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Do priority effects outweigh environmental filtering in a guild of dominant freshwater macroinvertebrates?

Little, Chelsea J ; Altermatt, Florian

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1 **Do priority effects outweigh environmental filtering in a guild of dominant freshwater**
2 **macroinvertebrates?**

3

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17

18 **Keywords:** Amphipod, aquatic ecology, community assembly, competition, metacommunity,
19 species distributions

20

21 Abstract

22 Abiotic conditions have long been considered essential in structuring freshwater
23 macroinvertebrate communities. Ecological drift, dispersal, and biotic interactions also structure
24 communities, and although these mechanisms are more difficult to detect, they may be of equal
25 importance in natural communities. Here, we hypothesized that in ten naturally-replicated
26 headwater streams in Eastern Switzerland, locally-dominant amphipod species would be
27 associated with differences in environmental conditions. We conducted repeated surveys of
28 amphipods and used a hierarchical joint species distribution model to assess the influence of
29 different drivers on species co-occurrences. The species had unique environmental requirements,
30 but a distinct spatial structure in their distributions was unrelated to habitat. Species co-occurred
31 much less frequently than predicted by the model, which was surprising because laboratory and
32 field evidence suggests they are capable of coexisting in equal densities. We suggest that niche
33 preemption may limit their distribution and that a blocking effect related to the specific linear
34 configuration of streams determines which species colonizes and dominates a given stream
35 catchment, thus suggesting a new solution a long-standing conundrum in freshwater ecology.

36 *“It is reasonable to suppose that the fundamental niches of the two species overlap, but*
37 *that within the overlap [the amphipod *Gammarus*] pulex is successful, while [the*
38 *amphipod *G.*] duebeni with a greater tolerance of salinity has a refuge in brackish water...*
39 *This case is as clear as one could want except that Hynes is unable to explain the absence*
40 *of *G. duebeni* from various uninhabited favorable localities in the Isle of Man and*
41 *elsewhere... These disconcerting empty spaces in the distribution of *Gammarus* may raise*
42 *doubts as to the completeness of the picture.” (Hutchinson 1957)*

43

44 **Introduction**

45 A central goal of ecology is to understand the factors determining the distribution of
46 species, and the mechanisms of how these species are structured into communities. For instance,
47 species distribution models based on environmental variables are commonly used to characterize
48 species’ niches – the set of abiotic and biotic conditions in which a species can survive and
49 reproduce (Hutchinson 1957) – and then to predict where they should be found. However, other
50 processes are also important in determining species distributions, such as dispersal (Macarthur &
51 Wilson 1967; Hubbell 2001; Leibold *et al.* 2004), interspecific interactions like competition
52 (Wisz *et al.* 2013), and processes like order of arrival or “priority effects” (Drake 1991; Chase
53 2003; De Meester *et al.* 2016). Particularly at the local scale, these processes may in effect
54 prevent the coexistence of species that are otherwise similarly suited to environmental conditions
55 (Fukami *et al.* 2016), and which do coexist at broader spatial scales. Compared to environmental
56 variables, factors like order of arrival and dispersal limitation are not easy to detect or quantify in
57 observational data, and so far have been largely neglected in species distribution models despite
58 widespread recognition of their importance (Guisan & Thuiller 2005; D’Amen *et al.* 2017).

59 Amphipods are one of the examples of organisms G. Evelyn Hutchinson used in his
60 seminal 1957 remarks positing the factors shaping species coexistence (see epigraph). While the
61 examples on plankton or plant community coexistence are much more widely referred to, the
62 relatively species-poor family of Gammaridae amphipods (Crustacea: Amphipoda) are an
63 enigmatic case because the individual species are highly similar to one another ecologically, for
64 instance using the same food resources, and are speculated to fill the same niches while also
65 predated on one another (as well as members of their own species) (Macneil *et al.* 1997).
66 Furthermore, in regions such as Europe and parts of Eurasia, they are the most dominant and
67 important decomposers in freshwater ecosystems, thus playing a key role in ecosystems and food
68 webs. In general, dominant species in a given community can structure communities and play an
69 essential role in determining ecosystem function (Hillebrand *et al.* 2008). This is also true for
70 amphipods, with greater dominance by the common central European species *Gammarus*
71 *fossarum* associated with higher decomposition rates in streams (Dangles & Malmqvist 2004).
72 Because of such ecosystem-level effects, the distribution and potential coexistence of amphipod
73 species are of particular interest. As noted by Hutchinson (1957) and others (for instance,
74 Pinkster *et al.* 1970 called the amphipod species distributions a "problem"), mechanisms behind
75 both these species' commonly observed coexistence, but also the equally-common apparent
76 exclusion of one by another, need clarification given that the species' niches are assumed to be so
77 similar.

78 In general, when a new species arrives from the regional species pool, there are three
79 relevant outcomes in a community, assuming that the species' abiotic requirements are met: (1)
80 the new species cannot establish in the community; (2) it establishes and coexists with the other
81 species; or (3) it establishes and replaces the previously-dominant species. The first case can
82 occur when the species are functionally similar and niche space is not wide enough for both to

83 coexist (niche preemption), or even when they are dissimilar but the previously-established
84 species has modified and erased the niche of the new species; such conditions result in priority
85 effects (Fukami 2015). The second case can occur when species have different niches, and among
86 competitors with similar niches can be promoted by spatial storage effects due to environmental
87 or temporal heterogeneity at a given scale (Hart *et al.* 2017). The third case, meanwhile, is typical
88 but not exclusive to invasive species. These cases illustrate that even when there is the
89 opportunity for multiple functionally-similar species to coexist, they not always do so.
90 Furthermore, the “final” outcome of species interactions after a new species’ arrival depends on
91 the temporal and spatial scale being considered. Species turnover due to competitive exclusion
92 often occurs very slowly (Yackulic 2017), thus coexistence in the short term may lead to species
93 replacement (succession) over a longer time frame.

94 To identify the mechanisms governing the distribution and coexistence of freshwater
95 amphipods, we surveyed 121 stream reaches distributed in ten headwater stream catchments in
96 Eastern Switzerland, sampling throughout the network topology of main and side stems, and
97 capturing temporal dynamics by visiting each stream seasonally for one year. Previous work
98 indicated that five amphipod species were present in the downstream lake, and three of these
99 species consistently occupy the tributary catchments (Altermatt *et al.* 2016). These omnivorous
100 species are comparable in size and functionally similar. They can move kilometers or tens of
101 kilometers per year when expanding their ranges (Dick *et al.* 1994; Bollache *et al.* 2004). By
102 comparison, the total stream length in our studied headwater catchments ranged from 2.8 to 4.8
103 kilometers. No genetic differentiation has been observed in this region’s native freshwater
104 amphipods at this spatial scale (Altermatt *et al.* 2016), and patterns of population genetic
105 differences of the same species in Germany did not indicate dispersal limitation but rather
106 colonization history and subsequent genetic drift (Weiss & Leese 2016). While there is genetic

107 isolation by distance at larger scales (Westram et al. 2013), we thus assumed that the distribution
108 of these different species across our comparatively small study catchments should be driven only
109 by niche differences with respect to abiotic conditions, biotic interactions, and/or stochastic
110 processes, rather than dispersal limitation. We also expected that we would find multiple species
111 coexisting in at least some locations, either as a result of equalizing or stabilizing mechanisms, or
112 as a transient state before eventual competitive exclusion. We hypothesized that:

113 (a) Species richness would be invariable throughout the sampling region, but with different
114 species or combinations of species in different locations comprising this diversity; *or*,

115 (b) Species richness would be higher at downstream points near the lake outlet. All of the
116 species previously found in the streams are present in the lake, so we conceptualize the lake as a
117 regional species pool. We would expect such a pattern of species richness both because
118 downstream points are closest to the regional species pool, and because of characteristic diversity
119 patterns found in river networks (Altermatt 2013); *and*,

120 (c) Species would have individual niches and habitat preferences. This has been
121 demonstrated for amphipod species in lakes (Hesselschwerdt *et al.* 2008) and larger rivers (Kley
122 & Maier 2005), and we expected that this niche partitioning would explain why species were
123 found in different locations. Such environmental requirements would lead to coexistence in
124 complex habitats and/or to spatial segregation of species into non-overlapping patches within a
125 catchment.

126

127 **Methods**

128 *Study location and sampling sites*

129 We studied ten naturally replicated catchments in eastern Switzerland, with the headwater
130 streams between 2.75 and 5 kilometers in total length (including main and side stems) and

131 running into Lake Constance (catchment sizes 115 to 453 hectares). Four streams were located in
132 the less-developed, steeper “Untersee” region to the west, and six were located in the more
133 heavily agricultural, flatter “Obersee” region to the east (Figure 1A). Catchments had varying
134 land use from primarily mixed deciduous and coniferous forest to primarily agriculture, with
135 pockets of higher density housing or industrial uses (Figure 1E). In each catchment, streams were
136 divided into 250-meter segments along the main stem. Side stems less than 450 meters in total
137 length were counted as single segments, while side stems greater than this length were divided
138 into 250-meter segments beginning from the confluence with the main stem. A sampling point
139 was established within each segment in a reach with representative habitat and stream flow, and
140 sampling points in different segments were placed as equidistantly as possible. This resulted in a
141 range of nine to 15 sampling points per catchment, and 121 sampling points in total.

142

143 *Data collection*

144 Sampling points were visited four times at roughly three-month intervals, between
145 April/May 2015 and January 2016. Repeat sampling points were within 10 meters of points at the
146 same location. We measured:

147 (1) *Substrate and habitat characterization*. Substrate type and complexity have previously
148 been shown to explain local distributions of amphipods (Kley & Maier 2005; Piscart *et al.* 2007;
149 Eisenring *et al.* 2016). Thus, we measured the width of the active channel and classified habitat
150 inside a 1 m long section using a 1 x 1 m sampling frame with 0.2 x 0.2 m gridlines. The number
151 of grid squares comprising different substrate types was estimated visually, as impermeable
152 surface (bedrock, solidly calcified benthic material, or concrete), rocks >20 cm in diameter,
153 gravel 2.5–20 cm diameter, fine gravel <2.5 cm diameter, sand, mud, or clay. A separate visual
154 estimation was made of the number of grid squares covered by dead leaves, living terrestrial and

155 large aquatic plants, roots and woody debris, or moss and algae, and allowed for the layered
156 structure of microhabitats such that the area covered by these components could sum to greater
157 than the two-dimensional area of the stream section.

158 (2) *Water chemistry*. A water sample was collected from each sample point and, in the lab,
159 measured for total phosphorus with a spectrophotometer (Varian Cary 50 Bio, Palo Alto,
160 California, USA), and total nitrogen, dissolved organic carbon (DOC), and total organic carbon
161 (TOC), all with a TOC analyzer (Shimadzu TOC-L, Kyoto, Japan). Further variation in water
162 chemistry was inferred to be captured indirectly through differences in land use (Johnson *et al.*
163 1997), described below.

164 (3) *Amphipod abundance and identity*. After leaf collection, kicknetting was performed
165 across the width of the stream section. Sampling effort was equal per meter of stream width, so
166 that the total time spent kicknetting was greater in wider stream segments, and each habitat and
167 substrate type was included in the sampling. Abundance of amphipods was estimated by order of
168 magnitude: 0, 1–10, 10–100, 100–1000, or >1000. From each sample up to ~40 amphipods were
169 collected and preserved in ethanol for subsequent identification in the lab; individuals were
170 chosen to represent the range of sizes present in the sample, but not including those which were
171 too small to reliably identify to species based on morphological characters. Depending on stream
172 temperature, the common amphipod species in this area may live 1–3 years and reach sexual
173 maturity at six months (Pöckl *et al.* 2003); thus we assumed that the smallest juveniles from the
174 spring and summer sampling visits could be counted/identified as medium-sized individuals in
175 subsequent sampling visits if they survived.

176

177 *Land-use data*

178 Amphipod species distributions have previously been associated with ammonia
179 concentration (Gergs *et al.* 2013), which in turn is associated with agricultural runoff in our study
180 region (Abbaspour *et al.* 2007). Thus, this and other important factors for amphipod distributions
181 such as riparian vegetation degradation (Mauchart *et al.* 2014) and pH and dissolved oxygen
182 (Meijering 1991) were assessed indirectly through land use type, integrating various unmeasured
183 factors. All spatial analysis was done using ArcGIS 10.2.2 (ESRI, Redlands, California, USA).
184 Spatial information about streams was extracted from the Swiss national 1:25,000 scale water
185 network and digital elevation models (Swisstopo 2003, 2007). We calculated elevation of each
186 sampling point, latitude/longitude, and its upstream distance from the outlet on Lake Constance.

187 Land cover within the catchments was classified using a combination of data sources. We
188 used as the basis the CORINE land cover (2012) land-use classification (Bossard *et al.* 2000),
189 produced from Indian Remote Sensing (IRS) P6 LISS III and RapidEye imagery with a Minimal
190 Mapping Unit of 25 hectares and positional accuracy of, at a minimum, 100 meters. To add
191 specificity to CORINE's agricultural classification and because orchards often have higher
192 herbicide application, we added the area of vine and orchard fruit cultivation from a 1:25,000
193 scale vector map (Swisstopo 2010), resulting in nine categories: discontinuous urban fabric,
194 industrial or commercial units, non-irrigated arable land, complex cultivation patterns, fruit
195 orchards and vine cultivation, broad-leaved forest, mixed forest, inland marshes, and water
196 bodies. The area of land falling into each land use category was calculated for each study
197 catchment in total, as well as for a 50-meter radius area at each sampling point.

198

199 *Statistical analysis*

200 All statistical analyses were performed in R version 3.3.2 (R Core Team 2016). The
201 presence or absence of amphipod species was examined using the 'HMSC' Bayesian joint

202 species distribution model (JDSM) package (Ovaskainen *et al.* 2017). This framework
203 incorporates aspects of traditional species distribution models by estimating the association
204 between species and environmental and/or spatial variables, but implements the model for
205 multiple species concurrently, which allows the residual variation from the environmental factors
206 to be used to detect associations between species that are not driven only by shared
207 environmental preferences (Ovaskainen *et al.* 2017; also other JDSM's, e.g., Pollock *et al.* 2014).
208 We incorporated environmental covariates and the sampling structure, with catchment and
209 sampling point as random factors representing spatial context. We used default priors and
210 modeled species occurrences using the Bernoulli distribution and a probit link function
211 (additional information on model specification in Appendix I). MCMC chains were run to
212 100,000 iterations, with a burn-in period of 1,000 iterations and subsequently thinned to include
213 only every 100th sample of the posterior distributions.

214 We primarily compared two models. The first included only the spatial random effects
215 (“S”). The second included three types of factors: spatial random effects, prior amphipod
216 occurrence, and environmental covariates (“SPE”). The environmental covariates included those
217 described previously: substrate and habitat information, water chemistry, latitude, elevation,
218 distance from the stream outlet, and land use at the point and catchment level. Because at the first
219 sampling timepoint, there was no prior presence-absence information, these two models were
220 made using data only from the second through fourth sampling timepoints. For comparison
221 purposes, we repeated the model with random effects plus environmental factors with the
222 complete dataset of all four timepoints, which necessitated excluding information about prior
223 amphipod occurrence (“SE_{Full}”). Finally, we ran two additional models using only the second
224 through fourth timepoints – one with spatial random effects plus the prior presence of amphipod

225 species (“SP”), and another with the random effects plus all other environmental covariates
226 described above (“SE”) – the results of which are presented in Appendix I.

227 Overall model fit was assessed using Tjur’s R^2 (Tjur 2009), the difference between the
228 mean fitted value of sampling units where species are present and the mean fitted values where
229 species are absent. Importance of environmental covariates was assessed in two ways: whether
230 the covariate had a significant effect, and what proportion of variance it actually explained. First,
231 parameter estimates of the association between environmental covariates and presence/absence of
232 individual species were extracted as 95% central credible intervals. Where this interval did not
233 overlap with zero, the covariate was deemed to have a strong directional association with the
234 species. Secondly, the explained variance in presence/absence of each species was partitioned
235 among all explanatory variables, which were grouped for presentation into broad categories, as
236 well as to random effects at the both sampling scales (catchment and sample point).

237 Finally, we assessed the potential co-occurrence of species, or “hypothetical species
238 association patterns” (Aivelo & Norberg 2017), by extracting the residual correlations between
239 species from the latent part of the model framework. A positive residual correlation indicates that
240 species occur together more frequently than would be predicted by their calculated niches, while
241 a negative residual correlation indicates that their niches would predict them to co-occur more
242 frequently than they do in practice. These putative species associations are depicted by the
243 median value of posterior samples.

244

245 **Results**

246 *Spatial and temporal patterns in distribution*

247 Our sampling revealed a pronounced spatial pattern in species distributions, with
248 *Gammarus fossarum* the only species present upstream of outlets in the western catchments and

249 three different species (*G. fossarum*, *G. pulex*, and *G. roeseli*) present in eastern catchments, but
250 rarely coexisting (Figure 1). Of these three, *G. fossarum* and *G. pulex* are native species while *G.*
251 *roeseli* is non-native but considered naturalized since it arrived in the 1800s. Across the whole
252 study region and sampling year, mean species richness at outlet points was 1.25 species (range 0–
253 3), and at non-outlet points was 0.69 species (range 0–2). No non-outlet point ever had three
254 species present. We concluded that outlets were more representative of the lake’s species pool of
255 five to six species (Altermatt *et al.* 2014, 2016) than of stream communities, and excluded outlet
256 points from subsequent analyses.

257 Site occupancy was fairly stable through time, with no change in species composition at a
258 sampling point in 78% of the possible transitions from one timepoint to the next. There were few
259 changes from single-species to multi-species occupancy (3% of possible transitions) or vice versa
260 (2% of possible transitions). There was also one change from a point being occupied by one to a
261 different species (0.3% of transitions; Figure 2). The most common change at the sampling point
262 level was from being occupied to being unoccupied (11% of possible transitions), in large part
263 due to seasonal drying of some stream reaches. Few (5/17) of these dried stream reaches were
264 reoccupied, and in all of these cases they were reoccupied by the same species which had been
265 present before the drying event. In one of the five cases, an additional species co-established at
266 the re-wetted stream reach. Overall, this shows that there is nearly zero turnover in species
267 dominance amongst occupied sampling points and little chance for “new” species to establish
268 after disturbance has rendered some patches unoccupied.

269

270 *Comparing joint species distribution models*

271 The spatial arrangement of the sampling points was important in explaining the presence
272 and absence of different species through several different metrics. The *S* model using only the

273 random effects of catchment and sampling point for the second through fourth timepoints
274 (n=390) explained 51% of the variation in species presence and absence. The full “SPE” model
275 (n=237) explained 71% of variation. The models with either prior amphipod occurrence or
276 environmental covariates separately had intermediate model fits (Appendix I). By comparison,
277 the SE_{Full} model across all sampling timepoints but using only spatial arrangement and
278 environmental covariates (n=367) explained 64% of variation. This suggests that both
279 environmental data and data about species distributions at prior sampling times are important and
280 do not convey the same information.

281

282 *Abiotic influences on species distribution*

283 In the *SPE* model, only a few variables had strong directional effects (defined using the
284 95% central credible interval of the posterior distribution of the association) on the presence or
285 absence of amphipod species (Table S1). Despite their strong directional effects, these variables
286 did not necessarily account for a large proportion of the variance in occurrence patterns (Figure
287 3); for instance, the association between the area of substrate covered by leaves and the
288 occurrence of *G. pulex* accounted for only 1.7% of the explained variation in the species’
289 occurrence. For *G. pulex*, the area of the streambed covered by leaf litter, the proportion of area
290 surrounding a point made up of arable land, and the previous presence of *G. pulex* were strong
291 predictors. For *G. fossarum*, latitude, the proportion of catchment area covered by orchards, the
292 dissolved organic carbon in the water, and the previous presence of *G. fossarum* were strong
293 predictors. And for *G. roeseli*, the proportion of area surrounding a point used for industrial or
294 commercial purposes and the previous presence of *G. pulex* were strong predictors. Other
295 important factors in the SE_{Full} model, such as the association between *G. fossarum* and previous
296 drying or the area of moss and algae on the substrate, no longer had strong directional effects

297 when both environment and previous species occurrence information were integrated into the
298 same model (Table S1). Although other factors measured at the sampling point or catchment
299 level did not have strongly directional effects, they nevertheless contributed greatly to explaining
300 the variation in species occurrences when a variance partitioning was conducted on the *SPE*
301 model (Figure 3). For example, land use in the catchment accounted for 32% of the explained
302 variation in the occurrence of *G. fossarum*, and 6% of the explained variation in *G. pulex*; while
303 variables measured at the point level which did not have strong directional effects nevertheless
304 combined to account for 24% of the explained variation in the occurrence of *G. fossarum*, 13% of
305 explained variation in *G. pulex*, and 5% of the explained variation in *G. roeseli*. The density of
306 posterior distributions of all associations between measured variables and species occurrences are
307 presented in Figure S1.

308

309 *Co-occurrence of amphipod species*

310 After accounting for these factors, putative species associations between different
311 amphipod species remained in the *SPE* model: weak positive correlations at the catchment level,
312 and strong positive and negative correlations at the sampling point level (Figure 4). At the
313 sampling point level, *G. fossarum* rarely co-occurred with either of the other species despite
314 somewhat-similar habitat requirements (median residual correlation = -0.74 to *G. pulex* and -0.75
315 to *G. roeseli*). Conversely, *G. pulex* and *G. roeseli* co-occurred much more frequently (median
316 residual correlation = 0.99) than would have been predicted either by random chance or based on
317 their individual habitat requirements. At the catchment level, pairs of species co-occurred slightly
318 more frequently (residual correlations of 0.10–0.25) than would have been predicted either by
319 random chance or by the niches constructed based on our measured factors (spatial arrangement,
320 previous species occurrence, and environmental covariates).

321

322 **Discussion**

323 It has been commonly observed that species do not always co-exist where might be
324 expected. We examined the distribution of three locally-dominant and occasionally co-occurring
325 amphipod species in order to disentangle the ecological processes behind their occupancy
326 patterns in stream catchments. As expected, environmental factors explained part of the variation
327 in these species' distribution between and within catchments. Overall, however, individual
328 environmental factors rarely had strongly positive or negative effects on species occurrences, and
329 a large amount of variance remained unexplained by environmental variables, as is commonly
330 found (Cottenie 2005; Heino *et al.* 2015). While we are confident that we included the most
331 important variables in our analysis, we cannot completely exclude that an unmeasured variable
332 that is not correlated to any of the included variables could define a niche-axis along which the
333 species segregate. We think, however, this to be unlikely, as our variable choice is based on
334 extensive existing knowledge on relevant variables (Kley & Maier 2005; Piscart *et al.* 2007;
335 Hesselschwerdt *et al.* 2008; Eisenring *et al.* 2016). Importantly, these three species are not
336 dispersal-limited at the scale of our studied headwater stream catchments (Altermatt *et al.* 2016),
337 ruling out another common mechanism shaping community composition.

338 Using a joint species distribution modeling approach, we show that this unexplained
339 variance can be assigned to putative species interactions. While much experimental work on
340 community assembly and species interactions has been done in plant communities -- where
341 individuals are immobile, order of arrival can be easily manipulated and neighbors may be
342 removed from a community (e.g., Choler *et al.* 2001) -- this is more challenging when working
343 with animals in flowing-water systems. We used an analytical approach which allowed us to infer
344 species interactions from observational data (Aivelo & Norberg 2017; Ovaskainen *et al.* 2017)

345 without performing manipulations. In past studies, competition has been assumed to be the
346 primary species interaction shaping amphipod communities: for example, *G. pulex* rarely co-
347 occurred with another sympatric species, *G. duebeni*, in rivers in France, and this was attributed
348 to hypothesized strong competition between the two species (Pinkster *et al.* 1970). However, in
349 no amphipod distribution study that we are aware of has competition been directly measured or
350 indirectly inferred. Our results now suggest a more nuanced role of competition.

351 After accounting for important environmental factors we found strong negative species
352 interactions, but because different species are dominant in different catchments, we ruled out that
353 one species has an absolute fitness and competitive advantage over the others; if this were true,
354 the same species should have dominated all of our catchments. Which species dominated which
355 catchment was also not satisfactorily explained by environmental variables alone, suggesting that
356 the identity of the “winner” is also not deterministically driven by niche differences. This we
357 conclude because at the catchment scale species coexisted more frequently than expected based
358 on environmental factors. In particular, in two catchments where multiple species co-occurred
359 throughout the length of the stream, they did so at roughly equal densities over the course of the
360 entire study period (Table S2). These two catchments were not particularly close to each other
361 and had different land use (Figure 1) and habitat characteristics (Supplementary Data), making it
362 improbable that some particular abiotic variable promoted coexistence. The ability of the species
363 to coexist was also found in laboratory experiments, where *G. fossarum* and *G. roeseli* each had
364 equal (~90%) survival over short-term experiments, regardless of whether maintained separately
365 or together in mesocosms at equal densities (Little & Altermatt 2018). This rules out strong,
366 density-independent competition between the species, to the degree that would cause competitive
367 exclusion when the species are at similar densities. And yet most strikingly, at the scale of
368 sampling reaches we found a putative negative species association between the two most

369 common species in the region, *G. fossarum* and *G. pulex*. Indeed, classic studies in France
370 (Pinkster *et al.* 1970; Piscart *et al.* 2007) and Britain (Hynes 1954) found that derived
371 environmental preferences (i.e., niche differences) were insufficient in explaining the distribution
372 of freshwater amphipods. Instead, in our data the previous occurrence of the same species at a
373 sampling point was the only strong positive predictor of the occurrence of *G. fossarum* and *G.*
374 *pulex*. Thus, it is clear that coexistence of species depends on scale (Hart *et al.* 2017), and we
375 indeed saw coexistence at the catchment but only rarely at the reach scale.

376 Thus, what is the source of these differing patterns of coexistence, and how are strong
377 negative association between the two most common species shaped? Neither a pure
378 environmental filtering nor competitive exclusion perspective offer convincing explanations in
379 our analysis. Alternatively, priority effects are thought to be common in various ecosystems
380 (Alford & Wilbur 1985; Almany 2003; De Meester *et al.* 2016). They are, however, generally
381 difficult to quantify through observational study because the history of community assembly is
382 rarely known (Fukami 2015). Several patch characteristics are associated with promoting priority
383 effects among functionally-similar species. These mechanisms typically allow early-arriving
384 species to quickly grow to large population sizes: for instance, small patch size and a stable
385 environment with high resource supplies and/or lack of predation (Fukami 2015). In linear habitat
386 networks such as streams, which are surrounded by an unsuitable (terrestrial) habitat matrix and
387 where each habitat patch (stream reach) is connected to only a very small number of other
388 patches, priority effects may play an outsized role due to spatial blocking. Notably, after a large-
389 scale disturbance, purely aquatic animals primarily colonize stream networks from the outlet up.
390 Thus, if a species first colonizes a stream reach near the outlets, this species encounters low
391 resistance while dispersing further upstream and may quickly rise to high densities in these
392 patches as well. Conversely, it may become very difficult for another newly-arriving species to

393 pass through these initial downstream habitat patches en route to suitable (potentially even
394 empty) upstream reaches, once a prior species is present. Distributions in an overlapping set of
395 streams, measured at a coarser scale, also showed little change over two years (Altermatt *et al.*
396 2016), however we assume that after events such as heavy pesticide application to surrounding
397 farm fields, species turnover in a catchment could occur if the disturbance extended downstream
398 and provided access from the regional species pool. Priority effects have been invoked to explain
399 macroinvertebrate community composition in individual reaches (McAuliffe 1984; Palmer *et al.*
400 1996), but as far as we are aware, the role of priority effects in excluding species at the catchment
401 or network level has not yet been investigated in natural riverine systems.

402 There are further mechanisms supporting/consistent with the role of priority effects in
403 structuring these amphipod communities. First, intraguild predation is thought to favor priority-
404 effects shaping community structure (for example, Blaustein & Margalit 1996). And indeed,
405 intraguild predation is common in various *Gammarus* species pairs, often at a stronger intensity
406 by one species than the other (Macneil *et al.* 1997). Secondly, mate limitation may also prevent
407 new species from moving into a catchment dominated by a single other species, and is a
408 characteristic destabilizing mechanism which can lead to priority effects (Fukami *et al.* 2016).
409 *Gammarus* species have been shown to have varying abilities to differentiate between potential
410 mates of different species (Kolding 1986; Dick & Elwood 1992). Some form interspecific
411 copulatory pairs even when mates of their own species are available, and no viable offspring can
412 be produced (Kolding 1986).

413

414 *Conclusion*

415 We found that although part of the variation in the distribution of *G. fossarum* could be
416 explained by environmental measures, multiple species rarely coexisted, even in reaches that

417 would seem to be suitable for more than one species. This leads to a classic problem: despite
418 knowledge of environmental conditions, it can be difficult to predict where a given species will
419 be found if other factors are preventing it from occupying all suitable niche space (Hutchinson
420 1957). Competition is often invoked as a probable cause for one species to exclude another, yet
421 here, competing species can coexist in some circumstances, but not others. Order of arrival may
422 be the key to understanding these different outcomes. Furthermore, river networks represent a
423 unique spatial setting for such considerations (Altermatt 2013), since colonization by aquatic
424 organisms is in many cases directional (downstream to upstream or vice versa). For example,
425 established dominant species in downstream reaches have a head start towards colonizing empty
426 upstream patches and may prevent newly-arriving species from passing through occupied habitat
427 patches to reach empty ones. While most studies of historical contingency, community assembly,
428 and priority effects have used plant communities, we show that priority effects may be important
429 in freshwater ecosystems as well, due in part to their specific spatial structure.

430

431 **Research Ethics:** No permits were required to collect invertebrate study organisms.

432

433 **Data Sharing:** The data for this study are archived at Dryad (DOI 10.5061/dryad.75jq1).

434

435 **Competing Interests:** We have no competing interests.

436

437 **Statement of Authorship:** CJL and FA jointly developed the field sampling protocol and
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440

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449
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632 **Figure Captions**

633

634 **Figure 1. (A)** Simplified diagram of 121 sampling points along the branches of ten headwater
635 stream catchments of Lake Constance in Eastern Switzerland. Sampling points are separated by,
636 on average, 250 meters. Colors of sampling points represent whether each species was ever found
637 at the point over a year of sampling effort; divided circles show that multiple species were found
638 at that point. Catchments varied by **(B)** maximum elevation (and thus stream slope), **(C)**
639 branching structure/network complexity, **(D)** catchment area, and **(D)** land use.

640

641 **Figure 2.** Maintenance (gray lines) and changes in occupancy (black lines) at the 111 sampling
642 sites (outlets were excluded in this analysis) over a year of visits. Five different possible states of
643 site occupancy are defined as follows: no amphipods (zero occupancy), occupancy by one of each
644 one of the three amphipod species separately, or occupancy by multiple species. Point size is
645 scaled to the proportion of sampling sites in a state at the given sampling timepoint, and the line
646 thickness connecting points at from one sampling visit to the next is scaled to the number of state
647 transitions which occurred over the given sampling interval. Less than ten sampling sites ever
648 contained multiple coexisting species (yellow points); the overall proportion of sites containing
649 zero species (white points) increased over the duration of the study, due in large part to sites
650 which dried out completely (dotted lines). Only some of these intermittent reaches were
651 recolonized when water returned in the final sampling visit (dash-dotted lines).

652

653 **Figure 3. (A)** The amount of variance in species occurrences (Tjur's R^2) explained by model
654 components for each species individually, and the number of times each species was detected in
655 the field sampling. **(B)** Variance partitioning of factors used in the *SPE* model (spatial random

656 effects, prior amphipod occurrence, environmental covariates) in relation to presence/absence of
657 each species found in the study. Stacked bars show the proportion of the total explained variance,
658 indicated in panel (A) for each species; overall, 71% of total variance in the dataset was
659 explained by the model.

660

661 **Figure 4.** Residual associations in occurrence between different species at the catchment and
662 sampling point level, after the influence of spatial relationships, environmental covariates and
663 previous amphipod site occupancy have been taken into account by the *SPE* model. Arrows are
664 colored by the strength of the association; positive associations (represented by solid lines)
665 indicate that species co-occur more frequently than would be predicted by covariates, while
666 negative associations (represented by dashed lines) indicate that species co-occur less frequently
667 than predicted.