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# Total population for a resource-limited single consumer model

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## Abstract

In the past several decades, much attention has been focused on the effects of dispersal on total populations of species. In Zhang (EL 20:1118–1128, 2017), a rigorous biological experiment was performed to confirm the mathematical conclusion: Dispersal tends to enhance populations under a suitable hypothesis. In addition, mathematical models keeping track of resource dynamics in population growth were also proposed in Zhang (EL 20:1118–1128, 2017) to understand this remarkable phenomenon. In these models, the self-regulated quantity “loss rate" of the population seems, in general, difficult to measure experimentally. Our main goal in this paper is to study the effects of relations between the loss rate and the resources, the role of dispersal, and the impact of their interactions on total populations. We compare the total population for small and large diffusion under various correlations between loss rate and the resources. Biological evidence seems to support some specific correlations between the loss rate and the resources.

**Keywords** Total population · Reaction-diffusion system · Consumer-resource model · Spatial heterogeneity

**Mathematics Subject Classification** 35B30 · 35B40 · 35J57 · 92D40

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## 1 Introduction

Total population plays a vital role in theoretical and applied ecology. Its understanding improves the schemes of species conservation and control of invasive species. As an essential strategy for populations to adapt to spatially and temporally varying environments, dispersal or diffusion noticeably influences the population's abundance or even survival. It is well-known that the carrying capacity in a constant environment determines the total population. However, in spatially heterogeneous environments, the total population is far more complex than the total carrying capacity. Numerous theories have been developed for both discrete and continuous models.

Discrete models go back at least to Freedman and Waltman (1977) and Holt (1985), in which a two-patch logistic model of a single population was studied. We refer interested readers to DeAngelis and Zhang (2014), Elbetch et al. (2021), and Gao and Lou (2022) for a more recent account of the development in this direction.

The classical logistic equation with diffusion has been traditionally used for single species as a continuous model, and it was first observed by Lou (2006) that total population always exceeds total carrying capacity in a heterogeneous environment when the intrinsic growth rate is proportional to the carrying capacity. This remarkable result was studied by DeAngelis et al. (2016) for a more general situation. In the case of small diffusion, they extended the work of Lou (2006) and showed that when the intrinsic growth rate of the population is positively correlated to the habitat's carrying capacity, dispersal benefits the species and its total population at equilibrium surpasses the (total) carrying capacities. On the contrary, assuming that the intrinsic growth rate is constant, i.e., independent of the local carrying capacity, Guo et al. (2020a) showed that diffusion harms the population, i.e., at equilibrium, the heterogeneous distribution of resources supports a population strictly smaller than the total carrying capacity. In addition to its own biological significance, the total population is also essential in analyzing the dynamics of the competition models of two species with diffusions. We refer interested readers to Cantrell and Cosner (1991, 1998), Guo et al. (2020a, b), He and Ni (2013a, b, 2016a, b, 2017), Lam and Ni (2012), Lou (2006, 2008) and references therein for further details.

The mathematical results above seem to raise an interesting question: *In reality, does dispersal help the total population to surpass carrying capacity?* Indeed, rigorous empirical validation was rare until the recent works of Zhang et al. (2017). Zhang et al. (2017) experimentally tested and confirmed the mathematical results of how dispersal, i.e., diffusion, influences the total population of a single species under a spatially heterogeneous environment. Zhang et al. (2017) conducted laboratory experiments of budding yeast, where the yeast and the amino acid tryptophan serve as the consumer and the resource, respectively. They set up a single "population" composed of a single row of 12 wells in a plate, and each well had either a heterogeneous or homogeneous distribution of resources (tryptophan). To control the diffusion, they transferred 3% of the volume to adjacent positions for each well using the liquid handling robot. Investigating the effects of the growth rate of the yeast in each heterogeneous and homogeneous environment, they further applied varying concentrations of the macrolide eukaryotic antibiotic cycloheximide, which is a translation inhibitor interfacing the growth rate of the yeast.

Their experiments confirmed that diffusion increases the total population under certain conditions, as predicted by logistic models. Moreover, to include resource dynamics in their experiments, which reflects a more accurate and realistic situation, new mathematical models were proposed in Zhang et al. (2017). However, as some of the parameters in their models, such as the loss rate, seem delicate and perhaps even difficult to measure experimentally, they also conducted numerical simulations to analyze these models for various value ranges of the loss rate. Indeed, their simulation results seemed to indicate that large diffusion might damage the total population in heterogeneous environments when the loss rate and resource inputs have certain relations. This raises an interesting point and seems to warrant further mathematical studies and clarifications.

One of the model proposed in Zhang et al. (2017) (see Model I therein) was

$$\begin{cases} Z_t = d\Delta Z + Z(\frac{r(x)N}{k+N} - g(x)Z) & \text{for } x \in \Omega, t > 0, \\ N_t = N_R(x) - \frac{r(x)NZ}{\gamma(k+N)} & \text{for } x \in \Omega, t > 0, \\ \partial_\nu Z = 0 & \text{for } x \in \partial\Omega, t > 0, \\ Z(x,0) = Z_0(x), N(x,0) = N_0(x) & \text{for } x \in \Omega. \end{cases} \tag{1.1}$$

Here, $Z(x,t)$ and $N(x,t)$ are the densities of consumer population and resource, respectively, the constant $d$ denotes the diffusion rate of the consumer, $r(x)$ is the intrinsic growth rate of the consumer, $k$ is the half-saturation rate, $g(x)$ is the loss rate due to self-regulation of the consumer population, $N_R(x)$ is the resource input, $\gamma$ is the yield rate, and $\Omega$, the habitat, is a bounded smooth domain in Euclidean space $\mathbb{R}^N$ with $\nu$ denotes its unit outward normal.

Throughout this paper we assume that $d$, $k$ and $\gamma$ are positive constants, and $r(x)$, $g(x)$ and $N_R(x)$ are (strictly) positive, smooth functions on $\bar{\Omega}$ $(= \Omega \cup \partial\Omega)$ where $\Omega$ is a bounded domain in Euclidean space $\mathbb{R}^N$, with smooth boundary $\partial\Omega$, while $Z_0$ and $N_0$ are non-negative, not identically zero and continuous functions on $\bar{\Omega}$.

The system (1.1) describes a diffusing population in an environment where the resources are exploited and renewed. It turns out that the yield rate $\gamma$ in the system (1.1) is very important, as the work He et al. (2019, 2023) showed. Following (He et al. 2019, 2023), we define

$$\gamma^*(d) := \inf\Big\{\gamma > 0 \,\Big|\, \inf_{\Omega}(N_R - \frac{1}{\gamma} r\theta_d) \geq 0\Big\} = \sup_{\Omega} \frac{r\theta_d}{N_R}, \tag{1.2}$$

and

$$\gamma_*(d) := \sup\Big\{\gamma > 0 \,\Big|\, \sup_{\Omega}(N_R - \frac{1}{\gamma} r\tilde{w}_d) < 0\Big\} = \sup\Big\{\gamma > 0 \,\Big|\, \sup_{\Omega} \frac{\gamma N_R}{r\tilde{w}_d} < 1\Big\}, \tag{1.3}$$

where $\theta_d$ is the positive solution of

$$\begin{cases} d\Delta\theta + \theta(r - g\theta) = 0 & \text{for } x \in \Omega, \\ \partial_\nu \theta = 0 & \text{for } x \in \partial\Omega, \end{cases} \tag{1.4}$$

and $\tilde{w}_d$ is the positive solution of

$$\begin{cases} d\Delta\tilde{w} + \gamma N_R - g\tilde{w}^2 = 0 & \text{for } x \in \Omega, \\ \partial_\nu \tilde{w} = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{1.5}$$

It is well-known that (1.4) has a unique positive solution $\theta_d$ (cf. Propositions 3.2 and 3.3 in Cantrell and Cosner (2003)). As for the existence and uniqueness of $\tilde{w}_d$ in (1.5), see the proofs of Theorem 3 and Corollary 2 in He et al. (2019).

Our starting point is the following fundamental result due to He et al. (2019, 2023).

**Theorem 1.1** (He et al. (2023), Theorem B, Theorem 1.3) *Suppose that $r(x)$, $N_R(x)$ and $g(x)$ are positive and Hölder continuous in $\bar{\Omega}$, then:*

*(i) If $\gamma \geq \gamma^*(d)$, then resource-unlimited positive steady state $(\theta_d, \infty)$ is globally asymptotically stable for system (1.1);*

*(ii) If $\gamma < \gamma_*(d)$, then system (1.1) has a unique resource-limited positive steady state $\left(\tilde{w}_d, \frac{\gamma k N_R}{r\tilde{w}_d - \gamma N_R}\right)$, which is globally asymptotically stable.*

*Here, as $t \to \infty$, the convergence of $Z(\cdot, t)$ is in the $C^1(\bar{\Omega})$-norm in both Parts (i) and (ii) and the convergence of $N(\cdot, t)$ is uniform on $\bar{\Omega}$ in Part (i) and is pointwise on $\Omega$ in Part (ii).*

The above results concluded that if the yield rate $\gamma \geq \gamma^*(d)$, the $(\theta_d, \infty)$ is the unique positive steady state of the system (1.1), and it is globally asymptotically stable. Here $\theta_d$ is the positive solution to the well-known logistic equation (1.4), which has been studied by many authors in the last few decades; see, e.g. Cantrell and Cosner (1991, 1998); DeAngelis et al. (2016); Guo et al. (2020a, b); Hastings (1983); He and Ni (2013a, b, 2016a, b, 2017); Lam and Ni (2012); Li and Lou (2019); Lou (2006, 2008).

If the yield rate $\gamma < \gamma_*(d)$, then $\left(\tilde{w}_d, \frac{\gamma k N_R}{r\tilde{w}_d - \gamma N_R}\right)$ is the unique positive steady state of the system (1.1) and it is globally asymptotically stable, where $\tilde{w}_d$ is the positive solution of (1.5). He et al. (2019) proved that the total population $\int_\Omega \tilde{w}_d \, dx$ is strictly increasing in $d$ for $d > 0$ if $N_R$ is nonconstant and $g$ is a constant. In addition, Yao and Li (2023) proved that if $N_R/g$ is nonconstant, $\max_{\bar{\Omega}} \tilde{w}_d$ is strictly decreasing and $\min_{\bar{\Omega}} \tilde{w}_d$ is strictly increasing in $d$ for $d > 0$.

Applying the maximum principle (cf. Lou and Ni (1999) Lemma 2.1) to (1.5), we have $g(x_0)\tilde{w}_d^2(x_0) \geq \gamma N_R(x_0)$, where $\tilde{w}_d(x_0) = \min_{\bar{\Omega}} \tilde{w}_d, x_0 \in \bar{\Omega}$. Thus, for all $d > 0$, $\tilde{w}_d \geq \sqrt{\gamma}\sqrt{\min_{\bar{\Omega}} \frac{N_R}{g}}$.

Denoting

$$\gamma_0 := \min_{\bar{\Omega}} \frac{r^2}{N_R^2} \min_{\bar{\Omega}} \frac{N_R}{g} > 0, \tag{1.6}$$

then by (1.3), for all $d > 0$, we have

$$\gamma_0 \leq \gamma_*(d), \tag{1.7}$$

which implies that for all $d > 0$, $\gamma_*(d)$ has a positive lower bound $\gamma_0 > 0$.

The primary purpose of this paper is to investigate the properties of the steady state of (1.1); or, more precisely, the positive solution of (1.5) for the case $\gamma < \gamma_0 \leq \gamma_*(d)$, for all $d > 0$, as Theorem 1.1 reduces the steady states of (1.1) to the solution of (1.5) when $\gamma$ is small.

Denoting

$$R(x) := \gamma N_R(x), \tag{1.8}$$

we rewrite (1.5) as follows for convenience:

$$\begin{cases} d\Delta u + R(x) - g(x)u^2 = 0 & \text{for } x \in \Omega, \\ \partial_\nu u = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{1.9}$$

Denote the unique positive solution of (1.9) by $u_d$ with diffusion rate $d$.

As we remarked earlier, the yield rate $\gamma$ is an important parameter: when $\gamma$ is large, the consumer $Z(\cdot, t)$ eventually converges to the steady state $\theta_d$ of the classical logistic equation (1.4), while the resource tends to $\infty$ (which seems a bit unrealistic). On the other hand, when $\gamma$ is small, the consumer $Z(\cdot, t)$ always converges to the unique steady state $\tilde{w}_d$ of (1.5) (or, $u_d$ of (1.9)), while the resource also reaches an equilibrium.

It seems obvious that the (effective) resource input $R$ is crucial - especially in the case of small $\gamma$; in fact, in this case, the loss rate $g$ also turns out to be important. In this paper we will focus on the properties of the total population $\int_\Omega u_d\, dx$, in terms of the loss rate $g(x)$ and the resources input $R(x)$.

In He et al. (2019), it was already established that if $g \equiv$ constant and $R \not\equiv$ constant, then the total population $\int_\Omega u_d\, dx$ is strictly increasing in $d > 0$. In Sect. 2 below, we shall prove that, on the contrary, if $R \equiv$ constant, and $g \not\equiv$ constant, then $\int_\Omega u_d\, dx$ is strictly decreasing in $d > 0$. Motivated by these facts, we shall systematically study the total population for more general cases, in terms of the loss rate $g$ and the resources input $R$.

It is not difficult to see that,

$$\lim_{d \to 0^+} \int_\Omega u_d\, dx = \int_\Omega \sqrt{R/g}\, dx.$$

(See Theorem 2.2 below for a more detailed statement.) On the other hand, denoting, $\bar{f} = \frac{1}{|\Omega|}\int_\Omega f(x)\,dx$ for continuous function $f$ on $\bar{\Omega}$, it is standard to show that,

$$\lim_{d\to\infty}\int_\Omega u_d\,dx = \int_\Omega \sqrt{\bar{R}/\bar{g}}\,dx.$$

(See Theorem 2.3 below for details.)

Therefore, as a primary step in our study, we compare these two quantities $\int_\Omega \sqrt{R/g}\,dx$ and $\int_\Omega \sqrt{\bar{R}/\bar{g}}\,dx$. It turns out that two more quantities $\int_\Omega \sqrt{\bar{R}/g}\,dx$ and $\int_\Omega \sqrt{R/\bar{g}}\,dx$ are playing roles in this approach, as the following inequalities (which follow from Hölder's inequality) indicate:

$$\int_\Omega \sqrt{\bar{R}/g}\,dx > \int_\Omega \sqrt{\bar{R}/\bar{g}}\,dx > \int_\Omega \sqrt{R/\bar{g}}\,dx, \tag{1.10}$$

where both $R$ and $g$ are nonconstants. With (1.10), we are able to formulate conditions on $R$ and $g$ to compare the total populations $\int_\Omega u_d\,dx$ for large and small dispersal rate $d$. This illustrates the role of dispersals in total populations and provides rigorous proofs for the numerical simulations in Zhang et al. (2017).

A mathematical example is included in Sect. 5 to illustrate the effects of various correlations between $R$ and $g$. We also briefly discuss the biological significance of the correlations between $R$ and $g$ in Sect. 6.

The paper is organized as follows: In Sect. 2, we introduce our main results. Section 3 studies the monotone properties of the total population. We investigate the effects of various correlations between $g$ and $R$ on the total population for small and large diffusion rates in Sect. 4. To illustrate our results, we include an example in Sect. 5. Section 6 contains further remarks and discussions.

## 2 Main results

In He et al. (2019), the authors proved that the total population $\int_\Omega u_d\,dx$, where $u_d$ is the unique positive solution of (1.9), strictly increases in $d$ if $0 < g \equiv$ constant and $0 < R \not\equiv$ constant. Our first result here shows that, on the contrary, if we have, instead, that $0 < R \equiv$ constant and $0 < g \not\equiv$ constant, then $\int_\Omega u_d\,dx$ is strictly decreasing in $d$.

**Theorem 2.1** *Assume that* $0 < R \equiv$ *const. and* $0 < g \not\equiv$ *const. on* $\bar{\Omega}$*, then* $\int_\Omega u_d\,dx$ *strictly decreases in* $d$*.*

To facilitate the comparisons of total populations for $d$ small and large and investigate the total population's monotone properties for small diffusion, our second result focuses on the total population $\int_\Omega u_d\,dx$ for $d > 0$ small.

**Theorem 2.2** *Assume that* $g > 0$ *and* $R > 0$ *on* $\bar{\Omega}$*. Then as* $d \to 0^+$,

$$u_d \to \sqrt{R/g} \text{ in } C(\bar{\Omega}) \cap H^1(\Omega), \tag{2.1}$$

*and*

$$\int_\Omega u_d\,dx=\int_\Omega \sqrt{R/g}\,dx+\frac{d}{8}\int_\Omega \frac{1}{R^2g}\nabla(R/g)\cdot\nabla(Rg)\,dx+o(d). \tag{2.2}$$

*In particular,*

*(i) if $\nabla(R/g)\cdot\nabla(Rg)\ \geq\ (\not\equiv)0$ in $\Omega$, then the total population $\int_\Omega u_d\,dx$ is strictly increasing as $d>0$ small;*

*(ii) if $\nabla(R/g)\cdot\nabla(Rg)\ \leq\ (\not\equiv)0$ in $\Omega$, then the total population $\int_\Omega u_d\,dx$ is strictly decreasing as $d>0$ small.*

Motivated by the work of Zhang et al. (2017), it seems reasonable to explore the various cases of the loss rate $g$ depending on specific correlations with the resource input $R$.

**Definition 1** We say two positive functions $\phi$ and $\psi$ on $\bar{\Omega}$ are positively correlated if

$$\phi(x_1)\geq\phi(x_2)\Longleftrightarrow\psi(x_1)\geq\psi(x_2),\forall x_1,x_2\in\bar{\Omega},$$

and two positive functions $\phi$ and $\psi$ on $\bar{\Omega}$ are negatively correlated if

$$\phi(x_1)\geq\phi(x_2)\Longleftrightarrow\psi(x_1)\leq\psi(x_2),\forall x_1,x_2\in\bar{\Omega}.$$

It turns out that the following correlations between $g$ and $R$ play vital roles in the study of the total population for both small and large dispersal:

($\mathcal{L}1$) $g/R$ and $Rg$ are positively correlated;
($\mathcal{L}2$) $R/g$ and $g$ are positively correlated.

To illustrate the roles of large and small diffusion rates, we study the behavior of the unique positive solution $u_d$ of (1.9) for $d\to\infty$ and compare $\lim\limits_{d\to\infty}\int_\Omega u_d\,dx$ with $\lim\limits_{d\to0^+}\int_\Omega u_d\,dx$.

**Theorem 2.3** *Assume that $g>0$, $R>0$ on $\bar{\Omega}$. Then as $d\to\infty$,*

$$u_d\to\sqrt{\bar{R}/\bar{g}}\ in\ C^2(\bar{\Omega}). \tag{2.3}$$

*Suppose further that $R/g\not\equiv$ const., then the following statements hold for the positive solution $u_d$:*

*(i) If $g$ and $R$ satisfy ($\mathcal{L}1$), i.e., $g/R$ and $Rg$ are positively correlated, then*

$$\lim_{d\to0^+}\int_\Omega u_d\,dx=\int_\Omega\sqrt{R/g}\,dx>\int_\Omega\sqrt{\bar{R}/\bar{g}}\,dx=\lim_{d\to\infty}\int_\Omega u_d\,dx; \tag{2.4}$$

*(ii) If $g$ and $R$ satisfy ($\mathcal{L}2$), i.e., $R/g$ and $g$ are positively correlated, then*

$$\lim_{d\to0^+}\int_\Omega u_d\,dx=\int_\Omega\sqrt{R/g}\,dx<\int_\Omega\sqrt{\bar{R}/\bar{g}}\,dx=\lim_{d\to\infty}\int_\Omega u_d\,dx. \tag{2.5}$$

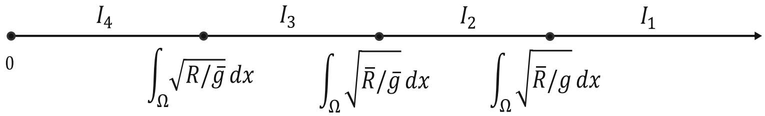

**Fig. 1** Four disjoint intervals $I_1$, $I_2$, $I_3$ and $I_4$ defined in (2.6)

As we shall see later, the following two more relations will play roles in the comparison between the quantities $\lim\limits_{d\to 0^+} \int_\Omega u_d\, dx$ and $\lim\limits_{d\to\infty} \int_\Omega u_d\, dx$ (See Theorem 2.4 for details):

($\mathcal{L}1^+$) $g/R$ and $R$ are positively correlated;
($\mathcal{L}1^-$) $Rg$ and $R$ are negatively correlated.

Note that relations ($\mathcal{L}1^+$) and ($\mathcal{L}1^-$) are opposite to each other in the sense that, ($\mathcal{L}1^+$) implies $g$ and $R$ are positively correlated while ($\mathcal{L}1^-$) implies $g$ and $R$ are negatively correlated. Moreover, if $g$ and $R$ satisfy ($\mathcal{L}1^+$) or ($\mathcal{L}1^-$), then $g$ and $R$ satisfy relation ($\mathcal{L}1$). (see Remark 4.2 for details.)

Assuming that $0 < R, g \not\equiv$ const. and $R/g \not\equiv$ const., by (1.10), we can split the interval $(0, +\infty)$ into four disjoint slots $I_1, I_2, I_3, I_4$ (also see Fig. 1), where

$$\begin{aligned} I_1 &:= \Big[\int_\Omega \sqrt{\bar{R}/g}\, dx, +\infty\Big), & I_2 &:= \Big(\int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx, \int_\Omega \sqrt{\bar{R}/g}\, dx\Big), \\ I_3 &:= \Big(\int_\Omega \sqrt{R/\bar{g}}\, dx, \int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx\Big], & I_4 &:= \Big(0, \int_\Omega \sqrt{R/\bar{g}}\, dx\Big]. \end{aligned} \tag{2.6}$$

We have the following sufficient conditions to determine which interval $I_i$, $1 \le i \le 4$ the quantity $\lim\limits_{d\to 0^+} \int_\Omega u_d\, dx = \int_\Omega \sqrt{R/g}\, dx$ falls within:

**Theorem 2.4** *Assume* $0 < R, g \not\equiv$ *const. and* $R/g \not\equiv$ *const., then:*

*(i) If g and R satisfy relation* ($\mathcal{L}1^-$)*, i.e., Rg and R are negatively correlated, then* $\int_\Omega \sqrt{R/g}\, dx \in I_1$*;*
*(ii) If g and R satisfy relation* ($\mathcal{L}1^+$)*, i.e., g/R and R are positively correlated, then* $\int_\Omega \sqrt{R/g}\, dx \in I_2$*;*
*(iii) If g/R and g are positively correlated, then* $\int_\Omega \sqrt{R/g}\, dx > \int_\Omega \sqrt{R/\bar{g}}\, dx$*. Moreover, we assume that* $|\Omega| = 1$, $\sqrt{R/g}$ *is a function of g, i.e.,*

$$\sqrt{R/g}(x) = l(g(x)), \forall x \in \Omega, \tag{2.7}$$

*with* $l(r) > 0, r > 0$*. Denoting* $L(r) := rl^2(r)$*, if l is a concave function and L is a convex function on* $[\min\limits_{\bar{\Omega}} g, \max\limits_{\bar{\Omega}} g]$*, then* $\int_\Omega \sqrt{R/g}\, dx \in I_3$*;*
*(iv) If* $R/g^2$ *and g are positively correlated, then* $\int_\Omega \sqrt{R/g}\, dx \in I_4$*.*

To reveal that $\int_\Omega \sqrt{R/g}\, dx$ can fall within each interval $I_i$ under specific correlations between $g$ and $R$, and to illustrate Theorem 2.4, we consider a special case $g = R^\alpha$, $\alpha \in \mathbb{R}$ and assume that $R$ is a positive, nonconstant, smooth function on $\bar{\Omega}$ with $|\Omega| = 1$ (See Sect. 5 for details).

Theorem 2.1 and Theorem 2.2 will be proved in Sect. 3. Section 4 will establish Theorems 2.3 and 2.4. Section 5 will illustrate Theorem 2.4 with the example $g = R^{\alpha}$.

## 3 Monotone properties of the total population

In this section, we first investigate the monotone properties of the total population for a spatially homogeneous environment and prove Theorem 2.1. Second, we study the behaviors of the positive solution $u_d$ and the monotone properties of total population $\int_{\Omega} u_d \, dx$ as $d \to 0^+$, where $u_d$ is the unique positive solution of (1.9).

Theorem 2.1 follows directly from Proposition 3.1, which is a more general result.

**Proposition 3.1** *Assume $R, g > 0$, $R/g \not\equiv const.$ on $\bar{\Omega}$, then for the positive solution $u_d$ of (1.9), $\int_{\Omega} Ru_d \, dx$ is strictly decreasing in $d > 0$.*

***Proof*** Denoting $\partial u_d/\partial d$ by $u_d'$ and differentiating both sides of (1.9) w.r.t. $d$, we obtain:

$$\begin{cases} d\Delta u_d' + \Delta u_d - 2g u_d u_d' = 0 & \text{for } x \in \Omega, \\ \partial_{\nu} u_d' = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{3.1}$$

Multiply (1.9) with $2u_d'$ and (3.1) with $u_d$, then subtract them to get

$$2d\Delta u_d u_d' + 2Ru_d' - d\Delta u_d' u_d - \Delta u_d u_d = 0, \ \text{for } x \in \Omega.$$

Integrating the above equation over $\Omega$, we have, by Divergence Theorem,

$$d\int_{\Omega} (\nabla u_d') \cdot (\nabla u_d) \, dx - \int_{\Omega} |\nabla u_d|^2 \, dx = 2\int_{\Omega} Ru_d' \, dx. \tag{3.2}$$

It suffices to show $\int_{\Omega} (\nabla u_d') \cdot (\nabla u_d) \le 0$ because $u_d \not\equiv$ const. To this end, multiplying (3.1) with $u_d'$ and taking integration over $\Omega$, we have

$$\int_{\Omega} (\nabla u_d') \cdot (\nabla u_d) \, dx = -\int_{\Omega} d|\nabla u_d'|^2 \, dx - 2\int_{\Omega} g u_d (u_d')^2 \, dx \le 0.$$

This completes the proof of Proposition 3.1. □

Next, we analyze the asymptotic behavior of the positive solution $u_d$ and the monotone behavior of the total population as $d \to 0^+$ and then prove Theorem 2.2. Our proof of Theorem 2.2 is motivated by the work of DeAngelis et al. (2016) and is organized as the following steps:

***Proof of Theorem 2.2*** Our first step is to show that

$$\lim_{d \to 0^+} \left\| u_d - \sqrt{R/g} \right\|_{C(\bar{\Omega})} = 0. \tag{3.3}$$

It suffices to show $\lim\limits_{d\to 0^+}\left\|u_d-\sqrt{R/g}\right\|_\infty=0$ due to the continuity of $\sqrt{R/g}$ and $u_d$.

Fix $\varepsilon>0$ small, there exists a function $\vartheta_\varepsilon^+\in C^2(\bar\Omega)$ s.t. $\sqrt{R/g}+\frac{\varepsilon}{2}\le\vartheta_\varepsilon^+\le\sqrt{R/g}+\varepsilon$ in $\Omega$ and $\partial_\nu\vartheta_\varepsilon^+=0$ on $\partial\Omega$. Since $\Delta\vartheta_\varepsilon^+$ is bounded in $\bar\Omega$, there exists $0<d_\varepsilon^+\ll 1$ s.t. $\forall 0<d<d_\varepsilon^+$,

$$d\Delta\vartheta_\varepsilon^+ + R - g(\vartheta_\varepsilon^+)^2\le d\Delta\vartheta_\varepsilon^+ + g\Big(-\varepsilon\sqrt{R/g}-\varepsilon^2/4\Big)\le 0. \tag{3.4}$$

Similarly, there exists a function $\vartheta_\varepsilon^-\in C^2(\bar\Omega)$ s.t. $\sqrt{R/g}-\varepsilon\le\vartheta_\varepsilon^-\le\sqrt{R/g}-\frac{\varepsilon}{2}$ in $\Omega$ and $\partial_\nu\vartheta_\varepsilon^-=0$ on $\partial\Omega$. Also, there exists $0<d_\varepsilon^-\ll 1$ s.t. $\forall 0<d<d_\varepsilon^-$,

$$d\Delta\vartheta_\varepsilon^- + R - g(\vartheta_\varepsilon^-)^2\ge d\Delta\vartheta_\varepsilon^- + g\Big(\varepsilon\sqrt{R/g}-\varepsilon^2/4\Big)\ge 0. \tag{3.5}$$

By (3.4) and (3.5), $\forall 0<d<\min\{d_\varepsilon^+,d_\varepsilon^-\}$, $(\vartheta_\varepsilon^+,\vartheta_\varepsilon^-)$ is a pair of upper and lower solution of (1.9) and $0<\vartheta_\varepsilon^-<\vartheta_\varepsilon^+$. By the uniqueness of positive solution $u_d$, we have $\vartheta_\varepsilon^-\le u_d\le\vartheta_\varepsilon^+$ and then $\left\|u_d-\sqrt{R/g}\right\|_\infty\le\varepsilon, \forall 0<d<d_\varepsilon$. So $\limsup\limits_{d\to 0^+}\left\|u_d-\sqrt{R/g}\right\|_\infty\le\varepsilon, \forall\varepsilon>0$ and this proves (3.3).

Our second step is to show that

$$\lim_{d\to 0^+}\left\|u_d-\sqrt{R/g}\right\|_{H^1(\Omega)}=0. \tag{3.6}$$

Setting $\hat u_d=u_d-\sqrt{R/g}$, it suffices to show $\lim\limits_{d\to 0^+}\int_\Omega|\nabla\hat u_d|^2\,dx\to 0$. Then, by (1.9),

$$d\Delta\hat u_d + d\Delta\sqrt{R/g}-g\hat u_d\Big(u_d+\sqrt{R/g}\Big)=0 \text{ for } x\in\Omega. \tag{3.7}$$

Multiplying (3.7) with $\frac{\hat u_d}{d}$ and taking integration over $\Omega$, then by Divergence Theorem,

$$\begin{aligned}\int_\Omega|\nabla\hat u_d|^2\,dx &= \int_{\partial\Omega}\hat u_d(\partial_\nu\hat u_d)\,dS+\int_\Omega\Delta\Big(\sqrt{R/g}\Big)\hat u_d\,dx-\frac{1}{d}\int_\Omega g\hat u_d^2\Big(u_d+\sqrt{R/g}\Big)dx\\ &\le\int_{\partial\Omega}\Big|\hat u_d\Big(\nabla\sqrt{R/g}\Big)\cdot\vec\nu\Big|\,dS+\int_\Omega\Big|\Delta\Big(\sqrt{R/g}\Big)\hat u_d\Big|\,dx\\ &\le\int_{\partial\Omega}||\hat u_d||_{C(\bar\Omega)}\cdot\Big\|\Big(\nabla\sqrt{R/g}\Big)\cdot\vec\nu\Big\|_\infty dS+\int_\Omega||\hat u_d||_{C(\bar\Omega)}\cdot\Big\|\Delta\Big(\sqrt{R/g}\Big)\Big\|_\infty dx\\ &\to 0 \text{ as } d\to 0^+ \text{ by (3.3)}.\end{aligned}$$

Our third step is to prove that

$$\lim_{d\to 0^+}\int_\Omega\Big|\nabla u_d\cdot\nabla\Big(\frac{1}{\sqrt{Rg}+gu_d}\Big)-\nabla\sqrt{R/g}\cdot\nabla\Big(\frac{1}{2\sqrt{Rg}}\Big)\Big|\,dx=0. \tag{3.8}$$

Notice that

$$
\begin{aligned}
&\int_\Omega \Big|\nabla u_d \cdot \nabla\Big(\frac{1}{\sqrt{Rg}+gu_d}\Big) - \nabla\sqrt{R/g}\cdot\nabla\Big(\frac{1}{2\sqrt{Rg}}\Big)\Big|\,dx\\
&\le \int_\Omega \Big|\nabla\Big(u_d-\sqrt{R/g}\Big)\cdot\nabla\Big(\frac{1}{\sqrt{Rg}+gu_d}\Big)\Big|dx\\
&\quad+\int_\Omega\Big|\nabla\sqrt{R/g}\cdot\nabla\Big(\frac{1}{\sqrt{Rg}+gu_d}-\frac{1}{2\sqrt{Rg}}\Big)\Big|dx\\
&=: I+II.
\end{aligned}
$$

Then Cauchy-Schwarz Inequaliy, boundedness of $\Big|\nabla\Big(\frac{1}{\sqrt{Rg}+gu_d}\Big)\Big|$ in $L^2(\Omega)$, (3.3) and (3.6) guarentee that $I \to 0$ as $d \to 0^+$. As for $II$, we have

$$
\frac{1}{\sqrt{Rg}+gu_d}-\frac{1}{2\sqrt{Rg}}=\frac{\sqrt{Rg}-gu_d}{2(\sqrt{Rg}+gu_d)\sqrt{Rg}}=\frac{1}{2R+2\sqrt{Rg}u_d}\Big(\sqrt{R/g}-u_d\Big).
$$

Then Cauchy-Schwarz Inequaliy, boundedness of $\frac{1}{2R+2\sqrt{Rg}u_d}$ in $C(\bar\Omega)\cap H^1(\Omega)$, (3.3) and (3.6) imply that $II \to 0$ as $d \to 0^+$.

Now, by (1.9), (3.3), (3.6) and (3.8),

$$
\begin{aligned}
\int_\Omega u_d\,dx &= \int_\Omega \sqrt{R/g}\,dx - d\int_\Omega \nabla(u_d)\cdot\nabla\Big(\frac{1}{\sqrt{Rg}+gu_d}\Big)dx\\
&=\int_\Omega \sqrt{R/g}\,dx - d\int_\Omega \nabla\sqrt{R/g}\cdot\nabla\Big(\frac{1}{2\sqrt{Rg}}\Big)\,dx+o(d)\\
&=\int_\Omega \sqrt{R/g}\,dx+\frac{d}{8}\int_\Omega\frac{1}{R^2g}\nabla(R/g)\cdot\nabla Rg\,dx+o(d),
\end{aligned}
$$

as $d \to 0^+$ and this completes the proof of Theorem 2.2. □

***Remark 3.2*** Under the assumption of Theorem 2.2, if we further assume $R/g$ is a function of $Rg$, i.e.,

$$
(R/g)(x) = f(Rg(x)), x \in \Omega,
$$

where $f$ is smooth and $f > 0$. Assume $R/g$, $Rg \not\equiv$ const., it is easy to verify that

(i) if $g$ and $R$ satisfy relation ($\mathcal{L}1$), then $f' \le (\not\equiv)0$, so $\nabla(R/g)\cdot\nabla(Rg) \le (\not\equiv)0$ in $\Omega$ and the total population $\int_\Omega u_d\,dx$ is strictly decreasing for $d > 0$ small;

(ii) if $g$ and $R$ satisfy relation ($\mathcal{L}2$), then $f' \ge (\not\equiv)0$, so $\nabla(R/g)\cdot\nabla(Rg) \ge (\not\equiv)0$ in $\Omega$ and the total population $\int_\Omega u_d\,dx$ is strictly increasing for $d > 0$ small.

To end this section, we consider some special correlations between $g$ and $R$:

**Proposition 3.3** *There are the following special correlations between $g$ and $R$:*

*(i) If* $R/g \equiv$ *constant* $C_1 > 0$*, then the total population is independent of the diffusion rate* $d$*, that is,* $\forall d > 0$*,* $\int_\Omega u_d\, dx = \sqrt{C_1}|\Omega|$*.*

*(ii) If* $0 < R, g \not\equiv$ *constant and* $Rg \equiv$ *constant* $C_2 > 0$*, then the total population* $\int_\Omega u_d\, dx$ *is decreasing for small* $d > 0$*. Moreover,* $\forall d > 0$*,*

$$\int_\Omega u_d\, dx < \lim_{d\to 0^+} \int_\Omega u_d\, dx. \tag{3.9}$$

Here, Part *(i)* is trivial. As for Part *(ii)*, we introduce another equation:

$$\begin{cases} d\Delta v + 2R - 2\sqrt{Rg}\, v = 0 & \text{for } x \in \Omega, \\ \partial_\nu v = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{3.10}$$

Since $\left(\max_{\bar\Omega} \sqrt{R/g}, \min_{\bar\Omega} \sqrt{R/g}\right)$ is a pair of upper and lower solutions, (3.10) has a positive solution, denoted as $v_d$, which is unique by Fredholm Alternative Theorem. By standard elliptic regularity, $v_d \in C^2(\bar\Omega)$, for $d > 0$.

**Proposition 3.4** *Suppose* $R, g > 0$*,* $\forall d > 0$*, the positive solution* $u_d$ *of (1.9) is a subsolution of (3.10). If we further assume* $R/g \not\equiv$ *const., then* $u_d \leq (\not\equiv) v_d$*.*

***Proof*** By (1.9), we have

$$d\Delta u_d + 2R - 2\sqrt{Rg}u_d = R + gu_d^2 - 2\sqrt{Rg}u_d = (\sqrt{R} - \sqrt{g}u_d)^2 \geq 0. \tag{3.11}$$

Thus $u_d$ is a subsolution of (3.10). Suppose the equality holds in (3.11), then $u_d \equiv \sqrt{R/g}$, so $\Delta u_d \equiv 0$ in $\Omega$ by (1.9). By $\partial_\nu u_d = 0$, $u_d \equiv$ const., that is, $R/g \equiv$ const. This completes our proof of Proposition 3.4. □

***Proof of Proposition 3.3 (ii)*** By Proposition 3.4, $u_d \leq (\not\equiv) v_d$, where $v_d$ satisfies

$$\begin{cases} d\Delta v_d + 2R - 2\sqrt{C_2} v_d = 0 & \text{for } x \in \Omega, \\ \partial_\nu v_d = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{3.12}$$

Integrating (3.12) over $\Omega$, by $\partial_\nu v_d = 0, \forall x \in \partial\Omega$ and Divergence Theorem,

$$\int_\Omega v_d\, dx = \frac{1}{\sqrt{C_2}} \int_\Omega R\, dx = \int_\Omega R/\sqrt{C_2}\, dx = \int_\Omega \sqrt{R/g}\, dx, \forall d > 0.$$

Since $u_d \leq (\not\equiv) v_d, \forall d > 0$, then $\int_\Omega u_d\, dx < \int_\Omega v_d\, dx = \int_\Omega \sqrt{R/g}\, dx = \lim_{d\to 0^+} \int_\Omega u_d\, dx$ by Theorem 2.2. This completes our proof of Proposition 3.3. □

## 4 Effects of correlations between *g* and *R* on the total population

In this Section, we investigate the effects of various correlations between $g$ and $R$ on the total population for small and large diffusion and prove Theorems 2.3 and 2.4.

Initially, we explore the correlations between positive functions $\phi$ and $\psi$ on $\bar{\Omega}$:

**Proposition 4.1** *Assume $\phi$ and $\psi$ are two positive functions on $\bar{\Omega}$. For any $n \in \mathbb{N}^+$,*

*(i) If $\phi$ and $\psi$ are positively correlated, then $\phi$ and $\phi\psi^n$ are positively correlated.*
*(ii) If $\phi$ and $\psi$ are negatively correlated, then $\phi$ and $\psi^n/\phi$ are negatively correlated.*

***Proof*** It is clear that for positive functions $\phi$ and $\psi$, we have

$$\phi \text{ and } \psi \text{ are positively correlated } \iff \phi \text{ and } 1/\psi \text{ are negatively correlated.} \tag{4.1}$$

By (4.1), it suffices to prove assertion *(i)*. Assuming $\phi$ and $\psi$ are positively correlated, for arbitrary $x_1, x_2 \in \bar{\Omega}$, we consider the following two cases:
if $\phi(x_1) \geq \phi(x_2)$, then $\psi(x_1) \geq \psi(x_2)$, so $\psi^n(x_1) \geq \psi^n(x_2)$ and $\phi\psi^n(x_1) \geq \phi\psi^n(x_2)$;
if $\phi(x_1) < \phi(x_2)$, then $\psi(x_1) \leq \psi(x_2)$, so $\psi^n(x_1) \leq \psi^n(x_2)$ and $\phi\psi^n(x_1) < \phi\psi^n(x_2)$.

Thus $\phi(x_1) \geq \phi(x_2) \iff \phi\psi^n(x_1) \geq \phi\psi^n(x_2)$. We complete the proof of Proposition 4.1. □

***Remark 4.2*** Applying Proposition 4.1 to ($\mathcal{L}1$), ($\mathcal{L}1^+$), ($\mathcal{L}1^-$) and ($\mathcal{L}2$), we have

(i) The two opposite relations ($\mathcal{L}1^+$) and ($\mathcal{L}1^-$) both imply ($\mathcal{L}1$). ($\mathcal{L}1^+$) is opposite to ($\mathcal{L}1^-$) in the sense that, ($\mathcal{L}1^+$) implies that $g$ and $R$ are positively correlated while ($\mathcal{L}1^-$) implies that $g$ and $R$ are negatively correlated.
(ii) ($\mathcal{L}2$) implies that $g/R$ and $Rg$ are negatively correlated, which is opposite to ($\mathcal{L}1$).

Next, we introduce the following proposition as the key to the proof of Theorem 2.4.

**Proposition 4.3** *Suppose $\phi$ and $\psi$ are two positive and smooth functions on $\bar{\Omega}$.*

*(i) If $\phi$ and $\psi$ are positively (negatively resp.) correlated, then*

$$|\Omega| \int_\Omega \phi\psi \, dx \geq (\leq \ resp.) \left(\int_\Omega \phi \, dx\right)\left(\int_\Omega \psi \, dx\right); \tag{4.2}$$

*(ii) If $\phi$ and $\psi/\phi$ are positively correlated, then*

$$|\Omega|(\int_\Omega \phi\psi \, dx)^2 \geq \left(\int_\Omega \phi^2 \, dx\right)\left(\int_\Omega \psi \, dx\right)^2. \tag{4.3}$$

Our approach for Proposition 4.3 is motivated by the work of DeAngelis et al. (2016). We approximate the integrals by their Riemann sums and apply the following lemmas. (See Appendix A for the proof of Proposition 4.3)

**Lemma 4.4** (DeAngelis et al. (2016) Lemma 26) *Suppose there are two finite sequences of nonnegative real numbers* $\{a_i\}_{i=1}^n$ *and* $\{b_i\}_{i=1}^n$, *s.t.* $\{a_i\}_{i=1}^n$ *is an increasing sequence.*
*If* $\{b_i\}_{i=1}^n$ *is an increasing (decreasing resp.) sequence, then*

$$\begin{aligned} &n(a_1b_1 + a_2b_2 + \cdots + a_nb_n) \geq (\leq \ \textit{resp.}) \\ &(a_1 + a_2 + \cdots + a_n)(b_1 + b_2 + \cdots + b_n). \end{aligned} \tag{4.4}$$

**Lemma 4.5** *Suppose that* $\{a_i\}_{i=1}^n$ *and* $\{b_i\}_{i=1}^n$ *are two finite increasing sequences of positive real numbers. If the sequence* $\left\{\frac{b_i}{a_i}\right\}_{i=1}^n$ *is also increasing, then*

$$\begin{aligned} &n(a_1b_1 + a_2b_2 + \cdots + a_nb_n)^2 \geq (a_1^2 + a_2^2 \\ &+ \cdots + a_n^2)(b_1 + b_2 + \cdots + b_n)^2. \end{aligned} \tag{4.5}$$

For the proof of Lemma 4.4, we refer to the work of DeAngelis et al. (2016). We prove Lemma 4.5 by induction and see Appendix A for the proof.

With Proposition 4.3, we come to the

***Proof of Theorem 2.4*** First, we prove *(i)* . Denote $\phi = \sqrt{R}$, $\psi = \sqrt{\frac{1}{g}}$, then $\psi/\phi = \sqrt{\frac{1}{Rg}}$ and $\phi$ and $\psi/\phi$ are positively correlated. Then $\lim\limits_{d\to 0^+} \int_\Omega u_d\, dx = \int_\Omega \sqrt{R/g}\, dx \geq \int_\Omega \sqrt{\bar{R}/g}\, dx$ is guaranteed by Proposition 4.3 *(ii)*.

Then, we prove *(ii)*, and to do this, we first prove $\int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx < \int_\Omega \sqrt{R/g}\, dx = \lim\limits_{d\to 0^+} \int_\Omega u_d\, dx$. By Hölder's inequality and the assumption $R/g \not\equiv$ const., we have $\int_\Omega \sqrt{Rg}\, dx < \sqrt{\int_\Omega R\, dx}\sqrt{\int_\Omega g\, dx}$. So

$$\int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx = |\Omega| \sqrt{\frac{\int_\Omega R\, dx}{\int_\Omega g\, dx}} < |\Omega| \frac{\int_\Omega R\, dx}{\int_\Omega \sqrt{Rg}\, dx}. \tag{4.6}$$

Since $(\mathcal{L}1^+)$ implies that $\sqrt{R/g}$ and $\sqrt{Rg}$ are negatively correlated by Remark 4.2, it follows directly from Proposition 4.3 *(i)* that

$$|\Omega| \int_\Omega R\, dx \leq \Big(\int_\Omega \sqrt{R/g}\, dx\Big)\Big(\int_\Omega \sqrt{Rg}\, dx\Big). \tag{4.7}$$

By (4.6) and (4.7), we have $\int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx < \int_\Omega \sqrt{R/g}\, dx$.

We now prove that $\lim\limits_{d\to 0^+}\int_\Omega u_d\,dx = \int_\Omega \sqrt{R/g}\,dx < \int_\Omega \sqrt{\bar{R}/g}\,dx$. By Remark 4.2, ($\mathcal{L}1^+$) implies that $1/g$ and $R$ are negatively correlated. Then, by Proposition 4.3 *(i)*,

$$\int_\Omega \sqrt{R/g}\,dx \le \frac{1}{|\Omega|}\int_\Omega \sqrt{R}\,dx \cdot \int_\Omega \sqrt{1/g}\,dx < \sqrt{\frac{\int_\Omega R\,dx}{|\Omega|}} \cdot \int_\Omega \sqrt{1/g}\,dx = \int_\Omega \sqrt{\bar{R}/g}\,dx.$$

Note that the strict inequality above follows from Hölder's inequality and the assumption $R \not\equiv$ const. Therefore, $\int_\Omega \sqrt{R/g}\,dx < \int_\Omega \sqrt{\bar{R}/g}\,dx$.

Next, we prove *(iii)*. As for $\int_\Omega \sqrt{R/\bar{g}}\,dx < \int_\Omega \sqrt{R/g}\,dx$, the proof is similar to that of $\int_\Omega \sqrt{R/g}\,dx < \int_\Omega \sqrt{\bar{R}/g}\,dx$ in *(ii)*. We include the proof here for completeness.

Note that $g/R$ and $g$ are positively correlated is equivalent to $R/g$ and $g$ are negatively correlated. Then by Proposition 4.3 *(i)*,

$$\int_\Omega \sqrt{R}\,dx \le \frac{1}{|\Omega|}\int_\Omega \sqrt{R/g}\,dx \int_\Omega \sqrt{g} < \int_\Omega \sqrt{R/g}\,dx \sqrt{\frac{\int_\Omega g\,dx}{|\Omega|}} = \sqrt{\bar{g}}\int_\Omega \sqrt{R/g}\,dx.$$

Here, the strict inequality above follows from Hölder's inequality and the assumption that $g \not\equiv$ const. Consequently, $\int_\Omega \sqrt{R/\bar{g}}\,dx < \int_\Omega \sqrt{R/g}\,dx$.

To prove $\int_\Omega \sqrt{R/g}\,dx \le \int_\Omega \sqrt{\bar{R}/\bar{g}}\,dx$, we assume functions $l$ and $L$ as in the assumption, then $\sqrt{R/g} = l(g)$ and $R = L(g)$. Since $l$ is a concave function, $L$ is a convex function and $|\Omega| = 1$, by Jensen's inequality, we have

$$\Big(\int_\Omega l(g)dx\Big)^2 \cdot \int_\Omega g\,dx \le l^2\Big(\int_\Omega g\,dx\Big)\cdot\Big(\int_\Omega g\,dx\Big) = L\Big(\int_\Omega g\,dx\Big) \le \int_\Omega L(g)dx. \tag{4.8}$$

This implies $\int_\Omega \sqrt{R/g}\,dx \le \int_\Omega \sqrt{\bar{R}/\bar{g}}\,dx$ and completes our proof for *(iii)*.

The proof of *(iv)* is similar to that of *(i)* with $\phi$, $\psi$ being replaced by $\phi = \sqrt{g}$, $\psi = \sqrt{R/g}$, and henceforth is omitted. Hence, we complete the proof of Theorem 2.4. □

To end this section, we determine the behavior of $u_d$ as $d \to \infty$ and complete the proof of Theorem 2.3.

***Proof of Theorem 2.3*** First, we prove (2.3), i.e., $u_d \to \sqrt{\bar{R}/\bar{g}}$ in $C^2(\bar{\Omega})$, as $d \to \infty$. Apply the maximum principle (cf. Lou and Ni (1999) Lemma 2.1) to (1.5), we have $g(x_1)u_d^2(x_1) \le R(x_1)$, where $u_d(x_1) = \max\limits_{\bar{\Omega}} u_d$, $x_1 \in \bar{\Omega}$. So $||u_d||_\infty \le ||\sqrt{R/g}||_\infty$, $\forall d > 0$. Then by standard elliptic regularity, $\{u_d : d \gg 1\}$ is a bounded subset in $C^{2,\alpha}(\bar{\Omega})$, where $0 < \alpha < 1$. Pass to a subsequence if necessary, $u_{d_k} \to$ some $u_\infty$ in $C^2(\bar{\Omega})$ as $k \to \infty$. Dividing (1.9) by $d$ on both sides, we have:

$$\Delta u_d + \frac{1}{d}(R - g u_d^2) = 0. \tag{4.9}$$

By (4.9), $\Delta u_\infty \equiv 0$ and $\partial_\nu u_\infty = 0$, then $u_\infty \equiv$ some const. $L$. Integrating both sides of (4.9) over $\Omega$, by $\partial_\nu u_{d_k} = 0$ on $\partial\Omega$, we have $\int_\Omega (R - g u_{d_k}^2)\,dx = 0$. Sending

$k \to \infty$, we have $\int_\Omega R\,dx = L^2 \int_\Omega g\,dx$, i.e., $L = \sqrt{\bar{R}/\bar{g}}$. Since this works for every subsequence $\{d_k\}_{k=1}^{\infty}$, we prove (2.3).

By (4.6), (4.7), Part *(i)* is directly derived from the proof of Theorem 2.4 *(ii)*. As for Part *(ii)*, it suffices to show $\Big(\int_\Omega \sqrt{R/g}\,dx\Big)^2\Big(\int_\Omega g\,dx\Big) < |\Omega|^2 \int_\Omega R\,dx$. By Hölder's inequality and Proposition 4.3 *(i)*, we have

$$\Big(\int_\Omega \sqrt{R/g}\,dx\Big)^2\Big(\int_\Omega g\,dx\Big) < |\Omega|\Big(\int_\Omega R/g\,dx\Big)\Big(\int_\Omega g\,dx\Big) \le |\Omega|^2 \int_\Omega R\,dx,$$

since $R/g$ and $g$ are positively correlated. (Here, strict inequality follows from Hölder's inequality and the assumption $R/g \not\equiv$ const.) This finishes our proof of Theorem 2.3. □

## 5 Illustration of Theorem 2.4 with $g = R^\alpha$

Assume $R$ is a positive, smooth, and nonconstant function on $\bar{\Omega}$ with $|\Omega| = 1$, and $g = R^\alpha, \alpha \in \mathbb{R}$. For simplicity, we assume $R \ge 1$ on $\bar{\Omega}$. Define $p_1, p_2, p_3, \mu$ as follows:

$$\begin{aligned} p_1(\alpha) &:= \int_\Omega \sqrt{\bar{R}/g}\,dx, \quad p_2(\alpha) := \int_\Omega \sqrt{\bar{R}/\bar{g}}\,dx, \\ p_3(\alpha) &:= \int_\Omega \sqrt{R/\bar{g}}\,dx, \quad \mu(\alpha) := \int_\Omega \sqrt{R/g}\,dx. \end{aligned} \tag{5.1}$$

(Here, quantities $p_i$'s and $\mu$ depend on $\alpha$ and are denoted as $p_i(\alpha)$'s and $\mu(\alpha)$.) We see that quantities $p_i$'s are the endpoints of intervals $I_i$'s and the quantity $\mu = \lim\limits_{d \to 0^+} \int_\Omega u_d\,dx$. By Hölder's Inequality and $R \not\equiv$ const., we have

$$p_1(\alpha) \ge p_2(\alpha) > p_3(\alpha), \forall \alpha \in \mathbb{R} \text{ and } p_1(\alpha) = p_2(\alpha) \Longleftrightarrow \alpha = 0. \tag{5.2}$$

By Theorem 2.4, with $g = R^\alpha$, we have:

$$\text{if } \alpha \le -1, \text{ then } g \text{ and } R \text{ satisfy } (\mathcal{L}1^-), \text{ so } p_1(\alpha) \le \mu(\alpha), \text{ i.e., } \int_\Omega \sqrt{R/g}\,dx \in I_1; \tag{5.3}$$

$$\begin{aligned} &\text{if } 0 \le \alpha \le 1/2, \text{ then } R/g^2 \text{ and } g \text{ are positively correlated, so } 0 < \mu(\alpha) \le p_3(\alpha), \\ &\text{i.e., } \int_\Omega \sqrt{R/g}\,dx \in I_4; \end{aligned} \tag{5.4}$$

$$\begin{aligned} &\text{if } 1 < \alpha, \text{ then } g \text{ and } R \text{ satisfy } (\mathcal{L}1^+), \text{ so } p_2(\alpha) < \mu(\alpha) < p_1(\alpha), \\ &\text{i.e., } \int_\Omega \sqrt{R/g}\,dx \in I_2. \end{aligned} \tag{5.5}$$

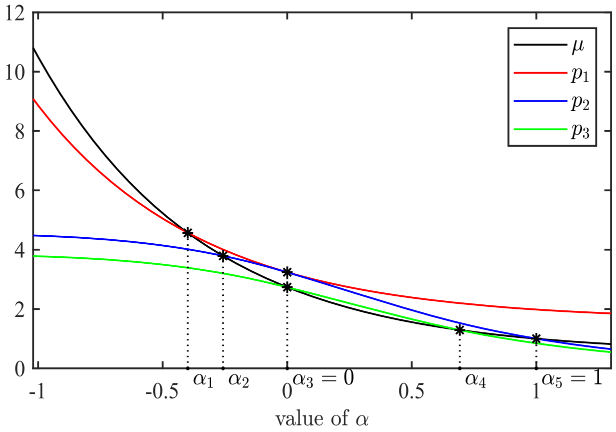

**Fig. 2** The behaviors of $\mu$, $p_1$, $p_2$, $p_3$ w.r.t. $\alpha$. (Here, the monotonicity of $\mu$, $p_1$, $p_2$, $p_3$ w.r.t. $\alpha$ is due to the assumption $R \geq 1$.)

Now, we present the behaviors of $\mu$, $p_1$, $p_2$, $p_3$ with respect to $\alpha$ (also see Fig. 2):

**Proposition 5.1** *For every positive smooth function $R \not\equiv const.$ on $\Omega$ with $|\Omega| = 1$ and $g = R^\alpha$, there is a unique group of numbers $(\alpha_1(R), \alpha_2(R), \alpha_3(R), \alpha_4(R), \alpha_5(R))$ with $-1 < \alpha_1(R) < \alpha_2(R) < \alpha_3(R) = 0 < \frac{1}{2} < \alpha_4(R) < \alpha_5(R) = 1$ satisfying:*

*(i)* $\mu(\alpha_1) = p_1(\alpha_1)$*;* $\mu(\alpha_2) = p_2(\alpha_2)$*;* $\mu(\alpha_3) = p_3(\alpha_3)$*;* $\mu(\alpha_4) = p_3(\alpha_4)$*;* $\mu(\alpha_5) = p_2(\alpha_5)$.

*(ii)* $\forall \alpha \in (-\infty, \alpha_1)$, $p_1(\alpha) < \mu(\alpha)$*, then* $\mu(\alpha) \in I_1$*;*
$\forall \alpha \in (\alpha_1, \alpha_2) \cup (\alpha_5, +\infty)$, $p_2(\alpha) < \mu(\alpha) < p_1(\alpha)$*, i.e.,* $\mu(\alpha) \in I_2$*;*
$\forall \alpha \in (\alpha_2, \alpha_3) \cup (\alpha_4, \alpha_5)$, $p_3(\alpha) < \mu(\alpha) < p_2(\alpha)$*, then* $\mu(\alpha) \in I_3$.
$\forall \alpha \in (\alpha_3, \alpha_4)$, $0 < \mu(\alpha) < p_3(\alpha)$*, then* $\mu(\alpha) \in I_4$.

Next, we investigate the derivatives of $p_1$, $p_2$, $p_3$, $\mu$ with respect to $\alpha$ to determine their behaviors at each $\alpha_i$, $1 \leq i \leq 5$.

**Proposition 5.2** *Suppose $R \not\equiv const.$ is a positive and smooth function on $\bar{\Omega}$ and $|\Omega| = 1$. Let $g = R^\alpha$, $p_1(\alpha) = \int_\Omega \sqrt{\bar{R}/g}\, dx$, $p_2(\alpha) = \int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx$, $p_3(\alpha) = \int_\Omega \sqrt{R/\bar{g}}\, dx$, and $\mu(\alpha) = \int_\Omega \sqrt{R/g}\, dx$. Then the following statements holds for $p_1$, $p_2$, $p_3$ and $\mu$:*

*(i)* $\forall \beta \in \mathbb{R}$ *satisfying* $p_1(\beta) = \mu(\beta)$*, we have* $\frac{\partial \mu}{\partial \alpha}(\beta) < \frac{\partial p_1}{\partial \alpha}(\beta)$*;*

*(ii) For* $i = 2, 3$, $\forall \beta \in \mathbb{R}$ *satisfying* $p_i(\beta) = \mu(\beta)$*, we have* $\frac{\partial \mu}{\partial \alpha}(\beta) < (>$ *resp.)* $\frac{\partial p_i}{\partial \alpha}(\beta)$*, given* $\beta < (>$ *resp.)* $1/3$.

To prove Proposition 5.2, we define $F(\eta) := \frac{\int_\Omega R^\eta \ln R\,dx}{\int_\Omega R^\eta\,dx}$, $\eta \in \mathbb{R}$, then by Hölder's inequality and $R \not\equiv$ const., we have, for $\eta \in \mathbb{R}$,

$$\begin{aligned}\frac{\partial}{\partial\eta}F(\eta) &= \frac{(\int_\Omega R^\eta \ln^2 R\,dx)(\int_\Omega R^\eta\,dx) - (\int_\Omega R^\eta \ln R\,dx)^2}{(\int_\Omega R^\eta\,dx)^2}\\ &\geq \frac{(\int_\Omega R^\eta |\ln R|^2\,dx)(\int_\Omega R^\eta\,dx) - (\int_\Omega R^\eta |\ln R| dx)^2}{(\int_\Omega R^\eta\,dx)^2} > 0,\end{aligned} \tag{5.6}$$

i.e., $F(\eta)$ is strictly increasing in $\eta \in \mathbb{R}$.

Next, we apply (5.6) repeatedly in the proof of Proposition 5.2.

***Proof of Proposition 5.2*** We first prove *(i)*. Notice

$$\begin{aligned}\frac{\partial\mu}{\partial\alpha}(\beta) < \frac{\partial p_1}{\partial\alpha}(\beta) &\Longleftrightarrow \int_\Omega R^{\frac{1-\beta}{2}}\ln R\,dx > \sqrt{\int_\Omega R\,dx}\int_\Omega R^{-\frac{\beta}{2}}\ln R\,dx\\ &\Longleftrightarrow \frac{\int_\Omega R^{\frac{1-\beta}{2}}\ln R\,dx}{\int_\Omega R^{\frac{1-\beta}{2}}\,dx} > \frac{\int_\Omega R^{-\frac{\beta}{2}}\ln R\,dx}{\int_\Omega R^{-\frac{\beta}{2}}\,dx},\end{aligned}$$

where the last equivalence follows from $\sqrt{\int_\Omega R\,dx}\int_\Omega R^{-\frac{\beta}{2}}\,dx = \int_\Omega R^{\frac{1-\beta}{2}}\,dx$, derived from $p_1(\beta) = \mu(\beta)$. Then by (5.6) and $\frac{1-\beta}{2} > -\frac{\beta}{2}$, $\forall\beta \in \mathbb{R}$, we prove $\frac{\partial\mu}{\partial\alpha}(\beta) < \frac{\partial p_1}{\partial\alpha}(\beta)$.

Second, we prove *(ii)*, and it suffices to prove for $i = 2$ (the proof for $i = 3$ is similar and henceforth is omitted). As the same process in *(i)*, we have:

$$\frac{\partial\mu}{\partial\alpha}(\beta) < (> \text{ resp.}) \frac{\partial p_2}{\partial\alpha}(\beta) \Longleftrightarrow \frac{\int_\Omega R^{\frac{1-\beta}{2}}\ln R\,dx}{\int_\Omega R^{\frac{1-\beta}{2}}}dx > (< \text{ resp.}) \frac{\int_\Omega R^\beta \ln R\,dx}{\int_\Omega R^\beta\,dx}.$$

By (5.6) and the fact $\frac{1-\beta}{2} > (< \text{ resp.})\,\beta$, $\forall\beta < (> \text{ resp.})\ 1/3$, we prove *(ii)*. This completes our proof of Proposition 5.2. □

***Proof of Proposition 5.1*** Fix positive smooth function $R \not\equiv$ const. on $\Omega$. We first prove the existence of a group of numbers $(\alpha_i, \alpha_2, \alpha_3, \alpha_4, \alpha_5)$ satisfying Proposition 5.1 *(i)* and

$$\alpha_2 \leq \alpha_3 \leq 0 < \alpha_4 < \alpha_5. \tag{5.7}$$

Notice that (5.2), (5.3), (5.4), (5.5) and continuity of $p_1, p_2, p_3, \mu$ w.r.t. $\alpha$ guarantee the existence of such $\alpha_i$'s, $1 \leq i \leq 5$, and moreover $\alpha_1 \leq \alpha_2$. Next, we prove the uniqueness of the above $\alpha_i$, $\forall 1 \leq i \leq 5$.

By Proposition 5.2 *(i)*, $\frac{\partial\mu}{\partial\alpha}(\alpha_1) < \frac{\partial p_1}{\partial\alpha}(\alpha_1)$, which guarantees the uniqueness of $\alpha_1$ for $\mu(\alpha_1) = p_1(\alpha_1)$. By (5.3), $-1 \leq \alpha_1$. Similarly, by Proposition 5.2 *(ii)*, $\alpha_2$ and $\alpha_3$

are unique for $\mu(\alpha_2) = p_2(\alpha_2)$, $\mu(\alpha_3) = p_3(\alpha_3)$ with $\alpha_2, \alpha_3 \le 0$. Moreover, we have $\alpha_3 = 0$ because $\mu(0) = p_3(0)$.

As for $\alpha_4$, by Proposition 5.2 *(ii)*, it suffices to show $\alpha_4 > 1/3$. Let $\tilde{\beta} = \min\{\beta > 0 | \mu(\beta) = p_3(\beta)\}$. By $\mu(0) = p_3(0)$ and Proposition 5.2 *(ii)*, we have $\frac{\partial \mu}{\partial \alpha}(0) < \frac{\partial p_3}{\partial \alpha}(0)$. So $\tilde{\beta} > 0$, $\mu(\tilde{\beta}) = p_3(\tilde{\beta})$ and $\frac{\partial \mu}{\partial \alpha}(\tilde{\beta}) \ge \frac{\partial p_3}{\partial \alpha}(\tilde{\beta})$. It remains to prove $\tilde{\beta} > 1/3$. By Proposition 5.2 *(ii)* again, if $\tilde{\beta} < 1/3$, then $\frac{\partial \mu}{\partial \alpha}(\tilde{\beta}) < \frac{\partial p_3}{\partial \alpha}(\tilde{\beta})$, which is a contradiction. Suppose $\tilde{\beta} = 1/3$, then derived from $\mu(\tilde{\beta}) = p_3(\tilde{\beta})$, we have $(\int_\Omega R^{1/2})^2\, dx = (\int_\Omega R^{1/3})^3\, dx$, which implies $R \equiv$ const. by Hölder's inequality, contradicting to our assumptions. Furthermore, by (5.5), we have $\alpha_4 \ge 1/2$.

Now, we consider $\alpha_5$ and $\alpha_5 \ge 1/2$ by (5.7). Proposition 5.2 *(ii)* guarantees the uniqueness of $\alpha_5$ for $\mu(\alpha_5) = p_2(\alpha_5)$ with $\alpha_5 > 0$, and $\alpha_5 = \{1\}$ because of $\mu(1) = p_2(1)$.

By (5.2), (5.3), (5.4), (5.5), (5.7) and uniqueness of the above $\alpha_i$'s, we have

$$-1 \le \alpha_1 < \alpha_2 < \alpha_3 = 0 < \frac{1}{2} \le \alpha_4 < \alpha_5 = 1 \tag{5.8}$$

and $\alpha_i$'s satisfy Proposition 5.1 *(ii)*.

Ultimately, we exclude the possibilities of $\alpha_1 = -1$ and $\alpha_4 = \frac{1}{2}$. If $\alpha_1 = -1$, then in $\mu(\alpha_1) = p_1(\alpha_1)$, we have $\int_\Omega R\, dx = (\int_\Omega \sqrt{R})^2\, dx$, which implies $R \equiv$ const. by Hölder's inequality, contradicting to our assumptions. Similarly, $\alpha_4 = \frac{1}{2}$ provides the same contradiction. Hence, we complete the proof of Proposition 5.1. ◻

***Remark 5.3*** By Proposition 5.1 above, we see that,

$$-1 < \alpha_1(R) < \alpha_2(R) < 0 \quad \text{and} \quad \frac{1}{2} < \alpha_4(R) < 1, \tag{5.9}$$

for all positive nonconstant smooth functions $R$. It seems natural to ask whether there are more precise lower and upper bounds. Here, we give a negative answer. Assume $N = 1$, $\Omega = (0, 1)$. After careful examination of the proofs, we see that Proposition 5.1 also holds for positive step functions on $\Omega$. Now, letting $M \ge 1$ be a constant, we consider the following step functions:

$$R_{1,M}(x) = \begin{cases} 1, & 0 < x < 1/2, \\ M, & 1/2 < x < 1; \end{cases} \text{ and } R_{2,M}(x) = \begin{cases} 1, & 0 < x < 1 - 1/M, \\ M, & 1 - 1/M < x < 1. \end{cases} \tag{5.10}$$

By Proposition 5.1, $\alpha_i(R_{1,M})$ and $\alpha_i(R_{2,M})$ exist for all $1 \le i \le 5$, and moreover,

$$\lim_{M\to\infty} \alpha_1(R_{1,M}) = \lim_{M\to\infty} \alpha_2(R_{1,M}) = 0, \qquad \lim_{M\to\infty} \alpha_4(R_{1,M}) = 1, \tag{5.11}$$

$$\lim_{M\to\infty} \alpha_1(R_{2,M}) = \lim_{M\to\infty} \alpha_2(R_{2,M}) = -1, \qquad \lim_{M\to\infty} \alpha_4(R_{2,M}) = \frac{1}{2}. \tag{5.12}$$

***Proof*** In order to prove (5.11) and (5.12), by (5.9), it suffices to show $\lim_{M\to\infty}\alpha_1(R_{1,M}) = 0$, $\lim_{M\to\infty}\alpha_4(R_{1,M}) = 1$, $\lim_{M\to\infty}\alpha_2(R_{2,M}) = -1$ and $\lim_{M\to\infty}\alpha_4(R_{2,M}) = \frac{1}{2}$. We show $\lim_{M\to\infty}\alpha_1(R_{1,M}) = 0$ here. The similar proof of other assertions is omitted.

Suppose to the contrary, there is a $\varepsilon_1 > 0$, there exists a sequence $\{M_k\}_{k=1}^{\infty}$ s.t. $M_k \to +\infty$ as $k \to \infty$ and $\alpha_1(R_{1,M_k}) \le -\varepsilon_1, \forall k \ge 1$. By direct calculation of $p_1(\alpha_1(R_{1,M_k})) = \mu(\alpha_1(R_{1,M_k}))$, we have

$$\frac{\left(\frac{1}{M_k}+1\right)\left(M_k^{\alpha_1(R_{1,M_k})/2}+1\right)^2}{\left(M_k^{(\alpha_1(R_{1,M_k})-1)/2}+1\right)^2} = 2. \tag{5.13}$$

As $k \to \infty$, since $\alpha_1(R_{1,M_k}) \le -\varepsilon_1 < 0$, $M_k \to +\infty$, (5.13) implies that $1 = 2$, which is impossible. This completes the proof of Remark 5.3. □

## 6 Concluding remarks and discussions

This paper investigates a consumer-resource model proposed by Zhang et al. (2017) whose global dynamics was investigated by He et al. (2019, 2023) for both large and small yield rates. For low yield rates, we study the properties of the resource-limited positive steady state of the model (1.1), namely, the positive solution of (1.9).

We first prove that the total population with homogeneously distributed resources but spatially heterogeneous loss rate strictly decreases as the diffusion rate increases. Next, we study the asymptotic behavior of the positive solution $u_d$ of (1.9) as the diffusion rate is small or large and analyze the corresponding dispersal effects for the total population. Moreover, we compare the total population for small and large dispersal under various correlations between loss rate $g$ and the (effective) resource input $R$.

Correlations between the loss rate $g$ and the resource input $R$ play a vital role in our study of the total population for both small and large diffusion rates. Biological evidence seems to support some specific correlations between $g$ and $R$. Biro et al. (2003) studied the effects of the daphnid food density on mortality and the mean autumn mass of young rainbow trout (*Oncorhynchus mykiss*). They concluded that mortality decreases and the mean autumn mass increases with more food (See Figure 5 in Biro et al. (2003)), which seems to imply that $g$ is negatively correlated to $R$ in their experiment. Moreover, increasing soil nutrients, e.g., fertilization use improves the population growth rate and decreases mortality for a few reasons. For instance, Davis (2007) has found a 40 % lower seed mortality rate with fertilizer applications due to a decrease in microbial predation.

However, over-fertilization can lead to higher mortality according to the well-accepted nitrogen-limitation hypothesis, which predicts a positive response in species performance to dietary nitrogen content and seems to imply a positive correlation between $g$ and $R$. For example, fertilization increased the nitrogen concentration of both host-plant species and decreased the survival of larvae in all six Lepidoptera species by at least one-third (see Kurze et al. (2018) Figures 3 and 4). Furthermore, eutrophication, owing to nitrogen and phosphorus enrichment in the sediments or aquatic system, is one of the major environmental threats to biodiversity conservation. For instance, eutrophication due to fertilizer use has been shown to have negative effects on the distribution and the abundance of waterbirds due to the long-term storage of nutrients (e.g., phosphorus) in sediment (Møller and Laursen (2015)).

It is important to study how diffusion affects populations in systems with multiple trophic levels in the context of high nutrient level (e.g., eutrophication), and we hope to take up this project in a future study to better map interactions between various biotic components (cf. Desprez et al. (1992), Dorgham (2014) and Johnson et al. (2007)).

Mathematically, it is possible to relax our assumptions on the resource input $g$ and the loss rate $R$ to allow them to be nonnegative instead of strictly positive. We shall leave the details to the interested readers.

By Theorem 2.2, Theorem 2.3 and (1.3),

$$\lim_{d\to 0^+}\gamma_*(d)=\min_{\bar\Omega}\frac{r^2}{gN_R}=:\gamma_1 \text{ and } \lim_{d\to\infty}\gamma_*(d)=\min_{\bar\Omega}\frac{r^2}{N_R^2}\cdot\frac{\int_\Omega N_R\,dx}{\int_\Omega g\,dx}=:\gamma_2. \tag{6.1}$$

Thus, we can apply Theorem 2.2, Theorem 2.3 and Theorem 2.4 to system (1.1) under the assumption $\gamma<\min\{\gamma_1,\gamma_2\}$, which is a relaxation of the assumption $\gamma<\gamma_0$.

To conclude this section, we briefly discuss the numerical simulations of the one-dimensional discrete version of system (1.1) described by Zhang et al. (2017) (See equations (2a), (2b) therein with $m_i\equiv 0$, for all $1\le i\le 12$ and $\eta=0$), for each $1\le i\le 12$:

$$\begin{cases}\partial_t U_i &= \frac{r_{\max}N_i}{k+N_i}U_i-g_iU_i^2-D(U_i-\frac{1}{2}U_{i-1}-\frac{1}{2}U_{i+1}),\\ \partial_t N_i &= N_{\text{input},i}-\frac{r_{\max}N_iU_i}{\gamma(k+N_i)}.\end{cases} \tag{6.2}$$

There are 12 patches in (6.2). Each patch is linked to others by nearest-neighbor diffusion, and there is only one-sided diffusion for two end patches (patches 1 and 12).

Set $r_{\max}=0.1$, $k=0.1$, $\gamma=0.01$ and set

$$g_i=\begin{cases}\text{positive constant } g_{\text{odd}} & \text{for odd } i,\\ 0.001 & \text{for even } i.\end{cases} \tag{6.3}$$

Set $N_{\text{input},i}=0.31$, for all $i$'s in the homogeneous case. For a heterogeneous case, set

$$N_{\text{input},i}=\begin{cases}0.02 & \text{for odd } i,\\ 0.6 & \text{for even } i.\end{cases} \tag{6.4}$$

By (6.1), for all $0 < g_{\text{odd}} < 100 * 10^{-3}$, we have

$$\min\{\gamma_1, \gamma_2\} \geq \frac{1}{6} > \gamma = 0.01. \tag{6.5}$$

Thus, with $R := \gamma N_R$, for all $0 < g_{\text{odd}} < 100 * 10^{-3}$, we can apply Theorems 1.1, 2.2 and 2.3 to model (6.2) to get

$$\begin{aligned} &\text{TRAPA}_{\text{hetero, no diffusion}} = \int_\Omega \sqrt{R/g}\, dx, \ \text{TRAPA}_{\text{hetero, diffusion}} = \int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx, \\ &\text{TRAPA}_{\text{homo, no diffusion}} = \int_\Omega \sqrt{\bar{R}/g}\, dx. \end{aligned} \tag{6.6}$$

In Figure 3 of Zhang et al. (2017), they numerically investigated the total populations exhibited in (6.6) as functions of $g_{\text{odd}}$ for both small and large diffusion. Our theoretical results of comparison between the integrals in (6.6) follow from Theorems 2.3 and 2.4, which seem consistent with the numerical simulation results of Zhang et al. (2017). (See Table 1 here.)

**Table 1** The value range of $g_{\text{odd}}$ guaranteeing that the following inequalities hold for theoretical estimates in this paper and numerical simulation in Zhang et al. (2017)

| | Theoretical results (by Theorems 2.3 and 2.4) | Numerical simulation results in Zhang et al. (2017) |
|---|---|---|
| $\int_\Omega \sqrt{R/g}\, dx < \int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx$ | $g_{\text{odd}} < \frac{1}{30} * 10^{-3}$ or $g_{\text{odd}} > 30 * 10^{-3}$ | $g_{\text{odd}} < 0.038 * 10^{-3}$ or $g_{\text{odd}} > 2.3 * 10^{-3}$ |
| $\int_\Omega \sqrt{R/g}\, dx > \int_\Omega \sqrt{\bar{R}/\bar{g}}\, dx$ | $\frac{1}{30} * 10^{-3} < g_{\text{odd}} < 10^{-3}$ | $0.038 * 10^{-3} < g_{\text{odd}} < 2.3 * 10^{-3}$ |
| $\int_\Omega \sqrt{R/g}\, dx < \int_\Omega \sqrt{\bar{R}/g}\, dx$ | $g_{\text{odd}} < 10^{-3}$ | $g_{\text{odd}} < 3.6 * 10^{-3}$ |
| $\int_\Omega \sqrt{R/g}\, dx > \int_\Omega \sqrt{\bar{R}/g}\, dx$ | $g_{\text{odd}} > 30 * 10^{-3}$ | $g_{\text{odd}} > 3.6 * 10^{-3}$ |

## Appendix A: Proof of Lemma 4.5 and Proposition 4.3

In Appendix, we present the proof of Lemma 4.5 and Proposition 4.3. First, we prove Lemma 4.5, and to do so, we introduce another lemma:

**Lemma A.1** *Assume $n \geq 2$. Suppose that $\{a_i\}_{i=1}^n$ and $\{b_i\}_{i=1}^n$ are two finite increasing sequences of positive real numbers. If the sequence $\left\{\frac{b_i}{a_i}\right\}_{i=1}^n$ is also increasing, then*

$$\sum_{j=1}^{n-1} a_j b_j \cdot \sum_{j=1}^{n-1} (a_j b_j + 2a_n b_n) \geq \sum_{j=1}^{n-1} b_j \cdot \sum_{j=1}^{n-1} (a_n^2 b_j + 2a_j^2 b_n). \tag{A.1}$$

***Proof of Lemma A.1*** We prove Lemma A.1 by induction.

Suppose $n = 2$, then (A.1) holds if $a_1 = a_2$. We consider the case $a_1 < a_2$, then

$$(A.1) \Longleftrightarrow 2b_1b_2a_1(a_2 - a_1) \geq (a_2^2 - a_1^2)b_1^2 \Longleftrightarrow 2b_2a_1 \geq (a_2 + a_1)b_1,$$

and $2b_2a_1 \geq (a_2 + a_1)b_1$ holds because $b_2 \geq b_1$ and $\frac{b_2}{a_2} \geq \frac{b_1}{a_1}$.

Now suppose the statement holds for $n = 2, \cdots, k-1$, we consider the case $n = k$:

$$\begin{aligned}
&\text{the left-handed side (abbreviated to L.H.S. for convenience) of } (A.1)\\
=&\Big[\Big(\sum_{j=1}^{k-2} a_jb_j\Big) + a_{k-1}b_{k-1}\Big]\cdot\Big[\sum_{j=1}^{k-2}(a_jb_j + 2a_kb_k) + a_{k-1}b_{k-1} + 2a_kb_k\Big]\\
=&\Big(\sum_{j=1}^{k-2} a_jb_j\Big)\cdot\sum_{j=1}^{k-2}(a_jb_j + 2a_kb_k) + a_{k-1}b_{k-1}(a_{k-1}b_{k-1} + 2a_kb_k)\\
&+ a_{k-1}b_{k-1}\sum_{j=1}^{k-2}(a_jb_j + 2a_kb_k) + (a_{k-1}b_{k-1} + 2a_kb_k)\cdot\sum_{j=1}^{k-2} a_jb_j;\\
&\text{the right-handed side (abbreviated to R.H.S. for convenience) of } (A.1)\\
=&\Big[\Big(\sum_{j=1}^{k-2} b_j\Big) + b_{k-1}\Big]\cdot\Big[\sum_{j=1}^{k-2}(a_k^2b_j + 2a_j^2b_k) + a_k^2b_{k-1} + 2a_{k-1}^2b_k\Big]\\
=&\Big(\sum_{j=1}^{k-2} b_j\Big)\cdot\sum_{j=1}^{k-2}(a_k^2b_j + 2a_j^2b_k) + b_{k-1}(a_k^2b_{k-1} + 2a_{k-1}^2b_k)\\
&+ (a_k^2b_{k-1} + 2a_{k-1}^2b_k)\cdot\Big(\sum_{j=1}^{k-2} b_j\Big) + b_{k-1}\sum_{j=1}^{k-2}(a_k^2b_j + 2a_j^2b_k).
\end{aligned}$$

By the induction hypothesis, we have

$$\Big(\sum_{j=1}^{k-2} a_jb_j\Big)\cdot\sum_{j=1}^{k-2}(a_jb_j + 2a_kb_k) \geq \Big(\sum_{j=1}^{k-2} b_j\Big)\cdot\sum_{j=1}^{k-2}(a_k^2b_j + 2a_j^2b_k),$$

and by the case $n = 2$, with $a_1, a_2, b_1, b_2$ replacing by $a_{k-1}, a_k, b_{k-1}, b_k$, respectively, we obtain

$$a_{k-1}b_{k-1}(a_{k-1}b_{k-1} + 2a_kb_k) \geq b_{k-1}(a_k^2b_{k-1} + 2a_{k-1}^2b_k).$$

It remains to show

$$\begin{aligned} a_{k-1}b_{k-1}\sum_{j=1}^{k-2}(a_jb_j+2a_kb_k)+(a_{k-1}b_{k-1}+2a_kb_k)\cdot\sum_{j=1}^{k-2}a_jb_j \\ \geq (a_k^2b_{k-1}+2a_{k-1}^2b_k)\cdot\Big(\sum_{j=1}^{k-2}b_j\Big)+b_{k-1}\sum_{j=1}^{k-2}(a_k^2b_j+2a_j^2b_k), \end{aligned} \tag{A.2}$$

which follows from the following claim: $\forall 1\leq j\leq k-2$,

$$\begin{aligned} a_{k-1}b_{k-1}(a_jb_j+2a_kb_k)+a_jb_j(a_{k-1}b_{k-1}+2a_kb_k) \\ \geq b_j(a_k^2b_{k-1}+2a_{k-1}^2b_k)+b_{k-1}(a_k^2b_j+2a_j^2b_k). \end{aligned} \tag{A.3}$$

Denote $c_1 := a_jb_{k-1}$, $d_1 := b_ja_{k-1}$, $c_2 := a_kb_j$, $d_2 := a_jb_k$, $c_3 := a_{k-1}b_k$, $d_3 := a_kb_{k-1}$. Then, we obtain $0<c_1\leq d_2$ and $0<d_1\leq c_2$. By direct calculation, we have

$$(d_2-c_1)(c_2-d_1)\geq 0,$$

that is,

$$c_1d_1+d_2c_2\geq c_1c_2+d_1d_2.$$

Similarly, as $0<c_1\leq d_3$, $0<d_1\leq c_3$ and $0<c_2\leq d_3$, $0<d_2\leq c_3$, we obtain

$$c_1d_1+d_3c_3\geq c_1c_3+d_3d_1 \quad\text{and}\quad c_2d_2+d_3c_3\geq c_2c_3+d_3d_2.$$

So, we have

$$\begin{aligned} \text{the L.H.S. of (A.3)} =&(c_1d_1+d_2c_2)+(c_1d_1+d_3c_3)+(c_2d_2+d_3c_3) \\ \geq&(c_1c_2+d_1d_2)+(c_1c_3+d_3d_1)+(c_2c_3+d_3d_2). \end{aligned} \tag{A.4}$$

Similarly, we have

$$\begin{aligned} \text{the R.H.S. of (A.3)} =&(d_1c_3+c_2d_3)+(c_2d_3+d_2c_1)+(d_1c_3+c_1d_2) \\ \leq&(d_1d_3+c_2c_3)+(c_2c_1+d_2d_3)+(d_1d_2+c_1c_3), \end{aligned} \tag{A.5}$$

by direct calculation and the facts that $0<d_1\leq c_2$, $0<d_3\leq c_3$, $0<c_2\leq d_2$, $0<c_1\leq d_3$, $0<d_1\leq c_1$, $0<d_2\leq c_3$.

Our assertion follows from (A.4) and (A.5). Now, the inequality (A.2) holds, and our proof of Lemma A.1 is complete. □

***Proof of Lemma 4.5*** We prove Lemma 4.5 by induction. When $n = 1$ the statement holds obviously. Suppose the statement holds for the $n = 1, 2, \cdots, k-1$ case, then we consider the case $n = k$. Notice that

$$\begin{aligned}
&\text{the L.H.S. of (4.5)}\\
&= k\Big[\Big(\sum_{j=1}^{k-1} a_j b_j\Big)^2 + 2a_k b_k\Big(\sum_{j=1}^{k-1} a_j b_j\Big) + a_k^2 b_k^2\Big]\\
&= (k-1)\Big(\sum_{j=1}^{k-1} a_j b_j\Big)^2 + \sum_{j=1}^{k-1} a_j b_j \cdot \sum_{j=1}^{k-1}(a_j b_j + 2a_k b_k) + a_k b_k \sum_{j=1}^{k-1}(2a_j b_j + a_k b_k) + a_k^2 b_k^2;\\
&\text{the R.H.S. of (4.5)}\\
&= \Big(\sum_{j=1}^{k-1} a_j^2 + a_k^2\Big)\cdot\Big[\Big(\sum_{j=1}^{k-1} b_j\Big)^2 + 2b_k \sum_{j=1}^{k-1} b_j + b_k^2\Big]\\
&= \Big(\sum_{j=1}^{k-1} a_j^2\Big)\cdot\Big(\sum_{j=1}^{k-1} b_j\Big)^2 + \Big(\sum_{j=1}^{k-1} b_j\Big)\cdot\Big[\sum_{j=1}^{k-1}(a_k^2 b_j + 2a_j^2 b_k)\Big] + b_k\Big[\sum_{j=1}^{k-1}(2a_k^2 b_j + a_j^2 b_k)\Big] + a_k^2 b_k^2.
\end{aligned}$$

By the induction hypothesis and Lemma A.1, it remains to show

$$a_k b_k \sum_{j=1}^{k-1}(2a_j b_j + a_k b_k) \geq b_k\Big[\sum_{j=1}^{k-1}(2a_k^2 b_j + a_j^2 b_k)\Big], \tag{A.6}$$

which is equivalent to show $\sum_{j=1}^{k-1}((a_k^2 - a_j^2)b_k) \geq \sum_{j=1}^{k-1}(2b_j a_k(a_k - a_j))$.

So $\forall 1 \leq j \leq k-1$, it suffices to show

$$(a_k^2 - a_j^2)b_k \geq 2b_j a_k(a_k - a_j). \tag{A.7}$$

If $a_k = a_j$, then (A.7) holds trivially. If $a_k > a_j$, then the inequality holds because $\frac{b_k}{a_k} \geq \frac{b_j}{a_j}$ and $b_k \geq b_j, \forall 1 \leq j \leq k-1$. This finishes the proof of Lemma 4.5. □

With Lemmas 4.4 and 4.5, we are ready for the

***Proof of Proposition 4.3*** We approximate the integrals by their Riemann sums and set

$$a_i = \phi(x_i), b_i = \psi(x_i), \forall i = 1, 2, \cdots, n, \tag{A.8}$$

where $\{x_i\}_{i=1}^n$ are uniformly distributed in $\Omega$. We can rearrange sequences $\{a_i\}_{i=1}^n$ and $\{b_i\}_{i=1}^n$ in the order that $\{a_i\}_{i=1}^n$ is ascending.

We prove *(i)* here, and the proof of *(ii)* is similar and henceforth is omitted. It suffices to prove for the case $\phi$ and $\psi$ are positively correlated, then $\{b_i\}_{i=1}^n$ is also ascending. By Lemma 4.4, we have the following inequality:

$$n\sum_{i=1}^n a_i b_i \geq \Big(\sum_{i=1}^n a_i\Big)\cdot\Big(\sum_{i=1}^n b_i\Big) \Longleftrightarrow \frac{1}{n}\sum_{i=1}^n \phi(x_i)\psi(x_i) \geq \frac{1}{n}\Big(\sum_{i=1}^n \phi(x_i)\Big)\cdot\frac{1}{n}\Big(\sum_{i=1}^n \psi(x_i)\Big).$$

Letting $n \to \infty$, we have (4.2) and finish the proof of Proposition 4.3. □

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## Declarations

**Conflict of interest** No potential conflict of interest was reported by the authors.

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