

LETTER

Directed movement changes coexistence outcomes in heterogeneous environments

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Abstract

Understanding mechanisms of coexistence is a central topic in ecology. Mathematical analysis of models of competition between two identical species moving at different rates of symmetric diffusion in heterogeneous environments show that the slower mover excludes the faster one. The models have not been tested empirically and lack inclusions of a component of directed movement toward favourable areas. To address these gaps, we extended previous theory by explicitly including exploitable resource dynamics and directed movement. We tested the mathematical results experimentally using laboratory populations of the nematode worm, *Caenorhabditis elegans*. Our results not only support the previous theory that the species diffusing at a slower rate prevails in heterogeneous environments but also reveal that moderate levels of a directed movement component on top of the diffusive movement allow species to coexist. Our results broaden the theory of species coexistence in heterogeneous space and provide empirical confirmation of the mathematical predictions.

KEYWORDS

C. elegans, coexistence, consumer-resource model, directed movement, experiment, theory

INTRODUCTION

Understanding mechanisms that promote coexistence has been a central goal of ecology since Gause (1934); Hutchinson (1959) and has remained a central topic in

both theoretical and applied ecology (Amarasekare & Nisbet, 2001; Levine & Hart, 2020; Silvertown, 2004). In the study of species competition in an environment in which fitness varies heterogeneously in space, theory has focused on two extremes concerning individual

movement patterns. One extreme finds expression in the ideal free distribution (IFD) (Fretwell, 1972; Fretwell & Lucas, 1969). The IFD assumes that individuals within a population will pursue a directed movement strategy that leads to a population distribution across heterogeneous landscape habitats such that any further movement by an individual would lead to a decrease in its fitness (McPeck & Holt, 1992). In the absence of any differences between species other than movement strategy, theory shows that use of an IFD is an evolutionarily stable strategy (Cantrell et al., 2007).

The opposite extreme from the IFD is symmetric diffusion, or purely random movement in space with no regard for differences in habitat quality. Assuming that there are no differences among species other than in the speed of their random movement in a heterogeneous landscape, theory again shows that there is one winning strategy; the species with the slower-moving individuals will always dominate and exclude the other. Although

this theoretical result may seem counter-intuitive, a large body of mathematical theory, based on Lotka-Volterra-type equations with resources included only implicitly, has shown that, with random movement, the slower mover outcompetes the faster one in spatially heterogeneous but temporally constant environments (e.g. Cantrell & Cosner, 2004; Dockery et al., 1998; Hastings, 1983; prediction is shown in Figure 1a). A heuristic explanation is that population growth in favourable habitat is higher, and that, with random movement, individuals of the fast species move on average from favourable to unfavourable locations at a greater rate than those of the slow species.

Therefore, models with both extreme assumptions on movement show a strategy that will exclude all other strategies, such that there is no coexistence. However, movement of real organisms is neither purely random nor purely directional (Amarasekare, 2010; Evans & Cain, 1995; Valdovinos et al., 2016), and there is reason to expect

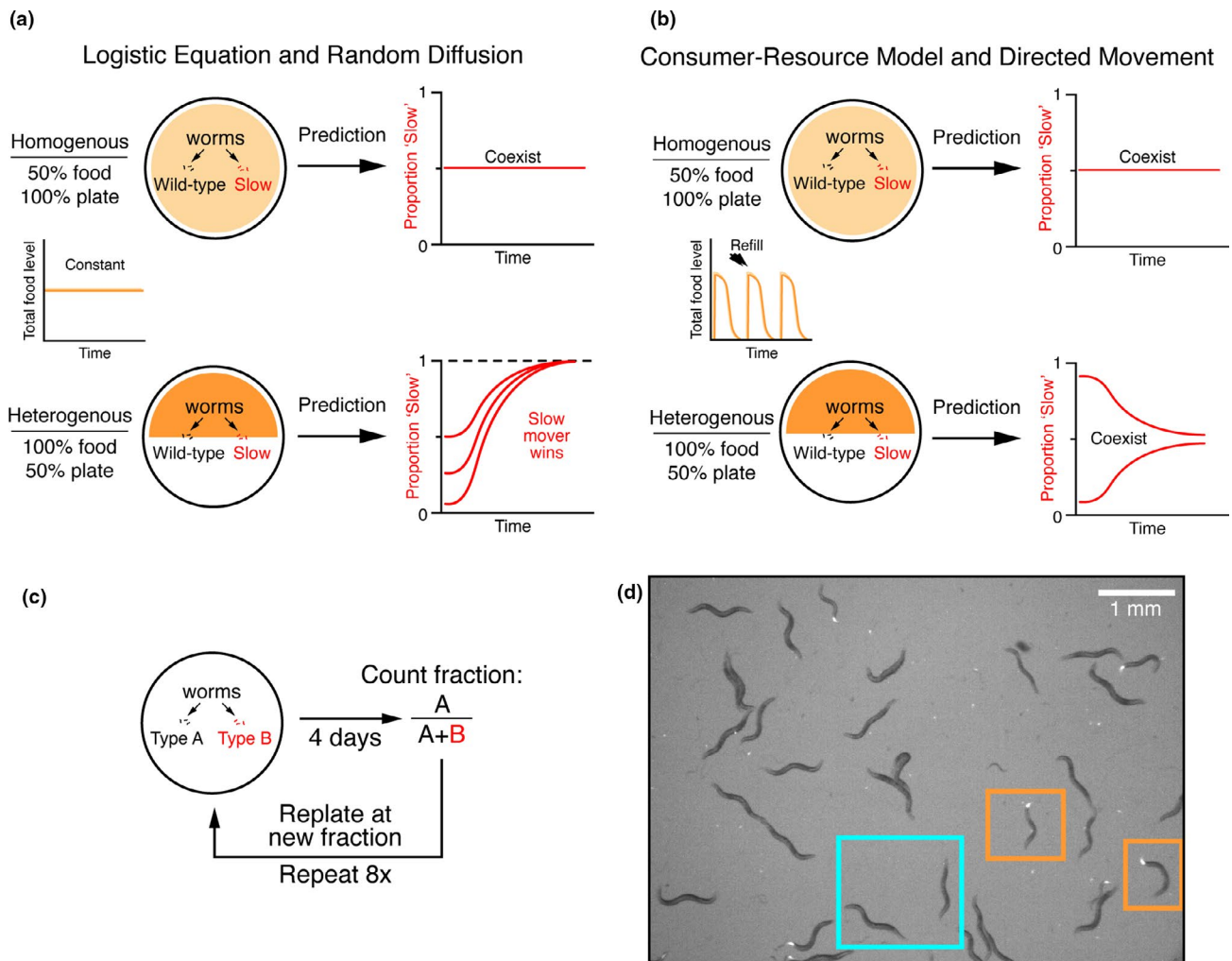


FIGURE 1 Schematic diagram of theoretical predictions. (a) Based on paired logistic equations with random diffusion. (b) Based on the paired consumer-resource model with directed movement. (c) Representation of experimental design on ‘transfer event’. (d) Same initial population size was used in both heterogeneous and homogeneous environments, which started with the same level of total resource concentration. Worms were counted after four days of growth in four randomly selected fields on each entire plate. Micro-graphed image with labelled strain (in orange boxes) and unlabelled strain (in blue boxes)

that coexistence could occur when movements of competitors are intermediate to those extremes. Therefore, there is motivation to generalise theory and models by including a certain degree of directed movement of both movers towards more favourable environmental conditions (Hamilton & May, 1977; Johnson & Gaines, 1990). In the case of two species, identical except for different rates of diffusion, it is obvious that, if the faster moving species is given a sufficient directed movement component towards the favourable environment, it could prevent its exclusion by the slower competitor. However, it is not obvious that coexistence of the two species would be attained.

In exploring that case using experiments in laboratory systems we realised that Lotka-Volterra equations, which ignore resource dynamics of the competing species, and therefore also the time scale involved in feedbacks between the competing species and their resource (Wilkinson, 2006), could not accurately represent the laboratory populations of our study of spatially heterogeneous systems (Arditi et al., 2015; Zhang et al., 2017). Hence, we adopted a consumer-resource model that accounts for resource dynamics as an additional variable (MacArthur, 1972; Tilman, 1982). Consumer-resource models are more suitable for describing the effects of environmental heterogeneity and movement, as recent empirical and theoretical studies have revealed (Van Dyken & Zhang, 2019; Zhang, DeAngelis, & Ni, 2020). By considering two competing consumer species identical except for the magnitude of the symmetric diffusion component of their movement, this study differs from some other studies, such as Wilson and Abrams (2005); Golubski et al. (2008); Schoolmaster et al. (2014), in which resource-exploitation abilities also differ between species.

It is challenging to empirically test this body of competition theory owing to the major hurdles of finding two species, or producing two strains within a species that are nearly identical in all aspects except for their movement rates, and then measuring their relative abundances when competing. Hence, the relevant empirical tests have long been lacking (Chesson, 2008; Siepielski & McPeck, 2010). To fill in the gap in empirically testing theoretical predictions, we performed experiments with strains of the nematode worm *Caenorhabditis elegans* with different rates of movement (Flavell et al., 2013). These strains have different rates of the random component of movement, but similar components of directed movement towards the areas of higher resource density. Along with the empirical study, we extended previous theory on the effect of movement on coexistence using the consumer-resource model with a component of directed movement on top of symmetric diffusion. We were able to provide a rigorous test of the hypothesis from model predictions that a combination of diffusion and directed movement in heterogeneous environments can lead to the coexistence of two species that are identical in all respects except for their rates of symmetric diffusion.

MATERIALS AND METHODS

Experimental system

The free-living soil nematode worm, *C. elegans*, was developed to understand the genetic basis for animal development and behaviour (Brenner, 1974), and the concerted effort in hundreds of labs over the last several decades has established it as one of the best laboratory models for empirical studies (Corsi et al., 2015). Unlike previous work of Friedenber (2003), which used the same system to test the evolution of dispersal in spatiotemporally variable microcosms, our study focused on investigating the novel consideration of exploitable resources and directed movement on affecting coexistence of two strains with different locomotion speeds in temporally constant but spatially varying environments. *C. elegans* is a self-fertilising hermaphrodite with a very low incidence of males. Nonetheless, we also carefully managed the culture environments to ensure no males were observed or quantified during the entire experiment.

Strain with directed movement

We paired genotypes of *C. elegans* hermaphrodites with different foraging speeds to determine their coexistence patterns. We used MT1073 *egl-4(n478)* IV to represent a fast mover (roamer) (L'Etoile et al., 2002). This strain also has a reduced egg laying rate, but this does not affect the overall brood size (Figure S1A in Appendix S1). Conversely, CX14295 *pdf-1(ok3425)* III with a slower moving speed on food was used as a slow mover (dweller) (Omura et al., 2012). Compared with the dweller, which tends to stay within a smaller area, the roamer moves much faster across a bacterial lawn and turns infrequently (Flavell et al., 2013). We did not test the roamer directly with the dweller. Instead, we paired both the roamer and dweller with a fluorescently labelled transgenic strain LX2004 *vsIs183 [nlp-3p::mCherry, nlp-3::GCaMP5, + lin-15(+)] lite-1(ce314) lin-15(n765ts)* X (Collins et al., 2016), which has an intermediate locomotion rate to quantify population shifts pairing with the unlabelled strains above. The *nlp-3* promoter/enhancer (Brewer et al., 2019) was used to drive expression of the mCherry reporter, and the pL15EK plasmid was used as a co-injection marker [*lin-15(+)*] to rescue the *lin-15(n765ts)* multi-vulva phenotype. The movement rate follows the rankings for the three strains: roamer > fluorescently labelled strain > dweller (Figure 1d). To ensure that the fluorescent strain is effectively neutral when competing against either the dweller or roamer, and there are no intrinsic fitness differences among strains, we quantified the brood size of each strain. Eleven sub-adult (L4) nematodes of each genotype were placed individually on 60 mm Petri plates. Food was provided by a lawn of *Escherichia coli* bacteria (strain OP50) grown on

nematode growth medium (NGM) agar from an inoculum of 100 μ l. The worms were transferred to fresh plates every ~24 h for 4 days (last transfer was done 84 h after original plating). Progeny on all plates were recorded and pooled.

Culture medium

The *C. elegans* populations were cultured at 20°C on Nematode Growth Medium agar plates seeded with OP50 *E. coli* bacteria as food source (Brenner, 1974). We had two designed environments, differing only in how the 200 μ l OP50 *E. coli* was distributed on each petri dish: homogeneously and heterogeneously. The homogeneous environment was prepared by uniformly spreading the *E. coli* bacteria across the entire surface of the petri dish while the heterogeneous environment was prepared by spreading the same volume of food onto one half of the dish. To compare how much time each strain spends on and off food in the heterogeneous environments, we recorded ~24-h adult animals from each strain for 2 h on 35-mm plates seeded with 30 μ l OP50. Two plates of five adults each were recorded for 2 h ($n = 10$ animals per strain). We calculated the proportion of time each animal spent on and off the food.

Strain without directed movement

To test the potential impact of directed movement on species coexistence patterns, we crossed each strain with PR694 *tax-2(p694)* I, a mutant that shows defects in chemotaxis and in direct movement (Dusenbery et al., 1975). The *tax-2(p694)* mutation was followed by duplex PCR using the following oligonucleotides: *tax-2(p694)*-mut-fwd, TGA CTG CTT GGC AAC GGA CTT; *tax-2(p694)*-wt-fwd: GAT AGA CAG GTA CAT AAT CTT CAG AAT CTG; and *tax-2(p694)*-rev: TGC AGA AAT GCT CGA AGT AGC CCA, generating MIA470 *tax-2(p694)* I; *vsIs183 lite-1(ce314) lin-15(n765ts)* X, MIA471 *tax-2(p694)* I; *egl-4(n478)* IV and MIA472 *tax-2(p694)* I; *pdf-1(ok3425)* III.

Transfer events

Four combinations of worms were used in both homogeneous and heterogeneous environments; Group 1 with directed movement: LX2004 (labelled) & CX14295 (dweller), and LX2004 (labelled) & MT1073 (roamer); Group 2 without directed movement: MIA470 (labelled, no chemotaxis) & MIA471 (dweller, no chemotaxis) and MIA470 (labelled, no chemotaxis) & MIA472 (roamer, no chemotaxis). A total of six late L4-stage worms were placed at the centre of each plate with three initial proportions of individuals of the slow-moving strain to

all individuals ($proportion_{slow} = 1/6, 1/2$ and $5/6$). Each condition had five replicates. We chose a total of six initial worms because they can nearly deplete the food on each plate after four days, when the majority of the worms reach the L4-stage, which along with adult animals, are easiest to score under the microscope. We also ran simulations, as described below, with different initial numbers (6 or 12 initial worms) and initial locations (all placed at the centre or equally distributed across the plate), confirming that the initial number of animals or their initial position on the plate had no effect on the predictions (Figures S2 and S3 in Appendix S1). Every 4 days, four fields were randomly selected on each plate using a Leica M165FC fluorescence microscope with a FLIR Grasshopper 3 USB3 camera, as described in Collins et al. (2016) and Munro et al. (2020). The numbers of fluorescent and non-fluorescent strains in each field were counted by using a custom script in MATLAB (2018). A new $proportion_{slow}$ was determined by the numbers of the slow mover to total numbers and the paired strain pooled from the four images. We then used the new $proportion_{slow}$ to calibrate the initial population abundance of the two genotypes for the next transfer (the initial population was always equal to six), rounding the starting population to the nearest integer. Note that we always used separately cultured L4-stage worms to start each transfer, instead of worms from the previous plates, to avoid any potential impacts of strain evolution. We repeated the transfer process eight times or until the proportion of paired genotypes stayed relatively stable (Figure 1c).

Statistical analysis

We performed a one-way ANOVA test with Bonferroni multiple comparison correction to compare the mean of the number of reproduced progeny, and the time spent on and off food among the three strains with directed movement. The difference in final proportion of the slow mover was assessed using ANOVA across initial proportions in both heterogeneous and homogeneous environments. Assumptions of equal variance and normality were examined by the residual plots along the fitted values and the normal quantile plot, respectively. Analyses were performed in R version 4.0.2 (Team 2013).

Mathematical model

To represent the experimental system where a consumer (nematodes) feeding on an exploitable resource (*E. coli*), we used a consumer-resource model, with consumers using explicit resources (Wilkinson, 2006; Zhang et al., 2017). We modelled paired competing consumers exploiting a common resource in a

one-dimensional patch system, where patches received different concentrations of resource that do not diffuse between the patches. Three patches are simulated, each with two competing consumer species, U and V (Equations 1a, 1b), and a single exploitable resource, N (Equation 1c). The equations for these (omitting movement) are

$$\frac{dU_i}{dt} = \frac{rN_iU_i}{k + N_i} - mU_i - g(U_i + V_i)U_i \quad (1a)$$

$$\frac{dV_i}{dt} = \frac{rN_iV_i}{k + N_i} - mV_i - g(U_i + V_i)V_i \quad (1b)$$

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

($i = 1, 2, 3$). Parameter r is the asymptotic growth rate under infinite resources, k is the half-saturation coefficient, m is the mortality rate, g is the density-dependent loss rate, N_{input} is the resource input rate, θ is the loss rate of nutrient from the system and γ is the yield (consumer individual reproduction per unit resource).

The movement of the two consumers between two adjacent patches, in this case from patch i to $i - 1$, is described for each of the two consumers, respectively, by

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

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

where d (resp. D) is the dispersal rate of slow (resp. fast) disperser. These terms are subtracted from the population of the donor patch and added to the recipient patch. We assumed all consumer parameters are identical, except for their symmetric diffusion rates, where $d < D$. The parameter α scales the relative importance of directed movement and β prevents a zero denominator. The equations are presented more fully in Appendix S1.

Directed movement

In the model the amounts of time individuals spent on each patch could be inferred from the proportions of the population sizes at equilibrium, which depends on the choice of movement parameters. Movement was directed towards the patch with the highest resource level, normalised by the resource level of the donor patch, represented as the constant α multiplied by the difference in resource level between the two patches

between which there was movement. We used the same level of α for both fast and slow movers since no significant difference in the percentage of time spent on and off the food was detected across the strains (Figure S1B in Appendix S1). For instance, if the resource levels for two patches are, respectively, N_1 for Patch 1 and N_2 for Patch 2, then directed movement rate from Patch 1 to Patch 2 $\sim (N_2 - N_1)/(N_1 + \beta)$ when $N_2 > N_1$. Precisely, if the phenotype has random movement rate d and directed movement rate α (from Patch 1 to Patch 2), then we expect the individual to spend $d/(2*d + \alpha)$ of time in Patch 1, and $(d + \alpha)/(2*d + \alpha)$ in Patch 2.

Model simulations

We developed a computational code based on the set of model equations to simulate a one-dimensional patch system. Two types of simulations were performed. In the first type the simulations were run with no interruptions over a sufficiently long time period for the population to approach an equilibrium. The second type of simulations imitated the experiments with transfer events between plates to mimic the experiment. At each transfer event, the resource levels were renewed, and the populations were re-established in the same proportions that existed at the end of the preceding time step but at the original total population size, so that the competitive dynamics could proceed.

Initial conditions

We first performed simulations in a two-patch system to consider a heterogeneous environment that is more similar to that used in the experiments where Patch 1 received nearly all input of resource, whereas Patch 2 received a very little input (Figure S2G-I, S3G-I in Appendix S1). Additionally, we considered that the experimental heterogeneous environments were created by putting food only on half of the plate, and worms were started in the middle of the plate; hence, we viewed the ‘middle part’ of the plate as a transition area between with and without food. We further ran simulations with a three-patch system where the patches differed only in resource input (N_{input}). Patch 1 received the largest input of resource, $N_{input,1}$ while Patch 2, in the middle, received about half of the resource of Patch 1, and Patch 3 received a very small input. Lastly, we extended the three-patch system to an n-patch system to increase model generality. Accordingly, in homogeneous environments, each patch received an equal proportion of the total resource inputs used in the heterogeneous environments. All models started with six initial population sizes with nine initial proportions of the slow mover (0.1, 0.2, ..., 0.9).

Transfer events

To reflect our experimental setup in the second type of simulation, we let six initial populations of the two species start in the middle patch (Patch 2), which then grew and moved among the three patches for a given amount of time steps. Finally, we recalculated the $proportion_{slow}$ based on the final total abundance of each consumer. We determined the number of time steps for each transfer event based on the time when most resource was depleted, so that the transfer event in simulations could represent the experimental transfer.

Sensitivity analysis

Parameter values that are listed in Table S1 in Appendix S1 were artificially assigned based on our best estimation. Additionally, we performed a sensitivity analysis regarding the effect of a 10% decrease or increase of all the six parameters (α , r , k , $gamma$, m , g).

RESULTS

Experimental results

All strains spent significantly more time on food than off ($p < 0.05$) (Figure S1A in Appendix S1). This result indicated that the strains have a net movement from a lower resource patch to a higher resource patch, which we called as ‘directed movement’. In the heterogeneous case with directed movement, the $proportion_{slow}$ across three initial values converged and the final $proportion_{slow}$ stayed close to 0.6, indicating that the two strains coexisted over eight transfer events despite differences in movement rates (Figure 2a,b). In contrast, we found that in the homogeneous environment, the $proportion_{slow}$ stayed nearly constant with some stochastic variation around the initial values (Figure 2c,d). Finally, experiments using mutant strains without directed movement converged to a slow-mover frequency of 0.9, reflecting its dominance (Figure 3a,b). Similar constant patterns were observed in homogeneous environments (Figure 3c,d).

Coexistence patterns with directed movement

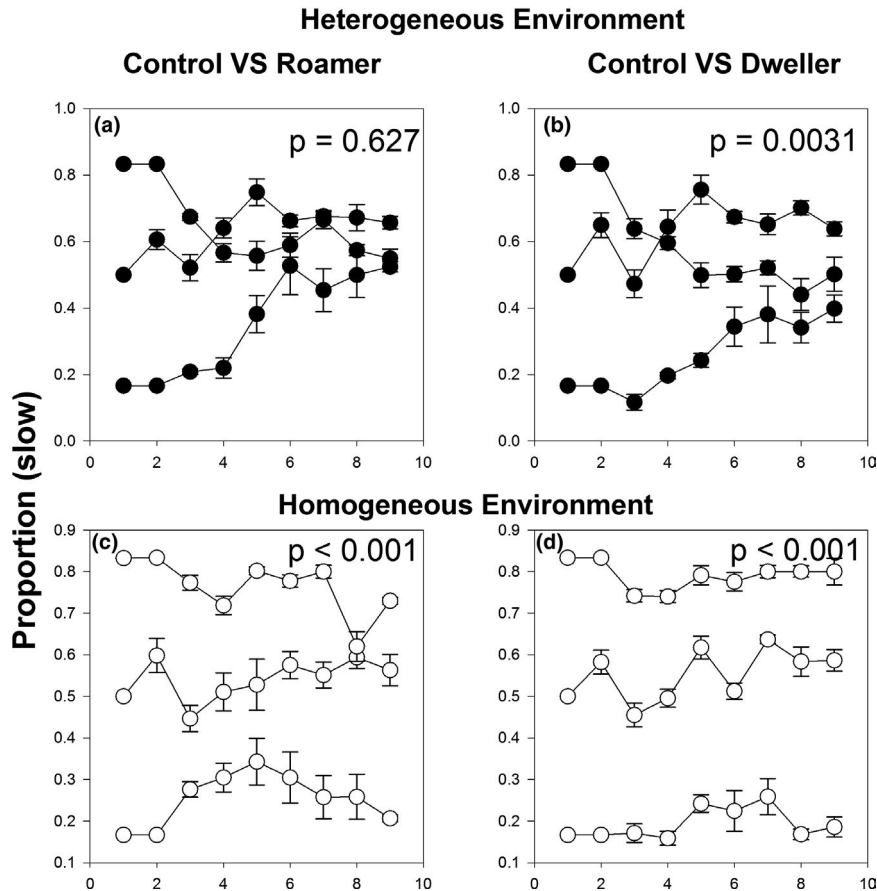


FIGURE 2 Dynamic change of proportion of slow mover ($proportion_{slow}$) in the group with directed movement. (a, c) LX2004 (labelled) paired with MT1073 (roamer); (b, d) LX2004 (labelled) paired with CX14295 (dweller), over eight transfers in heterogeneous environments (dark dots) and in homogeneous environments (empty dots). Significance of difference in the final proportions of slow mover ($proportion_{slow}$) between the different initial proportions in each condition were analysed using Analysis of Variance (ANOVA). p values indicate the significance of comparisons

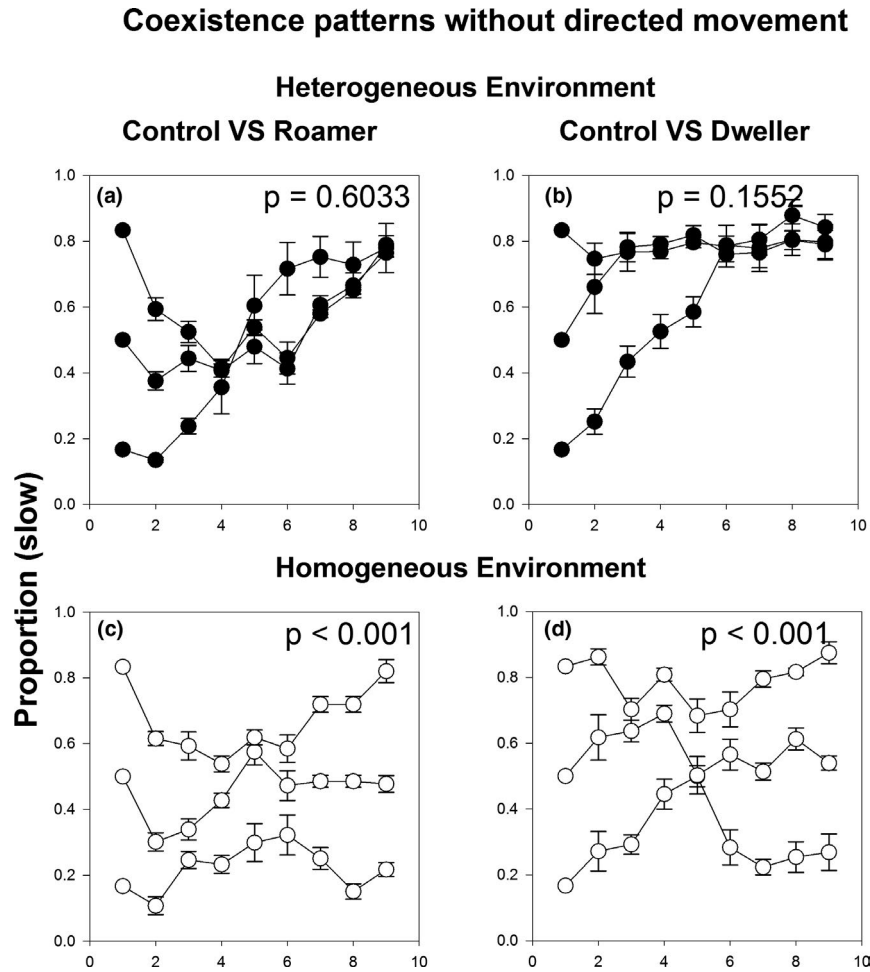


FIGURE 3 Dynamic change of proportion of slow mover ($proportion_{slow}$) in the group without directed movement. (a, c) MIA470 (labelled, no chemotaxis) paired with MIA472 (roamer, no chemotaxis); (b, d) MIA470 (labelled, no chemotaxis) paired with MIA471 (dweller, no chemotaxis), over nine transfers in heterogeneous environments (dark dots) and in homogeneous environments (empty dots). Significance of difference in the final proportions of slow mover ($proportion_{slow}$) between the different initial proportions in each condition were analysed using Analysis of Variance (ANOVA). p values indicate the significance of comparisons

The final $proportion_{slow}$ was significantly higher without directed movement than with it ($p < 0.0001$), which suggest that directed movement underlies the ability of fast movers to compete in heterogenous environments.

Results of the numerical model simulation

In the first set of simulations, the model equations were run over sufficient time to reach equilibrium without breaking the simulation into smaller segments separated by transfer events to new plates. For all initial proportions, the population size reached by the slow and fast movers at equilibrium varied as a function of the coefficient of directed movement, α , as shown in Figure 4 for Patches 1 and 2 (populations on Patch 3 were much smaller and not shown). Small values of the directed movement component ($\alpha \leq 0.075$) caused extinction of the fast-mover. For large, directed movements of both strains towards Patch 1 ($\alpha \geq 0.35$), the reverse occurred; with the slow mover being excluded. For intermediate levels of

directed movement ($0.1 < \alpha < 0.35$) the two competitors distributed themselves among the different patches (the slow mover mainly on Patch 1 and the fast mover more evenly distributed between Patches 1 and 2), so that coexistence occurred. These simulation results, showing a range of values of α for which coexistence could occur, are proved analytically in Appendix S2.

The second set of simulations imitated the experiments in more detail, including the periodic transfer events of the populations to new plates. In the simulations of heterogeneous environments, for a range of intermediate values of α ($0.1 < \alpha < 0.35$), the two species coexisted and the final convergence point ($proportion_{slow}$) depended on levels of directed movement (higher when α was small and smaller when α was large). We set $\alpha = 0.125$ in Figure 5b which led to a final $proportion_{slow}$ close to the experimental result (Figure 2a,b). When α was smaller than 0.1, $proportion_{slow}$ increased to 1, indicating that the slow mover won (Figure 5a); conversely, when α was larger than 0.35, $proportion_{slow}$ declined to 0, indicating that the fast mover won (Figure 5c). For comparison, in a homogeneous setting, the

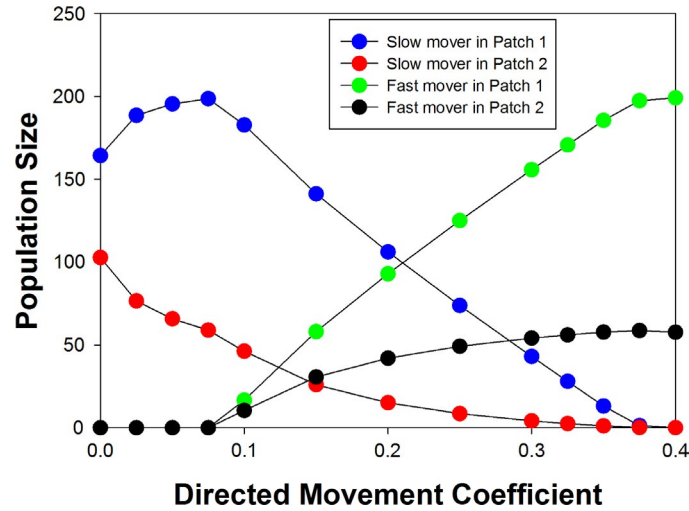


FIGURE 4 Simulations of population sizes of slow movers (U_1 and U_2) on Patches 1 and 2, respectively, and fast movers (V_1 and V_2), on Patches 1 and 2, respectively, as functions of the coefficient of directed movement coefficient, α

proportions all stayed close to their initial values independent of changes in α (Figure 5d–f). We also obtained analytical results regarding the invasibility of both the slow and fast movers when initially rare, given that the resident competitor was at the equilibrium state, and these results were consistent with the simulations. The analytical results, presented in Appendix S2, prove that coexistence is possible only when directed movement is intermediate, while the slower (resp. faster) mover is favoured when the directed movement is weak (resp. strong). We have extended the three-patch system to an n -patch system (Appendix S2), and showed the overall conclusion regarding exclusion versus coexistence to be robust across patch numbers. Although the final proportions between the competing species do change with some parameters (α and r), especially in heterogeneous environments, the general conclusion regarding exclusion versus coexistence was robust across parameter range (Figure S3 in Appendix S1, Appendix S2).

Overall, the two sets of simulations showed similar results for the two species with an identical rate of directed movement and different rates of their symmetric diffusion components of movement. Stable coexistence occurred over a range of intermediate rates of directed movement. For rates of directed movement below this range, the slower mover always ultimately excluded the faster mover. For rates above this range, the fast mover excluded the slow mover.

DISCUSSION

Our mathematical and empirical results both support previous mathematical theory and extend it. Our experiments supported the existing theory that with different levels of symmetric diffusion but no directed movement, the slow mover always prevails in heterogeneous environments (Hastings, 1983). New here are the results,

experimentally and mathematically, of coexistence for intermediate rates of directed movement and, mathematically, exclusion of the slower mover at high rates of directed movement. An intuitive explanation for the exclusion of the slow mover for large directed movement is that, both strains towards the patch with higher resource, both populations squeeze into that patch, experiencing high intraspecific and interspecific competition, and thus high mortality. However, the fast mover, by virtue of its faster diffusion rate, is able to ‘leak’ out of the patch at a much faster rate than its competitor to the patch with lower resource, where, with little competition, it builds up population to dominate on that patch and spreads back to the good patch in sufficient numbers to exclude the slow mover from the system. This explanation is supported by observation of the population dynamics on the patches in the simulations. Therefore, in contrast with the situation in which there is no directed movement, fast diffusion may be advantageous when competing consumers have identical directed movements.

This mechanism relies on direct density-dependent competition built into Equations (1a, 1b) through coefficient g , and thus the coexistence of the two consumers that occurs ($0.075 < \alpha < 0.35$) also appears to depend on the density-dependent competition, which also occurs in the mathematical proof in Appendix S2. We were unable to find through simulations cases of coexistence without this density dependence; that is, when the species competed through exploitative competition alone. The importance of direct density-dependent competition is further corroborated by the finding from a previous study that Lotka-Volterra-type competition, based on direct density-dependent competition under certain conditions, can also lead to coexistence when random movement rate is small and directed movement large (Chen et al., 2012; Lam & Lou, 2014).

The competition studied here can be thought of in the context of the two extreme idealisations of movement

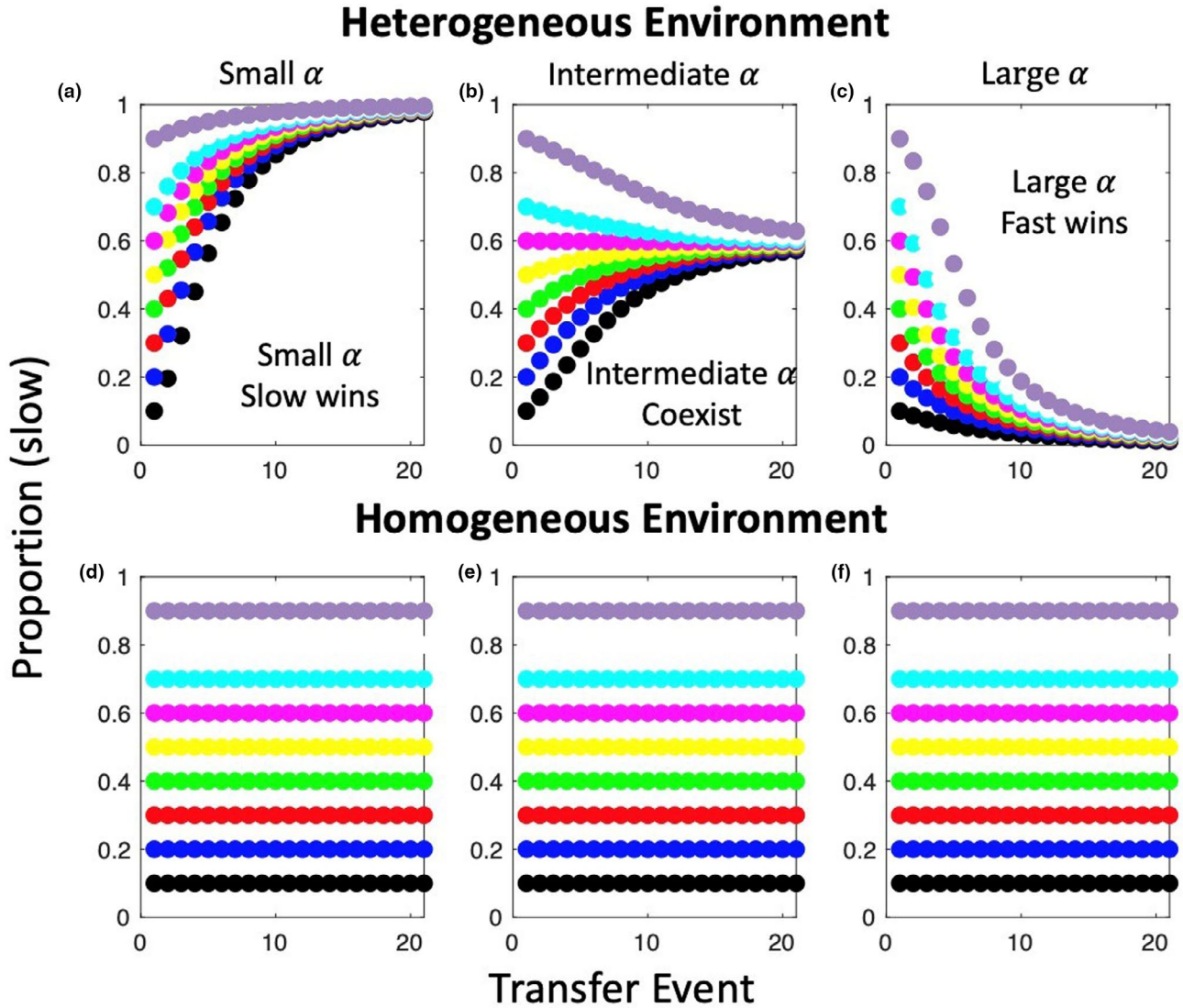


FIGURE 5 Simulations of the proportion of slow mover ($proportion_{slow}$) over 20 transfer events with a series of initial proportions (0.1–0.9) in heterogeneous environments with (a) small α (≤ 0.1); (b) intermediate α ($= 0.125$); (c) large α (≥ 0.35); and in homogeneous environments with (d) small α (≤ 0.1); (e) intermediate α ($= 0.125$); (f) large α (≥ 0.35). Each dot represents the $proportion_{slow}$ of each transfer event, and colours represent different initial proportions. Initial resource levels in the three patches in heterogeneous environments are (200, 100 and 1) and in homogeneous environments are 100, 100 and 100, respectively. To evaluate the results, we used the proportion of slow mover as $proportion_{slow} = \sum_{i=1}^3 U_i / (\sum_{i=1}^3 U_i + \sum_{i=1}^3 V_i)$ to represent the dominance of slow mover

in heterogeneous space, one being directed movement towards the Ideal Free Distribution and the other random movement or symmetric diffusion. Neither extreme likely occurs in reality, and the outcomes of competition depend on the relative degrees of the two types of movement. Here, under the assumption that both competitors have identical directed movement, the slow mover does better the smaller is the component of directed movement. When directed movement rate α is lowered below 0.075 and the fast mover is excluded, its distribution on the patches approaches that of a perfectly diffusing population. The fast mover does better the larger the directed movement component is, and when α exceeds 0.35 and the slow mover is excluded, the distribution of the fast mover approaches the IFD as α is increased further.

Between those thresholds, neither of those ideal movement types can be approached closely enough that only one competitor can survive, so the competitors coexist. The values of these thresholds depend, of course, on the other parameters of the equations.

Consumer-resource models are ubiquitous in ecological theory but have been used less often than Lotka-Volterra models in studying competition in heterogeneous environments. The consumer-resource model used here was based on the Zhang et al. (2017); Zhang, DeAngelis, Ni, Wang, et al. (2020) model for a single species, extended to describe paired competing consumers exploiting a common resource. To represent the experimental system in which both species showed a similar net directional movement from a lower resource area

to a higher resource area, identical directed movement component was added to the symmetric movement of the competitors. The numerical simulations and mathematical analysis of the model, showing stable coexistence with an intermediate level of directed movement, were in close agreement with the experimental results, in which the two consumers could coexist for a long time. This indicates that the consumer-resource approach is useful in this context. Besides the role of movement studied here, environmental heterogeneity plays an important role in other models, where it can promote species coexistence (Amarasekare et al., 2004; MacArthur & Levins, 1967; Snyder & Chesson, 2004). However, unlike our approach, those studies assume that different species differ in their abilities in exploiting resources.

This study has various ecological implications. For instance, *C. elegans* shows a directional movement in its foraging, from a lower resource patch to a higher resource patch (Meisel & Kim, 2014). Environmental conditions are ever-changing, temporally and spatially; hence, if individuals can obtain clues of neighbouring environments, to determine the best direction to disperse, the benefit of high dispersal can be enhanced (Nichols et al., 2020). Additionally, it is a complex and highly challenging problem to predict the metacommunity dynamics in heterogeneous environments because the differences in dispersal rates among competing species alter their dominance and community structure (Tilman, 1994). Thus, concepts from this study may be useful in explaining coexistence in a metacommunity (Leibold et al., 2004), where metacommunity is defined as a set of local communities that are linked by dispersal (Gilpin, 2012; Wilson, 1992). Anthropogenic actions and climate change are fragmenting the environment and putting more emphasis on the role of organism movement to favourable habitats, which sustains population survivorship and biodiversity (Fahrig, 2003). Species with various movement strategies, such as having a fast or slow movement rate, could have different adaptations to the environmental change, ultimately mediating coexistence (Schlägel et al., 2020). For this reason, movement is increasingly considered to be a critical process in ecological dynamics models to predict species adaptation under changing environments (Clobert et al., 2012).

We acknowledge limitations to our study. Our empirical findings showed that the two species can coexist for least eight transfer events. Friedenberg (2003) performed evolution experiments with *C. elegans* for five generations (each transfer event is nearly equal to one generation); hence, the experimental time length we conducted is believed to be long enough. There is still a possible mismatch between the timescale of the mathematical theory and practical experimental limitation because mathematical models usually project long-term behaviours of the system reaching a stable and equilibrium state. In contrast, biological experiments are mostly performed on shorter timescales relative to the life cycle

of the organism (Liu et al., 2019). It is possible that the coexistence observed in our experiment is an example of long transient behaviour. Such transient dynamics (Hastings, 2001, 2004; Kermack & McKendrick, 1927), have been shown to play a critical role in understanding species coexistence. However, detecting this transient behaviour is still a ‘black-box’ in both mathematics and biology (Hastings et al., 2018). Our study, as a pioneering effort, looked at species coexistence at both relatively short timescale (experiment) and the longer timescale (mathematics) and showed that short term experiments can provide a reasonably good match with the theoretical prediction.

We focused on an experimental heterogeneous pattern via distributing all the food resource onto one half of the dish, more patterns should be considered in the future, such as creating a large and small patch. We have only investigated the effect of local movement on species coexistence. Extending such study to include comprehensive understanding of multiple dimensions of movement (e.g. long-distance movements, density-dependent movement) is crucial because it can provide more realistic representations of nature (Nunez-Mir et al., 2019). Additionally, a rich theory on evolution of movement in heterogeneous environments has been developed (Cantrell et al., 2018; Cote et al., 2017; Levin et al., 2003; McPeck & Holt, 1992; Travis & Dytham, 2002), and Friedenberg (2003) performed the first experimental study with *C. elegans* to demonstrate evolution of movement in spatiotemporally variable microcosms. Hence, the experimental system of *C. elegans* will be a suitable system to test for long term evolution of movement under more complex environments. Lastly, our work focused on the case assuming the competing two species are completely identical except for their symmetric movement rates, whereas, such assumption may not be realistic in nature (Tilman, 1994). Hence, including trade-offs in competitive and colonisation abilities with the context of consumer-resource interactions and information of movement could fill in substantial gaps in our understanding of how movement in heterogeneous regions affects the competition and coexistence of multiple species.

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AUTHOR CONTRIBUTIONS

Bo Zhang and Kevin M. Collins designed the experiment; Bo Zhang, Rossana Signorelli, Zhiyuan Fu and Lu Zhai collected and analysed data; Bo Zhang performed the simulations; King-Yeung Lam, Weiming Ni, Yuan Lou, Donald L. DeAngelis and Alan Hastings provided mathematical proof. BZ, King-Yeung Lam, Donald L. DeAngelis and Alan Hastings wrote the first draft, and all authors contributed substantial revisions.

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