



Dispersal and spatial heterogeneity: single species

Donald L. DeAngelis¹ · Wei-Ming Ni^{2,3} ·
Bo Zhang¹

Received: 20 October 2014 / Revised: 15 March 2015 / Published online: 11 April 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract A recent result for a reaction-diffusion equation is that a population diffusing at any 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. This has so far been proven by Lou for the case in which the reaction term has only one parameter, $m(x)$, varying with spatial location x , which serves as both the intrinsic growth rate coefficient and carrying capacity of the population. However, this striking result seems rather limited when applies to real populations. In order to make the model more relevant for ecologists, we consider a logistic reaction term, with two parameters, $r(x)$ for intrinsic growth rate, and $K(x)$ for carrying capacity. When $r(x)$ and $K(x)$ are proportional, the logistic equation takes a particularly simple form, and the earlier result still holds. In this paper we have established the result for the more general case of a positive correlation between $r(x)$ and $K(x)$ when dispersal rate is small. We review natural and laboratory systems to which these results are relevant and discuss the implications of the results to population theory and conservation ecology.

✉ Wei-Ming Ni
wmni@umn.edu

Donald L. DeAngelis
ddeangelis@bio.miami.edu

Bo Zhang
bo@bio.miami.edu

- ¹ Department of Biology, University of Miami, Coral Gables, FL 33124, USA
- ² Center for Partial Differential Equations, East China Normal University, Minhang, Shanghai 200241, People's Republic of China
- ³ School of Mathematics, University of Minnesota, Minneapolis, MN 55455, USA

Keywords Diffusion · Spatial heterogeneity · Mathematical ecology

Mathematics Subject Classification 35K57 · 92D25

1 Introduction

Levin (1992) noted that the “effort to explain the distribution of populations in terms of the movements of individuals is an extension of one of the most successful applications of mathematics to ecological phenomena, the use of random walk and diffusion models to describe dispersal”. Although the movements of animals and the seeds of plants are complex, the diffusion approximation often provides a very good description of such movement and hence has been a central assumption in spatial ecology, especially in the important area of reaction-diffusion models (Skellam 1951; Okubo 1980; Berg 1983; Hastings 1983; Kareiva 1983; Czarán 1998; Turchin 1998; Cantrell and Cosner 2003; Malchow et al. 2008; Cosner 2014). Studying diffusion, or more general forms of dispersal, in heterogeneous environments has been one of the key approaches to understanding growth and survival of individual populations and coexistence of species (Kadmon and Allouche 2007; Tamburello et al. 2013). For example, dispersal in heterogeneous environments results in movement between areas of greater and lesser suitability (e.g., differences in growth rate), with consequences for the population that need to be determined (Holt 1993; Mouquet and Loreau 2002, 2003). At the community level, sufficient dispersal in a heterogeneous environment with associated niche differences will promote species-sorting along resource gradients and promote coexistence (Chase and Leibold 2003).

Although real environments are highly heterogeneous in their underlying abiotic properties, the resource availability for consumers, and other conditions, mathematical studies of organism diffusion typically have assumed homogeneous environments. It is, therefore, important to extend theory to heterogeneous environments. Some progress is being made, however, in incorporating heterogeneity into theory and models (Turchin 1998; Cantrell and Cosner 2003; Ovaskainen et al. 2008; Ritchie 2010). Mathematical studies of reaction-diffusion models have revealed a number of interesting results that serve to stimulate active research in this area. Here we review some recent mathematical results and discuss a basic ingredient in extending these to a context that is relevant to key areas of ecological theory.

Using the classical Lotka-Volterra competition-diffusion system, Dockery et al. (1998) showed that, in a spatially heterogeneous environment, given two competing species with different dispersal rates but are otherwise identical, the *slower* competitor always wipes out the faster one regardless of their initial values. This is the celebrated result known as “*the slower diffuser always prevails!*”

In an attempt to understand this phenomenon, Lou (2006) adopted the weak competition approach and discovered another remarkable result. It has been known for decades that, for the classical Lotka-Volterra system in a *homogeneous* environment, *two weakly competing species will always co-exist regardless of their (random) dispersal rates or initial values*. (See e.g. Hsu 1978.) However, Lou (2006) proved, among other things, that *in a spatially heterogeneous environment, certain weakly competing*

species with appropriate dispersal rates can no longer co-exist, again, regardless of their initial values! Furthermore, Lou (2006) proposed an interesting conjecture which would further clarify the dynamics of 2×2 Lotka-Volterra weak competition-diffusion system when one of the inter-specific competition coefficients is small.

Progress was made first by Lam and Ni (2012), and then, Lou’s conjecture was finally established by He and Ni (in review). In fact, the result of He and Ni (in review) goes beyond Lou’s conjecture - it encompasses both the *entire* dynamics for 2×2 Lotka-Volterra weak competition-diffusion system, *without the smallness assumption on the inter-specific coefficients*, and the “slower diffuser always prevails”; moreover, it has proceeded further to investigate more general systems where the two competing species are allowed to have different intrinsic growth rates and carrying capacities.

It turns out that the starting point of Lou’s approach is a special case of the single logistic equation

$$\begin{cases} u_t = d \Delta u + u(m(x) - u) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu u = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \end{cases} \tag{1}$$

where $u(x, t)$ represents the population density of a species at location $x \in \Omega$ and at time $t > 0$, which is therefore assumed to be non-negative; Ω , the habitat, is a bounded domain in \mathbb{R}^N with smooth boundary $\partial\Omega$; d is the dispersal rate of u ; $\Delta = \sum_{i=1}^N \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator, and $\partial_\nu = \nu \cdot \nabla$, where ν denotes the outward unit normal vector on $\partial\Omega$, is the normal derivative on the boundary. The zero Neumann (no-flux) boundary condition is to ensure that no individual crosses the boundary of the habitat. The function $m(x)$ represents both the local carrying capacity and the intrinsic growth rate of the species u , which reflects the environmental influence on the species.

It is well known that for every $d > 0$ Eq. (1) has a unique positive steady state θ_d , which is globally asymptotically stable (see e.g. Cantrell and Cosner 2003). In addition, Lou (2006) made the following observation: For every $d > 0$

$$\int_{\Omega} \theta_d > \int_{\Omega} m. \tag{2}$$

In other words, *in a heterogeneous environment, when (random) dispersal is allowed, the total population is always strictly greater than the total carrying capacity!* Another striking observation!

A seemingly natural question arises: *Do these results apply to real biological systems?* A problem with applying Eq. (1) to real systems seems to be the hypothesis that the function $m(x)$ represents both the local carrying capacity and the intrinsic growth rate of the species u , which reflects the environmental influence on the species. However, in real ecological environments, the intrinsic growth rate and carrying capacity are not the same in general. In fact, it is fundamental in the ecology of population life histories that intrinsic growth rate, $r(x)$, and carrying capacity, $K(x)$, are distinct parameters related to a species population. In classical r - and K -theory, the r -endpoint of the r -, K -spectrum represents the quantitative extreme situation that the optimal strategy is to maximize energy input into early reproduction and to produce as many

progeny as possible. The K -endpoint represents the qualitative extreme that competition is keen and the optimal strategy is to maximize energy into maintenance, at the cost of a lower maximum intrinsic growth rate (e.g., fewer offspring) (Pianka 1970; Luckinbill 1978; Parry 1981; Boyce 1984). This suggests that it is important to treat r and K differently. Certainly intrinsic growth rate and carrying capacity are not identical in general, as Eq. (1) states. But this does not mean that for a given species $r(x)$ and $K(x)$ may not be correlated in some fashion across an environmental gradient; in fact, it will be assumed here that some degree of correlation can exist (see Sect. 3 below for more discussion on this issue). Note that in this paper we consider intrinsic growth $r(x)$ to be not the maximum rate of increase that a population can grow in ideal conditions, but the maximum growth rate under conditions at the spatial location x . Thus, we shall consider the following equation where r and K are used separately (instead of m alone) and determine how this modifies the result (2) which holds for Eq. (1):

$$\begin{cases} u_t = d\Delta u + r(x)u \left(1 - \frac{u}{K(x)}\right) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_\nu u = 0 & \text{on } \partial\Omega \times \mathbb{R}^+. \end{cases} \tag{3}$$

We note that when $r(x)$ is proportional to $K(x)$, i.e. $r(x) = cK(x)$, for some constant $c > 0$, (3) reduces to (1) by rescaling the time variable. In fact, (3) is generally referred to as the *logistic* equation.

For the general logistic Eq. (3) it can be shown, as we shall see below in Sect. 2, that (3) has a unique positive steady state, denoted by u_d , which is globally asymptotically stable. However, the corresponding property (2), namely,

$$\int_\Omega u_d > \int_\Omega K, \tag{4}$$

no longer holds without additional correlation between r and K . Thus, all the interesting phenomena mentioned above for the corresponding two species Lotka-Volterra competition-diffusion systems with general r and K are now in doubt.

The purpose of this paper is to investigate the properties of the positive steady state u_d of (3); namely, the solution of the following equation

$$\begin{cases} d\Delta u + r(x)u \left(1 - \frac{u}{K(x)}\right) = 0, & \text{in } \Omega, \\ \partial_\nu u = 0 & \text{on } \partial\Omega. \end{cases} \tag{5}$$

After establishing the existence, uniqueness, and asymptotic stability of the steady state u_d , we are interested in understanding the various properties of u_d , in term of the intrinsic growth rate $r(x)$ and the carrying capacity $K(x)$; in particular, if and when (4) holds - a property which is of vital importance for competition between two species.

It seems reasonable to assume that the intrinsic growth rate $r(x)$ should have some relationship to the carrying capacity $K(x)$ (which reflects the resources available at location $x \in \Omega$); that is, if $K(x_1) = K(x_2)$, then $r(x_1) = r(x_2)$ (see Sect. 3). In other words, r is a function of K , i.e.

$$r(x) = h(K(x)), x \in \Omega \tag{6}$$

for some function h . We say that r and K are *positively (negatively, resp.) correlated* if h is monotonically increasing (decreasing, resp.).

Our first main result is as follows.

Theorem 11 *Assume that both $0 < r(x) \not\equiv \text{const.}$ and $0 < K(x) \not\equiv \text{const.}$ on $\bar{\Omega}$, and both $r(x), K(x) \in C^2(\bar{\Omega})$. Then the following statements hold for the positive steady state u_d of (3):*

1. *As $d \rightarrow 0, u_d \rightarrow K$ in $L_\infty \cap H_1$.*
2. *Suppose that r and K are positively (negatively, resp.) correlated. Then the total population is always strictly increasing (decreasing, resp.) for $d > 0$ small. In fact,*

$$\left(\int_\Omega u_d \right)' \Big|_{d=0} = - \int_\Omega \nabla K \cdot \nabla \left(\frac{1}{r} \right) > 0 \quad (< 0, \text{ resp.}).$$

Theorem 11 shows that for positively correlated r and K , (4) always holds for $d > 0$ small.

It seems interesting to point out that to obtain the convergence $u_d \rightarrow K$ in H_1 as $d \rightarrow 0$ in Theorem (11) above, we need first to show that the rate of convergence of $u_d \rightarrow K$ in L_∞ as $d \rightarrow 0$ is bounded above by Cd for some constant C , which seems new and interesting of its own.

For $d \rightarrow \infty$, we have the following result.

Theorem 12 *Assume that both $0 < r(x) \not\equiv \text{const.}$ and $0 < K(x) \not\equiv \text{const.}$ on $\bar{\Omega}$. Then the following statements hold for the positive steady state u_d of (3):*

1. *As $d \rightarrow \infty, u_d$ tends to a constant; more precisely,*

$$u_d \rightarrow L \equiv \frac{\int_\Omega r(x)}{\int_\Omega \frac{r(x)}{K(x)}}.$$

2. *If $h(s)/s$ is (strictly) decreasing in $s > 0$, then*

$$L(<) \leq \bar{K} \equiv \left(\frac{1}{|\Omega|} \right) \int_\Omega K(x).$$

3. *If $h(s)/s$ is (strictly) increasing in $s > 0$, then $L(>) \geq \bar{K}$.*

Observe that $L = \bar{K}$ when $r \equiv cK$ for some positive constant c .

From the two results above we see that even when r and K are positively correlated, inequality (4) is guaranteed to hold only for d small, but will not always hold for d large. Whether (4) holds for *all* $d > 0$ under the additional hypothesis that $h(s)/s$ is increasing for all $s > 0$ remains open.

The proofs of all our results are included in Sect. 2. Section 3 contains further remarks and discussions.

2 Proofs

In this section, we include the proofs of all the results we mentioned in the Introduction concerning (5).

First of all, for simplicity we will always assume in this section that both the intrinsic growth rate $r(x)$ and the carrying capacity $K(x)$ are smooth and positive everywhere throughout the entire domain (the habitat) $\bar{\Omega}$. More precisely, we assume throughout this section that *both* $0 < r(x), 0 < K(x) \in C^1(\bar{\Omega})$, and $r(x), K(x) \neq \text{constant}$.

Discussions on relaxing this assumption, both mathematically and biologically, will be included in Sect. 3.

Sometimes it is convenient to write (5) as

$$\begin{cases} d\Delta u + \xi(x)u(K(x) - u) = 0, & \text{in } \Omega, \\ \partial_\nu u = 0 & \text{on } \partial\Omega, \end{cases} \tag{7}$$

where

$$\xi(x) \equiv \frac{r(x)}{K(x)} > 0$$

on $\bar{\Omega}$.

Now we begin to establish the first basic result—the existence, uniqueness and asymptotic stability of the positive steady state for (5).

Proposition 21 *For every $d > 0$, (7), and therefore (5), has a unique positive solution u_d , which is globally asymptotically stable.*

Proof The proof is standard, and is based on the well known upper- and lower-solutions method, thus we shall be brief. Setting

$$\bar{u} \equiv \max_{\bar{\Omega}} K(x), \quad \underline{u} \equiv \min_{\bar{\Omega}} K(x),$$

we see easily that \bar{u} is an upper solution for (7), \underline{u} is a lower solution for (7), and $\bar{u} > \underline{u}$ on $\bar{\Omega}$. Thus, (7) has a solution $\bar{u} > u_d > \underline{u}$.

The uniqueness of u_d also follows from standard arguments, hence is omitted here. The global asymptotic stability of u_d follows from the uniqueness and the fact that any constant larger than \bar{u} defined above is an upper solution and any constant smaller than \underline{u} is a lower solution. □

Next we proceed to show that $u_d \rightarrow K$ as $d \rightarrow 0$ in $L_\infty \cap H_1$. To this end, we need first that $u_d \rightarrow K$ as $d \rightarrow 0$ in L_∞ with a rate linear in d .

Proposition 22 *For $d > 0$ small, $\|u_d - K\|_{L_\infty} \leq C_*d$ where $C_* = \frac{2\|\Delta K\|_{L_\infty}}{(\min_{\bar{\Omega}} r(x))}$.*

Proof The idea is to get a sequence of appropriate upper and lower solutions in terms of d . For each $d > 0$, letting $\bar{u} = K + C_*d$, we compute

$$\begin{aligned}
 d\Delta\bar{u} + \xi(x)\bar{u}(K - \bar{u}) &= d[\Delta K - C_*r(1 + C_*d/K)] \\
 &\leq d[\Delta K - C_*r] \leq d[\Delta K - 2\|\Delta K\|_{L^\infty}] \leq 0;
 \end{aligned}$$

i.e. \bar{u} is an upper solution.

Setting $\underline{u} = K - C_*d$, we see that for $d > 0$ small, $\underline{u} > 0$. Then we compute, for $d > 0$ small

$$\begin{aligned}
 d\Delta\underline{u} + \xi(x)\underline{u}(K - \underline{u}) &= d\left[\Delta K + C_*r - C_*^2(rd/K)\right] \\
 &= d\left[\Delta K + \frac{1}{2}C_*r + C_*r\left(\frac{1}{2} - C_*\frac{d}{K}\right)\right] \\
 &\geq d\left[\Delta K + \frac{1}{2}C_*r\right] \geq 0;
 \end{aligned}$$

i.e. \underline{u} is a lower solution. Clearly, $\bar{u} > \underline{u}$. Therefore, $\bar{u} > u_d > \underline{u}$, and our proof is complete. □

Our next estimate is crucial.

Proposition 23 $\|u_d - K\|_{H_1} \rightarrow 0$ as $d \rightarrow 0$.

Proof Setting $v = u_d - K$, we have

$$d\Delta v + d\Delta K + \xi u_d(-v) = 0.$$

Multiplying this equation by v/d and integrating over Ω , we obtain

$$\int_{\Omega} |\nabla v|^2 = \int_{\Omega} v(\Delta K) - \int_{\Omega} v\xi u_d \left(\frac{v}{d}\right) \leq \int_{\Omega} v\|\Delta K\|_{L^\infty},$$

which tends to 0 as $d \rightarrow 0$ by Proposition 22. This concludes the proof. □

For our purposes the following result is useful.

Proposition 24 $\int_{\Omega} |\nabla u_d \cdot \nabla\left(\frac{1}{\xi u_d}\right) - \nabla K \cdot \nabla\left(\frac{1}{r}\right)| \rightarrow 0$ as $d \rightarrow 0$.

Proof

$$\begin{aligned}
 &\int_{\Omega} \left| \nabla u_d \cdot \nabla\left(\frac{1}{\xi u_d}\right) - \nabla K \cdot \nabla\left(\frac{1}{r}\right) \right| \\
 &\leq \int_{\Omega} \left| \nabla(u_d - K) \cdot \nabla\left(\frac{1}{\xi u_d}\right) \right| + \int_{\Omega} \left| \nabla K \cdot \nabla\left(\frac{1}{\xi u_d} - \frac{1}{r}\right) \right| \\
 &\leq \left(\int_{\Omega} |\nabla(u_d - K)|^2\right)^{1/2} \left(\int_{\Omega} \left|\nabla\left(\frac{1}{\xi u_d}\right)\right|^2\right)^{1/2} + \|\nabla K\|_{L^\infty} \int_{\Omega} \left|\nabla\left(\frac{1}{\xi u_d} - \frac{1}{r}\right)\right| \\
 &\equiv I + II
 \end{aligned}$$

The first term in I tends to 0 by Proposition 23. The second term in I

$$\nabla \left(\frac{1}{\xi u_d} \right) = \frac{\xi \nabla u_d + u_d \nabla \xi}{(\xi u_d)^2}$$

is bounded in L_2 , again by Proposition 23. Thus $I \rightarrow 0$ as $d \rightarrow 0$.

For II we proceed as follows.

$$\int_{\Omega} \left| \nabla \left(\frac{1}{\xi u_d} - \frac{1}{r} \right) \right| \leq \int_{\Omega} \frac{1}{(\xi u_d)^2} |\nabla(\xi u_d) - \nabla r| + \int_{\Omega} |\nabla r| \left| \frac{1}{(\xi u_d)^2} - \frac{1}{r^2} \right|$$

$$\equiv III + IV$$

The term $III \rightarrow 0$ since

$$\int_{\Omega} |\nabla(\xi u_d) - \nabla r| = \int_{\Omega} \left| \nabla \left[\frac{r}{K} (u_d - K) \right] \right|$$

which tends to 0 by Proposition 23; and the term $IV \rightarrow 0$ as

$$\frac{1}{(\xi u_d)^2} - \frac{1}{r^2} = \frac{1}{(r \xi u_d)^2} (r + \xi u_d)(r - \xi u_d) = \frac{K^2}{(r u_d)^2} (K + u_d)(K - u_d)$$

which tends to 0 in L_2 again by Proposition 23. This finishes our proof. □

Dividing the equation in (7) by ξu_d , integrating over Ω , by Proposition 24 and the Divergence Theorem, we obtain the following useful formula.

Proposition 25 *For $d > 0$ small, it holds that*

$$\int_{\Omega} u_d = \int_{\Omega} K - d \left[\int_{\Omega} \nabla K \cdot \nabla \left(\frac{1}{r} \right) + o(1) \right]. \tag{8}$$

Now we are ready for the proof of Theorem 11. Part 1 already follows from Propositions 22 and 23. Since $\int_{\Omega} u_d \rightarrow \int_{\Omega} K$ as $d \rightarrow 0$, Part 2 follows directly from Proposition 25 since, by (6)

$$\nabla K \cdot \nabla \left(\frac{1}{r} \right) = -h' \frac{|\nabla K|^2}{r^2}.$$

Our next goal is to determine the asymptotic behavior of u_d as $d \rightarrow \infty$, and to prove Theorem 12. Dividing the equation in (5) by d , we have

$$\Delta u + \frac{1}{d} r(x) u \left(1 - \frac{u}{K(x)} \right) = 0, \quad \text{in } \Omega. \tag{9}$$

Integrating the Eq. (9) over Ω , by the boundary condition $\partial_\nu u = 0$, we see immediately that

$$\int_{\Omega} r(x)u \left(1 - \frac{u}{K(x)}\right) = 0. \tag{10}$$

Now, recall that u_d is bounded in L_{∞} , standard elliptic regularity estimates for (9) guarantee that, for d large, $\{u_d | d \gg 1\}$ is a bounded subset in $C^{2,\alpha}(\bar{\Omega})$. By passing to a subsequence if necessary, u_{d_k} converges in $C^2(\bar{\Omega})$, as $k \rightarrow \infty$, to u_{∞} . From Eq. (9), we see that

$$\Delta u_{\infty} = 0,$$

with $\partial_{\nu}u_{\infty} = 0$ on $\partial\Omega$. This implies that $u_{\infty} \equiv L$, where $L \geq 0$ is a constant.

Suppose that $L = 0$. Then $u_{d_k} \rightarrow 0$ uniformly on $\bar{\Omega}$. It follows that, for k large, $1 - u_{d_k}/K > 0$ on $\bar{\Omega}$. Since $u_{d_k} > 0$ on $\bar{\Omega}$ also, we then have

$$\int_{\Omega} r(x)u_{d_k} \left(1 - \frac{u_{d_k}}{K(x)}\right) > 0$$

for all k large, which contradicts (10). Therefore, the constant $L > 0$.

As u_{d_k} also satisfies (10), letting $k \rightarrow \infty$, we obtain

$$0 = \int_{\Omega} r(x)L \left(1 - \frac{L}{K(x)}\right) = L \int_{\Omega} r(x) \left(1 - \frac{L}{K(x)}\right).$$

From $L > 0$, we conclude that

$$L = \frac{\int_{\Omega} r(x)}{\int_{\Omega} \frac{r(x)}{K(x)}}.$$

Since this works for every sequence $d \rightarrow \infty$, Part 1 of Theorem 12 is established.

The proofs of Parts 2 and 3 of Theorem 12 are similar, we therefore will only prove Part 2 here.

Our strategy for proving Part 2 is to approximate the integrals involved by their Riemann sums, and then establish the corresponding inequality for their Riemann sums. The core of the proof is the following simple inequality.

Lemma 26 *Suppose there are two sequences of nonnegative real numbers such that $a_1 \geq a_2 \geq \dots \geq a_n \geq 0$ and $0 \leq b_1 \leq b_2 \leq \dots \leq b_n$. Then*

$$n(a_1b_1 + a_2b_2 + \dots + a_nb_n) \leq (a_1 + a_2 + \dots + a_n)(b_1 + b_2 + \dots + b_n).$$

Proof We use induction. When $n = 1$, this is obvious. Now assume that the above inequality holds when $n = k$, we need to show that it holds for $n = k + 1$.

To this end, we first observe that

$$a_1b_1 + \dots + a_kb_k + ka_{k+1}b_{k+1} \leq a_{k+1}(b_1 + \dots + b_k) + (a_1 + \dots + a_k)b_{k+1} \tag{11}$$

since

$$a_{k+1} [(b_{k+1} - b_1) + \dots + (b_{k+1} - b_k)] \leq a_1(b_{k+1} - b_1) + \dots + a_k(b_{k+1} - b_k).$$

Now we proceed as follows. By induction hypothesis and (11)

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

This finishes the proof. □

We now turn to the proof of Part 2 in Theorem 12. Approximate the integrals by their Riemann sums and set

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

Since we can rearrange the terms in the Riemann sums in the order that b_i is ascending (then a_i is automatically descending by our assumption on h), we see that

$$\frac{1}{n} \sum_{i=1}^n \frac{h(K(x_i))}{K(x_i)} K(x_i) \leq \left(\frac{1}{n} \sum_{i=1}^n \frac{h(K(x_i))}{K(x_i)} \right) \left(\frac{1}{n} \sum_{i=1}^n K(x_i) \right)$$

by Lemma 26. The *strict* inequality in Part 2 of Theorem 12 follows from a careful examining of the proof above (in particular, the proof of Lemma 26). Our proof of Theorem 12 is now complete.

3 Discussions and concluding remarks

Mathematically, formula (8) is interesting especially when compared to a previous result obtained by Lou, namely, Theorem 1.5 in Lou (2006), which deals with the special case when the dimension $N = 1, r \equiv cK$ for some constant $c > 0$, but K changes sign. In this case, Lou showed that if K has only nondegenerate zeros, then, as $d \rightarrow 0$, the unique positive steady state θ_d , if exists, has the property that $\theta_d \rightarrow K_+ = \max\{K, 0\}$ and

$$\int_{\Omega} \theta_d - \int_{\Omega} K_+ \geq Cd^{2/3} \tag{12}$$

for d small, which is *much larger* than the exact estimate given by (8). (Lou also has a conjecture on the upper bound.) In any case, it seems interesting to note that the estimates (8) and (12) exhibit different nature of the two cases: $K > 0$ and K changes sign even in the simplest case $r \equiv cK$.

Mathematically, it is possible to relax our assumptions on the positivity of r and K , with similar proofs. However, to make our presentation as simple as possible, we have not included this slightly more general case.

Biologically, it seems that K should not be negative anywhere - as K represents the carrying capacity of the environment. However, it seems that K could be 0 somewhere, either at a point or in a region. Moreover, it seems that the intrinsic growth rate r should always be *nonpositive* wherever K is *nonpositive*. Likewise, r should be positive wherever K is positive, if K is to represent all the information we have from the environment for the species u .

Our use of the logistic density-dependent population growth term, in the form shown in Eq. (3),

$$ru \left(1 - \frac{u}{K} \right), \tag{13}$$

to study the effects of dispersal and spatial heterogeneity on total population size, raises some issues that will be discussed here. Our motivation is that the logistic equation is ubiquitous in ecological models, where it is used both in modeling individual populations and in modeling basal populations within food webs. Note that the reaction term in Eq. (1) from Lou (2006) can be rewritten in the same structural form as (13)

$$u(m(x) - u) = m(x)u \left(1 - \frac{u}{m(x)} \right). \tag{14}$$

We took the logical first step in generalizing Eq. (1) by allowing the intrinsic growth rate and carrying capacity to have potentially different forms; that is, we modify (14) to

$$r(x)u \left(1 - \frac{u}{K(x)} \right). \tag{15}$$

Whereas in (14) the maximum growth rate and the carrying capacity are the same function, in (15) $r(x)$ and $K(x)$ may differ. In fact, it is basic to ecological populations that the relationship between the intrinsic growth rate and the carrying capacity can be distinct, rather than being identical functional forms, as they are in Eq. (1). Function (15) is a step towards greater potential realism in describing population growth as a logistic equation. However, it should be noted that the logistic equation itself has inspired controversy, as it represents $K(x)$ as “carrying capacity”, or the maximum population size (whether in terms of number or biomass) that can be maintained in a habitat. Carrying capacity may seem to be a simple concept, but in fact it has been interpreted in many different ways (McLeod 1997 and references therein); in particular, regarding what environmental factors should be included in determining the carrying capacity; e.g., available food, spatial area, or other factors. Therefore, its representation as a fixed characteristic of a population is too restrictive an assumption. A number of authors on the logistic model recommend a more general form of the logistic equation

$$u_t = ru - \alpha u^2, \tag{16}$$

where $\alpha > 0$ and r can be positive or negative (e.g., see Mallet 2012). The advantage of this form is that carrying capacity is not prescribed in terms of a single parameter as in function (15), but the population size emerges from the density-independent term, ru , and the density-dependent term, αu^2 . For example, if both population birth and mortality rates, B and M , have density-independent and density-dependent parts; i.e., $B = B_0 - B_1u$ and $M = M_0 + M_1u$, then $r = B_0 - M_0$ and $\alpha = B_1 + M_1$. No relationship between r and α is implied in this case. However, when the form of the logistic (13) is used, then $r = B_0 - M_0$ and $K = (B_0 - M_0)/(B_1 + M_1)$. This implies a possible relationship if a change in resource levels changes not only B_1 and/or M_1 , but also B_0 and M_0 . Therefore, empirical data on the effect of resource levels on density-dependent birth and mortality rates are of great interest as indicators of correlations of r and K . It is also important that in (13) r can take on negative values without it being necessary to simultaneously change the sign of α for the model to make sense.

Our present analysis is restricted to the logistic expressed in the form (15) and we have shown that it implies that $r(x)$ and $K(x)$ must be positively correlated to guarantee the results of Lou (2006) to hold; that is, for total population size to exceed total carrying capacity in a heterogeneous system with diffusion. Although it has generally been assumed by ecologists that r and K are independent parameters, evidence for a positive correlation along resource gradients in some populations has been reviewed by Mallet (2012). We speculate, then, that the functional relationship, $r(x) = h(K(x))$, may apply in many situations, so Theorem 1.2 generalizes the basic result of Lou (2006) in an important way. For example, available resources may vary with x , and with it carrying capacity, whereas the intrinsic growth rate of the population may stay the same or change only slightly with changes over the same range of x . At the other extreme, the quality of resources, or other factors such as temperature, may vary with x in such a way that the intrinsic growth rate varies strongly with x , but the quantity of resources may stay relatively constant, such that the carrying capacity changes little with x . Therefore, further extension of the results concerning the effects of the relationship between $r(x)$ and $K(x)$ should be sought in the future.

The new results for Eq. (3) can have some implications for important concepts of spatial ecology. A key area of spatial ecology is that of source-sink theory, which deals with the occurrence of sources and sinks on landscapes. Sources are areas in which surplus population is created (reproduction and growth exceed losses) and sinks are areas in which losses exceed births and growth. Populations in better quality patches are more productive and should produce more emigrants to lower quality patches (Donahue et al. 2003). This concept has implications for conservation ecology, because it is possible that individuals may diffuse from high quality areas to sink areas, in which they die or fail to reproduce, threatening the population (Pulliam 1988). Pulliam's influential paper has been followed by many others, expanding on the idea (Amarasekare 2004; Amezcuca and Holyoak 2000; Dias 1996; Holt 1997; Howe et al. 1991; Loreau and DeAngelis 1997; Watkinson and Sutherland 1995; Wilson 2001; Ritchie 1997). Equation (3) and the analysis here cannot easily be applied to sinks, as a sink area would be one in which $r(x)$ becomes negative, while the results here apply to $K(x)$, $r(x) \geq 0$. But the simple source and sink idea has been replaced by a more complex picture in which pseudo-sinks are included (Watkinson and Sutherland 1995). Pseudo-sinks are areas into which net population influxes from other areas may

be observed at times. However, these areas are actually self-sustaining (i.e., $r(x) > 0$) and the net influx occurs only because there are more productive sources nearby from which individuals migrate. The pseudo-sink concept is highly relevant to conservation, because both fundamental population ecology issues and population management issues often involve questions over what strategy of occupation of space is best for a population. A basic question is whether it is best for a population to be restricted to a relatively small region in which $r(x)$ is large, although the total range is limited, or for the population to occupy a much larger range, which may also include areas of small $r(x)$. In the latter case, the diffusion from the higher- into the lower- $r(x)$ parts of the range could more than offset the advantage of larger total area.

A modeling study that attempted to answer this question was carried out by Pulliam and Danielson (1991). They simulated a bird population on a model landscape in which poor-quality habitat, corresponding to poor reproductive success such that r was small or negative, could be added to a constant amount of high-quality habitat, which had a high r that produced surplus population. The authors also assumed that the larger the ratio of poor-quality to high quality habitat, the more likely it was that individuals would choose the poorer quality habitat. This amounted to an “effective diffusion” away from the high- to the poor-quality habitat. Therefore, they expected that an increase in poor-quality habitat might reduce the total population size, because of higher migration from high-quality habitat. However, the trend of total population biomass was not monotonically decreasing with lower ratio of high-quality to low-quality habitat. In fact, there was a peak for an intermediate ratio (their Figure 7B). Therefore, despite the increased diffusion away from high-quality habitat as poor-quality habitat was added, the high-quality habitat produced enough of a surplus in reproduction that the population could expand into and occupy poor-quality habitat fast enough to overcompensate for poor reproductive success there.

Experimental tests of the application of mathematical results for populations in heterogeneous environments have rarely been tested. However, Zhang et al. (2015) set out to experimentally test the mathematical result of Lou (2006) of how a single plant population responds to spatial heterogeneity, as it disperses, i.e. diffuses. They planted duckweed (*Lemna minor* Linn) in situations where the limiting resources (nutrients) were distributed heterogeneously in different concentrations in five containers used to represent patches. They manually controlled rates of diffusion; that is, 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. They found, in agreement with the mathematical theory (Lou 2006), that steady state total biomass was maximized at an intermediate rate of diffusion and that the total biomass exceeded that reached in the heterogeneous system without diffusion; that is, exceeded total carrying capacity. In the computer model that was used to simulate the experiment, the authors found that the best fit to the model was achieved when $r(x)$ and $K(x)$ were approximately linearly related, i.e. $r(x) \equiv cK(x)$. This seems to apply here because nutrient concentrations in the equal-sized containers probably act equally on growth rate and carrying capacity.

Testing the applicability of the mathematical theory in the field would be more difficult, as dynamics of a population in nature are affected by a large number of

factors that are difficult to control. This is especially true for animal populations, the individuals of which are unlikely to move by diffusion (i.e., randomly). Nevertheless, dispersal of populations of both plants and animals over long time scales can often be represented as diffusive, and, in that case, it may be possible to observe steady state patterns of biomass density on landscapes as influenced by the interactions of heterogeneity and diffusion.

A case in point is an experiment described by [Keddy \(1981, 1982\)](#) and [Watkinson \(1985\)](#). The authors manipulated densities of seeds of the plant *Cakile edentula* 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. A model by [Watkinson \(1985\)](#) describing this experiment showed that the plants were most abundant in the sink sites because of the high seed migration from the source. This high quantity of plants in the poor habitat appears to signify that it is a case where diffusion in a heterogeneous environment creates an overall biomass that exceeds that which would be achieved in a homogeneous environment.

Such experiments are rare and are prone to much uncertainty. To test the results presented above greater efforts are needed in designing both field studies and laboratory experiments. Experimental systems using microbial organisms can be tightly controlled and carried out with many variations in treatments and replications (e.g., [Van Dyken et al. 2013](#)), and so show great promise in that direction. In that approach one can manipulate yeast strains to disperse with many different dispersal rates in various heterogeneous environments, which will improve and double-check what [Zhang et al. \(2015\)](#) found in their duckweed experiments. Also, in the future, such an approach could simulate the competition of yeast strains with different dispersal rates in a heterogeneous system, which has not been done in laboratory experiment so far, to further extend testing of mathematical theory.

Acknowledgments Research supported in part by NSF (USA), NSFC (PRC), “111-Project” (PRC) and “1000 Talents Project” (PRC).

References

- Amarasekare P (2004) The role of density-dependent dispersal in source-sink dynamics. *J Theor Biol* 226:159–168
- Amezcuca AB, Holyoak M (2000) Empirical evidence for predator-prey source-sink dynamics. *Ecology* 81:3087–3098
- Berg H (1983) *Random Walks in Biology*. Princeton University Press, Princeton
- Boyce MS (1984) Restitution of r- and K-selection as a model of density-dependent natural selection. *Annu Rev Ecol Syst* 15:427–447
- Cantrell RS, Cosner C (2003) *Spatial ecology via reaction-diffusion equations*. Wiley, Chichester
- Chase JM, Leibold MA (2003) *Ecological Niches*. University of Chicago Press, Chicago
- Cosner C (2014) Reaction-diffusion-advection models for the effects and evolution of dispersal. *Discrete Contin Dyn Syst* 34:1701–1745
- Czaran T (1998) *Spatiotemporal Models of Populations and Community Dynamics*. Chapman and Hall, London
- Dias PC (1996) Sources and sinks in population biology. *Trends Ecol Evol* 11:326–330
- Dockery J, Hutson V, Mischaikow K, Pernarowski M (1998) The evolution of slow dispersal rates: A reaction-diffusion model. *J Math Biol* 37:61–83

- Donahue MJ, Holyoak M, Feng C (2003) Patterns of dispersal and dynamics among habitat patches varying in quality. *Am Nat* 162:302–317
- Hastings A (1983) Can spatial variation alone lead to selection for dispersal? *Theor Popul Biol* 24:244–251
- He XQ, Ni WM (2013) The effects of diffusion and spatial variation in Lotka–Volterra competition–diffusion system I: heterogeneity vs. homogeneity. *J Diff Equ* 254:528–546
- He XQ, Ni WM (in review) Global dynamics of the Lotka–Volterra competition–diffusion system: diffusion and spatial heterogeneity, I
- Holt RD (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs RE, Schluter D (eds) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, pp 77–88
- Holt RD (1997) On the evolutionary stability of sink populations. *Evol Ecol* 11:723–731
- Howe R, Davis WGJ, Mosca V (1991) The demographic significance of sink populations. *Biol Conserv* 57:239–255
- Hsu SB (1978) Limiting behavior for competing species. *SIAM J Appl Math* 34:760–763
- Kadmon R, Allouche O (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *Am Nat* 170:443–454
- Kareiva P (1983) Local movements in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Ecol Monogr* 52:261–282
- Keddy PA (1981) Experimental demography of the sand-dune annual, *Cakile-Edentula*, growing along an environmental gradient in Nova-Scotia. *J Ecol* 69:615–630
- Keddy PA (1982) Population ecology on an environmental gradient - *Cakile-Edentula* on a sand dune. *Oecologia* 52:348–355
- Lam KY, Ni WM (2012) Uniqueness and complete dynamics in the heterogeneous competition–diffusion systems. *SIAM J Appl Math* 72:1695–1712
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- Loreau M, DeAngelis DL (1997) Source–sink dynamics and the coexistence of species on a single resource. *Theor Popul Biol* 51:79–93
- Lou Y (2006) On the effects of migration and spatial heterogeneity on single and multiple species. *J Diff Equ* 223:400–426
- Luckinbill LS (1978) R and K selection in experimental populations of *Escherichia coli*. *Science* 202:1201–1203
- Malchow HS, Petrovski V, Venturino E (2008) *Spatiotemporal patterns in ecology and epidemiology: theory, models, and simulation*. Chapman and Hall/CRC, London
- Mallet J (2012) The struggle for existence: how the notion of carrying capacity, K, obscures the links between demography, Darwinian evolution, and speciation. *Evol Ecol Res* 14:627–665
- McLeod SR (1997) Is the concept of carrying capacity useful in variable environments? *Oikos* 79:529–542
- Mouquet N, Loreau M (2002) Coexistence in metacommunities: the regional similarity hypothesis. *Am Nat* 159:420–426
- Mouquet N, Loreau M (2003) Community patterns in source–sink metacommunities. *Am Nat* 162:544–557
- Okubo A (1980) *Diffusion and ecological problems: mathematical models*. Springer, Berlin
- Ovaskainen O, Luoto M, Ikonen I, Rekola H, Meyke E, Kuussaari M (2008) An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *Am Nat* 171:610–619
- Parry GD (1981) The meaning of r- and K-selection. *Oecologia* 48:260–264
- Pianka ER (1970) On r- and K-selection. *Am Nat* 104:592–597
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661
- Pulliam HR, Danielson BJ (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am Nat* 137:S50–S66
- Ritchie ME (1997) *Wildlife and landscape ecology: effects of pattern and scale*. Springer, New York
- Ritchie ME (2010) *Scale, heterogeneity, and the structure and diversity of ecological communities*. Princeton University Press, Princeton
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38:196–218
- Tamburello L, Benedetti-Cecchi L, Masini L, Bulleri F (2013) Habitat heterogeneity promotes the coexistence of exotic seaweeds. *Oecologia* 172:505–513
- Turchin P (1998) *Quantitative analysis of movement*. Sinauer Associates, Sunderland
- Van Dyken JD, Muller MJI, Mack KML, Desai MM (2013) Spatial population expansion promotes the evolution of cooperation in an experimental prisoners dilemma. *Current Biol* 23:919–923
- Watkinson AR (1985) On the abundance of plants along an environmental gradient. *J Ecol* 73:569–578

- Watkinson AR, Sutherland WJ (1995) Sources, sinks and pseudo-sinks. *J Anim Ecol* 64:126–130
- Wilson HB (2001) The evolution of dispersal from source to sink populations. *Evol Ecol Res* 3:27–35
- Zhang B, Li X, DeAngelis D, Ni WM, Wang G (2015) Effects of dispersal on total biomass in a patchy, heterogeneous system: analysis and experiment. *Math Biosci*. doi:[10.1016/j.mbs.2015.03.005](https://doi.org/10.1016/j.mbs.2015.03.005)