in their replication of various parameters.  
18 509 Firstly, no experiment has attempted to simulate flowing water, and although  
19 510 hydraulic cues that break dormancy are poorly understood (Brock *et al.*, 2003), simple  
20 511 inundation may not trigger development in some taxa (Danks, 1987). Second, while  
21 512 some studies have replicated a natural light/dark cycle (e.g. Datry *et al.*, 2012), others  
22 513 have covered containers to prevent loss of emerging insects (e.g. Stubbington *et al.*,  
23 514 2009), obscuring photoperiod-related cues (Chapman, 1998). Third, some studies  
24 515 have kept samples at ambient temperatures (e.g. Stubbington *et al.*, 2009), while  
25 516 others have followed constant temperature regimes (e.g. Datry *et al.*, 2012),  
26 517 suppressing thermal development triggers (Zwick, 1996). Other relevant factors  
27 518 include the occurrence of aquatic and riparian predators (Larned *et al.*, 2007), and the  
28 519 duration of rehydration. The latter should be sufficient for macroinvertebrates to  
29 520 develop to an identifiable stage, which may exceed the 28-32 d duration typically  
30 521 used (Jackson & Sweeney, 1995), particularly since physiological desiccation  
31 522 tolerance often involves entering a resting state (Williams, 1996) and subsequent  
32 523 development in response to inundation may be delayed (Wickson *et al.*, 2012). It is  
33 524 noteworthy that the sole plecopteran (*Brachyptera risi*) recorded by Stubbington (R.  
34 525 Stubbington, unpublished a) occurred in a single RS sample rehydrated for 9 months.  
35 526 Future rehydration experiments should seek to manipulate biotic and abiotic  
36 527 parameters to promote development of seedbank inhabitants.

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38 529 Current estimates of seedbank richness may be underestimates due to the spatial  
39 530 design of sampling strategies. Invertebrates may follow a receding waterline in

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3 531 preference to burrowing into sediments, and such movements may concentrate  
4 532 individuals into the last microhabitats to lose free water (Larimore, Childers &  
5 533 Heckrotte, 1959; Tronstad, Tronstad & Benke, 2005b; Stubbington, Wood & Reid,  
6 534 2011) prior to other behaviours such as vertical migration, egg deposition and  
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8 535 entrance into a desiccation-resistant dormant state. This relocation over small spatial  
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10 536 scales increases existing heterogeneity in invertebrate distribution. Sampling designs  
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12 537 should therefore be informed by observation of hydrological conditions preceding the  
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14 538 dry phase.  
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#### 17 540 *Seedbank importance in a changing climate*

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19 541 Previous conceptualisation of dry riverbeds as biologically inactive (Stanley, Fisher &  
20 542 Grimm, 1997) has left dry reaches vulnerable to anthropogenic impacts (Larned *et al.*,  
21 543 2010). However, recognition that dry sediments contribute to aquatic community  
22 544 persistence provides impetus for their protection (Steward *et al.*, 2012). In addition,  
23 545 the total biota supported by temporary rivers may be high, due to temporal transitions  
24 546 between wet and dry phases and use of dry sediments by terrestrial and amphibious  
25 547 communities (Fritz & Feminella, 2011; Datry *et al.*, 2012; Corti & Datry, 2012).  
26 548 Communities may be interdependent due to reciprocal energy exchanges (Nakano &  
27 549 Murakami, 2011; Fritz & Feminella, 2011), with aquatic taxa providing prey for  
28 550 riparian predators (Paetzold, Bernet & Tockner, 2006; Greenwood & McIntosh, 2010)  
29 551 and aquatic predators exploiting inputs of terrestrial prey engulfed by advancing  
30 552 wetted fronts (Corti & Datry, 2012).  
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34 554 With climate change scenarios predicting an increase in drought severity (Solomon *et*  
35 555 *al.*, 2007) and therefore in the extent and duration of riverbed drying (Sponseller *et al.*,  
36 556 2010; Döll and Schmied, 2012), ensuring the integrity of persistence mechanisms  
37 557 used by temporary river communities is an increasing priority. Climate change  
38 558 adaptation strategies need to be system specific (Aldous *et al.*, 2011) and the  
39 559 importance of protecting dry sediments as a feature promoting community resistance  
40 560 should therefore be judged on a site-by-site basis. Where the seedbank is found to be  
41 561 of high value, action may be required to protect its ecological integrity. Our analysis  
42 562 identified strong relationships between sediment moisture and taxon richness, and  
43 563 rehabilitation and management strategies should therefore aim to maintain moisture  
44 564 content during periods of low precipitation. Such efforts could manipulate any  
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3 565 parameter influencing moisture including, for example, sediment organic matter  
4 566 content or shading of the dry reach. As such, consideration of both riparian and  
5 567 instream habitats may help to maintain a rich seedbank that promotes community  
6 568 resistance to riverbed drying.  
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3 869 **Figure legends**  
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6 871 **Fig. 1** Relationship between the proportion of flowing river (FR) taxa in rehydrated  
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8 872 sediments (RS) and environmental harshness (see text for determination; 1 = least  
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10 873 harsh; 6 = most harsh). Arc-sine square-root transformed data. See Table 1 for site  
11 874 details.  
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14 876 **Fig. 2** Two-dimensional non-metric multidimensional scaling (NMDS) plot of  
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16 877 macroinvertebrate assemblages in flowing river (FR) and rehydrated sediment (RS)  
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18 878 samples across a gradient of environmental harshness (see text for determination;  
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20 879 numbers indicate harshness ranks, where 1 = least harsh and 6 = most harsh). Filled  
21 880 symbols = FR samples; open symbols = RS samples; lines link FR and RS samples  
22 881 from the same system.  
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24 882

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26 883 **Fig. 3** Relationship between environmental harshness, and Bray-Curtis similarity  
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28 884 between flowing-river and rehydrated sediment samples. See text for determination of  
29  
30 885 harshness; 1 = least harsh; 6 = most harsh.  
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33 887 **Fig. 4** Two-dimensional non-metric multidimensional scaling (NMDS) plot of  
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35 888 macroinvertebrate assemblages in rehydrated sediment samples, along a spatial or  
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37 889 temporal gradient of increasing dry period. Numbers indicate dry period duration (d).  
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40 891 **Fig. 5** Metrics for the macroinvertebrate community persisting in riverbed sediments  
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42 892 during dry periods of different durations: mean  $\pm$  1 S.E. (a) taxa per sample; (b)  
43 893 individuals  $\text{kg}^{-1}$  sediment. Number of samples per duration: 0.1-7 d,  $n = 14$ ; 8-30 d,  $n$   
44 894 = 7; 31-63 d,  $n = 7$ ; 64-287 d,  $n = 17$ .  
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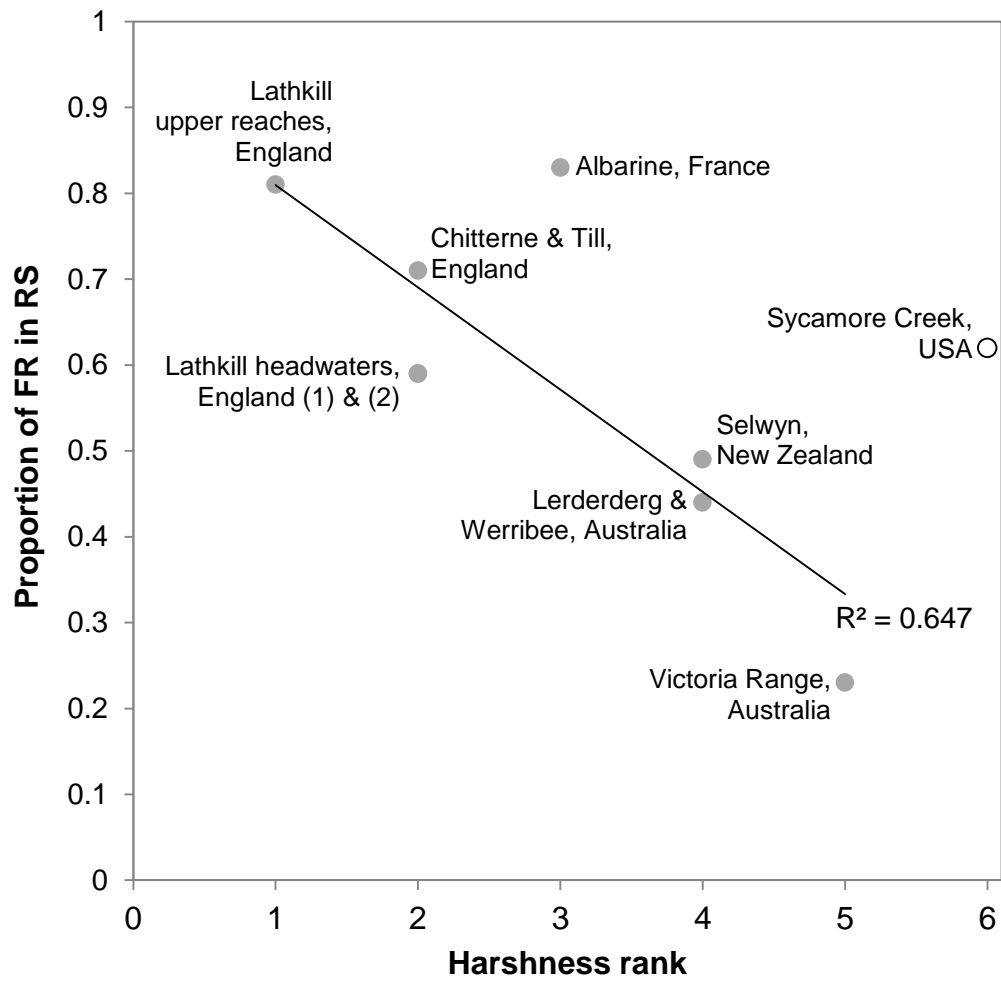
46 895

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48 896 **Fig. 6** Relationship between macroinvertebrate community metrics and sediment  
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50 897 moisture content in experimentally rehydrated riverbed sediments: (a) total number of  
51 898 taxa; (b) densities (individuals  $\text{kg}^{-1}$ ). See Table 1 for site details.  
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2 **Fig. 1**  
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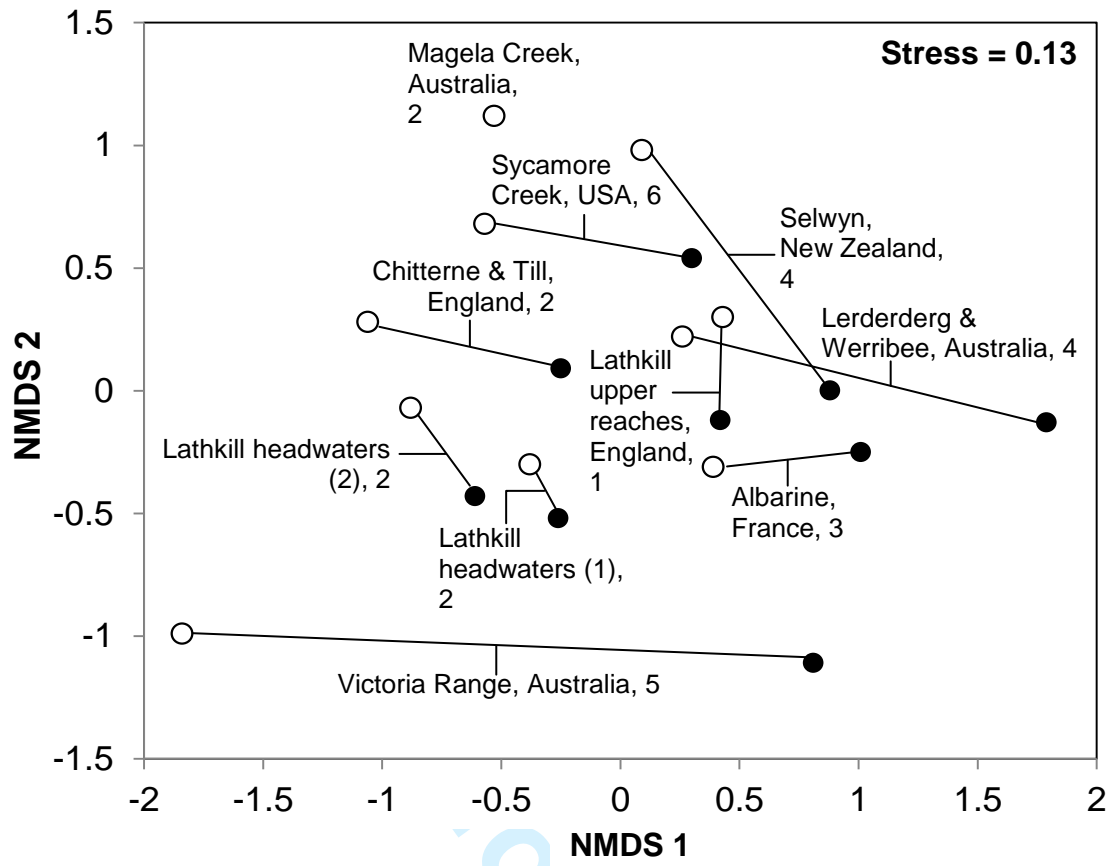
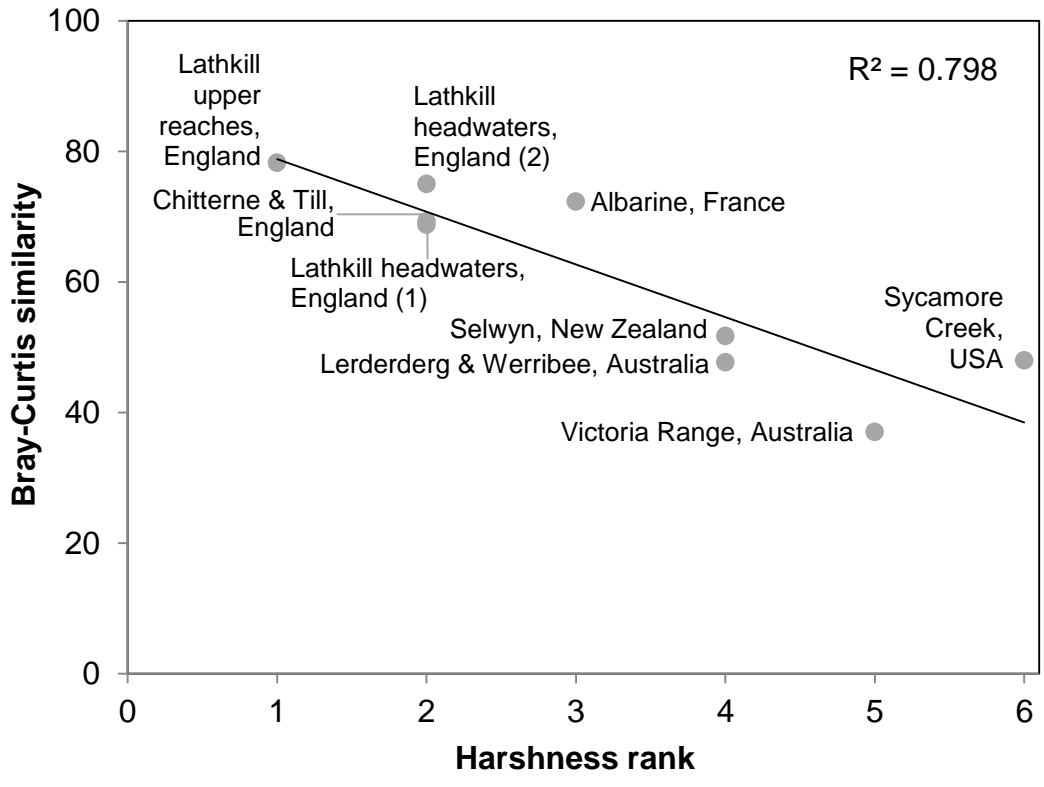


Fig. 2

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For Review



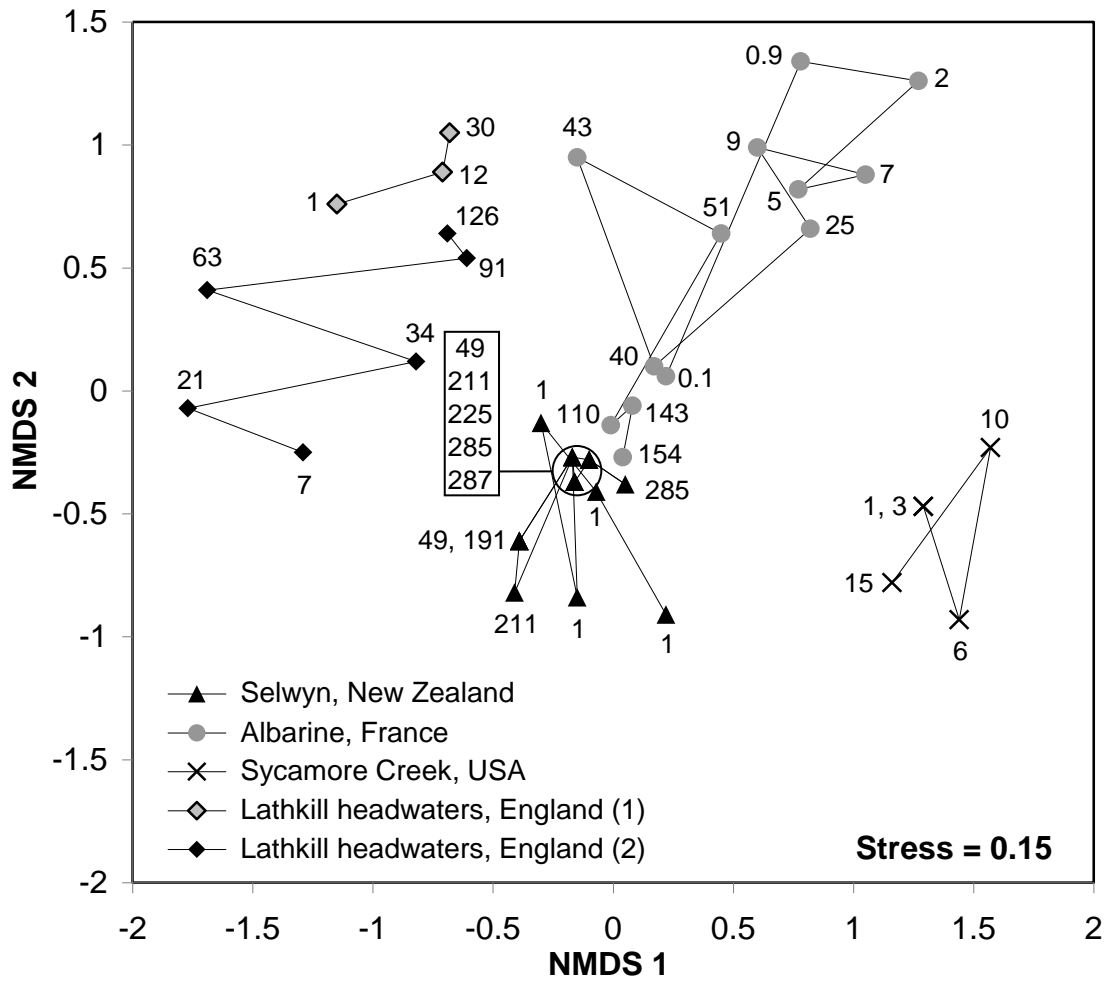


Fig. 4

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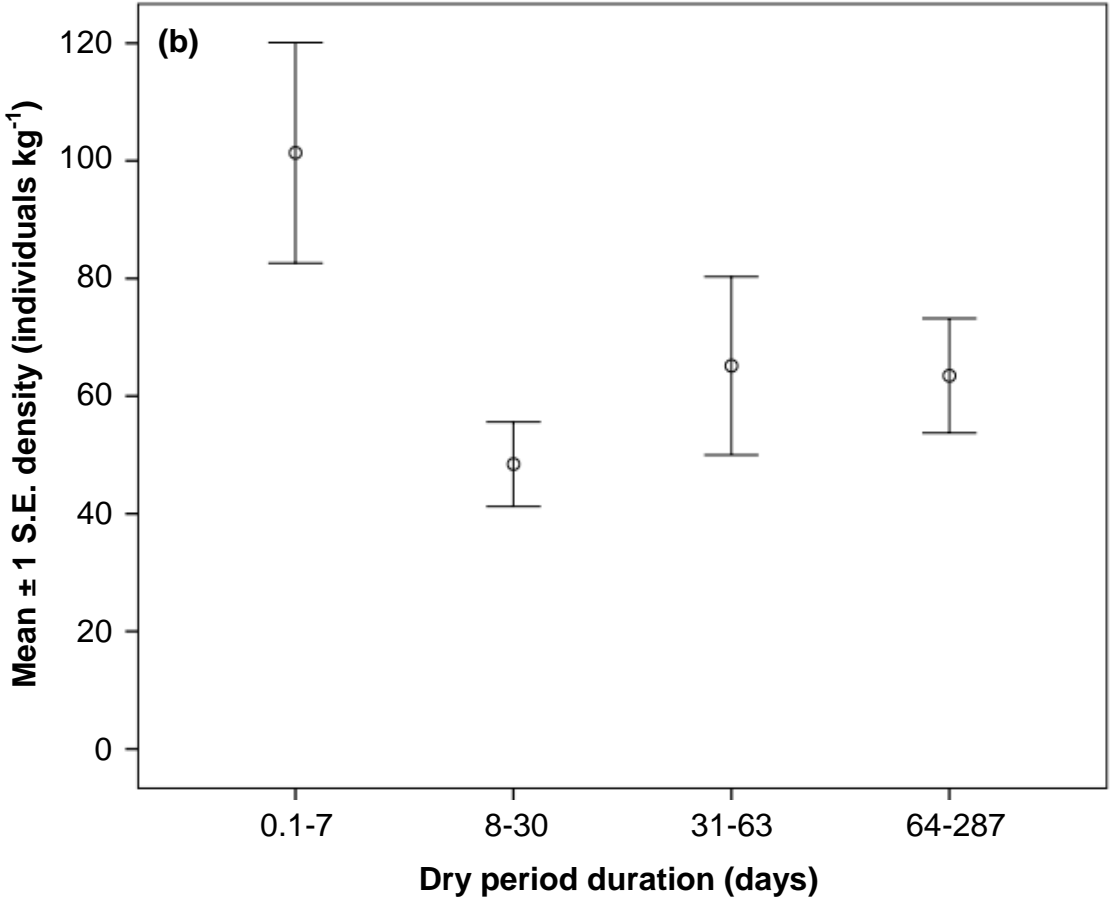
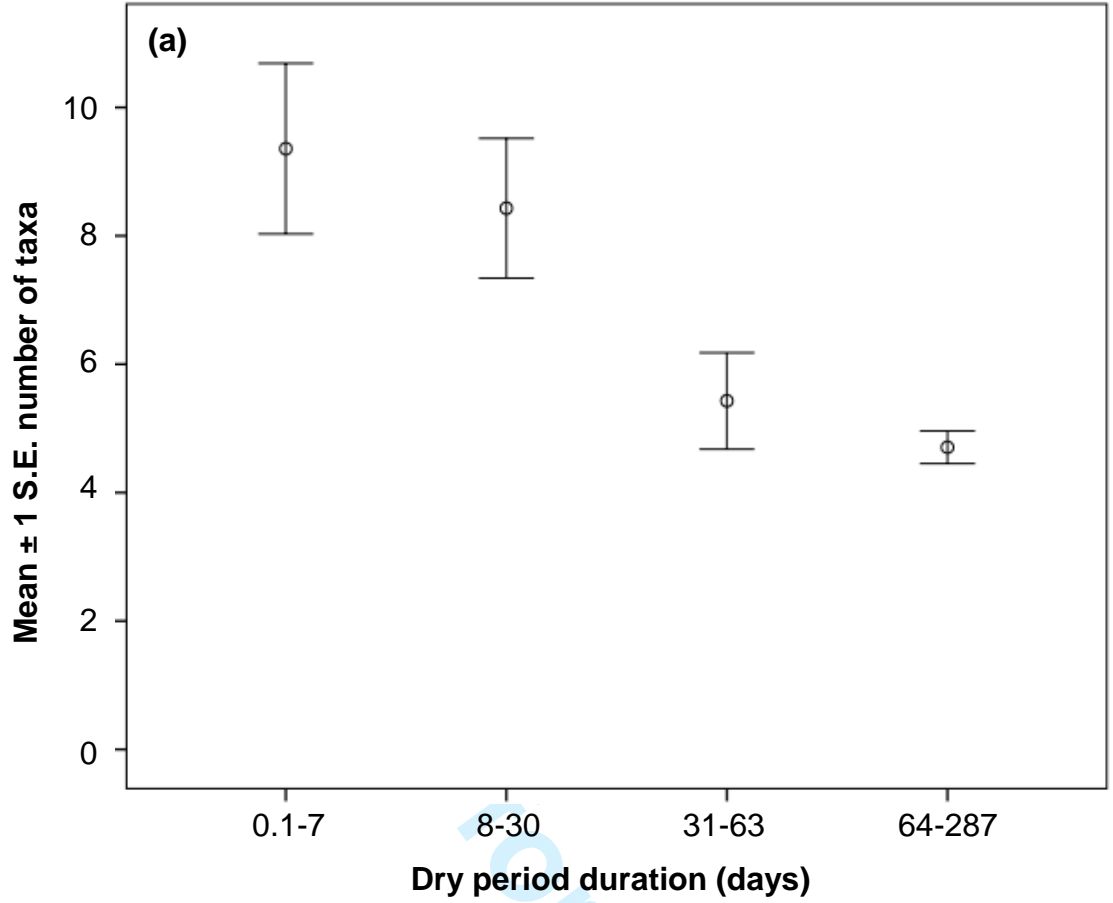


Fig. 5

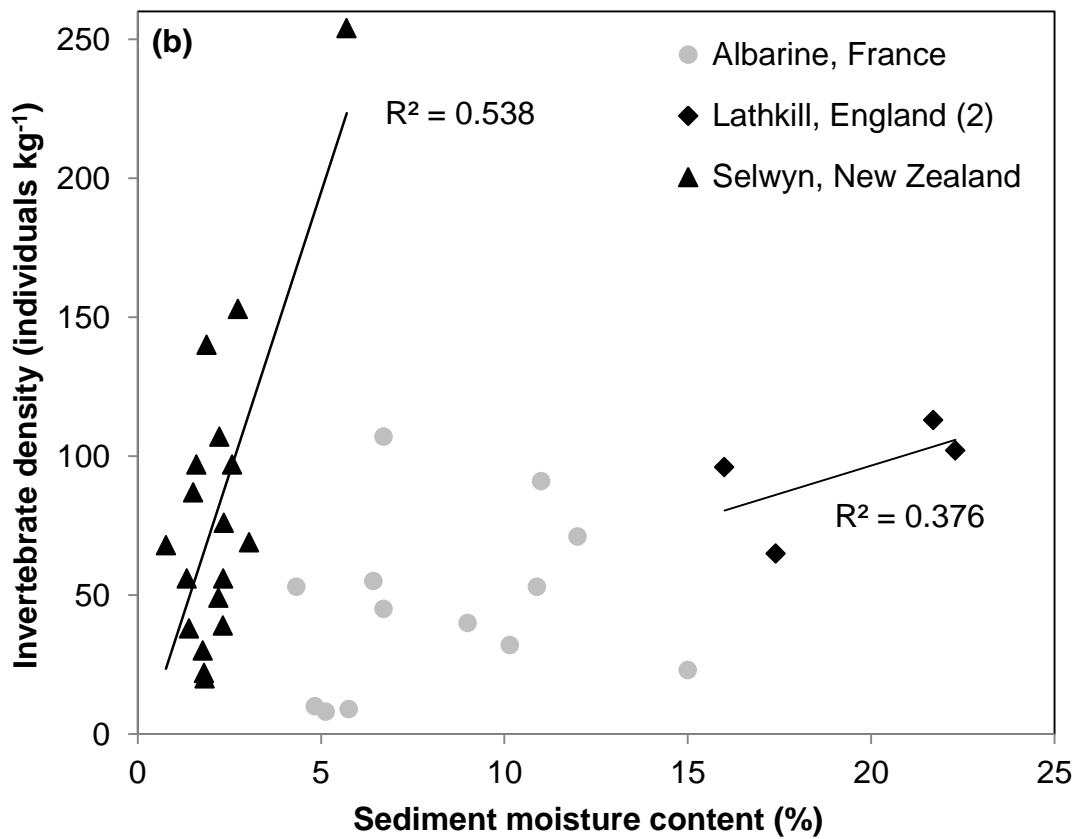
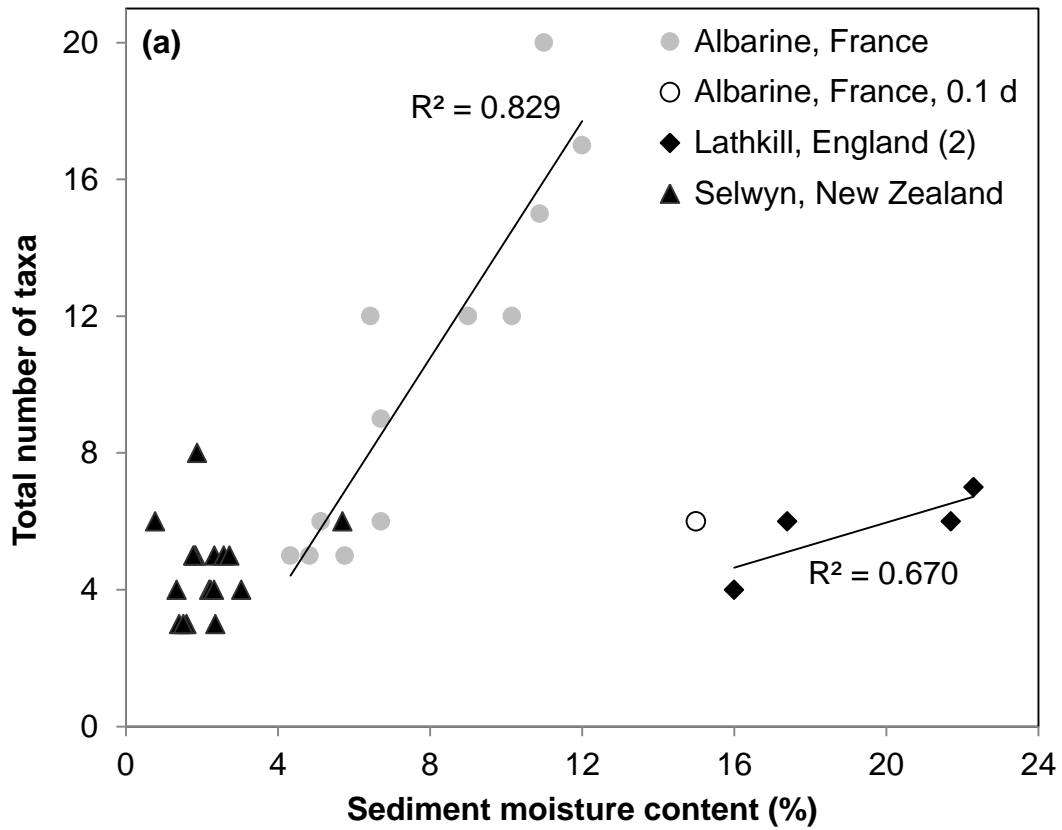


Fig. 6

1 **Table 1** Characteristics of river systems included in the analysis of the  
 2 macroinvertebrate seedbank

Authors	Location	Climate	Typical dry period, mo p.a.	Geology / sediments
Boulton, 1989	Werribee and Lerderderg Rivers, Victoria, Australia	Temperate	2	Cobble-gravel sediments over mixed alluvium
Chester & Robson, 2011	16 streams, Victoria mountain range, Australia	Mediterranean to semi-arid	Varied between streams	Boulder and cobble sediments over sandstone
Datry, Corti & Philippe, 2012	Lower reaches, Albarine River, France	Temperate	0.1-5	Glacio-fluvial deposits
Larned, Datry & Robinson, 2007	Mid-reaches, Selwyn River, New Zealand	Temperate	0.1-10	Glacio-fluvial deposits
Paltridge et al., 1997	Lowland reach, Magela Creek, Australia.	Tropical / Monsoonal	5	Sand-dominated sediments over sandstone
Stanley et al., 1994	Mid-basin, Sycamore Creek, Sonoran Desert, USA	Arid	<9	Coarse sand and pebble dominated sediments
Stubbington et al., 2009 / R. Stubbington, unpublished a*	Headwaters, River Lathkill, England	Temperate	5-6	Soil / bedrock over karst limestone
R. Stubbington, unpublished b	Upper reaches, River Lathkill, England	Temperate	2-3	Mixed sediments over karst limestone
P. J. Wood, unpublished	Chitterne Brook and River Till, England	Temperate	6	Gravel dominated sediment over chalk

3 \*referred to as *Lathkill headwaters (1)* and *(2)* respectively in figures

1 **Table 2** Sampling strategy and experimental procedures of analysed datasets

Authors	Study reach (km)	Flowing river samples						Dry sediment samples						Weight (kg, each/total)	Rehydr-ation duration	Physical data
		Type	Pre-, post- or during drying	No. sites (a)	No. per site (b)	Dates (c)	(a)*(b)*(c) = no. of samples	Area (m <sup>2</sup> )	Sample depth (cm)	No. sites (a)	No. per site (b)	Dates (c)	(a)*(b)*(c) = no. of samples			
Boulton 1989	2 & 5	Sweep, various	Pre-, post	<4	10	23	= 845	~0.06	0-10	4	Riffles, pools	1	= 61	estimated 1.5 / 90	14 d	Moisture
Chester & Robson, 2011	16 x 0.5	Surber	Post- + after 1 yr	16	6	3	= 192	0.2	NS	16	6	1	= 96	estimated > 1 / >96	21 d	None
Datry, Corti & Philippe, 2012	15	Hess	Pre-, Post-	5	4	2	= 40	0.2	0-10	13	2-3	1	= 34	2.5 / 85	32 d	Moisture
Larned, Datry & Robinson, 2007	32	Surber	Pre-, Post-	16	2	2-11	= 73	NS	0-10 & 10-20	9	3 x 2 depths,	1	= 54	2.5 / 135	17 d	Moisture; OM; GSD
Paltridge et al., 1997	22	Various	Post-	3	6	6	= 108	0.16	0-5	3	10	1	= 30	estimated 3 / 90	14 d	None
Stanley et al., 1994	122 & 140m	80 cm <sup>2</sup> cores	Pre- Post-	2 1	5 5	NS, ≥4 3	= ≥40 = 15	80cm <sup>2</sup>	0-10	5	2	5	= 50	estimated 0.25 / 13	1 d	Moisture
Stubbington et al., 2009	<1	Surber Kick	Pre-, Post-	<6	1-3	<7	= 35	~0.1	0-5	6	1	3	= 18	1 / 18	28 d	Not available
R. Stubbington, unpublished a	<1	Surber Kick	Pre-	1	4	1	= 4	~0.1	0-5	7	1	6	= 42	0.5-1 / <42	28 d	Moisture; OM; GSD
R. Stubbington, unpublished b	<1	Surber	During	2	3-4	1	= 7	0.05	0-10	2	1	1	= 2	1.5 / 3	28 d	Moisture; OM; GSD
P. J. Wood, unpublished	2 x <1	Surber	Pre-	3	3-4	1	= 10	0.1	0-10	3	3	1	= 9	2 / ~18	28 d	None

2 NS = not stated. Physical data abbreviations: moisture = sediment moisture content; OM = sediment organic matter content; GSD = sediment  
3 grain size distribution

1 **Table 3** Estimation of relative harshness of river systems from which rehydrated  
 2 sediments were extracted

Study	Sediment moisture (%)			Air temperature (average monthly max. during DP; °C)	Rain (average monthly total during DP; mm)	Organic matter (%)	Shading	Harshness (Rank 1-6)
	Mean	Min	Trend					
Stanley et al., 1994	NS; rapid moisture loss noted			Actual max >60 C in previous year	NS 1-3 at Phoenix	NS	Unshaded	6
Chester & Robson, 2011	NS	NS	None	NS 16-34 at Horsham December to May	NS 13-31 at Horsham March to May	NS	Forest	5
Larned, Datry & Robinson, 2007	2.2	NS	None	NS 14 at Christchurch September	NS 46 at Christchurch September	1.8	Unshaded	4
Boulton 1989	NS			Actual max 35	NS 26-45 at Ballan, Jan-Apr long term mean	NS	Part-shaded	4
Datry, Corti & Philippe, 2012	8.3	4.8	Decline	NS 20-27 at Lyon June to September	NS 56-93 at Lyon June to September	NS	Part-shaded	3
R.Stubbington, unpublished a	20.0	8.9	Stable	24 Actual max during DP	65-118 Actual monthly total during DP	<1 - 26	Part shaded	2
Stubbington et al., 2009	NS			14.5 monthly mean (not max)	NS 93-108 in Manchester August to September	<1 - 26	Part shaded	2
P. J. Wood, unpublished	Sediments moist			20 at Heathrow in June	53 at Bracknell June	Organic rich	Part shaded	2
Paltridge et al., 1997	NS; temperate micro-climate under leaf litter			Actual max 39 at Jabiru Airport in sampling month	168 total	NS	Dense riparian plants	2
R.Stubbington, unpublished b	NS	NS	None	24 Actual max during DP month	118 Actual total during DP month	NS	Wooded	1

3 NS = not stated or not available; DP = dry period.

**Table 4** Macroinvertebrate taxa present in sediments extracted from dry riverbeds and experimentally rehydrated. Numbers indicate the presence of  $\geq 1$  representative of the taxon stated, where: F = family; G = genus; S = species; SF = sub-family

<i>Taxa</i>	Boulton, 1989	Chester & Robson, 2011	Datry, Corti & Philippe, 2012	Larned, Datry & Robinson, 2007	Paltridge et al., 1997	Stanley et al., 1994	Stubbington et al., 2009	R. Stubbington, unpublished a	R. Stubbington, unpublished b	P. J. Wood, unpublished	Occurrence ( /10)
Acarina	2F			✓	✓	✓			✓		5
Bivalvia			✓				✓	✓	✓		4
Cnidaria			✓	✓							2
Coleoptera			✓								1
							✓			✓	3
	5S		3G	✓					2S		4
							✓	✓	✓	✓	4
									✓		1
						✓	✓		✓		3
	✓										1
	✓										1
Crustacea			2F				✓				2
			✓								1
					✓						1
Diptera	2G	✓	✓		✓	✓	✓	✓	✓		8
	6G	✓	3SF	3G		✓	✓	✓	✓	✓	9
							✓				1
	✓										1
	✓		✓					✓	✓		4
	✓				✓				✓		3
	✓								✓		2
			✓								1
					✓						1
	✓										1
			✓			✓					2
Ephemeroptera	2G				✓	✓				✓	4
			2G		✓						2
			✓								1
	✓		✓								2
Gastropoda	✓										1
	✓										1
	✓										1
			✓					✓		✓	3
						✓					1
			✓			✓				✓	2
			✓								1
Megaloptera				✓							1
Oligochaeta	✓		✓	4F	✓	✓	✓	✓	✓	✓	9
Plecoptera	✓	✓									2
			✓						✓		2
							✓				1
								✓			1
Trichoptera	✓							✓			1
				✓							1
									✓		1
			✓								1
	✓		✓								2
			✓				✓		✓		3

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	Odontoceridae			✓								1
	Polycentropodidae			✓								1
	Psychomyiidae									✓		1
	Sericostomatidae				✓							1
Tricladida		✓		✓		✓		2G	✓			5
	Total taxa	22	3	24	9	9	9	12	9	17	7	
	kg of sediment	90	96	85	55	90	13	39	42	3	18	

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1 **Table 5** A comparison of the taxonomic composition of flowing river (FR) and  
 2 rehydrated sediment (RS) samples

	Boulton, 1989	Chester & Robson, 2011	Datry, Corti & Philippe, 2012	Larned, Datry & Robinson, 2007	Stanley et al., 1994	Stubbington et al., 2009	R. Stubbington, unpublished a	R. Stubbington, unpublished b	P. J. Wood, unpublished
Community metric									
% of FR taxa in RS	18	5	54	22	33	31	31	52	42
No. FR taxa in RS	33	1	27	13	7	5	4	16	5
No. taxa in RS only	1	2	3	1	2	8	5	2	2
No. taxa in FR only	147	21	23	47	14	11	9	15	7
FR Orders not in RS	A B Cn H I M O	Co E Tr	None	A E G H P Tl	E H O Tr	E G H	A I Tr	A E G I	E
Sampling strategy									
No. / type of FR samples	845 sweep + other	192 Surber	8 Hess	10 Surber	NS / cores	15 kick + 20 Surber	1 kick + 3 Surber	7 Surber	6 Surber
FR area, where RS area = 1	>1	>1*	<1	<1	>1	1	<1	>1	1
FR sample times (pre, post-, during drying)	Pre-, post	Post-	Pre-; post-	Pre-; post	Pre-; post-	Pre-	Pre-	During	Pre-

3 Order abbreviations: A, Amphipoda; B, Bivalvia; Cn, Cnidaria; Co, Coleoptera; E,  
 4 Ephemeroptera; G, Gastropoda; H, Hemiptera; I, Isopoda; M, Megaloptera; O,  
 5 Odonata; P, Plecoptera; Tl, Tricladida; Tr, Trichoptera.

**Table 6** Occurrence and numerical importance of alternative recolonist sources. P = proportion (the number of taxa found in the habitat as a proportion of the number in rehydrated sediments); ✓ = habitat occurred but distance/extent not described; NS = not stated/refuge potential cannot be determined; \* = combined values for >1 habitat; high = qualitative author assessment of importance; RS = rehydrated sediment samples (values in final column reproduced from Table 5).

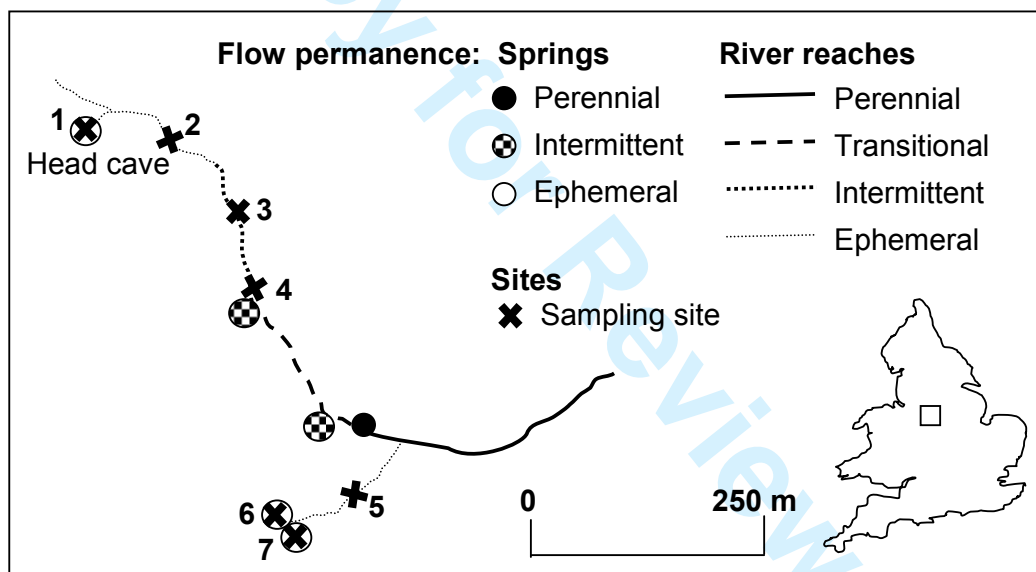
	External to the dry channel								Within the dry channel						
	Upstream reaches		Downstream reaches		Perennial lentic waters		Groundwater springs		Perennial pools		Hyporheic zone		Microhabitats		RS
	Distance / Extent	P	Distance	P	Distance / Extent	P	Distance / Extent	P	Extent	P	Extent	P	Extent	P	P
Boulton, 1989	None	0	NS	-	>6 km / 0.02m <sup>2</sup> 1 lake	0.29	NS	-	Several; NS	0.87	NS	0.10	Leaves, wood algae, , roots, burrows	0.24	0.35
Chester & Robson, 2011	Distance NS 7 of 16 sites	0.95	NS	-	NS	-	Supply pools in the dry channel	-	Many, 1-10m length, fed by groundwater	1.1	<0.5m to bedrock	-	Under stones, leaf litter	0.27	0.05
Datry, Corti & Philippe, 2012	0-15km away >30km extent	-	<1km	-	NS	-	NS	-	NS	-	✓ dry	-	NS	-	0.57
Larned, Datry & Robinson, 2007	<0.1km away 10km extent	-	13 km	-	NS	-	NS	-	NS	-	✓	-	NS	-	0.23
Stanley et al., 1994	0.8-2.5 km	1*	0.8-1.2 km	1*	NS	-	NS	-	NS	-	✓ dry	<0.1	None	0	0.41
Stubbington et al., 2009	None	0	<1 km	1.8	NS	-	<0.5km. 1 cave/ 3 springs of 0.5m <sup>2</sup>	0.56	None	0	None	0	Under stones, bryophytes	-	0.31
R.Stubbington, unpublished a	None	0	<1 km	2.7	NS	-	<0.5km. 1 cave, 3 springs of 0.5m <sup>2</sup>	0.57	None	0	None	0	Under stones, bryophytes	-	0.42
R.Stubbington, unpublished b	<1 m	2.3*	<1 m	2.3*	NS	-	<1km. 2 springs of 0.5m <sup>2</sup>	-	NS	-	Widespread, depth 0.5m	2.0	Marginal vegetation	-	0.53
P. J. Wood, unpublished	None	0	5-9 km	-	<1 km away 1 pond	-	Location NS 1 spring, 1 well	0.36	None	0	Widespread, depth >0.3m	0.45	NS	-	0.36

## Appendix S1 Supporting information on unpublished studies

### Study sites and research aims

#### *R. Stubbington (unpublished a)*

Stubbington (R. Stubbington, unpublished a) collected samples from the ephemeral karstic headwaters of the River Lathkill (Derbyshire, UK; Fig. S1). This is the same area as described and studied by Stubbington et al. (2009), but with an additional seventh site located within the reach (Fig. S1; Table 1). This study was conducted in a year of typical hydrological conditions, to complement the work of Stubbington et al. (2009), which characterised seedbank composition during an unusually short dry phrase preceded by a high-magnitude flood event.

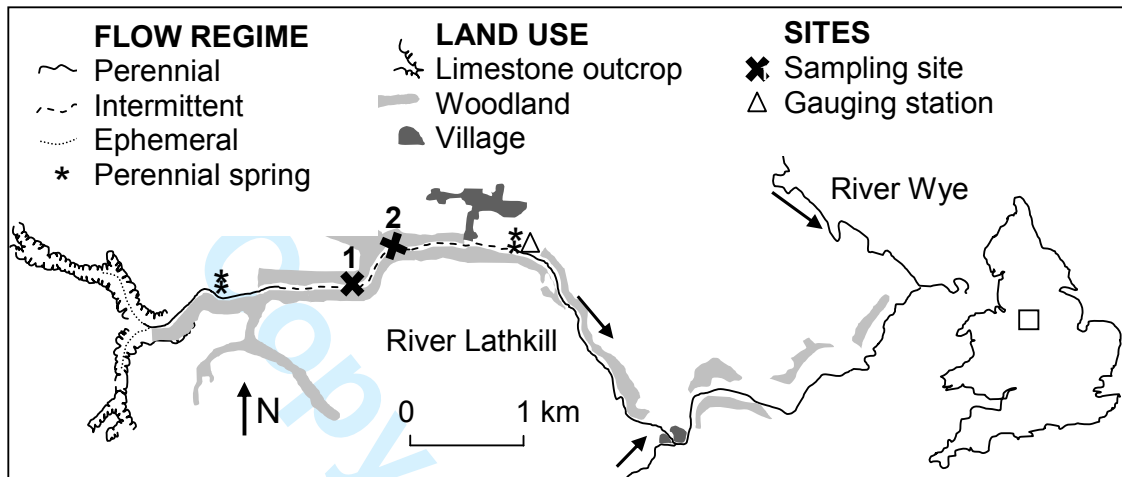


**Fig. S1** Map of the River Lathkill, indicating the location of the seven sampling site in the study of Stubbington (R. Stubbington, unpublished a). Small-scale spatial variability in the flow regime is described by Stubbington et al. (2009). Originally published in Stubbington et al. (2009) and adapted for reproduction here from the author's original figure.

#### *R. Stubbington (unpublished b)*

Stubbington (R. Stubbington, unpublished b) studied the upper reaches of the River Lathkill (Derbyshire, UK), <2 km downstream of the headwaters, in which flow is

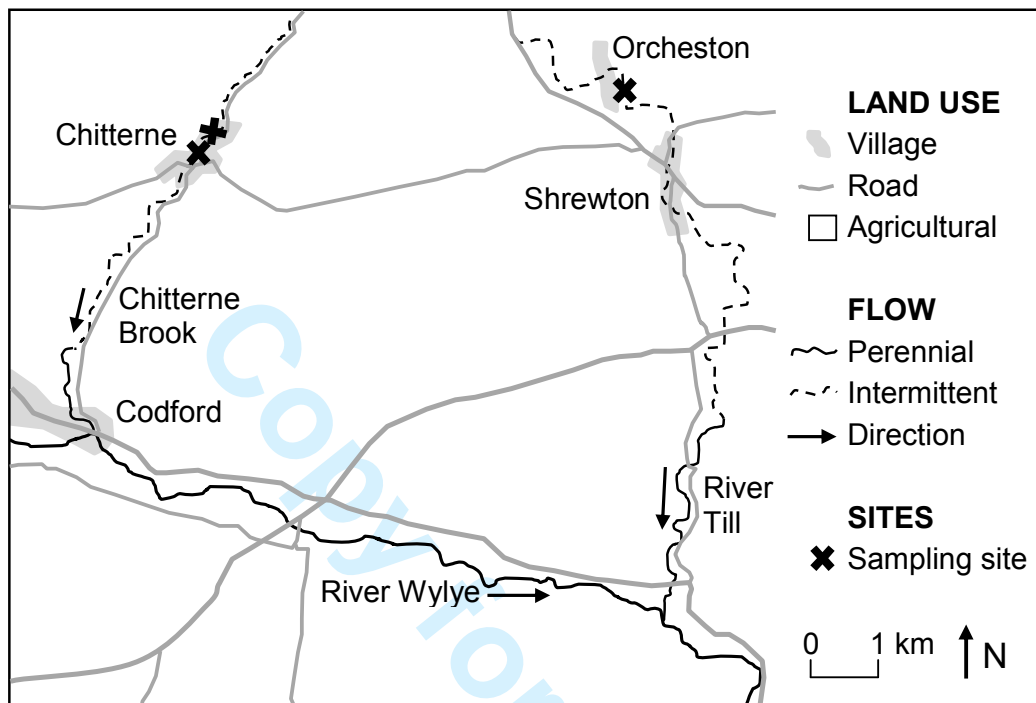
intermittent and the karst bedrock is overlain by mixed alluvium (Fig. S2). Samples were collected opportunistically as part of a wider study (see Stubbington et al., 2011) following localised sediment drying at two sites (Fig. S2); samples were treated as described in Stubbington et al. (2009).



**Figure S2** Map of the River Lathkill, indicating the location of the sampling sites in the study of Stubbington (R. Stubbington, unpublished b; originally published in Stubbington et al. (2011) and adapted for reproduction here from the author's original figure).

*P. J. Wood (unpublished)*

This study examined invertebrate persistence in dry sediments of temperate-zone headwater streams underlain by chalk geology. Such streams, which are not associated with perennial springs, typically experience a period of drying from late spring until autumn then a period of surface flow during winter, and hence are locally termed 'winterbourne streams' (Wright et al., 1984; Berrie, 1992). The study examined the intermittent headwaters of two chalk streams, the Chitterne Brook and River Till, which are adjacent tributaries of the River Wylde (Wiltshire, UK;  $51^{\circ} 12.3\text{N}$ ,  $-1^{\circ} 57.6\text{W}$ ). The catchment is predominantly agricultural, with numerous small villages and minor roads (Fig. S3)



**Figure S3** Map of Chitterne Brook and the River Till, indicating the location of the sampling sites in the study of Wood (P. J. Wood, unpublished; original drawing).

### Methods

All unpublished studies were conducted by the same research group and rehydration and subsequent sample processing were conducted following the procedure outlined in Stubbington et al. (2009). However, other aspects of these studies differed, as detailed below.

#### *R. Stubbington (unpublished a)*

Flowing river (FR) samples comprised one 3-minute kick sample and three 30-second Surber samples taken at one site (site 3; Fig. S1) on one occasion two months prior to the dry phase. One sediment sample was then collected for rehydration at each of sites 1-7 (Fig. S1) within 7 d of sediment drying, and then again 14 d, 34 d, 63 d, 91 d and 126 d after this first sampling occasion.

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3 Sediment moisture content was determined for two samples taken on day 34 and for  
4 all samples taken on days 63, 91 and 126. A sediment sample of approx. 50 g was  
5 extracted from the same area as the RS sample, sealed in sample bag, and returned to  
6 the laboratory. Samples were placed in pre-weighed aluminium dishes and the weight  
7 determined using an electronic balance. Samples were then oven-dried at 50 °C until  
8 the weight remained constant for 12 hours, and % moisture calculated using the  
9 original and final weights.  
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16 Sediment grain size distribution (GSD) was determined for three sets (day 63, 91 and  
17 126) of seven RS samples, following completion of the rehydration experiment.  
18 Clasts estimated to have an  $a$ -axis  $>100$   $\mu\text{m}$  were excluded from the sample, to  
19 reduce the influence of atypically large particles on the calculated percentage of fine  
20 sediment. Course particulate organic matter was also removed. Sediments were oven  
21 dried at 105 °C until the sample weight remained constant over a 12 hour period.  
22 Where oven drying caused aggregation of fine sediments, dried samples were gently  
23 disaggregated using a porcelain pestle and mortar, with care taken not to apply undue  
24 force which could result in particle abrasion. Disaggregated sediments were dry-  
25 sieved through a sieve tower (8, 4, 2, and 1 mm, 500, 250, 125 and 63  $\mu\text{m}$ ) using a  
26 sieve shaker (Endecotts Ltd, London, UK) for five minutes, and each size fraction  
27 then weighed. The % of grains in each fraction was determined and the mean of the  
28 three samples calculated.  
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40 *R. Stubbington (unpublished b)*

41 A single sediment sample was collected for rehydration at each of sites 1 and 2 (Fig.  
42 S2) on a single date following contraction of the submerged area. The short duration  
43 of marginal drying prevented further samples being taken. FR samples comprised 3-4  
44 30-second Surber samples taken within 50 m of the two RS sampling points, on the  
45 same date that RS samples were extracted.  
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51 The GSD was examined for one set of two replicates sample per site. Sediment  
52 samples were collected using a MacNeil sampler, following the procedure outlined by  
53 Bunte and Abt (2001), collecting samples of approx. 5 kg each. These were processed  
54 using the method outlined for Stubbington (R. Stubbington, unpublished a). Sediment  
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moisture was analysed in situ using a ThetaProbe soil moisture sensor (Delta-T Devices, Cambridge, UK).

*P. J. Wood (unpublished)*

FR samples comprised three 30-second Surber samples taken at each site from which dry sediments were later sampled (Fig. S3). Following drying, three sediment samples were collected from each site and rehydrated.

## Results

The taxa recorded in both FR and rehydrated sediment (RS) samples in the studies of Stubbington (R. Stubbington, unpublished a), Stubbington (R. Stubbington, unpublished b) and Wood (P. J. Wood, unpublished) are shown in Tables S1-S3, respectively. Sediment moisture and GSD data is then provided for Stubbington (R. Stubbington, unpublished a) in Tables S4 and S5, and GSD data for Stubbington (R. Stubbington, unpublished b) in Tables S6.

**Table S1** Invertebrate taxa recorded in the karstic headwaters of the River Lathkill by Stubbington (R. Stubbington, unpublished a). FR = flowing river samples; RS = rehydrated sediment samples; a = adult; l = larvae; p = pupae. Sample numbers (*n*) are detailed in the text.

		Site:	1	2	3	3	4	5	6	7
		RS	RS	RS	FR	RS	RS	RS	RS	RS
Coleoptera	Dytiscidae spp. (l)				✓					
	<i>Helophorus</i> sp. (l.)		✓							
	<i>Helophorus brevipalpis</i> (a)				✓					
Crustacea	<i>Gammarus pulex</i>				✓					
	Cyclopoida						✓		✓	
	Harpacticoida	✓					✓	✓	✓	✓
	<i>Asellus aquaticus</i>				✓					
	Ostracoda	✓	✓	✓		✓	✓	✓	✓	✓
	Diptera									✓
Diptera	Ceratopogonidae (l)								✓	✓
	Chironomidae (l)			✓	✓				✓	✓
	Chironomidae (p)			✓						
	Diptera (unidentified) (l)	✓		✓	✓		✓	✓	✓	✓
	Diptera (unidentified) (p)									✓
	Empididae (l)			✓					✓	✓
	Psychodidae (l)						✓			
	Tipulidae (l)				✓					
Gastropoda	<i>Lymnaea</i> spp.			✓	✓					
	Sphaeriidae	✓	✓	✓				✓		✓
Nematoda		✓	✓	✓	✓	✓	✓	✓	✓	✓
Oligochaeta		✓	✓	✓	✓	✓	✓	✓	✓	✓

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Plecoptera	<i>Nemoura cambrica</i>								✓
	<i>Brachyptera risi</i>				✓				
Trichoptera	<i>Limnephilus lunatus</i> (l)								✓
	<i>Micropterna lateralis</i> (l)								✓
	<i>Micropterna sequax</i> (l)								✓
Tricladida	<i>Phagocata vitta</i>	✓	✓	✓			✓	✓	✓
	<i>Polycelis</i> spp.								✓

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**Table S2** Invertebrate taxa recorded the upper reaches of the River Lathkill by Stubbington (R. Stubbington, unpublished b). FR = flowing river samples; RS = rehydrated sediment samples; a = adult; l = larvae; p = pupae. Sample numbers (*n*) are detailed in the text.

		Site 1		Site 2	
		FR	RS	FR	RS
Acarina	Hydracarina		✓	✓	
Coleoptera	<i>Oreodytes sanmarkii</i> (a)	✓			
	<i>Elmis aenea</i> (l)	✓	✓	✓	✓
	<i>Elmis aenea</i> (a)	✓	✓	✓	
	<i>Limnius volckmari</i> (a)			✓	
	<i>Oulimnius</i> spp. (a)	✓			
	<i>Riolus</i> spp. (l)	✓	✓	✓	
	<i>Riolus subviolaceus</i> (a)	✓	✓	✓	
	<i>Helophorus</i> spp. (l)		✓		
	<i>Helophorus brevipalpis</i> (a)	✓	✓	✓	✓
	<i>Hydraena</i> spp. (l)	✓	✓		✓
	<i>Hydraena</i> spp. (a)	✓		✓	
	<i>Anacaena globulus</i> (a)		✓		
Crustacea	Copepoda				✓
	<i>Asellus meridianus</i>			✓	
	<i>Gammarus pulex</i>	✓		✓	
	Ostracoda		✓		✓
Diptera	Ceratopogonidae (l)		✓	✓	
	Chironomidae (l)	✓	✓	✓	✓
	Chironomidae (p)	✓		✓	
	Diptera (unidentified) (p)			✓	
	Empididae (l)	✓	✓	✓	
	<i>Dicranota</i> spp. (l)			✓	
	Muscidae (l)	✓			
	Psychodidae (l)	✓	✓		✓
	Simuliidae (l)	✓		✓	
	Stratiomyidae (l)		✓		
Ephemeroptera	<i>Baetis</i> spp.	✓		✓	
	<i>Serratella ignita</i>	✓		✓	
Gastropoda	<i>Ancylus fluviatilis</i>	✓			
	<i>Lymnaea peregra</i>			✓	
	Sphaeriidae			✓	✓
Nematoda		✓	✓	✓	✓
Oligochaeta		✓	✓	✓	✓
Plecoptera	<i>Leuctra</i> spp.	✓	✓	✓	
	<i>Nemoura</i> sp.			✓	
Trichoptera	<i>Dinocras cephalotes</i> (l)	✓	✓	✓	
	<i>Agapetus fuscipes</i> (l)	✓			✓
	<i>Chaetopteryx villosa</i> (l)			✓	
	<i>Drusus annulatus</i> (l)			✓	
	<i>Drusus annulatus</i> (p)	✓	✓	✓	
	<i>Micropterna-Stenophylax</i> group (l)	✓			
	<i>Limnephilus lunatus</i> (l)			✓	
	<i>Tinoides dives</i> (l)	✓	✓		

*Rhyacophila obliterata* (l)

✓

**Table S3** Invertebrate taxa recorded in two chalk streams by Wood (P. J. Wood, unpublished). FR = flowing river samples; RS = rehydrated sediment samples. Sample numbers (*n*) are detailed in the text.

		Chitterne Brook				River Till	
		Site 1		Site 2			
		FR	RS	FR	RS	FR	RS
Coleoptera	<i>Agabus biguttatus</i>					✓	
	<i>Hydroporus</i> sp.				✓		
	Dytiscidae sp.	✓		✓		✓	
	<i>Helophorus</i> sp.		✓				
	Hydrophilidae	✓					
Crustacea	<i>Niphargus aquilex</i>	✓		✓		✓	
	Copepoda		✓		✓		✓
	<i>Asellus aquaticus</i>					✓	
	Ostracoda				✓	✓	✓
Diptera	Chironomidae	✓	✓	✓		✓	✓
	<i>Simulium angustitarse</i>	✓					
	<i>Simulium latipes</i>	✓					
	Tipulidae						✓
Ephemeroptera	<i>Baetis rhodani</i>					✓	
	<i>Paraleptophlebia wernerii</i>	✓					
Gastropoda	<i>Lymnaea stagnalis</i>						✓
	<i>Lymnaea truncatula</i>		✓		✓		✓
	<i>Anisus leucostoma</i>		✓	✓	✓		✓
Hirudinea	Glossiphoniidae					✓	
Oligochaeta		✓	✓	✓	✓	✓	✓

**Table S4** Moisture content (%) recorded in sediments extracted from the karstic headwaters of the River Lathkill by Stubbington (R. Stubbington, unpublished a). SD = standard deviation; d = days (duration of dry phase).

Site	% moisture				
	34 d	63 d	91 d	126 d	Mean
1	17.5	15.8	16.0	19.8	17.3
2	14.5	17.9	8.9	17.4	14.7
3	-	16.9	12.1	18.7	15.9
4	-	16.7	17.4	15.7	16.6
5	-	19.7	14.7	17.4	17.2
6	-	17.1	13.1	21.8	17.3
7	-	47.9	39.6	45.3	44.3
Mean	16.0	21.7	17.4	22.3	
SD	2.1	11.6	10.2	10.3	

**Table S5** Grain size distribution of sediments extracted from the karstic headwaters of the River Lathkill by Stubbington (R. Stubbington, unpublished a). Numbers indicate the mean % of grains in a size fraction; SD = standard deviation.

		Size fraction (mm)							
		>8	>4	>2	>1	>0.5	>0.25	>0.125	<0.125
Site 1	Mean	29.2	20.0	17.3	15.2	8.9	5.8	3.3	0.3
	SD	1.7	1.4	0.4	3.0	0.2	1.8	1.1	0.2
Site 2	Mean	47.0	17.1	7.0	8.4	8.6	6.7	4.8	0.5
	SD	20.1	1.8	3.6	6.0	5.7	4.0	2.5	0.2
Site 3	Mean	34.2	16.8	7.3	13.5	14.6	8.5	4.8	0.3
	SD	11.3	1.8	0.6	3.3	5.2	3.1	2.1	0.1
Site 4	Mean	45.0	20.4	8.8	7.3	7.5	5.6	4.5	0.4
	SD	5.3	1.7	1.4	1.4	1.8	2.3	2.2	0.3
Site 5	Mean	29.4	18.5	10.0	13.7	12.1	9.9	6.2	0.3
	SD	8.4	1.9	2.4	1.5	1.4	1.8	1.3	0.1
Site 6	Mean	34.5	19.7	16.8	15.0	8.5	3.6	1.6	0.3
	SD	6.0	2.0	2.2	2.0	1.4	0.4	0.1	0.1
Site 7	Mean	19.3	2.0	5.0	12.2	22.7	16.1	17.9	4.8
	SD	33.4	3.2	5.3	10.5	8.1	6.4	16.5	4.0

**Table S7** Grain size distribution of sediments extracted from the upper reaches of the River Lathkill by Stubbington (R. Stubbington, unpublished b). Numbers indicate the mean % of grains in a size fraction; SD = standard deviation.

		Size fraction (mm)							
		>8	>4	>2	>1	>0.5	>0.25	>0.125	<0.125
Site 1	Mean	52.3	12.2	11.1	10.7	7.4	3.1	1.5	1.7
	SD	6.4	1.4	0.1	2.4	2.8	1.5	0.8	0.5
Site 2	Mean	25.7	23.5	13.7	10.2	10.4	9.4	4.2	3.1
	SD	1.1	2.3	1.9	1.8	0.6	2.3	2.0	1.2

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