

# Effects of diffusion on total biomass in heterogeneous continuous and discrete-patch systems

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**Abstract** Theoretical models of populations on a system of two connected patches previously have shown that when the two patches differ in maximum growth rate and carrying capacity, and in the limit of high diffusion, conditions exist for which the total population size at equilibrium exceeds that of the ideal free distribution, which predicts that the total population would equal the total carrying capacity of the two patches. However, this result has only been shown for the Pearl-Verhulst growth function on two patches and for a single-parameter growth function in continuous space. Here, we provide a general criterion for total population size to exceed total carrying capacity for three commonly used population growth rates for both heterogeneous continuous and multi-patch heterogeneous landscapes with high population diffusion. We show that a sufficient condition for this situation is that there is a convex positive relationship between the

maximum growth rate and the parameter that, by itself or together with the maximum growth rate, determines the carrying capacity, as both vary across a spatial region. This relationship occurs in some biological populations, though not in others, so the result has ecological implications.

**Keywords** Population dynamics · Spatial heterogeneity · Diffusion · Growth functions

## Introduction

The quality of habitat of an ecological population typically varies across its range. The quality of habitat can vary gradually across a continuum of habitat or it can vary discontinuously across patches of habitat. In both cases, key questions asked by ecologists are how populations of mobile animals disperse across the heterogeneous environment, foraging, searching for mates, etc. and how this dispersal affects the population size and distribution across the environment. Mathematical and simulation models are often used to address these questions. Often, the models have patches of habitat rather than a continuum, as the mathematics is easier to describe, so we will largely use that conceptualization here but will produce results for both patchy and continuous habitats.

The majority of models of animal dispersal in heterogeneous environments fall into one of two broad categories, balanced dispersal models and source-sink models (Diffendorfer 1998). In the first category, habitat patches vary in carrying capacity, but are all capable of supporting a population. In this idealization, the population on each patch reaches the carrying capacity at steady state and the population flux of animals moving among patches is balanced such that the number of animals on each patch stays the same through time. This implies that the probability of an animal moving out

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of a patch per unit time is inversely proportional to the carrying capacity of the patch (McPeck and Holt 1992). The distribution across patches is an ideal free distribution (IFD) (Fretwell and Lucas 1970). According to the IFD, if other factors besides carrying capacity of a patch, such as predator density, can be ignored and animals are free to move, and move in a way to maximize fitness, then they will continue to move until they cannot do any better in terms of fitness, which is the point at which the subpopulation on each patch matches its carrying capacity. The IFD theory is idealized in the sense that it assumes individual organisms have perfect knowledge of the environment and freedom to move. The IFD evens out the fitnesses of individuals of the given population across the landscape, because patches that are poorer in quality, due to lower resources, will have lower densities of individuals. The IFD has been used to describe the distributions of foraging animals in the field (e.g., Harper 1982; Oksanen et al. 1995; Lin and Batzli 2001; Pusenius and Schmidt 2002; Jones et al. 2006). Because at steady-state, no individual can improve fitness by moving to another patch, the IFD corresponds to an evolutionarily stable strategy (ESS), a strategy that cannot be invaded by another strategy that is initially rare (e.g., Cressman et al. 2004; Cantrell et al. 2007; Křivan et al. 2008).

In the second broad category, source-sink theory, animal movement is not directed preferentially towards maximizing fitness, but animals may move from better to poorer resource areas, as well as the reverse (Pulliam 1988). Because in this concept, animals can move, by accident or intention, into non-habitat patches, source-sink models include not only habitat patches but also patches in which population growth is negative. Thus, dispersal occurs, through random or directed movements, from areas of high resource levels and positive growth (sources) into areas of low resources and negative growth (sinks). This movement pattern can lower the overall growth rate and size of the population and even lead to population extinction, if the population growth rate in sources cannot keep up with the loss in sinks. Even if extinction is avoided, the overall population size in a source-sink system is less than would be supported by the sources alone because of population loss to sinks. Many papers have expanded on this idea, with Holt (1985) providing a first mathematical analysis of a source-sink model so that source-sink theory is well developed (e.g., Amarasekare 2004; Amezcua and Holyoak 2000; Dias 1996; Dunning et al. 1992; Gunderson et al. 2001; Holt 1997; Howe et al. 1991; Kristan 2003; Loreau and DeAngelis 1997; Ritchey 1997; Watkinson and Sutherland 1995; Wilson 2001).

A variation on source-sink theory sees heterogeneous landscapes not simply as areas of dichotomous sources and sinks, but also of regions that may appear to be sinks but are actually capable of net positive production and thus of independently sustaining subpopulations. Net

population fluxes from high-growth rate sources may be observed at times into these low-growth rate patches; hence, the latter may seem to be sinks and are thus called “pseudo-sinks” (Watkinson and Sutherland 1995). Pseudo-sink areas are actually self-sustaining, and the net flux occurs only because there are more productive sources nearby from which individuals migrate. Populations in the better-quality patches are more productive and should produce emigrants to the low-quality patches (Donahue et al. 2003), but all patches contribute to supporting the population. Environments consisting purely of sources and pseudo-sinks are somewhat intermediate between balanced dispersal and source-sink situations. Because all landscapes vary in habitat quality, there will generally be a distribution of sources and pseudo-sinks, as well as true sinks. Here, we will consider landscapes consisting only of sources and pseudo-sinks and will assume that animals do not move optimally in a pattern that leads to an IFD, but that they move in a random manner that can be described as diffusion.

When a population is spread across its range of sources and pseudo-sinks, it may be thought that the total population size will surely be less than if it were distributed through balanced dispersal, or IFD. But that is not always the case. It has been recognized that under certain circumstances, a population in which individuals move randomly on a landscape with heterogeneously distributed resources can reach higher populations than populations following the IFD. We will study this analytically and derive general proofs for discrete and continuous systems and for a few commonly used population growth functions. In particular, we show that a sufficient condition for this situation is that there is a convex positive relationship between the maximum growth rate and the carrying capacity, as both vary across a spatial region. These are novel results, but build on previous work on specific models described below.

## Mathematical background

The counter-intuitive result that a population diffusing in a heterogeneous spatial region could reach a larger population size than the total carrying capacity of the region was shown by Lou (2006) (see also He and Ni 2013a, b). He considered a population of consumers of total biomass  $u$ , described by the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = D\Delta u + [g(x)-u]u, \quad (1)$$

where  $g(x)$  varies with the spatial distance  $x$  but is fixed temporally, and where the population diffuses at some constant rate  $D$ , with Neumann (no-flux) boundary conditions on  $u$ . Lou

(2006) showed, by dividing the terms of the right-hand side by  $u$  and integrating over all space  $\Omega$ , that the following holds at equilibrium

$$D \int_{\Omega} \frac{|\nabla u|^2}{u^2} + \int_{\Omega} [g(x)-u(x)]dx = 0 \tag{2}$$

Because the first term is necessarily positive, i.e.,

$$D \int_{\Omega} \frac{|\nabla u|^2}{u^2} > 0, \tag{3}$$

this implies that

$$\int_{\Omega} [u(x)-g(x)]dx > 0; \tag{4}$$

The qualitative interpretation of this result is that diffusion of individuals away from areas of high-growth rate keeps the population levels in those areas below carrying capacity, so that new production exceeds losses at steady state in those areas. The diffusion from areas of higher to lower levels of resource allows higher population levels to be attained in other areas than their carrying capacities would allow in the absence of diffusion. The result is that the total population overall space exceeds that which would occur in a homogeneous space with the same total carrying capacity, or even for an IFD in heterogeneous space. In Eq. (1),  $g(x)$  represents both carrying capacity and maximum growth rate, and (4) holds for positive  $g(x)$ . But in general, the properties of growth rate and carrying capacity for a population will differ and need to be described by different parameters. Population models used in ecology, such as the logistic equation, have separate parameters for maximum growth rate and carrying capacity. In fact, results analogous to those of Lou (2006) were observed earlier for a two-patch system in which the population on the two patches was described by logistic equations (Freedman and Waltman 1977; Holt 1985); i.e., for a model of the form,

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - \varepsilon N_1 + \varepsilon N_2 \tag{5a}$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - \varepsilon N_2 + \varepsilon N_1 \tag{5b}$$

(Holt 1985). In these papers, it was shown that for high movement rates between the compartments,  $\varepsilon$ , that is, high in relation to population growth rates, the total population at equilibrium could exceed the sum of the carrying capacities of the two patches, for certain combinations of the parameters,  $r_i$  and  $K_i$ ; in particular, if  $K_j > K_i$  and  $r_j/K_j > r_i/K_i$ . This is shown graphically in Fig. 2 of Holt (1985). Therefore, the conclusion that total population size at equilibrium may exceed the sum

of carrying capacities holds for the basic logistic equation model, at least in the two-patch case with high dispersal rates. Recently, this two-patch model has been more thoroughly analyzed (Arditi et al. 2015).

The continuous landscape version of this effect of heterogeneity has also been studied recently. Assuming that both maximum population growth rate and carrying capacity vary spatially, DeAngelis et al. (2016) extended Lou’s (2006) results to the logistic equation in continuous space,

$$\frac{\partial u}{\partial t} = D \Delta u + r(x) \left[1 - \frac{u}{K(x)}\right] u, \tag{6}$$

showing that both for small values of the diffusion rate,  $D$ , and for  $D \rightarrow \infty$ , conditions could be found on  $r(x)$  and  $K(x)$ , for which it is true that

$$\int_{\Omega} [u(x)-K(x)]dx > 0 \tag{7}$$

The utility of the logistic model, written in the form of Eq. (6), especially in extension to spatial situations, has been questioned, as has the notion implicit in that model that a carrying capacity can be defined in terms of a constant such as  $K$  (Mallet 2012; Arditi et al. 2015). Therefore, to show that these results have more universal importance in ecology, our goal is to extend the above results beyond the logistic model in the form of Eq. (6) both to a more general version of the logistic and to another commonly used function for population growth. In particular, we show the relationships that must hold between the spatially dependent parameters of the model for the result of total population size to exceed total carrying capacity at equilibrium. It is convenient to demonstrate the results in a discrete multi-patch system in which the patches are in a one-dimensional array connected by diffusion and then show the extension to continuous space in any dimension. The continuous space equivalent expressions are derived in Appendix A and the multi-patch case is in Appendix B. We will also be less general here than in DeAngelis et al. (2016) and show results mathematically only for  $D \rightarrow \infty$ , though numerical results will be given for the whole range of values of  $D$ .

### Methods

A general method is used to determine criteria for total population size at equilibrium to exceed total carrying capacity in a one-dimensional discrete-patch version of the general reaction-diffusion model;

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u, x)u, \tag{8}$$

where  $F(u, x)$  is the reaction or growth term, which can take on different forms. We will consider three different forms of  $F(u, x)$ ;

$$F_1(u, x)u = (r(x) - \alpha(x)u)u \tag{9a}$$

$$F_2(u, x)u = r(x) \left( 1 - \frac{u}{K(x)} \right) u \tag{9b}$$

$$F_3(u, x)u = \left( \frac{r(x)}{a + u} - q(x) \right) u \tag{9c}$$

We refer to these functions for rate of population growth as the “original Verhulst growth,” the “Pearl-Verhulst growth,” and the “Monod growth”, respectively. As Mallet (2012) notes, Eq. (9a) is the form of the non-linear growth function in the form originally described by Verhulst (1838), while (9b) is the form that Pearl (1927) adopted, with carrying capacity  $K$ , commonly referred to as the logistic. In Eq. (9c), a Monod saturating growth form is used. All these models were originally used in a non-spatial context. We assume that the functions  $r(x)$ ,  $K(x)$ ,  $\alpha(x)$ , and  $q(x)$ , though varying in space, like  $g(x)$  earlier, are all constant in time.

Consider the patch model equivalent to (8), with  $n$  compartments, which have biomasses represented by the variables  $U_1, U_2, \dots, U_n$  (for example, grams biomass per patch). 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., wrap-around conditions);

$$\frac{dU_i}{dt} = F(U_i, x_i)U_i - DU_i + \frac{1}{2}DU_{i-1} + \frac{1}{2}DU_{i+1} \quad (i = 1, \dots, n) \tag{10}$$

where  $i - 1 = n$  when  $i = 1$  and  $i + 1 = 1$  when  $i = n$ .

We examine the behavior of this and the other functions in the limit that  $D \rightarrow \infty$ . Let  $D$  approach very large values ( $D \gg F(U, x)$ ). This implies that  $U_i - U_{i-1} \rightarrow 0$  for all  $i$ . This must be true because  $F(U_i, x_i)$ , if considered only as non-negative, is bounded for all values of  $U_i$ . To determine the total biomass at equilibrium, we can write a set of equilibrium conditions as follows.  $U_1 \approx U_2 \dots \approx U_n \approx Z$ , to obtain at steady state,

$$F(Z, x_i)Z = \left( \frac{1}{2} \right) D(U_{i+1} - U_i) + \left( \frac{1}{2} \right) D(U_i - U_{i-1}) \quad (i = 2, \dots, n-1) \tag{11a}$$

plus the two end patches, which have wraparound conditions

$$F(Z, x_1)Z = \left( \frac{1}{2} \right) D(U_1 - U_n) - \left( \frac{1}{2} \right) D(U_1 - U_2), \tag{11b}$$

$$F(Z, x_n)Z = \left( \frac{1}{2} \right) D(U_{n-1} - U_n) - \left( \frac{1}{2} \right) D(U_n - U_1) \tag{11c}$$

We do not substitute  $Z$  for the  $U_i$ s on the right-hand side, but cancel those terms by adding the  $n$  equations (11a,b,c) together to obtain the equation

$$\sum_{i=1}^n F(Z, x_i)Z = 0, \tag{12}$$

which can be solved for the non-zero value of  $Z$ . Then,

$$U_{\text{total}} = \sum_{i=1}^n U_i \text{ is equal to } nZ.$$

### Results

The above approach is applied to each of the three growth functions in the reaction diffusion model, modified here as a one-dimensional discrete-patch system.

#### Case 1 Original Verhulst model

Consider the original Verhulst function, using the parameters in Eq. (2) of Mallet (2012);

$$F_1(u, x)u = (r(x) - \alpha(x)u)u \tag{13}$$

in the discrete patch model

$$\begin{aligned} \frac{dU_i}{dt} = & r_i U_i - \alpha_i U_i^2 - DU_i + \frac{1}{2} DU_{i-1} \\ & + \frac{1}{2} DU_{i+1} \quad (i = 1, \dots, n) \end{aligned} \tag{14}$$

The steady state equilibrium biomass of each isolated patch is given by  $r_i/\alpha_i$ , so the total steady state biomass summed over  $n$  patches, represented in the following as  $K_{\text{total}}$ , is

$$K_{\text{total}} = \sum_{i=1}^n \frac{r_i}{\alpha_i}. \tag{15}$$

At equilibrium, for  $D \rightarrow \infty$ , we can assume that

$$U_1 = U_2 = \dots = U_n \equiv Z. \tag{16}$$

By summing all the  $n$  equations at equilibrium, we obtain

$$\sum_{i=1}^n F(Z, x_i)Z = \sum_{i=1}^n (r_i Z - \alpha_i Z^2) = 0, \tag{17}$$

because all of the terms multiplied by  $D$  cancel, so that the non-zero solution of  $Z$  is

$$Z = \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i}. \tag{18}$$

If

$$U_{\text{total}} = nZ > K_{\text{total}}, \tag{19}$$

then the total population of the system with diffusion is greater than the sum of the individual equilibria of the patches and vice versa. Note that when  $\alpha_i = \alpha$  for all values of  $i$ ,

$$U_{\text{total}} = nZ = K_{\text{total}},$$

In [Appendix A](#), for continuous  $x$ , we let  $r(x) = h(\alpha(x))$  and show that if  $h(s)/s$  increasing in  $s > 0$ , then  $U_{\text{total}}$  ( $L$  in [Appendix A](#))  $> K_{\text{total}}$  ( $\bar{K}$  in [Appendix A](#)). This is extended to the discrete  $x_i$  case in [Appendix B](#). Thus, for (19) to hold, it is sufficient that the relationship between  $r_i$  and  $\alpha_i$  is positive convex. A special case of a convex relationship is  $r_i \propto (\alpha_i/b)^\gamma$ , where  $b$  is a constant and  $\gamma > 1$ . Numerical simulations were performed to find the total equilibrium population in a five-compartment version of (14). We assumed that  $r_i \propto (\alpha_i/b)^\gamma$  and determined total population size versus  $\gamma$  from a numerical solution of the five-compartment model, as well as from the analytic expression (18). We compare these with the total carrying capacity or total population size at IFD with no diffusion (Fig. 1a). Note that the switch from  $U_{\text{total}} < K_{\text{total}}$  to  $U_{\text{total}} > K_{\text{total}}$  occurs at  $\gamma = 1$ , which is the switch from a positive concave to a positive convex relationship. For each of the nine values of  $\gamma$  used, the total biomass at equilibrium is plotted against the diffusion coefficient,  $D$  (Fig. 1b). Note that the values of

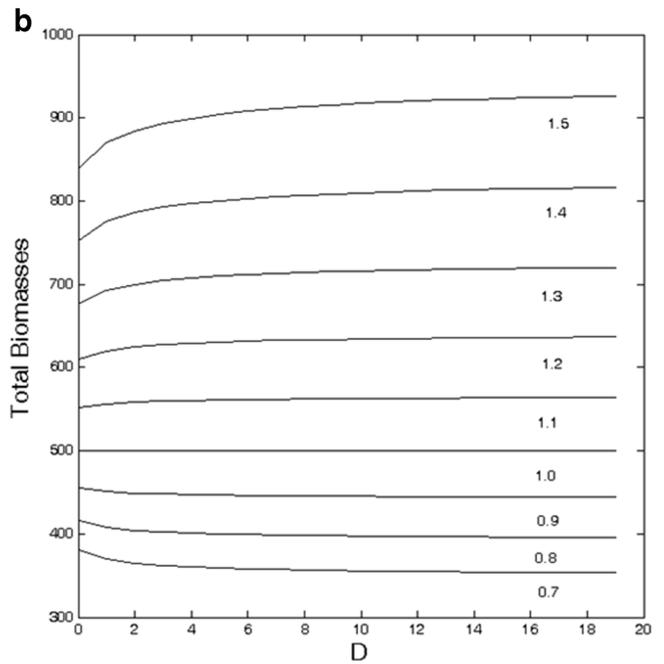
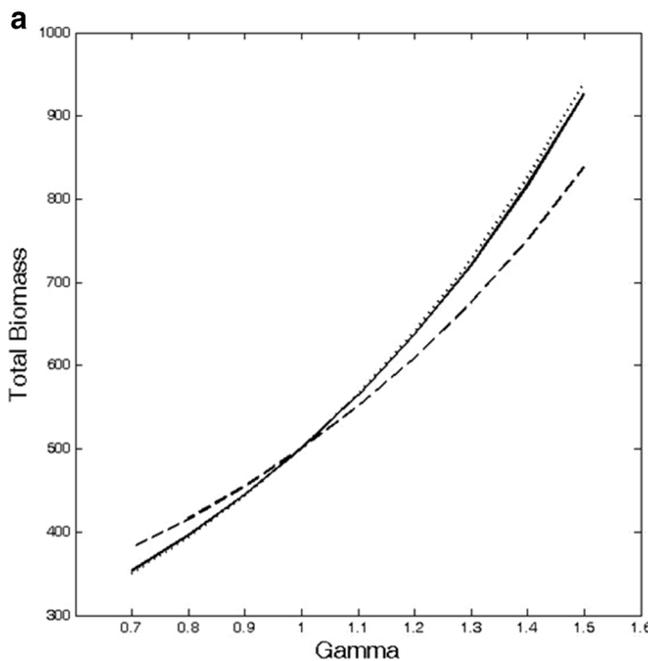
carrying capacity for each patch,  $r_i/\alpha_i$ , vary with  $\gamma$  in this case, because these carrying capacities are functions of  $r_i$  as well as of  $\alpha_i$ . While a convex relationship, such as  $r_i \propto (\alpha_i/b)^\gamma$ , where  $\gamma > 1$ , is sufficient for inequality (19) to hold, it is not necessary. Relationships that are partly convex and partly concave can be demonstrated to result in (19). For example,  $r_i \propto \alpha_i^2/(1 + \gamma\alpha_i^2)$  can lead to (19) holding over a range of values of  $\gamma$ , even though the relationship may be concave over part of the range of  $\alpha_i$ , as long as the convex part of the curve is sufficiently preponderate.

Case 2 (Pearl-Verhulst growth). See [Appendix C](#) (Supplementary material) for the analysis. The numerical results are shown in Fig. 2a, b.

Case 3 (Monod growth). See [Appendix C](#) (Supplementary material) for the analysis. The numerical results are shown in Fig. 3a, b.

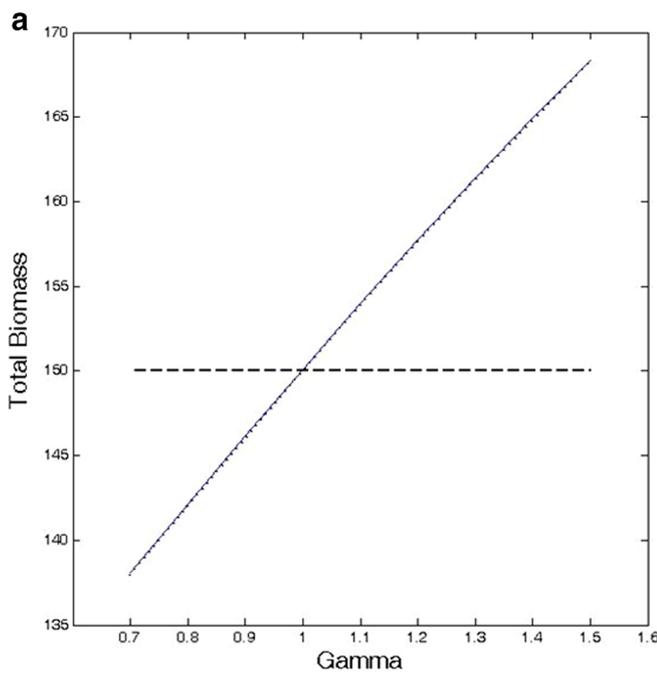
### Discussion

We have shown that three different population growth functions can all lead to the possibility that in a heterogeneous resource environment, in which individuals can diffuse through random movement, the total population size can exceed the mathematically defined total carrying capacity. The ecologically counterintuitive nature of this

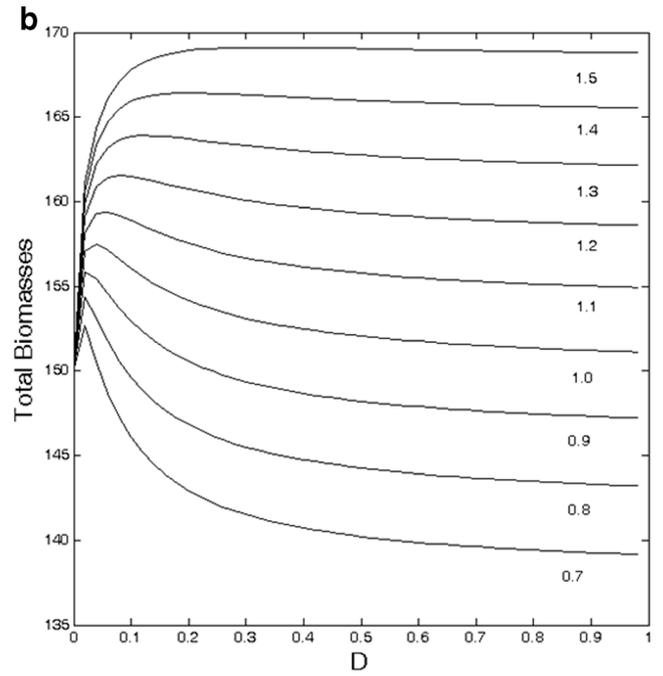


**Fig. 1** **a** Total population  $U_{\text{total}}$  from numerical solution of five-patch original Verhulst growth model with diffusion (solid line), overlapping with the analytic calculation from equations (26) (dotted lines), and total carrying capacity with no diffusion (dashed line). Parameter values  $r_i$  increase as a power of  $\gamma$ :  $r_1 = 1$ ,  $r_2 = 2^\gamma$ ,  $r_3 = 3^\gamma$ ,  $r_4 = 4^\gamma$ ,  $r_5 = 5^\gamma$ .

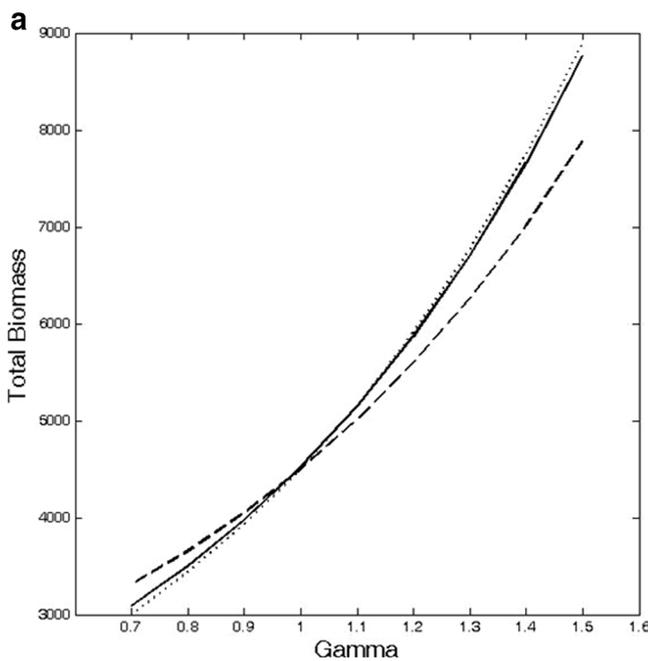
Parameter values of  $\alpha_i$  increase linearly:  $\alpha_1 = 0.01$ ,  $\alpha_2 = 0.02$ ,  $\alpha_3 = 0.03$ ,  $\alpha_4 = 0.04$ ,  $\alpha_5 = 0.05$ . **b** Example of total population size  $U_{\text{total}}$  as function of  $D$  for  $U_{\text{total}} < K_{\text{total}}$ :  $\gamma = 0.7$  through  $\gamma = 1.5$  in intervals of 0.1. The values of  $\gamma$  are shown in the figure



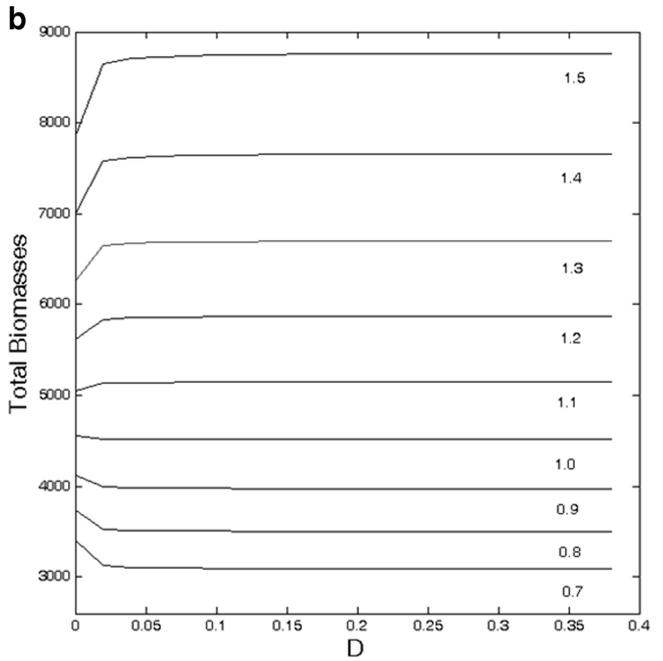
**Fig. 2 a** Total population  $U_{total}$  from numerical solution of five-patch Pearl-Verhulst growth model with diffusion (solid line), overlapping with the analytic calculation from equation (dotted line), and total carrying capacity with no diffusion (dashed line). Parameter values  $r_i$  increase as a power of  $\gamma$ :  $r_1 = 0.01$ ,  $r_2 = 0.01 * 2^\gamma$ ,  $r_3 = 0.01 * 3^\gamma$ ,



$r_4 = 0.01 * 4^\gamma$ ,  $r_5 = 0.01 * 5^\gamma$ ; parameter values of  $K_i$  increase linearly:  $K_1 = 10.$ ,  $K_2 = 20.$ ,  $K_3 = 30.$ ,  $K_4 = 40.$ ,  $K_5 = 50.$  **b** Example of total population size  $U_{total}$  as a function of  $D$ , for  $\gamma = 0.7$  through  $\gamma = 1.5$  in intervals of 0.1. The values of  $\gamma$  are shown in the figure



**Fig. 3 a** Total population size  $U_{total}$  from numerical solution of five-patch Monod growth model with diffusion (solid line), overlapping with the analytic calculation from Eq. (32) (dotted line), carrying capacity with no diffusion (dashed line). Parameter values  $r_i$  increase as a power of  $\gamma$ :  $r_1 = 1$ ,  $r_2 = 2^\gamma$ ,  $r_3 = 3^\gamma$ ,  $r_4 = 4^\gamma$ ,  $r_5 = 5^\gamma$ . Parameter values  $q_i$



increase linearly:  $q_1 = 0.001$ ,  $q_2 = 0.002$ ,  $q_3 = 0.003$ ,  $q_4 = 0.004$ ,  $q_5 = 0.005$ ,  $a = 100.$  **b** Example of total population size  $U_{total}$  as function of  $D$  for  $U_{total} < K_{total}$ :  $\gamma = 0.7$  through  $\gamma = 1.5$  in intervals of 0.1. The values of  $\gamma$  are shown in the figure

result, which shows that a randomly diffusing population can exceed the size of a population in which individuals attempt to optimize fitness (that is, the IFD), was first pointed out by Holt (1985) for a two-patch system. Oddly, passive diffusion results in a larger population size than active seeking of optimal fitness. For both continuous and patchy systems, however, this depends on a relationship between the local maximum growth rates and local carrying capacities of the system. It is sufficient that the growth rate is convex positively correlated with carrying capacity, meaning that the growth rate increases faster than carrying capacity along a gradient of carrying capacity in the environment. The implication of the theorem in Appendix A is more general, however, and has not been completely explored.

The contrasting results for equilibrium population size for rapid diffusion and the balanced dispersal of the IFD reflect the different sets of assumptions in their derivation, which can be stated in succinct form. In particular, starting with equation

$$\frac{dU_i}{dt} = F(U_i, x_i)U_i - DU_i + \frac{1}{2}DU_{i-1} + \frac{1}{2}DU_{i+1} \quad (i = 1, \dots, n)$$

the IFD is derived by assuming that each

$$F(U_i, x_i) = 0,$$

leading to populations in each patch reaching carrying capacity of that patch. On the other hand, rapid diffusive movement among patches implies that  $U_i - U_{i-1} \rightarrow 0$  for all values of  $i$ , leading to

$$\sum_{i=1}^n F(U_i, s_i) = \sum_{i=1}^n F(Z, s_i) = 0$$

An underlying assumption of this study is that spatially varying parameters describing the growth and carrying capacity in the models are not independent, but that they positively covary with changes in  $x$ . For the Pearl-Verhulst equation, we assumed a positive relationship between  $r(x)$  and  $K(x)$ ; for the original Verhulst model, we assumed a relationship between  $r(x)$  and  $\alpha(x)$ ; and for the Monod model, we assumed a positive relationship between  $r(x)$  and  $q(x)$ .

Concerning the widely used Pearl-Verhulst equation, traditionally, ecologists have considered maximum growth rate,  $r(x)$ , and carrying capacity,  $K(x)$ , to be independent, but this is a perception based on the way that the equation is written. It is clear from the study of the other equations (e.g., Verhulst and Monod) that the maximum growth rate and the carrying capacity should be related and that “carrying capacity” is not an independent property of an ecological system, but arises from the balance of terms of gain and loss, with density dependence in the loss.

There have been few studies directed specifically at determining a relationship between  $r$  and  $K$  of the logistic equation applied to populations. A main source of information is from ecotoxicologists, who have measured in the laboratory the effects of different stressors on both  $r(x)$  and  $K(x)$ , where now  $x$  refers to some level of stress. Hendriks et al. (2005) reviewed 128 studies of that sort, showing a high correlation of  $r(x)$  with  $K(x)$ , with a slope close to 1 (their Fig. 4). As the authors point out, the data show that standardized carrying capacities decreased proportionally to standardized growth rates. Although these studies impose an artificial stress on populations, it is not unreasonable to generalize to stresses in general, which can include any deviation from optimal environmental conditions of a population. Although there have been few studies outside of the ecotoxicological realm that combine measurements of growth rate, some studies exist. For example, a study of leafhopper populations exists in which both  $r$  and  $K$  were measures along a rearing temperature gradient for four species of rice feeding leafhoppers, of the genus *Nephotettix* (Valle et al. 1989). For each species, growth rate and carrying capacity were affected proportionally. This paper, as well as studies of Luckinbill (1978, 1979) and Fitzsimmons et al. (2010) are evidence of the generality of positive relationships between  $r$  and  $K$ .

Our study has shown the importance of the way in which growth rate  $r(x)$  and a parameter related to carrying capacity,  $K(x)$ ,  $\alpha(x)$ , or  $q(x)$ , are related. If the relationship is such that the maximum growth rate increases more rapidly than the carrying capacity along a gradient of increasing carrying capacity, then  $U_{\text{total}} > K_{\text{total}}$ , while if the relationship is concave, the reverse is true. The ecotoxicological measurements of  $r$  and  $K$  in Hendriks et al. (2005, their Fig. 4), while showing a positive relationship between  $r$  and  $K$  in 128 studies, does not give information on the shapes of the relationships as a function of pollutant concentration. However, a closer look at the specific studies gives some information. Wong and Chang (1988) studied the effect of herbicides and insecticides on growth and steady state biomass of the alga *Chlamydomonas reinhardtii*. Most of the studies with different chemicals show a concave relationship between  $r$  and  $K$ , though at least one shows a convex relationship. Similarly, the study of Valle et al. (1989) of four leafhopper species shows a concave relationship for two species and a convex relationship for the two others.

All species populations are distributed on ranges in which fitness is a function of abiotic and biotic conditions and stresses (Watkinson 1985; Holt et al. 2005). To better understand how total population size may relate to these conditions and stresses, the relationships between maximum growth rate and the density-dependent parameters determining carrying capacity need to be understood.

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**Appendix A. Comparisons of total population and carrying capacity for large diffusion rate in the continuous space case**

We begin with a general equation that can facilitate all three cases, original Verhulst, Pearl-Verhulst, and Monod growth models, although analysis of the latter two is completed in the Supplementary Material;

$$u_t = D\Delta u + uF(u, x) \text{ in } \Omega \times (0, T) \tag{A.1}$$

$$\partial_\nu u = 0 \text{ on } \partial\Omega \times (0, T)$$

where  $T \leq \infty$ ,  $\Omega$  is a bounded domain in  $\mathcal{R}^N$ ,  $\nu$  is the unit outward normal on the smooth boundary  $\partial\Omega$  (thus,  $\partial_\nu u$  represents the normal derivative of  $u$ ), and  $F(u, x)$  satisfies:

(F1) For every  $x \in \overline{\Omega}$ , there exists a unique  $K(x) > 0$  such that  $F(K(x), x) = 0$ , and

(F2) for every  $x \in \overline{\Omega}$ ,  $F(u, x)$  is decreasing in  $0 \leq u \leq K(x)$ .

Under these hypotheses, the existence and uniqueness of a positive steady state for (A.1) is guaranteed by standard arguments (see, e.g., Cantrell and Cosner 2003, DeAngelis et al. 2016).

**Proposition A.1** For every  $D > 0$ , (A.1) has a unique positive steady state,  $u_D$ , which is globally asymptotically stable. Moreover,  $\max_{x \in \overline{\Omega}} u_D(x) \leq \max_{x \in \overline{\Omega}} K(x)$ .

Note that all three cases of interest, Pearl-Verhulst, original Verhulst, and Monod growth models, satisfy both (F1) and (F2).

**Proposition A.2** As  $D \rightarrow \infty$ ,  $u_D \rightarrow L$ , where  $L$  is a positive constant such that

$$\int_{\Omega} F(L, x) dx = 0 \tag{A.2}$$

**Proof.** Dividing the equation for  $u_D$

$$D\Delta u_D + u_D F(u_D, x) = 0 \tag{A.3}$$

by  $D$ , we obtain

$$\Delta u_D = -\frac{1}{D} u_D F(u_D, x).$$

Since the term  $u_D F(u_D, x)$  is uniformly bounded in  $x \in \overline{\Omega}$  and for all  $D$ , the right-hand side of the equation above tends to 0 as  $D \rightarrow \infty$ . Standard elliptic regularity estimates guarantee that by passing to a (sub)sequence

if necessary,  $u_D \rightarrow u_\infty$  as  $D \rightarrow \infty$  and the limit function  $u_\infty$  satisfies

$$\Delta u_\infty = 0 \text{ in } \Omega$$

$$\partial_\nu u_\infty = 0 \text{ on } \partial\Omega$$

which, in turn, implies that  $u_\infty \equiv \text{constant}$ . Clearly,  $u_\infty \geq 0$ .

Integrating the equation (A.3) over  $\Omega$ , we have

$$\int_{\Omega} u_D F(u_D, x) = 0. \tag{A.4}$$

Passing to the limit as  $D \rightarrow \infty$ , we see that

$$u_\infty \int_{\Omega} F(u_\infty, x) = 0 \tag{A.5}$$

since  $u_\infty$  is a constant.

If  $u_\infty = 0$ , i.e.,  $u_D \rightarrow 0$  as  $D \rightarrow \infty$ . On the other hand, since  $u_D > 0$  and  $F(u, x) > 0$  for  $u \in (0, K(x))$ , it follows that  $u_D F(u_D, x) > 0$  for all  $x \in \overline{\Omega}$ . This contradicts (A.4). Therefore,  $u_\infty > 0$ . From (A.5), we conclude

$$\int_{\Omega} F(u_\infty, x) dx = 0$$

and thus,  $u_\infty = L$ . Since this holds for every possible subsequence, our proof is complete.

We are now ready for comparing the total population  $\int_{\Omega} u_\infty dx$  with the total carrying capacity  $\int_{\Omega} K dx$  for the original Verhulst model.

**Theorem A.1** For the original Verhulst model

$$F(u, x) = (r(x) - \alpha(x)u)$$

we have

$$L = \frac{\int_{\Omega} r(x) dx}{\int_{\Omega} \alpha(x) dx}, \quad \overline{K} = \frac{1}{|\Omega|} \int_{\Omega} \frac{r(x)}{\alpha(x)} dx,$$

If  $r(x) = h(\alpha(x))$ , then the following statements hold:

- (i) If  $h(s)/s$  is increasing in  $s > 0$ , then  $L > \overline{K}$ .
- (ii) If  $h(s)/s$  is decreasing in  $s > 0$ , then  $L < \overline{K}$ .
- (iii) If  $h(s)/s$  is a constant in  $s > 0$ , then  $L = \overline{K}$ .

**Theorem A.2** For the Pearl-Verhulst model (see Supplementary material)

**Theorem A.3** For the Monod growth model (see Supplementary material)

The proofs of all three theorems above are similar, and they all follow from the crucial inequalities below.

**Proposition A.3**

(i) For two sequences of real numbers  $0 \leq a_1 \leq a_2 \leq \dots \leq a_n$  and  $0 \leq b_1 \leq b_2 \leq \dots \leq b_n$ , it always holds that

$$n(a_1b_1 + a_2b_2 + \dots + a_nb_n) \geq (a_1 + a_2 + \dots + a_n)(b_1 + b_2 + \dots + b_n) \tag{A.6}$$

(ii) For two sequences of real numbers  $a_1 \geq a_2 \geq \dots \geq a_n \geq 0$  and  $0 \leq b_1 \leq b_2 \leq \dots \leq b_n$ , it always holds that

$$n(a_1b_1 + a_2b_2 + \dots + a_nb_n) \leq (a_1 + a_2 + \dots + a_n)(b_1 + b_2 + \dots + b_n) \tag{A.7}$$

**Proof.** Part (ii) is proved in [DeAngelis et al. 2016, Lemma 2.6]. As we will need these inequalities in Appendix B below in a crucial way, we include a short proof here for part (i).

We use induction. Obviously, (A.6) holds for  $n = 1$ . Now, assume that (A.6) holds for  $n = k$  then we proceed to show that (A.6) holds for  $n = k + 1$ . First, observe that

$$a_1b_1 + \dots + a_kb_k + ka_{k+1}b_{k+1} \geq a_{k+1}(b_1 + \dots + b_k) + (a_1 + \dots + a_k)b_{k+1} \tag{A.8}$$

since

$$a_{k+1}[(b_{k+1}-b_1) + \dots + (b_{k+1}-b_k)] \geq a_{k+1}(b_{k+1}-b_1) + \dots + a_k(b_{k+1}-b_k)$$

From the induction hypothesis and (A.8), it follows that

$$\begin{aligned} & (a_1b_1 + \dots + a_kb_k + a_{k+1}b_{k+1})(k + 1) \\ &= (a_1b_1 + \dots + a_kb_k)k + (a_1b_1 + \dots + a_kb_k) + a_{k+1}b_{k+1}(k + 1) \\ &\geq (a_1 + \dots + a_k)(b_1 + \dots + b_k) + a_{k+1}(b_1 + \dots + b_k) \\ &\quad + (a_1 + \dots + a_k)b_{k+1} + a_{k+1}b_{k+1} \\ &= (a_1 + \dots + a_k + a_{k+1})(b_1 + \dots + b_k + b_{k+1}) \end{aligned}$$

This complete the proof.

(A.7) is a “dual” version of (A.6), and it can be proved by reversing all the inequalities in the proof of (A.6) above.

We are now ready for the proofs of Theorems A.1

*Proof of Theorem A.1.*

The values of  $L$  follow from a simple computation of (A.2).

The proofs of parts (i) and (ii) are almost identical; thus, we will only present the proof of part (i) here.

We first approximate all integrals by their Riemann sums and set, for  $i = 1, \dots, n$ ,

$$a_i = r(x_i) = \frac{h(\alpha(x_i))}{\alpha(x_i)}, \quad b_i = \alpha(x_i), \quad i = 1, 2, \dots, n.$$

Since we can arrange the terms in the Riemann sum in such a way that  $\{b_i\}$  is ascending (then,  $\{a_i\}$  is also ascending since  $h(s)/s$  is increasing), we have, by (A.6), that

$$\begin{aligned} \frac{1}{n} \sum_{i=1}^n r(x_i) &= \frac{1}{n} \sum_{i=1}^n \frac{h(\alpha(x_i))}{\alpha(x_i)} \alpha(x_i) \geq \left( \frac{1}{n} \sum_{i=1}^n \frac{h(\alpha(x_i))}{\alpha(x_i)} \right) \left( \frac{1}{n} \sum_{i=1}^n \alpha(x_i) \right) \\ &= \left( \frac{1}{n} \sum_{i=1}^n \frac{r(x_i)}{\alpha(x_i)} \right) \left( \frac{1}{n} \sum_{i=1}^n \alpha(x_i) \right). \end{aligned}$$

Letting  $n \rightarrow \infty$ , we obtain

$$\frac{1}{|\Omega|} \int_{\Omega} r(x) dx \geq \left( \frac{1}{|\Omega|} \int_{\Omega} \frac{r(x)}{\alpha(x)} dx \right) \left( \frac{1}{|\Omega|} \int_{\Omega} \alpha(x) dx \right),$$

i.e.,  $L \geq \bar{K}$ . Again, the strict inequality follows from a careful examination of the arguments above.

The proof of part (iii) is immediate.

**Appendix B. Discrete case (patch model)**

In this appendix, we will establish the discrete version of Theorems A.1 for patchy models, which we have used in the main text. First, we remark that the existence and uniqueness of the steady state solutions for all three n-patch models (with any diffusion rate  $D > 0$ ) follow from similar considerations for the continuous PDE-model (as in Appendix A above). We refer to (Lou 2016) for a rigorous mathematical proof.

As before, we treat only the original Verhulst growth model here, while the Pearl-Verhulst and Monod growth models are presented in the Supplementary material. In fact, all three cases follow directly from Proposition A.3 directly.

**Theorem B.1** The total population in the n-patch original Verhulst model,  $F(u,x) = r(x) - \alpha(x)u$  approaches the limit

$$nZ = n \frac{\sum_{i=1}^n r_i}{\sum_{i=1}^n \alpha_i}$$

as  $D \rightarrow \infty$ . Suppose that  $r(x) = h(\alpha(x))$ ; then the following statements hold:

- (i) If  $h(s)/s$  is increasing in  $s > 0$ , then  $nZ > \sum_{i=1}^n \frac{r_i}{\alpha_i}$ .
- (ii) If  $h(s)/s$  is decreasing in  $s > 0$ , then  $nZ < \sum_{i=1}^n \frac{r_i}{\alpha_i}$ .
- (iii) If  $h(s)/s$  is a constant in  $s > 0$ , then  $nZ = \sum_{i=1}^n \frac{r_i}{\alpha_i}$ .

**Proof.** Again, the derivation of  $nZ$  was included in the main text, and the rest of the assertions follow from Proposition A.3 directly by setting  $a_i = \frac{r_i}{\alpha_i}$  and  $b_i = \alpha_i$ ,  $i = 1, \dots, n$ , arranged in ascending order of  $\{b_i\}$ .

**Theorem B.2** *Pearl-Verhulst model (see Supplementary material)*

**Theorem B.3** *Monod growth mode (see Supplementary Material)*

We therefore conclude that in an  $n$ -patch system, the total population is larger than the total carrying capacity for large diffusion rate for all three models, Pearl-Verhulst, original Verhulst, and Monod growth models, if the intrinsic growth rate,  $r$ , is a convex function of the other parameter.

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