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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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32 which implies

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

33 The diffusion of individuals away from the areas of high productiv-
 34 ity keeps the population levels in those areas below carrying capacity,
 35 so that high production continues. The diffusion allows higher popu-
 36 lation levels to be attained in the lower resource areas than the
 37 carrying capacity would predict. The result is that the total popula-
 38 tion over all space exceeds that which would occur in a homogeneous
 39 space with the same total resource production. In order to apply the
 40 above results to typical ecological models, it is necessary to extend
 41 (1) to a logistic equation

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

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

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

56 2. Methods

57 2.1. Discrete patch model

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

57 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 experi-
 ment in which diffusion occurred continuously in time. Instead, an
 artificial experiment was designed, in which diffusion was simul-
 ated 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 rep-
 resent 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 regu-
 lar time intervals:

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

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

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 (dif-
 fusion) 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 contin-
 uous rate of diffusion. Because it was not possible to control K_i and
 r_i independently in the experiment through different nutrient con-
 centrations, 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.

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