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Dispersal syndromes can impact ecosystem functioning in spatially structured freshwater populations

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Abstract: Dispersal can strongly influence ecological and evolutionary dynamics. Besides the direct contribution of dispersal to population dynamics, dispersers often differ in their phenotypic attributes from non-dispersers, which leads to dispersal syndromes. The consequences of such dispersal syndromes have been widely explored at the population and community level; however, to date, ecosystem-level effects remain unclear. Here, we examine whether dispersing and resident individuals of two different aquatic keystone invertebrate species have different contributions to detrital processing, a key function in freshwater ecosystems. Using experimental two-patch systems, we found no difference in leaf consumption rates with dispersal status of the common native species *Gammarus fossarum*. In *Dikerogammarus villosus*, however, a Ponto-Caspian species now expanding throughout Europe, dispersers consumed leaf litter at roughly three times the rate of non-dispersers. Furthermore, this put the contribution of dispersing *D. villosus* to leaf litter processing on par with native *G. fossarum*, after adjusting for differences in organismal size. Given that leaf litter decomposition is a key function in aquatic ecosystems, and the rapid species turnover in freshwater habitats with range expansions of non-native species, this finding suggests that dispersal syndromes may have important consequences for ecosystem functioning.

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1 **Dispersal Syndromes Can Impact Ecosystem Functioning In Spatially**
2 **Structured Freshwater Populations**

3

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5

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19

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23

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25

26 **Abstract**

27 Dispersal can strongly influence ecological and evolutionary dynamics.
28 Besides the direct contribution of dispersal to population dynamics, dispersers often
29 differ in their phenotypic attributes from non-dispersers, which leads to dispersal
30 syndromes. The consequences of such dispersal syndromes have been widely
31 explored at the population and community level, however, to date, ecosystem-level
32 effects remain unclear. Here, we examine whether dispersing and resident individuals
33 of two different aquatic keystone invertebrate species have different contributions to
34 detrital processing, a key function in freshwater ecosystems. Using experimental two-
35 patch systems, we found no difference in leaf consumption rates with dispersal status
36 of the common native species *Gammarus fossarum*. In *Dikerogammarus villosus*,
37 however, a Ponto-Caspian species now expanding throughout Europe, dispersers
38 consumed leaf litter at roughly three times the rate of non-dispersers. Furthermore,
39 this put the contribution of dispersing *D. villosus* to leaf litter processing on par with
40 native *G. fossarum*, after adjusting for differences in organismal size. Given that leaf
41 litter decomposition is a key function in aquatic ecosystems, and the rapid species
42 turnover in freshwater habitats with range expansions of non-native species, this
43 finding suggests that dispersal syndromes may have important consequences for
44 ecosystem functioning.
45

46 **Introduction**

47 Dispersal, the movement from a natal site to another site or habitat patch with
48 potential consequences for gene flow, is an essential process in ecology and evolution
49 [1,2]. Dispersal connects local populations and allows for colonization of new
50 patches, and thus governs the spatial distribution of biodiversity. Although it is often
51 treated as a stochastic event, dispersal between patches is neither neutral with respect
52 to species [3] nor to individuals within species [4]. Within species, individuals may
53 disperse depending on their own phenotype (dispersal syndrome) [5–7]. Across the
54 animal kingdom, dispersing and non-dispersing individuals have identifiable
55 differences in a broad range of phenotypic characteristics [2,4,8]. These phenotypic
56 differences can have consequences in the newly colonized habitats.

57 To date, the effects of dispersal syndromes have primarily been considered at
58 the population and community levels. For example, in Glanville fritillary butterflies,
59 polymorphism in an isomerase gene is such that heterozygotes disperse 70% more
60 often than homozygotes, and because this gene is also associated with differences in
61 clutch size, life span, and other traits, this contributes to colonization-extinction
62 dynamics [2]. In western bluebirds, the increased aggressiveness of dispersers has
63 community-level effects because this enables them to out-compete mountain bluebirds
64 in patches they colonize [9].

65 While such correlations are interesting in the context of population and
66 community dynamics, ecosystems could also be impacted by dispersal syndromes, via
67 resource flux, a measure of ecosystem functioning [10]. In fact, some work has
68 demonstrated that dispersers consume resources differently than non-dispersers; for
69 example, mosquitofish which had dispersed between pools in an experimental stream
70 were four times as efficient at reducing prey abundance after arriving in a new

71 location as are non-dispersers, though this effect attenuated over time [11]. However,
72 this finding was framed in a behavioral context of behavior, rather than addressing its
73 potential implications for ecosystem-level fluxes. Thus, resource dynamics, and
74 resource consumption in particular, are a potentially unexplored consequence of
75 dispersal syndromes on ecosystems [12].

76 Detritus consumption by detritivores is a strong determinant of decomposition
77 rate, one of the key fluxes in ecosystems [13,14]. Decomposition of organic matter is
78 especially important in freshwater ecosystems, because it enables terrestrial detritus to
79 subsidize the aquatic food web [15], and shredding of leaf litter by invertebrate
80 detritivores is a key step in the decomposition process [16,17]. Here, we used
81 shredding freshwater detritivores to test whether dispersers differ in their leaf litter
82 consumption rate and thus their contribution to ecosystem function (decomposition).
83 We used one native and one non-native species of amphipod (Crustacea: Amphipoda),
84 a guild of dominant shredding invertebrates in European streams [18]. Amphipod
85 abundance can drive total terrestrial leaf litter shredding [19,20], however these two
86 species are functionally non-equivalent in their shredding activity [21–23]. After an
87 initial experiment where we allowed individuals to disperse in experimental two-patch
88 landscapes, we examined whether dispersers and non-dispersers (henceforth
89 “residents”) differed in leaf consumption rates.

90

91 **Methods**

92 We used one native amphipods species, *Gammarus fossarum* (Koch), and one
93 non-native amphipod species, *Dikerogammarus villosus* (Sowinsky), in our
94 experiments. *Gammarus fossarum* is very common in headwater streams throughout
95 Switzerland and central Europe [24]. We collected adult *G. fossarum* from the

96 Sagentobelbach stream in Dübendorf, Switzerland (47.39° N, 8.59° E) in November
97 2016. In the laboratory, amphipods were placed in holding containers of ~500
98 individuals, gradually brought up to 18 °C, and acclimated to laboratory conditions
99 for 60 hours, during which ad libitum alder (*Alnus glutinosa* (Gaertner)) leaves were
100 available as food. This was repeated in January 2017 with *D. villosus*, a species which
101 originates in the Ponto-Caspian region and has expanded into central Europe in the
102 last two decades [25], with individuals collected from Lake Constance at Kesswil,
103 Switzerland (47.60° N, 9.32° E). For each species, the experiment was conducted in
104 two steps: a dispersal experiment followed by a leaf consumption experiment.
105 Experimental protocols, including length of dispersal phase and length of
106 consumption experiment, were adapted depending on the species' activity levels and
107 consumption rates, based on pilot experiments. *Gammarus fossarum* used in the
108 experiment had a mean dry weight of 3.30 mg (s.d. ±1.33), and *D. villosus* had a mean
109 dry weight of 8.59 mg (s.d. ±2.60).

110

111 *Dispersal experiment*

112 One of the most common methods for examining the causes and consequences
113 of dispersal is to allow organisms to disperse through linked experimental patches in
114 systems ranging from two-patch pairings [26] to larger grids or networks [27,28]. The
115 dispersal experiments were run according to the Dispersal Network (DispNet)
116 distributed experiment protocol, detailed in [26]. Briefly, we set up 40 replicates of a
117 two-patch mesocosm system, with 10 replicates each in a factorial design of resource
118 availability (alder leaves vs. no food) and predator cues (fish kairomones vs. no
119 kairomones). Because we found no effect of the resource or predator cue context on
120 dispersal rates in amphipods [26], we pooled data from the different treatments

121 together for this analysis and only considered the effect of dispersal status (disperser
122 vs. resident) on subsequent leaf consumption. Residuals from the models (described
123 below) confirmed that no additional variation in leaf consumption rates was explained
124 by experimental context/treatment (Figure S2).

125 Each patch was a 3 L (198 x 198 mm) polypropelene box, and each pair of
126 patches (one “origin” and one “target” patch, with their relative positions randomized
127 within each pair) was connected by 30 cm of silicon tubing with 20 mm diameter.
128 Patches were covered with a black lid to reduce light permeability, while the
129 connection tube was left uncovered; this light difference between patches and matrix
130 rendered the connection tube a hostile matrix, since photophobia is an antipredation
131 strategy in amphipods [29]. We also measured movement (gross swimming speed,
132 extracted from videos of the animals using the ‘BEMOVI’ package [30] in R), and
133 this did not differ significantly between residents and dispersers (Figure S1). Thus, we
134 are confident that relocation from the origin to target patch was not simply due to
135 routine movement in the course of foraging, but indeed represented dispersal.

136 Twenty amphipods were placed in each origin patch and allowed to habituate
137 for 30 minutes. We then opened a clamp that had been used to close the connection
138 and amphipods could disperse for a period of 4 ½ hours (*G. fossarum*) or 7 hours (*D.*
139 *villosus*) before the connection tube was closed again.

140

141 *Consumption experiment*

142 After the dispersal experiment, amphipods were transferred to new single-
143 patch mesocosms (2 L plastic containers with 0.4 m² of substrate area) to measure leaf
144 litter consumption. The density of amphipods used in the leaf consumption
145 experiment was standardized between dispersers and residents to account for possible

146 effects of density on leaf consumption rates [31]. Thus, from each two-patch system,
147 all dispersers were moved to one new mesocosm, and an identical number of
148 haphazardly-chosen residents was moved to a separate new mesocosm. Densities
149 remained highly correlated at the replicate block level throughout the experiment (*G.*
150 *fossarum*: $r = 0.89$, $p < 0.001$; *D. villosus*, $r = 0.53$, $p = 0.05$). Mesocosms were
151 provisioned with 1.5 g (dry weight) of conditioned alder leaves. The leaf consumption
152 experiments were run for 19 (*G. fossarum*) and 12 (*D. villosus*) days, respectively, at
153 which point leaves from the mesocosms were collected and dried for 48 h at 60 °C,
154 then weighed to calculate mass loss from the beginning of the experiment. Amphipods
155 were counted every two to three days throughout the experiments to track mortality;
156 overall, survival was 76.3% for *G. fossarum* and 95.4% for *D. villosus*. These
157 mortality estimates were used to calculate an average daily amphipod density for each
158 mesocosm over the length of the experiment. At the end of the experiment, amphipods
159 were sacrificed and dried for 48 h at 60 °C. The average daily biomass in a mesocosm
160 (mg m^{-2}) was then calculated as the average daily density (above) multiplied by the
161 average weight of individuals in the mesocosm. Leaf consumption rates were
162 calculated as the dry weight of leaf litter consumed per milligram of amphipod dry
163 weight per day.

164

165 *Analysis*

166 Consumption rates were compared between residents and dispersers of each
167 species separately using linear mixed-effects models with the ‘lme4’ package, version
168 1.1-18-1 [32], in R version 3.5.0 (R Core Team, Vienna, Austria, 2018). Distributions
169 of consumption rates were positively skewed, so to meet assumptions regarding error
170 structure the *G. fossarum* data were square-root transformed and the *D. villosus* data

171 were inverse-transformed (response = 1/consumption rate) before analysis. For both
172 species, the response was modeled with dispersal status (disperser vs. resident) as a
173 fixed factor, and replicate block (the two-patch experimental metapopulation from
174 which dispersers and residents originated) as a random intercept. The replicate block
175 accounted for all potential differences associated with the experimental
176 metapopulation of origin and density. After building the mixed-effect models, a
177 conditional R^2 value (accounting for both random and fixed effects) was calculated
178 using the ‘MuMIn’ package, version 1.42.1 [33]. Differences in consumption rates
179 between dispersers and residents were tested using Tukey HSD tests using the
180 ‘multcomp’ package, version 1.4-8 [34].

181

182 **Results**

183 For *G. fossarum*, the estimated difference between square-root transformed
184 daily consumption rates of residents and dispersers was 0.020 (standard error of the
185 estimate = 0.121; model $R^2 = 0.38$) (Table 1). For *D. villosus*, the estimated difference
186 between inverse-transformed daily consumption rates of residents and dispersers was
187 0.208 (standard error of the estimate = 0.063; model $R^2 = 0.82$), which was significant
188 according to post-hoc testing ($z = 3.31$, $p < 0.001$, Table 1). Dispersing *D. villosus*
189 had similar biomass-adjusted consumption rates to *G. fossarum*, and approximately
190 three times higher than non-dispersing *D. villosus* (Figure 1).

191

192 **Discussion**

193 We identified a dispersal syndrome with consequences for ecosystem
194 functioning in a non-native but not a native species: *D. villosus* dispersers consumed
195 leaf litter at roughly three times the rate of residents, while there was no difference in

196 leaf consumption rate with dispersal status in *G. fossarum*. To date, most research
197 addressing consumption rates in relation to dispersal status or range fronts has been in
198 a behavioral context, addressing personality and aggression as contributions to
199 predator-prey interactions [11,35,36]. To our knowledge there has been little research
200 into consumption of basal resources as a component of nonrandom dispersal. This is
201 despite the importance of such traits to energy flows through food webs and
202 ecosystems. Furthermore, differences in traits that may depend on resource
203 consumption – such as size, metabolism, and growth rates [2,8] – with dispersal
204 propensity render resource consumption a logical component of a dispersal
205 phenotype, and thus one which could have consequences for energy fluxes through
206 food webs and ecosystems.

207 Our study species are omnivorous aquatic invertebrates, which despite a wide
208 diet breadth contribute the bulk of leaf litter processing in central European headwater
209 streams [19]. Our results show that in *D. villosus*, dispersers make a greater
210 contribution to the detritus-based pathway integrating terrestrial energy into the food
211 web than do residents. This species also has lower overall contributions to leaf litter
212 processing than *G. fossarum* [21–23], but we suggest that both species identity and
213 dispersal status of individuals within a species could jointly determine their
214 contribution to ecosystem function.

215 Predicting these populations' contributions to ecosystem function is important
216 because *D. villosus* has deemed one of the 100 worst invaders in European freshwater
217 ecosystems [38]. Therefore, its dispersal syndrome should be considered in that
218 context. Because the non-native species is undergoing an active range expansion, the
219 signature of either tradeoffs for increased dispersal ability or selection for success in
220 new habitats is likely more prominent than in populations which are in their range

221 core (such as the *G. fossarum* populations used in our experiment), consistent with
222 spatial selection theory [41]. Identifying whether this is true or whether the dispersal
223 syndrome is consistent across the range of *D. villosus* would require performing
224 experiments with *D. villosus* from its range core in the Ponto-Caspian region. This
225 would also address whether it is appropriate to make interspecific comparisons of this
226 and other phenotypic traits using populations with different recent dispersal/range
227 expansion histories, depending on the research question.

228 Regardless, how non-native species will affect ecosystem function is a central
229 question in the era of global change and increased connectivity [42]. As the location
230 of suitable habitat shifts and human activity continues to increase organismal dispersal
231 globally, the potential effects of phenotype-dependent dispersal should be considered
232 when attempting to predict impacts on ecosystem function. This may be challenging,
233 because it means that predictions made based on species contributions to ecosystem
234 function in their range core may not be valid at the edges of their range expansions
235 [42]. However, considering prior evidence of how dispersal phenotypes can alter
236 community dynamics, it is crucial to extend this understanding into the realm of
237 ecosystem function.

238

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245

246 **Author contributions**

247 EAF conceived the dispersal experiment and all authors together designed the
248 consumption experiment. CJL and EAF ran the experiments. CJL analyzed the data
249 and drafted the manuscript. All authors contributed to revisions, gave final approval
250 for publication, and agreed to be held accountable for the work within the article.

251

252 **Data accessibility**

253 Data will be made available on Dryad and code will be posted to GitHub upon the
254 manuscript's acceptance; both are available to reviewers as extra supplementary
255 material.

256

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261

262 **Competing interests**

263 We have no competing interests.

264

265 **Ethical statement**

266 No ethics approval was required for this experiment. Work with non-native species
267 was carried out according to the laws of Switzerland.

268

269 **Figure/table legends**

270

271 **Figure 1.** Daily average leaf litter consumption by dispersing and non-dispersing
272 (“resident”) amphipods of *G. fossarum* (n = 73 mesocosms) and *D. villosus* (n = 53),
273 adjusted for biomass of the individuals in each experimental replicate. Error bars
274 show standard error of the mean, and gray dots show raw data points from
275 experimental mesocosms. Asterisk shows a significant difference ($p < 0.05$) between
276 consumption rates of dispersers and residents according to a linear mixed effect
277 model.

278

279 **Table 1.** Results from the linear mixed-effects models of biomass-adjusted
280 consumption rates as a function of dispersal status, for *Gammarus fossarum* (n=73
281 mesocosms) and *Dikerogammarus villosus* (n=53). Estimates and their standard errors
282 are drawn from linear mixed-effects models, and z- and p-values for the effect of
283 dispersal status are from Tukey’s HSD tests; variance associated with the random
284 factor of replicate blocks, and its standard deviation, is reported in italics.

285

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411

412 **Tables**

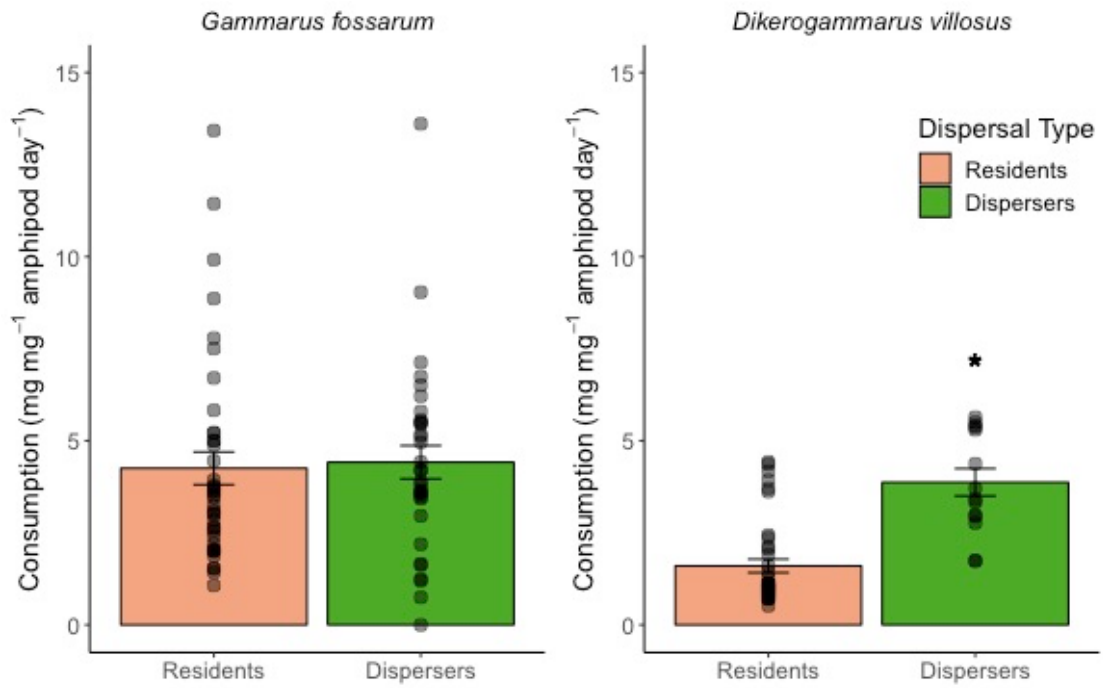
413 **Table 1**

	Coefficient	Std. Error/ Std. Dev.	z	p
<i>G. fossarum</i> (square-root transformed daily consumption)				
Intercept (residents)	1.951	0.110		
Dispersers	0.019	0.121	0.163	0.87
<i>Variance due to replicates:</i>	<i>0.156</i>	<i>0.395</i>		
<i>D. villosus</i> (inverse-transformed daily consumption)				
Intercept (residents)	0.666	0.080		
Dispersers	0.209	0.063	3.311	< 0.001
<i>Variance due to replicates:</i>	<i>0.125</i>	<i>0.354</i>		

414

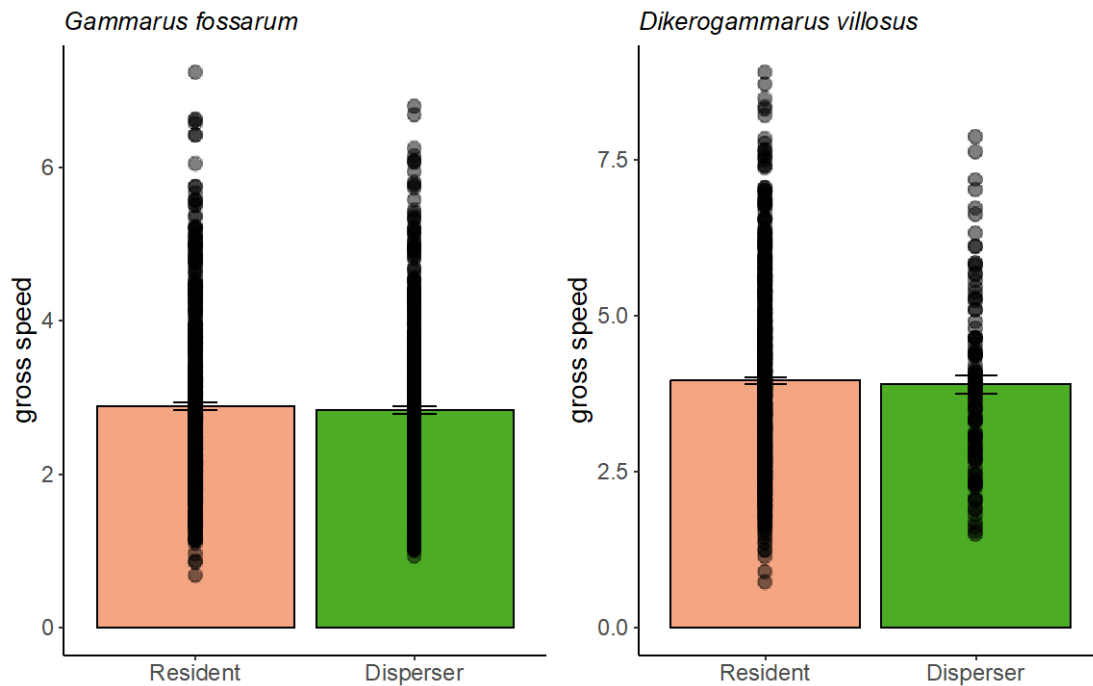
415 **Figures**

416



417

418 **Figure 1.**

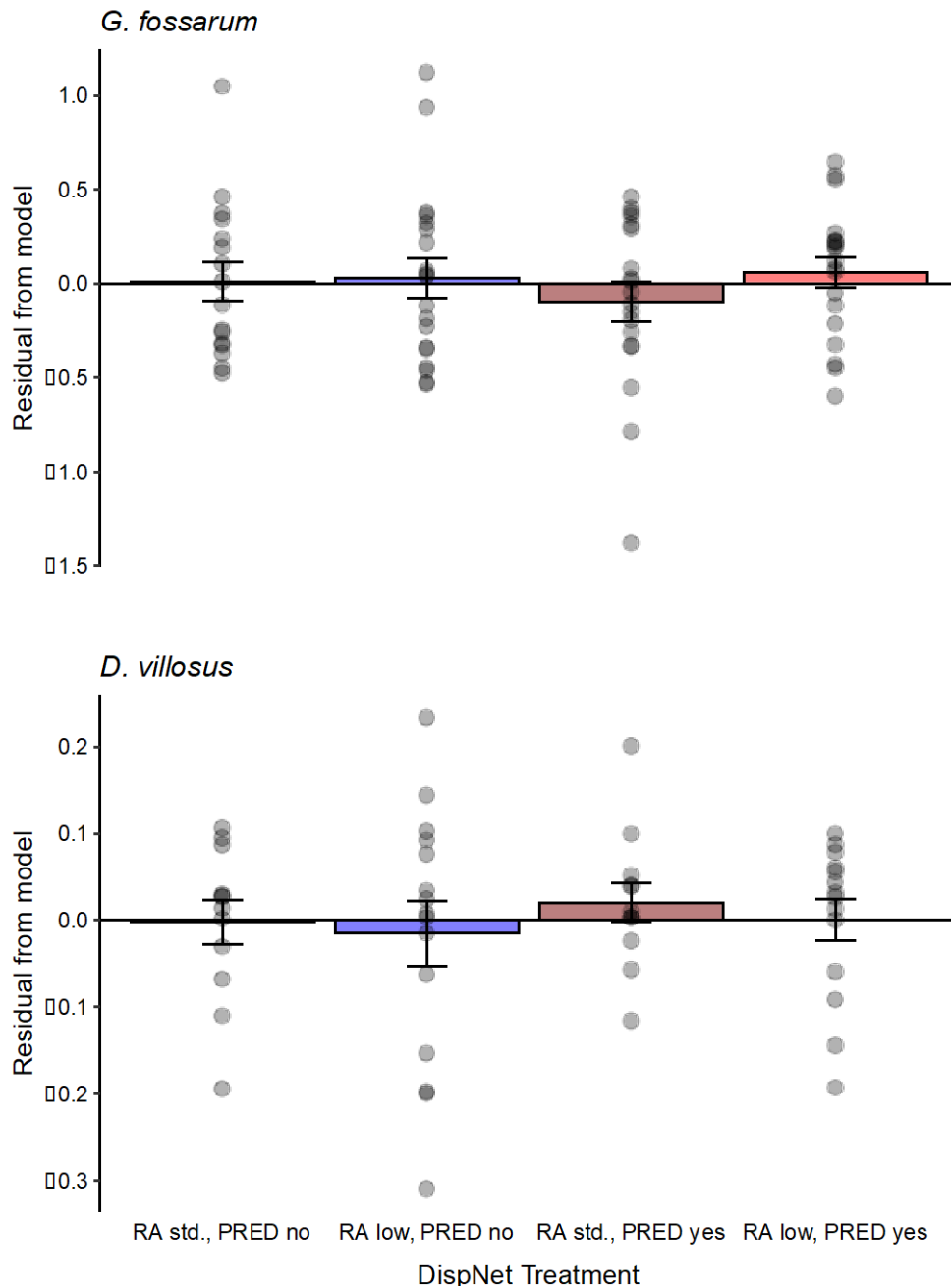


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422 **Figure S1.** Gross swimming speed of residents and dispersers, from video analysis using
423 the 'BEMOVI' package in R. Before being placed into the consumption mesocosms,
424 residents and dispersers were (separately) placed into an experimental arena and and
425 allowed to move freely for three minutes. Each time an amphipod moved it was
426 detected it was given an object identifier and the movement was described; gray dots
427 in the figure represent each movement, and error bars show the standard error of
428 speed for residents and dispersers. There were no significant differences in swimming
429 speed between residents and dispersers based on simple linear models in either *G.*
430 *fossarum* ($F_{1,1109} = 0.57$, $p = 0.44$) or *D. villosus* ($F_{1,824} = 0.17$, $p = 0.68$).

431

432



433

434 **Figure S2.** Model residuals from the mixed-effect models (transformed consumption

435 rate ~ dispersal status + (1|replicate block)) plotted against treatments from the

436 dispersal experiment: RA = resource availability (standard or low), PRED = predator

437 cues (no or yes). Linear models of residuals as a response of dispersal experiment

438 treatment showed no significant effects (*G. fossarum*: $F_{3,69} = 0.49$, $p = 0.69$; *D.*

439 *villosus*: $F_{3,49} = 0.25$, $p = 0.86$). Error bars show standard error of the mean, and gray

440 points show residuals from individual experimental replicates.