Journal of Mathematical Biology (2019) 78:1605–1636
https://doi.org/10.1007/s00285-018-1321-z

Mathematical Biology

Dynamics of a consumer–resource reaction–diffusion model

Homogeneous versus heterogeneous environments

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Received: 29 May 2018 / Revised: 30 November 2018 / Published online: 2 January 2019

Abstract

We study the dynamics of a consumer–resource reaction–diffusion model, proposed recently by Zhang et al. (Ecol Lett 20(9):1118–1128, 2017), in both homogeneous and heterogeneous environments. For homogeneous environments we establish the global stability of constant steady states. For heterogeneous environments we study the existence and stability of positive steady states and the persistence of time-dependent solutions. Our results illustrate that for heterogeneous environments there are some parameter regions in which the resources are only partially limited in space, a unique feature which does not occur in homogeneous environments. Such difference between homogeneous and heterogeneous environments seems to be closely connected with a recent finding by Zhang et al. (2017), which says that in consumer–resource models, homogeneously distributed resources could support higher population abundance than heterogeneously distributed resources. This is opposite to the prediction by Lou (J Differ Equ 223(2):400–426, 2006. https://doi.org/10.1016/j.jde.2005.05.010) for logistic-type models. For both small and high yield rates, we also show that when a consumer exists in a region with a heterogeneously distributed input of exploitable renewed limiting resources, the total population abundance at equilibrium can reach a greater abundance when it diffuses than when it does not. In contrast, such phenomenon may fail for intermediate yield rates.

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Keywords Spatial heterogeneity · Global asymptotic stability · Consumer–resource model · Reaction–diffusion equations

Mathematics Subject Classification 92D25 · 92D40 · 35K57 · 35B40

1 Introduction

Population abundance, or biomass of populations, is often the critical factor in deciding management strategies for the protection of endangered species and the control of exotic invasive species. For homogeneous environments in which the resources are evenly distributed in space, the total population of a single population is usually determined by the carrying capacity. However, when the environment is spatially varying across the habitat, the connection between biomass and carrying capacity may potentially be complicated, partly due to different movement behaviors of organisms. This issue has largely been addressed in theoretical studies, in both discrete and continuous spatial models. For a two-patch system of a single population with logistic growth,it was shown by Freedman and Waltman (1977) and Holt (1985) that for high movement rates, the total biomass of population at equilibrium could exceed the sum of the carrying capacities of the two patches. See also a recent thorough study of the two-patch system by Arditi et al. (2015).

The continuous model for a single population with logistic growth and diffusion is studied by DeAngelis et al. (2016b), in which it is assumed that both intrinsic growth rate and carrying capacity vary spatially. DeAngelis et al. showed that if the growth rate is positively correlated with the carrying capacity, then the total population at equilibrium could exceed the total carrying capacity. This extended the results of Lou (2006), where the growth rate is assumed to be proportional to the carrying capacity. The total population of a single species model also plays an important role in determining the interesting dynamics of models of two competing species which diffuse in heterogeneous environments, e.g., it could occur that without diffusion two competing species will coexist at any location, but with diffusion one competitor can wipe out the other at every location. We refer interested readers to Cantrell and Cosner (1991, 1998), Hastings (1983), He and Ni (2013a, b, 2016a, b, 2017), Lam and Ni (2012), Lou (2006) and references therein for further details.

In contrast to these theoretical developments, empirical works in validating the theoretical predictions are lacking until the recent works of Zhang et al. (2015) and of DeAngelis et al. (2016a). In their experimental studies Zhang et al. (2015) measured the growth of the duckweed in a five-patch system with different nutrient levels, by manually moving a portion of the duckweed between the adjacent patches in a fixed time period. Their experimental results showed that the total population of the duckweed is higher than the total carrying capacity of the system and it is peaked at a relatively low diffusion (or mixing) rate, in agreement with the theoretical predictions from both discrete and continuous spatial models.

The experimental work of Zhang et al. (2015) mimicked the classical logistic model with diffusion, in which carrying capacity is held to be spatially varying but temporally constant. Such considerations neglected several important factors, one of which is the feedback of resources from exploitations by consumers. To remedy such restrictions, Zhang et al. (2017) first experimentally tested several hypotheses suggested previously by the logistic model, and then, based on their experiments, extended the logistic models to consumer–resource reaction–diffusion models to include *exploitable renewed resources*. Their experiments also confirmed that spatial diffusion will increase the total population in heterogeneous environments, as predicted by logistic models. Surprisingly, their experimental results also showed that homogeneously distributed resources actually supported higher population abundance than heterogeneously distributed resources, which is opposite to the prediction from logistic models. In Appendix E of the supplementary materials in Zhang et al. (2017), a mathematical proof of this fact was given under some suitable assumptions. In this paper we will analytically study the dynamics of a consumer–resource model proposed by Zhang et al. (2017).

The paper is organized as follows: In Sect. 2 we will introduce the mathematical model and discuss our main results. In Sect. 3 we study the persistence of consumer and resource populations in heterogeneous environments and establish the existence of a positive steady state. The linear stability of the positive steady state is investigated in Sect. 4. Section 5 is devoted to studying the dynamics of the model in homogeneous environments, in which we show that the constant positive steady state is unique and globally asymptotically stable. In Sect. 6 we study some qualitative properties of the positive steady state determined in Sect. 3 and investigate two hypotheses raised by Zhang et al. (2017). We conclude with discussions in Sect. 7.

2 Mathematical model and main results

Consider the following consumer–resource model derived, based on the experiments, by Zhang et al. (2017) (see Model I therein)

$$\begin{cases} Z_t = d\Delta Z + Z\left(\frac{r(x)N}{k+N} - g(x)Z\right) & \text{for } x \in \Omega, t > 0, \\ N_t = N_R(x) - \frac{r(x)NZ}{\gamma(k+N)} & \text{for } x \in \Omega, t > 0, \\ \partial_n Z = 0 & \text{for } x \in \partial\Omega, t > 0, \\ Z(x,0) = Z_0(x), \quad N(x,0) = N_0(x) & \text{for } x \in \Omega. \end{cases} \tag{1}$$

Here $Z(x,t)$ and $N(x,t)$ are the densities of consumer and resource populations at location x and time t, respectively. d is the diffusion rate of the consumer, $\Delta = \Sigma_{i=1}^{N} \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator, $r(x)$ is the growth rate of the consumer under unlimited resources, 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, and γ is the yield rate (measured as individuals per unit resources).

Throughout this paper we assume that d, k and γ are positive constants, and $r(x)$, $g(x)$ and $N_R(x)$ are positive, Hölder continuous functions in $\bar{\Omega} = \Omega \cup \partial\Omega$, where Ω is a bounded domain in Euclidean space $\mathbb{R}^N$, with smooth boundary $\partial\Omega$. $n(x)$ is the outward unit normal vector at $x \in \partial\Omega$, and $\partial_n Z := n \cdot \nabla Z$. The zero Neumann boundary condition for Z means that there is no flux of consumer population across the boundary. We assume that Z_0 and N_0 are non-negative, not identically zero and continuous in $\bar{\Omega}$.

Our first observation is that for solutions of (1), it may occur that $N(x,t) \to \infty$ as $t \to \infty$, i.e. the resources become unlimited in space. Accordingly, set

$$U(x,t) := \frac{Z(x,t)}{\gamma}, \quad M(x,t) := \frac{N(x,t)}{k + N(x,t)},$$

then we obtain the equivalent system

$$\begin{cases} U_t = d\Delta U + U\,(rM - \gamma g U) & \text{for } x \in \Omega, t > 0, \\ kM_t = (1-M)^2(N_R - rMU) & \text{for } x \in \Omega, t > 0, \\ \partial_n U = 0 & \text{for } x \in \partial\Omega, t > 0, \\ U(x,0) = U_0(x), \quad M(x,0) = M_0(x) & \text{for } x \in \Omega. \end{cases} \tag{2}$$

Here $U_0 = Z_0/\gamma$ and $M_0 = N_0/(k + N_0)$ satisfy $U_0 \geq 0$, $U_0 \not\equiv 0$, $M_0 \geq 0$, $M_0 \not\equiv 0$, and $M_0 < 1$ in $\bar{\Omega}$. Our first result settles the homogeneous case.

Theorem 1 *Suppose that $r(x)$, $N_R(x)$ and $g(x)$ are positive constant functions, denoted by $\bar{r}$, $\bar{N}_R$ and $\bar{g}$, respectively. Then the positive constant steady state of* (2)*, given by*

$$\min\left\{1, \frac{\sqrt{\gamma\bar{g}\bar{N}_R}}{\bar{r}}\right\} \cdot \left(\frac{\bar{r}}{\gamma\bar{g}}, 1\right)$$

is globally asymptotically stable among all solutions of (2) *with initial data* (U_0, M_0) *satisfying*

$$U_0(x) \geq 0,\ M_0(x) \geq 0,\ U_0(x) \not\equiv 0,\ M_0(x) \not\equiv 0 \textit{ and } M_0(x) < 1 \textit{ for all } x \in \bar{\Omega}. \tag{3}$$

That is, the following statements hold:

(a) *If $\gamma \geq \frac{\bar{r}^2}{\bar{g}\bar{N}_R}$, then $\left(\frac{\bar{r}}{\gamma\bar{g}}, 1\right)$ is globally asymptotically stable;*

(b) *If $\gamma < \frac{\bar{r}^2}{\bar{g}\bar{N}_R}$, then $\left(\sqrt{\frac{\bar{N}_R}{\gamma\bar{g}}}, \frac{\sqrt{\gamma\bar{g}\bar{N}_R}}{\bar{r}}\right)$ is globally asymptotically stable.*

Theorem 1 fully determines the dynamics of system (1) in the homogeneous case. Namely, if the yield rate is greater than or equal to some critical value, part (a) implies that the resource density will grow to infinity in Ω as $t \to \infty$, which we refer as the case of *unlimited resources*; in contrast, part (b) illustrates that if the yield rate is smaller than the critical value, the resource density will remain bounded in Ω as $t \to \infty$, i.e. *the resources are limited uniformly in space*. In other words, for homogeneous environments the resources are either unlimited across the habitat or limited everywhere. We shall see that the situation will be more complicated for heterogeneous environments.

We now consider system (2) with general positive $r(x)$, $N_R(x)$ and $g(x)$, for which $(U, M) = (0, 1)$ is always a non-negative steady state. We focus on positive steady states $(\tilde{U}, \tilde{M})$ of (2) that satisfy $\tilde{U} > 0$ and $0 < \tilde{M} \leq 1$ in $\bar{\Omega}$. Note that $\left(\frac{1}{\gamma}\theta, 1\right)$ is always a positive steady state of (2), where $\theta = \theta(x)$ is the unique positive solution of the scalar problem

$$\begin{cases} d\Delta\theta + \theta\,[r(x) - g(x)\theta] = 0 & \text{for } x \in \Omega, \\ \partial_n \theta = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{4}$$

(It is a standard fact that the above equation has a unique positive solution; see e.g. Propositions 3.2 and 3.3 of Cantrell and Cosner 2003.) A natural question is whether system (2) has any positive steady state other than $\left(\frac{1}{\gamma}\theta, 1\right)$. This is addressed in the next result.

Theorem 2 *Suppose that $r(x)$, $N_R(x)$ and $g(x)$ are positive and Hölder continuous in $\bar{\Omega}$.*

(a) *If $\gamma \geq \sup_{x\in\Omega} \frac{r(x)\theta(x)}{N_R(x)}$, then $\left(\frac{1}{\gamma}\theta, 1\right)$ is globally asymptotically stable. In particular, $\left(\frac{1}{\gamma}\theta, 1\right)$ is the only positive steady state of (2);*

(b) *If $\gamma < \sup_{x\in\Omega} \frac{r(x)\theta(x)}{N_R(x)}$, then (2) has at least one additional positive steady state, denoted by (u^*, m^*), satisfying $u^* > 0$, $0 < m^* \leq 1$ and $m^* \not\equiv 1$ in $\bar{\Omega}$. Moreover, u^* is the unique positive solution of*

$$d\Delta u^* + u^* \left[r \min\left\{ \frac{N_R}{ru^*}, 1 \right\} - \gamma g u^* \right] = 0 \text{ in } \Omega, \quad \partial_n u^*|_{\partial\Omega} = 0, \tag{5}$$

and m^* is given by $m^* = \min\left\{\frac{N_R}{ru^*}, 1\right\}$.

(c) *The positive steady state (u^*, m^*) is linearly stable whenever it exists.*

A natural question is whether (u^*, m^*), if it exists, is unique. It turns out that, due to the degeneracy of the second equation of (2) when $M = 1$, the system can admit infinitely many steady states in general. In view of the linear stability result of part (c), we conjecture that the steady state (u^*, m^*) given by part (b) is globally asymptotically stable among all solutions of (2) with initial data (U_0, M_0) satisfying (3). See Remark 1 for additional discussion.

By a priori estimates $\inf_\Omega \frac{r}{g} \leq \theta \leq \sup_\Omega \frac{r}{g}$, which follows readily from the maximum principle, we have the following more explicit result:

Corollary 1 *Suppose that $r(x)$, $N_R(x)$ and $g(x)$ are positive and Hölder continuous in $\bar{\Omega}$.*

(a) *If $\gamma \geq \sup_\Omega \frac{r}{N_R} \cdot \sup_\Omega \frac{r}{g}$, then $\left(\frac{1}{\gamma}\theta, 1\right)$ is globally asymptotically stable.*

(b) *If $\gamma < \sup_\Omega \frac{r}{N_R} \cdot \inf_\Omega \frac{r}{g}$, then (2) has at least one additional positive steady state, denoted by (u^*, m^*), satisfying $u^* > 0$, $0 < m^* \leq 1$ and $m^* \not\equiv 1$ in $\bar{\Omega}$. Furthermore, u^* can be determined by (5).*

Next we proceed to discuss qualitative properties of positive steady state (u^*, m^*) and illustrate some differences between heterogeneous and homogeneous cases. We write the unique positive solution of (5) as $u^*(x, \gamma)$ to stress its dependence on γ. Since $u^*(x, \gamma)$ is strictly decreasing in γ, i.e. $u^*(x, \gamma_1) < u^*(x, \gamma_2)$ in $\bar{\Omega}$ if $\gamma_1 > \gamma_2$, the following concise result is a consequence of Theorem 2.

Corollary 2 *For any $d > 0$, there exist two positive constants $\gamma_*(d)$ and $\gamma^*(d)$ satisfying*

$$\left(\inf_{\Omega} \frac{r^2}{N_R^2}\right)\left(\inf_{\Omega} \frac{N_R}{g}\right) \le \gamma_*(d) \le \gamma^*(d) \le \left(\sup_{\Omega} \frac{r}{N_R}\right)\left(\sup_{\Omega} \frac{r}{g}\right) \tag{6}$$

and that:

(a) *If $0 < \gamma < \gamma_*(d)$, then $m^* < 1$ in $\bar{\Omega}$;*
(b) *If $\gamma_*(d) \le \gamma < \gamma^*(d)$, both sets $\{x \in \Omega : m^*(x) = 1\}$ and $\{x \in \Omega : m^*(x) < 1\}$ are non-empty;*
(c) *If $\gamma \ge \gamma^*(d)$, then $m^* \equiv 1$ in $\bar{\Omega}$.*

The proof of Corollary 2 is given at the end of Sect. 3. Cases (a) and (c) correspond to the cases of limited and unlimited resources, respectively, which is similar to the homogeneous case. However, for the homogeneous case $\gamma_* = \gamma^* = \bar{r}^2/(\bar{g}\bar{N}_R)$ holds, thus case (b) is null for the homogeneous case. For the heterogeneous case, i.e. $r(x)$, $N_R(x)$ and $g(x)$ are non-constant functions, it holds generally that $\gamma_* < \gamma^*$, and case (b) implies that the resources are unlimited in some locations but limited elsewhere. Such scenario can be regarded as resources partially limited in space, which is a unique feature for heterogeneous environments. This will be further elaborated in Sect. 6.

Three hypotheses were proposed and tested by Zhang et al. (2017) both mathematically and experimentally, of which two can be stated as follows:

Hypothesis A When a consumer exists in a region with a heterogeneously distributed input of exploitable renewed limiting resources, the total population abundance at equilibrium can reach a greater abundance when it diffuses than when it does not.

Hypothesis B A consumer diffusing in a region with a heterogeneously distributed input of exploitable renewed limiting resources can have greater total population abundance at equilibrium than a population diffusing in a space with the same total amount of resources distributed homogeneously.

For logistics models of single populations, it was previously shown by Lou (2006) that both hypotheses hold when the intrinsic growth rate and the carrying capacity are proportional to each other. The situation becomes more complicated otherwise, as is shown by DeAngelis et al. (2016b). One of the main findings by Zhang et al. (2017), *experimentally as well as mathematically* for the consumer–resource model and its discrete counterpart, is that Hypothesis B is false when the diffusion rate is small.

In Sect. 6 we study some qualitative properties of steady state u^* of (5) under the additional assumption that $g \equiv 1$. Our main findings are: (i) both Hypotheses A and

B hold when the resources are unlimited everywhere in space (large γ); (ii) when the resources are limited everywhere in space, Hypothesis A holds but Hypothesis B fails (small γ); (iii) when the resources are partially limited in space, both Hypotheses A and B may fail (intermediate γ).

3 Persistence and existence of positive steady states

In this section we study positive steady states of (2) and the persistence of time-dependent solutions of (2). Part (a) of Theorem 1 and parts (a) and (b) of Theorem 2 follow directly from the following result:

Theorem 3 *Suppose that $r(x)$, $N_R(x)$ and $g(x)$ are positive and Hölder continuous in $\bar{\Omega}$.*

(a) *Suppose $\gamma \geq \sup_{x\in\Omega} \frac{r(x)\theta(x)}{N_R(x)}$, then $\left(\frac{1}{\gamma}\theta, 1\right)$ is globally asymptotically stable;*

(b) *Suppose $\gamma < \sup_{x\in\Omega} \frac{r(x)\theta(x)}{N_R(x)}$, then*

  (i) *the steady state $\left(\frac{1}{\gamma}\theta, 1\right)$ is weakly repelling, i.e. there is no solution (U, M) of (2) with initial data satisfying (3) such that $(U, M) \to \left(\frac{1}{\gamma}\theta, 1\right)$ as $t \to +\infty$;*

  (ii) *system (2) has at least one additional positive steady state, denoted by (u^*, m^*), satisfying $u^* > 0$, $0 < m^* \leq 1$ and $m^* \not\equiv 1$ in $\bar{\Omega}$. Furthermore, u^* is the unique positive solution of*

$$d\Delta u^* + u^*\left[r\min\left\{\frac{N_R}{ru^*}, 1\right\} - \gamma g u^*\right] = 0 \text{ in } \Omega, \quad \partial_n u^*|_{\partial\Omega} = 0;$$

and m^* is given by $m^* = \min\left\{\frac{N_R}{ru^*}, 1\right\}$.

Remark 1 (i) Here we adopt the notion of weak repeller with respect to the set of initial data satisfying (3) from Definition 8.15 of Smith and Thieme (2011).

(ii) The linear stability of the steady state (u^*, m^*) given in Theorem 3(b)(ii) will be established in Sect. 4. We conjecture that the steady state (u^*, m^*) is actually globally asymptotically stable with respect to all initial conditions satisfying (3).

(iii) If we relax the initial condition (u_0, m_0) of (2) so that for some open subset Ω_0 of $\bar{\Omega}$,

$$\begin{cases} u_0(x) \geq 0, \ m_0(x) \geq 0, \ u_0(x) \not\equiv 0, \\ m_0(x) < 1 \text{ for } x \in \Omega_0 \text{ and } m_0(x) = 1 \text{ for } x \in \Omega\backslash\Omega_0, \end{cases}$$

then we conjecture that the corresponding solution $(U(\cdot, t), M(\cdot, t)) \to (u^*_{\Omega_0}, m^*_{\Omega_0})$ as $t \to \infty$, where the latter are determined by

$$\begin{cases} d\Delta u^*_{\Omega_0} + u^*_{\Omega_0}\left[rm^*_{\Omega_0} - \gamma g u^*_{\Omega_0}\right] = 0 & \text{in } \Omega, \ \partial_n u^*_{\Omega_0}|_{\partial\Omega} = 0; \\ m^*_{\Omega_0}(x) = \begin{cases} \min\left\{\frac{N_R(x)}{ru^*_{\Omega_0}(x)}, 1\right\} & x \in \Omega_0, \\ 1 & x \in \bar{\Omega}\backslash\Omega_0, \end{cases} \end{cases}$$

whenever $(\theta/\gamma, 1)$ is unstable. Note that $m^*_{\Omega_0}(x)$ may potentially be discontinuous.

(iv) Concerning the domain of attraction of the steady state (u^*, m^*) given in Theorem 1(b), we conjecture that $\lim_{t\to\infty}(U(\cdot,t), M(\cdot,t)) = (u^*, m^*)$, provided that $\{x \in \Omega : m_0(x) = 1\} \subset \{x \in \Omega : m^*(x) = 1\}$.

(v) The above discussion also explains the connection with the case when $m_0 \equiv 1$, in which case it must hold that $U(x,t) \to \frac{1}{\gamma}\theta(x)$ as $t \to \infty$.

Before we prove Theorem 3, we first state and prove two lemmas:

Lemma 1 *Let $V(x,t)$ be twice continuously differentiable in x and continuously differentiable in t and satisfy*

$$\begin{cases} V_t - a_{ij}V_{x_ix_j} - b_jV_{x_j} \geq f(x,t,V) & \text{for } x \in \Omega,\ t \geq t_0, \\ \partial_n V \geq 0 & \text{for } x \in \partial\Omega,\ t \geq t_0, \\ \inf_{x\in\Omega} V(x,t_0) > -\infty, \end{cases}$$

where the coefficients $a_{ij}(x,t)$ and $b_j(x,t)$ are assumed to be Hölder continuous, with (a_{ij}) being uniformly positive-definite on $\bar{\Omega} \times [t_0, \infty)$, and the Einstein convention is used so that repeated indices are summed. Assume also that $f(x,t,s)$ is Hölder continuous in x and t and Lipschitz continuous in s, and there exist $\eta, \delta > 0$ such that

$$f(x,t,s) \geq \frac{\eta}{1+t} \quad \text{for } x \in \Omega,\ t \geq t_0,\ \text{and } s \leq \frac{\delta}{1+t}. \tag{7}$$

Then there exists $T > t_0$ such that

$$V(x,t) > \frac{\delta}{1+t} \quad \text{for } x \in \Omega,\ t \geq T.$$

Proof We claim that it is enough to show that

$$\inf_{x\in\Omega} V(x,T) \geq \frac{\delta}{1+T} \quad \text{for some } T \geq t_0. \tag{8}$$

Suppose that (8) holds. Using $\frac{\delta}{1+t}$ as a comparison function, by standard arguments involving the strong maximum principle, we have

$$V(x,t) > \frac{\delta}{1+t} \quad \text{for } x \in \bar{\Omega},\ t > T.$$

In particular, the lemma is proved in case $\inf_{x\in\Omega} V(x,t_0) \geq \frac{\delta}{1+t_0}$.

Suppose now that $\inf_{x\in\Omega} V(x,t_0) < \frac{\delta}{1+t_0}$, then there exists $T > t_0$ such that

$$\inf_{x\in\Omega} V(x,t_0) + \eta \log\left(\frac{1+T}{1+t_0}\right) = \frac{\delta}{1+T}.$$

Define the auxiliary function

$$\underline{V}(t) = \inf_{x\in\Omega} V(x, t_0) + \eta \log\left(\frac{1+t}{1+t_0}\right) \quad \text{for } t_0 \le t < T.$$

Claim $\underline{V}$ has the following properties in $t_0 \le t \le T$:

(i) $\underline{V}_t - a_{ij}\underline{V}_{x_i x_j} - b_j \underline{V}_{x_j} \le f(x, t, \underline{V})$ for $x \in \Omega$ and $t \in [t_0, T]$;
(ii) $\partial_n \underline{V} = 0$ for $x \in \partial\Omega$ and $t_0 \le t \le T$;
(iii) $\underline{V}(t_0) \le V(x, t_0)$ for $x \in \Omega$.

It suffices to verify the differential inequality (i) as assertions (ii) and (iii) clearly hold. For (i), observe that $\underline{V}(t) \le \frac{\delta}{1+t}$ for all $t \in [t_0, T]$. Hence, by (7)

$$\underline{V}_t - a_{ij}\underline{V}_{x_i x_j} - b_j \underline{V}_{x_j} = \frac{\eta}{1+t} \le f(x, t, \underline{V}(t)) \quad \text{for } x \in \Omega,\ 0 \le t < T.$$

This proves the claim.

By the above claim, we may apply the parabolic maximum principle to conclude that $V(x, t) \ge \underline{V}(t)$ for all $x \in \Omega$ and $t_0 \le t \le T$. In particular, (8) holds. □

Corollary 3 *Let $f(t, s)$ be a Lipschitz continuous function from $[t_0, +\infty) \times \mathbb{R}$ to $\mathbb{R}$, and $\delta, \eta > 0$ are given such that*

$$f(t, s) \ge \frac{\eta}{1+t} \quad \textit{for } t \ge t_0 \textit{ and } s \le \frac{\delta}{1+t}.$$

If $\tilde{V}(t) \in C^1([t_0, +\infty))$ satisfies the differential inequality

$$\tilde{V}' \ge f(t, \tilde{V}) \quad \textit{for } t \ge t_0,$$

then there exists $T > t_0$ such that

$$\tilde{V}(t) > \frac{\delta}{1+t} \quad \textit{for } t \ge T.$$

Lemma 2 *Let (U, M) be a solution of (2) with initial data (U_0, M_0) satisfying (3). Then*

(a) *For each time-dependent solution of (2), there exists $C_1 > 0$ such that*

$$M(x, t) \le 1 - \frac{C_1}{1+t} \quad \textit{for } x \in \bar{\Omega} \textit{ and } t \ge 0.$$

(b) *There exist $T_1 > 0$ and $0 < \delta_1 < 1$, depending on initial data, such that*

$$U(x, t) \le \frac{1}{\gamma}\theta(x)\left(1 - \frac{\delta_1}{1+t}\right) \quad \textit{for } t \ge T_1.$$

Proof First, we prove (a). Fix a non-negative, non-trivial initial data (U_0, M_0) such that $M_0 < 1$ for $x \in \bar{\Omega}$ and consider the corresponding time-dependent solution of (2). Let $C_1 = \min\left\{\inf_\Omega(1 - M_0), \frac{k}{\sup_\Omega N_R}\right\}$.

It suffices to observe, by the equation of M, that

$$k\left(\frac{1}{1-M}\right)_t \le (\sup N_R)$$

so that

$$\frac{1}{1-M(x,t)} \le \frac{1}{1-M_0(x)} + \frac{(\sup N_R)}{k}t \le \frac{1+t}{C_1}.$$

This proves (a).

For (b), setting $w(x,t) := \gamma\frac{U(x,t)}{\theta(x)}$, we have

$$\begin{cases} w_t - d\Delta w - 2d\frac{\nabla\theta}{\theta}\cdot\nabla w \le g\theta w\left[-\inf_{x\in\Omega}\left(\frac{r}{g\theta}\right)\frac{C_1}{1+t} + 1 - w\right] & x \in \Omega,\ t > 0, \\ \partial_n w = 0 & x \in \partial\Omega,\ t > 0, \\ w(x,0) = \gamma U_0(x)/\theta(x) & x \in \Omega. \end{cases} \tag{9}$$

Now, observe that $V_1(x,t) := 1 - w(x,t)$ satisfies

$$(V_1)_t - d\Delta V_1 - 2d\frac{\nabla\theta}{\theta}\cdot\nabla V_1 \ge f_1(x,t,V_1) \quad \text{for } x \in \Omega, t \ge 0, \tag{10}$$

where

$$f_1(x,t,s) = g(x)\theta(x)(1-s)\left[\inf_{x\in\Omega}\left(\frac{r}{g\theta}\right)\frac{C_1}{1+t} - s\right].$$

Moreover, letting

$$\delta_1 = \frac{1}{2}\min\left\{1, C_1\inf_{x\in\Omega}\left(\frac{r}{g\theta}\right)\right\} \quad \text{and} \quad \eta_1 = \frac{C_1}{4}\left(\inf_{x\in\Omega} g\theta\right)\left(\inf_{x\in\Omega}\frac{r}{g\theta}\right),$$

it holds that

$$f_1\,(x,t,s) \ge g(x)\theta(x)\,(1-s)\left[\inf_{x\in\Omega}\left(\frac{r}{g\theta}\right)\frac{C_1}{1+t} - s\right] \ge \frac{\eta_1}{1+t} \tag{11}$$

for $t \ge 0$ and $s \le \frac{\delta_1}{1+t}$.

By Lemma 1, there exists $T_1 \ge 0$ such that

$$V_1(x,t) > \frac{\delta_1}{1+t} \quad \text{for } x \in \Omega,\ t \ge T_1.$$

This proves (b). □

Next, we prove Theorem 3.

Proof We first prove (a). Suppose $\gamma \geq \sup_{x\in\Omega} \frac{r(x)\theta(x)}{N_R(x)}$, i.e. $N_R(x) \geq \frac{1}{\gamma} r(x)\theta(x)$ in $\bar{\Omega}$. Recall that $M \leq 1$, then

$$kM_t = (1-M)^2(N_R - rMU) \geq (1-M)^2 r\left(\frac{1}{\gamma}\theta - U\right), \quad \text{for } x \in \bar{\Omega},\ t \geq 0.$$

By Lemma 2, we deduce that $M(x,t) < 1$ for $t \geq 0$, and $M_t(x,t) > 0$ for $x \in \Omega$ and $t \geq T_1$. This implies that $m_\infty(x) := \lim_{t\to\infty} M(x,t)$ exists and satisfies $m_\infty(x) \leq 1$ for all $x \in \Omega$.

It remains to show that $m_\infty(x) \equiv 1$. Suppose to the contrary that $m_\infty(x) < 1$ somewhere. Next, let μ_1 be the principal eigenvalue of

$$d\Delta\varphi + rm_\infty\varphi + \mu\varphi = 0 \quad \text{in } \Omega, \quad \text{and} \quad \partial_n\varphi = 0 \quad \text{on } \partial\Omega.$$

Define $\hat{w} \equiv 0$ when $\mu_1 \geq 0$; and when $\mu_1 < 0$, define $\hat{w}$ to be the unique positive solution of

$$\begin{cases} d\Delta\hat{w} + \hat{w}(rm_\infty - g\hat{w}) = 0 & \text{in } \Omega, \\ \partial_n\hat{w} = 0 & \text{on } \partial\Omega. \end{cases} \tag{12}$$

Then, when $\mu_1 < 0$, $\frac{1}{\gamma}\hat{w}$ is the unique positive solution of

$$d\Delta\left(\frac{1}{\gamma}\hat{w}\right) + \left(\frac{1}{\gamma}\hat{w}\right)\left[rm_\infty - \gamma g\left(\frac{1}{\gamma}\hat{w}\right)\right] = 0 \quad \text{in } \Omega.$$

In either case, $\lim_{t\to\infty} U(x,t) = \frac{1}{\gamma}\hat{w}(x)$ uniformly for $x \in \bar{\Omega}$. Since $m_\infty \leq 1, \not\equiv 1$, we may deduce by comparison that $\hat{w} < \theta$ in $\bar{\Omega}$. Now, choose δ', T' so that

$$U(x,t) \leq \frac{1}{\gamma}\hat{w}(x) + \delta' < \frac{1}{\gamma}\theta(x) - \delta' \quad \text{for all } x \in \overline{\Omega},\ t \geq T'.$$

Then

$$k\partial_t\left(\frac{1}{1-M}\right) = \frac{kM_t}{(1-M)^2} = N_R - rMU \geq r\left(\frac{1}{\gamma}\theta - U(x,t)\right) \geq r\delta'$$

for all $x \in \bar{\Omega}$ and $t \geq T'$. This implies that $m_\infty(x) = \lim_{t\to\infty} M(x,t) = 1$, which is a contradiction. This proves (a).

Next, we prove (b)(i). Suppose to the contrary that there is some time-dependent solution $(U(x,t), M(x,t))$ of (2), with non-negative, non-trivial initial data (U_0, M_0) such that $M_0 < 1$ for $x \in \bar{\Omega}$, which is attracted to $\left(\frac{1}{\gamma}\theta, 1\right)$ as $t \to \infty$. By the hypothesis, there exists $x_0 \in \Omega$ such that $N_R(x_0) < \frac{1}{\gamma} r(x_0)\theta(x_0)$. Fix $x = x_0$, then for all sufficiently large t,

$$\begin{aligned} kM_t(x_0,t) &= (1-M(x_0,t))^2\,[N_R(x_0)-r(x_0)M(x_0,t)U(x_0,t)] \\ &= (1-M(x_0,t))^2\left[N_R(x_0)-r(x_0)M(x_0,t)\left(\tfrac{1}{\gamma}\theta(x_0)+o(1)\right)\right] \\ &< 0, \end{aligned}$$

rendering it impossible that $M(x_0,t)\to 1$ as $t\to\infty$. This proves (b)(i).

To show assertion (b)(ii), let $(\tilde{\mu}_1,\tilde{\varphi}_1)$ be the principal eigenpair of

$$d\Delta\tilde{\varphi}+r\tilde{\varphi}+\tilde{\mu}\tilde{\varphi}=0 \quad \text{in } \Omega, \quad \text{and} \quad \partial_n\tilde{\varphi}=0 \quad \text{on } \partial\Omega.$$

Then

$$\tilde{\mu}_1=-\int_\Omega \frac{\Delta\tilde{\varphi}_1+r\tilde{\varphi}_1}{\tilde{\varphi}_1}\,dx=-\int_\Omega\left(\frac{|\nabla\tilde{\varphi}_1|^2}{\tilde{\varphi}_1^2}+r\right)dx<0.$$

Now, for $0<\epsilon\ll 1$, $\epsilon\tilde{\varphi}_1$ and $\frac{1}{\gamma}\theta$ gives a pair of strict lower and upper solutions of

$$\begin{cases} d\Delta\tilde{u}+\tilde{u}\left[r\min\left\{\frac{N_R(x)}{r\tilde{u}(x)},1\right\}-\gamma g\tilde{u}\right]=0 & \text{for } x\in\Omega, \\ \partial_n\tilde{u}=0 & \text{for } x\in\partial\Omega. \end{cases} \tag{13}$$

Here we have used the condition $\gamma<\sup_{x\in\Omega}\frac{r(x)\theta(x)}{N_R(x)}$ to ensure that $\frac{1}{\gamma}\theta$ is a strict upper solution. This proves the existence of at least one positive solution u^* to (13) such that $u^*(x)<\frac{1}{\gamma}\theta(x)$ in $\bar{\Omega}$. The uniqueness of u^* follows from the fact that $f(x,u):=r(x)\min\{\frac{N_R(x)}{r(x)u},1\}-\gamma gu$ is decreasing in u and Hölder continuous in x; see, e.g. Proposition 3.3 of Cantrell and Cosner (2003). (Alternatively, one may also argue by the subhomogeneity of the semiflow, see Theorem 2.3.4 of Zhao 2017.)

Setting $m^*(x)=\min\left\{\frac{N_R(x)}{ru^*(x)},1\right\}$, we obtain the existence of a positive steady state (u^*,m^*). Finally, since $u^*(x)\not\equiv\frac{1}{\gamma}\theta$, we must have $m^*(x)\not\equiv 1$. This proves Theorem 3. □

Finally we establish Corollary 2.

Proof of Corollary 2. For any $d>0$, define

$$\gamma^*(d)=\sup_\Omega\frac{r(x)\theta(x)}{N_R(x)} \quad \text{and} \quad \gamma_*(d)=\sup\left\{\gamma>0:\ \sup_\Omega\frac{N_R}{r\tilde{u}}<1\right\}, \tag{14}$$

where θ is the unique positive solution of (4) and $\tilde{u}$ is the unique positive solution of

$$d\Delta\tilde{u}+(N_R-\gamma g\tilde{u}^2)=0 \ \text{ in } \Omega. \quad \partial_n\tilde{u}\big|_{\partial\Omega}=0. \tag{15}$$

Let (u^*,m^*) be the steady state of (2) as given by Theorem 2. Then $m^*=\min\left\{1,\frac{N_R}{ru^*}\right\}$ and u^* is the unique solution to (5). If $m^*\equiv 1$ in Ω, then $u^*=\theta/\gamma$ and $\frac{N_R}{ru^*}\geq 1$ in $\bar{\Omega}$. This implies $m^*\equiv 1$ in Ω iff $\gamma\geq\gamma^*(d)$.

Next, suppose that $m^* < 1$ somewhere in Ω. Then $m^* < 1$ in $\bar{\Omega}$ iff

$$u^* = \tilde{u}, \quad \text{and} \quad \sup_{\Omega} \frac{N_R}{r\tilde{u}} < 1.$$

Hence, fixing all parameters except γ, then

$$m^* < 1 \ \text{ in } \bar{\Omega} \quad \text{iff } \gamma \text{ is such that } \sup_{\Omega} \frac{N_R}{r\tilde{u}} < 1.$$

The definition of $\gamma_*(d)$ follows from the fact that $\tilde{u}$ is strictly decreasing in γ.

Finally, the inequalities in (6) are direct consequences of the definitions of $\gamma_*(d)$, $\gamma^*(d)$, and that $\sup_{\Omega} \theta \le \sup_{\Omega} \frac{r}{g}$, $\inf_{\Omega} \tilde{u}^2 \ge \inf_{\Omega} \frac{N_R}{\gamma g}$. This establishes Corollary 2.

4 Linear stability of positive steady states

In this section we consider the linear stability of positive steady state (u^*, m^*), which is given in Theorem 2. The main result is stated as follows:

Theorem 4 *If the steady state (u^*, m^*) exists, then it is linearly stable; i.e. if $\lambda \in \mathbb{C}$ is an eigenvalue of the linear problem*

$$\begin{cases} -k\lambda\Psi = (-ru^*\Psi - rm^*\Phi)(1-m^*)^2 & \textit{for } x \in \Omega, \\ -\lambda\Phi = d\Delta\Phi + \Phi(rm^* - 2\gamma g u^*) + ru^*\Psi & \textit{for } x \in \Omega, \\ \partial_n \Phi = 0 & \textit{for } x \in \partial\Omega, \end{cases} \tag{16}$$

then necessarily $\operatorname{Re}\lambda > 0$ *holds.*

We caution the readers that in the first equation of (16), the term $-2(1-m^*)(N_R - rm^*u^*)\Psi$ actually vanishes, as a consequence of the definition of m^* after (5).

Remark 2 Let (u^*, m^*) be a steady state given by Theorem 3(b)(ii). Define $\Omega_0 := \{x \in \Omega : m^*(x) < 1\}$. Then the above linearization concerns perturbations from the steady state (u^*, m^*) within the function space

$$\mathbf{X}_1 = \left\{(\tilde{u}, \tilde{m}) \in C(\bar{\Omega}; \mathbb{R}^+ \times [0,1]) : \tilde{m}(x) < 1 \ \text{ in } \Omega_0, \ \tilde{m}(x) = 1 \ \text{ in } \Omega \backslash \Omega_0 \right\}.$$

Proof We eliminate Ψ by the substitution

$$\Psi = \mathcal{X}_{\{x:m^*(x)<1\}} \frac{rm^*}{\frac{k\lambda}{(1-m^*)^2} - ru^*} \Phi = \mathcal{X}_{\{x:m^*(x)<1\}} \frac{(1-m^*)^2}{k} \left[\frac{rm^*}{\lambda - \frac{ru^*(1-m^*)^2}{k}} \right] \Phi$$

to obtain the nonlinear eigenvalue problem

$$\begin{cases} d\Delta\Phi + \Phi \left[rm^* - 2\gamma g u^* + \lambda + \mathcal{X}_{\{x:m^*(x)<1\}} \frac{(1-m^*)^2}{k} \frac{r^2 u^* m^*}{\lambda - \frac{ru^*(1-m^*)^2}{k}} \right] = 0 & \text{for } x \in \Omega, \\ \partial_n \Phi = 0 & \text{for } x \in \partial\Omega. \end{cases} \tag{17}$$

Claim The following holds:

$$\inf_{\varphi \in H^1(\Omega)} \int_\Omega [d|\nabla\varphi|^2 - (rm^* - \gamma g u^*)\varphi^2]\, dx = 0. \tag{18}$$

This assertion follows by observing that 0 is an eigenvalue (with positive eigenfunction $\varphi_1 = u^*$) of the problem

$$\begin{cases} d\Delta\varphi + (rm^* - \gamma g u^*)\varphi + \mu\varphi = 0 & \text{for } x \in \Omega, \\ \partial_n \varphi = 0 & \text{for } x \in \partial\Omega. \end{cases}$$

We further claim that for each constant $k > 0$, the nonlinear eigenvalue problem (17) does not admit any eigenvalue with non-positive real part. Suppose to the contrary that $\lambda = \alpha + i\beta$ is an eigenvalue, with $\alpha \le 0$, $\beta \in \mathbb{R}$, and eigenfunction $\Phi = \phi + i\psi$, where ϕ, ψ are real-valued functions. Then

$$\begin{cases} -d\Delta\phi + A\phi = B\psi & \text{for } x \in \Omega, \\ -d\Delta\psi + A\psi = -B\phi & \text{for } x \in \Omega, \\ \partial_n\phi = \partial_n\psi = 0 & \text{for } x \in \partial\Omega, \end{cases} \tag{19}$$

where A and B are given by

$$\begin{aligned} A &= -rm^* - \alpha + 2\gamma g u^* \\ &\quad + \mathcal{X}_{\{x: m^*(x)<1\}} \frac{(1-m^*)^2 u^* r^2 m^*}{k} \cdot \frac{-\alpha + ru^*(1-m^*)^2/k}{\beta^2 + (-\alpha + ru^*(1-m^*)^2/k)^2} \end{aligned}$$

and, respectively,

$$B = \beta\left(-1 + \mathcal{X}_{\{x: m^*(x)<1\}} \frac{(1-m^*)^2 u^* r^2 m^*}{k} \cdot \frac{1}{\beta^2 + (-\alpha + ru^*(1-m^*)^2/k)^2}\right).$$

Claim There exists $\sigma_0 > 0$ independent of k, such that

$$\sigma_0 \int \varphi^2\, dx \le \int \left[d|\nabla\varphi|^2 + A\varphi^2\right] dx \quad \text{for all } \varphi \in H^1(\Omega). \tag{20}$$

To establish our assertion, we make use of (18) to get

$$\begin{aligned} &\inf_{\varphi \in H^1(\Omega)} \frac{\int [d|\nabla\varphi|^2 + A\varphi^2]\, dx}{\int \varphi^2\, dx} \\ &\ge \inf_{\varphi \in H^1(\Omega)} \frac{\int [d|\nabla\varphi|^2 + (-rm^* + \gamma g u^*)\varphi^2]\, dx}{\int \varphi^2\, dx} + \frac{\int \gamma g u^* \varphi^2\, dx}{\int \varphi^2\, dx} \\ &\ge \gamma \inf_\Omega (g u^*) > 0. \end{aligned}$$

Multiplying the equation of ϕ by ϕ, the equation of ψ by ψ, integrating the results by parts and adding them together, we obtain (by using (20))

$$\sigma_0 \int (\phi^2 + \psi^2)\,dx \le \int \left[d|\nabla\phi|^2 + d|\nabla\psi|^2 + A(\phi^2+\psi^2) \right] dx$$
$$= \int [B\psi\phi - B\phi\psi]\,dx = 0.$$

Hence $\phi \equiv \psi \equiv 0$, and this shows that any λ with $\mathrm{Re}\,\lambda \le 0$ is not an eigenvalue. This concludes the proof of the theorem. □

5 Global asymptotic stability in the homogeneous case

Throughout this section $r(x)$, $N_R(x)$ and $g(x)$ are positive constant functions, denoted by $\bar{r}$, $\bar{N}_R$ and $\bar{g}$, respectively. We establish Theorem 1 for the case $\gamma < \bar{r}^2/(\bar{g}\bar{N}_R)$ as the other case $\gamma \ge \bar{r}^2/(\bar{g}\bar{N}_R)$ is covered by part of (a) of Theorem 3. For the ease of notation we drop the bars and write them as N_R, g and r for the rest of this section.

Proposition 1 *For each time-dependent solution of* (2)*, there exist* $\delta_0 > 0$ *and* $T_0 > 0$ *such that*

$$\frac{N_R}{r} + \frac{\delta_0}{1+t} \le U(x,t) \le \frac{r}{\gamma g} - \frac{\delta_0}{1+t} \quad \textit{and}$$
$$\frac{\gamma g N_R}{r^2} + \frac{\delta_0}{1+t} \le M(x,t) \le 1 - \frac{\delta_0}{1+t}$$

for $x \in \Omega$ *and* $t \ge T_0$.

Proof By Lemma 2, there exist $C_1, T_1 > 0$ and $0 < \delta_1 < \min\left\{1, \frac{r}{\gamma g}\right\}$ such that

$$M(x,t) \le 1 - \frac{C_1}{1+t} \quad \text{and} \quad U(x,t) \le \frac{r}{\gamma g} - \frac{\delta_1}{1+t} \quad \text{for } x \in \Omega,\ t \ge T_1,$$

where we have used the fact that $\frac{1}{\gamma}\theta = \frac{r}{\gamma g}$.

Claim There exist $\delta_2 > 0$ and $T_2 > 0$ such that $M(x,t) \ge \frac{\gamma g N_R}{r^2} + \frac{\delta_2}{1+t}$ for $x \in \Omega$ and $t \ge T_2$.

Fix $x \in \Omega$, and let $V_2(t) = M - \frac{\gamma g N_R}{r^2}$, then for $t \ge T_1$,

$$k(V_2)' = \left(1 - \frac{\gamma g N_R}{r^2} - V_2\right)^2 \left[N_R - r\left(V_2 + \frac{\gamma g N_R}{r^2}\right) U(x,t) \right]$$
$$\ge \left(1 - \frac{\gamma g N_R}{r^2} - V_2\right)^2 \left[N_R - r\left(V_2 + \frac{\gamma g N_R}{r^2}\right)\left(\frac{r}{\gamma g} - \frac{\delta_1}{1+t}\right) \right]$$
$$= \left(1 - \frac{\gamma g N_R}{r^2} - V_2\right)^2 \left[\left(-\frac{r^2}{\gamma g} + \frac{r\delta_1}{1+t}\right) V_2 + \frac{\gamma g N_R \delta_1}{r} \frac{1}{1+t} \right].$$

Hence, we define $f_2(t,s) = \left(1 - \frac{\gamma g N_R}{r^2} - s\right)^2 \left[\left(-\frac{r^2}{\gamma g} + \frac{r\delta_1}{1+t}\right) s + \frac{\gamma g N_R \delta_1}{r} \frac{1}{1+t}\right]$, so that

$$k(V_2)' \geq f_2(t, V_2) \quad \text{for } t \geq T_1.$$

Setting $\delta_2 = \frac{1}{2} \min \left\{1 - \frac{\gamma g N_R}{r^2}, \frac{\gamma^2 g^2 N_R \delta_1}{r^3}\right\}$, we deduce that, for $t \geq T_1$ and $s \leq \frac{\delta_2}{1+t}$,

$$\begin{aligned} f_2(t,s) &\geq \left(1 - \frac{\gamma g N_R}{r^2} - s\right)^2 \left[\left(-\frac{r^2}{\gamma g} + \frac{r\delta_1}{1+t}\right) \frac{\delta_2}{1+t} + \frac{\gamma g N_R \delta_1}{r} \frac{1}{1+t}\right] \\ &\geq \left(1 - \frac{\gamma g N_R}{r^2} - s\right)^2 \left[-\frac{r^2}{\gamma g} \frac{\delta_2}{1+t} + \frac{\gamma g N_R \delta_1}{r} \frac{1}{1+t}\right] \\ &\geq \frac{1}{4} \left(1 - \frac{\gamma g N_R}{r^2}\right)^2 \frac{\gamma g N_R \delta_1}{2r} \frac{1}{1+t}. \end{aligned}$$

By Corollary 3, there exists $T_2 \geq T_1$ such that $V_2(t) \geq \frac{\delta_2}{1+t}$ for all $t \geq T_2$. This proves the claim.

Claim There exist $\delta_3 > 0$ and $T_3 > 0$ such that $U(x,t) \geq \frac{N_R}{r} + \frac{\delta_3}{1+t}$ for $x \in \Omega$ and $t \geq T_3$.

By the previous claim, we deduce that

$$\begin{cases} U_t - d\Delta U \geq U\left[\gamma g \left(\frac{N_R}{r} - U\right) + r\frac{\delta_2}{1+t}\right] & \text{for } x \in \Omega,\ t \geq T_2, \\ \partial_n U = 0 & \text{for } x \in \partial\Omega, t \geq T_2. \end{cases}$$

By comparison it is not hard to show that $\liminf_{t\to\infty} U(x,t) \geq \dfrac{N_R}{r}$. In particular, there exists $T_2' \geq T_2$ such that

$$\inf_{x\in\Omega} U(x,t) \geq \frac{N_R}{2r} \quad \text{for } t \geq T_2'. \tag{21}$$

Let $V_3(x,t) = U(x,t) - \frac{N_R}{r}$, then

$$(V_3)_t - d\Delta V_3 \geq f_3(x,t,V_3) \quad \text{for } x \in \Omega, \text{ and } t \geq T_2',$$

where, using (21),

$$f_3(x,t,s) := \begin{cases} \left(s + \frac{N_R}{r}\right)\left(\frac{r\delta_2}{1+t} - \gamma g s\right) & \text{when } \gamma g s \geq \frac{r\delta_2}{1+t}, \\ \frac{N_R}{2r}\left(\frac{r\delta_2}{1+t} - \gamma g s\right) & \text{when } \gamma g s \leq \frac{r\delta_2}{1+t}. \end{cases}$$

Setting $\delta_3 = \frac{r\delta_2}{2\gamma g}$, we have, for all $t \geq T_2'$ and $s \leq \frac{\delta_3}{1+t}$,

$$f_3(x,t,s) \geq \frac{N_R}{2r}\left(\frac{r\delta_2}{1+t} - \gamma g \frac{\delta_3}{1+t}\right) \geq \frac{N_R}{2r} \cdot \frac{r\delta_2}{2} \cdot \frac{1}{1+t}.$$

And Lemma 1 again implies the existence of $T_3 \geq T_2'$ such that $V_3(t) \geq \frac{\delta_3}{1+t}$ for all $t \geq T_3$. This proves the claim.

Finally, the proposition follows by letting $T_0 = \max\{T_1, T_2, T_3\}$ and $\delta_0 = \min\{C_1, \delta_1, \delta_2, \delta_3\}$. □

Theorem 5 *Suppose $\gamma < r^2/(gN_R)$, then the positive (constant) steady state (u^*, m^*) for (2) is globally asymptotically stable among initial values (U_0, M_0) satisfying (3).*

Proof Suppose the constant parameters satisfy $\gamma < r^2/(gN_R)$, then the steady state

$$(u^*, m^*) = \left(\sqrt{\frac{N_R}{\gamma g}}, \frac{\sqrt{\gamma g N_R}}{r}\right)$$

is determined by

$$rm^* = \gamma g u^* \quad \text{and} \quad N_R = rm^*u^*.$$

Clearly, $m^* < 1$.
Step 1. Suppose the initial condition satisfies (3), then there exists $T_0 > 0$ such that

$$\frac{N_R}{r} < U(x, T_0) < \frac{r}{\gamma g} \quad \text{and} \quad \frac{\gamma g N_R}{r^2} < M(x, T_0) < 1 \quad \text{for } x \in \overline{\Omega}. \tag{22}$$

This follows from Proposition 1. Thus we may assume without loss of generality that the initial data (U_0, M_0) satisfies (22).

Define, for $\xi \in \left(u^*, \frac{r}{\gamma g}\right)$,

$$\overline{U}(\xi) := \xi, \quad \underline{U}(\xi) := \frac{N_R}{\gamma g \xi}, \quad \overline{M}(\xi) := \frac{\gamma g}{r}\xi, \quad \text{and} \quad \underline{M}(\xi) := \frac{N_R}{r\xi}$$

where, by construction, for all $x \in \bar{\Omega}$ it holds that

$$\frac{N_R}{r} < \underline{U} < u^* < \overline{U} < \frac{r}{\gamma g}, \quad \frac{\gamma g N_R}{r^2} < \underline{M} < m^* < \overline{M} < 1, \quad \overline{M}\underline{U} = \underline{M}\overline{U} = \frac{N_R}{r}.$$

Next, define the family of (invariant) sets $\Gamma(\xi)$ as follows:

$$\Gamma(\xi) := \left\{(y_1, y_2) \in \mathbb{R}^2 : \underline{U}(\xi) \leq y_1 \leq \overline{U}(\xi) \text{ and } \underline{M}(\xi) \leq y_2 \leq \overline{M}(\xi)\right\}.$$

By Step 1, it is possible to choose $\xi \in \left(u^*, \frac{r}{\gamma g}\right)$ close enough to $\frac{r}{\gamma g}$ such that

$$(U(x,0), M(x,0)) \in \text{int}\,\Gamma(\xi) \quad \text{for all } x \in \bar{\Omega}. \tag{23}$$

Step 2. Let $\xi \in \left(u^*, \frac{r}{\gamma g}\right)$. We claim that if $(U(x,0), M(x,0)) \in \operatorname{int}\Gamma(\xi)$ for all $x \in \bar{\Omega}$ then $(U(x,t), M(x,t)) \in \operatorname{int}\Gamma(\xi)$ for all $x \in \bar{\Omega}$ and $t \geq 0$.

Suppose to the contrary that Step 2 is false, then for some $t_1 > 0$,

$$(U(x,t), M(x,t)) \in \operatorname{int}\Gamma(\xi) \quad \text{for all } x \in \bar{\Omega} \text{ and } t \in [0, t_1),$$

and one of the following alternatives holds (in the following we suppress the dependence of ξ in $\overline{U}, \underline{U}, \overline{M}, \underline{M}$):

(i) $U(x_1, t_1) = \overline{U}$ or $U(x_1, t_1) = \underline{U}$ for some $x_1 \in \bar{\Omega}$.
(ii) $\underline{U} < U(x, t_1) < \overline{U}$ for all $x \in \bar{\Omega}$, but $M(x_1, t_1) = \overline{M}$ or $M(x_1, t_1) = \underline{M}$ for some $x_1 \in \bar{\Omega}$.

For case (i), we observe that for $t \in [0, t_1]$, $\underline{M} \leq M(x,t) \leq \overline{M}$ for all $x \in \bar{\Omega}$ and hence

$$\begin{cases} \gamma g U(\underline{U} - U) \leq U_t - d\Delta U \leq \gamma g U(\overline{U} - U) & \text{for } x \in \Omega, t \in [0, t_1], \\ \partial_n U = 0 & \text{for } x \in \partial\Omega, t \in [0, t_1]. \end{cases} \tag{24}$$

Since $\underline{U} < U(x,0) < \overline{U}$ for $x \in \bar{\Omega}$, the strong maximum principle for parabolic equations yields that $\underline{U} < U(x,t) < \overline{U}$ for all $x \in \bar{\Omega}$ and $t \in [0, t_1]$; a contradiction, i.e. case (i) is impossible.

For case (ii), for $x = x_1$ and $t \in [0, t_1]$, we have

$$\begin{aligned} M_t &= \frac{(1-M)^2}{k}[r\underline{M}\overline{U} - rM\overline{U} + rM(\overline{U} - U)] \\ &= -\frac{r(1-M)^2}{k}\overline{U}(M - \underline{M}) + \frac{r(1-M)^2}{k}M(\overline{U} - U) \end{aligned}$$

and also

$$\begin{aligned} M_t &= \frac{(1-M)^2}{k}\left[r\overline{M}\underline{U} - rM\underline{U} - rM(U - \underline{U})\right] \\ &= \frac{r(1-M)^2}{k}\underline{U}(\overline{M} - M) - \frac{r(1-M)^2}{k}M(U - \underline{U}) \end{aligned}$$

i.e. (still fixing $x = x_1$)

$$(M - \underline{M})_t = -\frac{r(1-M)^2}{k}\overline{U}(M - \underline{M}) + \frac{r(1-M)^2}{k}M(\overline{U} - U) \tag{25}$$

and

$$(\overline{M} - M)_t = -\frac{(1-M)^2}{k}r\underline{U}(\overline{M} - M) + \frac{r(1-M)^2}{k}M(U - \underline{U}). \tag{26}$$

Since $\underline{U} < U(x,t) < \overline{U}$ for $x \in \bar{\Omega}$ and $t \in [0, t_1]$, we have

$$M(x_1, t_1) - \underline{M} > \exp\left(-\int_0^{t_1} \frac{r\overline{U}}{k}(1 - M(x_1, s))^2\, ds\right)(M(x_1, 0) - \underline{M}) \geq 0.$$

Similarly, we deduce that $\overline{M} - M(x_1, t_1) > 0$, a contradiction, i.e. case (ii) is also impossible. This finishes Step 2.

Step 3. Let $t_0 \geq 0$, and let $\xi \in \left(u^*, \frac{r}{\gamma g}\right)$ be fixed so that

$$(U(x, t_0), M(x, t_0)) \in \Gamma(\xi) \quad \text{for } x \in \bar{\Omega}, \tag{27}$$

then

$$(U(x,t), M(x,t)) \in \Gamma(\xi) \quad \text{for } x \in \bar{\Omega}, \ \text{ and } \ t > t_0. \tag{28}$$

To show Step 3, suppose (27) holds. Then $(U(x, t_0), M(x, t_0)) \in \operatorname{int} \Gamma(\hat{\xi})$ for all $x \in \bar{\Omega}$ and for all $\hat{\xi} \in \left(\xi, \frac{r}{\gamma g}\right)$. In view of Step 2, for all $\hat{\xi} \in \left(\xi, \frac{r}{\gamma g}\right)$, we have

$$(U(x,t), M(x,t)) \in \operatorname{int} \Gamma(\hat{\xi}) \quad \text{for all } x \in \bar{\Omega},\ t \geq t_0.$$

Since $\cap_{\hat{\xi} \in \left(\xi, \frac{r}{\gamma g}\right)} \operatorname{int} \Gamma(\hat{\xi}) = \Gamma(\xi)$, this implies (28).

Step 4. Define

$$\xi_* := \inf\left\{\xi \in \left(u^*, \frac{r}{\gamma g}\right) : \exists t_0 \text{ s.t. } (U(x,t), M(x,t)) \in \Gamma(\xi) \text{ for } x \in \bar{\Omega},\ t \geq t_0\right\}.$$

By Steps 1 and 3, $\xi_* \in \left[u^*, \frac{r}{\gamma g}\right)$ is well-defined. If $\xi_* = u^*$, then $(U(\cdot, t), M(\cdot, t)) \to (u^*, m^*)$ as $t \to \infty$, and we are done.

Suppose to the contrary that $\xi_* \in \left(u^*, \frac{r}{\gamma g}\right)$. By parabolic regularity theory and a standard diagonal process, passing to a sequence $t_j \to \infty$, we may assume that $U(x, t + t_j) \to \tilde{U}(x,t)$ weakly in $W^{2,1,p}_{loc}(\Omega \times [0, \infty))$ and strongly in $C^{1+\alpha,(1+\alpha)/2}(\bar{\Omega} \times [0, \infty))$. Moreover, denoting $\overline{U} = \overline{U}(\xi_*)$ and similarly for $\underline{U}$, $\overline{M}$, $\underline{M}$, we have for each $\epsilon > 0$, there exists $t_0 > 0$ such that

$$(U(x,t), M(x,t)) \subset \Gamma(\xi_* + \epsilon) \quad \text{for all } x \in \bar{\Omega},\ t \geq t_0,$$

so that if we let $t \to \infty$ and then $\epsilon \to 0$, we have

$$\limsup_{t \to +\infty} \sup_{x \in \Omega} M(x,t) \leq \overline{M}, \quad \text{and} \quad \liminf_{t \to +\infty} \inf_{x \in \Omega} M(x,t) \geq \underline{M} \tag{29}$$

and that

$$\limsup_{t\to+\infty}\sup_{x\in\Omega} U(x,t) \le \overline{U}, \quad \text{and} \quad \liminf_{t\to+\infty}\inf_{x\in\Omega} U(x,t) \ge \underline{U}. \tag{30}$$

Passing to the weak limit for the equation of U, we deduce differential inequalities for the nonnegative functions $(\overline{U} - \tilde{U})$ and $(\tilde{U} - \underline{U})$ that are similar to (24),

$$\begin{cases} (\overline{U} - \tilde{U})_t - d\Delta(\overline{U} - \tilde{U}) = -\tilde{U}_t + d\Delta\tilde{U} \ge -\gamma g\tilde{U}(\overline{U} - \tilde{U}), & (x,t) \in \Omega \times [0,\infty), \\ (\tilde{U} - \underline{U})_t - d\Delta(\tilde{U} - \underline{U}) = \tilde{U}_t - d\Delta\tilde{U} \ge -\gamma g\tilde{U}(\tilde{U} - \underline{U}), & (x,t) \in \Omega \times [0,\infty), \\ \partial_n(\overline{U} - \tilde{U}) = \partial_n(\tilde{U} - \underline{U}) = 0 & (x,t) \in \partial\Omega \times [0,\infty), \\ \overline{U} - \tilde{U} \ge 0 \quad \text{and} \quad \tilde{U} - \underline{U} \ge 0 & (x,t) \in \Omega \times [0,\infty). \end{cases} \tag{31}$$

By the weak Harnack inequality for strong solutions of parabolic equations (see Theorem 7.37 of Lieberman 1996) applied to $(\overline{U} - \tilde{U})$ and $(\tilde{U} - \underline{U})$, there can only be three cases:

(i) there exists $t_0 > 0$ such that $\underline{U} < \tilde{U}(x,t) < \overline{U}$ for $(x,t) \in \bar{\Omega} \times (t_0, \infty)$;
(ii) $\tilde{U}(x,t) \equiv \underline{U}$ for $(x,t) \in \bar{\Omega} \times [0,\infty)$;
(iii) $\tilde{U}(x,t) \equiv \overline{U}$ for $(x,t) \in \bar{\Omega} \times [0,\infty)$.

We will make use of the following technical lemma, whose proof will be postponed to the end of this section.

Lemma 3 *Suppose $t_j \to +\infty$ and $\tilde{U}(x,t) = \lim_{j\to\infty} U(x,t+t_j)$ weakly in $W^{2,1,p}_{loc}(\Omega \times [0,\infty))$.*

(a) *If $\tilde{U} < \overline{U}$ in $\bar{\Omega} \times [1,3]$, then there exist $\delta_1 > 0$ and $j_0 \in \mathbb{N}$ such that for all $j \ge j_0$,*

$$M(x, t_j + t) > \underline{M} + \delta_1 \quad \textit{and} \quad U(x, t_j + t) < \overline{U} - \delta_1 \quad \textit{in } \bar{\Omega} \times [2,3];$$

(b) *If $\tilde{U} > \underline{U}$ in $\bar{\Omega} \times [1,3]$, then there exist $\delta_1 > 0$ and $j_0 \in \mathbb{N}$ such that for all $j \ge j_0$,*

$$M(x, t_j + t) < \overline{M} - \delta_1 \quad \textit{and} \quad U(x, t_j + t) > \underline{U} + \delta_1 \quad \textit{in } \bar{\Omega} \times [2,3].$$

In both assertions δ_1 is independent of $j \ge j_0$.

Assume the lemma holds. Then for case (i),

$$\underline{U} < \tilde{U}(x,t) < \overline{U} \quad \text{for } x \in \bar{\Omega} \text{ and } t_0 + 1 \le t \le t_0 + 3.$$

By parts (a) and (b) of Lemma 3, we deduce that for $j \ge j_0$,

$$\underline{M}(\xi_*) + \delta_1 < M(x, t_j + t_0 + t) < \overline{M}(\xi_*) - \delta_1,$$
$$\underline{U}(\xi_*) + \delta_1 < U(x, t_j + t_0 + t) < \overline{U}(\xi_*) - \delta_1,$$

for $x \in \bar{\Omega}$ and $t \in [2, 3]$. Hence, there exists ξ_{**} such that $u^* < \xi_{**} < \xi_*$ and

$$(U(x, t_j + t_0 + 2), M(x, t_j + t_0 + 2)) \in \Gamma(\xi_{**}) \quad \text{for} \quad x \in \bar{\Omega}.$$

By the invariance of $\Gamma(\xi_{**})$ (proved in Step 3), we deduce

$$(U(x, t), M(x, t)) \in \Gamma(\xi_{**}) \quad \text{for } x \in \bar{\Omega},\ t \geq t_j + t_0 + 2.$$

This contradicts the minimality of ξ_*. Thus case (i) is impossible.

Next we consider case (ii), where $\tilde{U} \equiv \underline{U}$. This implies, by way of Lemma 3(a), that for some constant δ_1 and for all $j \geq j_0$,

$$M(x, t_j + t) - \underline{M} \geq \delta_1 \quad \text{for } x \in \bar{\Omega},\ t \in [2, 3].$$

Hence the second differential inequality in (31) can be improved to

$$\begin{cases} \tilde{U}_t - d\Delta\tilde{U} \geq \gamma g \tilde{U}\left(\underline{U} + \frac{r\delta_1}{\gamma g} - \tilde{U}\right) & \text{for } x \in \Omega,\ t \in [2, 3], \\ \partial_n \tilde{U} = 0 & \text{for } x \in \partial\Omega,\ t \in [2, 3], \\ \tilde{U} \geq \underline{U} & \text{for } x \in \Omega,\ t \in [2, 3]. \end{cases}$$

Standard comparison yields that $\tilde{U}(x, t) > \underline{U}$ for $x \in \bar{\Omega}$ and $t \in (2, 3]$. This is a contradiction to $\tilde{U} \equiv \underline{U}$ for all $x \in \bar{\Omega}$ and $t \geq 0$. Thus case (ii) is impossible. Similarly, we can deduce that case (iii) is also impossible. We thus have arrived at a contradiction from the assumption that $\xi_* > u^*$. Thus $\xi_* = u^*$ and we are done.

Finally, we supply the proof of Lemma 3. We only prove (a), as the proof of (b) is analogous. Solving (25) in the interval $[t_j, t_j + t]$, we have

$$\begin{aligned} &M(x, t_j + t) - \underline{M} \\ &\quad = \exp\left(-\int_{t_j}^{t_j+t} \frac{r\overline{U}}{k}(1 - M(x, s))^2 ds\right) \\ &\quad\quad \times \left[(M(x, t_j) - \underline{M}) + \int_{t_j}^{t_j+t} \exp\left(\int_{t_j}^{t_j+\tau} \frac{r\overline{U}}{k}(1 - M(x, s))^2 ds\right)\right. \\ &\quad\quad \left. \times \frac{r(1 - M(x, \tau))^2}{k} M(x, \tau)(\overline{U} - U(x, \tau)) d\tau\right]. \end{aligned}$$

Choose, by Step 1, a parameter $\xi_0 \in \left(u^*, \frac{r}{\gamma g}\right)$ such that

$$(U(x, 0), M(x, 0)) \in \Gamma(\xi_0) \quad \text{for all } x \in \bar{\Omega},$$

and set $\overline{M}_0 = \overline{M}(\xi_0) < 1$, and $\underline{M}_0 = \underline{M}(\xi_0) > 0$. By Step 3, we have $(U(x, t), M(x, t)) \in \Gamma(\xi_0)$ for all $x \in \bar{\Omega}$ and $t \geq 0$, i.e. $\underline{M}_0 \leq M(x, t) \leq \overline{M}_0$ for all $x \in \bar{\Omega}$ and $t \geq 0$.

By assumption, $\tilde{U}(x,t) = \lim_{j\to\infty} U(x, t+t_j) < \overline{U}$ in the compact set $\bar{\Omega}\times[1,3]$. Hence it is possible to choose δ_0 and j_1 so that for all $j \geq j_1$,

$$\begin{cases} \overline{U} - U(x, t_j + t) \geq \delta_0 & \text{for } x \in \bar{\Omega},\ t \in [1,3], \\ \inf_{x\in\Omega}(M(x,t_j) - \underline{M}) \geq -\frac{1}{2}\left[\frac{r(1-\overline{M}_0)^2}{k}\underline{M}_0\delta_0\right], \end{cases}$$

where we have made use of (29). Hence, for each $x \in \bar{\Omega}$ and $t \in [2,3]$,

$$\begin{aligned} &M(x, t_j + t) - \underline{M} \\ &\quad \geq \exp\left(-\int_{t_j}^{t_j+t} \frac{r\overline{U}}{k}(1 - M(x,s))^2 ds\right) \\ &\qquad \cdot \left[\inf_{x\in\Omega}(M(x,t_j) - \underline{M}) + \int_{t_j+1}^{t_j+t} \frac{r(1-\overline{M}_0)^2}{k}\underline{M}_0\delta_0 d\tau\right] \\ &\quad \geq \exp\left(-\int_{t_j}^{t_j+t} \frac{r\overline{U}}{k}(1 - M(x,s))^2 ds\right) \\ &\qquad \cdot \left[\inf_{x\in\Omega}(M(x,t_j) - \underline{M}) + \frac{r(1-\overline{M}_0)^2}{k}\underline{M}_0\delta_0\right] \\ &\quad \geq \exp\left(-\int_{t_j}^{t_j+3} \frac{r\overline{U}}{k} ds\right) \cdot \frac{1}{2} \cdot \left[\frac{r(1-\overline{M}_0)^2}{k}\underline{M}_0\delta_0\right] \\ &\quad = \exp\left(-\frac{3r\overline{U}}{k}\right)\left[\frac{r(1-\overline{M}_0)^2}{2k}\underline{M}_0\delta_0\right] \\ &\quad := \delta_1 > 0. \end{aligned}$$

Since the last expression is independent of $x \in \bar{\Omega}$ and $t \in [2,3]$, part (a) of Lemma 3 is proved. The proof of part (b) is analogous and is skipped. □

Remark 3 In fact, it is not difficult to construct a Lyapunov function as follows:

$$V(t) := \max_{x\in\bar{\Omega}} \left\{ U(x,t), \frac{r}{\gamma g}M(x,t), \frac{N_R}{\gamma g U(x,t)}, \frac{N_R}{rM(x,t)} \right\}.$$

However, due to the lack of compactness of the semiflow generated by (2), one cannot directly invoke LaSalle's Invariance Principle to conclude the global asymptotic stability of the homogeneous steady state (u^*, m^*).

6 Qualitative properties of steady state: Case $g \equiv 1$

In this section we study some qualitative properties of the unique positive steady state u^* of (5), under the condition $g \equiv 1$. The main goal of this section is to determine when Hypothesis A and Hypothesis B hold or fail for the special case $g \equiv 1$.

Throughout this section we assume that $g \equiv 1$ and rewrite (5) as

$$\begin{cases} d\Delta u^* + u^* \left[\min\left\{ \frac{N_R}{u^*}, r \right\} - \gamma u^* \right] = 0 & \text{in } \Omega, \\ \partial_n u^* = 0 & \text{on } \partial\Omega. \end{cases} \tag{32}$$

Note that u^* depends upon d and γ. For the sake of brevity we write it as u^* instead of $u^*(x, d, \gamma)$. By Theorem 3 we may assume that if $\gamma \geq \sup_{x\in\Omega} \frac{r(x)\theta(x)}{N_R(x)}$, then $u^* = \theta/\gamma$.

In terms of u^*, Hypothesis A is equivalent as

$$\int_\Omega u^*\, dx > \lim_{d\to 0} \int_\Omega u^*\, dx$$

holds for all $d > 0$, and Hypothesis B is equivalent to

$$\int_\Omega u^*\, dx > \lim_{d\to \infty} \int_\Omega u^*\, dx$$

holds for all $d > 0$.

We start with a few properties for u^* which hold for all γ.

Lemma 4 *For any $d > 0$ and $\gamma > 0$,*

$$\max_{\bar\Omega} u^* \leq \min\left\{ \frac{\max_{\bar\Omega} r}{\gamma}, \frac{\max_{\bar\Omega} \sqrt{N_R}}{\sqrt{\gamma}} \right\}; \quad \min_{\bar\Omega} u^* \geq \min\left\{ \frac{\min_{\bar\Omega} r}{\gamma}, \frac{\min_{\bar\Omega} \sqrt{N_R}}{\sqrt{\gamma}} \right\}. \tag{33}$$

Proof Suppose that $\max_{\bar\Omega} u^* = u^*(x_0)$ for some $x_0 \in \bar\Omega$. By Proposition 2.2 of Lou and Ni (1996),

$$\gamma u^*(x_0) \leq \min\left\{ \frac{N_R(x_0)}{u^*(x_0)}, r(x_0) \right\},$$

from which the first inequality of (33) follows. The proof for the second inequality of (33) is similar and thus omitted. □

The proofs of the following two results are also standard; See DeAngelis et al. (2016b).

Lemma 5 *As $d \to 0+$,*

$$u^*(x) \to u_0(x) := \min\left\{ \sqrt{\frac{N_R(x)}{\gamma}}, \frac{r(x)}{\gamma} \right\}$$

uniformly in $x \in \bar\Omega$.

Lemma 6 *As $d \to \infty$, $u^* \to u_\infty$ uniformly in $x \in \bar\Omega$, where u_∞ is the positive constant uniquely determined by*

$$\gamma|\Omega|u_\infty = \int_\Omega \min\left\{\frac{N_R(x)}{u_\infty}, r(x)\right\} dx.$$

We consider three scenarios: large, small and intermediate γ, and determine whether Hypotheses A and B hold or fail in these parameter regions. Our main findings are as follows.

(i) (large γ) When the resources are unlimited everywhere in space, then Hypotheses A and B hold.
(ii) (small γ) When the resources are limited everywhere in space, then Hypothesis A holds but Hypothesis B fails.
(iii) (intermediate γ) When the resources are partially limited in space, then both Hypotheses A and B may fail.

6.1 Large γ case

Theorem 6 *Suppose that* $\gamma \geq \bar{\gamma} := \max_{\bar{\Omega}} r \cdot \max_{\bar{\Omega}} \frac{r}{N_R}$ *and* $r(x)$ *is non-constant. Then for any* $d > 0$,

$$\int_\Omega u^*\, dx > \lim_{d\to 0+} \int_\Omega u^*\, dx = \lim_{d\to\infty} \int_\Omega u^*\, dx.$$

Theorem 6 implies that for suitably large γ, both Hypothesis A and B hold, similarly as predictions on logistic models. This is not surprising as u^* satisfies the logistic equation, as asserted in the following result:

Lemma 7 *If* $\gamma \geq \bar{\gamma}$, *then* u^* *satisfies*

$$\begin{cases} d\Delta u^* + u^*\left[r - \gamma u^*\right] = 0 & in\ \Omega, \\ \partial_n u^* = 0 & on\ \partial\Omega. \end{cases} \tag{34}$$

Proof By Lemma 4,

$$\max_{\bar{\Omega}} u^* \leq \frac{\max_{\bar{\Omega}} r}{\gamma} \leq \min_{\bar{\Omega}} \frac{N_R}{r},$$

whenever $\gamma \geq \overline{\gamma}$. Hence, $N_R/u^* \geq r$ in $\bar{\Omega}$, and thus u^* satisfies (34). □

The proof of Theorem 6 follows from Lemmas 5, 6 and 7; see, e.g., the proof of Lou (2006).

From the proof of Lemma 7 we see that if γ is suitably large, then $m^* = \min\{\frac{N_R}{ru^*}, 1\} \equiv 1$ in $\bar{\Omega}$. This implies that $N(x,t) \to \infty$ as $t \to \infty$, i.e. the resources are unlimited everywhere in space. In other words, both Hypotheses A and B hold when the resources are unlimited everywhere in space.

6.2 Small γ case

This is the case when the resources are limited everywhere in space, which is opposite to the case of large γ. In this case, we will show that Hypothesis A holds but Hypothesis B fails.

Theorem 7 *Suppose that* $0 < \gamma \le \underline{\gamma}$, *where*

$$\underline{\gamma} := \left\{ \left(\min_{\bar{\Omega}} \frac{r^2}{N_R^2} \right) \left(\min_{\bar{\Omega}} N_R \right), \left(\min_{\bar{\Omega}} r \right) \left(\min_{\bar{\Omega}} \frac{r}{N_R} \right) \right\},$$

and $N_R(x)$ *is non-constant. Then* $\int_\Omega u^*\,dx$ *is strictly increasing in* d. *In particular,*

$$\lim_{d\to 0} \int_\Omega u^*\,dx < \int_\Omega u^*\,dx < \lim_{d\to\infty} \int_\Omega u^*\,dx.$$

holds for any $d > 0$.

Lemma 8 *If* $\gamma \le \underline{\gamma}$, *then* $u^* = \tilde{u}$, *where* $\tilde{u} = \tilde{u}(\cdot; d)$ *is the uniquely positive solution of*

$$\begin{cases} d\Delta\tilde{u} + N_R - \gamma\tilde{u}^2 = 0 & \text{in } \Omega, \\ \partial_n \tilde{u} = 0 & \text{on } \partial\Omega. \end{cases} \tag{35}$$

Proof By Lemma 4,

$$\min_{\bar{\Omega}} u^* \ge \min\left\{ \frac{\min_{\bar{\Omega}} r}{\gamma}, \frac{\min_{\bar{\Omega}} \sqrt{N_R}}{\sqrt{\gamma}} \right\} \ge \max_{\bar{\Omega}} \frac{N_R}{r},$$

where the last inequality follows from $\gamma \le \underline{\gamma}$. Hence, $N_R/u^* \le r$ in $\bar{\Omega}$, and thus u^* satisfies (35). □

Lemma 9 *Let* $\tilde{u} = \tilde{u}(\cdot; d)$ *be the unique positive solution of* (35). *Suppose that* N_R *is non-constant. Then* $\int_\Omega \tilde{u}(x; d)\,dx$ *is strictly increasing in* d.

Proof We denote $\partial\tilde{u}/\partial d$ as $\tilde{u}'$. Differentiating (35) with respect to d, we have

$$\begin{cases} d\Delta\tilde{u}' + \Delta\tilde{u} - 2\gamma\tilde{u}\tilde{u}' = 0, & x \in \Omega, \\ \partial_n \tilde{u}' = 0 & x \in \partial\Omega. \end{cases} \tag{36}$$

Set $\mathcal{L} := (-d\Delta + 2\gamma\tilde{u})^{-1}$, i.e. the inverse of the operator $-d\Delta + 2\gamma\tilde{u}$ subject to the Neumann boundary condition. By (35) and (36) we have

$$\tilde{u} = \mathcal{L}(N_R + \gamma\tilde{u}^2), \quad \text{and} \quad d\tilde{u}' = \mathcal{L}(d\Delta\tilde{u}) = \mathcal{L}(\gamma\tilde{u}^2 - N_R).$$

Hence

$$\begin{aligned} d\left(\int_\Omega \tilde{u}\right)' &= d\int_\Omega \tilde{u}' \\ &= d\int_\Omega \mathcal{L}(\Delta\tilde{u}) \\ &= \int_\Omega \mathcal{L}(d\Delta\tilde{u}) \\ &= \int_\Omega \mathcal{L}(\gamma\tilde{u}^2 - N_R) \\ &= \int_\Omega \mathcal{L}(2\gamma\tilde{u}^2) - \int_\Omega \mathcal{L}(\gamma\tilde{u}^2 + N_R) \\ &= \int_\Omega \mathcal{L}(2\gamma\tilde{u}^2) - \int_\Omega \tilde{u}. \end{aligned} \tag{37}$$

It remains to show that

$$\int_\Omega \mathcal{L}(2\gamma\tilde{u}^2) > \int_\Omega \tilde{u},$$

from which it follows that $\int_\Omega \tilde{u}$ is strictly increasing in d.

To prove our assertion, let $v = \mathcal{L}(2\gamma\tilde{u}^2)$, i.e. v satisfies

$$\begin{cases} -d\Delta v + 2\gamma\tilde{u}v = 2\gamma\tilde{u}^2, & x \in \Omega, \\ \partial_n v = 0 & x \in \partial\Omega. \end{cases} \tag{38}$$

By the maximum principle, $v > 0$ in $\bar{\Omega}$. As $\tilde{u}$ is non-constant, v is also non-constant. Dividing (38) by v and integrating the result in Ω we obtain

$$-d\int_\Omega \frac{|\nabla v|^2}{v^2} + 2\gamma\int_\Omega \tilde{u} = 2\gamma\int_\Omega \frac{\tilde{u}^2}{v}.$$

Since v is non-constant, we have

$$\int_\Omega \tilde{u} > \int_\Omega \frac{\tilde{u}^2}{v},$$

which can be written as

$$\int_\Omega \frac{\tilde{u}(v-\tilde{u})}{v} > 0.$$

Note that

$$\int_\Omega (v-\tilde{u}) - \int_\Omega \frac{(v-\tilde{u})^2}{v} = \int_\Omega \frac{\tilde{u}(v-\tilde{u})}{v}.$$

Hence,

$$\int_{\Omega}(v-\tilde{u}) > \int_{\Omega}\frac{(v-\tilde{u})^2}{v} \geq 0,$$

which proves the assertion. □

Theorem 7 now follows from Lemmas 8 and 9.

6.3 Intermediate γ

The results from previous two subsections illustrate that Hypothesis A hold for small and large γ. In this subsection we show that Hypothesis A could fail for intermediate values of γ.

Theorem 8 *Suppose that* $\max_{\bar{\Omega}}\frac{r^2}{N_R} < \frac{\int_{\Omega} r}{|\Omega|}\max_{\bar{\Omega}}\frac{r}{N_R}$ *holds. Then*

$$\lim_{d\to 0}\int_{\Omega} u^*\,dx > \lim_{d\to\infty}\int_{\Omega} u^*\,dx$$

for

$$\gamma \in \left[\max_{\bar{\Omega}}\frac{r^2}{N_R}, \frac{\int_{\Omega} r}{|\Omega|}\max_{\bar{\Omega}}\frac{r}{N_R}\right).$$

Remark 4 It is easy to construct functions N_R and r for which $\max_{\bar{\Omega}}\frac{r^2}{N_R} < \frac{\int_{\Omega} r}{|\Omega|}\max_{\bar{\Omega}}\frac{r}{N_R}$ holds; for instance, it holds when r is non-constant and N_R is proportional to r^2. We also note that $\max_{\bar{\Omega}}\frac{r^2}{N_R} < \frac{\int_{\Omega} r}{|\Omega|}\max_{\bar{\Omega}}\frac{r}{N_R}$ does not hold when N_R is proportional to r.

In fact, when $N_R(x) = kr(x)$ for some $k > 0$, then $\lim_{d\to 0}\int_{\Omega} u^*\,dx \leq \lim_{d\to\infty}\int_{\Omega} u^*\,dx$ holds for every $\gamma > 0$. Precisely, by Lemmas 4 and 5,

$$u_\infty = \sqrt{\frac{\bar{r}}{\gamma}}\min\left\{\sqrt{k}, \sqrt{\frac{\bar{r}}{\gamma}}\right\}, \quad \text{and} \quad u_0(x) = \sqrt{\frac{r(x)}{\gamma}}\min\left\{\sqrt{k}, \sqrt{\frac{r(x)}{\gamma}}\right\}$$

Hence, by Schwartz's inequality,

$$\int_{\Omega} u_0\,dx \leq \int_{\Omega}\sqrt{\frac{kr(x)}{\gamma}}\,dx = \frac{\sqrt{k}|\Omega|}{|\Omega|}\int_{\Omega}\sqrt{\frac{r(x)}{\gamma}}\,dx \leq \sqrt{k}|\Omega|\sqrt{\frac{\bar{r}}{\gamma}} = \int_{\Omega} u_\infty\,dx$$

in case $k < \frac{\bar{r}}{\gamma}$; and

$$\int_{\Omega} u_0\,dx \leq \int_{\Omega}\frac{r(x)}{\gamma}\,dx = \frac{\bar{r}}{\gamma}|\Omega| = \int_{\Omega} u_\infty\,dx$$

in case $k \geq \frac{\bar{r}}{\gamma}$.

An immediate corollary of Theorem 8 says that for γ belong to the interval $[\max_{\bar{\Omega}} \frac{r^2}{N_R}, \frac{\int_\Omega r}{|\Omega|} \max_{\bar{\Omega}} \frac{r}{N_R})$, $\lim_{d\to 0} \int_\Omega u^* \, dx > \int_\Omega u^* \, dx$ for large d; in particular, Hypothesis A could fail for large d.

One can also construct examples such that Hypothesis B fails for intermediate values of γ and small d.

Given two functions F, G on $\bar{\Omega}$, define

$$A := \left(\int_\Omega \min\{F, G\} \, dx\right)^2 - \int_\Omega \min\left\{|\Omega| F^2, \left(\int_\Omega \min\{F, G\} \, dx\right) G\right\}.$$

Lemma 10 *Suppose that $F, G \in C(\bar{\Omega})$ and $F \geq G$ in $\bar{\Omega}$. Then $A \geq 0$ holds. Furthermore, $A = 0$ if and only if $|\Omega| F^2 \geq \left(\int_\Omega G\right) G$ in $\bar{\Omega}$.*

Proof By $F \geq G$,

$$\begin{aligned}
A &= \left(\int_\Omega G\right)^2 - \int_\Omega \min\left\{|\Omega| F^2, \left(\int_\Omega G\right) G\right\} \\
&= \left(\int_\Omega G\right)^2 - \int_\Omega G \cdot \int_{\{x:|\Omega|F^2 \geq (\int_\Omega G)G\}} G - \int_{\{x:|\Omega|F^2 < (\int_\Omega G)G\}} |\Omega| F^2 \\
&= \int_\Omega G \cdot \int_{\{x:|\Omega|F^2 < (\int_\Omega G)G\}} G - \int_{\{x:|\Omega|F^2 < (\int_\Omega G)G\}} |\Omega| F^2 \\
&= \int_{\{x:|\Omega|F^2 < (\int_\Omega G)G\}} \left[\left(\int_\Omega G\right) G - |\Omega| F^2\right] \\
&\geq 0,
\end{aligned}$$

and the last equality holds if and only if the set $\{x : F^2 < (\int_\Omega G)G\}$ has zero measure, i.e. $|\Omega| F^2 \geq (\int_\Omega G \, dx) G$ in $\bar{\Omega}$. □

Proof of Theorem 8 For $s \in (0, \infty)$, set

$$f(s) = \gamma |\Omega| s^2 - \int_\Omega \min\{N_R(x), s r(x)\} \, dx.$$

As $f(s)/s$ is strictly increasing, $f(s)$ is positive for large s and negative for small s, $f(s) = 0$ has a unique positive root, which is precisely given by u_∞, by the definition of u_∞ (Lemma 6). Recall that $u^* \to u_0 = \min\left\{\sqrt{\frac{N_R}{\gamma}}, \frac{r}{\gamma}\right\}$ as $d \to 0$ and $u^* \to u_\infty$ as $d \to \infty$. Hence, to compare $\lim_{d\to 0} \int_\Omega u^* \, dx$ and $\lim_{d\to\infty} \int_\Omega u^* \, dx$, it suffices to determine the sign of $f\left(\frac{1}{|\Omega|} \int_\Omega u_0 \, dx\right)$. More precisely, if $f\left(\frac{1}{|\Omega|} \int_\Omega u_0 \, dx\right) > 0$, then $\frac{1}{|\Omega|} \int_\Omega u_0 \, dx$ is strictly greater than the unique root u_∞ of f, and thus $\lim_{d\to\infty} \int_\Omega u^* \, dx = |\Omega| u_\infty < \int_\Omega u_0 \, dx = \lim_{d\to 0} \int_\Omega u^* \, dx$.

By direct computation we have

$$\frac{|\Omega|}{\gamma} f\left(\frac{\int_\Omega u_0}{|\Omega|}\right) = \left(\int_\Omega \min\left\{\sqrt{\frac{N_R}{\gamma}}, \frac{r}{\gamma}\right\}\right)^2 - \int_\Omega \min\left\{|\Omega|\frac{N_R}{\gamma}, \left(\int_\Omega \min\left\{\sqrt{\frac{N_R}{\gamma}}, \frac{r}{\gamma}\right\}\right)\cdot\frac{r}{\gamma}\right\}.$$

By choosing $F = \sqrt{N_R/\gamma}$ and $G = r/\gamma$ we see that

$$\frac{|\Omega|}{\gamma} f\left(\frac{\int_\Omega u_0}{|\Omega|}\right) = A.$$

By assumption $\gamma \geq \max_{\bar{\Omega}} \frac{r^2}{N_R}$, $F = \sqrt{N_R/\gamma} \geq G = r/\gamma$ in $\bar{\Omega}$. Hence, by Lemma 10, $A \geq 0$ and $A = 0$ holds if and only if $\gamma \geq \frac{\int_\Omega r}{|\Omega|} \max_{\bar{\Omega}} \frac{r}{N_R}$. This completes the proof of Theorem 8. □

7 Discussions

In this paper we have investigated the dynamics of a consumer–resource reaction–diffusion model, proposed recently by Zhang et al. (2017), for both homogeneous and heterogeneous environments. For homogeneous environments we have established the global stability of the constant steady state. In particular, if the yield rate is greater than or equal to some critical value, the resources will become unlimited across the habitat; if the yield rate is smaller than the critical value, the resources are limited in the whole habitat. For heterogeneous environments we have studied the existence and stability of positive steady states and the persistence of time-dependent solutions. For heterogeneous environments, our results imply that the resources will be unlimited across the habitat for large yield rate and limited in the space for sufficiently small yield rate. However, there is some range of yield rates in which the resources are partially limited in space, a unique feature which does not occur in homogeneous environments.

As was mentioned in the Introduction, an experiment performed by Zhang et al. (2017) showed, surprisingly, that Hypothesis B was false. In fact, this can be easily seen by comparing Figure 4 in p. 1124 and Figure 6 in p. 1126. A mathematical proof of this fact was included in the Appendix E of Zhang et al. (2017) for the case when γ is small. For the reader's convenience, we include it here for comparison purposes.

Proposition 2 *Let u_d and v_d be respectively the unique positive solution of the following problems*

$$\begin{cases} d\Delta u + N_R - \gamma g u^2 = 0 & \text{in } \Omega, \\ \partial_n u = 0 & \text{on } \partial\Omega, \end{cases} \tag{39}$$

and

$$\begin{cases} d\Delta v + \bar{N}_R - \gamma g v^2 = 0 & \text{in } \Omega, \\ \partial_n v = 0 & \text{on } \partial\Omega. \end{cases} \tag{40}$$

where $\bar{N}_R = \frac{1}{|\Omega|}\int_\Omega N_R\, dx$. *Then, for* d *small*

$$\int_\Omega u_d < \int_\Omega v_d$$

provided that N_R *and* g *are positively correlated and, either* N_R *or* g *is nonconstant.*

The proof follows from the following lemma which compares the respective carrying capacities of the two systems.

Lemma 11

$$\int_\Omega \sqrt{\frac{N_R}{\gamma g}}\, dx < \int_\Omega \sqrt{\frac{\bar{N}_R}{\gamma g}}\, dx$$

if N_R *and* g *are positively correlated and, either* N_R *or* g *is nonconstant.*

Proof If N_R and g are positively correlated, then N_R and $1/g$ are negatively correlated, then by Lemma 26 in p. 247 of DeAngelis et al. (2016b), it follows that

$$\int_\Omega \sqrt{\frac{N_R}{\gamma g}}\, dx \le \frac{1}{|\Omega|}\int_\Omega \sqrt{\bar{N}_R}\int_\Omega \sqrt{\frac{1}{\gamma g}} = \int_\Omega \sqrt{\frac{\bar{N}_R}{\gamma g}}\, dx$$ □

Combining Proposition 2 and Theorem 7, we see that, for γ small, we now have a fairly good understanding of why Hypothesis B fails. This seems particularly relevant, as the experiments performed by Zhang et al. (2017) seem to indicate that the parameter γ is quite small.

Another hypothesis proposed by Zhang et al. (2017) stated that when a consumer exists in a region with a heterogeneously distributed input of exploitable renewed limiting resources, the total population abundance at equilibrium can reach a greater abundance when it diffuses than when it does not. While we show that such hypothesis holds for both small and high yield rates, a new finding of this paper is that this second hypothesis proposed by Zhang et al. (2017) may fail for intermediate values of yield rates.

The phenomenon of partially limited resources in space can be regarded as a transition between the current consumer–resource model with small yield rates and the classical logistic model. The details of such transition in terms of parameters such as the diffusion rate and the yield rate yet remain to be understood and invite further investigation. To illuminate the situation, we make some comments to clarify the general conditions on the critical yield rates given in Theorem 3 and Corollary 2 versus those in Sect. 6 (Theorems 6, 7, 8). To this end, for any given $d > 0$, recall the following critical rates specified in (14) (see also Corollary 2):

$$\gamma^*(d) = \sup_{\Omega} \frac{r(x)\theta(x)}{N_R(x)} \quad \text{and} \quad \gamma_*(d) = \sup\left\{\gamma > 0 : \sup_{\Omega} \frac{N_R}{r\tilde{u}} \leq 1\right\}.$$

Since $\max_{\bar{\Omega}} \theta < \max_{\bar{\Omega}} r$ and $\min_{\bar{\Omega}} \theta > \min_{\bar{\Omega}} r$ when $g = 1$, it is easy to show

$$\underline{\gamma} < \inf_{d>0} \gamma_*(d) < \sup_{d>0} \gamma^*(d) < \overline{\gamma},$$

which implies that $m^* \equiv 1$ everywhere for those values of γ as given in Theorem 6, whereas $m^* < 1$ everywhere in case of Theorem 7. This in particular implies that $\gamma - \gamma^*(d)$ does not change sign for those values of γ as given in Theorems 6 and 7, respectively. In contrast, for those γ in Theorem 8, $\gamma - \gamma^*(d)$ always changes sign as it holds that

$$\left(\max_{\bar{\Omega}} \frac{r^2}{N_R}, \frac{\int_\Omega r}{|\Omega|} \max_{\bar{\Omega}} \frac{r}{N_R}\right) \subset \left(\inf_{d>0} \gamma^*(d), \sup_{d>0} \gamma^*(d)\right),$$

which follows from $\gamma^*(d) \to \max_{\bar{\Omega}} \frac{r^2}{N_R}$ when $d \to 0$ and $\gamma^*(d) \to \frac{\int_\Omega r}{|\Omega|} \max_{\bar{\Omega}} \frac{r}{N_R}$ when $d \to \infty$.

Determining the shapes of $\gamma^*(d)$ and $\gamma_*(d)$ will be useful in understanding the transition between the consumer–resource model with small yield rates and the classical logistic model. For the case of $N_R(x)$ proportional to $r(x)$, it was conjectured by Lou and Wang (2017) that $\gamma^*(d)$ is strictly monotone decreasing in d; see also the work by Li and Lou (2018) for recent development. It seems interesting but challenging to determine the general shapes of $\gamma^*(d)$ and $\gamma_*(d)$, as functions of the diffusion rate d.

Acknowledgements We sincerely thank the anonymous referees for their comments which help improve the presentation of the paper. The research of X. He is supported in part by NSFC (11601155), Recruitment Program of Global Experts in China, and Science and Technology Commission of Shanghai Municipality (No. 18dz2271000); the research of K.-Y. Lam and Y. Lou is partially supported by NSF Grant DMS-1411476; the research of W.-M. Ni is partially supported by the Presidential Chair Fund at CUHK (SZ), NSF Grants DMS-1210400 and DMS-1714487, and NSFC Grant Nos. 11571363, 11431005. Part of the research was carried out while K.-Y. Lam was visiting the Center for PDE, ECNU and while Y. Lou was visiting the NCTS at the National Taiwan University.

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