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The ideal free strategy with weak Allee effect

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1. Introduction

Biological dispersal plays a fundamental role in understanding the distribution, dynamics, and persistence of competing species in a habitat. From an ecological vantage point, the movement of organisms has received much attention, resulting in many studies with varied approaches. Within this body of work, an important research direction incorporates reaction–diffusion models in order to understand the impact of species movement on competitive aspects such as invasion, coexistence and exclusion, especially when the habitat varies spatially. A number of papers in this context demonstrated two species competition results, indicating which dispersal strategies lead to exclusion and in some cases coexistence [4,6,7,11]. While the question of which strategies produce winners, losers, or coexistence began to be answered, the underlying ‘why’ remained unclear. Recently, however, Cantrell

et al. [5] explained that the affect of spatial variation of resources on species competition relates to the notion that diffusion usually gives rise to a mismatch between population density and the quality of the environment. That is, the dominant competitor is able to distribute itself in the environment so as to have the 'right' balance of population to available resource.

Because our study uses [5] as a departure point, we present their model which allows for the possibility that populations can "match the environmental quality perfectly":

$$\begin{cases} u_t = \mu \nabla \cdot [\nabla u - u \nabla P] + u(m - u - v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \nabla \cdot [\nabla v - v \nabla Q] + v(m - u - v) & \text{in } \Omega \times (0, \infty), \\ [\nabla u - u \nabla P] \cdot n = [\nabla v - v \nabla Q] \cdot n = 0 & \text{on } \partial \Omega \times (0, \infty). \end{cases} \quad (1.1)$$

In (1.1), $u(x, t)$ and $v(x, t)$ represent the densities of species u and v at location x and time t , respectively, μ and ν are the positive diffusion rates for the respective species, $P(x)$ and $Q(x) \in C^2(\bar{\Omega})$ provide advective directions as well as regulate speed in those directions and $m(x)$ is the intrinsic growth rate at location x in the habitat. We suppose that $m(x) > 0$ and non-constant in Ω , indicating that the habitat is spatially variable. Also, we define the habitat Ω to be a bounded domain in \mathbb{R}^N with smooth boundary $\partial \Omega$ for $N > 1$. Notice that (1.1) has no flux boundary conditions so that no species can leave the environment.

If we set $v = 0$ in (1.1) the single species equation for u has $u^* \equiv m$ as a positive steady state when $P = \ln(m)$. Notice the net flux for species u satisfies $\nabla u^* - u^* \nabla \ln(m) = 0$ in Ω and the fitness of species u is the same at every location in Ω : $m/u^* \equiv 1$. A species manifesting this type of spatial structure is said to be at an ideal free distribution, as the density of the species at any location $x \in \Omega$ is proportional to the habitat quality $m(x)$. In light of this, Cantrell et al. termed $P = \ln(m)$ an 'ideal free strategy' [5].

Cantrell et al. [5] showed that selection prefers the ideal free strategy over 'nearby' strategies. They also hypothesized that the ideal free strategy should be able to defeat any other strategy, and therefore be a global evolutionary stable strategy. Averill et al. [1] validated this conjecture in the following result.

Theorem 1.1. (See [1].) *Suppose that m is a positive, non-constant function and $m \in C^2(\bar{\Omega})$. If $P = \ln(m)$ and $Q = \ln(m)$ is non-constant, then $(m, 0)$ is the globally asymptotically stable steady state of (1.1) among initial data that are nonnegative and not identically zero.*

Theorem 1.1 illustrates competitive exclusion in that the species playing the ideal free strategy will drive the species playing a different strategy to extinction.

Our main question for the present work is this: does Theorem 1.1 still hold when the reaction term, $u(m - u - v)$, in the equation for u in (1.1), is replaced by $u^2(m - u - v)$? To address this question, we narrow the possible movement strategies, setting $P = \ln(m)$ and $Q = \beta \ln(m)$, where $\beta \in [0, \infty)$. Because P and Q set the bias in each species' movement, we can now interpret the advection of both species to be directed towards resource maxima, that is, maxima of m in Ω [1,2,5,8]. With these definitions of P and Q , we want to examine how the dynamics of the following model change as we vary β :

$$\begin{cases} u_t = \mu \nabla \cdot [\nabla u - u \nabla \ln(m)] + u^2(m - u - v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \nabla \cdot [\nabla v - \beta v \nabla \ln(m)] + v(m - u - v) & \text{in } \Omega \times (0, \infty), \\ [\nabla u - u \nabla \ln(m)] \cdot n = [\nabla v - \beta v \nabla \ln(m)] \cdot n = 0 & \text{on } \partial \Omega \times (0, \infty). \end{cases} \quad (1.2)$$

The competition of species u and v in this context is interesting for a number of reasons. First, we see that the new reaction term, $u^2(m - u - v)$, in the equation for u in (1.2), indicates that u has a disadvantage at low populations. This phenomenon of decreased fitness for low population densities, is known as the Allee effect [17]. Because the fitness of u is reduced, as opposed to being negative for small populations, the reaction term for u in (1.2) produces a 'weak' Allee effect [15].

Of particular interest is the influence such population dynamics have on biological invasions. Taylor and Hastings [17] put forth an excellent review of work in this area, highlighting the ecological consequences of Allee effects on invasive species dynamics as well as implications for biological control. The present work fits into this thread of research, as our main question connects to how the interplay between the ideal free strategy and the weak Allee effect influence a species' potential for invasion and long term survival. However, this question is mathematically difficult as invasion dynamics no longer give useful information for any $\beta \in [0, \infty)$. In other words, the long term population growth rates for rare species u trying to invade resident species v or rare species v trying to invade resident species u are both zero. The dynamics of (1.2) are therefore more subtle than (1.1), requiring more specialized techniques.

In terms of results, we demonstrate analytically that for small values of β , species u drives species v to extinction, just as in Theorem 1.1. We also show that for large values of β , u can invade v and numerics suggest that u will again drive v to extinction. Recall that species u plays the ideal free strategy, a balance of advection and diffusion which allows it to eventually have total control on the available resources. We reason that for small values of β , v acts too much like a generalist, missing not only the resource maxima, but eventually is even driven out of areas with less favorable resources. Species u is able to exploit resource maxima, growing to overcome any lasting influence from the Allee effect. For large values of β , v is too specialized, concentrating at resource maxima and foregoing resources in most other locations. Again, as species u grows in number, the Allee effect wanes, and the competition becomes like that of Theorem 1.1. On the other hand, numerical simulations suggest that for intermediate values of β , species v not only survives, but can drive species u to extinction. This differs dramatically from the result in Theorem 1.1, indicating that some combination of intermediate advection with diffusion allows species v to distribute itself in a way that keeps u from establishing itself at any location in the habitat.

2. Main results

Working from model (1.2), we want to develop a picture of its dynamics as we vary $\beta \in [0, \infty)$. Our first result concerns the $\beta = 0$ case.

Theorem 2.1. *Suppose $m \in C^2(\bar{\Omega})$ is positive and non-constant. Then for $\beta = 0$ and any $\mu, \nu > 0$, any solution (u, v) of (1.2) with nonnegative, not identically zero initial data converges to $(m, 0)$ in $L^\infty(\Omega)$ as $t \rightarrow \infty$.*

While the Allee effect usually decreases the chances that an invasive species can establish itself [17], this result says that species u cannot only invade, but as the ideal free disperser, u will drive species v to extinction no matter its diffusion rate.

We find that a similar result holds true even when we allow v to have weak advection.

Theorem 2.2. *Suppose $m \in C^2(\bar{\Omega})$ is positive and non-constant. Then there exists $0 < \beta^* < 1$ such that for all $\beta \in (0, \beta^*)$ and any $\mu, \nu > 0$, any solution (u, v) of (1.2) with nonnegative, not identically zero initial data converges to $(m, 0)$ in $L^\infty(\Omega)$ as $t \rightarrow \infty$.*

Remark 1. We conjecture based on Lemma 4.1 and numerical results that Theorem 2.2 holds for all $\beta \in (0, 1)$.

Remark 2. System (1.2) has a continuum of steady states of the form $(sm, (1-s)m)$ for $s \in (0, 1)$ when $\beta = 1$. Notice that in this case, both species are playing the ideal free strategy and hence can coexist.

For large values of β , we find a related result to the above, as the following theorem implies that u can invade v .

Theorem 2.3. *Suppose $m \in C^2(\bar{\Omega})$ is positive and non-constant. Then there exists $1 \ll \beta^{**}$ such that for all $\beta > \beta^{**}$, the semi-trivial steady state $(0, v^*)$ of (1.2) is unstable.*

In line with Theorem 2.3, numerics indicate that u should be the sole survivor in the large β case and we anticipate that (1.2) does not have positive steady states. Therefore, for large β , we propose that the dynamics of (1.2) tend globally to $(m, 0)$ as in Theorem 2.2.

For intermediate advection rates, the analysis is difficult and we suspect the dynamics are more complicated. Interestingly, we see for β in this domain, the stability of $(0, v^*)$ changes, indicating that species v cannot only invade the ideal free disperser, but can induce its extinction. This is a departure from the result in Theorem 1.1 and will be discussed in Section 6.

We outline this paper as follows: Theorems 2.1, 2.2, and 2.3 are substantiated in Sections 3–5, respectively. In Section 6 we synthesize our conclusions and discuss some open problems.

3. Proof of Theorem 2.1

Before proving Theorem 2.1, we want to justify that system (1.2) has two semi-trivial steady states. It is well known that the steady state equation for v in (1.2) (set $u = 0$) has a unique positive steady state v^* since $m > 0$ and non-constant in Ω . It is also clear that $u^* \equiv m$ satisfies the steady state equation for the following single species system,

$$\begin{aligned} u_t &= \mu \nabla \cdot [\nabla u - u \nabla \ln(m)] + u^2(m - u) \quad \text{in } \Omega \times (0, \infty), \\ [\nabla u - u \nabla \ln(m)] \cdot n &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \quad (3.1)$$

We claim that $u^* \equiv m$ is the unique positive steady state of system (3.1). To prove this, we make use of a Lyapunov function approach with an infinite dimensional version of LaSalle's invariance principle. See [10,12] for details concerning the technique and statement of LaSalle's invariance principle.

To begin, we define $E : C(\bar{\Omega}) \rightarrow \mathbb{R}$ by $E(u) = \int_{\Omega} u + \frac{m^2}{u}$.

Lemma 3.1. *For any solution $u(x, t)$ of (3.1),*

$$\frac{d}{dt} E(u(\cdot, t)) = - \int_{\Omega} \frac{\mu 2m |\nabla(u/m)|^2}{(u/m)^3} - \int_{\Omega} (m^2 - u^2)(m - u) \leq 0. \quad (3.2)$$

Proof. Integrating the equation for u , we get $\frac{d}{dt} \int_{\Omega} u = \int_{\Omega} u^2(m - u)$. Next, we see that

$$\frac{d}{dt} \int_{\Omega} \frac{m^2}{u} = - \int_{\Omega} \frac{\mu \nabla(m \nabla(u/m))}{(u/m)^2} + m^2(m - u).$$

Integrating by parts, we see that

$$- \int_{\Omega} \frac{\mu \nabla(m \nabla(u/m))}{(u/m)^2} = - \int_{\Omega} \frac{\mu 2m |\nabla(u/m)|^2}{(u/m)^3},$$

from which our result follows. \square

Lemma 3.2. *Let $u(x, t)$ be any solution of (3.1) with $u(x, 0) > 0$ for some $x \in \Omega$. Then there exists $t_0 > 0$ such that for $t > t_0$, $u(x, t)$ has a positive uniform lower bound on Ω .*

Proof. Let $y = (u/m)$. Then y satisfies the following

$$\begin{aligned} y_t &= \mu \Delta y + \mu \nabla y \cdot \nabla \ln(m) + my^2(m - my) \quad \text{in } \Omega \times (0, \infty), \\ \nabla y \cdot n &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \quad (3.3)$$

By the maximum principle [13], since $y(x, 0) = u(x, 0)/m > 0$ for some $x \in \Omega$, $y(x, t) > 0$ in $\Omega \times (0, \infty)$ [13]. Let $t_0 > 0$ such that $\inf_{\Omega} y(x, t_0) = \epsilon_0$, where $0 < \epsilon_0 < 1$. Notice that ϵ_0 is a subsolution to (3.3). Because (3.3) is strongly monotone [3], $y(x, t) \geq \epsilon_0$ in $\Omega \times (t_0, \infty)$. Hence we see that any solution y with nonnegative, not identically zero initial conditions, eventually has a positive uniform lower bound. Because $u = ym$, we have the same result for u . \square

For any $\chi > 0$, set $G = \{u \in C(\bar{\Omega}): u > 0 \text{ in } \bar{\Omega}, E(u) \leq E(m) + \chi\}$. For any $u(x, 0) \in G$, by Lemma 3.1, $E(u(x, t)) \leq E(u(x, 0))$. Thus, $u(x, t) \in G$ for any $t > 0$. By Lemmas 3.1 and 3.2, we see that E is a Lyapunov functional on G , that is, it decreases along trajectories and is continuous on \bar{G} .

Define $M = \{u \in \bar{G}: \frac{d}{dt}E(u) = 0\}$. The maximal invariant subset of M is $\{m\}$. To see this, consider the formula for $\frac{d}{dt}E$ in (3.2). It is clear that $\frac{d}{dt}E = 0$ if and only if $u \equiv m$.

Proposition 1. $u^* \equiv m$ is the unique positive steady state of (3.1).

Proof. We show that $u^* \equiv m$ is the globally asymptotically stable positive steady state of (3.1). Since E is a Lyapunov functional on \bar{G} and the largest invariant subset of M is $\{m\}$, to apply LaSalle's invariance principle, we must demonstrate that solution trajectories of (3.1) are pre-compact. This fact follows from Redlinger's result in [14], i.e. given any $\delta > 0$, there are constants $\tau \in (0, 1)$ and $C^* > 0$ such that

$$\sup_{t \geq \delta} \|u(\cdot, t)\|_{C^{2,\tau}(\bar{\Omega})} \leq C^*.$$

With all the ingredients in place, LaSalle's invariance principle implies that for any solution u of (3.1) with nonnegative, not identically zero initial conditions, $u \rightarrow m$ uniformly on Ω as $t \rightarrow \infty$. \square

Remark 3. Actually, $u^* \equiv m$ is the unique positive steady state of the single species equation for any reaction term $u^\kappa(m - u)$ with $\kappa > 1$. We can apply the same arguments as above with $E(u) = \int_{\Omega} u + \frac{m^\kappa}{u^{\kappa-1}}$.

In light of these results, we see that (1.2) has exactly two semi-trivial steady states: $(m, 0)$ and $(0, v^*)$. To determine the dynamics of (1.2), a typical approach is to linearize the system at both semi-trivial steady states and then combine this local information with monotone system theory. However, one can see that the principal eigenvalues associated to the linearized operators both at $(m, 0)$ and $(0, v^*)$ (coming from (1.2)) are zero for all $\beta \geq 0$. Therefore, even the local stability of both semi-trivial steady states is non-trivial. In light of this, we are forced to handle the non-linearity of (1.2) directly.

For the rest of this section, we set $\beta = 0$ in (1.2) so our model becomes

$$\begin{cases} u_t = \mu \nabla \cdot [\nabla u - u \nabla \ln(m)] + u^2(m - u - v) & \text{in } \Omega \times (0, \infty), \\ v_t = v \Delta v + v(m - u - v) & \text{in } \Omega \times (0, \infty), \\ [\nabla u - u \nabla \ln(m)] \cdot n = \nabla v \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \quad (3.4)$$

In order to prove Theorem 2.1, we first show that (3.4) has no strictly positive steady states. We will then show that $(0, v^*)$ is unstable and because (3.4) is a strongly monotone system, we can conclude by monotone dynamical system theory [3,16] that $(m, 0)$ is globally asymptotically stable.

Lemma 3.3. *System (3.4) has no strictly positive equilibrium states.*

Proof. Suppose (3.4) has a positive equilibrium (\bar{u}, \bar{v}) , i.e., both components are positive on Ω and the pair satisfies

$$\begin{aligned}\mu \nabla \cdot [\nabla \bar{u} - \bar{u} \nabla \ln(m)] + \bar{u}^2(m - \bar{u} - \bar{v}) &= 0 \quad \text{in } \Omega, \\ \nu \Delta \bar{v} + \bar{v}(m - \bar{u} - \bar{v}) &= 0 \quad \text{in } \Omega, \\ [\nabla \bar{u} - \bar{u} \nabla \ln(m)] \cdot n = \nabla \bar{v} \cdot n &= 0 \quad \text{on } \partial\Omega.\end{aligned}\tag{3.5}$$

Now, if we multiply the equation for \bar{v} in (3.5) by \bar{v} and integrate in Ω , we obtain

$$0 = -\nu \int_{\Omega} |\nabla \bar{v}|^2 + \int_{\Omega} \bar{v}^2(m - \bar{u} - \bar{v}).\tag{3.6}$$

Next, integrating the equation for \bar{u} in Ω ,

$$0 = \int_{\Omega} \bar{u}^2(m - \bar{u} - \bar{v}).\tag{3.7}$$

Third, we see that multiplying the equation for \bar{u} by $-(m/\bar{u})^2$ and integrating yields

$$0 = -\mu \int_{\Omega} \frac{2m|\nabla(\bar{u}/m)|^2}{(\bar{u}/m)^3} - \int_{\Omega} m^2(m - \bar{u} - \bar{v}).\tag{3.8}$$

Finally, if we multiply the equation for \bar{u} by $2(m/\bar{u})$ and then integrate, we have

$$0 = \mu \int_{\Omega} \frac{2m|\nabla(\bar{u}/m)|^2}{(\bar{u}/m)^2} + \int_{\Omega} 2m\bar{u}(m - \bar{u} - \bar{v}).\tag{3.9}$$

Combining Eqs. (3.6), (3.7), (3.8), and (3.9), gives us

$$0 = -\mu \int_{\Omega} \frac{2m|\nabla(\bar{u}/m)|^2(1 - (\bar{u}/m))}{(\bar{u}/m)^3} - \nu \int_{\Omega} |\nabla \bar{v}|^2 - \int_{\Omega} ((m - \bar{u})^2 - \bar{v}^2)(m - \bar{u} - \bar{v}).\tag{3.10}$$

Now, since m is a super solution to the equation of \bar{u} (we can change variable here and use maximum principle arguments [3,13]), we have that $\bar{u} \leq m$ in Ω . Thus every term in (3.10) is nonpositive and the whole expression is zero if and only if $\bar{u}/m = c_1$, $\bar{v} = c_2$, and $m - \bar{u} = \bar{v}$ in Ω , where c_1 and c_2 are constants. However, this means that $m(1 - c_1) = c_2$, implying that if $1 - c_1 \neq 0$, then m is constant in Ω . But m is assumed to be non-constant in Ω . Hence, $c_1 = 1$ and $c_2 = 0$. But this contradicts the positivity of \bar{v} in Ω and finishes the proof. \square

Lemma 3.4. *The semi-trivial steady state $(0, v^*)$, of (3.4), is unstable.*

Proof. Suppose $(0, v^*)$ is stable. Then for all $\epsilon > 0$, there exists a $\tau(\epsilon)$, where $0 < \tau(\epsilon) < \epsilon$, such that if $|u(x, 0) - 0| + |v(x, 0) - v^*(x)| < \tau$ in Ω , then $|u(x, t) - 0| + |v(x, t) - v^*(x)| < \epsilon$ in $\Omega \times (0, \infty)$.

Using the equation of u in (3.4), we see that

$$\begin{aligned}
\frac{d}{dt} \int_{\Omega} \frac{m^2}{u} &= - \int_{\Omega} \frac{2\mu m |\nabla(u/m)|^2}{(u/m)^3} - \int_{\Omega} m^2(m - u - v) \\
&\leq - \int_{\Omega} m^2(m - u - v) \\
&= - \int_{\Omega} (m^2 - (v^*)^2)(m - u - v^* + v^* - v) - \int_{\Omega} (v^*)^2(m - u - v^* + v^* - v) \\
&= - \int_{\Omega} (m^2 - (v^*)^2)(m - v^*) - \int_{\Omega} (m^2 - (v^*)^2)(-u + v^* - v) \\
&\quad - \int_{\Omega} (v^*)^2(m - v^*) - \int_{\Omega} (v^*)^2(-u + v^* - v) \\
&\leq - \int_{\Omega} (v^*)^2(m - v^*) + \epsilon,
\end{aligned}$$

where the last inequality follows from the definition of stability for $(0, v^*)$, the fact that $(m^2 - (v^*)^2)(m - v^*) \geq 0$ in Ω , and that both m and v^* have positive upper and lower uniform bounds in Ω .

Next, note that if we multiply the equation for v^* (set $u = 0$ in (3.4)) by v^* and integrate in Ω , because m is non-constant, we have that $\int_{\Omega} (v^*)^2(m - v^*) = \eta > 0$. Thus from the above inequality, we see that if we choose ϵ small enough, then for $t > 0$,

$$\frac{d}{dt} \int_{\Omega} \frac{m^2}{u} \leq -\eta/2 < 0. \tag{3.11}$$

Eq. (3.11) implies that for all $t > 0$,

$$\int_{\Omega} \frac{m^2}{u} \leq \left(\int_{\Omega} \frac{m^2}{u(x, 0)} \right) - (\eta/2)t. \tag{3.12}$$

But since the left-hand side of (3.12) is always positive, we have a contradiction. We see then that $(0, v^*)$ must be unstable. \square

Finally, we note as above that (3.4) has two semi-trivial steady states, $(m, 0)$ and $(0, v^*)$. Combining the results from Lemmas 3.3 and 3.4, we see that (3.4) has no strictly positive equilibria and $(0, v^*)$ is unstable. Because we can change variables and show that (3.4) gives rise to a strongly monotone dynamical system, by the usual monotone dynamical system theory [3,16], $(m, 0)$ must be globally asymptotically stable. This completes the proof of Theorem 2.1.

4. Proof of Theorem 2.2

Lemma 4.1. For $\beta \in (0, 1)$, $(0, v^*)$ is unstable.

Proof. Suppose $(0, v^*)$ is stable. Then for all $\epsilon > 0$, there exists a $\tau(\epsilon)$, where $0 < \tau(\epsilon) < \epsilon$, such that if $|u(x, 0) - 0| + |v(x, 0) - v^*(x)| < \tau$ in Ω , then $|u(x, t) - 0| + |v(x, t) - v^*(x)| < \epsilon$ in $\Omega \times (0, \infty)$.

Using the equation of u in (1.2), we have

$$\begin{aligned} \frac{d}{dt} \int_{\Omega} \frac{m^2}{u} &= - \int_{\Omega} \frac{2\mu m |\nabla(u/m)|^2}{(u/m)^3} - \int_{\Omega} m^2(m - u - v) \\ &\leq - \int_{\Omega} m^2(m - u - v) \\ &= - \int_{\Omega} m^2(m - v^*) - \int_{\Omega} m^2(-u - v + v^*) \\ &\leq - \int_{\Omega} m^2(m - v^*) + \epsilon, \end{aligned}$$

where the last inequality follows from the definition of stability of $(0, v^*)$.

We claim that $\int_{\Omega} m^2(m - v^*) = \sigma > 0$. To see this, note that

$$\begin{aligned} \int_{\Omega} m^2(m - v^*) &= \int_{\Omega} (m^2 - (v^*)^2)(m - v^*) + \int_{\Omega} (v^*)^2(m - v^*) \\ &\geq \int_{\Omega} (v^*)^2(m - v^*) - \int_{\Omega} v^*(m - v^*) \left(\frac{v^*}{m^{\beta}}\right)^{\frac{1}{1-\beta}} + \int_{\Omega} v^*(m - v^*) \left(\frac{v^*}{m^{\beta}}\right)^{\frac{1}{1-\beta}} \\ &= \int_{\Omega} (v^*)^2(m - v^*) \left(\frac{m^{\frac{\beta}{1-\beta}} - (v^*)^{\frac{\beta}{1-\beta}}}{m^{\frac{\beta}{1-\beta}}}\right) + \int_{\Omega} v^*(m - v^*) \left(\frac{v^*}{m^{\beta}}\right)^{\frac{1}{1-\beta}}. \end{aligned}$$

Since $\beta \in (0, 1)$, the first term in the last inequality is nonnegative. Multiplying the equation of v^* (set $u = 0$ in (1.2)) by $(\frac{v^*}{m^{\beta}})^{\frac{1}{1-\beta}}$ and then integrating by parts,

$$\int_{\Omega} v^*(m - v^*) \left(\frac{v^*}{m^{\beta}}\right)^{\frac{1}{1-\beta}} = \int_{\Omega} \frac{v}{1-\beta} \left| \nabla \left(\frac{v^*}{m^{\beta}}\right) \right|^2 \left(\frac{v^*}{m^{\beta}}\right)^{\frac{\beta}{1-\beta}} > 0,$$

since m is non-constant in Ω . Thus, $\int_{\Omega} m^2(m - v^*) = \sigma > 0$.

Therefore, choosing ϵ small enough, we can say that for $t > 0$,

$$\frac{d}{dt} \int_{\Omega} \frac{m^2}{u} \leq -\sigma/2 < 0. \quad (4.1)$$

As in the proof of Lemma 3.4, this leads to a contradiction. \square

Lemma 4.2. *There exists $0 < \beta^* < 1$ such that for all $\beta \in (0, \beta^*)$, there are no positive solutions to the steady state equation for (1.2).*

Proof. Suppose not. Then there exists a sequence of positive steady state solutions (U_k, V_k) to (1.2) with $\beta_k \rightarrow 0^+$ as $k \rightarrow \infty$. By the maximum principle [13] we see that for $0 < \beta_k \ll 1$, (U_k, V_k) is uniformly bounded in $L^\infty(\bar{\Omega})$. Also, by elliptic regularity and the Sobolev embedding theorem [9], (U_k, V_k) is uniformly bounded in $C^{1,\eta}(\bar{\Omega})$ for some $\eta \in (0, 1)$. Passing to a subsequence if necessary, we have that (U_k, V_k) converges to (U^*, V^*) in $C^1(\bar{\Omega})$, satisfying

$$\begin{aligned} \mu \nabla \cdot [\nabla U^* - U^* \nabla \ln(m)] + (U^*)^2 (m - U^* - V^*) &= 0 \quad \text{in } \Omega, \\ \nu \Delta V^* + V^* (m - U^* - V^*) &= 0 \quad \text{in } \Omega, \\ [\nabla U^* - U^* \nabla \ln(m)] \cdot n = \nabla V^* \cdot n &= 0 \quad \text{on } \partial \Omega. \end{aligned} \quad (4.2)$$

By Lemma 3.3, we know that (4.2) has no positive coexistence states. Thus, (U^*, V^*) must be either $(0, 0)$, $(0, v^*)$, or $(m, 0)$. Suppose first that $(U_k, V_k) \rightarrow (0, 0)$ as $\beta_k \rightarrow 0^+$. Let $\hat{v}_k = \frac{V_k}{\|V_k\|_{L^\infty(\bar{\Omega})}}$. Then by elliptic regularity [9], $\hat{v}_k \rightarrow v^1$ in $C^1(\bar{\Omega})$ as $\beta_k \rightarrow 0^+$, where v^1 satisfies

$$\nu \Delta v^1 + v^1 m = 0 \quad \text{in } \Omega, \quad \nabla v^1 \cdot n|_{\partial \Omega} = 0. \quad (4.3)$$

Integrating (4.3) gives us that $\int_{\Omega} v^1 m = 0$. But this is a contradiction since $v^1 \geq 0$ in Ω and $\|v^1\|_{L^\infty(\bar{\Omega})} = 1$.

Now suppose that $(U_k, V_k) \rightarrow (0, v^*)$ as $\beta_k \rightarrow 0^+$. Consider the equation for U_k (coming from steady state equation of (1.2)). If we multiply this equation by $-(m/U_k)^2$ and integrate, then for small enough $\beta_k > 0$,

$$\begin{aligned} 0 &= - \int_{\Omega} \frac{2\mu m |\nabla(U_k/m)|^2}{(U_k/m)^3} - \int_{\Omega} m^2 (m - U_k - V_k) \\ &\leq - \int_{\Omega} m^2 (m - U_k - V_k) = - \int_{\Omega} m^2 (m - v^*) - \int_{\Omega} m^2 (-U_k - V_k + v^*) \\ &\leq - \int_{\Omega} m^2 (m - v^*) + C\beta_k < 0, \end{aligned}$$

where C is some positive constant. Note that the last inequality holds since $\int_{\Omega} m^2 (m - v^*) > 0$ (see Lemma 4.1 and put $\beta = 0$) and (U_k, V_k) converges to $(0, v^*)$. We again arrive at a contradiction.

Therefore, we are left with the case that (U_k, V_k) converges to $(m, 0)$. Considering the equation for V_k (coming from the steady state of (1.2)), we can divide by $\|V_k\|_{L^\infty(\bar{\Omega})}$ to get

$$\begin{aligned} \nu \nabla \cdot \left[m^{\beta_k} \nabla \left(\frac{V_k}{m^{\beta_k} \|V_k\|_{L^\infty(\bar{\Omega})}} \right) \right] + \left[\frac{V_k}{\|V_k\|_{L^\infty(\bar{\Omega})}} \right] (m - U_k - V_k) &= 0 \quad \text{in } \Omega, \\ \left[m^{\beta_k} \nabla \left(\frac{V_k}{m^{\beta_k} \|V_k\|_{L^\infty(\bar{\Omega})}} \right) \right] \cdot n &= 0 \quad \text{on } \partial \Omega. \end{aligned} \quad (4.4)$$

Letting $\beta_k \rightarrow 0^+$, by elliptic regularity [9], $\frac{V_k}{\|V_k\|_{L^\infty(\bar{\Omega})}} \rightarrow v_2$ in $C^1(\bar{\Omega})$ where v_2 satisfies $\Delta v_2 = 0$ in Ω and $\nabla v_2 \cdot n|_{\partial \Omega} = 0$ with $\|v_2\|_{L^\infty} = 1$. This implies that $v_2 \equiv 1$ in Ω .

Next, notice that we can rearrange the equation for U_k as follows

$$\begin{aligned} \mu \nabla \cdot \left[m \nabla \left(\frac{U_k - m}{m \|V_k\|_{L^\infty(\bar{\Omega})}} \right) \right] + m(U_k)^2 \left[\left(\frac{m - U_k}{m \|V_k\|_{L^\infty(\bar{\Omega})}} \right) - \frac{V_k}{\|V_k\|_{L^\infty(\bar{\Omega})} m} \right] &= 0 \quad \text{in } \Omega, \\ \left[m \nabla \left(\frac{U_k - m}{m} \right) \right] \cdot n &= 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (4.5)$$

Let $\varphi_k = \frac{(U_k - m)}{m \|V_k\|_{L^\infty(\bar{\Omega})}}$. Then by elliptic regularity [9], $\varphi_k \rightarrow \phi$ in $C^1(\bar{\Omega})$ as $\beta_k \rightarrow 0^+$, where ϕ satisfies

$$\begin{aligned} \mu \nabla \cdot [m \nabla \phi] - m^3 \phi - m^2 &= 0 \quad \text{in } \Omega, \\ \nabla \phi \cdot n &= 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (4.6)$$

Now if we integrate the steady state equation for V_k in (1.2) we see that

$$\begin{aligned} 0 &= \int_{\Omega} V_k(m - U_k - V_k) \\ &= \int_{\Omega} \left(\frac{V_k}{\|V_k\|_{L^\infty(\bar{\Omega})}} \right) \left[-m\varphi_k - \frac{V_k}{\|V_k\|_{L^\infty(\bar{\Omega})}} \right] \rightarrow \int_{\Omega} m\phi + 1 \end{aligned} \quad (4.7)$$

as $\beta_k \rightarrow 0^+$. Using the maximum principle [13] with Eq. (4.6), we conclude that $\phi < 0$ in Ω . Let $f = -m\phi > 0$ in Ω . Note that from (4.7), $\int_{\Omega} f = |\Omega|$.

Multiplying (4.6) by ϕ^2 and then integrating by parts gives us

$$\begin{aligned} 0 &= \mu \int_{\Omega} \phi^2 \nabla \cdot (m \nabla \phi) - \int_{\Omega} m^3 \phi^3 + m^2 \phi^2 \\ &= -\mu \int_{\Omega} 2\phi m |\nabla \phi|^2 - \int_{\Omega} m^3 \phi^3 + m^2 \phi^2 \\ &= 2\mu \int_{\Omega} f |\nabla \phi|^2 - \int_{\Omega} f^2 (1 - f). \end{aligned} \quad (4.8)$$

So from (4.8), $\int_{\Omega} f^2 (1 - f) = 2\mu \int_{\Omega} f |\nabla \phi|^2 > 0$, since m is non-constant in Ω . Therefore, $\int_{\Omega} f^2 > \int_{\Omega} f^3$. We claim that this is a contradiction. To see this notice

$$\begin{aligned} 0 &\leq \int_{\Omega} (f + 1)(f - 1)^2 \\ &= \int_{\Omega} (f^2 - 1)(f - 1) \end{aligned}$$

$$\begin{aligned}
&= \int_{\Omega} f^2(f-1) - \int_{\Omega} (f-1) \\
&= \int_{\Omega} f^2(f-1). \tag{4.9}
\end{aligned}$$

Thus from (4.9), $\int_{\Omega} f^3 \geq \int_{\Omega} f^2$. As previously claimed, this is a contradiction, finishing the proof. \square

Using Lemmas 4.1 and 4.2, we see that for $\beta \in (0, \beta^*)$, system (1.2) has no coexistence states and the semi-trivial steady state $(0, v^*)$ is unstable. Because we can change variables to show that (1.2) is a strongly monotone system, we apply the monotone dynamical system theory [3,16] to conclude that $(m, 0)$, the other semi-trivial steady state, is globally asymptotically stable. This completes the proof of Theorem 2.2.

5. Proof of Theorem 2.3

In this section we show that $(0, v^*)$ is unstable for sufficiently large β . Suppose on the contrary that $(0, v^*)$ is stable. Consider once again the expression

$$\begin{aligned}
\frac{d}{dt} \int_{\Omega} \frac{m^2}{u} &= - \int_{\Omega} \frac{2\mu m |\nabla(u/m)|^2}{(u/m)^3} - \int_{\Omega} m^2(m-u-v) \\
&\leq - \int_{\Omega} m^2(m-u-v) \\
&= - \int_{\Omega} m^3 - \int_{\Omega} m^2(-u-v+v^*) + \int_{\Omega} m^2 v^* \\
&\leq - \int_{\Omega} m^3 - \int_{\Omega} m^2(-u-v+v^*) + \|m^2\|_{L^\infty(\Omega)} \int_{\Omega} v^* \\
&\leq - \int_{\Omega} m^3 + \epsilon
\end{aligned}$$

where the last inequality follows from the definition of stability of $(0, v^*)$ and the fact that $\int_{\Omega} v^* \rightarrow 0$ as $\beta \rightarrow \infty$ [4]. Since $\int_{\Omega} m^3 = \bar{\delta} > 0$, we can choose $\epsilon > 0$ small enough and β large enough such that

$$\frac{d}{dt} \int_{\Omega} \frac{m^2}{u} \leq -\bar{\delta}/2 < 0$$

for all $t > 0$. As in the proof of Lemma 3.4 this leads to a contradiction and completes the proof of Theorem 2.3.

6. Discussion

This study explores the competition of two species subject to different population dynamics and dispersal strategies in a spatially variable habitat. In particular, we suppose that one species undergoes a weak Allee effect, having limited growth at small populations, but plays a movement strategy that is ideal free. In other words, while the species has reduced fitness (in comparison with the other

species) at small populations, its steady state distribution in the absence of a competitor is in proportion to the resource quality at each location in the habitat. When both species have the same population dynamics (no Allee effect), it was shown that the species playing the ideal free strategy reigns supreme, driving the less “optimal” mover to extinction [1] (here we use “optimal” in terms of a single species’ ability at steady state to match the resource distribution). However, we find that this result is not always true as we study the competition between an “optimal” disperser u with more restrictive population dynamics and a less capable disperser v without restrictive population dynamics.

To summarize the global dynamics of (1.2) while varying the advection rate β of species v on the interval $[0, \infty)$, we divide this interval into several parts, commenting on the results and some open problems:

- $\beta \in [0, \beta^*)$.
Combining the results in Theorems 2.1 and 2.2, we show that $(m, 0)$ is globally asymptotically stable. Biologically, this means that u cannot only invade v , but species u will cause v to go extinct. Therefore, we see that v as a pure diffuser or diffuser with weak advection is not able to overcome the resource matching ability of u . As stated before, we suggest that u has enough advection to take advantage of better resources, and therefore is less affected by the initial reduction in fitness.
- $\beta \in [\beta^*, 1)$.
We conjecture based on numerical simulations and Lemma 4.1 that $(m, 0)$ is globally asymptotically stable for $\beta \in (0, 1)$. The difficulty here is showing that (1.2) has no positive steady state solutions for this range of β . We suspect that a clever Lyapunov functional can be defined to solve this problem. For instance, lurking behind the scenes in the proof of Lemma 3.3 is the functional $E : C(\Omega) \times C(\Omega) \rightarrow \mathbb{R}$ defined by

$$E(u, v) = \int_{\Omega} \frac{m^2}{u} + 2m \ln u - u + \frac{v^2}{2}$$

as the zero derivative along trajectories, $dE/dt = 0$ is given in Eq. (3.10).

- $\beta = 1$.
For $\beta = 1$, both species are playing the ideal free strategy and thus can coexist. Here we have a continuum of steady state solutions (see Remark 1).
- Intermediate values of $\beta > 1$.
For intermediate values of β , the analysis is more difficult. Numerical simulations suggest that there exists a $\tilde{\beta}$ such that $(0, v^*)$ is globally asymptotically stable for $\beta \in (1, \tilde{\beta}]$ and there exists a $\hat{\beta}$ such that both species can coexist in a possibly small interval given by $(\tilde{\beta}, \hat{\beta})$. This result shows that the dynamics of (1.2) are more intricate than those in (1.1), suggesting that there are a range of strategies for v that cannot be invaded even by an ideal free disperser. That is to say, even if a rare species plays an “optimal” movement strategy in comparison with a resident competitor, a slight reduction in fitness at small populations can be enough to prevent its invasion. Supporting such claims analytically would be an interesting and challenging direction for future work.
- $\beta \in [\beta^{**}, \infty)$.
For large values of β , we were able to show analytically that $(0, v^*)$ is unstable, implying that u can invade. This is somewhat surprising since v , moving with strong advection, establishes itself at the best resources, i.e. maxima of m . However, we maintain that since β is so large, v concentrates too much near these maxima, giving u an opportunity to grow in quite favorable regions of the habitat. Based on this and simulations, we propose that $(m, 0)$ is globally asymptotically stable, leaving it as an open problem (even showing local stability is non-trivial). The crux here involves proving that (1.2) has no positive steady states for large enough β . Again, perhaps an insightful Lyapunov functional can be used to “tie up” the loose ends.

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