



Effects of dispersal on total biomass in a patchy, heterogeneous system: Analysis and experiment



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ABSTRACT

An intriguing recent result from mathematics is that a population diffusing at an intermediate rate in an environment in which resources vary spatially will reach a higher total equilibrium biomass than the population in an environment in which the same total resources are distributed homogeneously. We extended the current mathematical theory to apply to logistic growth and also showed that the result applies to patchy systems with dispersal among patches, both for continuous and discrete time. This allowed us to make specific predictions, through simulations, concerning the biomass dynamics, which were verified by a laboratory experiment. The experiment was a study of biomass growth of duckweed (*Lemna minor* Linn.), where the resources (nutrients added to water) were distributed homogeneously among a discrete series of water-filled containers in one treatment, and distributed heterogeneously in another treatment. The experimental results showed that total biomass peaked at an intermediate, relatively low, diffusion rate, higher than the total carrying capacity of the system and agreeing with the simulation model. The implications of the experiment to dynamics of source, sink, and pseudo-sink dynamics are discussed.

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1. Introduction

The effects of spatial heterogeneity and dispersal on populations and on ecosystem properties such as productivity are key issues in ecology. An interesting recent result from mathematics is that a population in an environment in which resources vary spatially will reach a higher total equilibrium biomass than the same population in an environment with the same total resources but where resources are distributed homogeneously [1–3], which they referred to as ‘a curious fact indeed’. The mathematical result depends on the population being able to diffuse in space. This result from mathematical theory has implications for ecology. Ecologists attempt to understand the factors regulating populations in spatially structured habitats with regional factors such as spatially distributed environmental heterogeneity and dispersal [4]. A number of ecological investigations carried out in recent years have established that spatial heterogeneity in the availability of soil-based resources can strongly influence the growth and patterns of biomass allocation of single plants [5]. How-

ever, these studies did not involve spatial diffusion, so results for the two factors of spatial heterogeneity and diffusion together have, to our knowledge, rarely been tested empirically, despite the relevance of dispersal to key ecological issues.

Lou [1] considered a population in an inhomogeneous environment; i.e., where the population growth rate is a function of distance, s , along one dimension, and $g(s) \neq \text{constant}$, and where the population can diffuse at some constant rate (D). He used an equation of the form

$$\frac{\partial X}{\partial t} = D \frac{\partial^2 X}{\partial s^2} + [g(s) - X]X, \quad (1.1)$$

with Neumann (no-flux) boundary conditions on X . Here ‘resources’, $g(s)$, represent both growth rate and carrying capacity, and the resource level is assumed fixed externally. Lou [1] noted that, at equilibrium, when both sides are divided by X and integration is performed over all space Ω , the following holds;

$$D \int_{\Omega} \frac{1}{X(s)^2} \left| \frac{\partial X(s)}{\partial s} \right|^2 > 0, \quad (1.2)$$

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which implies

$$\int_{\Omega} [X(s) - g(s)] ds > 0. \tag{1.3}$$

The diffusion of individuals away from the areas of high productivity keeps the population levels in those areas below carrying capacity, so that high production continues. The diffusion allows higher population levels to be attained in the lower resource areas than the carrying capacity would predict. The result is that the total population over all space exceeds that which would occur in a homogeneous space with the same total resource production. In order to apply the above results to typical ecological models, it is necessary to extend (1.1) to a logistic equation

$$\frac{\partial X}{\partial t} = D \frac{\partial^2 X}{\partial s^2} + r(s) \left[1 - \frac{X}{K(s)} \right] X, \tag{1.4}$$

where the maximum growth rate, $r(s)$, and carrying capacity, $K(s)$, are standard parameters in ecological models. It is useful at first to switch from continuous to discrete space (patches or compartments) to demonstrate in a simple manner how to make the extension. The discrete space model can then be used to simulate planned empirical experiments.

The first objective of this research is to determine if the mathematical result of Lou [1] has relevance to empirical systems. That is, will a diffusing population in an environment with spatially varying resources reach a higher total equilibrium biomass than the population in an environment with the same total resources distributed homogeneously with diffusion? The second objective is to test the mathematical result that a hump-shaped pattern appears when the equilibrium biomass is plotted as a function of the rate of diffusion.

2. Methods

2.1. Discrete patch model

The discrete patch model analogous to (1.4) uses logistic growth equations in which carrying capacities can be specified for a one-dimensional series of compartments linked through population diffusion. Consider n compartments, which have biomasses represented by the variables X_1, X_2, \dots, X_n (for example, grams dry weight biomass). Relevant equations for continuous diffusion among compartments are the following, in which there are fluxes between the two patches on either end as well (i.e., wraparound conditions);

$$\frac{dX_i}{dt} = r_i(1 - X_i/K_i)X_i - DX_i + \frac{1}{2}DX_{i-1} + \frac{1}{2}DX_{i+1} \quad (i = 1, \dots, n) \tag{2.1}$$

where it is understood that $i-1 = n$ when $i = 1$ and $i+1 = 1$ when $i = n$.

The system is described by the parameters, r_i , K_i , and D . Here, r_i (for example, day^{-1}) is the maximum growth rate in patch i , while K_i (for example, grams dry weight biomass) is the carrying capacity for patch i , with $r_i(1 - X_i/K_i)$ being the actual growth rate at any time. The parameter D (day^{-1}) is the diffusion coefficient.

Use of two parameters, r and K , rather than the single parameter, g , differs from the mathematical model (1), but is more flexible in describing population growth. When r_i and K_i take on independent values for each compartment i , it can be shown that there is no guarantee that diffusion in a heterogeneous environment leads to greater equilibrium biomass than in the absence of diffusion. Specifically, it can be shown that the inequality

$$\sum_{i=1,n} \frac{r_i}{K_i} (X_i - K_i) > 0 \tag{2.2}$$

holds for this system (see Appendix A), but this does not necessarily imply that

$$\sum_{i=1,n} (X_i - K_i) > 0; \tag{2.3}$$

i.e., the total biomass is greater in a heterogeneous system with diffusion than without diffusion (analogous to (1.3)). However, a criterion for (2.3) can be found (see Appendix B); that is, the inequality

$$\sum_{i=1,n} \left(\frac{(r_i - r_{i-1})(K_i - K_{i-1})}{r_i r_{i-1}} \right) > 0 \tag{2.4}$$

guarantees that

$$X_{\text{total}} = \sum_{i=1,n} X_i$$

increases as D increases from zero for small values of D , so that (2.3) holds at least for small values of D . A sufficient condition for criterion (2.4) to be satisfied is that K_i and r_i both be increasing or both be decreasing together. We have used simulations to exhaustively test this result. A criterion parallel to (2.4) can be found for the spatially continuous form with $r(s)$ and $K(s)$; that is, for

$$\frac{\partial X}{\partial t} = D \frac{\partial^2 X}{\partial s^2} + r(s) \left[1 - \frac{X(s)}{K(s)} \right] X(s). \tag{2.5}$$

The criterion for $X_{\text{total}} = \int_{\Omega} X(s)$ to increase for small increases in D from zero is now,

$$\int_{\Omega} \frac{\partial K}{\partial s} \cdot \frac{\partial}{\partial s} \left(\frac{1}{r} \right) < 0. \tag{2.6}$$

The proof is outlined in Appendix C. Both (2.4) and (2.6) are new mathematical results.

2.2. Discrete patch, discrete time model simulations

System (2.1), as written, represents continuous-in-time but discrete-in-space diffusion. It was impractical to design an experiment in which diffusion occurred continuously in time. Instead, an artificial experiment was designed, in which diffusion was simulated by manual transfer of floating aquatic plants between containers (patches) with different nutrient levels. To represent this in a model, Eq. (2.1) was discretized in time and the number of compartments were set to $n = 5$. In the time-discretized version designed to represent the experiment, growth was assumed to occur according to the logistic equation over equal time periods (Eq. (2.7a)), and then amounts of biomass were transferred among compartments at regular time intervals:

$$\frac{dX_i}{dt} = r_i(1 - X_i/K_i)X_i \quad (t_{j(+)} \leq t \leq t_{j+1(-)}) \tag{2.7a}$$

$$X_i(t_{j(+)}) = X_i(t_{j(-)})(1 - M) + \frac{1}{2}MX_{i-1}(t_{j(-)}) + \frac{1}{2}MX_{i+1}(t_{j(-)}) \tag{2.7b}$$

for $t = t_j$

where compartment numbers $i + 1 = 1$ when $i = 5$ and $i - 1 = 5$ when $i = 1$, and where $t_{j(-)}$ means the value before biomass transfer (diffusion) and $t_{j(+)}$ means the value after transfer. The new parameter M represents the fraction moved between compartments at discrete time intervals (every 4 days in the experiment), rather than a continuous rate of diffusion. Because it was not possible to control K_i and r_i independently in the experiment through different nutrient concentrations, the mathematical results above imply that success of the experiment in showing higher biomass at non-zero diffusion rates depend on K_i and r_i being positively correlated.

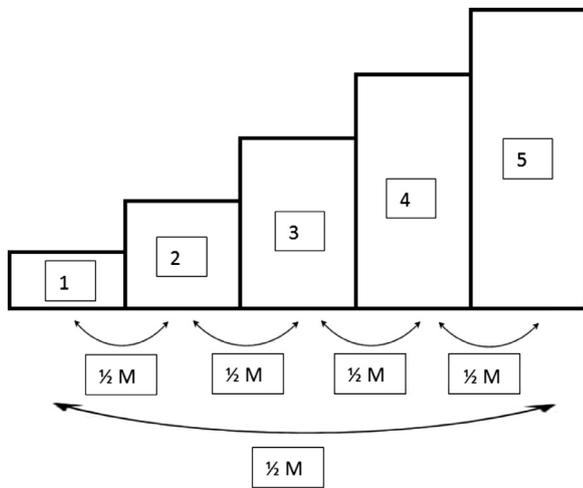


Fig. 1. Model configuration, showing that five containers with gradient in nutrient supply (in the proportions 0:0.5:1:1.5:2, from compartment 1 to compartment 5) with rates of diffusion (M). Half of the biomass removed from each container was transferred to the container on the right and half to the container on the left (this included moving plant biomass between containers 1 and 5).

Simulations were performed to help design and interpret an experiment.

2.3. Experiment

The objective of the experiment was to determine whether there is a non-zero diffusion rate that maximizes total vegetation biomass in a region in which resources are distributed heterogeneously, and to estimate that diffusion rate and the maximum vegetation biomass. We used duckweed (*Lemna minor* Linn.) in our experiment. Duckweed is an aquatic plant that floats on or just beneath the surface of still or slow-moving bodies of fresh water and wetlands. These plants are simple, lacking an obvious stem or leaves. Duckweed was convenient to use, because it is easy to maintain in laboratory containers, as well as to manipulate to simulate a specific type of movement, namely density-independent diffusion in this case. This was done through transfers between a row of five compartments (containers in which duckweed was grown) with different nutrient levels (Fig. 1 shows a schematic of the experimental arrangement). Biomass could also easily be measured through time. The experiment is described in online supplementary material.

3. Results

3.1. Simulation model

A comparison of simulations of total biomass through time in the homogeneous and heterogeneous five-compartment systems, with diffusion in both cases, is shown in Fig. 2. Note that the solid wavy line in the heterogeneous system results from the biomass transfers every 4 days. The parameter values, r_i and K_i , were chosen to best fit the experiment. Higher overall biomass is clear in the heterogeneous system with $M = 0.20$. However, in the absence of diffusion, the final total biomasses in the homogeneous and heterogeneous treatments were precisely the same (dashed line in Fig. 2).

In order to compare the total biomasses resulting in a heterogeneous distribution of resources for different diffusion rates, a sequence of values of transfer from $M = 0$ –0.25 were used. Because we did not know *a priori* the growth rates, r_i , and carrying capacities, K_i , of the individual containers, we examined results for a reasonable range of parameters. All simulations showed a peak in total biomass as a function of M , when the values of r_i and K_i obeyed criterion (2.4). The

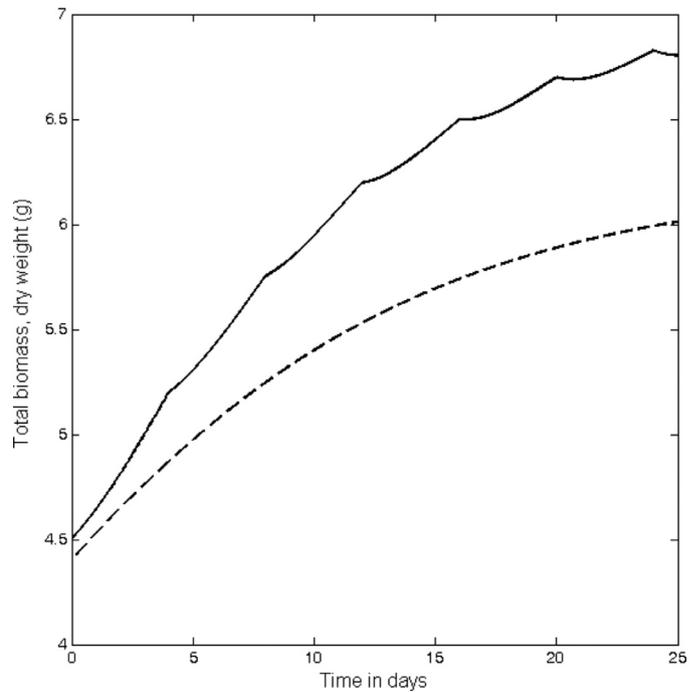


Fig. 2. Simulations of total biomass as a function of time under heterogeneous conditions with 20% diffusion (solid curve). Homogeneous conditions with 20% diffusion and without diffusion, heterogeneous condition without diffusion, all those three cases followed the same biomass growth (dashed curve). The diffusion, M , for each condition was 20% every 4 days. The result shows that there was a higher total biomass in the heterogeneous case. The parameter values for the heterogeneous case are $r_1 = 0.011$, $r_2 = 0.033$, $r_3 = 0.077$, $r_4 = 0.11$, $r_5 = 0.275$ day⁻¹, $K_1 = 0.135$, $K_2 = 0.405$, $K_3 = 0.945$, $K_4 = 1.35$, $K_5 = 3.37$ g dW. The parameter values of the homogeneous case are $r_i = 0.10$ and $K_i = 1.242$ for $i = 1, 2, \dots, 5$.

best fit to the total experimental population biomass (see below) as a function of diffusion rate, M , is shown in Fig. 3 (values of r_i and K_i are in caption), with a peak in total biomass at about $M = M_{\max} = 0.07$. In addition, the biomass of each of the containers is plotted as a function of M (Fig. 4). It is clear that the biomasses of the five compartments converge as a function of increasing D , as predicted from theory.

3.1.1. Sensitivity analysis of model simulation

The plots shown in Figs. 3 and 4 represent parameter sets that best fit the experimental data below. These parameters showed a somewhat more non-linear gradient of values than we expected based on the nutrients added; i.e. the best set of values were $r_1 = 0.0068$, $r_2 = 0.0204$, $r_3 = 0.0476$, $r_4 = 0.0680$, $r_5 = 0.1700$ day⁻¹, $K_1 = 0.2$, $K_2 = 0.6$, $K_3 = 1.4$, $K_4 = 2.0$, $K_5 = 5.0$ g dW. Note that we are assuming $r_i/K_i = \text{constant}$.

We explored the sensitivity of the simulation results to the mean values of the r_i s (solid lines) and K_i s (dotted lines), as well as to the mean gradients, S , of resources across the patches represented by the sets r_i s and K_i s. Each of these was changed by $\pm 10\%$ and $\pm 20\%$ and the sensitivity to these of the peak biomass, the diffusion coefficient at which the peak in total biomass occurs, M_{\max} , and the sharpness of the peak (ratio of peak biomass to biomass in the absence of diffusion) was calculated. In the case of the gradient, S , sensitivity to a $\pm 10\%$ change was created by, respectively increasing or decreasing r_1 and K_1 by 10%, r_2 and K_2 by 5%, and respectively decreasing or increasing r_5 and K_5 by 10% and r_4 and K_4 by 5%. It can be seen that all three, r , K , and S , have a positive effect on maximum total biomass (Fig. 5a). Parameters K_i and S have a positive effect on M_{\max} , but r_i has a negative effect (Fig. 5b). Parameters K_i and S have a positive effect on sharpness of the peak, but r_i has no effect (Fig. 5c). More generally, through exhaustive simulations, we confirmed that satisfaction

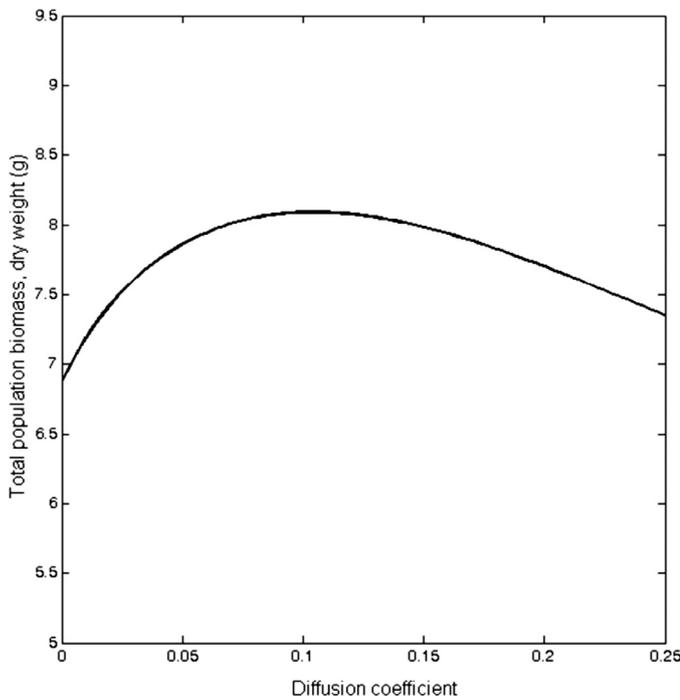


Fig. 3. Total biomass versus diffusion rate in model simulations. Other parameters were chosen within reasonable ranges to fit the experimental data (see Fig. 6). These are $r_1 = 0.0068$, $r_2 = 0.0204$, $r_3 = 0.0476$, $r_4 = 0.0680$, $r_5 = 0.1700 \text{ day}^{-1}$, $K_1 = 0.2$, $K_2 = 0.6$, $K_3 = 1.4$, $K_4 = 2.0$, $K_5 = 5.0 \text{ g dW}$.

of criterion (2.4) guarantees that (2.3) is true, at least for small values of diffusion. The condition that whenever $K_i > K_{i-1}$, it is also true that $r_i > r_{i-1}$, and vice versa is sufficient to guarantee that (2.4) holds, but is not a necessary condition.

3.2. Experiment

The central goal of the experiment was to determine which diffusion rate may lead to the peak biomass in the heterogeneous

system. We found a significantly higher biomass in heterogeneous system than homogeneous system with 20% diffusion (Fig. 6). We conducted further experiments to measure the total dry biomass with 0%, 6% and 10% diffusion rates. Although experiments 1 and 2 were carried out 20 days apart, biomass for the heterogeneous resource distribution and 0% diffusion did not differ between the two experiments ($p = 0.194$). Thus we assumed that we could compare the total biomasses with four different diffusion rates, ($M = 0\%$, 6%, 10% and 20%), under the heterogeneous conditions described in the Methods section. Therefore, we had a total of four treatments (0%, 6%, 10% and 20% diffusion rates) with 0% diffusion rate having 6 replicates and other treatments having 3 replicates. The diffusion rate significantly affected biomass, with non-zero values of the diffusion rate having significantly higher biomass than 0% diffusion. The highest biomass occurred at $M = 6\%$ (Fig. 7), which is close to the peak of the simulation results (Fig. 4a) which are also plotted in Fig. 7.

4. Discussion

We set out to experimentally test the mathematical result of Lou [1] of how a single plant population responds to spatial heterogeneity and dispersal through diffusion. We first extended Lou's results to a logistic growth model and to a discretized model. For the experimental test, we planted duckweed (*Lemna minor* Linn.) in situations of both heterogeneously and homogeneously distributed resource. We manually controlled rates of diffusion, i.e., the percentage of duckweed transferred from each water container to adjacent ones. Based on this experimental design, a simulation model was developed to determine the range of results expected from the laboratory experiment.

The experiment, in which the diffusion was applied artificially every 4 days at levels of 6% and 10%, in addition to a 0% control, confirmed that a moderate level of diffusion increased total biomass above the level of the non-diffusing population in a heterogeneous environment. In particular, 6% diffusion produced a total biomass that appears to be close to a peak value. In the heterogeneous system, without diffusion, the biomass growth will follow the resource distribution, the total biomass increases to total carrying capacity. But with a moderate level of diffusion, the biomass exported from

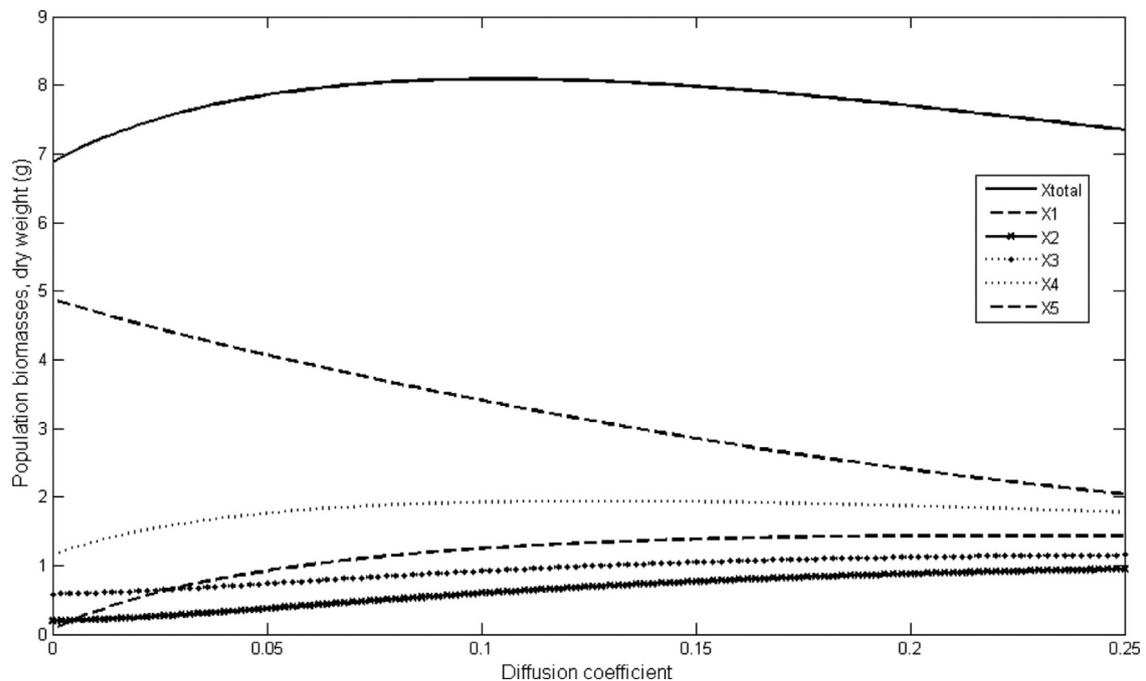


Fig. 4. Biomasses of all five compartments and total biomass versus diffusion rate. Other estimated parameter values are the same as in Fig. 3.

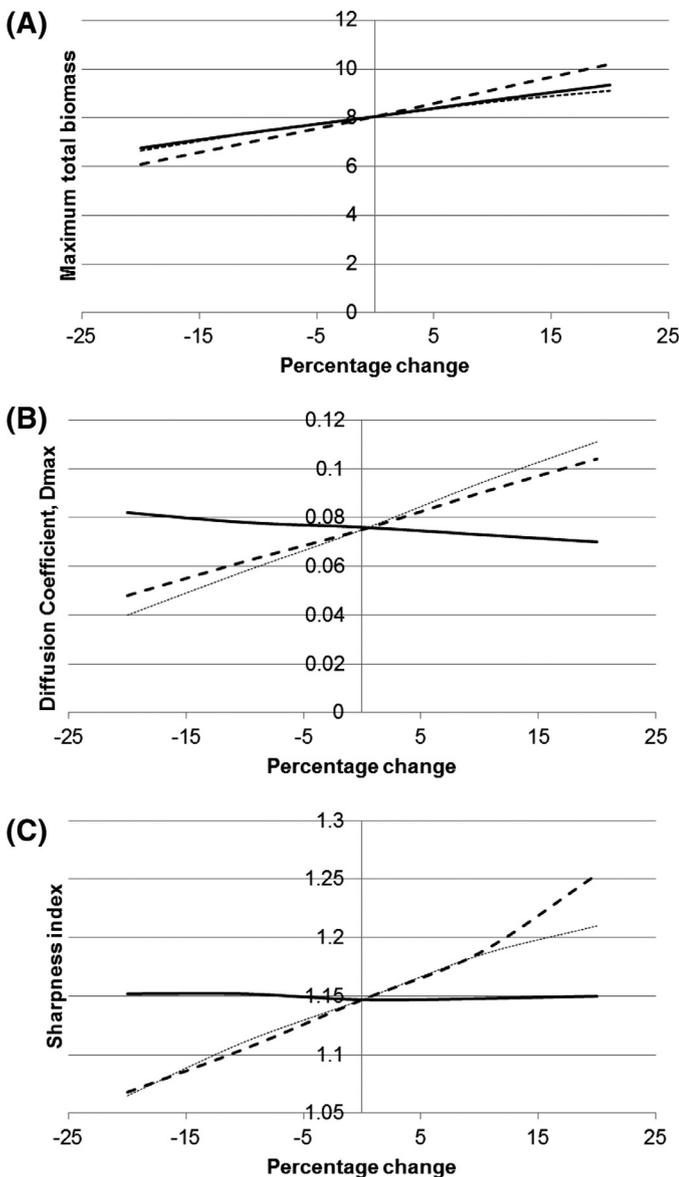


Fig. 5. Sensitivity analysis for (a) maximum total biomass, (b) diffusion coefficient, M_{\max} , at which maximum total biomass occurs, and (c) sharpness of the peak (ratio of height at M_{\max} to height when $M = 0$). The values are simulated for ($\pm 10\%$ and $\pm 20\%$) of all the $r_i(s)$ (solid line), all the $K_i(s)$ (dotted line) and slope, S , of the resource gradient across the containers, S .

the higher productivity region results in larger increase in standing stock biomass in lower resource areas than the decrease in biomass in higher resource areas. This can increase the total biomass level of the whole system to be greater than total carrying capacity. However, as diffusion is increased to high levels, biomass becomes homogeneous over the whole region and the total biomass again becomes equal to the total carrying capacity.

Modeling studies of this phenomenon are rare. But a somewhat analogous result to biomass maximization at intermediate diffusion rates was obtained by Pulliam and Danielson [6]. Pulliam and Danielson simulated different relative amounts of high- and poor-quality habitat, in which population movement from high- to low-quality habitat was more likely the lower the ratio of the former to the latter. However, in this study the trend of total population biomass was not monotonically decreasing with lower ratio of high-quality to low-quality habitat, and, in fact, there was a peak for an intermediate ratio. The reason seems to be related to our finding that intermediate

diffusion levels maximize total biomass; that is, as long as the population levels in the high-quality sites are not too negatively affected by movement into low-quality sites, the enhancement of population at the low-quality sites causes the total population to be higher.

Our model simulation and experiment relate to an important concept of spatial ecology, the occurrence of sources and sinks on landscapes. Sources are the areas in which surplus population is created (reproduction and growth exceed losses) and sinks are the areas in which losses exceed births and growth. This concept has implications for conservation ecology, because it is possible that individuals may be attracted to sink areas, where they die or fail to reproduce, threatening the population [7]. That influential paper has been followed by many others, expanding on the idea [8–17]. The simple source and sink idea have been replaced by a more complex picture in which ‘pseudo-sinks’ are included [14]. Pseudo-sinks are areas into which net population fluxes may be observed at times. However, these areas are actually self-sustaining and the net flux occurs only because there are more productive sources nearby from which individuals migrate. Habitat patches that vary in quality can cause population dynamics to differ between patches. Populations in better quality patches are more productive and should produce more emigrants [18].

Our experiment is relevant to the concept of pseudo-sinks, because none of the containers in the experiment was actually a sink. All the individual containers, in isolation, could maintain populations, though at different levels. Containers become pseudo-sinks in the context of receiving input from more productive containers. The model simulation and empirical experiments show how pseudo-sinks may provide a positive role in maintaining a population and also imply that, under certain conditions of resource heterogeneity, there is higher total vegetation biomass than under homogeneous conditions.

The experiments and model suggest that different rates of dispersal among sources and pseudo-sinks in nature can affect regional population size and there might be rates of diffusion that maximize the size of the total population in a heterogeneous region. However, this would in general be difficult to test in the field, as dynamics of a population in nature are affected by a large number of factors that were eliminated in our experiment. This is especially true for animal populations, the individuals of which are unlikely to move by diffusion (i.e., randomly). They more often move within home ranges, with frequent returns to core areas, or show directed movements in response to environmental gradients. Nevertheless, dispersal of populations of both plants and animals over long time scales can often be represented as diffusive (e.g., Kareiva [19]), and, in that case, steady state patterns of biomass density on landscapes may be influenced by the interactions of heterogeneity and diffusion. A part of the population will diffuse from the most productive areas, and that surplus population can enhance the population of the less productive areas and increase the total population level of the whole system.

Manipulations of simple systems in nature that demonstrate such effects are possible. In an experiment described by Keddy [20,21] and Watkinson [14], densities of seeds of the plant *Cakile edentula* were manipulated along a sand dune gradient. The seaward or beach end of the gradient was a source, while the middle and landward sites were shown to be net sinks where mortality was higher than reproduction. Interestingly, in a model by Watkinson [14], the plants were most abundant in the sink sites because of the high seed migration from the source. Watkinson’s work suggests that in his system diffusion can cause the overall population in a heterogeneous environment to exceed that in a homogeneous environment.

The experiments of Keddy [20,21] and the model of Pulliam and Danielson [6], as well as our experiment and model, simplify the importance of spatial configuration. Our experiment used a very specific one-dimensional spatial configuration of containers with a linear gradient of resources, the relative levels of which were at least roughly known. In nature, the configurations of sources, sinks, and pseudo-sinks may take highly complex forms in two dimensions [22,23].

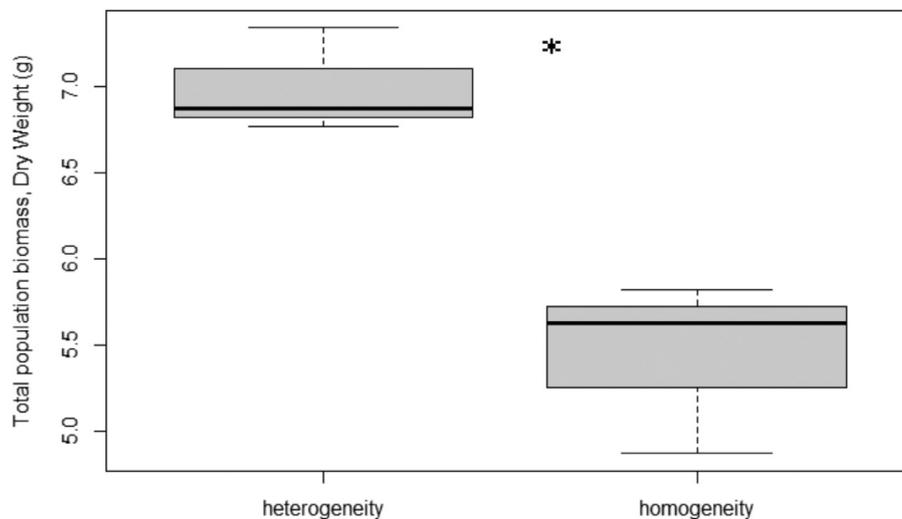


Fig. 6. Experimental values of mean and standard deviation of total dry biomass. The left bar shows the dry weight of duckweed from the heterogeneous treatment group with 20% diffusion rate and the right bar shows the dry weight from homogeneous treatment group with 20% diffusion rate. In both treatments total nutrients were the same. Stars above the error bars indicate significant differences ($P < 0.05$) between treatments. Each treatment was replicated 3 times.

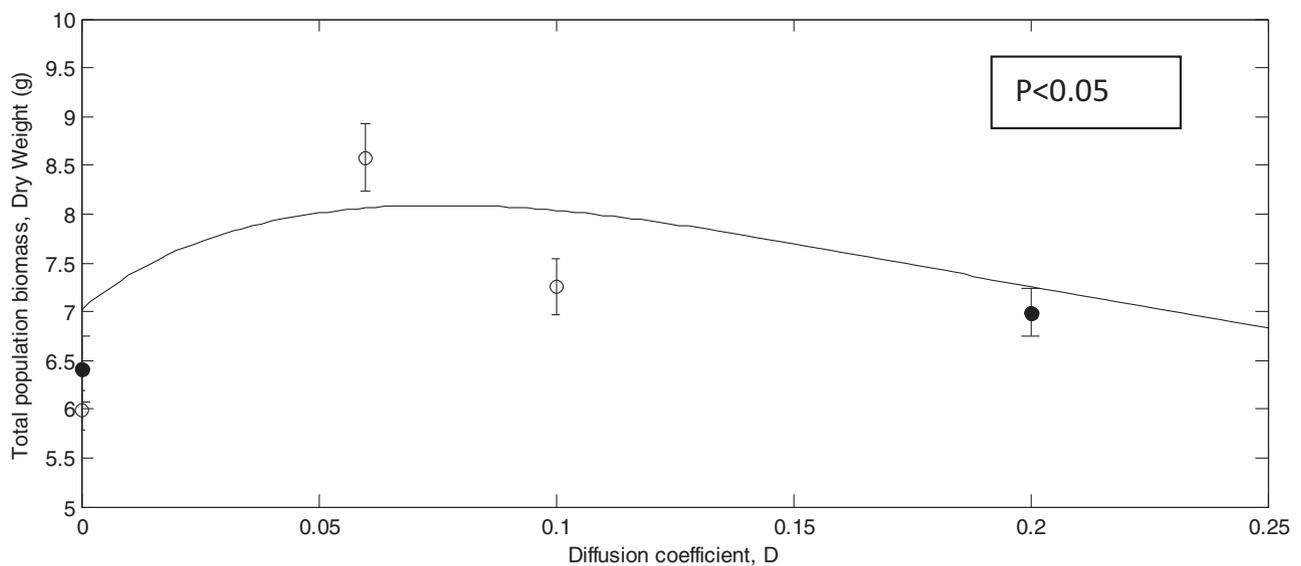


Fig. 7. Mean and standard deviation of total dry biomass as functions of diffusion coefficient from experiment and model simulation. The dark dots show the total dry weight under heterogeneous condition with different diffusion rates (0%, 20%) from first experiment. The empty dots show the total dry weight under heterogeneous conditions with different diffusion rates (0%, 6%, 10%) from the second experiment. $P < 0.05$ indicates significant differences between treatments. The solid line shows results for dry mass as a function of diffusion coefficient (from 0% to 25%) from the simulation model.

In addition, carrying capacities of different natural habitats are difficult to estimate, as they depend on many factors that are difficult to measure. It is still possible, however, that more complex, but still quantifiable experiments in the field, could be carried out in the future.

Our experiment involved only biomass of a single population. Spatial heterogeneity and diffusion also have implications for species richness. The interaction of spatial movement and competition in shaping ecological communities have been the object of much study [24–30], with spatial heterogeneity playing an important role in the interaction [24,31,32]. A trade-off between competition and dispersal can lead to regional coexistence of competing species [33]. Also, given enough heterogeneity in the resources over the area occupied by the community, many species could, in principle, coexist [25,29,34]. Therefore, spatial heterogeneity is an important consideration of species coexistence [35]. The general relationship between richness and ecosystem functioning remains valid in open systems,

but the maintenance of ecosystem processes significantly depends on the effects of dispersal on species richness and local interactions. Without dispersal, experimental systems lack a key process counteracting competitive exclusion [36]. Moderate to intermediate dispersal rates between local communities can weaken local competitive exclusion either by a colonization–competition trade-off and/or by source-sink dynamics when resource availability is spatially distributed [4].

Our experiment had a number of limitations. Due to the uncertainties in the amount of light and nutrient level in each container during the course of the experiment, we can only estimate that light was approximately the same for all containers and the nutrient levels had a strong gradient across the containers. A larger amount of experimental replicates with different levels of heterogeneity and additional diffusion rates would have helped to better confirm our results. But our experiments fit a model well and give reasonable support to our hypothesis that diffusion in a heterogeneous environment can increase biomass over an equivalent homogeneous environment.

The model simulation provides a perspective how population biomass is regulated by the interacting effects of spatial heterogeneity and diffusion in natural system. Our future plan is going to test our results in a natural system, and also possibly to test two-species competition of limited resource in heterogeneous conditions.

Acknowledgments

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Appendix A. Spatially discrete environment with parameters r_i and K_i

Use of two parameters, r and K , rather than the single parameter, g , differs from the mathematical model (1.1), but can still produce the results found by Lou [1] if r_i and K_i scale in proportion. To show that, we can write the equilibrium equation for one compartment in a general n -compartment model with terms

$$\frac{D}{2}(X_{i-1} - 2X_i + X_{i+1}) + r_i \left(1 - \frac{X_i}{K_i}\right) X_i = 0 \quad (i = 1, n) \quad (\text{A.1})$$

and with periodic boundary conditions; $X_{n+1} = X_1$.

Dividing by X_i and summing over n , we obtain

$$\frac{D}{2} \sum_{i=1, n} \frac{K_i}{r_i X_i} (X_{i-1} - 2X_i + X_{i+1}) + \sum_{i=1, n} r_i - \sum_{i=1, n} \frac{r_i}{K_i} X_i = 0 \quad (\text{A.2})$$

or

$$\frac{D}{2} \sum_{i=1, n} \frac{1}{X_i} (X_{i-1} - 2X_i + X_{i+1}) = \sum_{i=1, n} \frac{r_i}{K_i} (X_i - K_i) \quad (\text{A.3})$$

We can manipulate the left hand side of (A.3) as follows

$$\begin{aligned} & \frac{D}{2} \sum_{i=1}^n \left[\frac{X_{i-1} - X_i}{X_i} + \frac{X_{i+1} - X_i}{X_i} \right] \\ &= \frac{D}{2} \sum_{i=1}^n \left[\frac{X_{i-1} - X_i}{X_i} \right] + \frac{D}{2} \sum_{i=2}^{n+1} \left[\frac{X_i - X_{i-1}}{X_{i-1}} \right] \\ &= \frac{D}{2} \left(\frac{X_0 - X_1}{X_1} \right) + \frac{D}{2} \sum_{i=2}^n \left[\frac{X_{i-1} - X_i}{X_i} \right] + \frac{D}{2} \sum_{i=2}^n \left[\frac{X_{i+1} - X_i}{X_i} \right] \\ & \quad + \frac{D}{2} \left(\frac{X_{n+1} - X_n}{X_n} \right) \end{aligned}$$

or, using $X_0 = X_n$ and $X_{n+1} = X_1$,

$$\begin{aligned} &= \frac{D}{2} \left(\frac{X_0 - X_1}{X_1} \right) + \frac{D}{2} \left(\frac{X_1 - X_0}{X_0} \right) + \frac{D}{2} \sum_{i=2}^n \left[\frac{X_{i-1} - X_i}{X_i} \right] \\ & \quad + \frac{D}{2} \sum_{i=2}^n \left[\frac{X_{i+1} - X_i}{X_i} \right] \\ &= \frac{D}{2} \sum_{i=1}^n \left[\frac{X_{i-1} - X_i}{X_i} + \frac{X_i - X_{i-1}}{X_{i-1}} \right] = \frac{D}{2} \sum_{i=1}^n \left[\frac{(X_i - X_{i-1})^2}{X_i X_{i-1}} \right]. \quad (\text{A.4}) \end{aligned}$$

From using (A.4) in (A.3) we find that

$$\sum_{i=1}^n \frac{r_i}{K_i} (X_i - K_i) = \frac{D}{2} \sum_{i=1}^n \left[\frac{(X_i - X_{i-1})^2}{X_i X_{i-1}} \right] \quad (\text{A.5})$$

from which it follows that

$$\sum_{i=1, n} \frac{r_i}{K_i} (X_i - K_i) > 0. \quad (\text{A.6})$$

Our goal is to determine the conditions under which X_i increases from its equilibrium value of K_i as D increases. Note that (A.6) does not imply that $\sum_{i=1, n} (X_i - K_i) > 0$. However, if r_i and K_i scale in proportion (that is, if the growth rate is proportional to the carrying capacity at a fixed constant, say r/K), then it follows that

$$\sum_{i=1, n} \frac{r_i}{K_i} (X_i - K_i) = \frac{r}{K} \sum_{i=1, n} (X_i - K_i) > 0 \quad \text{and} \quad \sum_{i=1, n} (X_i - K_i) > 0. \quad (\text{A.7})$$

In this case, r_i/K_i is equivalent to a single parameter g_i . We can further deduce that $X_{\text{total}} = \sum_{i=1, n} X_i$ will always increase initially as D increases from zero, by taking the derivative of equation (A.7) with respect to D :

$$\begin{aligned} \frac{d}{dD} \left(\sum_{i=1, n} (X_i - K_i) \right) &= \frac{d}{dD} \left(\sum_{i=1, n} X_i \right) = \frac{d}{dD} \left(\frac{D}{2} \sum_{i=1, n} \frac{(X_i - X_{i-1})^2}{X_i X_{i-1}} \right) \\ &= \frac{1}{2} \sum_{i=1, n} \frac{(X_i - X_{i-1})^2}{X_i X_{i-1}} + D \frac{d}{dD} \left(\sum_{i=1, n} \frac{(X_i - X_{i-1})^2}{X_i X_{i-1}} \right) \end{aligned} \quad (\text{A.8})$$

The right hand side of (A.8) is positive for $D = 0$, which implies that X_{total} will initially increase. It must also eventually decrease, because it can be shown that as $D \rightarrow \infty$, $X_i \rightarrow X_{\text{mean}}$ (for all i), where $X_{\text{mean}} = \frac{1}{n} \sum_{i=1, n} X_i$.

It is shown in Appendix B that more general criteria can be found for X_{total} increasing with increasing values of D .

Appendix B. Criterion for X_{total} to increase as D increases from zero

The objective is to show that

$$\sum_{i=1, n} \left(\frac{(r_i - r_{i-1})(K_i - K_{i-1})}{r_i r_{i-1}} \right) > 0 \quad (\text{B.1})$$

(Criterion 2.4 in text) is a sufficient condition for X_{total} to increase as D increases from zero. It is straightforward to demonstrate that this holds for any n .

To show that, we again write the equilibrium equation for one compartment in a general n -compartment model with terms

$$\frac{D}{2}(X_{i-1} - 2X_i + X_{i+1}) + r_i \left(1 - \frac{X_i}{K_i}\right) X_i = 0 \quad (\text{B.2})$$

Multiplying both sides by $K_i/r_i X_i$ and summing over n , we obtain

$$\frac{D}{2} \sum_{i=1, n} \frac{K_i}{r_i X_i} (X_{i-1} - 2X_i + X_{i+1}) + \sum_{i=1, n} K_i - \sum_{i=1, n} X_i = 0 \quad (\text{B.3})$$

or

$$\frac{D}{2} \sum_{i=1, n} \frac{K_i}{r_i X_i} (X_{i-1} - 2X_i + X_{i+1}) = \sum_{i=1, n} (X_i - K_i) \quad (\text{B.4})$$

Our goal is to determine the conditions under which X_i increases from its equilibrium value of K_i as D increases. To determine this, we

differentiate both sides of (A.3) to obtain

$$\frac{1}{2} \sum_{i=1}^n \frac{K_i}{r_i X_i} (X_{i-1} - 2X_i + X_{i+1}) + \frac{D}{2} \frac{d}{dD} \left[\sum_{i=1}^n \frac{K_i}{r_i X_i} (X_{i-1} - 2X_i + X_{i+1}) \right] = \frac{d}{dD} \left[\sum_{i=1}^n (X_i - K_i) \right]$$

Setting $D = 0$, and $X_i = K_i$ ($i = 1, n$), we obtain

$$\frac{1}{2} \sum_{i=1}^n \frac{K_i}{r_i K_i} (K_{i-1} - 2K_i + K_{i+1}) = \frac{d}{dD} \left(\sum_{i=1}^n X_i \right) = \frac{dX_{\text{total}}}{dD}$$

or

$$\begin{aligned} \frac{dX_{\text{total}}}{dD} &= \frac{1}{2} \sum_{i=1}^n \frac{1}{r_i} (K_{i-1} - 2K_i + K_{i+1}) \\ &= \frac{1}{2} \sum_{i=1}^n \frac{1}{r_i} [(K_{i+1} - K_i) - (K_i - K_{i-1})] \end{aligned} \tag{B.5}$$

Now we use a general formula for integration by parts

$$\begin{aligned} \sum_{i=1}^n (a_{i+1} - a_i) b_i &= \sum_{i=1}^n a_{i+1} b_i - \sum_{i=1}^n a_i b_i \\ &= \sum_{i=2}^{n+1} a_i b_{i-1} - \sum_{i=1}^n a_i b_i \\ &= a_{n+1} b_n - a_1 b_0 + \sum_{i=1}^n a_i b_{i-1} - \sum_{i=1}^n a_i b_i \\ &= a_{n+1} b_n - a_1 b_0 + \sum_{i=1}^n a_i (b_{i-1} - b_i) \end{aligned}$$

Because $a_{n+1} = a_1$ and $b_0 = b_n$, the first two terms in the last line cancel and we have

$$\sum_{i=1}^n (a_{i+1} - a_i) b_i = \sum_{i=1}^n a_i (b_{i-1} - b_i) \tag{B.6}$$

Let $a_i = K_i - K_{i-1}$, and $b_i = 1/r_i$, and use (A.5) in (A.4) to determine that

$$\frac{dX_{\text{total}}}{dD} = \frac{1}{2} \sum_{i=1}^n \left(\frac{1}{r_i} - \frac{1}{r_{i-1}} \right) (K_i - K_{i-1}) \tag{B.7}$$

or

$$\sum_{i=1, n} \left(\frac{(r_i - r_{i-1})(K_i - K_{i-1})}{r_i r_{i-1}} \right) > 0$$

Equation (A.6) implies that if the relationship between the $r_i(s)$ and $K_i(s)$ is such that the right hand side of (A.6) is greater than zero, then X_{total} will increase with an increase in D , at least in the vicinity of the equilibrium point $X_i = K_i$ ($i = 1, n$). This suggests a general criterion for X_{total} to increase with D for any value of n .

Appendix C. Outline of proof of Criterion 9

A criterion parallel to (2.4) can be found for the spatially continuous one-dimensional form with $r(s)$ and $K(s)$; that is, for

$$\frac{\partial X(s)}{\partial t} = D \frac{\partial^2 X(s)}{\partial s^2} + r(s) \left[1 - \frac{X(s)}{K(s)} \right] X(s), \tag{C.1}$$

where $r(s) > 0$ and $K(s) > 0$ and both are continuous and non-constant in a bounded domain Ω . Neumann (zero flux) boundary conditions

are assumed. Denoting the solution at equilibrium still by $X(s)$, i.e.;

$$d\Delta X + r(s)X \left(1 - \frac{X}{K(s)} \right) = 0 \text{ in space } \Omega, \tag{C.2}$$

in paper in preparation, the criterion for X_{total} , $X_{\text{total}} = \int_{\Omega} X(s)$, to increase for small increases in D from zero is now,

$$\int_{\Omega} \frac{\partial K}{\partial s} \frac{\partial}{\partial s} \left(\frac{1}{r} \right) < 0 \tag{C.3}$$

or, more generally

$$\int_{\Omega} \nabla K \cdot \nabla \frac{1}{r} < 0 \tag{C.4}$$

A full proof for this result will be given in the paper in preparation. However, we note here that at equilibrium it is shown that the solution, $X(s)$, approaches $K(s)$ at all points in the domain Ω as $D \rightarrow 0$. Dividing both sides of (c.2) by $r(s)X(s)/K(s)$, and integrating over Ω , we obtain,

$$\begin{aligned} 0 &= \int_{\Omega} \left[d\Delta X \cdot \frac{K(s)}{r(s)X} + (K(s) - X) \right] \\ &= -d \int_{\Omega} \nabla X \cdot \nabla \left(\frac{K(s)}{r(s)X} \right) + \int_{\Omega} (K(s) - X). \end{aligned}$$

From

$$\int_{\Omega} \left| \nabla X(s) \cdot \nabla \left(\frac{1}{\xi X(s)} \right) - \nabla K \cdot \nabla \frac{1}{r} \right| \rightarrow 0 \text{ as } d \rightarrow 0,$$

where ξ is equal to r/K (proof in paper in preparations), it follows that

$$\int_{\Omega} X = \int_{\Omega} K - d \left[\int_{\Omega} \nabla K \cdot \nabla \frac{1}{r} + o(1) \right]$$

So that the criterion for $X_{\text{total}} = \int_{\Omega} X(s)$ to increase when $\int_{\Omega} \nabla K \cdot \nabla \frac{1}{r} < 0$ or, for the one-dimensional case, when $\int_{\Omega} \frac{\partial K}{\partial s} \frac{\partial}{\partial s} \left(\frac{1}{r} \right) < 0$, follows.

Supplementary Materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.mbs.2015.03.005](https://doi.org/10.1016/j.mbs.2015.03.005).

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