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INVADING THE IDEAL FREE DISTRIBUTION

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Dedicated to Professor Chris Cosner on the occasion of his 60th birthday

Abstract. Recently, the ideal free dispersal strategy has been proven to be evolutionarily stable in the spatially discrete as well as continuous setting. That is, at equilibrium a species adopting the strategy is immune against invasion by any species carrying a different dispersal strategy, other conditions being held equal. In this paper, we consider a two-species competition model where one of the species adopts an ideal free dispersal strategy, but is penalized by a weak Allee effect. We will show rigorously in this case that the ideal free disperser is invasible by a range of non-ideal free strategies, illustrating the trade-off between the advantage of being an ideal free disperser and the setback caused by the weak Alee effect. Moreover, a sharp integral criterion is given to determine the stability/instability of one of the semi-trivial steady state, which is always linearly neutrally stable due to the degeneracy caused by the weak Allee effect.

1. Introduction.

Habitat selection plays a pivotal role in a species' life history, i.e. its endeavor to survive and reproduce. While accounting for all factors in this complicated process is a formidable task, ecologists attempt to identify elements which capture the essential mechanisms of habitat choice. One such perspective is known as *ideal free distribution* (IFD) theory, proposed by Fretwell and Lucas in their study of birds [10]. This framework operates from two assumptions: (i) each individual has complete knowledge of its environment to determine the most favorable locations for growth and (ii) each individual is able to freely move to these "best" spots. Provided the assumptions hold, the theory predicts that the resulting distribution of the species will be proportional to the amount of available resources at each location in the habitat [10].

Although the presuppositions of IFD theory are regarded by some in the empirical research community as being overly simplistic [15], there are a number of

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experimental studies confirming its predictions (see for example [9, 12, 21]). More importantly, this simple principle provides a striking, quantitative link between habitat choice and evolution of dispersal that allows for rigorous theoretical investigation.

For instance, a kind of dispersal behavior known as "balanced dispersal" arises from the evolution of dispersal in patchy environments. Balanced dispersal, as described in [3], "implies that at equilibrium individuals in any patch will have the same fitness, namely zero, because all populations are at carrying capacity". Hence it is capable of producing an ideal free distribution. Since individuals at all locations have the same fitness, there is no advantage for anyone to move to another location to increase fitness. Furthermore, if the resident species adopts the balanced dispersal strategy, then it cannot be invaded by another rare species playing a different strategy. In the game-theoretic setting, the balanced dispersal strategy, regarded as a strategy played by the resident population, is an *evolutionarily stable strategy* (ESS).

The spatially continuous case is taken up by Cantrell et. al. [5] where a reaction-diffusion-advection model of two competing species was proposed. (See system (1) below.) The species disperses via a combination of diffusion and advection, the latter component captures the conditional, or biased, aspect of dispersal. Among all of the advection modes (admissible under their formulation), only one allows for the possibility for the resident to equilibrate to a form of ideal free distribution. Sufficient conditions were obtained for the ideal free dispersal strategy to be able to defend against any invader, showing that IFD is a local ESS. Later it was further shown in [1] that this IFD strategy is a global ESS. (See Theorem 2.1.)

All of the above lines of research show that in the context of an environment that is spatially variable but temporally constant, the species adopting IFD is able to resist invasion by any other dispersal strategies, with other properties being held equal. But how robust is this conclusion? For instance, can the ideal free disperser, vulnerable to some fitness cost or constraint, still resist invasion by a rare species? The subtlety of this question lies in the fact that at equilibrium, an ideal free dispersing resident leaves absolutely no resource for an invader to draw upon for growth.

We narrow our inquiry into this multi-faceted question by assuming that the ideal free disperser is subjected to a weak Allee effect, which causes a reduction in its fitness at low density. This question was first posed in [23], where numerical evidence presented therein suggested that the ideal free disperser can indeed be invaded by a certain range of non-IFD strategies. Our present paper presents analytical justification for this phenomenon, and offers conditions and intuition as to how the ideal free disperser may give way to an invading species, and in some cases even be driven to extinction.

2. **Model and Main Results.**

Let Ω be a bounded domain in $\mathbb{R}^N$ for $N \geq 2$, with smooth boundary $\partial\Omega$. Consider the following reaction-diffusion-advection model of Lotka-Volterra type:

$$\begin{cases} u_t = \nabla \cdot (d_1 \nabla u - u \nabla \tilde{P}(x)) + u(m(x) - u - v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nabla \cdot (d_2 \nabla v - v \nabla \tilde{Q}(x)) + v(m(x) - u - v) & \text{in } \Omega \times (0, \infty), \\ d_1 \partial_n u - u \partial_n \tilde{P} = d_2 \partial_n v - v \partial_n \tilde{Q} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{1}$$

where $u(x,t)$ and $v(x,t)$ represent species' densities at location $x \in \Omega$ and time t; d_1 and d_2 are their respective diffusion rates; $\tilde{P}(x)$, $\tilde{Q}(x) \in C^2(\bar{\Omega})$ specify the advective direction and the corresponding speeds; $m(x)$ describes the quality of the habitat at location x. Throughout this paper, we assume that

(M1): $m \in C^2(\bar{\Omega})$ is positive and non-constant.

Finally, ∂_n is the outward normal derivative on $\partial\Omega$ and reflecting boundary conditions are imposed, i.e. there is no net movement across any point on $\partial\Omega$.

Note that the species u and v in (1) have identical population dynamics but different movement strategies. Setting $P(x) = \frac{\tilde{P}(x)}{d_1}$ and $Q(x) = \frac{\tilde{Q}(x)}{d_2}$, we reformulate our system to match the model in [5]:

$$\begin{cases} u_t = d_1 \nabla \cdot (\nabla u - u \nabla P(x)) + u(m(x) - u - v) & \text{in } \Omega \times (0,\infty), \\ v_t = d_2 \nabla \cdot (\nabla v - v \nabla Q(x)) + v(m(x) - u - v) & \text{in } \Omega \times (0,\infty), \\ \partial_n u - u \partial_n P = \partial_n v - v \partial_n Q = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{2}$$

As pointed out in [5], if we set $P = \ln m$, then $(m,0)$ is a steady state of (2). That is, in the absense of competitor, the species adopting dispersal strategy $P = \ln m$ exactly matches the local carrying capacity at equilibrium $\tilde{u} \equiv m$. (Note also that the net flux is zero as well: $\nabla \tilde{u} - \tilde{u} \nabla \ln m \equiv 0$.) Hence $P = \ln m$ is a form of IFD strategy. The significance here is that the strategy yielding IFD is a globally evolutionarily stable strategy (Theorem 1.2 in [1]). Mathematically, the result can be stated as follows:

Theorem 2.1. *Suppose $m \in C^2(\bar{\Omega})$ is non constant and positive. Given any $d_1, d_2 > 0$, if $P = \ln m$, and $Q - \ln m$ is not constant, then $(m,0)$ is the globally asymptotically stable steady state of (2) among any nonnegative and not identically zero initial data.*

Theorem 2.1 holds on the premise that both species have identical population dynamics. To explore the robustness of IFS, we subject the ideal free disperser to a weak Allee effect by replacing the reaction term for species u in (2) by $u^2(m-u-v)$ [23]. Our question then becomes, *is the ideal free disperser subject to a weak Allee effect invadable by a species playing a different strategy?* Suppose that $P \equiv \ln m$ and $Q = \beta \ln m$ ($0 \le \beta < \infty$), we obtain

$$\begin{cases} u_t = d_1 \nabla \cdot (\nabla u - u \nabla \ln m) + u^2(m - u - v) & \text{in } \Omega \times (0,\infty), \\ v_t = d_2 \nabla \cdot (\nabla v - \beta v \nabla \ln m) + v(m - u - v) & \text{in } \Omega \times (0,\infty), \\ \partial_n u - u \partial_n \ln m = \partial_n v - \beta v \partial_n \ln m = 0 & \text{in } \partial\Omega \times (0,\infty), \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x) & \text{in } \Omega. \end{cases} \tag{3}$$

Mathematically, our goal is to find $\beta \in [0,\infty)$ such that $(m,0)$ is unstable in system (3).

Before stating our main results, we make a few preliminary remarks. System (3) has two semitrivial steady states $(m,0)$ and $(0,v^*)$, where v^* is the unique positive solution of

$$\begin{cases} d_2 \nabla \cdot (\nabla v - \beta v \nabla \ln m) + v(m - v) = 0 & \text{in } \Omega, \\ \partial_n v - \beta v \partial_n \ln m = 0 & \text{on } \partial\Omega. \end{cases} \tag{4}$$

In this paper, we are interested in the local and global stabilities of the steady states of (3). The mathematical subtlety lies in the fact that, due to the degeneracy caused by the IFD and the weak Allee effect, both of the semi-trivial steady states are linearly neutrally stable. i.e. the principal eigenvalues of the linearized system at $(m,0)$ or $(0,v^*)$ are identically zero. Therefore, we need to argue for nonlinear stability/instability directly. Our staring point is the following integral characterization of the local stability of $(0,v^*)$, proved in Section 3.

Theorem 2.2. *Let v^* be the unique positive solution of (4).*

(i) If $\int_\Omega m^2(m-v^*) < 0$, then $(0,v^*)$ is locally asymptotically stable.
(ii) If $\int_\Omega m^2(m-v^*) \geq 0$ and $\beta \neq 1$, then $(0,v^*)$ is unstable.

Using the criterion in Theorem 2.2, we can determine the local behavior of system (3) near $(0,v^*)$ for β close to 1. Confirming the conjecture in [23], we demonstrate that $(0,v^*)$ does indeed change stability as β crosses the threshold value of 1.

Proposition 2.3. *There exists $\epsilon_0 > 0$ such that*

(i) If $\beta \in [0,1)$, then $(0,v^*)$ is unstable.
(ii) If $\beta \in (1, 1+\epsilon_0)$, then $(0,v^*)$ is locally asymptotically stable.

If we assume in addition that

(M2): *$m \in C^3(\Omega)$ has a unique critical point $x_0 \in \Omega$, which is a non-degenerate local (hence global) maximum, and $\partial_n m|_{\partial\Omega} \leq 0$.*

then $(0,v^*)$ is unstable for all β sufficiently large.

Biologically, Proposition 2.3 (ii) indicates that there is a range of strategies which prevent invasion by an ideal free disperser. This is interesting because we can mathematically justify that the cost of the weak Allee effect is enough to offset the invasion success enjoyed by a resource matching strategy.

One can actually say more. By demonstrating that system (3) has no positive coexistence states for β near but larger than 1 (see Section A), the local asymptotic stability of $(0,v^*)$ actually determines the global dynamics of (3), thanks to the general theory of monotone dynamical systems [7, 13, 14, 19, 26]. In particular, this means that $(m,0)$ is unstable for some β. This line of attack can be found also in [5]. The local stability of the IFD steady state $(m,0)$ is often difficult to assess directly, considering the degeneracy associated to linearizing (3) at $(m,0)$. To state the global result, we prescribe the following assumption for m.

(M3): Suppose $\Omega = B_R \subseteq \mathbb{R}^N$, $m = m(r)$ is non-constant, $m_r(0) = 0$, $m_{rr} < 0$ in $[0,R)$ and satisfies $m + 2rm_r \geq 0$ in $(0,R)$.

Theorem 2.4. *(i) (Theorem 2.1 and 2.2 in [23]) There exists $0 < \beta_1 < 1$ such that for all $\beta \in (0,\beta_1)$ and any $d_1, d_2 > 0$, the steady state $(m,0)$ of (3) is globally asymptotically stable.*
(ii) Assume (M3). There exists $0 < \beta_2 < 1$ such that for all $\beta \in (\beta_2, 1)$ and any $d_1, d_2 > 0$, the steady state $(m,0)$ of (3) is globally asymptotically stable.
(iii) Assume (M3). There exists $\beta_3 > 1$ such that for all $\beta \in (1,\beta_3)$ and any $d_1, d_2 > 0$, the steady state $(0,v^*)$ of (3) is globally asymptotically stable.
(iv) Assume (M2). There exists $\beta_4 \gg 1$ such that for all $\beta > \beta_4$ and any $d_1, d_2 > 0$, the steady state $(m,0)$ of (3) is globally asymptotically stable.

While the mathematics are compelling in their own right, the biological implications of the instability of $(m,0)$ are quite strong: a rare species v can invade an ideal free disperser with significant resident population and drive it to extinction. This result seems counter intuitive as species u should have large enough density to minimize the cost of the weak Allee effect (which expresses itself mostly when the species is rare) and therefore dominate resource acquisition throughout the habitat. However, because v has slightly stronger advection, numerical simulations suggest that v is able to quickly establish itself at resource maxima. Focusing on the most abundant resource sites, species v eventually overtakes u, forcing it towards less favorable locations and eventually to extinction.

The paper is organized as follows: In Section 3 we determine conditions for the local stability of $(0, v^*)$. In Section 4, we discuss and prove the global dynamics of system (3), making use of the non-existence results of positive steady states contained in the appendix sections. Finally, we present our conclusions and discuss the intuition behind Theorem 2.2 in Section 5.

3. Local Stability of $(0, v^*)$.

In this section we discuss the local asymptotic stability of $(0, v^*)$. First, we recall several definitions from dynamical systems.

Definition 3.1. *(i) A steady state $(\tilde{u}, \tilde{v})$ of (3) is unstable if there is some $\epsilon_0 > 0$ such that for all $\delta > 0$, there exists non-negative initial data (u_0, v_0) and t_0 such that*

$$\|u_0 - \tilde{u}\|_{L^\infty(\Omega)} + \|v_0 - \tilde{v}\|_{L^\infty(\Omega)} < \delta$$

and the corresponding solution (u, v) of (3) satisfies

$$\|u(\cdot, t_0) - \tilde{u}\|_{L^\infty(\Omega)} + \|v(\cdot, t_0) - \tilde{v}\|_{L^\infty(\Omega)} \geq \epsilon_0.$$

(ii) A steady state $(\tilde{u}, \tilde{v})$ of (3) is locally asymptotically stable if for some $\delta > 0$, the solution $(u(x,t), v(x,t))$ of (3) with non-negative initial data (u_0, v_0) such that

$$\|u_0 - \tilde{u}\|_{L^\infty(\Omega)} + \|v_0 - \tilde{v}\|_{L^\infty(\Omega)} < \delta$$

satisfies

$$\|u(\cdot, t) - \tilde{u}\|_{L^\infty(\Omega)} + \|v(\cdot, t) - \tilde{v}\|_{L^\infty(\Omega)} \to 0. \tag{5}$$

(iii) A steady state $(\tilde{u}, \tilde{v})$ of (3) is globally asymptotically stable if (5) holds for each non-negative, not identically zero initial data (u_0, v_0).

Next, we state and prove the integral characterization of local stability of $(0, v^*)$.

Theorem 3.2. *Let v^* be the unique positive solution of (4).*

(i) If $\int_\Omega m^2(m - v^*) < 0$, then $(0, v^*)$ is locally asymptotically stable.
(ii) If $\int_\Omega m^2(m - v^*) \geq 0$ and $\beta \neq 1$, then $(0, v^*)$ is unstable.

Remark 1. *In [18], a PDE model in population genetics was considered where a degeneracy analogous to Allee effect is present. Amoung other things, the change in stability of the trivial solution was demonstrated via variational and degree-theoretical methods and a similar integral condition was obtained (See Theorem 1.1 therein). In our local stability analysis of $(0, v^*)$, a non-variational proof using the upper and lower solution method is presented. Our approach has the advantage of being more transparent and shows that a kind of transcritical bifurcation is present (see Remark 2). See also [25] for a Crandall-Rabinowitz type bifurcation analysis of a single species model with a non-degenerate type of Allee effect.*

Proof of Theorem 3.2. Define

$$C_\beta := \int_\Omega m^2(m - v^*).$$

First we prove (i). Suppose $C_\beta = \int_\Omega m^2(m-v^*) < 0$. We will construct, for all $\epsilon > 0$ sufficiently small, a pair of super/subsolution of the form

$$\begin{aligned} \bar{u}(x) &= \epsilon m + \epsilon^2 w(x) \\ \underline{v}(x) &= v^* + \epsilon z_\epsilon(x) \end{aligned} \tag{6}$$

such that

$$\begin{cases} d_1\nabla\cdot(\nabla\bar{u} - \bar{u}\nabla(\ln m)) + \bar{u}^2(m-\bar{u}-\underline{v}) < 0 & \text{in } \Omega, \\ d_2\nabla\cdot(\nabla\underline{v} - \beta\underline{v}\nabla\ln m) + \underline{v}(m-\bar{u}-\underline{v}) = 0 & \text{in } \Omega, \\ \partial_n\bar{u} - \bar{u}\partial_n(\ln m) = \partial_n\underline{v} - \beta\underline{v}\partial_n(\ln m) = 0 & \text{on } \partial\Omega, \end{cases} \tag{7}$$

and $z_\epsilon \to -v^*$ uniformly as $\epsilon \to 0$. Now we begin the construction. Firstly, let w be the unique solution to

$$\begin{cases} d_1\nabla\cdot\left[m\nabla\left(\frac{w}{m}\right)\right] = -m^2(m-v^*) + C_\beta & \text{in } \Omega, \\ \partial_n\left(\frac{w}{m}\right) = 0 \quad \text{on } \partial\Omega, & \int_\Omega \frac{w}{m} = 0. \end{cases} \tag{8}$$

Note that the existence of w follows from the fact that $\int_\Omega[-m^2(m-v^*)+C_\beta] = 0$. Secondly, for z_ϵ, we have the following lemma.

Lemma 3.3. *There exists $\epsilon_0 > 0$, and a small neighborhood $\mathcal{U}$ of $-v^*$, such that for all $\epsilon \in (-\epsilon_0, \epsilon_0)$, the problem*

$$\begin{cases} d_2\nabla\cdot\left(m^\beta\nabla\left(\frac{z}{m^\beta}\right)\right) + z[(1-\epsilon)m - \epsilon^2 w - 2v^* - \epsilon z] - v^*(m+\epsilon w) = 0 & \text{in } \Omega, \\ \partial_n\left(\frac{z}{m^\beta}\right) = 0 & \text{on } \partial\Omega. \end{cases} \tag{9}$$

has a unique solution z_ϵ in $\mathcal{U}$. Moreover, $z_\epsilon \to -v^*$ uniformly as $\epsilon \to 0$.

Proof of Lemma 3.3. Define $\mathcal{F} : \left\{y \in C^{2,\alpha}(\bar\Omega) : \partial_n\left(\frac{z}{m^\beta}\right)\big|_{\partial\Omega} = 0\right\} \times \mathbb{R} \to C^\alpha(\bar\Omega)$ by

$$\mathcal{F}(z,\epsilon) := d_2\nabla\cdot\left(m^\beta\nabla\left(\frac{z}{m^\beta}\right)\right) + z[(1-\epsilon)m - \epsilon^2 w - 2v^* - \epsilon z] - v^*(m+\epsilon w) = 0$$

Then $\mathcal{F}(-v^*, 0) = 0$ and

$$D_z\mathcal{F}(-v^*,0)[y] = d_2\nabla\cdot\left[m^\beta\nabla\left(\frac{y}{m^\beta}\right)\right] + (m-2v^*)y.$$

Claim 3.4. *$D_z\mathcal{F}(-v^*, 0)$ is an isomorphism.*

First, from the equation of v^*, we observe that zero is the principal eigenvalue of

$$\begin{cases} d_2\nabla\cdot\left[m^\beta\nabla\left(\frac{\varphi}{m^\beta}\right)\right] + (m-v^*)\varphi + \sigma\varphi + \mu\varphi = 0 & \text{in } \Omega, \\ \partial_n\left(\frac{\varphi}{m^\beta}\right) = 0 & \text{on } \partial\Omega, \end{cases}$$

i.e.

$$\inf_{\psi\in C^1(\bar\Omega)} \frac{\int_\Omega\left[d_2 m^\beta\left|\nabla\frac{\psi}{m^\beta}\right|^2 + (v^*-m)m^{-\beta}\psi^2\right]}{\int_\Omega m^{-\beta}\psi^2} = 0$$

Hence, the principal eigenvalue σ_1 of

$$\begin{cases} d_2\nabla\cdot\left[m^\beta\nabla\left(\frac{\varphi}{m^\beta}\right)\right] + (m-2v^*)\varphi + \sigma\varphi + \sigma_1\varphi = 0 & \text{in } \Omega, \\ \partial_n\left(\frac{\varphi}{m^\beta}\right) = 0 & \text{on } \partial\Omega, \end{cases}$$

satisfies

$$\begin{aligned}\sigma_1 &= \inf_{\psi\in C^1(\bar\Omega)} \frac{\int_\Omega \left[d_2 m^\beta \left|\nabla \frac{\psi}{m^\beta}\right|^2 + (2v^* - m)m^{-\beta}\psi^2\right]}{\int_\Omega m^{-\beta}\psi^2}\\
&> \inf_{\psi\in C^1(\bar\Omega)} \frac{\int_\Omega \left[d_2 m^\beta \left|\nabla \frac{\psi}{m^\beta}\right|^2 + (v^* - m)m^{-\beta}\psi^2\right]}{\int_\Omega m^{-\beta}\psi^2} = 0.\end{aligned}$$

Therefore $\sigma_1 > 0$ and zero is not an eigenvalue of $D_z\mathcal{F}$ and the claim is proved. Lemma 3.3 follows from an application of the Implicit Function Theorem. □

Now, define $\bar u$ and $\underline{v}$ as in (6). Then the second equation of (7) is equivalent to (9), which holds by definition of z_ϵ. It remains to show the first inequality in (7):

$$\begin{aligned}&d_1\nabla\cdot\left(m\nabla\left(\frac{\bar u}{m}\right)\right) + \bar u^2(m - \bar u - \underline{v})\\
&= \epsilon^2 d_1\nabla\cdot\left(m\nabla\left(\frac{w}{m}\right)\right) + (\epsilon m + \epsilon^2 w(x))^2(m - \epsilon m - \epsilon^2 w(x) - v^* - \epsilon z)\\
&= \epsilon^2\left\{d_1\nabla\cdot\left(m\nabla\left(\frac{w}{m}\right)\right) + m^2(m - v^*) + O(\epsilon)\right\}\\
&= \epsilon^2\left\{C_\beta + O(\epsilon)\right\} < 0\end{aligned}$$

since $C_\beta < 0$ is independent of ϵ small. This proves (i).

Now, we take up (ii). Suppose $C_\beta = \int_\Omega m^2(m - v^*) \geq 0$ and $\beta \neq 1$. We now construct, for $\epsilon > 0$ sufficiently small, a pair of super/subsolution $(\underline{u}, \bar v)$ of the form

$$(\underline{u}, \bar v) = (\epsilon m + \epsilon^2 w + \epsilon^3 y', v^* + \epsilon z'_\epsilon), \tag{10}$$

satisfying

$$\begin{cases} d_1\nabla\cdot(\nabla\underline{u} - \underline{u}\nabla(\ln m)) + \underline{u}^2(m - \underline{u} - \bar v) > 0 & \text{in } \Omega,\\ d_2\nabla\cdot(\nabla\bar v - \beta\bar v\nabla\ln m) + \bar v(m - \underline{u} - \bar v) = 0 & \text{in } \Omega,\\ \partial_n\underline{u} - \underline{u}\partial_n(\ln m) = \partial_n\bar v - \beta\bar v\partial_n(\ln m) = 0 & \text{on } \partial\Omega,\end{cases} \tag{11}$$

First we define w to be the unique solution to (8). Multiplying by $\frac{w}{m}$ and integrating by parts, using the fact that $v^* \neq m$ if $\beta \neq 1$, we deduce that $\frac{w}{m}$ is non-constant and

$$\int_\Omega mw(m - v^*) = d_1\int_\Omega m\left|\nabla\frac{w}{m}\right|^2 + C_\beta\int_\Omega\frac{w}{m} > 0. \tag{12}$$

Next, define y' to be the unique solution to

$$\begin{cases} d_1\nabla\cdot\left[m\nabla\left(\frac{y'}{m}\right)\right] + 2mw(m - v^*) - m^2(m - v^*) = 2\int_\Omega mw(m - v^*) - C_\beta \text{ in } \Omega,\\ \partial_n\left(\frac{y'}{m}\right) = 0 \quad \text{on } \partial\Omega, \quad \int_\Omega\frac{y'}{m} = 0.\end{cases}$$

And we define z'_ϵ to be the unique solution close to $-v^*$ to

$$d_2\nabla\cdot\left(m^\beta\nabla\left(\frac{z'}{m^\beta}\right)\right) + z'[(1-\epsilon)m - \epsilon^2 w - \epsilon^3 y - 2v^* - \epsilon z'] - v^*(m + \epsilon w) = 0$$

satisfying $\partial_n\left(\frac{z'}{m^\beta}\right) = 0$ on $\partial\Omega$.

Note that, as in (i), the existence of z'_ϵ can be deduced from Implicit Function Theorem, and that

$$z'_\epsilon \to -v^* \quad \text{uniformly as } \epsilon \to 0. \tag{13}$$

Then the second equation of (11) follows from the definition of z'_ϵ. It remains to verify the differential inequality in (11):

$$\begin{aligned}
&d_1\nabla\cdot(\nabla\underline{u}-\underline{u}\nabla(\ln m))+\underline{u}(m-\underline{u}-\bar{v})\\
&=d_1\nabla\cdot\left(m\nabla\frac{\underline{u}}{m}\right)+\epsilon^2(m+\epsilon w+\epsilon^2y')^2(m-\epsilon m+\epsilon^2 w+\epsilon^3 y'-v^*-\epsilon z'_\epsilon)\\
&=\epsilon^2\Bigg\{d_1\nabla\cdot\left(m\nabla\frac{w}{m}\right)+m^2(m-v^*)\\
&\qquad+\epsilon\left[d_1\nabla\cdot\left(m\nabla\frac{y'}{m}\right)+2mw(m-v^*)-m^2(m-v^*)-m^2(v^*+z)\right]+O(\epsilon^2)\Bigg\}\\
&=\epsilon^2\left\{C_\beta+\epsilon\left[2\int_\Omega mw(m-v^*)-C_\beta-m^2(v^*+z_\epsilon)\right]+O(\epsilon^2)\right\}\\
&=\epsilon^2\left\{(1-\epsilon)C_\beta+\epsilon\left[2\int_\Omega mw(m-v^*)-m^2(v^*+z_\epsilon)\right]+O(\epsilon^2)\right\}\\
&>0
\end{aligned}$$

where the last strict inequality follows from $C_\beta\geq 0$, (12) and (13). □

Remark 2. *An examination of the proof of Theorem 3.2(ii) yields the following result: Suppose that there exists $\beta_0>1$ and $\delta>0$ such that $C_{\beta_0}=0$ and $C_\beta>0$ for $\beta\in(\beta_0,\beta_0+\delta)$, then there exists $\epsilon_0>0$ such that for all $\beta\in[\beta_0,\beta+\delta)$, if (u,v) is a steady state of (3) and $\inf_\Omega u<\epsilon_0$, then $(u,v)=(0,v^*)$. i.e. $(0,v^*)$ is an isolated steady state with a uniform neighborhood for $\beta\in[\beta_0,\beta_0+\delta)$.*

3.1. **Local stability of $(0,v^*)$ when $\beta\approx 1$.**

Proposition 3.5. *There exists $\epsilon_0>0$ such that*
- *(i) If $\beta\in[0,1)$, then $(0,v^*)$ is unstable.*
- *(ii) If $\beta\in(1,1+\epsilon_0)$, then $(0,v^*)$ is locally asymptotically stable.*

Note that (i) is Lemma 3.4 and Lemma 4.1 from [23]. We need some perparation for the proof of (ii).

Let $\beta=1+\epsilon$, for $0<\epsilon\ll 1$. Then we know that v^* satisfies:

$$\begin{cases} d_2\nabla\cdot(\nabla v^*-(1+\epsilon)v^*\nabla(\ln m))+v^*(m-v^*)=0 & \text{in }\Omega,\\ \partial_n v^*-(1+\epsilon)v^*\partial_n(\ln m)=0 & \text{on }\partial\Omega.\end{cases}\tag{14}$$

Put $\hat{w}=\frac{v^*}{m^{1+\epsilon}}$. Then $\hat{w}$ satisfies:

$$\begin{cases} d_2\nabla\cdot(m^{1+\epsilon}\nabla\hat{w})+m^{1+\epsilon}\hat{w}(m-m^{1+\epsilon}\hat{w})=0 & \text{in }\Omega,\\ \partial_n\hat{w}=0 & \text{on }\partial\Omega.\end{cases}\tag{15}$$

Note that (15) can be rewritten as

$$\begin{cases} d_2\Delta\hat{w}+d_2\nabla[\ln(m^{1+\epsilon})]\nabla\hat{w}+\hat{w}(m-m^{1+\epsilon}\hat{w})=0 & \text{in }\Omega,\\ \partial_n\hat{w}=0 & \text{on }\partial\Omega.\end{cases}\tag{16}$$

By the implicit function theorem, we can write $\hat{w}=1+\epsilon w_1+O(\epsilon^2)$. Plugging in this expression to (16), we find that w_1 satisfies:

$$\begin{cases} d_2\Delta w_1+d_2\nabla(\ln m)\nabla w_1-m(w_1+\ln m)=0 & \text{in }\Omega,\\ \partial_n w_1=0 & \text{on }\partial\Omega.\end{cases}\tag{17}$$

Lemma 3.6. $\int_\Omega m^3(w_1+\ln m)>0$.

Proof. Let $w_1 = \varphi - \ln m$, then φ satisfies

$$\begin{cases} d_2 \nabla \cdot (m\nabla\varphi - \nabla m) - m^2\varphi = 0 & \text{in} \quad \Omega, \\ m\partial_n \varphi - \partial_n m = 0 & \text{on} \quad \partial\Omega. \end{cases} \tag{18}$$

Claim 3.7. *$\int_\Omega m^3 \varphi e^{-\varphi} \geq 0$.*

To see the claim, multiply (18) by $me^{-\varphi}$ and integrate the resulting equation in Ω,

$$\begin{aligned} \int_\Omega m^3\varphi e^{-\varphi} &= d_2 \int_\Omega \nabla \cdot (m\nabla\varphi - \nabla m) \cdot \left(me^{-\varphi}\right) \\ &= -d_2 \int_\Omega (m\nabla\varphi - \nabla m) \cdot \nabla \left(me^{-\varphi}\right) \\ &= -d_2 \int_\Omega (m\nabla\varphi - \nabla m) \cdot e^{-\varphi} \left(-m\nabla\varphi + \nabla m\right) \\ &= d_2 \int_\Omega e^{-\varphi} m^2 |\nabla(\varphi - \ln m)|^2 \geq 0. \end{aligned}$$

This proves Claim 3.7. Finally,

$$\int_\Omega m^3 \varphi \geq \int_\Omega m^3\varphi - \int_\Omega m^3 \varphi e^{-\varphi} = \int_\Omega m^3 e^{-\varphi}(\varphi - 0)(e^\varphi - e^0) > 0,$$

where φ is non-constant as m is non-constant. □

We now directly prove Proposition 3.5(ii):

Proof of Proposition 3.5(ii). Since $\beta = 1+\epsilon$, by Theorem 3.2, we need only demonstrate that $\int_\Omega m^2(m - v^*) < 0$ for all $\epsilon > 0$ sufficiently small. Using Lemma 3.6, $v^* = m^{1+\epsilon}\hat{w}$, and the expansion of $\hat{w}$ for ϵ small, we see that for $0 < \epsilon \ll 1$,

$$\begin{aligned} \int_\Omega m^2(m - v^*) &= \int_\Omega m^2[m - (m^{1+\epsilon}(1 + \epsilon w_1))] + O(\epsilon^2) \\ &= \int_\Omega m^2(m - m - \epsilon m w_1 - \epsilon m \ln m) + O(\epsilon^2) \\ &= -\epsilon \int_\Omega m^3(w_1 + \ln m) + O(\epsilon^2) < 0 \end{aligned}$$

for ϵ sufficiently small. This completes the proof. □

Remark 3. *We have actually proved that $\frac{d}{d\beta} \int_\Omega m^2(m - v^*)\big|_{\beta=1} < 0$. This also gives an alternative proof of (i) for β less than and close to 1.*

3.2. **Local stability of $(0, v^*)$ when $\beta \gg 1$.** We impose the following non-degeneracy condition on m.

- **(M2):** $m \in C^3(\Omega)$ has a unique critical point $x_0 \in \Omega$, which is a non-degenerate local (hence global) maximum, and $\partial_n m|_{\partial\Omega} \leq 0$.

Proposition 3.8. *Suppose* (M2) *holds, then there exists $\beta_0 > 1$ such that $(0, v^*)$ is unstable for all $\beta \in [\beta_0, \infty)$.*

Proof. First, we state the following result which follows from Theorem B.1 in Appendix B.

Lemma 3.9. *$v^* \to 0$ in $L^2(\Omega)$ as $\beta \to \infty$.*

Therefore $\int_\Omega m^2(m-v^*) < 0$ for β sufficiently large, and the proposition follows from Theorem 3.2. ☐

Remark 4. *The assumption* (M2) *can be relaxed here. In fact, by the proof of Theorem 3.5 of* [4] *(with modification as in Lemma 2.2(ii) of* [16]*), the conclusion of Lemma 3.9 and hence Proposition 3.8 hold provided the set of critical points of* m *is of measure zero.*

Because of the degeneracy of the linearization of (3) at $(m,0)$, we will determine the local stability of $(m,0)$ indirectly through the global dynamics, which is the subject of the following section.

4. **Global dynamics.** We now discuss the global dynamics of system (3) for $\beta \in [0,\infty)$. We begin with a result from [23].

Theorem 4.1. (*Theorem 2.1 and 2.2 in* [23]) *Suppose* $m \in C^2(\bar\Omega)$ *is positive and non-constant. Then there exists a* $0 < \beta^* \ll 1$*, such that for all* $\beta \in [0,\beta^*)$*,* $(m,0)$ *is globally asymptotically stable.*

Since (3) gives rise to a strongly monotone dynamical system, the proof of Theorem 4.1 in [23] follows a standard procedure: establish the stability of one of the two semi-trivial steady states and then show that the system does not admit any strictly positive steady states. We already know that $(0,v^*)$ is unstable for all $\beta \in (0,1)$ (Lemma 4.1 in [23]). In order to ensure the non-existence of positive steady states, we prescribe the following restriction on m and Ω.

(M3): Suppose $\Omega = B_R \subseteq \mathbb{R}^N$, $m = m(r)$ is non-constant, $m_r(0) = 0$, $m_{rr} < 0$ in $[0,R)$ and satisfies $m + 2rm_r \geq 0$ in $(0,R)$.

Proposition 4.2. *Suppose* (M3) *holds. Then there exists* $\epsilon_1 > 0$ *such that if* $0 < |\beta - 1| < \epsilon_1$*, then* (3) *does not have any positive steady states.*

Proof. See Section A. ☐

With non-existence of positive steady states for β sufficiently close to 1, we can infer the global dynamics of the system from the local stability results of $(0,v^*)$ established in the previous section.

Theorem 4.3. *Suppose* (M3) *holds. Then for* $\beta \in (1-\epsilon_1, 1)$*,* $(m,0)$ *is globally asymptotically stable.*

Proof. By Lemma 4.1 in [23] we have that $(0,v^*)$ is unstable for all $\beta \in (0,1)$. Proposition 4.2 says that for all $\beta \in (1-\epsilon_1,1)$, (3) has no positive steady states. Hence by monotone dynamical system theory [13, 26], the result is established. ☐

As the stability of $(0,v^*)$ depends on the fact that $\int_\Omega m^2(m-v^*) > 0$ and this quantity remains positive for all $\beta \in (0,1)$, we conjecture that $(m,0)$ will be globally attracting for all $\beta \in (0,1)$. Biologically, this means that the IFD strategy remains dominant even with the "penalty" of a weak Allee effect. However, this result dramatically changes when species v plays a strategy with advection slightly larger than 1. This is when v approximately attains an IFD while slightly overmatching the global maximum of m.

Theorem 4.4. *Suppose* (M3) *holds. Then there exists* $\epsilon' > 0$ *such that for all* $\beta \in (1, 1+\epsilon')$*,* $(0,v^*)$ *is globally asymptotically stable.*

Proof. By Proposition 3.5 (ii), $(0, v^*)$ is locally asymptotically stable for $\beta \in (1, 1+\epsilon_0)$. Also, Proposition 4.2 ensures us that for $\beta \in (1, 1+\epsilon_1)$, (3) has no positive steady states. Set $\epsilon' = \min\{\epsilon_0, \epsilon_1\}$. Then by monotone dynamical system theory [13, 26], $(0, v^*)$ is globally stable for all $\beta \in (1, 1+\epsilon')$. □

This result provides analytic justification to the prediction made in [23] and demonstrates that the ideal free disperser not only may be driven to extinction, but it may not be able to even invade.

However, as β grows larger, the stability of $(0, v^*)$ changes to be unstable again (see Theorem 2.3 in [23]), indicating that the ideal free disperser is not significantly affected by weak Allee effect. In order to capture the global picture, we want to demonstrate that (3) has no positive steady states for large β.

Proposition 4.5. *Suppose* (M1) *holds. Then for some* $\beta_1 > 1$, (3) *has no positive steady states for* $\beta > \beta_1$.

Proof. See Appendix B. □

This immediately leads to the global stability result:

Theorem 4.6. *Suppose* (M1) *holds. Then for some* $\beta' > 1$, $(m, 0)$ *is globally asymptotically stable for* $\beta > \beta'$.

Proof. Proposition 3.8 indicates that for $\beta > \beta_0$, $(0, v^*)$ is unstable. By Proposition 4.5, we have that for $\beta > \beta_1$, (3) has no positive steady states. Let $\beta' = \max\{\beta_0, \beta_1\}$. Then by monotone dynamical system theory [13, 26], $(m, 0)$ is globally asymptotically stable for all $\beta > \beta'$. □

5. **Discussion.** This study builds on the work in [1], where it was proven that the IFD strategy adopted by species u is evolutionarily stable. In other words, everything else being held equal, an established population of u is immune against invasion by any rare competitor species adopting a different dispersal strategy. In this paper, by establishing the global asymptotic stability of $(0, v^*)$ for β close to but greater that 1, we have shown that the ideal free disperser u is sometimes invadable by a rare competitor species v with a dispersal strategy that is not ideal free, provided that the fitness of u has a weak Allee effect. This illustrates the trade-off, in the dynamics of competing species in a spatially variable environment, between the advantage of an IFD strategy on the one hand, and the setback of a weak Allee effect on the other.

Not only is this biologically interesting, but the mathematics on which this notion rests are curious. First, the instability of the semi-trivial steady state $(m, 0)$ is established indirectly, through the local asymptotic stability and the non-existence of positive steady states. This indirect method is adopted due to the highly degenerate nature of $(m, 0)$ as a steady state of (3).

Second, we discuss the local stability of $(0, v^*)$, or equivalently, the invasibility of species v, when established, by species u. As shown above (see Section 3), the invasibility of u depends on the sign of the following integral condition:

$$C_\beta = \int_\Omega m^2(m - v^*). \tag{19}$$

To give an intuitive connection between (19) and the growth/decay of a rare ideal free disperser u, we first linearize system (3) at $(0, v^*)$, setting $u(x,t) = \epsilon\psi(x)e^{-\lambda t} + O(\epsilon^2)$ and $v(x,t) = v^* + \epsilon\phi(x)e^{-\lambda t} + O(\epsilon^2)$. Substituting these expressions into (3)

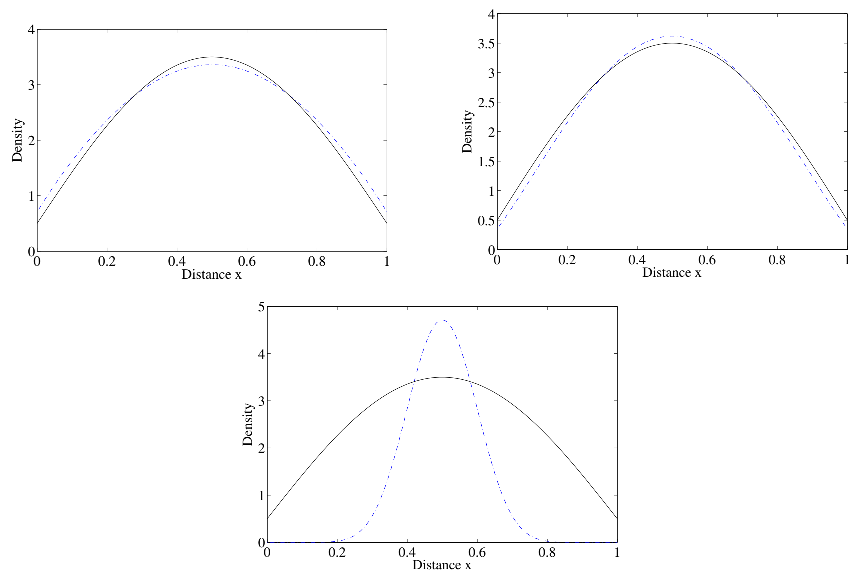

FIGURE 1. Three steady state profiles of species v: (i) $\beta \in (\beta_2, 1)$ (ii) $\beta \in (1, \beta_3)$ (iii) $\beta \gg 1$. Note the resource $m(x) = 3\sin(\pi x)+0.5$ is black and the dotted blue curve represents v^* in each subfigure.

and letting $\epsilon \to 0$, we can show that $\lambda = 0$ is the principal eigenvalue and ψ satisfies the following:

$$\begin{cases} d_1 \nabla \cdot \left(m \nabla \left(\dfrac{\psi}{m} \right) \right) = 0 & \text{in } \Omega, \\ \partial_n(\psi/m) = 0 & \text{on } \partial\Omega. \end{cases} \tag{20}$$

By the maximum principle and after suitable rescaling, $\frac{\psi}{m} \equiv 1$ in Ω, and therefore, $\psi = m$ in Ω. This means that apart from the principal eigenfunction m, all other modes of invasion for species u decay exponentially to zero. Therefore, we can write $u(x,t) = \epsilon m + O(\epsilon^2, e^{-\lambda_2 t})$, where $\lambda_2 > 0$ is the second eigenvalue of system (3) linearized at $(0, v^*)$.

If we integrate the equation for u in (3) over Ω we have:

$$\begin{aligned} \frac{d}{dt}\int_\Omega u &= \int_\Omega u^2(m-u-v) \\ &= \int_\Omega u^2(m-u-v+v^*-v^*) \\ &= \epsilon^2 \int_\Omega m^2(m-v^*) + O(\epsilon^3, e^{-\lambda_2 t}) \end{aligned}$$

Thus, we see that the growth or decay (on average) of u depends on the sign of C_β.

What is remarkable is that C_β changes from positive to negative as β increases to surpass the critical value 1. Locally, this means that $(0, v^*)$ changes from being unstable (for $\beta < 1$) to asymptotically stable for $\beta > 1$. Using steady state profiles, we further illustrate this connection:

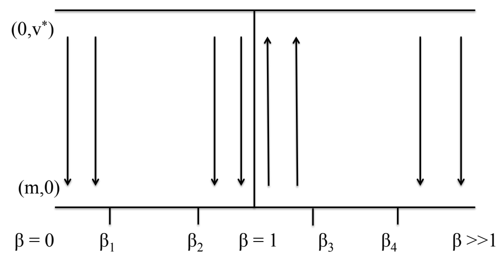

FIGURE 2. Bifurcation diagram illustrating the ideal free strategy tradeoff with the weak Allee effect.

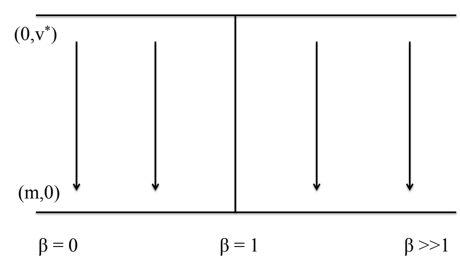

FIGURE 3. Bifurcation diagram illustrating the ideal free strategy as a global ESS for species with identical population dynamics.

- For $\beta \in (\beta_2, 1)$, v^* under-matches m near the global maximum x_0 and over-matches away from this maximum (see Figure 1(i)) In this case, (19) is positive, indicating that u can invade. Here u, when rare, will have a positive growth rate for all time near the maximum point x_0, which is enough for it to overcome the weak Allee effect.
- For $\beta \in (1, \beta_3)$, we see that v^* over matches near x_0 and under matches elsewhere (see Figure 1(ii)). While u can have positive growth rates away from x_0, the integral condition specifies that this is not enough to overcome the Allee effect and compete with resident species v^*.
- For larger β, while v^* still dominates resource acquisition near x_0, its concentration near x_0 implies that C_β is negative again (see Figure 1(iii)) and, by making use of resources away from x_0, u is able to invade.

We summarize the global results for system (3) in Figure 2. For convenience, we also summarize the global results for system (3) when u is not subject to the weak Allee effect (coming from [1]) in Figure 3.

Appendix A. Non-existence of Positive Steady States when $\beta \approx 1$.

Lemma A.1. *For each $t \in [0,1]$, there exists non-negative eigenfunction (ϕ', ψ') satisfying*

$$\begin{cases} d_1\nabla\cdot(m\nabla\phi') - (1-t)^2 m^3\phi' + tm^2\psi' = 0 & \text{in } \Omega, \\ d_2\nabla\cdot(m\nabla\psi') + (1-t)^2 m^3\phi' - tm^2\psi' = 0 & \text{in } \Omega, \\ \partial_n\phi' = \partial_n\psi' = 0 & \text{on } \partial\Omega. \end{cases} \tag{21}$$

Moreover,

(i) $d_1\phi' + d_2\psi' = const.$;
(ii) If $t \in (0,1)$, then $\phi' > 0$ and $\psi' > 0$ in $\bar{\Omega}$;
(iii) If we normalize by $d_1\phi' + d_2\psi' = 1$, then ψ' is give by

$$\begin{cases} \nabla\cdot(m\nabla\psi') - \left[\frac{(1-t)^2}{d_1}m^3 + \frac{t}{d_2}m^2\right]\psi' = -\frac{(1-t)^2}{d_1 d_2}m^3 & \text{in } \Omega, \\ \partial_n\psi' = 0 & \text{on } \partial\Omega, \end{cases} \tag{22}$$

and satisfies $\lim_{t\to 0}\psi' = \psi'\big|_{t=0} = \frac{1}{d_2}$.

Proof. By the spectral theory of cooperative system, there exists a principal eigenvalue λ' with non-negative eigenfunction (ϕ', ψ'), satisfying

$$\begin{cases} \nabla\cdot(m\nabla\phi') - \frac{(1-t)^2}{d_1}m^3\phi' + \frac{t}{d_1}m^2\psi' + \lambda'\phi' = 0 & \text{in } \Omega, \\ \nabla\cdot(m\nabla\psi') + \frac{(1-t)^2}{d_2}m^3\phi' - \frac{t}{d_2}m^2\psi' + \lambda'\psi' = 0 & \text{in } \Omega, \\ \partial_n\phi' = \partial_n\psi' = 0 & \text{on } \partial\Omega. \end{cases}$$

To show (i), it remains to show that $\lambda' = 0$. To this end, multiply the first equation by d_1 and the second equation by d_2, and then add the two equation. We then see that $\rho = d_1\phi' + d_2\psi' \geq 0$ is a non-negative eigenfunction of

$$\begin{cases} \nabla\cdot(m\nabla\rho) + \lambda'\rho = 0 & \text{in } \Omega, \\ \partial_n\rho = 0 & \text{on } \partial\Omega. \end{cases}$$

Hence $\lambda' = 0$ and ρ is a positive constant. This proves (i). (ii) follows from the fact that when $t \in (0,1)$, then (21) is irreducible. For (iii), (22) follows by substituting $\phi' = 1/d_1 - d_2\psi'/d_1$ into the second equation of (21). The final claim follows by observing that $1/d_2$ is the unique solution of (22) when $t = 0$. □

Lemma A.2. *Suppose* (M3) *holds, then for all $t \in (0,1)$, $\int_\Omega \nabla m\cdot\nabla\psi' \neq 0$. Moreover,*

$$\liminf_{t\to 0^+}\frac{1}{t}\left|\int_\Omega \nabla m\cdot\nabla\psi'\right| > 0.$$

Proof. Assume (M3), then $m = m(r)$ implies, by uniqueness, that ψ' is radially symmetric, i.e. $\psi' = \psi'(r)$. Written in radial coordinate, (22) becomes

$$\begin{cases} m\psi'_{rr} + \left[\frac{N-1}{r} + m_r\right]\psi'_r - \left[\frac{(1-t)^2}{d_1}m^3 + \frac{t}{d_2}m^2\right]\psi' = -\frac{(1-t)^2}{d_1 d_2}m^3 & \text{in } (0,R), \\ \psi'_r 0 = \psi'_r(R) = 0. \end{cases} \tag{23}$$

Note that $\psi' > 0$ in Ω by the maximum principle. Differentiating (23) with respect to r and multiplying the result by m, we deduce that

$$\begin{aligned}
&m^2\psi'_{rrr} + \left(2mm_r + m^2\frac{N-1}{r}\right)\psi'_{rr}\\
&\quad + \left\{mm_r\frac{N-1}{r} - m^2\frac{N-1}{r^2} + mm_{rr} - m\left[\frac{(1-t)^2}{d_1}m^3 + \frac{t}{d_2}m^2\right]\right\}\psi'_r\\
=&3m_r\left[\frac{(1-t)^2}{d_1}m^3 + \frac{t}{d_2}m^2\right]\psi' - \frac{t}{d_2}m^2m_r\psi' - \frac{(1-t)^2}{d_1d_2}3m^3m_r\\
=&3m_r\left[m\psi'_{rr} + m\frac{N-1}{r}\psi'_r + m_r\psi'_r\right] - \frac{t}{d_2}m^2m_r\psi'.
\end{aligned}$$

where we used equation (22) in the second to last equality. In conclusion, ψ'_r satisfies the inhomogeneous linear elliptic equation

$$\begin{cases}
m^2\psi'_{rrr} + \left(-mm_r + m^2\dfrac{N-1}{r}\right)\psi'_{rr}\\
+\left\{-m\dfrac{N-1}{r}\left(\dfrac{m}{r} + 2m_r\right) + mm_{rr} - 3m_r^2 - m\left[\dfrac{(1-t)^2}{d_1}m^3 + \dfrac{t}{d_2}m^2\right]\right\}\psi'_r\\
= -\dfrac{t}{d_2}m^2m_r\psi' \quad \text{in} \quad \Omega, \quad \psi'_r(0) = \psi'_r(R) = 0.
\end{cases} \tag{24}$$

Because of the assumptions on m and the fact that $\psi' > 0$ in Ω, for all $t \in (0,1)$, the strong maximum principle implies that $\psi'_r < 0$ in $(0,R)$. Hence, $\int_\Omega m_r\psi'_r \neq 0$. Moreover, by Lemma A.1, $\lim_{t\to 0}\psi' \to 1/d_2$. Hence, $\rho = \lim_{t\to 0}\psi'_r/t$ satisfies

$$\begin{cases}
m^2\rho_{rr} + \left(-mm_r + m^2\dfrac{N-1}{r}\right)\rho_r\\
\quad + \left[-m\dfrac{N-1}{r}\left(\dfrac{m}{r} + 2m_r\right) + mm_{rr} - 3m_r^2 - \dfrac{m^4}{d_1}\right]\rho\\
= -\dfrac{1}{d_2^2}m^2m_r \quad \text{in} \quad \Omega, \quad \rho(0) = \rho(R) = 0.
\end{cases} \tag{25}$$

and we see that $\rho < 0$ in $(0,R)$. Therefore, $\lim_{t\to 0} t^{-1}\left|\int_\Omega m_r\psi'_r\right| = \left|\int_\Omega m_r\rho\right| > 0$. ☐

A.1. **Proof of Proposition 4.2.** Suppose to the contrary that for a sequence of $\epsilon = \beta - 1$, system (3) has a corresponding positive steady state $(u,v) = (u(\epsilon), v(\epsilon))$. By compactness, we see that as $\epsilon \to 0$, (u,v) converges to a non-negative solution of

$$\begin{cases}
d_1\nabla\cdot\left(m\nabla\left(\dfrac{u}{m}\right)\right) + u^2(m-u-v) = 0 & \text{in} \quad \Omega,\\
d_2\nabla\cdot\left(m\nabla\left(\dfrac{v}{m}\right)\right) + v(m-u-v) = 0 & \text{in} \quad \Omega,\\
\partial_n\left(\dfrac{u}{m}\right) = \partial_n\left(\dfrac{v}{m}\right) = 0 & \text{on} \quad \partial\Omega.
\end{cases} \tag{26}$$

Claim A.3. *If $(\tilde{u},\tilde{v})$ is a non-negative solution of (26), then either $(\tilde{u},\tilde{v}) = 0$ or $(\tilde{u},\tilde{v}) = ((1-t_0)m, t_0m)$ for some $t_0 \in [0,1]$.*

If one of $\tilde{u}$ or $\tilde{v}$ is identically zero, it is easy to see that

$$(\tilde{u},\tilde{v}) = (0,0), \ \ (m,0), \ \ \text{or} \ \ (0,m).$$

Suppose $\tilde{u}$, $\tilde{v}$ are both not identically zero, then by the maximum principle (see also Proposition 2.2 of [17]), we have

$$0 < \tilde{u} < m \text{ and } 0 < \tilde{v} < m \text{ in } \bar{\Omega}.$$

Let t_0 be the maximal positive number such that $\tilde{u} \le (1-t_0)m$ and $\tilde{v} \ge t_0 m$, then one of the non-negative functions $w := (1-t_0)m - \tilde{u}$ and $z := \tilde{v} - t_0 m$ vanishes somewhere in $\bar{\Omega}$. It suffices to show that $w \equiv z \equiv 0$. Note that w, z satisfies

$$\begin{cases} d_1 \nabla \cdot \left(m \nabla \left(\frac{w}{m} \right) \right) - \tilde{u}^2 m(w/m) = -\tilde{u}^2 z \le 0 & \text{in} \quad \Omega, \\ d_2 \nabla \cdot \left(m \nabla \left(\frac{z}{m} \right) \right) - \tilde{v} m(z/m) = -\tilde{v} w \le 0 & \text{in} \quad \Omega, \\ \partial_n \left(\frac{w}{m} \right) = \partial_n \left(\frac{z}{m} \right) = 0 & \text{on} \quad \partial\Omega. \end{cases} \tag{27}$$

Suppose that $w(x_0) = 0$ for some $x_0 \in \bar{\Omega}$. If $w > 0$ in Ω and $x_0 \in \partial\Omega$, then by Hopf's boundary point lemma, $\partial_n(w/m)(x_0) < 0$ and this contradicts the boundary condition of w. Therefore we must have $x_0 \in \Omega$, but then by the strong maximum principle, $w \equiv 0$ and hence $z \equiv 0$. This shows that $(\tilde{u}, \tilde{v}) = ((1-t_0)m, t_0 m)$ for some $t_0 \in (0,1)$. The case where z vanishes somewhere in $\bar{\Omega}$ can be handled similarly. This proves Claim A.3.

Claim A.4. *As $\epsilon \to 0$, by passing to a subsequence, the positive steady state (u,v) converges to $((1-t_0)m, t_0 m)$ for some $t_0 \in [0,1]$.*

By Claim A.3, it suffices to show that $(u,v) \not\to (0,0)$. Suppose to the contrary that $(u,v) \to (0,0)$, then $v/\|v\|_\infty \to \hat{v}$ in $C^1(\bar{\Omega})$ where $\hat{v}$ is non-negative, $\|\hat{v}\|_\infty = 1$ and satisfies

$$\begin{cases} d_2 \nabla \cdot \left(m \nabla \frac{\hat{v}}{m} \right) + m\hat{v} = 0 & \text{in } \Omega, \\ \partial_n \left(\frac{\hat{v}}{m} \right) = 0 & \text{on } \partial\Omega. \end{cases}$$

Integrating over Ω, we have $\int m\hat{v} = 0$. This contradiction proves Claim A.4.

Lemma A.5. *For all ϵ sufficiently small, there exists $u_1, v_1 \in C^1(\bar{\Omega})$ such that $\|u_1\|_{C^1} + \|v_1\|_{C^1} \le O(\epsilon)$ and*

$$(u - u_1, v - v_1) \in \left\{ ((1-t)m, tm) \,\middle|\, t \in \mathbb{R} \right\}.$$

In particular, $\|m - u - v\|_{C^1} \le O(\epsilon)$.

Proof of Lemma A.5. Let $X = \{(w,z) \in [W^{2,p}(\Omega)]^2 \,|\, \partial_n w = \partial_n z = 0 \text{ on } \partial\Omega\}$ for some $p > N$, and let X_1 be a proper subspace of X, such that

$$X_1 + \operatorname{span}\{(1,1)\} = [W^{2,p}(\Omega)]^2.$$

Then for any $(u,v) \in X$, we can decompose

$$(u,v) = ((1-t)m - mw_1, tm^{1+\epsilon} + m^{1+\epsilon} z_1) \tag{28}$$

for some $t \in \mathbb{R}$ and $(w_1, z_1) \in X_1$ satisfying

$$\begin{cases} d_1 \nabla \cdot (m \nabla w_1) - m^3 (1 - t - w_1)^2 [t + w_1 - m^\epsilon (t + z_1)] = 0 & \text{in } \Omega, \\ d_2 \nabla \cdot \left(m^{1+\epsilon} \nabla z_1 \right) + m^{2+\epsilon} (t + z_1)[t + w_1 - m^\epsilon (t + z_1)] = 0 & \text{in } \Omega, \\ \partial_n w_1 = \partial_n z_1 = 0 & \text{on } \partial\Omega. \end{cases} \tag{29}$$

Let us define $\mathcal{F} : X_1 \times (-\epsilon_0, \epsilon_0) \times (-\delta, 1+\delta) \to [L^p(\Omega)]^2$ (with δ as given in Claim A.6 below) as

$$\mathcal{F}(w,z,\epsilon,t) := \begin{pmatrix} d_1 \nabla \cdot (m \nabla w) - m^3 (1 - t - w_1)^2 [t + w_1 - m^\epsilon (t + z_1)] \\ d_2 \nabla \cdot \left(m^{1+\epsilon} \nabla z \right) + m^{2+\epsilon} (t + z_1)[t + w_1 - m^\epsilon (t + z_1)] \end{pmatrix}$$

then the Frechét derivative $D_{(w,z)}\mathcal{F}$ at $(w,z,\epsilon,t) = (0,0,0,t)$ is given by $L_t\big|_{X_1}$, where $L_t : X \to [L^p(\Omega)]^2$ is given by

$$L_t(\phi,\psi) = \begin{pmatrix} d_1\nabla\cdot(m\nabla\phi) + (1-t)^2m^3(-\phi+\psi) \\ d_2\nabla\cdot(m\nabla\psi) + tm^2(\phi-\psi) \end{pmatrix}.$$

Claim A.6. *For some $\delta > 0$, $\ker L_t = \operatorname{span}\{(1,1)\}$ for all $t \in [-\delta, 1+\delta]$.*

It is easy to see the claim when $t = 0, 1$. For $t \in (0,1)$, L_t is an irreducible, cooperative operator with zero as an eigenvalue corresponding a positive eigenfunction $(1,1)$. It follows that zero must be the principal eigenvalue, and is necessarily simple. This proves the claim for $t \in [0,1]$, and the rest follows by continuity.

Hence $\ker L_t \cap X_1 = \{(0,0)\}$. On the other hand, since zero is the principal eigenvalue of the cooperative operator L_t (for $t \in [0,1]$), one can deduce that $L_t - \sigma I : X \to [L^p(\Omega)]^2$ is invertible for any $\sigma > 0$ and $t \in [0,1]$. Therefore, L_t is Fredholm with index zero for $t \in (-\delta, 1+\delta+1)$, for some $\delta > 0$ small, i.e., (together with Claim A.6)

$$\dim\operatorname{coker} L_t = \dim\ker L_t = 1 \quad \text{for all } t \in (-\delta, 1+\delta). \tag{30}$$

Next, we define a projection operator

$$P_t(f,g) = \frac{\int(f\phi' + g\psi')}{\int[(\phi')^2 + (\psi')^2]}\begin{pmatrix}\phi' \\ \psi'\end{pmatrix},$$

where (ϕ',ψ') is given in Lemma A.1. Observe that the range of L_t is given by $\ker P_t$ (by Range of $L_t \subseteq \ker P_t$ and (30)), and hence L_t is an isomorphism from X_1 to $\ker P_t$. As $(I-P_t)\mathcal{F}(\cdot,\cdot,\epsilon,t) : X_1 \to \ker P_t$ satisfies

$$D_{(w,z)}[(I-P_t)\mathcal{F}]\big|_{(w_1,z_1,\epsilon,t)=(0,0,0,t)} = (I-P_t)L_t = L_t,$$

we may apply the Implicit Function Theorem to $(I-P_t)\mathcal{F}$. For each steady state (u,v) of (3), by the decomposition (28) and Claim A.4, we have $(u,v) = ((1-t)m - mw_1, tm + mz_1)$, for some $t \in [-\delta, 1+\delta]$ and $(w_1,z_1) \in X_1$ close to $(0,0)$, which satisfies

$$\mathcal{F}(w_1,z_1) = 0 \Longrightarrow (I-P_t)\mathcal{F}(w_1,z_1) = 0.$$

Now, (i) if $\epsilon = 0$, then $(w_1,z_1) = 0$ for all t (Claim A.3), and (ii) for ϵ sufficiently small, any steady state (u,v) of (3) is close to $\{(1-t)m, tm) | t \in (-\delta, 1+\delta)\}$. If we decompose (u,v) as in (28), then the Implicit Function Theorem implies $\|w_1\|_{C^1} + \|z_1\|_{C^1} \le O(\epsilon)$, uniformly for $t \in (-\delta/2, 1+\delta/2)$. Finally, the conclusion follows by setting $u_1 = -mw_1$ and $v_1 = tm(m^\epsilon - 1) + m^{1+\epsilon}z_1$. □

It remains to consider three cases: (1) $(u,v) \to ((1-t_0)m, t_0m)$ for some $t_0 \in (0,1)$; (2) $(u,v) \to (m,0)$; (3) $(u,v) \to (0,m)$.

Case (1): $(u,v) \to ((1-t_0)m, t_0m)$ as $\epsilon \to 0$, for some $t_0 \in (0,1)$.

By Proposition A.5, we may write $u = (1-t)m - u_1$ and $v = tm + v_1$ for some t and (u_1,v_1) such that $|t - t_0| = o(1)$ with $\|u_1\|_{C^1} + \|v_1\|_{C^1} \le O(\epsilon)$. Divide (29) by ϵ and pass to the limit, letting $\phi_1 := \lim_{\epsilon\to 0} u_1/\epsilon$ and $\psi_1 := \lim_{\epsilon\to 0} v_1/\epsilon$. Then ϕ_1

and ψ_1 satisfies

$$\begin{cases} d_1\nabla\cdot\left(m\nabla\dfrac{\phi_1}{m}\right)+[(1-t_0)m]^2(-\phi_1+\psi_1)=0 & \text{in } \Omega,\\ d_2\nabla\cdot\left(m\nabla\dfrac{\psi_1}{m}\right)+t_0m(\phi_1-\psi_1)=d_2t_0\Delta m & \text{in } \Omega,\\ \partial_n\left(\dfrac{\phi_1}{m}\right)=0,\quad \partial_n\left(\dfrac{\psi_1}{m}\right)=\dfrac{t_0}{m}\partial_n m & \text{on } \partial\Omega. \end{cases} \tag{31}$$

Note that $(\phi_1,\psi_1)\neq(0,0)$, otherwise $\Delta m=0$ in Ω and $\partial_n m=0$ on $\partial\Omega$, which contradicts the assumption that m is non-constant. Let (ϕ',ψ') be the principal eigenfunction guaranteed by Lemma A.1, i.e. $\phi',\psi'>0$ in $\bar{\Omega}$ satisfies (21) with $t=t_0\in(0,1)$. Multiply the first equation of (31) by ϕ' and integrate by parts, we have

$$\int\left\{\frac{\phi_1}{m}d_1\nabla\cdot(m\nabla\phi')+[(1-t_0)m]^2(-\phi_1+\psi_1)\phi'\right\}=0. \tag{32}$$

Multiply the second equation of (31) by ψ' and integrate by parts, we have

$$\int\left\{\frac{\psi_1}{m}d_2\nabla\cdot(m\nabla\psi')+t_0m(\phi_1-\psi_1)\psi'\right\}=-d_2t_0\int\nabla m\cdot\nabla\psi'. \tag{33}$$

Adding (32) and (33), we deduce by (21) that

$$\begin{aligned} 0&=\int\frac{\phi_1}{m}\left[d_1\nabla\cdot(m\nabla\phi')-(1-t_0)^2m^3\phi'+t_0m^2\psi'\right]\\ &\quad+\int_\Omega\frac{\psi_1}{m}\left[d_2\nabla\cdot(m\nabla\psi')+(1-t_0)^2m^3\phi'-t_0m^2\psi'\right]\\ &=-d_2t_0\int\nabla m\cdot\nabla\psi' \end{aligned}$$

which is impossible, as the last integral is non-zero by Lemma A.2.

Case (2): $(u,v)\to(m,0)$ as $\epsilon\to0$.

Claim A.7. *Let* $\delta:=(\|u-m\|_\infty+\|v\|_\infty)/(2\|m\|_\infty)$*, then*

$$\left(\frac{m-u}{\delta},\frac{v}{\delta}\right)\to(m,m)\qquad \text{in } C^1(\bar{\Omega}).$$

To see the claim, we write $u=m-\delta u_2$ and $v=\delta v_2$, then $u_2,v_2\geq0$ and by definition $\|u_2\|_\infty+\|v_2\|_\infty=2\|m\|_\infty$. Moreover, u_2,v_2 satisfy

$$\begin{cases} d_1\nabla\cdot\left[m\nabla\left(\dfrac{u_2}{m}\right)\right]-(m-\delta u_2)^2(u_2-v_2)=0 & \text{in } \Omega,\\ d_2\nabla\cdot\left[m\nabla\left(\dfrac{v_2}{m}\right)\right]+v_2(\delta u_2-\delta v_2)=d_2\epsilon\nabla\cdot[v_2\nabla\ln m] & \text{in } \Omega,\\ \partial_n u_2-\dfrac{u_2}{m}\partial_n m=\partial_n v_2-(1+\epsilon)\dfrac{v_2}{m}\partial_n m=0 & \text{on } \partial\Omega. \end{cases}$$

By elliptic estimates, we may let $u_2 \to \phi_2$ and $v_2 \to \psi_2$ in $C^1(\bar{\Omega})$, where ϕ_2, ψ_2 satisfy (weakly) the following system

$$\begin{cases} d_1 \nabla \cdot \left[m \nabla \left(\dfrac{\phi_2}{m} \right) \right] - m^2(\phi_2 - \psi_2) = 0 & \text{in } \Omega, \\ d_2 \nabla \cdot \left[m \nabla \left(\dfrac{\psi_2}{m} \right) \right] = 0 & \text{in } \Omega, \\ \partial_n \left(\dfrac{\phi_2}{m} \right) = \partial_n \left(\dfrac{\psi_2}{m} \right) = 0 & \text{on } \partial\Omega, \\ \|\phi_2\|_\infty + \|\psi_2\|_\infty = 2\|m\|_\infty. \end{cases}$$

which implies that $(\phi_2, \psi_2) = (m, m)$. This proves Claim A.7.

Hence, we may write

$$u = (1 - \delta)\, m - u_3, \quad v = \delta m + v_3, \quad \|u_3\|_{C^1} + \|v_3\|_{C^1} \le o(\delta).$$

Moreover, u_3, v_3 satisfies

$$\begin{cases} d_1 \nabla \cdot \left[m \nabla \left(\frac{u_3}{m} \right) \right] + \left[(1 - \delta)\, m - u_3 \right]^2 (-u_3 + v_3) = 0 & \text{in } \Omega, \\ d_2 \nabla \cdot \left[m \nabla \left(\frac{v_3}{m} \right) \right] + (\delta m + v_3)(u_3 - v_3) = d_2 \epsilon \nabla \cdot \left[(\delta m + v_3) \nabla \ln m \right] & \text{in } \Omega \\ \partial_n u_3 - \frac{u_3}{m} \partial_n m = 0, \quad \partial_n v_3 - \frac{v_3}{m} \partial_n m = \frac{\epsilon}{m} (\delta m + v_3)\, \partial_n m & \text{on } \partial\Omega. \end{cases} \tag{34}$$

Similar to Lemma A.1, we have the following result.

Lemma A.8. *For all $\epsilon = \beta - 1$ small (hence $\delta > 0$ small), there exists a pair of positive eigenfunctions $(\hat{\phi}, \hat{\psi})$ satisfying $d_1 \hat{\phi} + d_2 \hat{\psi} = 1$, and*

$$\begin{cases} d_1 \nabla \cdot (m \nabla \hat{\phi}) - \left[(1 - \delta) m - u_3 \right]^2 m \hat{\phi} + (\delta m + v_3) m \hat{\psi} = 0 & \text{in } \Omega, \\ d_2 \nabla \cdot (m \nabla \hat{\psi}) + \left[(1 - \delta) m - u_3 \right]^2 m \hat{\phi} - (\delta m + v_3) m \hat{\psi} = 0 & \text{in } \Omega, \\ \partial_n \hat{\phi} = \partial_n \hat{\psi} = 0 & \text{on } \partial\Omega, \end{cases} \tag{35}$$

where $\hat{\psi}$ is given by the unique solution to

$$\begin{cases} \nabla \cdot (m \nabla \hat{\psi}) - \left\{ \frac{m}{d_1} \left[(1 - \delta) m - u_3 \right]^2 + \frac{m}{d_2} (\delta m + v_3) \right\} \hat{\psi} = -\frac{m}{d_1 d_2} [(1 - \delta) m - u_3]^2 \\ \hfill \text{in } \Omega, \\ \partial_n \hat{\psi} = 0 \hfill \text{on } \partial\Omega, \end{cases} \tag{36}$$

and satisfies $\lim_{\epsilon \to 0} \hat{\psi} = 1/d_1$. Moreover, if (M3) *holds, then $\|\nabla \hat{\psi}\|_\infty = O(\delta)$ and*

$$\liminf_{\epsilon \to 0} \frac{1}{\delta} \left| \int \nabla m \cdot \nabla \hat{\psi} \right| > 0.$$

Proof of Lemma A.8. The existence of $(\hat{\phi}, \hat{\psi})$ and the limit $\lim_{\epsilon \to 0} \hat{\psi} = 1/d_1$ can be proven in a similar manner as Lemma A.1 and is omitted. For the remaining part, we assume (M3) and write the equation of $\hat{\psi}$ in radial coordinate:

$$\begin{cases} m \hat{\psi}_{rr} + \left[\frac{N-1}{r} m + m_r \right] \hat{\psi}_r - \left\{ \frac{m}{d_1} [(1 - \delta) m - u_3]^2 + \frac{m}{d_2} (\delta m + v_3) \right\} \hat{\psi} \\ \quad = -\frac{m}{d_1 d_2} [(1 - \delta) m - u_3]^2 & \text{in } (0, R), \\ \psi_r(0) = \psi_r(R) = 0. \end{cases} \tag{37}$$

Differentiate (37) with respect to r, we deduce

$$\begin{aligned} &m^2\hat{\psi}_{rrr} + \left[-mm_r + \frac{N-1}{r}m^2\right]\hat{\psi}_{rr} - \left\{\frac{m^2}{d_1}[(1-\delta)m - u_3]^2 + \frac{m^2}{d_2}(\delta m + v_3)\right\}\hat{\psi}_r \\ &\quad + \left\{-\frac{N-1}{r}m\left(2m_r + \frac{m}{r}\right) + mm_{rr} - 3m_r^2\right\}\hat{\psi}_r \\ &= -\frac{\delta}{d_2}m^2 m_r\hat{\psi} + O(\|u_3\|_{C^1} + \|v_3\|_{C^1}) \\ &= -\frac{\delta}{d_2}m^2 m_r\hat{\psi} + o(\delta) > 0, \end{aligned}$$

where the last inequality follows from the fact that $\hat{\psi} \to 1/d_1$ as $\epsilon \to 0$. Hence $\|\nabla\hat{\psi}\|_\infty = \|\hat{\psi}_r\|_\infty = O(\delta)$ and $\hat{\psi}_r < 0$ for ϵ sufficiently small. The rest of the proof is similar to the proof of Lemma A.2 and is omitted. □

Now, similar to the procedure in Case (i), let $(\hat{\phi}, \hat{\psi})$ be given by Lemma A.8. Multiply the first equation of (34) by $\hat{\phi}$ and the second by $\hat{\psi}$. Upon integrating by parts and adding the equations, we have

$$\begin{aligned} 0 = &\int \left\{\frac{u_3}{m}\left[d_1\nabla\cdot(m\nabla\hat{\phi}) - \left[(1-\delta)\,m\hat{\phi} + u_3\right]^2 m\hat{\phi} + (\delta m + v_3)m\psi'\right]\right. \\ &\quad \left. + \frac{v_3}{m}\left[d_2\nabla\cdot(m\nabla\hat{\psi}) + [(1-\delta)\,m\phi' + u_3]^2\, m\hat{\phi} - (\delta m + v_3)m\psi'\right]\right\} \\ = &-d_2\epsilon\int(\delta m + v_3)\,\nabla\ln m\cdot\nabla\hat{\psi} \\ = &-d_2\epsilon\left[\delta\int\nabla m\cdot\nabla\hat{\psi} + o(\delta^2)\right], \end{aligned}$$

where in the last line, we have used the fact that $\|\nabla\hat{\psi}\|_\infty \le O(\delta)$ (Lemma A.8). By Lemma A.8, the last term is non-zero for sufficiently small ϵ, δ. This is a contradiction.

Case (3): $(u, v) \to (0, m)$ as $\epsilon \to 0$.

Write

$$u = sm + u_4, \quad \int u_4 m = 0, \quad \text{and} \quad v = (1-s)v^* + v_4$$

where $v^* = v^*(\epsilon)$ is the positive steady state of (4) when $\beta = 1 + \epsilon$. By Lemma A.5, $s = o(1)$. Moreover,

$$u_4 + v_4 = (u + v - m) + (1-s)(m - v^*) = O(\epsilon), \tag{38}$$

as $u + v - m = O(\epsilon)$ by Lemma A.5 and $m - v^* = O(\epsilon)$.

Claim A.9. $\|u_4\|_\infty \le o(s)$.

To see the claim, first observe that $\frac{u}{\|u\|_\infty} \to \frac{m}{\|m\|_\infty}$ in C^1 (by dividing the equation of u by $\|u\|_\infty$, and using compactness). Hence,

$$sm + u_4 = \frac{\|u\|_\infty}{\|m\|_\infty}m + o(\|u\|_\infty). \tag{39}$$

Multiply (39) by m and integrate, we have

$$s\int m^2 = \frac{\|u\|_\infty}{\|m\|_\infty}\int m^2 + o(\|u\|_\infty),$$

and hence $\|u\|_\infty = \|m\|_\infty s + o(s)$. Therefore by (39), we deduce

$$sm + u_4 = sm + o(s).$$

And the desired conclusion follows upon canceling sm from both sides.

Claim A.10. $\|u_4\|_{C^1} + \|v_4\|_{C^1} \leq o(\epsilon)$.

First, observe that u_4 satisfies

$$\begin{cases} d_1\nabla\cdot\left(m\nabla\frac{u_4}{m}\right) = -u^2[(1-s)(m-v^*) - u_4 - v_4] = o(\epsilon) \\ \partial_n \frac{u_4}{m}\big|_{\partial\Omega} = 0 \quad \text{and} \quad \int u_4 m = 0 \end{cases}$$

where the estimate follows from (38). Hence by Poincaré's inequality, $\|u_4\|_{C^1} \leq o(\epsilon)$. Next, observe that v_4 satisfies

$$\begin{cases} d_2\nabla\cdot\left(m\nabla\frac{v_4}{m}\right) + [(1-s)(m-2v^*) - (u_4+v_4)]v_4 \\ \quad = (1-s)v^*u_4 + (1-s)sv^*(m-v^*) \\ \partial_n \frac{v_4}{m^\beta}\big|_{\partial\Omega} = 0 \quad \text{and} \quad \int u_4 m = 0. \end{cases}$$

Simplifying,

$$\begin{cases} d_2\nabla\cdot\left(m\nabla\frac{v_4}{m}\right) + [(m-2v^*) + o(1)]v_4 = O(\|u_4\|_{C^1} + s\epsilon) = o(\epsilon) \\ \partial_n \frac{v_4}{m^\beta}\big|_{\partial\Omega} = 0. \end{cases}$$

By the uniform invertibility of the corresponding linear problem (see Claim 3.4), we have $\|v_4\|_{C^1} \leq o(\epsilon)$. This proves Claim A.10.

Next, by integrating the equation of u over Ω and dividing by s^2, we have

$$\begin{aligned} 0 &= \int \left(\frac{u}{s}\right)^2 (m-u-v) \\ &= \int \left(m + \frac{u_4}{s}\right)^2 [(1-s)(m-v^*) - u_4 - v_4] \\ &= (1-s)\int \left(m + \frac{u_4}{s}\right)^2 (m-v^*) - \int \left(m + \frac{u_4}{s}\right)^2 (u_4+v_4) \\ &= (1-s)\int m^2(m-v^*) + (1-s)\int \frac{u_4}{s}\left(2m + \frac{u_4 m}{s}\right)(m-v^*) \\ &\quad - \int \left(m + \frac{u_4}{s}\right)^2 (u_4+v_4) \\ &= (1-s)\left[\frac{\partial}{\partial\beta}\int m^2(m-v^*)\Big|_{\beta=1}\right]\epsilon + o(\epsilon) \end{aligned}$$

by Claims A.9 and A.10. Recalling that $\frac{\partial}{\partial\beta}\int m^2(m-v^*)|_{\beta=1} < 0$ (see Remark 3), the last line is nonzero for all s, ϵ sufficiently small. This contradiction completes the proof of Proposition 4.2.

Appendix B. Appendix B: Non-existence of Positive Steady States when $\beta \gg 1$.

Theorem B.1. *Suppose* (M1) *holds. For each $d > 0$, there exists $\beta_1 > 0$ large and $C, \epsilon > 0$ such that*

$$v^*(x) \leq C\left(\frac{m(x)}{\max_{\bar\Omega} m}\right)^{\epsilon\beta} \qquad \text{in } \Omega, \tag{40}$$

whenever $\beta \geq \beta_1$ and $d_2 \geq d$. In particular, for all $p \in [1,\infty)$, $v^* \to 0$ in $L^p(\Omega)$ as $\beta \to \infty$.

Proof of Theorem B.1. This is a special case of Theorem 1.6 of [16]. For completeness' sake, we shall give a short proof here, which follows from the methods developed in [6]. First, we fix, by the non-degeneracy of x_0, two positive constants $\kappa, K > 0$ such that

$$\kappa|x-x_0|^2 \leq m(x_0)-m(x) \leq K|x-x_0|^2, \quad \kappa|x-x_0|^2 \leq |\nabla m(x)|^2 \leq K|x-x_0|^2 \quad (41)$$

Let $M = M(d_2, \beta) = \|v^*\|_{L^\infty(\Omega)}$ and fix $\epsilon \in (0,1)$. Define

$$\bar{v}(x) = CM \left(\frac{m(x)}{\max_{\bar{\Omega}} m} \right)^{\epsilon\beta}.$$

Fix $R_0 > 0$ large so that for all $\beta \geq 2/\epsilon$,

$$\frac{\epsilon\beta - 1}{2\beta} \kappa R_0^2 \geq \|m\Delta m\|_{L^\infty(\Omega)}. \quad (42)$$

Then there exists $\beta_1 = \beta_1(d) \geq 2/\epsilon$ such that

$$d_2(1-\epsilon)(\epsilon\beta - 1)\frac{\kappa R_0^2}{2} > \|m\|^3_{L^\infty(\Omega)} \quad \text{for all } \beta \geq \beta_1 \text{ and } d_2 \geq d. \quad (43)$$

If we define

$$N[\phi] := \nu\nabla \cdot (\nabla\phi - \beta\phi\nabla \ln m) + (m - u_k - v_k)\phi, \quad (44)$$

then by (42) and (43),

$$N[\bar{v}] = \frac{\bar{v}}{m^2}\left\{ m^2(m - v^*) - d_2\beta(1-\epsilon)[(\epsilon\beta - 1)|\nabla m|^2 + m\Delta m] \right\} \leq 0$$

in $\Omega \setminus \bar{B}_{R_0/\sqrt{\beta}}(x_0)$ whenever $\beta \geq \beta_1$ and $d_2 \geq d$. Choose now $C > 0$ so that for all $\beta \geq \beta_1$ (and independent of d_2),

$$\inf_{B_{R_0/\sqrt{\beta}}(x_0)} \bar{v} \geq M \quad \text{in } B_{R_0/\sqrt{\beta}}(x_0). \quad (45)$$

This is possible in view of (41). Then v^* satisfies

$$\begin{cases} d_2\nabla \cdot (\nabla v - \beta v\nabla \ln m) + (m - v^*)v = 0 & \text{in } \Omega' := \Omega \setminus \bar{B}_{R_0/\sqrt{\beta}}(x_0), \\ \partial_n v - \beta v\partial_n \ln m = 0 & \text{on } \partial\Omega' \cap \partial\Omega, \\ v = v^* & \text{on } \partial\Omega' \cap \Omega, \end{cases}$$

while $\bar{v}$ satisfies

$$\begin{cases} d_2\nabla \cdot (\nabla v - \beta v\nabla \ln m) + (m - v^*)v \leq 0 & \text{in } \Omega' := \Omega \setminus \bar{B}_{R_0/\sqrt{\beta}}(x_0), \\ \partial_n v - \beta v\partial_n \ln m \geq 0 & \text{on } \partial\Omega' \cap \partial\Omega, \\ v \geq \|v^*\|_{L^\infty(\Omega)} \geq v^* & \text{on } \partial\Omega' \cap \Omega. \end{cases}$$

Now by the equation of v^*, the principal eigenvalue of

$$\begin{cases} d_2\nabla \cdot (\nabla\varphi - \beta\varphi\nabla \ln m) + (m - v^*)\varphi + \mu\varphi = 0 & \text{in } \Omega, \\ \partial_n v - \beta v\partial_n \ln m = 0 & \text{on } \partial\Omega, \end{cases}$$

is zero. By Proposition 3.2 of [2], it is apparent that the principal eigenvalue of

$$\begin{cases} d_2\nabla \cdot (\nabla\varphi - \beta\varphi\nabla \ln m) + (m - v^*)\varphi + \mu\varphi = 0 & \text{in } \Omega' := \Omega \setminus \bar{B}_{R_0/\sqrt{\beta}}(x_0), \\ \partial_n v - \beta v\partial_n \ln m = 0 & \text{on } \partial\Omega' \cap \partial\Omega, \\ \varphi = 0 & \text{on } \partial\Omega' \cap \Omega, \end{cases}$$

is positive. According to Theorem 2.4 of [1], one can infer by the strong maximum principle that

$$v^* \leq \bar{v} \quad \text{in } \Omega' = \Omega \setminus \bar{B}_{R_0/\sqrt{\beta}}(x_0).$$

Since we also have $v^* \le \|v^*\|_{L^\infty(\Omega)} \le \bar{v}$ in $\bar{B}_{R_0/\sqrt{\beta}}(x_0)$ (by (45)), we have

$$v^* \le \bar{v} \quad \text{in } \Omega. \tag{46}$$

It remains to show that $M = \|v^*\|_{L^\infty(\Omega)}$ is bounded independent of β large. Now by (46),

$$\int_\Omega m v^* \le \int_\Omega m\bar{v} \le CM\beta^{-N/2}. \tag{47}$$

On the other hand, by fixing $R_1 > R_0$ suitably large, we have (independent of β large)

$$v^* \le \bar{v} \le \frac{M}{2} = \frac{1}{2}\|v^*\|_{L^\infty(\Omega)} \quad \text{in } \Omega \setminus \bar{B}_{R_1/\sqrt{\beta}}(x_0).$$

Therefore, the maximum of v^* is attained in $B_{R_1/\sqrt{\beta}}(x_0)$ for all β large. If we write the equation of v^* as

$$\begin{cases} d_2\Delta v^* - \frac{\beta}{m}\nabla m \cdot \nabla v^* + v^*\left(m - v^* + \beta\frac{|\nabla m|^2}{m^2} - \beta\frac{\Delta m}{m}\right) = 0 & \text{in } \Omega, \\ \partial_n v^* - \beta(\partial_n m)v^* = 0 & \text{on } \partial\Omega, \end{cases}$$

then (since $\beta(\partial_n m) \le 0$ on $\partial\Omega$), we have by maximum principle

$$\|v^*\|_{L^\infty(\Omega)} \le O(\beta). \tag{48}$$

Next, we change coordinates $x = x_0 + \frac{y}{\sqrt{\beta}}$, then $V(y) = v^*(x_0 + \frac{y}{\sqrt{\beta}})$ is a positive solution to

$$d_2\Delta_y V - \frac{\sqrt{\beta}}{m}\nabla_x m\left(x_0 + \frac{y}{\sqrt{\beta}}\right)\cdot\nabla_y V + \frac{m - V + \beta|\nabla m|^2 m^{-2} - \beta m^{-1}\Delta m}{\beta}V = 0 \tag{49}$$

in $B_{2R_1}(0)$. By (48) and

$$\sqrt{\beta}\nabla_x m\left(x_0 + \frac{y}{\sqrt{\beta}}\right) \to D_x^2 m(x_0)y \quad \text{uniformly for } y \in B_{2R_1}(0),$$

all the coefficients of (49) are bounded. We may apply the Harnack inequality to V in $B_{2R_1}(0)$, which implies that for some c depending on dimension and $m(x)$, but independent of β large,

$$v^* \ge c\|v^*\|_\infty \quad \text{for } x \in B_{R_1/\sqrt{\beta}}(x_0) \text{ (or } y \in B_{R_1}(0)).$$

Hence

$$\int_\Omega (v^*)^2 \ge \int_{B_{R_1/\sqrt{\beta}}} (v^*)^2 \ge cM^2\beta^{-N/2}. \tag{50}$$

Combining (47) and (50) by the identity $\int_\Omega v^*(m - v^*) = 0$ (obtained by integrating the equation of v^* over Ω), we have

$$cM^2\beta^{-N/2} \le \int_\Omega (v^*)^2 = \int_\Omega m v^* \le CM\beta^{-N/2}.$$

Hence $M = \|v^*\|_{L^\infty(\Omega)}$ is bounded independent of β large. This proves the theorem. □

Next, we show the nonexistence of positive steady states when β is sufficiently large.

Proof of Proposition 4.5. Suppose to the contrary that for some fixed $d_1, d_2 > 0$, there exists a sequence $\beta_k \to \infty$ and positive solution (u_k, v_k) of (3) corresponding to $\beta = \beta_k$.

By a comparison argument, $u_k < m$ in $\bar{\Omega}$ for each k.

Claim B.2. *$u_k \to m$ weakly in $W^{2,p}(\Omega)$ for all $p \in [1,\infty)$ and strongly in $C^{1,\alpha}(\bar\Omega)$ for all $\alpha \in (0,1)$.*

To see the claim, notice that $0 < v_k < v^*$ (by comparison) and $v^* \to 0$ in $L^p(\Omega)$ for all $p \in [1,\infty)$ (by Theorem B.1). Hence the claim follows from elliptic L^p estimates applied to the equation of u.

Claim B.3. *There exists C such that $\|v_k\|_{L^\infty(\Omega)} \leq C\|m - u_k\|_{L^\infty(\Omega)}$ for all k.*

For $t = \|m - u_k\|_{L^\infty(\Omega)}/\min_{\bar\Omega} m$, we have $\|m - u_k\|_{L^\infty(\Omega)} \leq tm$. Hence by comparison, $v_k \leq v(t)$, where $v(t)$ is the unqiue positive solution of

$$\begin{cases} d_2\nabla\cdot(\nabla v - \beta v\nabla \ln m) + v(tm - v) = 0 & \text{in } \Omega, \\ \partial_n v - \beta v\partial_n(\ln m) = 0 & \text{on } \partial\Omega. \end{cases} \tag{51}$$

And $v' = v(t)/t$ satisfies

$$\begin{cases} t^{-1}d_2\nabla\cdot(\nabla v' - \beta v'\nabla \ln m) + v'(m - v') = 0 & \text{in } \Omega, \\ \partial_n v' - \beta v'\partial_n(\ln m) = 0 & \text{on } \partial\Omega. \end{cases} \tag{52}$$

And is bounded independent of β (large) and t (small) by Theorem B.1. Hence $v_k \leq Ct = C\|m - u_k\|_{L^\infty(\Omega)}/\min_{\bar\Omega} m$. This proves Claim B.3.

Next, we prove the key lemma.

Lemma B.4. *For each $p \geq 1$,*

$$\frac{v_k}{\|m - u_k\|_{L^\infty(\Omega)}} \to 0 \quad \text{in } L^p(\Omega) \text{ as } \beta \to \infty.$$

Proof. Let $\hat v = C\|m - u_k\|_{L^\infty(\Omega)}\left(\frac{m}{\max_{\bar\Omega} m}\right)^{\epsilon\beta}$. Then, as in Proof of Theorem B.1, there exists $\beta_2, R_0 > 0$ large such that

$$N[\hat v] = \hat v\left\{m - u_k - v_k - d_2(1-\epsilon)\beta\left[(\epsilon\beta - 1)\frac{|\nabla m|^2}{m^2} + \frac{\Delta m}{m}\right]\right\} \leq 0 \quad \text{in } \Omega\backslash B_{R_0/\sqrt{\beta_k}}(x_0), \tag{53}$$

where N is defined in (44). Hence by comparing v_k and $\hat v$ in $\Omega\backslash B_{R_0/\sqrt{\beta_k}}(x_0)$ (details similar to proof of Theorem B.1)

$$v_k \leq \begin{cases} \|v_k\|_\infty \leq C\|m - u_k\|_\infty & \text{in } \bar B_{R_0/\sqrt{\beta_k}}(x_0) \\ C\|m - u_k\|_\infty\left(\frac{m}{\max_{\bar\Omega} m}\right)^{\epsilon\beta} & \text{in } \Omega \setminus \bar B_{R_0/\sqrt{\beta_k}}(x_0). \end{cases}$$

And Lemma B.4 follows from Bounded Convergence Theorem. □

Rewriting the equation of u_k, we have

$$-d_1\nabla\cdot\left[\nabla(m - u_k) - (m - u_k)\frac{\nabla m}{m}\right] + u_k^2(m - u_k - v_k) = 0$$

$$-d_1\nabla\cdot\left[m\nabla\left(\frac{m - u_k}{m}\right)\right] + u_k^2(m - u_k) = u_k^2 v_k$$

Divide by $\|m - u_k\|_{L^\infty(\Omega)}$, letting $w = (m - u_k)/(m\|m - u_k\|_{L^\infty(\Omega)})$,

$$-d_1\nabla\cdot[m\nabla w] + mu_k^2 w = u_k^2\frac{v_k}{\|m - u_k\|_{L^\infty(\Omega)}}.$$

where $mu_k^2 \to m^3$ in $L^\infty(\Omega)$ and the right hand side goes to zero in $L^p(\Omega)$. Hence by L^p estimate, $w \to 0$ weakly in $W^{2,p}(\Omega)$ and strongly in $C^{1,\alpha}(\bar\Omega)$. i.e.

$$\frac{m - u_k}{\|m - u_k\|_{L^\infty(\Omega)}} \to 0 \quad \text{uniformly in } \Omega \text{ as } \beta_k \to \infty. \tag{54}$$

This is a contradiction. Therefore, (3) has no positive solutions for β large. □

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