

24 **ABSTRACT (150 words)**

25 Understanding the mechanisms that promote coexistence is a central topic in ecology. Among
26 plausible mechanisms of coexistence are different dispersal rates of competing types in
27 heterogeneous environments. A large body of mathematical theory, based on Lotka-Volterra-like
28 equations, proved non-coexistence, with the slower dispersing competitor always excluding the
29 faster disperser. Notably, these results have not been tested empirically and these predictions
30 considered mostly symmetric dispersal. To address these gaps, we not only extended previous
31 theory by including exploitable resources and a component of directed movement, but also tested
32 the new mathematical results experimentally using laboratory populations of the nematode
33 worm, *Caenorhaditis elegans*. In contrast to previous predictions, our novel results reveal, both
34 theoretically and empirically, that even with different symmetric dispersal, two identical
35 competing species with moderate levels of directed components can coexist. Our results advance
36 coexistence theories and underscore the role of directed dispersal in species coexistence in
37 heterogeneous environments.

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39 **Key words:** Consumer-resource model, directed movement, *C. elegans*, coexistence, theory,
40 experiment

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45 INTRODUCTION

46 Understanding the mechanisms that promote coexistence of competing species has been a
47 central goal of community ecology at least since Gause¹, Hutchinson² and has remained a
48 central topic in both theoretical and applied ecology^{3,4,5}. An important step was the
49 classification of all such mechanisms promoting coexistence into equalizing mechanisms and
50 stabilizing mechanisms. Specifically, the former refers to those mechanisms that reduces fitness
51 differences between species, while the latter refers to those that reduce niche overlap^{6,7}. In
52 particular, stabilizing mechanisms can be characterized by differences in how species exploit
53 spatially and temporally varying common resources⁸.

54 Spatial heterogeneity plays a crucial role in promoting coexistence and many studies have
55 found that heterogeneous environments support more species than homogeneous ones^{9,10}. The
56 effects of spatial heterogeneity could be related to several mechanisms proposed by Chesson⁸,
57 two of which are relevant to this study. The first one is the storage effect, which suggests that
58 different species may differ in what for them is high quality habitat, and so may segregate
59 spatially to some extent, thus decreasing interspecific competition relative to intraspecific
60 competition. The second mechanism is called the growth-density covariance, which describes the
61 overcrowding of populations in spatial areas with high maximum growth rates. Both of these
62 mechanisms can lead to mutual invasibility (i.e., intra-specific competition > inter-specific
63 competition), which ensures that the population of each species is bounded from below.

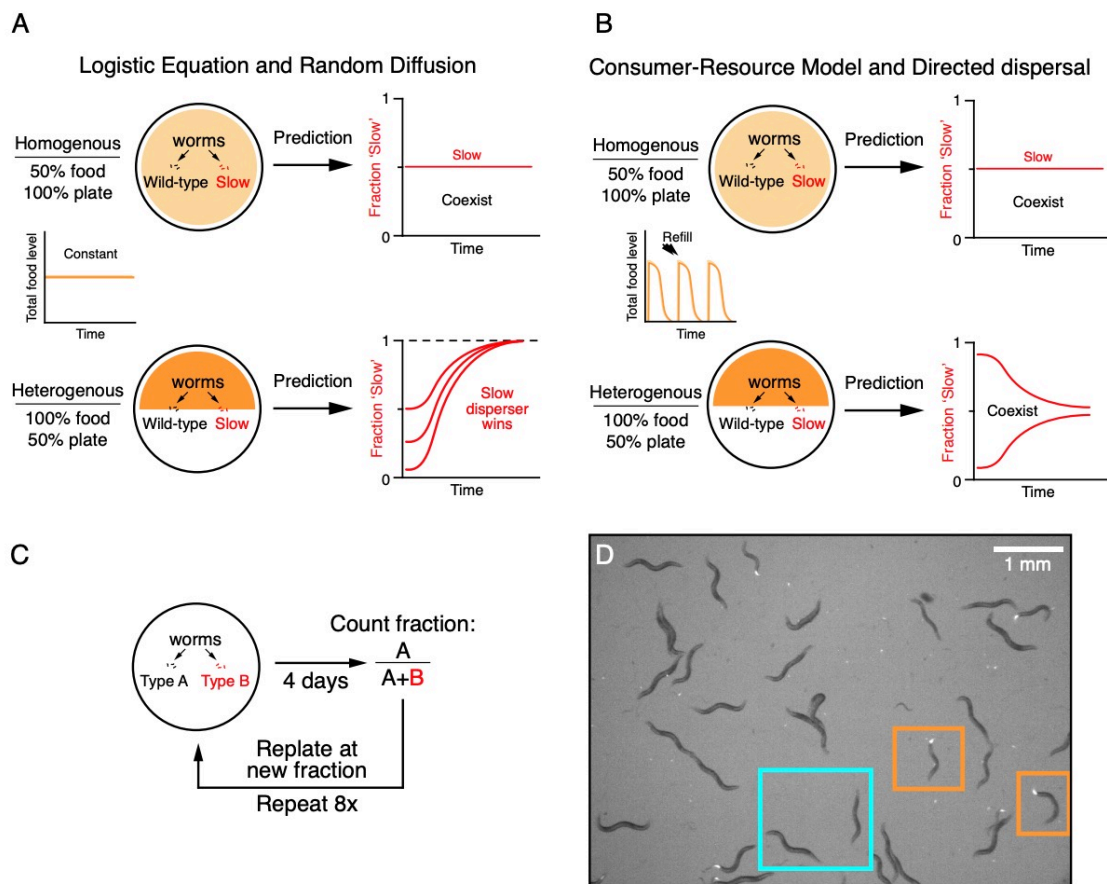
64 In parallel to the large body of coexistence theory in the ecology literature, a body of
65 mathematical theory, based on Lotka-Volterra-like equations, has specifically examined the
66 competition of two species dispersing at different rates in heterogeneous environments. The
67 theory considers a special but illuminating case where two competing species are entirely similar

68 except for their dispersal rates (i.e., slow *vs.* fast dispersers). Many theoretical studies have
69 shown that with random movement the slower disperser always outcompetes the faster one in
70 heterogeneous environments (e.g., Hastings ¹¹, Dockery, Hutson ¹², He and Ni ¹³, Cantrell and
71 Cosner ¹⁴) (Prediction is shown in Fig. 1A). A heuristic explanation is that population density in
72 favorable habitat is higher, so with random movement, the fast disperser moves from favorable
73 to unfavorable locations at a greater rate than the slow disperser, which gives an advantage to the
74 slow disperser.

75 A critical limitation of the above mathematical theory is the assumption that the two
76 competing dispersers only undergo pure diffusion (i.e., non-directed movement), whereas,
77 dispersal in nature is typically driven in part by spatial cues instead of being purely random ^{15, 16},
78 ¹⁷. Therefore, there is motivation to improve the assumption by including a certain degree of
79 directed movement of both dispersers towards more favorable environmental conditions^{18, 19}.
80 Another constraint of previous theory based on Lotka-Volterra-like equations is that it does not
81 explicitly consider the time scales of feedbacks between the organisms and their resource ²⁰, so
82 that it may not accurately represent real populations when applied to spatially heterogeneous
83 systems ^{21, 22}. Hence, we adopt a consumer-resource model that accounts for the resource
84 dynamics as an additional variable ^{23, 24}, which is more suitable for describing the effects of
85 environmental heterogeneity and dispersal ^{22, 25, 26, 27, 28}.

86 It is challenging to empirically test this body of competition theory owing to the major
87 hurdles of producing two phenotypes of a species that are nearly identical in all aspects except
88 for the dispersal rates, and then measuring their relative abundances when competing. Hence, the
89 relevant empirical tests are still lacking ^{29, 30}. To fill in the gap in our understanding of how
90 dispersal in heterogeneous regions affects coexistence outcome, we first extended the theory on

91 the effect of movement on coexistence using the consumer-resource model with directed
 92 movement of consumers (Prediction is shown in Fig. 1B). We performed rigorous experiments
 93 with different strains of the nematode, *Caenorhaditis elegans*, to validate our theoretical
 94 predictions. These strains have different rates of the random component of movement, but
 95 comparable components of directed movement towards areas of higher resource density³¹. We
 96 were able to provide a rigorous test of the hypothesis that a combination of diffusion and directed
 97 movement in heterogeneous environments can lead to coexistence of two species that are
 98 identical in all respects except for their rates of symmetric diffusion.



99

100 Figure 1. Schematic diagram of theoretical predictions, A: Based on paired logistic equations
 101 with random diffusion; B: Based on the paired consumer-resource model with directed
 102 movement; C: Representation of experimental design on “transfer event”; D: Micro-graphed
 103 image with labeled progeny (in orange boxes) and unlabeled progeny (in blue boxes).

104

105 **RESULTS**

106 **Overview**

107 Here, we provide an overview of our modeling and experimental methods, with full
108 details presented below. We first modeled paired competing consumers exploiting a common
109 resource/nutrient on three patches, where the patches have differing nutrient concentrations that
110 do not diffuse, and the consumers are identical except for differences in dispersal rate, which was
111 a close match to the theoretical assumption. In the experiments, we paired progeny of *C. elegans*
112 with distinguished roaming (roamer) and dwelling (dweller) locomotion (fast and slow
113 dispersing) behaviors to determine whether the two strains, identical except for their rates of
114 symmetric diffusion rates, can coexist. Compared to the dweller, which tends to stay within a
115 smaller area, the roamer moves much faster across a bacterial lawn and turns infrequently³¹. In
116 order to be able to visually compare the dweller and roamer in competition, we paired both with
117 a fluorescently labeled strain, which was intermediate in movement. In total, the locomotion rate
118 follows the ranking: roamer > fluorescently labeled strain > dweller (see labeled and unlabeled
119 strains in Fig. 1D).

120 The paired strains were allowed to forage in both heterogeneous and homogeneous
121 environments of bacteria prey (resource). The homogeneous environment was prepared by
122 uniformly spreading the *E. coli* bacteria across the entire surface of the petri dish while the
123 heterogeneous environment was prepared by spreading the same volume of food onto one half of
124 the dish (see schematic figures in Fig.1 A and B).

125

126 Numerical model simulation results

127 Our goal was to determine the effect of a combination of diffusion and directed
128 movement on the competition between two consumer species that are identical in all respects
129 except for their rates of symmetric diffusive movement. The two consumers were described by
130 Appendix A, Eqs. (1a-q) in a three-patch system, Patch 1 received the largest input of limiting
131 resource, $N_{input,1}$, while Patch 2 received about half of the resource of Patch 1, and Patch 3
132 received a very small input. Note that the three-patch system were modeled for consistency with
133 the experiment described below and the results hold in a two-patch system (Patch 1 received
134 nearly all input of limiting resource, while Patch 2 received a very small input).

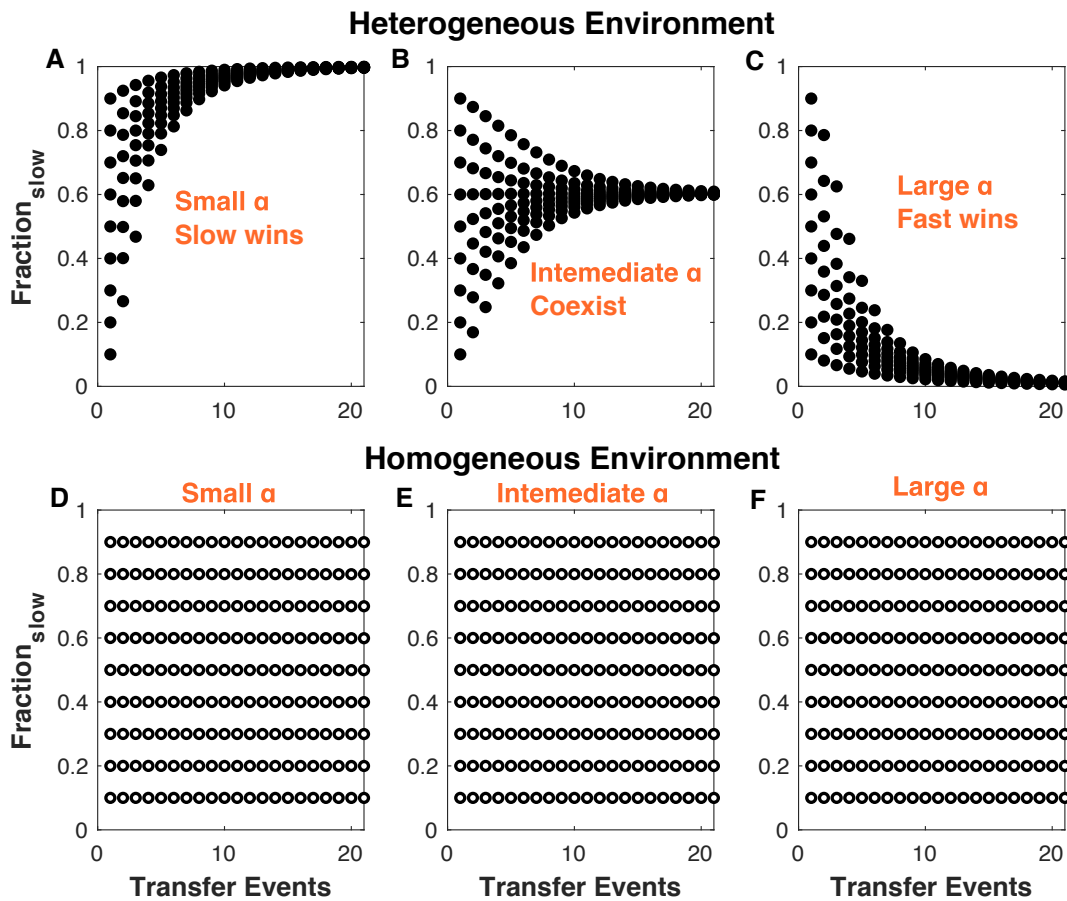
135 The first set of simulations was run over a long enough time to reach equilibrium without
136 breaking the simulation into smaller segments separated by transfer events to new plates, which
137 would match the experiments. As in the experiments, however, both populations started initially
138 on Patch 2 in different proportions (or fractions). For all initial fractions, the equilibrium absolute
139 values reached by the slow and fast dispersers varied as a function of the coefficient of directed
140 movement, α , as shown in Fig. S1 in Supporting Information Appendix A for Patches 1 and 2
141 (populations on Patch 3 were much smaller and not shown). For small directed movement ($\alpha \leq$
142 0.1), the slower disperser excluded the fast disperser, because the slow disperser maintained both
143 a higher population size and higher growth rate on Patch 1. For large directed movement, the
144 movement towards Patch 1 ($\alpha \geq 0.35$), both populations experienced high intraspecific and
145 interspecific competition, limiting their sizes through high rates of density-dependent mortality.
146 However, the fast disperser was able to escape Patch 1 at a faster rate to Patch 2 and build up
147 population, dominate on that patch through priority effect on that patch, and spread back to Patch
148 1 to exclude the slow disperser from the system. For intermediate levels of directed movement

149 (0.1 < α < 0.35) the two competitors partially specialized on different patches (the slow disperser
150 on Patch 1 and the fast disperser on Patch 2), so that coexistence occurred. These results are
151 proved analytically in Supporting Information, Appendix B.

152 The second set of simulations imitated the experiments, in which transfer events to new
153 plates were periodically used. Each transfer event was defined as a process of renewing nutrient
154 levels in each patch, and the populations were reestablished in the same fractions that existed at
155 the end of the preceding time step, so that the competitive dynamics could proceed (Fig. 1C). In
156 the simulations of heterogeneous environments, for a range of intermediate value of α (0.1 < α <
157 0.35) the trajectories for all starting fractions of the slow disperser, $fraction_{slow}$, converged on the
158 same final point (Fig. 2B). It is important to note that the convergence point ($fraction_{slow}$)
159 depends on levels of directed movement; it was higher when α was small and smaller when α
160 was large. We set $\alpha = 0.125$ in Fig. 2B which led to a final $fraction_{slow}$ close to the experimental
161 result (0.6). When α was smaller than 0.1, $fraction_{slow}$ increased to 1, indicating that the slow
162 disperser wins (Fig. 2A); conversely, when α was larger than 0.35, $fraction_{slow}$ declined to 0,
163 indicating that the fast disperser wins (Fig. 2C). In comparison, in a homogeneous setting, the
164 fractions all stayed close to their initial values independent of changes in α (Fig. 2D-F). We have
165 also obtained analytical results concerning the invasibility of the both the slower and faster
166 disperser when initially rare, given that the competitor is at the equilibrium state, which were
167 consistent with the simulations. The analytical results, presented in Supporting Information
168 Appendix B, proves that coexistence is possible only when directed movement is intermediate,
169 while the slower (resp. faster) disperser is favored when the directed movement is weak (resp.
170 strong).

171 Overall, the two sets of simulations showed similar results that for the two species with
 172 an identical rate of directed movement and different rates of their symmetric diffusion
 173 components of movement, stable coexistence occurs over a range of intermediate rates of
 174 directed movement. For rates of directed movement below this range, the slower disperser
 175 always ultimately excludes the faster disperser. For rates above this range, the fast disperser
 176 excludes the slow disperser.

177



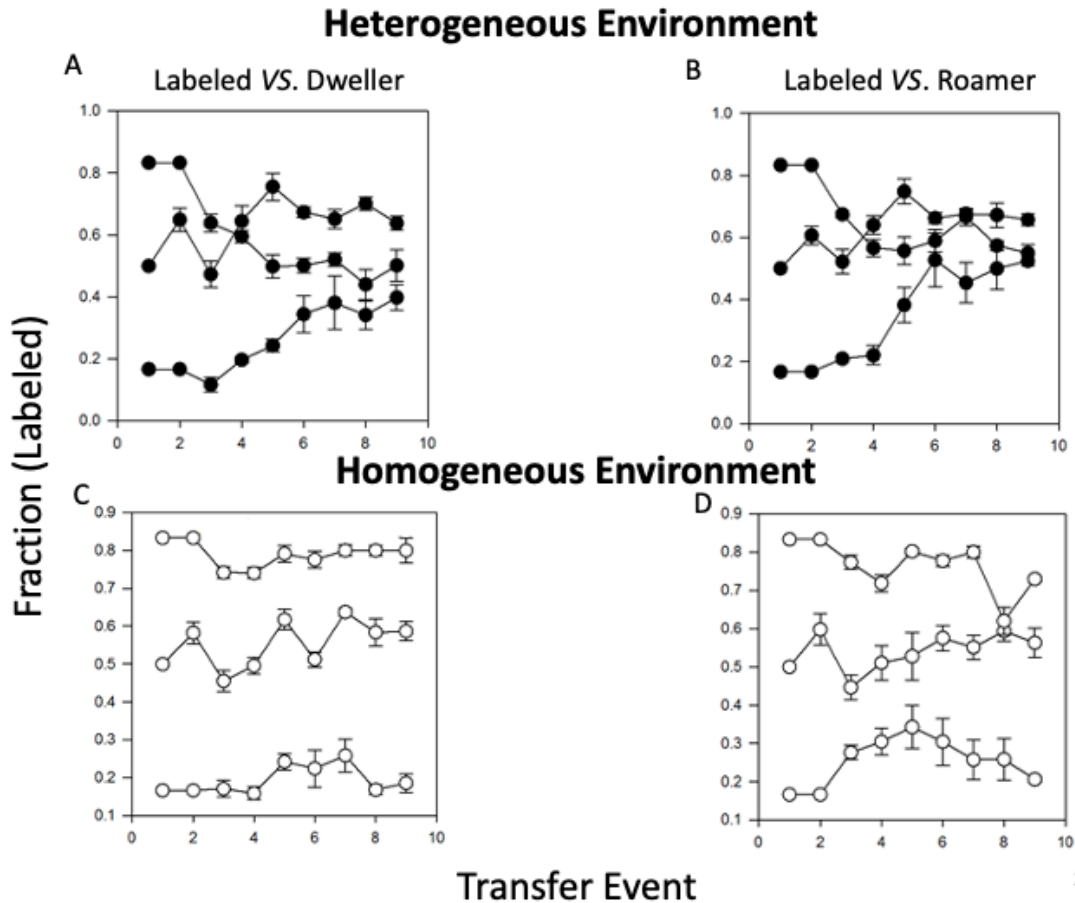
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179 Figure 2. The fraction of slow disperser over 20 transfer events with a series of initial fractions
 180 (0.1 – 0.9) in heterogeneous environments with A: small α (≤ 0.1); B: intermediate α (0.1 ~
 181 0.35); C: large α (≥ 0.35); and in homogeneous environments with D: small α (≤ 0.1); E:
 182 intermediate α (0.1 ~ 0.35); F: large α (≥ 0.35). Each dot represents the $fraction_{slow}$ of each
 183 transfer event, black filled dots represent heterogeneous environments and empty dots represent

184 homogeneous environments. Initial nutrient levels in the three patches in heterogeneous
185 environments are (200, 100 and 1) and in homogeneous environments are 100, 100 and 100. To
186 evaluate the results, we used the fraction of slow disperser as $fraction_{slow} = \frac{\sum_{i=1}^3 U_i}{\sum_{i=1}^3 U_i + \sum_{i=1}^3 V_i}$
187 to represent the dominance of slow disperser.
188

189 **Experimental results**

190 We paired labeled strain & dweller, labeled strain & roamer growing in both the
191 heterogeneous and homogeneous environments. Each environment contained 200 μ l total OP50
192 bacteria grown in B broth on 60 mm NGM plates. The labeled strain explored about 70% of the
193 lawn during a 16 hr interval on average. Differently, over the same interval, known mutants with
194 elevated dwelling behavior (dweller) explored less than 20% of the lawn, and the *egl-4* mutant
195 with elevated roaming behavior (roamer) explored more than 90% of the lawn³¹. Six late L4-
196 stage worms in total were placed on the center of each plate with three different initial fractions
197 of the fluorescently labelled progeny, which were 1:5, 3:3 and 5:1. In the heterogeneous case,
198 when the labeled control progeny was paired with both dweller and roamer, a similar convergent
199 pattern was shown in both cases, and the final fraction stayed closely to 0.6, suggesting that the
200 two strains coexisted over eight transfer events (Fig. 3A, B). Contrary to the heterogeneous
201 environment, we found that in the homogeneous environment, the $fraction_{labeled}$ stayed nearly
202 constant around the initial values (Fig. 3C, D). The experimental results were a close match with
203 our theoretical results described above.



204

205 Figure 3. Dynamic change of fraction of LX2004 (labeled) with A,C: dweller, B,D: roamer over
 206 eight transfers in heterogeneous environments (dark dots) and in homogeneous environments
 207 (empty dots).

208

209 **DISCUSSION**

210

211 A consumer-resource model, rather than a Lotka-Volterra model, is a better framework to
 212 describe the competing *C. elegans* strains, as it appropriately describes feeding on an exploitable
 213 resource, such that the competition is exploitative, as in the experiments^{22, 32}. Additionally, a key
 214 difference with the model we used here is that “Lotka-Volterra model” assumed instantaneous
 215 feedback between resource and consumer (i.e. complete separation of time scale), which is not
 216 accurate. By a novel experimental design, we were able to obtain empirical results concerning
 the competition of two species with different dispersal strategies. Moreover, we combined

217 experimental, numerical and mathematical approach to extend previous work from a single
218 species to a pair of competing species ²². Our results demonstrate that the consumer-resource
219 model, with a directed dispersal component, provides a suitable modeling approach to explore
220 the effect of environmental heterogeneity and dispersal on species coexistence.

221 In contrast to the paired logistic equation model with different levels of symmetric
222 diffusion but no directed movement, which has been used previously and which predicted that
223 the slow disperser always prevails in heterogeneous environments ¹¹, our experiments showed a
224 relatively stable coexistence pattern between the two species with different dispersal rates in
225 heterogeneous environments, over a range of intermediate speeds of directed movement.
226 Consistent with the logistic equation prediction, the experimental fraction of the two species
227 stayed constant in homogeneous environments. To explain the mismatch between the
228 experiments and logistic model's theoretical predictions in heterogeneous environments, we
229 modified the consumer-resource model, based on Zhang, Kula ²², to describe paired competing
230 consumers exploiting a common resource. Further, to represent the experimental system in which
231 both species showed a similar net directional movement from a lower nutrient area to a higher
232 nutrient area, a directed dispersal component was added to the symmetric (or unbiased) dispersal
233 in our new model.

234 The numerical simulations and mathematical analysis of the new model are in close
235 agreement with the experimental results, in which the two consumers could coexist for a long
236 time when they had an intermediate level of directed dispersal. When directed dispersal was zero
237 or small, the model showed the slower disperser excluding the faster one, which is consistent
238 with Hastings ¹¹ and Dockery, Hutson ¹². When directed dispersal was large, both species were
239 not using the resource (or choosing the habitat) optimally but were exposed to high density-

240 dependent limitation in Patch 1 from intra- and interspecific competition. In that case, greater
241 dispersal outweighed the disadvantage of greater diffusion from the more productive patch, so
242 faster disperser excluded the slower disperser. Thus, intermediate levels of directed dispersal can
243 be viewed as a transition between the two extreme cases, in which coexistence can occur.
244 Besides dispersal, environmental heterogeneity plays an important role contributing to species
245 coexistence^{33, 34, 35}. In this study, the heterogenous environment was designed such that only
246 50% of the available habitat was covered by resource, so it can be considered as a source-sink
247 system. Therefore, both our model and experimental results support the hypothesis that a trade-
248 off between competition and dispersal should lead to regional coexistence of competing species
249^{5, 36}.

250 This study highlighted two important novel insights in understanding species coexistence
251 in heterogeneous environments: 1. Compared to the simple logistic model, it is more realistic to
252 use the consumer-resource model developed here because it takes into account of the dynamic
253 change of the resource²⁰. Nonetheless, it is still important to note that the logistic model with
254 directed movement can also lead to coexistence when random dispersal rate is small and
255 advection large³⁷. Thus, the consumer-resource model is a mechanistic approach that reflects the
256 environmental requirements of a population and the effects of that population on the
257 environment simultaneously^{24, 38, 39}. 2. It is essential to investigate the combined effects of
258 dispersal and environmental heterogeneity on spatially extended dynamics^{40, 41}, as the ability of
259 a species to disperse to newly available habitats is crucial to ensure species survival, especially
260 under the changing climate⁴².

261 This study has various ecological implications. For instance, *C. elegans*, as a live animal,
262 shows a net movement from a lower nutrient patch to a higher nutrient patch⁴³. Environmental

263 conditions are ever-changing, temporally and spatially; hence, if individuals can obtain clues of
264 neighboring environments, to determine the best direction to disperse, the benefit of high
265 dispersal can be enhanced ⁴⁴. Additionally, it is a complex and highly challenging problem to
266 predict the metacommunity dynamics in heterogeneous environments because the differences in
267 dispersal rates among competing species alter their dominance and community structure ⁴⁵. Thus,
268 concepts from this study would be useful in explaining coexistence ⁴⁶, where metacommunity is
269 defined as a set of local communities that are linked by dispersal ^{47, 48}.

270

271 **LIMITATIONS AND FUTURE EXPLORATIONS**

272 Our empirical findings showed that the two species can coexist for least eight transfer
273 events. Friedenber^g ⁴⁹ performed evolution experiment with *C. elegans* for five generations (each
274 transfer event is nearly equal to one generation), hence the experimental time length we
275 conducted is believed to be long enough. There is still a possible mismatch between the
276 timescale of the mathematical theory and practical experimental limitation, since mathematical
277 models often project long-term behaviors where the system reaches a stable and equilibrium
278 state. In contrast, biological experiments are mostly performed on shorter timescales relative to
279 the life cycle of the organism ⁵⁰. It is possible that the coexistence observed in our experiment is
280 an example of long transient behavior. This mismatch as the transient dynamics ^{51, 52, 53}, have
281 been shown to plays a critical role in understanding species coexistence. However, detecting this
282 transient behavior is still a “black-box” in both mathematics and biology ⁵⁴. Our study, as a
283 pioneering effort, looked at species coexistence at both relatively short timescale (experiment)
284 and longer timescale (mathematics), and showed that short term experiments can provide a
285 reasonably good match with the theoretical prediction.

286 We have only investigated the effect of dispersal rate on species coexistence. Extending
287 such study to include comprehensive understanding of multiple dimensions of dispersal (e.g.,
288 distances involved, directionality of movement) is crucial because it can provide more realistic
289 representations of nature. For instance, considering dispersal distance is important as it is
290 necessary to accurately model natural phenomena; e.g., Nunez - Mir, Guo ⁵⁵ showed that
291 invasive species could have longer dispersal distance than native species. Dispersal direction is
292 also a critical factor, as it has been well accepted that conditional dispersal confers a strong
293 advantage in variable environments, as long as ecological cues give an accurate prediction of the
294 habitat ⁵⁶. Additionally, a rich theory on dispersal evolution in heterogeneous environments has
295 been developed ^{57, 58}, and Friedenbergr ⁴⁹ performed the first experimental study with *C. elegans*
296 to demonstrate evolution of dispersal in spatiotemporally variable microcosms. Hence, the
297 experimental system of *C. elegans* will be a suitable system to test for long term evolution of
298 dispersal under more complex environments. It is possible to modify our experimental set-up to
299 demonstrate how coexistence patterns could vary over time. Lastly, our work was able to
300 examine competition of two species that are completely identical except their dispersal rates. As
301 tradeoffs in competitive and colonization abilities have been analyzed in models ⁴⁵, we know of
302 no studies that combine such tradeoffs with the context of consumer-resource interactions and
303 information of dispersal. Including the consideration of these factors could fill in substantial gaps
304 in our understanding of how dispersal in heterogeneous regions affects the competition and
305 coexistence of multiple species.

306

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317

318 **Competing interests**

319 None declared.

320

321 **Materials and Correspondence**

322 Requests should be addressed to A.H.

323

324 **MATERIALS AND METHODS**

325 **Mathematical Model**

326 To model competition between organisms, we adopt a consumer-resource model that
327 differs from the classical Lotka-Volterra type models that are often used in the mathematical
328 ecology literature. Lotka-Volterra models are based on logistic growth of individual populations,

329 which incorporate carrying capacity, which has had a confusing history in empirical ecology⁵⁹.
330 Those models do not consider feedbacks between the organisms and their abiotic environment²⁰
331 and they also have limitations when applied to spatially heterogeneous systems^{21,22}. Because the
332 experiments in the study involve a consumer (nematodes) feeding on an exploitable resource (*E.*
333 *coli*), we use a consumer-resource model. However, it should be noted that the main
334 mathematical results presented here are the same for both the consumer-resource and Lotka-
335 Volterra models.

336 By accounting for the resource dynamics as an additional variable^{23,24}, the consumer-
337 resource modeling is a bottom-up approach that is more suitable for describing the effects of
338 environmental heterogeneity and dispersal, as the recent empirical and theoretical studies have
339 revealed^{22,25,26,27,28}. In the following, we analyze a model involving two consumers on a single
340 spatially distributed resource. The two consumers are identical except for their dispersal
341 strategies, which include a symmetric diffusion component that differs between the species, and
342 a directed component that is assumed to be identical for the two species.

343 *Model* - We modeled paired competing consumers exploiting a common resource/nutrient
344 on three patches, where the patches have differing nutrient concentrations that do not diffuse
345 between the patches, and the consumers are identical except for differences in dispersal rate. This
346 situation can be described by the following general model, which was modified based on Zhang,
347 Kula²² to describe the consumer-resource dynamics, and can be written in the form of a one-
348 dimensional n -patch system, where the two consumer populations, resource, and diffusion rates
349 for each patch as follows:

350
$$\frac{dU_i}{dt} = \frac{rN_iU_i}{k + N_i} - mU_i - g(U_i + V_i)V_i$$

351
$$- (d_{i,i-1} + d_{i,i+1})U_i + d_{i-1,i}U_{i-1} + d_{i+1,i}U_{i+1} \quad (1a)$$

352
$$\frac{dV_i}{dt} = \frac{rN_iV_i}{k + N_i} - mV_i - g(V_i + U_i)V_i$$

353
$$- (D_{i,i-1} + D_{i,i+1})V_i + D_{i-1,i}V_{i-1} + D_{i+1,i}V_{i+1} \quad (1b)$$

354

355
$$\frac{dN_i}{dt} = N_{input,i} - \theta N_i - \frac{rN_iU_i}{\gamma(k+N_i)} - \frac{rN_iV_i}{\gamma(k+N_i)} \quad (1c)$$

356

357
$$d_{i-1,i} = d + \alpha \frac{N_i - N_{i-1}}{N_{i-1} + \beta} \quad (1d)$$

358
$$D_{i-1,i} = D + \alpha \frac{N_i - N_{i-1}}{N_{i-1} + \beta} \quad (1e)$$

359

360 where the n patches are connected in a linear fashion and no-flux conditions are assumed at the
 361 ends. To simulate the experimental system, $n = 3$. The complete set of equations for the three-
 362 patch system used in the numerical simulation can be found in Supporting Information Appendix
 363 A.

364 Here U_i is the consumer with slow dispersal rate and V_i is the consumer with fast
 365 dispersal rate, and N_i is the limiting nutrient level, where i represents patch i ($i = 1, 2, 3$),
 366 Parameter r is the asymptotic growth rate under infinite resources, k is the half-saturation
 367 coefficient, γ is the yield (consumer individual reproduction per unit nutrient), m is the mortality
 368 rate, g is the density-dependent loss rate, N_{input} is the nutrient input rate, and d (resp. D) is the
 369 dispersal rate of slow (resp. fast) disperser. We assume all consumer parameters are identical,
 370 except for their dispersal rates, where $d < D$. The parameter α scales the relative importance of
 371 directed movement and β prevents a zero denominator.

372 **Model Simulations**

373 We developed a simulation code, using Matlab 2018, based on Appendix A, Eqs. (1a-i)
374 and using the parameter values listed in Table S1 in Appendix A. Two types of simulations were
375 performed. In the first type the simulations were run over a sufficiently long time period for the
376 population to approach an equilibrium. In the second type the simulations imitated the
377 experiments with transfer events to mimic the experiment. At each transfer event, the nutrient
378 levels were renewed, and the populations were reestablished in the same fractions that existed at
379 the end of the preceding time step but, as described below, at the original total absolute values,
380 so that the competitive dynamics could proceed.

381 *Initial Conditions* - To match the experiment, in heterogeneous environments, Patch 1
382 received the largest input of limiting resource, $N_{input,1}$, while Patch 2 received about half of the
383 resource of Patch 1, and Patch 3 received a very small input. In homogeneous environments, the
384 three patches received the same resource level, each receiving a third of the total resource levels
385 in heterogeneous environments. The model started with six initial subpopulations of the two
386 populations on Patch 2, which match with our experimental designs that are described below.
387 The two populations of slow and fast dispersers were initiated in nine different initial fractions
388 ($fraction_{slow}$). That is, each population started out as a fraction 0.1, 0.2, ... , 0.9 of the total
389 population in nine different simulations.

390 *Transfer Events* - The experiment consisted of intervals of continuous dynamics of the
391 nematodes, punctuated with resetting the resource amounts to mimic continuous resource input.
392 To reflect our experimental setup, we let the initial populations grow and disperse among the
393 three patches for a given amount of time steps, then recalculated the $fraction_{slow}$ based on the
394 final total abundance of each consumer. We determined the number of time steps of each transfer

395 event based on the time when most resource was depleted, so that the transfer event in
396 simulations could represent the experimental transfer.

397 *Directed Dispersal* – The individuals in the experimental system could show different
398 levels of net directional movement, so the model represented individuals having a net movement
399 from a lower nutrient patch to a higher nutrient patch^{15,43}. Hence, the diffusion terms (Eqs. 1d,e)
400 had two parts, a pure diffusion term, d for the slow disperser and D for the fast disperser, and a
401 term that specified directed movement towards the patch with highest resource level. The
402 directed dispersal term was determined by the difference in nutrient level between every two
403 patches. For instance, directed dispersal rate from Patch 1 to Patch 2 = $(N_2 - N_1)/N_1$ when $N_2 > N_1$.
404 The parameter α determined the strength of the directed movement.

405

406 **Experimental System**

407 *Strain and culture medium* – The free-living soil nematode worm, *Caenorhabditis*
408 *elegans* (*C. elegans*), has emerged as a powerful system to address basic ecological questions of
409 animal foraging strategies^{31, 60, 61} and context-dependent changes in animal locomotion^{62, 63, 64}.
410 The *C. elegans* model was developed to understand the genetic basis for animal development and
411 behavior⁶⁵, and the concerted effort in hundreds of labs over the last several decades has
412 established it as one of the best laboratory models for empirical studies⁶⁶. Unlike previous work
413 of Friedenber⁴⁹, which used the same system to test evolution of dispersal in spatiotemporally
414 variable microcosms, this study focused on investigating the novel consideration of exploitable
415 resources and directed movement on coexistence of two progenies with different locomotion, in
416 a temporal constant environment. *C. elegans* is a self-fertilizing hermaphrodite that can be grown

417 cheaply and easily on agar plates seeded with *E. coli* bacteria food. Each ~1 mm hermaphrodite
418 can produce ~300 genetically identical hermaphrodite progeny that reach reproductive maturity
419 within ~3 days. No males were observed during the entire experiment.

420 Three genotypes of *C. elegans* hermaphrodites with various foraging behaviors were used
421 to perform our experiments. We used MT1073 *egl-4(n478)* IV to represent a fast disperser
422 (roamer)⁶⁷. Conversely, CX14295 *pdf-1(ok3425)* III with slower moving speed was used as a
423 slow disperser (dweller)⁶⁸. The transgenic strain LX2004 *vsIs183 [nlp-3p::mCherry, nlp-*
424 *3::GCaMP5, + lin-15(+)] lite-1(ce314) lin-15(n765ts)* X, which has an intermediate dispersal
425 rate and expresses the mCherry fluorescent reporter, was used as a control to quantify population
426 shifts pairing with the unlabeled strains above⁶⁹. Thus, fluorescently labeled LX2004 was used to
427 pair with roamer and dweller strains, allowing for quantitation of progeny fractions under the
428 microscope. For the three strains, the dispersal rate follows the rankings: roamer > fluorescently
429 labeled progeny > dweller (Fig. 1D).

430 The *C. elegans* populations were cultured at 20°C on Nematode Growth Medium agar
431 plates seeded with OP50 *E. coli* bacteria as food source, as previously described⁶⁵. We used
432 petri dishes (60 mm) to perform the long-time experiment, details of which are described below.
433 We had two designed environments, differing only in how the OP50 *E. coli* was distributed on
434 the plates: homogeneously and heterogeneously.

435 To examine the change of fraction of a paired genotype with exploitable resources
436 renewed periodically, we conducted an eight-generations long experiment on 60 mm NGM
437 plates seeded with 200 µl OP50 *E. coli* per petri dish. Two combinations of worms were used in
438 both homogeneous and heterogeneous environments, which were: LX2004 (labeled) & CX14295
439 (dweller), and LX2004 (labeled) & MT1073 (roamer). Six late L4-stage worms in total were

440 placed at the center of each plate with three initial fractions of LX2004, which were 1:5, 3:3 and
441 5:1. Each treatment had five replicates. Each plate grew for four days till the food was nearly
442 depleted, and the majority of the worms were at the stage that were easy to be counted under the
443 microscope (most of them were around the L4-stage). As above, four fields were randomly
444 selected on each plate using a Leica M165FC fluorescence microscope with a FLIR Grasshopper
445 3 USB3 camera, as described in Collins, Bode ⁶⁹, Munro, Nguyen ⁷⁰. The numbers of fluorescent
446 and non-fluorescent progeny in each field were counted by using Matlab 2018. A new
447 *fraction_{labeled}* was determined by the total number of fluorescent (labeled) and non-fluorescent
448 progeny in the four images. We then used the new *fraction_{labeled}* to calibrate the initial population
449 abundance of the two genotypes for the next transfer (initial population always equal to six). For
450 the next transfer, we rounded the population number to the nearest integer. For instance, if the
451 *fraction_{labeled}* was 0.4, then we moved 2 L4-stage labeled worms ($6 \text{ worms} * 0.4 = 2.4 \approx 2$), and 4
452 L4-stage unlabeled worms ($6 \text{ worms} - 2 \text{ worms} = 4$) to the new plate. Additionally, we used
453 separately cultured L4-stage worms to start each transfer, instead of worms from the previous
454 plates, to avoid evolution impact. The new plate repeated previous processes and eight transfers
455 in total were performed when *fraction_{labeled}* stayed relatively stable (Fig.1 C). In the following,
456 we always report the fraction of labeled strain because this strain was used in all treatments.

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