

1 **Broad-scale patterns of invertebrate richness and community composition**
2 **in temporary rivers: effects of flow intermittence**

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25

26 **Abstract** (251 words)

27 Temporary rivers are increasingly common freshwater ecosystems, but there have been no
28 global syntheses of their community patterns. In this study, we examined the responses of
29 aquatic invertebrate communities to flow intermittence in 14 rivers from multiple
30 biogeographic regions and covering a wide range of flow intermittence and spatial
31 arrangements of perennial and temporary reaches. Hydrological data were used to describe
32 flow intermittence (FI, the proportion of the year with zero-flow) gradients. Linear mixed-
33 effects models were used to examine the relationships between FI and community structure
34 and composition. We also tested if communities at the most temporary sites were nested
35 subsets of communities at the least temporary and perennial sites. Taxon richness decreased
36 as FI increased and invertebrate communities became dominated by ubiquitous taxa. The
37 number of *resilient* taxa (with high dispersal capacities) decreased with increased FI, whereas
38 the number of *resistant* taxa (with adaptations to desiccation) was not related to FI. River-
39 specific and river-averaged model comparisons indicated that most FI-community
40 relationships did not differ statistically among rivers. Community nestedness along FI
41 gradients was detected in most rivers and there was little or no influence of the spatial
42 arrangement of perennial and temporary reaches. These results indicate that FI is a primary
43 driver of aquatic communities in temporary rivers, regardless of the biogeographic species
44 pool. Community responses are largely due to resilience rather than resistance mechanisms.
45 However, contrary to our expectations, resilience was not strongly influenced by spatial
46 fragmentation patterns, suggesting that colonist sources other than adjacent perennial reaches
47 were important.

48 **Keywords:** climate change, temporary rivers, habitat fragmentation, resistance, resilience,
49 biodiversity, life-history traits

50

51 **Introduction**

52 Identifying general relationships between environmental drivers and community responses is
53 a perennial goal in ecology. Common environment-community relationships are represented
54 by linear or curvilinear relationships that are congruent in direction (increasing or decreasing)
55 and magnitude (slope or inflection) for geographically separated and/or phylogenetically
56 distinct communities. For example, the shapes of relationships between water availability and
57 primary productivity (drivers) and the diversity of bat, amphibian, and bird communities
58 (responses) are remarkably similar over wide biogeographic ranges (Mittelbach et al. 2001,
59 McCain 2007). These observations suggest that some environmental factors are “master
60 variables” with strong direct or indirect effects on most communities in a given taxonomic
61 group or habitat type (Menéndez et al. 2007). Other environmental factors are subsidiary;
62 their effects on community structure are weak or localized. General relationships between
63 environmental drivers and community structure can provide mechanistic explanations for
64 widely observed spatial patterns, including latitudinal and altitudinal gradients in community
65 diversity (McCain 2007), regional beta-diversity patterns (Melo et al. 2009), species-area
66 relationships (Öckinger et al. 2010) and intercontinental community convergence (Lamouroux
67 et al. 2002).

68

69 Although temporary rivers drain all terrestrial biomes and represent the dominant freshwater
70 ecosystems in many areas, they have only recently been considered by ecologists (Larned et
71 al. 2010, Datry et al. 2011, Steward et al. 2012). As a result, the organisation of aquatic
72 communities in these systems has never been analysed across different biogeographic regions.
73 The periodic loss of surface water (hereafter “flow intermittence”) is a fundamental challenge
74 for aquatic organisms and may be a major driver of aquatic community diversity and
75 composition. Alteration of aquatic communities caused by flow intermittence may also have

76 cascading effects on biotic communities in adjacent ecosystems, such as riparian and
77 floodplain areas (McCluney and Sabo 2012) or hyporheic zones (Datry et al. 2007). There are
78 some indications that aquatic invertebrate communities in geographically distant river systems
79 display similar responses to variation in flow intermittence. For example, invertebrate taxon
80 richness in temporary rivers of France, New Zealand and the USA decreased linearly as the
81 severity of flow intermittence increased (Fritz and Dodds 2004, Arscott et al. 2010, Datry
82 2012). Partial and complete overlap in taxonomic composition has also been reported for
83 invertebrate communities from adjacent temporary and perennial reaches (e.g., del Rosario
84 and Resh 2000, Chester and Robson 2011). These observations suggest that intermittence-
85 specialist taxa are rare. However, the previous studies of aquatic invertebrates in temporary
86 rivers have been site- or river-specific and differed in aims and methods, preventing the
87 identification of general community patterns and mechanisms.

88
89 Aquatic communities of temporary rivers persist through disturbances using both resistance
90 and resilience mechanisms (Fritz and Dodds 2004, Bêche et al. 2009). Resistance reflects the
91 capacity of communities to persist unchanged through periods without surface water and
92 involves a range of physiological adaptations allowing organisms to survive within dry
93 riverbed sediments or remnant pools (Lytle and Poff 2004, Williams 2006). For example,
94 species from several invertebrate groups (e.g., oligochetes, copepods, dipterans) can persist
95 for years in dry river sediments as cysts and cocoons, or in a state of diapause as larvae or
96 adults (Williams, 2006). In this way, resistance can be viewed as a form of temporal dispersal
97 (Bohonak and Jenkins 2003). Resilience reflects the ability of communities to return to their
98 pre-drying state soon after flow resumes. Resilience to flow intermittence may be related to
99 aerial or instream dispersal capacity, which governs the rate at which taxa return to a rewetted
100 river channel from aquatic refuges (Stanley et al. 1994, Chester and Robson 2011).

101

102 While the respective roles of resistance and resilience mechanisms in structuring diversity
103 patterns in temporary rivers are currently unclear, a global analysis of diversity patterns across
104 temporary rivers might help disentangle the roles of these mechanisms. If resistance is the
105 principal persistence mechanism for invertebrates in temporary rivers, relationships between
106 flow intermittence and invertebrate taxon richness should be weak or nonexistent (**Fig. 1A**).
107 Additionally, the composition of temporary-reach communities should differ from those in
108 perennial reaches because of a progressive replacement of taxa along flow intermittence
109 gradients, particularly if there is a cost associated with desiccation-resistance adaptations
110 (**Fig. 1B**). In contrast, if resilience is the principal persistence mechanism, the progressive
111 colonization of previously-dry reaches by taxa from nearby aquatic refuges should result in
112 negative relationships between flow intermittence and taxon richness, and these relationships
113 should be congruent across rivers (**Fig. 1A**). In addition, taxa -poor communities at the most
114 temporary reaches should be nested-subsets of taxa -rich communities found at the least
115 temporary and/or perennial reaches (**Fig. 1B**).

116

117 Flow intermittence in river networks can lead to different spatial arrangements of perennial
118 and temporary reaches and thus different patterns of habitat fragmentation (Lake 2003). In
119 many river networks, temporary reaches are concentrated in the upper, middle or lower
120 reaches of rivers (**Fig. 1C**). These large-scale drying patterns can influence the effects of
121 fragmentation on dispersal and create mismatches in the geometries of dispersal and
122 disturbance (drying phase) (Fagan 2002). Downstream transport of materials (via stream
123 flow) is a dominant feature in lotic ecosystems and not all aquatic invertebrate taxa frequently
124 disperse overland (Bohonak and Jenkins 2003). Therefore, the accessibility of refuges for
125 aquatic invertebrates during dry periods, and dispersal pathways from these refuges following

126 rewetting may differ due to the variable spatial arrangements of temporary and perennial
127 reaches (**Fig. 1C**). The overall responses of aquatic organisms to flow intermittence should
128 thus vary with the pattern of habitat fragmentation, particularly if (instream?) dispersal is an
129 overriding mechanism for explaining community persistence in temporary rivers.

130

131 In this study, we investigated the responses of aquatic invertebrate communities to flow
132 intermittence in multiple biogeographic regions. We hypothesized that the persistence of
133 communities in temporary rivers is primarily associated with resilience mechanisms, not
134 resistance mechanisms. Based on the attributes of resilience-structured invertebrate
135 communities described above and in Figure 1, we predicted that invertebrate communities in
136 temporary rivers would be characterized by negative taxon richness-flow intermittence
137 relationships, and by community nestedness along flow intermittence gradients. Given
138 dispersal limitations of many invertebrate taxa, we expected these patterns to vary with the
139 spatial arrangement of temporary reaches within river systems. To test our predictions, we
140 used data from 128 sites in 14 temporary rivers across Europe, North America, and New
141 Zealand. The datasets encompassed a wide range of flow intermittence and spatial
142 arrangements of perennial and temporary reaches.

143

144 **Method**

145 **Data sets**

146 We compiled datasets from aquatic invertebrate studies of 14 temporary rivers in Europe
147 (seven rivers), North America (five rivers), and New Zealand (two rivers). The datasets
148 consisted of matrices of invertebrate taxa, abundances and sampling dates at multiple sites
149 within temporary and perennial river reaches. The average number of days between two
150 consecutive sampling events on a given site was 146.5 ± 74.5 d (SD?), and the average

151 distance between sites was 3.1 ± 2.6 km. At each site, invertebrates were collected from riffle
152 habitats using standardized and comparable sampling methods (Surber, Hess, and kick-net
153 samplers with mesh sizes ranging from 250 to 500 μm) from at least three sites per river
154 (**Table 1**). The datasets were classified by the spatial arrangement of perennial and temporary
155 reaches (upper, middle and lower reach drying, **Table 1**). For further information on the
156 individual studies, see the references in Table 1, and details about methods and sites in
157 **Appendix S1**.

158

159 **Quantification of flow intermittence**

160 For each data set, annual flow intermittence (FI), the proportion of the year with zero-flow,
161 was calculated for each sampling site. One of three procedures outlined below was used to
162 calculate FI values for the sampling sites in each river, reflecting the type of flow
163 measurement and quantity of discharge data available in each study. River discharge was
164 standardized to L s^{-1} .

165

166 *Hydrological modelling*. For five datasets (Albarine, Asse, Little Stour, Orari, Selwyn), mean
167 daily flow (including zero-flow) at sampling sites were estimated using the statistical model
168 ELFMOD (Larned et al. 2011). For each river, the input data consisted of manual
169 measurements of discharge at sampling sites on \geq nine dates, and continuous discharge from
170 at least two permanent recorders that bounded the study reaches. The discharge time-series
171 from each recorder was \geq 10 years long, and included the study period during which
172 invertebrate samples were collected. Modelled mean daily discharge was used to calculate FI
173 for each site each year.

174

175 *Direct measurement.* For four datasets (Garden, Huachuca, Little Lusk, Sycamore), water-
176 state loggers were used to record the presence or absence of water during the invertebrate
177 sampling period (Fritz et al. 2006, Jaeger and Olden 2012). FI was calculated for each
178 sampling site from the logged time-series. Estimates of FI based on ELMOD and water-state
179 loggers at sampling sites along the Albarine River were highly correlated ($r = 0.93$, $P <$
180 0.001 , $n = 9$).

181

182 *Direct observations.* For five datasets (Alme, Ellerbach, Fish Brook, Menne, Sauer) FI was
183 estimated at sampling sites using weekly to bi-monthly observations of flow state (flowing or
184 completely dry) for three to 12 months. Point gauging data and discharge data from adjacent
185 gauging stations were then used to assess flow-state patterns between consecutive
186 observations (Meyer et al. 2003).

187

188 **Invertebrate variables**

189 For each sample in the invertebrate datasets, taxon richness (TR) was calculated as the
190 number of taxa per sample. To account for differences in taxonomic resolution among
191 datasets, TR was calculated at three levels of resolution: fine (TR1), medium (TR2), and
192 coarse (TR3). The degree of taxonomic consistency among datasets increases and taxonomic
193 precision decreases from TR1 to TR3. The taxonomic groups used at each level of resolution
194 are shown in **Table 2**.

195

196 To describe the communities in each dataset in terms of taxonomic composition and life-
197 history traits, the relative abundances of Coleoptera, Diptera, Oligochaeta, and the sum of
198 Ephemeroptera, Plecoptera and Trichoptera (hereafter 'EPT') were calculated in each sample.
199 In addition, each taxon in each dataset was classified into one of four classes using life-history

200 and biological traits: *resistant*, *resilient*, both *resistant* and *resilient*, or neither *resistant* nor
201 *resilient*. Trait classification was undertaken at the coarsest taxonomic level (TR3) to
202 maximize consistency across datasets although this reduced our ability to detect fine-scale
203 patterns. We assigned the following traits to the *resilient* class: long adult lifespan, high
204 female dispersal, strong adult flying ability, common occurrence in drift, and strong
205 swimming ability. We assigned the following traits to the *resistant* class: presence of
206 desiccation-resistance forms (e.g., cysts, cocoons, diapause stages), body armouring limiting
207 water loss (including the use of external cases), plastron/spiracle respiration, and low
208 rheophily. We used published (Tachet et al., 2002, Poff et al. 2006, Bonada and Doledec
209 2011) and unpublished (V. Archaimbault, *personal communication*) trait information to
210 classify each taxon (**Appendix S2**). Given the coarse taxonomic resolution used (TR 3), we
211 assigned to each taxon the traits which were dominant across the constituent families, genera
212 or species. When the traits assigned to a taxon were from the *resistant* class exclusively, it
213 was classified as *resistant* (n = 37 taxa). Conversely, when the traits assigned to a taxon were
214 from the *resilient* class exclusively, it was classified as *resilient* (n = 37 taxa). When the traits
215 assigned to a taxon were from both the *resistant* and *resilient* classes, it was classified as
216 *resistant* and *resilient* (n = 26 taxa). Last, when no traits from the *resistant* or *resilient* classes
217 were assigned to a taxon, it was classified as neither *resistant* nor *resilient* (n = 25 taxa). For
218 12 out of 125 taxa, there was no information available regarding resistance and resilience
219 traits, and classification was based on closely related taxa for which there was some
220 information and authors' knowledge.

221

222 **Statistical analyses**

223 The invertebrate community variables described above were used as dependant variables in
224 linear mixed-effects models with Gaussian error distributions. Analyses were undertaken

225 using the lme4 package for R (R Development Core Team 2008). For each dependent
226 variable, we tested for effects of FI and then tested if these effects differed between rivers and
227 spatial drying patterns. We compared three nested mixed-effects models that progressively
228 increased in complexity. The first model (null) was a null model with a random intercept. The
229 second model (average) was an average model with a fixed effect of FI across all rivers. The
230 third model (river-specific) was a model with a random effect of FI, which was allowed to
231 vary among rivers (Bolker et al. 2009). River was entered as a random effect in each model.
232 When slopes differed among rivers, we fitted additional models adding longitudinal drying
233 pattern as a fixed effect to test for possible systematic effects of the spatial arrangement of
234 perennial and temporary reaches. The statistical significance levels for the fixed and random
235 effects in the best-fitting models were determined using likelihood-ratio tests on models with
236 and without each effect (Bolker et al. 2009). To select the most parsimonious models, we used
237 the minimum Akaike's Information Criterion (AIC). We checked for normality and
238 homogeneity by visual inspections of plots of residuals against fitted values. When average
239 models were selected, we used individual linear regressions to analyse how much individual
240 rivers contributed to the average model.

241

242 Nestedness analyses were used to determine whether invertebrate communities at the most
243 temporary sites were nested subsets of communities found at the least temporary and
244 perennial sites. Such patterns would indicate a selective loss of taxa susceptible to drying
245 rather than a replacement of perennial-flow specialists with intermittent-flow specialists along
246 flow intermittence gradients. We tested for community nestedness of both taxa incidence and
247 composition along the flow intermittence gradient at each river and at each taxonomic level
248 (TR1, 2 and 3) using the Brualdi and Sanderson discrepancy index, which provides a
249 conservative test for nestedness (Ulrich and Gotelli 2007). The significance of nestedness was

250 then tested against constrained null models (showing the same marginal totals as the original
251 data) using the “quasiswap” method (Miklós and Podani 2004).

252

253 **Results**

254 **Taxon richness and flow intermittence**

255 Taxon richness decreased for all taxonomic resolutions with increasing FI (Likelihood ratio
256 tests between null and average models, $\chi^2 = 232.59, 248.33, \text{ and } 179.78$ for TR1, TR2 and
257 TR3, respectively; $P < 0.001$; **Fig. 2**). The slopes of the taxon richness-FI relationships did
258 not differ statistically among rivers as indicated by the comparisons between average and
259 river-specific models ($\chi^2 = 1.08, 1.07, \text{ and } 1.76$; $P = 0.582, 0.586 \text{ and } 0.414$, for TR1, TR2
260 and TR3, respectively, **Fig. 2**). On average, a 10% increase in FI resulted in the loss of two
261 taxa at the fine taxonomic level (TR1: *slope* = -0.20, 95% *CI*: -[0.22 : 0.18]), one and a half
262 taxa at the medium taxonomic level (TR2: *slope* = -0.16, 95% *CI*: -[0.18 : 0.15]), and one
263 taxon at the coarse taxonomic level (TR3: *slope* = -0.12, 95% *CI*: -[0.13 : 0.10]) (**Fig. 2**).

264

265 **Resistance and resilience traits, community composition and flow intermittence**

266 The significant negative relationships between FI and taxon richness were maintained when
267 *resilient* taxa and those without *resistant* nor *resilient* traits were considered separately
268 (Likelihood ratio tests between null and average models, $\chi^2 = 125.93 \text{ and } 136.03$,
269 respectively; $P < 0.001$), but were not significant for *resistant* taxa or those with both
270 *resistant* and *resilient* traits ($\chi^2 = 13.61 \text{ and } 4.77$, $P = 0.1611 \text{ and } 0.8622$, respectively). For
271 *resilient* taxa and those without *resistant* nor *resilient* traits, the slopes of the taxon richness-
272 FI relationships differed statistically among rivers as indicated by the comparisons between
273 average and river-specific models ($\chi^2 = 15.09, \text{ and } 41.61$, respectively ; $P < 0.001$). However,
274 these relationships did not differ with respect to the spatial arrangement of perennial and

275 temporary reaches (Likelihood ratio test, $\chi^2 = 1.87$ and 3.11 ; $P = 0.7596$ and 0.5384 ,
276 respectively).

277

278 The relative abundances of EPT and Coleoptera decreased, and the relative abundance of
279 Diptera increased among rivers as FI increased (Likelihood ratio tests between null and
280 average models, $\chi^2 = 72.89$, 19.26 , and 73.44 , respectively; $P < 0.001$, **Fig. 3 and 4**). The
281 slopes of these relationships did not differ statistically among rivers (Likelihood ratio tests
282 between average and river-specific models, $\chi^2 = 0.27$, 5.19 , and 6.46 ; $P = 0.871$, 0.078 , and
283 0.065 , respectively, **Fig. 3 and 4**). On average, for every 10% increase of FI, there was a 4%
284 reduction in the relative abundance of EPT taxa (*slope* = -0.37 , 95% *CI*: $-[0.45 : 0.28]$), a
285 0.5% reduction in the relative abundance of Coleoptera (*slope* = -0.06 , 95% *CI*: $-[0.09 : 0.04]$)
286 and a 4% increase in the relative abundance of Diptera (*slope* = 0.38 , 95% *CI*: $[0.30 : 0.47]$).
287 There were no detectable relationships between the relative abundance of Oligochaeta and FI
288 (Likelihood ratio tests between null and average models, $\chi^2 = 4.79$; $P = 0.092$).

289

290 **Community nestedness along flow intermittence gradients**

291 At the fine taxonomic level, invertebrate communities at the most temporary sites were nested
292 subsets of communities at the least temporary and perennial sites in 10 of the 14 rivers (**Table**
293 **3**). At medium and coarse levels of taxonomic resolution, nestedness tended to occur
294 primarily in rivers with downstream drying patterns (**Table 3**).

295

296 **Discussion**

297 We demonstrated general and significant effects of FI on invertebrate taxon richness across 14
298 rivers in Europe, North America and New Zealand. As FI increased, invertebrate communities
299 in these rivers became increasingly taxa-poor. More importantly, the rate of decline in the

300 number of taxa along gradients of FI was not statistically different among the 14 rivers tested
301 for each of the three different levels of taxonomic resolution, despite these rivers representing
302 a wide range of climatic and biogeographic conditions and differing markedly in size and
303 spatial drying patterns. Therefore, our results demonstrate a wide-spread congruence in the
304 responses of invertebrates to FI and suggest that FI is a “master variable” driving river
305 community structure and composition. Given the increasing intensity and spatial extent of FI
306 in rivers due to anthropogenic water abstraction and climate change (Meybeck 2003, Larned
307 et al. 2010), our findings indicate the potential for widespread declines in river biodiversity
308 resulting from increased flow intermittence.

309

310 Our analysis of diversity patterns helps to disentangle the respective roles of resistance and
311 resilience mechanisms in structuring invertebrate communities in temporary rivers. There are
312 three ways in which our results suggest that, as we hypothesized, invertebrate community
313 patterns along FI gradients are primarily a function of resilience rather than resistance. First,
314 the relationships between taxon richness and FI held across rivers for *resilient* taxa and for
315 taxa without *resistant* nor *resilient* traits, when coded at the family level. In contrast, no
316 relationships were detected between FI and *resistant* taxa or taxa with both *resistant* and
317 *resilient* traits. Second, the relative abundances of groups such as EPT and Coleoptera
318 decreased with FI; many species in these groups are susceptible to desiccation (Williams
319 2006, Datry et al. 2012) and have *resilient* traits that facilitate recolonization, such as long
320 life-span or strong flying abilities (Petersen et al. 1999, Bohonak and Jenkins 2003). In
321 contrast, the relative abundance of dipteran taxa increased with FI, and desiccation-resistant
322 traits such as diapause and anhydrobiosis are prevalent among many dipteran families (Frouz
323 et al. 2003). Desiccation-resistant traits are not likely to be uniform across the Diptera as a
324 group, however, and do not constrain their persistence in perennial habitats. Many dipterans

325 thrive in perennial sites, and their relative abundances were on average > 25% in our 14 study
326 rivers. Third, a significant level of community nestedness occurred along most of the FI
327 gradients in this study, which indicates that taxa-poor communities in the most temporary
328 sites were nested-subsets of taxa-rich communities in the least temporary and perennial sites.
329 Community nestedness was probably the result of both limited dispersal from source
330 communities in perennial reaches and local extinction along FI gradients (McAbendroth et al.
331 2005). This suggests that the distribution of aquatic refuges across river landscapes, combined
332 with taxa-specific differences in dispersal abilities may explain much of the colonization and
333 succession dynamics in temporary rivers.

334

335 Although dispersal appears to be an overriding mechanism for explaining community
336 persistence in temporary rivers, there was very little evidence that the pattern of habitat
337 fragmentation (i.e., different spatial arrangements of perennial and temporary reaches) had a
338 strong influence on the responses of invertebrate communities to FI. The FI-taxonomic
339 richness relationships did not vary among spatial arrangements of perennial and temporary
340 reaches. Community nestedness at the coarsest taxonomic level was restricted to rivers with
341 downstream drying patterns. While this partly supports our initial prediction, it also indicates
342 that confounding factors may obscure the effect of spatial fragmentation patterns on aquatic
343 invertebrate communities. It is likely that the magnitude and dynamics of drying and
344 rewetting alter the effects of spatial drying patterns on the responses of invertebrate
345 communities to FI. Complete riverbed drying can occur within a few hours, or disconnected
346 pools can persist for several weeks in otherwise dry riverbeds. Rewetting may be gradual
347 (e.g., expanding pools driven by groundwater upwelling) or rapid (e.g., flash-flood bores
348 driven by runoff). These variable transitions between wet and dry periods are likely to
349 influence the ability of invertebrates to disperse to and from refuges (Bogan et al. 2013). Last,

350 refuges adjacent to (parafluvial ponds, lakes, springs) and beneath (hyporheic zone) river
351 channels were not included in this study, and could play significant roles in maintaining
352 communities in temporary rivers (Boulton et al. 1998, Williams 2006).

353

354 Invertebrate communities in reaches with the highest FI were consistently dominated by
355 generalist and ubiquitous taxa, rather than by temporary-habitat specialists. Even in the three
356 rivers where chironomids (Huachuca and Garden) or coleopterans (Little Stour) were
357 identified to the species level, there was still little evidence of temporary-specialist taxa.
358 Because rivers with natural flow regimes are characterized by large variations in discharge,
359 including drought periods (Lake 2003, Lytle and Poff 2004), drying may not be an
360 evolutionary force restricted to temporary rivers as previously thought (c.f., Williams 2006,
361 Steward et al. 2012). The absence of apparent temporary-specialist taxa in these rivers
362 contrasts with community patterns in temporary lentic habitats, such as ponds or wetlands,
363 where taxa replacements along decreasing hydroperiod gradients from perennial to
364 temporary-specialists are common (e.g., Wellborn et al. 1996). Such patterns are thought to be
365 driven by trade-offs between traits that facilitate survival in temporary environments (e.g.,
366 dormancy stages, desiccation-resistant eggs) and traits that reduce vulnerability to predators
367 (e.g., low activity rates, antipredator morphology) (Skelly 1995, Wellborn et al. 1996). Top
368 aquatic predators (invertebrates, fish) often occur in temporary river reaches (Labbe and
369 Faush 2000), and perhaps such trade-offs do not occur along FI gradients in rivers. However,
370 biotic interactions, including competition and predation, have not been as thoroughly
371 examined in temporary rivers compared to temporary lentic habitats (e.g., Skelly 1995,
372 Wellborn et al. 1996, Spencer et al. 1999), and empirical data to support this hypothesis are
373 currently lacking. If FI increases in extent and severity in the future, we anticipate an
374 increased biotic homogenization of riverine communities, which will in turn modify the

375 functioning and resilience of river ecosystems (McKinney and Lockwood 1999, Spencer et al.
376 1999).

377

378 We demonstrated that invertebrate communities have congruent responses to FI gradients
379 across a range of river sizes in multiple biogeographic regions, and that the spatial
380 arrangement of perennial and temporary reaches had very little influence on these responses.
381 This suggests that FI is a primary driver of aquatic communities in temporary rivers around
382 the world. Resilience explained invertebrate diversity patterns along FI gradients to a greater
383 degree than resistance. However, invertebrate colonization following the resumption of flow
384 remains a poorly-known process and many questions remain (Chester and Robson 2011). For
385 instance, we do not know to what degree successional patterns are predictable, and what
386 abiotic (e.g., distances to refuges, distribution of refuges across landscapes) or biotic drivers
387 (e.g., predation, competition) control succession. Metacommunity and metapopulation
388 dynamics deserve more attention in temporary rivers and more manipulative experiments are
389 needed to improve our understanding of their effects on diversity patterns. In the context of a
390 worldwide biodiversity crisis, whose severity in freshwater ecosystems has been carefully
391 documented (Dudgeon et al. 2006), the general relationships generated in this study may help
392 water managers mitigate the effects of dams, flow diversion, and water abstraction, and will
393 help scientists predict future changes in river biodiversity.

394

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417

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533 **Supplementary Material**

534

535 Additional Supporting Information may be found in the online version of this article:

536 **Appendix S1** {Characteristics of individual studies}

537 **Appendix S2** {List of life-history traits coded to assign each taxon to the following class: 0;

538 neither *resistant* nor *resilient*, 1:*resilient*, 2:*resistant* and 3: *resilient* and *resistant*}

539

540 **Table 1.** Description of the 14 temporary rivers. More details are available on Appendix 1. Unpub.: unpublished data.

Country	State/Region	River names	Climate type	Catchment area (km ²)	Spatial drying pattern	FI range (%)	Sampling method	Duration (yr)	No. dates	No. sites	Sample size	References
France	Provence	Asse	Mediterranean	657	Middle	0-20	Hess	3	5	13	49	unpub.
France	Rhône-Alpes	Albarine	Temperate	313	Lower	0-90	Hess	3	5	18	76	Datry 2012
Germany	East Westphalia	Alme	Temperate	763	Middle	0-35	Kick-net	3	3	7	21	unpub
Germany	East Westphalia	Ellerbach	Temperate	91	Lower	0-77	Surber	1	4	3	12	unpub.
Germany	East Westphalia	Menne	Temperate	8	Lower	0-40	Surber	1	2	3	6	Meyer et al. 2003
Germany	East Westphalia	Sauer	Temperate	109	Lower	0-60	Kick-net	5	2 to 4	14	36	unpub
New Zealand	Canterbury	Orari	Temperate	850	Middle	0-80	Hess	2	2	11	22	unpub.
New Zealand	Canterbury	Selwyn	Temperate	975	Middle	0-92	Hess	5	2 to 10	16	73	Arscott et al. 2010
UK	Kent	Little Stour	Temperate	213	Middle	0-20	Kick-net	9	8	9	72	Wood and Armitage 2004
US	Massachusetts	Fish	Temperate	47	Upper	0-30	Surber	2	3	8	24	Santos and Stevenson 2011
US	Arizona	Garden	Arid	34	Lower	0-95	Kick-net	1	1	9	9	Bogan et al. 2013.
US	Arizona	Huachuca	Arid	25	Lower	0-90	Kick-net	1	1	9	9	Bogan et al. 2013.
US	Illinois	Little Lusk	Temperate	43	Upper	0-82	Hess	2	2	4	7	unpub.
US	Indiana	Sycamore Branch	Temperate	3	Upper	0-65	Hess	2	2	4	7	unpub.

541 **Table 2. Number of taxa (No.) and corresponding proportion (%) across species, genera,**
542 **families and other taxonomic units for the different levels of taxonomic resolution used**
543 **in the study (TR1, 2 and 3). The taxonomic resolution for each group of taxa is also**
544 **detailed.** Ph: phylum, c: class, sc: sub-class, f: family, sf: sub-family, g: genus, s: species.
545 EPT: Ephemeroptera, Plecoptera and Trichoptera.
546

	TR1		TR2		TR3	
	No.	%	No.	%	No.	%
Species	249	43	0	0	0	0
Genera	234	40	256	72	0	0
Families	85	15	85	24	118	94
Others	17	3	17	5	7	6
Total	585	100	358	100	125	100

Taxonomic
resolution

Plecoptera	f, g, s	f, g	f
Trichoptera	f, g, s	f, g	f
Ephemeroptera	f, g, s	f, g	f
Coleoptera	f, g, s	f, g	f
Diptera	f, sf, g, s	f, sf, g	f
Odonata	f, g, s	f, g	f
Megaloptera	f, g, s	f, g	f
Hemiptera	f, g, s	f, g	f
Heteroptera	f, g, s	f, g	f
Amphipoda	f, g, s	f, g	f
Decapoda	f, g, s	f, g	f
Isopoda	f, g, s	f, g	f
Copepoda	sc	sc	sc
Ostracoda	c	c	c
Cladocera	o	o	o
Mollusca	f, g, s	f, g	f
Oligochaeta	sc, f, s	sc, f	sc
Hirudinae	sc, f	sc, f	sc
Platyhelminth	ph, f	ph, f	ph, f
Nemathelminthes	ph	ph	ph
Nematomopha	ph, f	ph, f	ph, f
Acari	sc	sc	sc
Hydrozoa	c	c	c

547 *Chironomidae subfamilies (Diamesinae, Orthocladinae, Podonominae, and Tanypodinae)
548 and tribes (Chironomini and Tanytarsini) were used across TR1, TR2, and TR3

549 **Table 3.** Community nestedness for different taxonomic levels (TR1, 2 and 3, see table 2). Values shown are the discrepancy indexes and the
 550 associated p-values from testing indexes against constrained null models. Italics indicate significant p-values.

551

Taxonomic level	Upper reach drying			Middle reach drying					Lower reach drying					
	Fish Brook	Sycamore Branch	Little Lusk	Asse	Orari	Selwyn	Little Stour	Alme	Albarine	Huachuca	Garden	Ellerbach	Menne	Sauer
TR1	53 ; <i>0.01</i>	30 ; 0.21	24 ; <i>0.03</i>	29 ; 0.55	81 ; <i>0.01</i>	123 ; <i>0.01</i>	75 ; 0.15	93 ; <i>0.01</i>	73 ; <i>0.01</i>	7 ; <i>0.01</i>	8 ; <i>0.01</i>	75 ; <i>0.01</i>	18 ; 0.49	257 ; <i>0.01</i>
TR2	39 ; <i>0.07</i>	28 ; 0.13	28 ; <i>0.05</i>	29 ; 0.51	54 ; <i>0.01</i>	69 ; 0.09	51 ; 0.45	75 ; <i>0.01</i>	60 ; <i>0.01</i>	3 ; <i>0.01</i>	3 ; <i>0.01</i>	57 ; <i>0.01</i>	16 ; 0.59	217 ; <i>0.01</i>
TR3	49 ; 0.98	17 ; 0.33	22 ; 0.49	24 ; 0.35	38 ; 0.23	45 ; 0.39	42 ; 0.31	57 ; <i>0.01</i>	87 ; <i>0.01</i>	1 ; <i>0.01</i>	1 ; <i>0.01</i>	33 ; <i>0.01</i>	10 ; 0.37	147 ; <i>0.01</i>

552

553 **Figure caption**

554 **Figure 1.** Conceptual diagrams for temporary rivers. A: predicted invertebrate taxon richness
555 patterns along flow intermittence gradients. B: predicted changes in invertebrate community
556 composition along flow intermittence gradients. C: spatial drying patterns in river networks
557 (after Lake, 2003). In B, greyscale boxes represent taxa present at different points along a
558 flow intermittence gradient. Communities structured by resilience are completely nested,
559 because taxa-poor communities at the most temporary reaches are subsets of taxa-rich
560 communities from the least temporary and perennial reaches. Communities structured by
561 resistance are only partially nested and have high rates of taxa replacement by temporary-flow
562 specialists along the flow intermittence gradient. In C, solid and dashed lines represent
563 perennial and temporary reaches, respectively.

564

565 **Figure 2.** Average mixed-effects models for the 14 data sets of TR1 (white circles, dotted
566 lines), TR2 (grey circles, plain gray line) and TR3 (black circles, plain black line) and FI as a
567 fixed slope, showing a congruent decrease in the number of taxa with increasing FI,
568 regardless of the taxonomic resolution. Linear regressions performed on each dataset
569 individually indicated significant relationships between taxon richness and FI in 11, 10 and 9
570 rivers out of 14, when considering TR1, 2 and 3, respectively.

571

572 **Figure 3.** Average (black) and river-specific (grey) mixed-effects models for the 14 data sets
573 of the relative abundance of EPT (Ephemeroptera, Plecoptera and Trichoptera) taxa in
574 communities and FI. Linear regressions performed on each dataset individually indicated
575 significant relationships in 6 rivers out of 14.

576

577 **Figure 4.** Average (black) and river-specific (grey) mixed-effects models for the 14 data sets
578 of the relative abundance of Diptera in communities and FI Linear regressions performed on
579 each dataset individually indicated significant relationships in 8 rivers out of 14.

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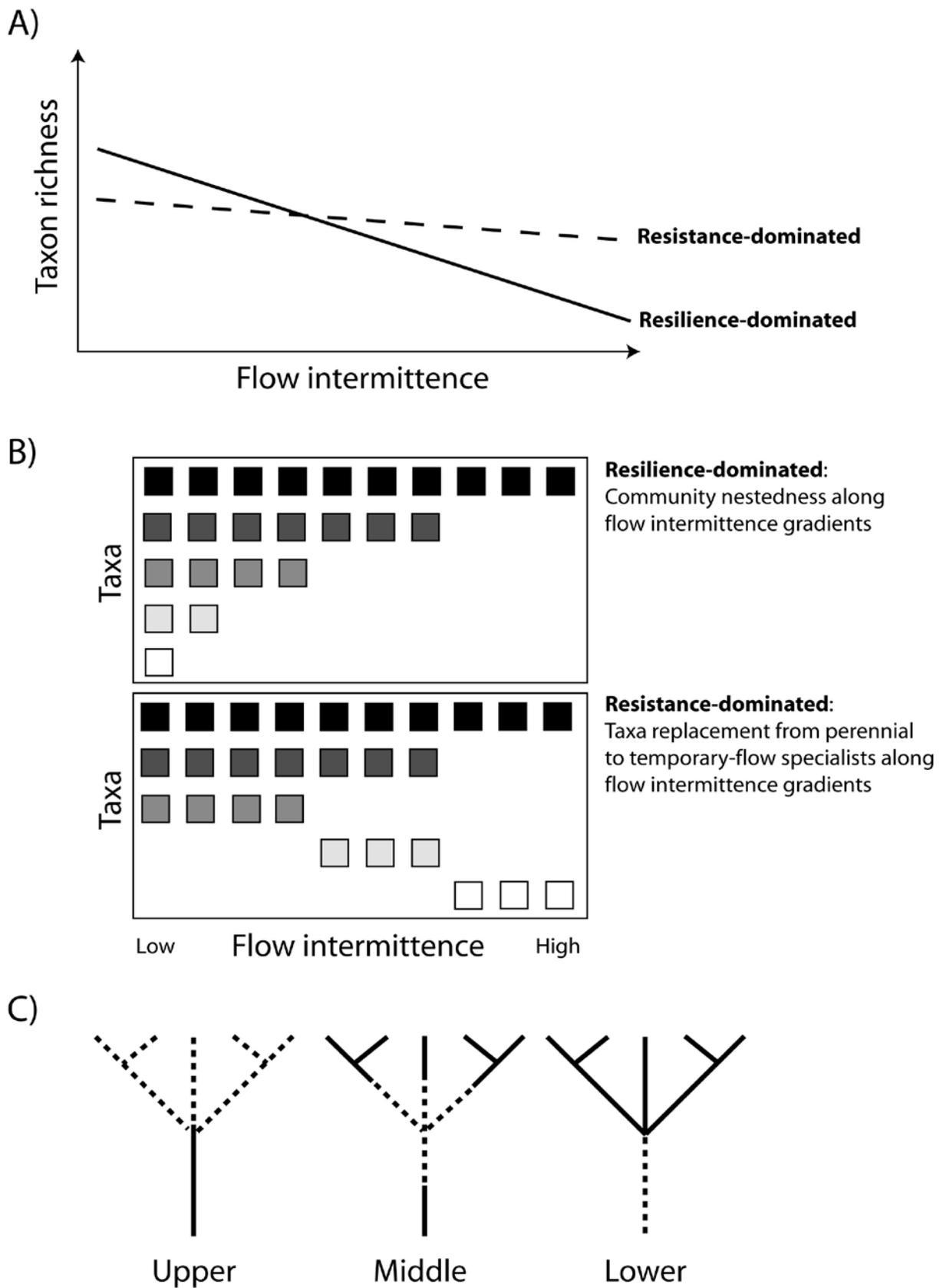
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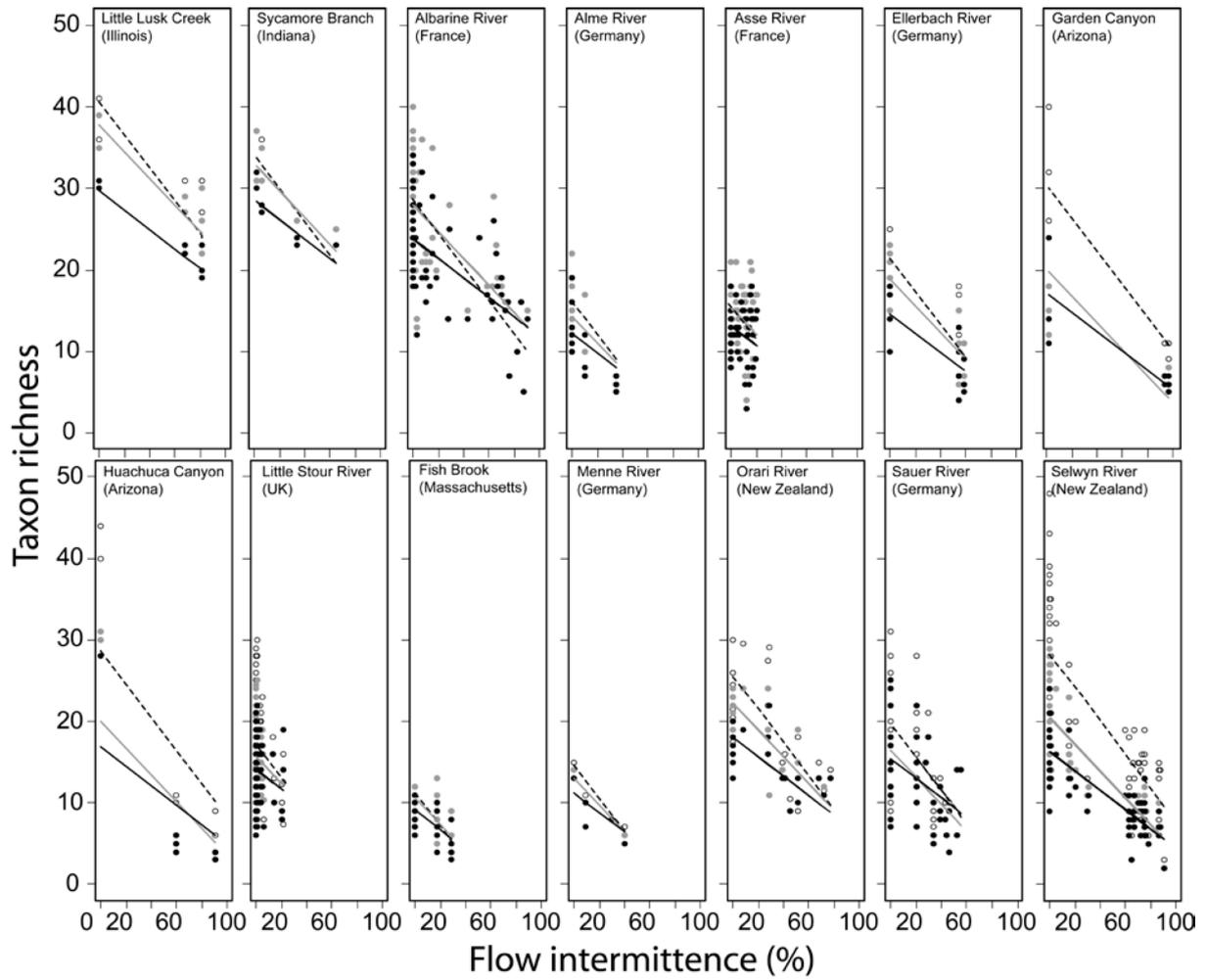
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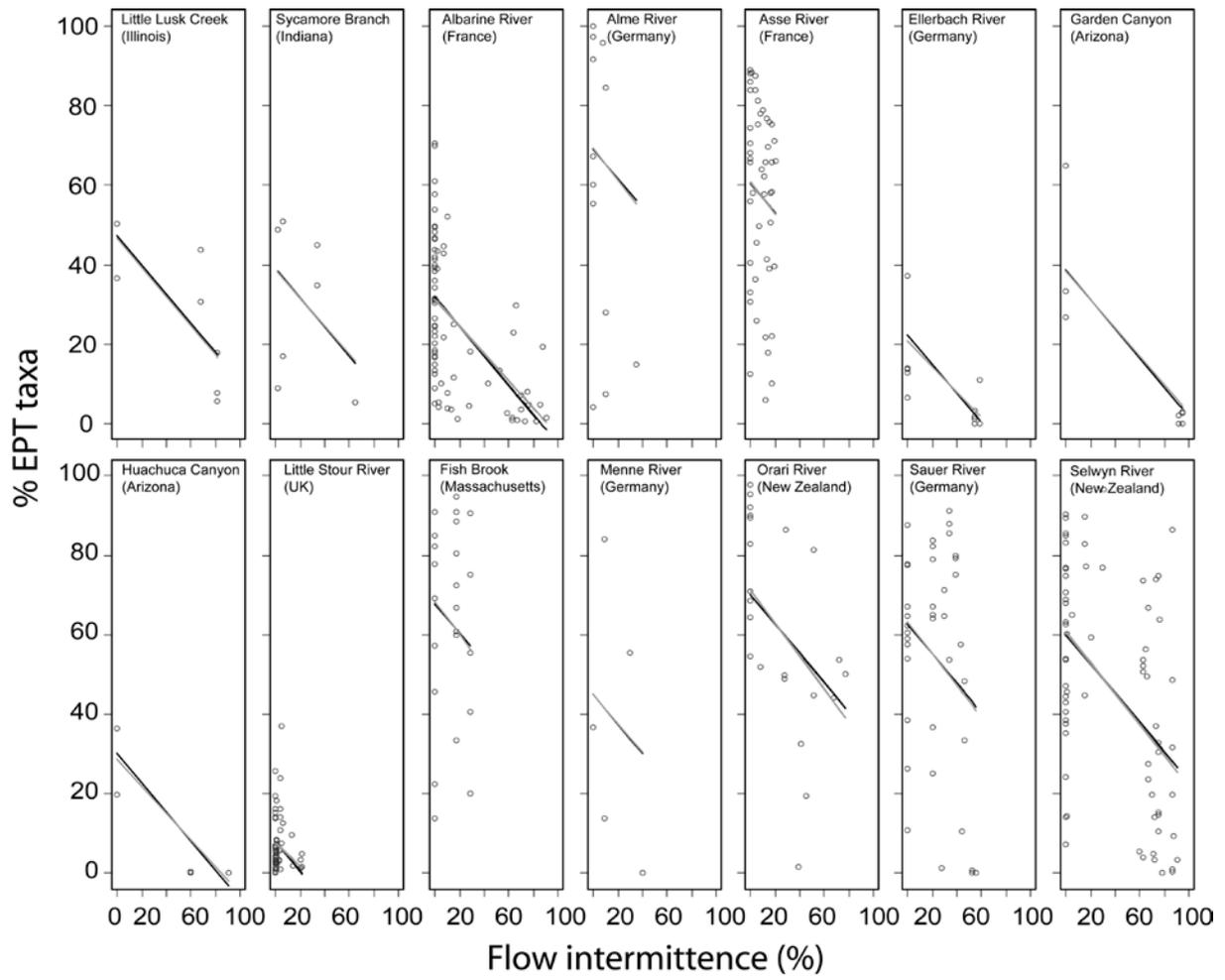
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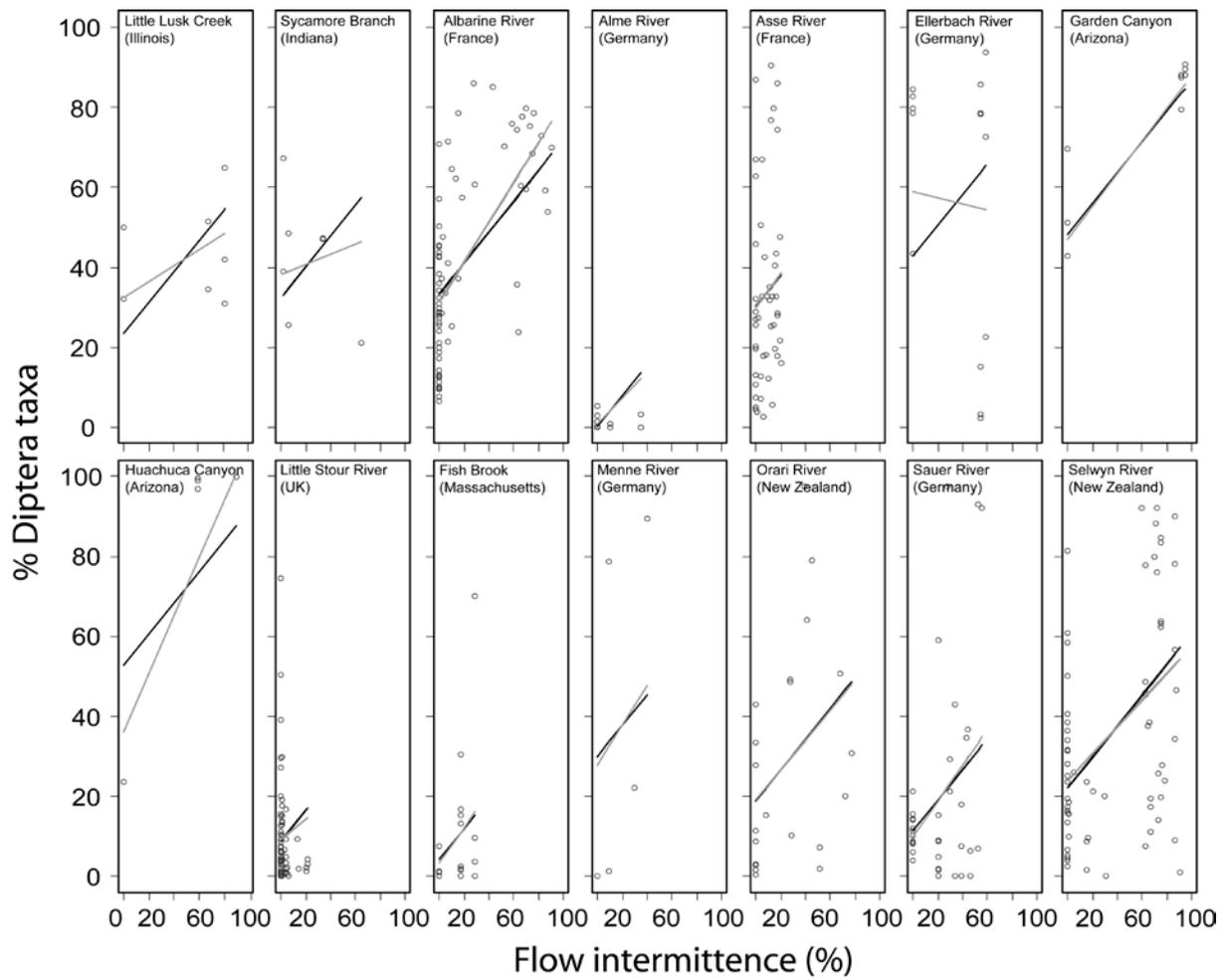
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632 Figure 4.

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Appendix S1: characteristics of individual studies.

Little Stour, United Kingdom

Physical setting

The Little Stour River is located in south-east England and drains a 213-km² catchment in permeable chalk terrain. The river flows 11.5 km from a perennial spring head to its confluence with the Great Stour River; sampling sites were located in the upper 2.5 km of the Little Stour. The chalk bedrock is overlain by alluvium in the mid-reaches of the river and there are high seepage losses into the porous alluvium during baseflow periods. The Little Stour flows along its entire length during most years; flow cessation has occurred on three occasions in the last century, in 1949, 1991-1992 and 1996-1997. Severe droughts in those years, in combination with groundwater abstraction for public water supplies, caused a 750 m reach to dry, 2 km downstream of the spring head. Flow and invertebrate data from the 1991-1992 and 1996-1997 droughts are included in this study. During both droughts, the 750 m-long temporary reach was dry for up to 15 months. Flow resumption occurred rapidly at the end of the droughts in the early winters of 1992 and 1997, although recovery of groundwater levels and surface flows to normal conditions took two years (Wood & Armitage 2004).

Invertebrate sampling

Invertebrates were collected from nine riffle-run habitats at nine sites (three temporary, six perennial) on the upper 2.5 km of the river during baseflow periods between 27 August and 3 September in each of nine years (1992-1999). Samples could not be collected from two dry sites in 1992 and 1997. Samples were collected using two-minute kick-samples with a hand-net (250- μ m mesh net). Samples were preserved in the field with 4% formaldehyde. Most aquatic insects were identified to species except dipterans, which were identified to family, and baetid mayflies, which were identified to genus. Molluscs were identified to species

except sphaeriid bivalves, which were identified to family. Oligochaetes and mites were identified to order. For more details on invertebrate sampling and processing, see Wood & Armitage (2004).

Albarine, France

Physical setting

The Albarine River is located in temperate eastern France and drains a 313-km² catchment. The river flows for 45 km through the Jura Mountains, then 15 km across an alluvial plain to its confluence with the Ain River. On the alluvial plain the river is perched 1-14 m above the regional water table, and the river loses flow to the underlying vadose zone and aquifer at an average rate of 0.4 m³ s⁻¹ km⁻¹. The entire alluvial plain reach is temporary due to the rapid seepage loss. Descriptions of the climate, geology and geomorphology of the Albarine River catchment are given in Datry (2012). Flow cessation begins in spring of most years at the confluence with the Ain River, and the drying front moves upstream over the summer. Flow resumption along the entire temporary reach generally occurs in late autumn/early winter. Flow intermittence and average annual dry event duration and frequency all increase with distance downstream. At the downstream end of the temporary reach, annual flow intermittence ranges from 50 to 90%.

Invertebrate sampling

Invertebrates were collected from riffles at 18 sites (seven perennial, 11 temporary) prior to flow cessation in spring (30 March 2009 and 27 May 2010) and autumn, ≥ 3 weeks after flow resumption (15 October 2008, 1 December 2010 and 12 October 2010). In October 2008, the five sites furthest downstream were not sampled because they dried two weeks after flow resumption. At each site and each sampling date, two invertebrate samples were collected at

each of two riffles and composited. Invertebrates were collected with a Hess sampler (0.125-m² area, 200- μ m mesh), and preserved with 96% ethanol. Most aquatic insects and all molluscs were identified to genus or species, and crustaceans, annelids and mites to genus, family or order. For more details on invertebrate sampling and processing, see Datry (2012).

Asse, France

Physical setting

The Asse River is located in the Provence region of southeastern France, and drains a 657-km² catchment in the southwestern French Alps. The main tributaries of the Asse River rise in the Préalpes de Digne, then converge 45 km downstream to form the Asse River mainstem, which flows for 30 km across an alluvial plain to its confluence with the Durance River. On the alluvial plain, the upper 15 km-long reach is perennial and the lower 15 km-long reach is temporary. Flow intermittence is caused by the combined effects of seepage into the underlying aquifer, high groundwater abstraction in the floodplain for agriculture, and bed aggradation. Along the temporary section, drying events occurred at two 4 km-long reaches spaced 7 km apart. Descriptions of the climate, geology and geomorphology of the Asse River catchment are given in Mano *et al.* (2009).

Invertebrate sampling

Invertebrates were collected from riffles at 13 sites (eight temporary, five perennial). Samples were collected in spring, just before the beginning of summer dry events (15 April March 2009 and 8 June 2010), and in autumn, at least 3 weeks after flow resumption (2 October 2008, 10 November 2010 and 19 October 2010). On each sampling date, two invertebrate samples were collected at each of two riffles per site, and the duplicate samples were composited. Invertebrates were collected using a Hess sampler (0.125-m² area, 200- μ m

mesh), and preserved with 96% ethanol. Most aquatic insects and all molluscs were identified to genus or species, and crustaceans, annelids and mites to family, order or genus.

Sycamore Branch, USA

Physical setting

Sycamore Branch drains a forested 3.1-km² catchment in the Charles C. Deam Wilderness Area of the Hoosier National Forest, south-central Indiana, USA. The stream flows for 3.4 km from its headwaters to the South Fork Arm of the Monroe Lake reservoir. The upper 2 km of Sycamore Branch have alternating perennial and temporary reaches, and the lower 1.4 km is perennial. Flow is primarily derived from overland flow, and secondarily from soil water and hillslope groundwater seepage. Drying occurs when soil water is depleted and the groundwater table falls below the streambed elevation. Flow intermittence generally decreases in the downstream direction. The uppermost study reach had the greatest flow intermittence (65%). Descriptions of the climate, geology, and vegetation of the area given in Homoya *et al.* (1984) and Thompson (2004).

Invertebrate sampling

Four 30-m long sampling reaches (two perennial, two temporary) were established along the upper 1.9 km of Sycamore Branch. Invertebrates were collected from riffles and pools in each reach. Samples were collected during wet (25 June 2003 and 7 April 2004) and dry periods (22 September 2003 and 11 August 2004) when surface water was present in each sampling reach. At each reach, four replicate samples from each habitat type were collected with a modified Hess sampler (0.053-m² area, 250- μ m mesh) and preserved in 70% ethanol. Invertebrates were identified to genus or species. For more details on invertebrate sampling and processing, see Fritz *et al.* (2006).

Little Lusk, USA

Physical setting

Little Lusk Creek drains a 43.2-km² catchment in Shawnee National Forest, southern Illinois, USA. The creek flows 15 km from its headwaters to its confluence with Lusk Creek. The upper 3 km are temporary and the lower 12 km are perennial. Flow is primarily derived from overland flow, and channel drying occurs in the late summer when saturated soil water is depleted and the groundwater table falls below the streambed elevation. Flow intermittence generally decreases in the downstream direction. The uppermost study reach had the greatest flow intermittence (82%). Descriptions of the climate, geology, and vegetation of the area are given in Schwegman (1973) and Thompson (2004).

Invertebrate sampling

Four 30-m long sampling reaches (one perennial, three temporary) were established along the upper 2.8 km of Little Lusk Creek. Invertebrates were collected from riffles and pools in each reach. Samples were collected during consecutive dry (30 August 2004) and wet (4 April 2005) seasons when surface was present in each sampling reach. Samples were collected and processed as described above for Sycamore Branch.

Orari, New Zealand

Physical setting

The Orari River drains an 850-km² catchment in the eastern foothills of New Zealand's Southern Alps and a portion of the alluvial Canterbury Plains to the east of the foothills. The river flows 45 km through the foothills to a gorge at the foothills-plains boundary, then 76 km across the Canterbury Plains to the Pacific Ocean. The section of the river used in the present study extended across the plains from the gorge to a point 3.5 km upstream from the river

mouth. The Canterbury Plains are composed of two hydrogeological regions, the inland and coastal plains. The inland plains are underlain by glacial and periglacial gravels. Aquifers in this area are separated from land surface by a deep vadose zone. The coastal plains are underlain by alternating layers of post-glacial gravels and marine clays deposited during high sea stands. Aquifers in this area form a vertical series with the uppermost aquifer at or near ground surface. Flow patterns in the Orari River reflect the contrasting hydrogeological structures. The inland-plains section of the Orari is perched, and the river progressively loses flow to the vadose zone; all flow is lost within 20 km of the gorge for part of most years. On the coastal plain, upwelling groundwater discharges into the Orari River, starting at a point ~ 49 km from the gorge and continuing to river mouth. The river gains groundwater with distance downstream in this section, and becomes perennial ~ 69 km downstream from the gorge. At the most temporary point of the river, annual average flow permanence is ~ 60%. When a dry section is present, it expands and contracts in length in response to groundwater level fluctuations and changes in run-off from upstream; the dry section varies from 0 - 50 km in length. Flow cessation occurs in late spring or early summer of most years. Descriptions of the climate, geology and geomorphology of the Orari River catchment are given in Larned *et al.* (2011).

Invertebrate sampling

Invertebrates were collected from riffles at 11 sites (five perennial, six temporary) on 24 October 2007 and 19 February 2008. The river was flowing over its entire length on both sampling dates. At each riffle, four replicate samples were collected with a Surber sampler (0.09-m², 250- μ m mesh), then two samples were combined into each of two composite samples and preserved in 70% isopropyl alcohol. Most aquatic insects and all molluscs were

identified to genus or species (some midges were identified to tribe). Crustaceans, annelids, and mites were identified to family or order.

Selwyn, New Zealand

Physical setting

The Selwyn River drains a 975-km² catchment located 90 km north of the Orari River. Like the Orari River, the Selwyn River rises in the foothills of the eastern Southern Alps and flows across the Canterbury Plains. The river mainstem flows 35 km through the foothills, then 54 km across inland and coastal plains to coastal Lake Ellesmere. The Selwyn River is perched over a deep vadose zone beneath the inland plains, and loses water with distance downstream. The first 3 km of the losing reach are perennial, and the next 43 km are temporary. In the coastal plains, upwelling groundwater causes progressive flow gains, and the river becomes perennial approximately 8 km from its terminus. The severity of intermittence is greater in the Selwyn River than the Orari River, as indicated by higher flow intermittence for most of its length. At the most temporary point of the river, annual average flow intermittence is approximately 70%. During extended droughts, the river dries for most of its length on the Canterbury Plains, and portions of the central reach may remain dry for more than 1 year. Descriptions of the climate, geology and geomorphology of the Selwyn River catchment are given in Larned *et al.* (2008).

Invertebrate sampling

Invertebrates were collected from riffles at 16 sites (three perennial, 13 temporary) on 11 dates between November 2003 and October 2004. At least one site was dry on each sampling date, so the total number of sampling dates at each cross-section varied from 2-11. At each site, four replicate samples were collected with a Surber sampler (0.09-m² area, 250- μ m

mesh), then two samples were combined into each of two composite samples and preserved in 70% isopropyl alcohol. Most insects and all molluscs were identified to genus or species (some midges were identified to tribe). Crustaceans, annelids, and mites were identified to family or order.

Garden and Huachuca, USA

Physical settings

Huachuca and Garden Canyons are arid-land streams that drain catchments in the Huachuca Mountains in southeast Arizona, USA. Huachuca Canyon drains a 25-km² catchment before joining the Babocomari River, a tributary of the San Pedro River. Garden Canyon drains a 34-km² catchment before joining the San Pedro River. In the uppermost 7 km of both streams, there is interrupted perennial flow through rugged canyons. Downstream of the canyons, the streams flow across alluvial fans where seepage losses are high; both streams become temporary at the canyon-alluvial fan boundaries. The temporary section of Huachuca Canyon extends 12.2 km to the confluence with the Babocomari River. The temporary section of Garden Canyon extends 22.1 km to the confluence with the San Pedro River. Flow intermittence in the temporary reaches of both streams increases with distance downstream. Flow intermittence ranges from 40% at the top of alluvial fans to 99% several kilometers down the fans. ~~Descriptions of the climate, geology and geomorphology of Garden and Huachuca Canyons are given in Bogan *et al.* (2013).~~ Descriptions of the climate, geology and geomorphology of Garden and Huachuca Canyons are given in Bogan *et al.* (2013).

Invertebrate Sampling

Invertebrates were collected from riffles at nine sites (three perennial, six temporary) from both Huachuca and Garden Canyons on 27-31 March 2010. Sampling sites were spaced 0.25

to 4 km apart. Perennial reaches were also sampled in November 2009 and 2010 and March 2011, but the temporary reaches were dry during these periods. During the March 2010 sampling period, the perennial and temporary reaches were connected by flow at both streams. At each sampling site, three replicate samples were collected with a D-net (0.09-m² area, 500- μ m mesh) by disturbing substrate to a depth of 5 cm to dislodge invertebrates. The three replicates samples at each site were composited and preserved in 95% ethanol. All aquatic insects, mites and amphipods were identified to genus or species. All other invertebrates were identified to family or order.

Fish Creek, USA.

Physical settings

Fish Brook drains a 47-km² catchment on the Atlantic Coastal Plain of north-eastern Massachusetts, USA. The Fish Brook mainstem flows 31.25 km from headwater wetlands to its confluence with the Ipswich River. Descriptions of the climate and geomorphology of the Ipswich River region are given in Zarriello & Ries (2000). The sampling sites used for this study were located on perennial Fish Brook and two of its temporary headwater tributaries. All sites were within a 1-km² area of deciduous forested swamp, 5 km upstream of the Ipswich River confluence.

Invertebrate Sampling

Invertebrates were collected from riffles and pools at eight sites (three perennial, five temporary) on eight days in July 2004, six days in September 2004, and six days in April 2005. At each sampling site, three replicate samples were collected with a D-net (0.1 m² area, 500- μ m mesh) and preserved in 80% ethanol. All invertebrates were identified to genus.

Alme and tributaries, Germany.

Physical setting

The Alme River drains a 763-km² catchment in East Westphalia, Germany. The river flows north for 60 km from its headwaters in the northeastern Sauerland region to its confluence with the Lippe River. The Alme River mainstem and three of its tributaries were sampled, the 28-km long Ellerbach River (catchment area 91 km²), the 8-km long Menne River (catchment area 8 km²), and the 30- km long Sauer River (catchment area 109 km²).

Seepage losses into limestone fissures and sinkholes cause flow intermittence in Alme and its tributaries. The Alme, Ellerbach and Sauer Rivers have perennial reaches extending from the headwaters downstream for 18–31 km, and temporary middle and lower reaches. The Menne River is in a completely karstified catchment and has alternating temporary and perennial reaches for its entire length. The 5-250 m-long perennial reaches in the Menne River are each downstream of a spring. The temporary reaches of the Ellerbach, Menne, and Sauer Rivers extend to their confluences with the Altenau River, which flows into the Alme. The temporary reach of the Alme River ends at the confluence with the Altenau, and the Alme is perennial from this point to its confluence with the Lippe River. Descriptions of the hydrology and geology of the Alme River and its catchment are given in Meyer & Meyer (2000), and Meyer *et al.* (2004).

Invertebrate sampling

In the Alme River, invertebrates were collected at seven sites (four perennial, three temporary) on three dates between 2005 and 2008. At each site, two or three replicate samples were taken with a Surber sampler (0.09-m², 250- μ m mesh). In the Ellerbach River, invertebrates were collected at three sites (one perennial, two temporary) on four dates in

2001. At each site, three replicate samples were taken with a Surber sampler (0.09-m², 250- μ m mesh). In the Menne River, invertebrates were collected at four sites (one perennial, three temporary) on three dates in 2000. At each site, two replicate samples were taken with a Surber sampler (0.09-m², 250- μ m mesh). In the Sauer River, invertebrates were collected at 14 sites (four perennial, 10 temporary) on three dates between 2000 and 2007. At each site, two replicate samples were taken with a Surber sampler (0.09-m², 250- μ m mesh). Invertebrate samples were preserved in 90% ethanol. All aquatic insects, mites, annelids, molluscs and amphipods were identified to genus or species. All other invertebrates were identified to family or order.

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Appendix S2. List of life-history traits coded to assign each taxon to the following class:

0 : neither *resistant* nor *resilient*; 1 : *resilient*; 2 : *resistant*; and 3 : *resilient* and *resistant*.

Given the coarse taxonomic resolution used (TR 3), we assigned to each taxon the traits which were dominant across the constituent families, genera or species. When a taxa showed exclusively traits from the *resistant* class, it was classified as *resistant* (n = 37 taxa). Conversely, when a taxa showed exclusively traits from the *resilient* class, it was classified as *resilient* (n = 37 taxa). When a taxa showed traits from both the *resistant* and *resilient* class, it was classified as *resistant* and *resilient* (n = 26 taxa). Last, when no traits was assigned to a taxa, it was classified as without *resistant* nor *resilient* (n = 25 taxa).

	united states codes	Long adult lifespan	High female dispersal	Strong adult flying capacity	Common occurrence in drift	Strong swimming ability		Desiccation resistance (long)	Body armor/ing	Plastron (anaerobic respiration)	Low metabolic
Plecoptera											
Capniidae	3				+			+			
Chloroperlidae	1				+						
Eustheniidae	0										
Gripopterygidae	0										
Leuctriidae	1				+						
Nemouridae	3				+			+			
Perlidae	1		+	+							
Perlodidae	0										
Taeniopterygidae	2							+			
Trichoptera											
Brachycentridae	2									+	
Calamoceratidae	2									+	
Conoesucidae	2							+		+	
Glossosomatidae	2									+	
Goeridae	2									+	
Helicopsychidae	2		+					+		+	
Hydrobiosidae	0										
Hydropsychidae	1		+	+	+						
Hydroptilidae	1		+			+					
Lepidostomatidae	0										
Leptoceridae	1		+								
Limnephilidae	2							+		+	
Molannidae	0										
Odontoceridae	2									+	
Philopotamidae	0										
Phryganeidae	2							+			
Polycentropodidae	1		+								
Psychomyiidae	1		+								
Rhyacophilidae	0										
Sericostomatidae	0										
Ulenoidea	2									+	
Ephemeroptera											
Baetidae	1				+	+					
Ameletidae	1					+					
Caenidae	2										+
Ephemerellidae	1				+						
Ephemeridae	2										+
Heptageniidae	1				+						
Leptophlebiidae	3				+						+
Leptophlebiidae	1				+						
Oligoneuridae	3					+					+
Siphonuridae	1				+	+					+
Coleoptera											
Brachypteridae	2							+		+	
Chrysomelidae	2							+		+	+
Dryopidae	2	+								+	
Dytiscidae	3	+	+	+		+			+	+	+
Elmidae	1	+			+			+			
Gyrinidae	3	+	+	+		+			+	+	+
Halplidae	1	+			+				+		
Hydraenidae	1	+			+					+	
Hydrophilidae	3	+			+					+	+
Psephenidae	0										
Ptilodactylidae	1	+	+	+							
Scarabaeidae	3	+	+	+					+	+	+
Scirtidae	3		+	+	+			+		+	+
Staphylinidae	3	+	+	+						+	+
Diptera											
Athericidae	0										
Ceratopogonidae	2							+			
Chironomidae	3		+		+			+			+
Culicidae	3	+	+					+		+	+
Cylindrotomidae	2							+			+
Damesinae	1		+		+						
Dixidae	2				+			+		+	
Dolichopodidae	3	+	+	+						+	+
Empididae	0										
Ephydriidae	3	+	+	+				+		+	+
Limoniidae	2							+			
Muscidae	3	+	+	+				+		+	
Orthocladinae	1		+		+			+			
Pediciidae	2							+			
Podonominae	1		+		+						
Psychodidae	2									+	+
Ptychopteridae	2							+		+	+
Rhagionidae	0										
Sciariidae	2							+			
Simuliidae	1			+	+						
Tabanidae	3		+	+				+		+	
Tanytopodinae	1		+		+						
Tanytarsini	1		+		+						
Tipulidae	2							+			
Odonata											
Aeshnidae	1	+	+	+		+					
Calopterygidae	1			+							
Coenagrionidae	0										
Cordulegastridae	1	+		+							+
Gomphidae	1	+		+							+
Lestidae	2										+
Libellulidae	1	+	+	+							+
Protoneturidae	1										
Megaloptera											
Corydalidae	0										
Sialidae	0										
Hemiptera											
Belostomatidae	3	+	+	+		+		+	+	+	+
Corixidae	3	+	+	+		+		+	+	+	+
Nepidae	2	+						+		+	+
Notonectidae	3	+	+	+		+		+	+	+	+
Heteroptera											
Mesovelidae	3	+				+		+		+	+
Velidae	3	+				+		+		+	+
Gerridae	3	+				+		+		+	+
Amphipoda											
Crangonyctidae	1	+	+		+			+			
Eusiridae	0										
Gammaridae	1	+			+	+					
Niphargidae	0										
Paraleptamphopidae	0										
Decapoda											