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EVOLUTION OF DISPERSAL AND THE IDEAL FREE DISTRIBUTION

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Dedicated to Horst R. Thieme on the Occasion of his 60th Birthday

Abstract. A general question in the study of the evolution of dispersal is what kind of dispersal strategies can convey competitive advantages and thus will evolve. We consider a two species competition model in which the species are assumed to have the same population dynamics but different dispersal strategies. Both species disperse by random diffusion and advection along certain gradients, with the same random dispersal rates but different advection coefficients. We found a conditional dispersal strategy which results in the ideal free distribution of species, and show that it is a local evolutionarily stable strategy. We further show that this strategy is also a global convergent stable strategy under suitable assumptions, and our results illustrate how the evolution of conditional dispersal can lead to an ideal free distribution. The underlying biological reason is that the species with this particular dispersal strategy can perfectly match the environmental resource, which leads to its fitness being equilibrated across the habitats.

1. Introduction.

Dispersal is an obvious and important feature of the life histories of many organisms, but its evolution and ecological effects remain poorly understood [11]. A question that has attracted the attention of a number of researchers is whether dispersal can evolve in habitats that are spatially heterogeneous but temporally constant, and if so, what dispersal strategies are likely to evolve. To address this question researchers typically have constructed models designed to describe what happens when a small number of individuals using a novel dispersal strategy are introduced into a population that is using another strategy. A viewpoint that is becoming more widespread in such modeling is that of adaptive dynamics, which connects the possibility of evolutionary invasion by a novel trait with the population dynamical processes that drive selection; see [18]. That approach has been used to a considerable extent in metapopulation models [18] but to a lesser degree in reaction-diffusion-advection models for dispersal in continuous space. An

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important idea in adaptive dynamics and similar approaches to evolutionary theory is the idea of evolutionarily stable strategies. A strategy is said to be evolutionarily stable if a population using it cannot be invaded by any small population using a different strategy. A related but different idea is that of convergent stable strategies. A strategy is convergent stable, roughly speaking, if small changes in nearby strategies are only favored (i.e., able to invade a resident population) if they are closer to the convergent stable strategy than the resident strategy. In other words, convergent stable strategies act as attractors for adaptive dynamics. In this paper we will use reaction-diffusion-advection models to examine the evolution of a type of conditional dispersal strategy, i.e., a nonrandom dispersal strategy that depends on environmental conditions [32]. To the extent possible we will frame our analysis in terms of adaptive dynamics, evolutionary stability, and related ideas. We will use the standard abbreviations ESS for "evolutionarily stable strategy" and CSS for "convergent stable strategy."

The starting point for the direction of research on the evolution of dispersal in spatially variable but temporally constant environments that we will pursue here is the paper [24]. In that paper Hastings showed that in simple diffusion models selection generally favors slower dispersal. A similar result was obtained in a more sophisticated modeling context in [20]. However, a close examination of the results of [20, 24] shows that their results hold because the population distribution resulting from diffusion creates a mismatch between population density and environmental quality as measured by the effective local population growth rate. In [32], McPeek and Holt found that in some simple discrete models selection could favor dispersal strategies that did not create such a mismatch. In this paper we will use the modeling approach of [20] but we will replace diffusion with a more subtle combination of advection and diffusion that allows populations to match environmental quality. Such strategies can be evolutionarily stable or convergent stable. They have the key features that at equilibrium individuals have the same fitness (as measured by the local population growth rate at their location) and there is no net movement of individuals, that is, the equilibrium density with the dispersal terms present in the model is the same as it would be if the dispersal terms were absent. These two features characterize a particular spatial distribution of a population known as the ideal free distribution; see [5]. The models considered in [5] included discrete diffusion systems of the form

$$\frac{du_i}{dt} = F_i(\vec{u})u_i + \sum_{\substack{j=1 \\ j\neq i}}^{n} [d_{ij}u_j - d_{ji}u_i] \quad \text{for} \quad i = 1, \dots, n. \tag{1.1}$$

In that setting a dispersal strategy defined by $\{d_{ij}\}$ is ideal free at an equilibrium $\vec{u}^* = (u_1^*, \dots, u_n^*)$ if

$$F_i(\vec{u^*}) = 0 \quad \text{and} \quad \sum_{\substack{j=1 \\ j\neq i}}^{n} \left[d_{ij}u_j^* - d_{ji}u_i^*\right] = 0 \quad \text{for} \quad i = 1, \dots, n. \tag{1.2}$$

In [5] it was shown that in the modeling formulation of [24], the ideal free property described in (1.2) is generally necessary and often sufficient for evolutionary stability of the strategy $\{d_{ij}\}$. Related results are obtained in [14, 30, 32, 33]. In the present paper we will consider the analogous situation for models of the form

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - u\nabla P] + u(m-u) & \text{in } \Omega\times(0,\infty), \\ [\nabla u - u\nabla P]\cdot n = 0 & \text{on } \partial\Omega\times(0,\infty), \end{cases} \tag{1.3}$$

where $u(x,t)$ represents the density of some species at location x and time t, $\mu > 0$ is the random diffusion rate, P and m are functions of x only, and m represents the intrinsic growth rate of species. The habitat Ω is a bounded domain in R^N with smooth boundary $\partial\Omega$, n is the outward unit normal vector on $\partial\Omega$, and the boundary condition in (1.3) means that there is no flux across the boundary.

In that setting the dispersal strategy determined by μ and P is ideal free if

$$\nabla\cdot[\nabla m - m\nabla P] = 0 \quad \text{in } \Omega, \tag{1.4}$$

which will hold if $P = \ln m + C$ for some constant C. (There are other ways that diffusive population models can support or approximate ideal free dispersal strategies, for example by nonlinear diffusion; see [8, 12].) We will show that the ideal free property is closely related to the evolutionary stability and convergent stability of dispersal strategies in (1.3). It turns out that the analysis of [24] can be applied to (1.3) by rewriting (1.3) in terms of the variable u/e^P if $P \neq \ln m + C$. In that case it follows that if $P \neq \ln m + C$ for any constant C then there will be selection for smaller μ, but in the ideal free situation the analysis of [24] does not apply. We will study the evolutionary properties of ideal free dispersal in (1.3) from the modeling viewpoint of [20]. The key idea is to consider the invading and resident populations as competitors that are ecologically identical but use different dispersal strategies. In this connection, consider the two species competition model

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - u\nabla P] + u(m-u-v) & \text{in } \Omega\times(0,\infty), \\ v_t = \nu\nabla\cdot[\nabla v - v\nabla Q] + v(m-u-v) & \text{in } \Omega\times(0,\infty), \\ [\nabla u - u\nabla P]\cdot n = [\nabla v - v\nabla Q]\cdot n = 0 & \text{on } \partial\Omega\times(0,\infty), \end{cases} \tag{1.5}$$

where $P, Q, m \in C^2(\bar\Omega)$. It is known that if $m > 0$ in Ω, then (1.5) has two semi-trivial steady states, denoted by $(u^*, 0)$ and $(0, v^*)$, respectively.

Throughout this paper we shall focus on the case when $\mu = \nu$. Assume $\mu = \nu$ and we can envision that system (1.5) models two competing species that are identical except their different dispersal strategies P and Q. An interesting question is whether there is any strategy in system (1.5) that is evolutionarily stable. In mathematical terms, the dispersal strategy P for the species with density u is a global evolutionarily stable strategy (ESS) if the semi-trivial steady state $(u^*, 0)$ is always locally stable, provided that Q is different from P (more precisely, $Q - P$ is non-constant in Ω). Similarly, we say that P is a local ESS if $(u^*, 0)$ is always locally stable provided that Q is close to P in $C^2(\bar\Omega)$ and $Q - P$ is nonconstant in Ω. The following result suggests that the ideal free strategy $P = \ln m$ (unique up to some constant as $\nabla P = \nabla(P + C)$ for any constant C) is a global ESS. The underlying reason is that when $P = \ln m$ (or $P = \ln m + C$ for some constant in general), $u^* \equiv m$ in Ω. That is, when the other competing species is not present, the species u with the dispersal strategy $P = \ln m$ can perfectly match the environmental resource which leads to its fitness being equilibrated across the habitats; i.e., $m - u^* \equiv 0$ in Ω.

Theorem 1. *Suppose that $\mu = \nu$, $m \in C^2(\bar\Omega)$ and $m > 0$ in $\bar\Omega$.*

a) *Suppose that* $P(x) = \ln m(x)$, $Q(x) = \ln m(x) + \epsilon R(x)$, *where* $R \in C^2(\bar{\Omega})$. *If* R *is non-constant, then* $(0, v^*)$ *is unstable and* $(u^*, 0)$ *is globally asymptotically stable for* $0 < |\epsilon| \ll 1$.

b) *Suppose that* $P(x) - \ln m$ *is non-constant. Then there exists some* $R \in C^2(\bar{\Omega})$ *such that for* $Q(x) = P(x) + \epsilon R(x)$, $(u^*, 0)$ *is unstable for* $0 < |\epsilon| \ll 1$.

In terms of the theory of Adaptive Dynamics [16, 17, 19, 21], part (a) illustrates that $P = \ln m$ is a local ESS and part (b) shows that no other strategy can be a local ESS. We conjecture that $P = \ln m$ is a global ESS.

Another related question is whether $\ln m$ is a global convergent stable strategy (CSS) of system (1.5). In biological terms, a strategy is convergent stable if selection favors strategies that are closer to it in an appropriate sense over strategies that are further away. Thus, evolution can be expected to drive strategies toward convergent stable strategies. (In general, evolutionarily stable strategies may or may not be convergent stable and vice-versa.) To be more precise, let $P = \ln m + \alpha R$ and $Q = \ln m + \beta R$ for some non-constant function R, where α, β are scalar numbers which represent a certain trait of the resident species with density u and the invading species with density v, respectively. We say that $\ln m$ is a global CSS if $(u^*, 0)$ is locally stable provided that $0 < \alpha < \beta$ or $\beta < \alpha < 0$, and locally unstable provided that $0 < \beta < \alpha$ or $\alpha < \beta < 0$. In this connection, we have:

Theorem 2. *Suppose that* $\mu = \nu$, $P(x) = \ln m + \alpha R$, $Q(x) = \ln m + \beta R$, $m > 0$. *We further assume that* $\Omega = (0, 1)$ *and* $R_x \neq 0$ *in* $[0, 1]$.

a) *If* $\alpha < \beta < 0$ *or* $0 < \beta < \alpha$, *then* $(u^*, 0)$ *is unstable and* $(0, v^*)$ *is stable. Moreover, given any* $\eta > 0$, *there exists* $\kappa > 0$ *such that if either* (i) $\alpha, \beta \in [-\eta, 0]$ *and* $0 < \beta - \alpha < \kappa$ *or* (ii) $\alpha, \beta \in [0, \eta]$ *and* $-\kappa < \beta - \alpha < 0$, *then* $(0, v^*)$ *is globally asymptotically stable.*

b) *If either* $\alpha < 0 < \beta$ *or* $\beta < 0 < \alpha$, *then both* $(u^*, 0)$ *and* $(0, v^*)$ *are unstable, and system* (1.5) *has at least one stable positive steady state.*

Part (a) of Theorem 2 not only shows that $\ln m$ is a global convergent stable strategy along suitable paths, it also determines the global dynamics of system (1.5) when the two strategies P and Q are close to each other. Note that the choice of κ in (a) is independent of α, β.

Part (b) of Theorem 2 is of independent interest as it provides a mechanism of coexistence of two competing species. The uniqueness and stability of the coexistence state remains unsettled. If we fix $\alpha \neq 0$ and let β be the parameter to vary, preliminary bifurcation analysis shows that a branch of coexistence states bifurcates from the semi-trivial steady state $(0, v^*)$ at $\beta = 0$, even without the assumption $\mu = \nu$. We plan to study how the branch of coexistence states bifurcates from the semi-trivial steady states for general μ, ν, α and β and report our progress in a forthcoming paper, among other things.

The case when m is constant is noteworthy as our results suggest that the optimal dispersal strategy for the homogeneous environment is not to adopt any sort of directed movements.

Concerning the general dynamics of (1.5), we have the following comments:

Remark 1.1. Suppose that $\mu = \nu$, $P = \ln m + \alpha R$, $Q = \ln m + \beta R$, $m > 0$ and R is non-constant. We conjecture that the dynamics of (1.5) and the structure of the coexistence states, in terms of α and β, can be described as follows:

a) If $\alpha < 0$, then $(u^*, 0)$ is globally asymptotically stable for $\beta < \alpha$, $(0, v^*)$ is globally asymptotically stable for $\beta \in (\alpha, 0]$, and system (1.5) has a unique coexistence state for $\beta > 0$, which is globally asymptotically stable.

b) If $\alpha = 0$, then $(u^*, 0)$ is globally asymptotically stable provided that $\beta \neq 0$.

c) If $\alpha > 0$, then (1.5) has a unique coexistence state for $\beta < 0$, which is globally asymptotically stable; $(0, v^*)$ is globally asymptotically stable for $\beta \in (0, \alpha)$, and $(u^*, 0)$ is globally asymptotically stable for $\beta > \alpha$.

This paper is arranged as follows. In Section 2, we discuss some general properties of system (1.5) including its monotonicity and establish some technical lemmas. Section 3 is devoted to understanding the stability of both semi-trivial steady states. In Section 4 we apply the Lyapunov-Schmidt procedure to study the structure of the solution set of system (1.5) for suitable P and Q, and establish several results on the non-existence of coexistence states of (1.5). The complete proofs of Theorem 1 and 2 are given in the end of Section 4. A brief nonmathematical discussion of the results is given in Section 5.

2. **Preliminary results.** In this section we first summarize some statements regarding solutions of system (1.5) and the stability of its steady states. By the maximum principle for cooperative systems [34], if the initial conditions of (1.5) are non-negative and not identically zero, the solutions of (1.5) are positive for $t \in (0, T)$, where $T \in (0, \infty]$ is the maximal existence time for the solutions of (1.5). By standard theory for parabolic equations [26], system (1.5) has a unique classical solution which exists for all time (i.e., $T = \infty$) and it defines a smooth dynamical system on $C(\bar{\Omega}) \times C(\bar{\Omega})$ [25, 35]. The stability of steady states of (1.5) is understood with respect to the topology of $C(\bar{\Omega}) \times C(\bar{\Omega})$.

A steady state $(\tilde{u}, \tilde{v})$ of (1.5) with both components positive is called a coexistence state; $(\tilde{u}, \tilde{v})$ is a semi-trivial steady state if one component is positive and the other is the zero function. When $m > 0$ in Ω, it can be shown that (1.5) has exactly two semi-trivial equilibria, denoted by $(u^*, 0)$ and $(0, v^*)$, respectively.

Definition 1. We say that (1.5) is a strongly monotone dynamical system if
a) $u_1(x, 0) \geq u_2(x, 0)$ and $v_1(x, 0) \leq v_2(x, 0)$ for all $x \in \Omega$ and
b) $(u_1(x, 0), u_2(x, 0)) \not\equiv (u_2(x, 0), v_2(x, 0))$
implies $u_1(x, t) > u_2(x, t)$ and $v_1(x, t) < v_2(x, t)$ for all $x \in \bar{\Omega}$ and $t > 0$.

The following result is a consequence of the maximum principle and the structure of (1.5).

Theorem 3. *The system* (1.5) *is a strongly monotone dynamical system.*

Proof. Set $w_i = u_i / e^P$ and $z_i = v_i / e^Q$. Then

$$\begin{cases} w_{i,t} = \mu e^{-P} \nabla \cdot [e^P \nabla w_i] + w_i (m - e^P w_i - e^Q v_i) & \text{in } \Omega \times (0, \infty), \\ z_{i,t} = \nu e^{-Q} \nabla \cdot [e^Q \nabla z_i] + z_i (m - e^P w_i - e^Q v_i) & \text{in } \Omega \times (0, \infty), \\ \nabla w_i \cdot n = \nabla z_i \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{2.1}$$

Since $w_1(x, 0) \geq w_2(x, 0)$ and $z_1(x, 0) \leq z_2(x, 0)$ in Ω, by the comparison principle for systems with two competitors (see [4, 25]) we have $w_1(x, t) \geq w_2(x, t)$ and $z_1(x, t) \leq z_2(x, t)$ in $\Omega \times (0, \infty)$; i.e., $u_1(x, t) \geq u_2(x, t)$ and $v_1(x, t) \leq v_2(x, t)$ in $\Omega \times (0, \infty)$. As $(w_1(x, 0), z_1(x, 0)) \not\equiv (w_2(x, 0), z_2(x, 0))$, from the strong maximum principle [34] we see that $w_1(x,t) > w_2(x,t)$ and $z_1(x,t) < z_2(x,t)$ in $\bar{\Omega} \times (0,\infty)$, i.e., $u_1(x,t) > u_2(x,t)$ and $v_1(x,t) < v_2(x,t)$ in $\bar{\Omega} \times (0,\infty)$. □

The following result is a consequence of Theorem 3 and the monotone dynamical system theory [25, 35]:

Theorem 4. *If system* (1.5) *has no coexistence state, then one of the semi-trivial steady states is unstable and the other one is globally asymptotically stable* [28]*; If both semi-trivial steady states are unstable, then* (1.5) *has at least one stable coexistence state* [15, 31].

For the rest of this section, we present two technical lemmas which will play important roles in the analysis later.

Let w be a solution of

$$\begin{cases} w_{xx} + b(x)w_x + \gamma(x)w\,[\kappa(x) - w] = 0 \quad \text{in } (0,1), \\ w_x(0) = w_x(1) = 0, \quad w > 0 \quad \text{in } [0,1], \end{cases} \tag{2.2}$$

where $b, \gamma \in C[0,1]$, $\kappa \in C^1[0,1]$, and $\gamma, \kappa > 0$ in $[0,1]$.

Lemma 2.1. *If $\kappa_x > 0$ in $[0,1]$, then $w_x > 0$ in $(0,1)$; if $\kappa_x < 0$ in $[0,1]$, then $w_x < 0$ in $(0,1)$.*

Proof. We consider the case $\kappa_x > 0$ in $[0,1]$ only. Set $h(x) := w(x) - \kappa(x)$. We claim that $h(0) > 0$. To establish this assertion, we argue by contradiction and assume that $h(0) \le 0$. Since $h_x(0) = w_x(0) - \kappa_x(0) = -\kappa_x(0) < 0$, then $h(x) < 0$ in $(0, \delta_1)$ for some $\delta_1 > 0$. By (2.2) we see that $w_{xx} + b(x)w_x < 0$ in $(0,\delta_1)$, i.e., $(e^{\int_0^x b} w_x)_x < 0$ in $(0,\delta_1)$. Since $w_x(0) = 0$, we have $w_x < 0$ in $(0,\delta_1)$. As $w_x(1) = 0$, we let $x^* \in (0,1]$ be the smallest number in $(0,1]$ such that $w_x(x^*) = 0$ and $w_x < 0$ in $(0,x^*)$. By the choice of x^*, $w_{xx}(x^*) \ge 0$. Thus, by (2.2) we see that $h(x^*) \ge 0$. However, as $w_x < 0$ in $(0,x^*)$ and $\kappa_x > 0$, we have $h_x = w_x - \kappa_x < 0$ in $(0,x^*)$. Since we assume that $h(0) \le 0$, then $h(x^*) < 0$, which is a contradiction.

Therefore, we must have $h(0) > 0$, so that $h > 0$ in $[0,\delta_2)$ for some $\delta_2 > 0$. By (2.2) we have $w_{xx} + b(x)w_x > 0$ in $(0,\delta_2)$, which implies that $(e^{\int_0^x b} w_x)_x > 0$ in $(0,\delta_2)$. As $w_x(0) = 0$, we see that $w_x > 0$ in $(0,\delta_2)$. Since $w_x(1) = 0$, we let $x^* \in (0,1]$ be the smallest number in $(0,1]$ such that $w_x(x^*) = 0$ and $w_x > 0$ in $(0,x^*)$. By the choice of x^*, $w_{xx}(x^*) \le 0$. By (2.2), we see that $h(x^*) \le 0$.

We claim that $x^* = 1$. If not, suppose that $x^* < 1$. Note that $h_x(x^*) = w_x(x^*) - \kappa_x(x^*) = -\kappa_x(x^*) < 0$. As $h(x^*) \le 0$, we may assume that $h < 0$ in $(x^*, x^* + \delta_3]$ for some $\delta_3 > 0$. We consider two different cases:

Case a. $h(x) < 0$ for $x \in (x^*, 1)$. By (2.2) we have $w_{xx} + bw_x < 0$ in $(x^*,1)$, i.e., $(e^{\int_0^x b} w_x)_x < 0$ in $(x^*,1)$. As $w_x(x^*) = 0$, we see that $w_x < 0$ in $(x^*,1]$, which contradicts $w_x(1) = 0$.

Case b. $h(x) = 0$ for some $x \in (x^*,1)$. Let $\bar{x}$ be the smallest number in $(x^*,1)$ such that $h(x) < 0$ in $(x^*,\bar{x})$ and $h(\bar{x}) = 0$. Then $w_{xx} + bw_x < 0$ in $(x^*,\bar{x})$. This along with $w_x(x^*) = 0$ implies that $w_x(\bar{x}) < 0$. On the other hand, by the choice of $\bar{x}$, $h_x(\bar{x}) \ge 0$, i.e., $w_x(\bar{x}) - \kappa_x(\bar{x}) \ge 0$. Hence, $w_x(\bar{x}) \ge \kappa_x(\bar{x}) > 0$, which is a contradiction.

Therefore, $x^* = 1$; i.e., $w_x > 0$ in $(0,1)$. This completes the proof of the case $\kappa_x > 0$. The proof of the other case is similar and is thus omitted. □

Lemma 2.2. *Suppose that $m, R \in C^1(\bar{\Omega})$ in $\bar{\Omega}$, $m > 0$ in $\bar{\Omega}$, and R is non-constant. Let w denote the unique solution of*

$$\begin{cases} \nabla \cdot [m\nabla w] - m^2(w+R) = 0 \quad \text{in } \Omega, \\ \dfrac{\partial w}{\partial n}|_{\partial\Omega} = 0. \end{cases} \tag{2.3}$$

Then

$$\int_\Omega m\nabla R \cdot \nabla w < 0. \tag{2.4}$$

Proof. Multiplying the equation of w by w and integrating in Ω, we have

$$-\int_\Omega m|\nabla w|^2 = \int_\Omega m^2 w(w+R).$$

Since R is not a constant function, we see that w is also non-constant. Hence,

$$\int_\Omega m^2 w(w+R) < 0.$$

Since

$$m^2 w(w+R) = m^2(R+w)^2 - m^2 R(R+w),$$

we have

$$\int_\Omega m^2 R(R+w) > \int_\Omega m^2(R+w)^2 \geq 0. \tag{2.5}$$

Multiplying the equation of w by R and integrating in Ω, we have

$$\int_\Omega m\nabla R \cdot \nabla w = -\int_\Omega m^2 R(R+w) < 0. \tag{2.6}$$

where the last inequality follows from (2.5). □

3. **Stability of semi-trivial steady states.** In this section we study the local stability of both semi-trivial steady states of the system (1.5). As we focus on the case when $\mu = \nu$ in this paper, without loss of generality we assume that $\mu = \nu = 1$ from now on.

The first result of this section is

Proposition 1. *Suppose that $\Omega = (0,1)$.*

a) $(u^*, 0)$ *is stable if* $(P_x - Q_x)(m/e^P)_x > 0$ *in* $[0,1]$, *unstable if* $(P_x - Q_x)(m/e^P)_x < 0$ *in* $[0,1]$.

b) $(0, v^*)$ *is stable if* $(P_x - Q_x)(m/e^Q)_x < 0$ *in* $[0,1]$, *unstable if* $(P_x - Q_x)(m/e^Q)_x > 0$ *in* $[0,1]$.

Proof. It suffices to prove part (a) as the proof of part (b) is identical. Rewrite the equation of u^* as

$$\begin{cases} \nabla \cdot \left[e^P \nabla(u^*/e^P)\right] + u^*(m - u^*) = 0 \quad \text{in } \Omega, \\ \nabla(u^*/e^P) \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{3.1}$$

The stability of $(u^*, 0)$ is determined by the sign of the principal eigenvalue of the linear problem

$$\begin{cases} \nabla \cdot [\nabla\psi - \psi\nabla Q] + \psi(m - u^*) = \sigma\psi \quad \text{in } \Omega, \\ [\nabla\psi - \psi\nabla Q] \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{3.2}$$

Rewrite (3.2) as

$$\begin{cases} \nabla \cdot \left[e^Q \nabla(\psi/e^Q)\right] + \psi(m-u^*) = \sigma\psi & \text{in } \Omega, \\ \nabla(\psi/e^Q)\cdot n = 0 & \text{on } \partial\Omega. \end{cases} \tag{3.3}$$

Set

$$\psi/e^Q = \varphi \cdot (u^*/e^P).$$

Then by (3.1) and (3.3) we see that φ satisfies $\nabla\varphi \cdot n = 0$ on $\partial\Omega$ and

$$\begin{aligned} &\frac{u^*}{e^{P-Q}}\Delta\varphi + \left[\nabla\left(\frac{u^*}{e^{P-Q}}\right) + e^Q\nabla\frac{u^*}{e^P}\right]\cdot\nabla\varphi + e^P\varphi\nabla(e^{Q-P})\cdot\nabla\left(\frac{u^*}{e^P}\right) \\ &= \sigma\frac{u^*}{e^{P-Q}}\varphi \end{aligned} \tag{3.4}$$

in Ω. The key is to determine the sign of $\nabla(e^{Q-P})\cdot\nabla\left(u^*/e^P\right)$.

For $\Omega = (0,1)$, we consider the situation when $(P_x - Q_x)(m/e^P)_x > 0$ in $[0,1]$. There are two cases: (1) $P_x > Q_x$ and $(m/e^P)_x > 0$ in $[0,1]$; (2) $P_x < Q_x$ and $(m/e^P)_x < 0$ in $[0,1]$.

Set $w = u^*/e^P$. Then w satisfies

$$\begin{cases} w_{xx} + P_x w_x + e^P w(m/e^P - w) = 0 & \text{in } (0,1), \\ w_x(0) = w_x(1) = 0. \end{cases}$$

We first consider the case (1). For this case, as $(m/e^P)_x > 0$ in $[0,1]$, by Lemma 2.1 we have $w_x > 0$ in $(0,1)$; i.e., $(u^*/e^P)_x > 0$ in $(0,1)$. Hence, as $P_x > Q_x$,

$$(e^{Q-P})_x \cdot \left(u^*/e^P\right)_x = e^{Q-P}(Q_x - P_x)\left(u^*/e^P\right)_x < 0 \quad \text{in } (0,1). \tag{3.5}$$

By (3.4), (3.5), and the comparison principle for principal eigenvalues it follows that $\sigma < 0$, i.e., $(u^*, 0)$ is stable.

For the case (2), as $(m/e^P)_x < 0$ in $[0,1]$, by Lemma 2.1 we have $w_x < 0$ in $(0,1)$; i.e., $(u^*/e^P)_x < 0$ in $(0,1)$. Hence, as $P_x < Q_x$, we see that (3.5) still holds, which again implies that $\sigma < 0$. Therefore, if $(P_x - Q_x)(m/e^P)_x > 0$ in $[0,1]$, $(u^*,0)$ is stable. Similarly, we can show that if $(P_x - Q_x)(m/e^P)_x < 0$ in $[0,1]$, $(u^*,0)$ is unstable. This completes the proof of part (a). □

The following lemma is a direct consequence of Proposition 1:

Lemma 3.1. *Suppose that $P = \ln m + \alpha R$, $Q = \ln m + \beta R$, $\Omega = (0,1)$, $m > 0$ and $R_x \neq 0$ in $[0,1]$. Then*

a) *$(u^*, 0)$ is unstable when $\alpha(\alpha - \beta) > 0$ and stable when $\alpha(\alpha-\beta) < 0$;*

b) *$(0, v^*)$ is unstable when $\beta(\alpha - \beta) < 0$ and stable when $\beta(\alpha - \beta) > 0$.*

Proof. For $P = \ln m + \alpha R$, $Q = \ln m + \beta R$,

$$(P_x - Q_x)(m/e^P)_x = \alpha(\beta - \alpha)e^{-\alpha R}R_x^2. \tag{3.6}$$

The conclusion of part (a) thus follows from (3.6) and part (a) of Proposition 1. The proof of part (b) is identical and is omitted. □

Next, we consider the situation when $Q(x) = P(x) + \epsilon R(x)$ for $|\epsilon| \ll 1$, i.e., when the two competing species are similar.

Lemma 3.2. *Suppose that $P(x) = \ln m$ and $Q(x) = \ln m + \epsilon R(x)$, where $R \in C^2(\bar\Omega)$. If $R(x)$ is non-constant, then $(0, v^*)$ is unstable for $0 < |\epsilon| \ll 1$.*

Proof. Note that $v^* = m$ when $\epsilon = 0$. For $|\epsilon| \ll 1$, as $v^* = m$ is non-degenerate, by the implicit function theorem we can expand v^* as $v^* = m + \epsilon v_1 + \epsilon^2 v_2 + \epsilon^3 v_3$, where v_1 is uniquely determined by

$$\begin{cases} \nabla \cdot [\nabla v_1 - v_1 \nabla(\ln m) - m\nabla R] - v_1 m = 0 \quad \text{in } \Omega, \\ [\nabla v_1 - v_1 \nabla(\ln m) - m\nabla R] \cdot n|_{\partial\Omega} = 0, \end{cases} \tag{3.7}$$

and v_2 is uniquely determined by

$$\begin{cases} \nabla \cdot [\nabla v_2 - v_2 \nabla(\ln m) - v_1\nabla R] - m v_2 - v_1^2 = 0 \quad \text{in } \Omega, \\ [\nabla v_2 - v_2 \nabla(\ln m) - v_1\nabla R] \cdot n|_{\partial\Omega} = 0, \end{cases} \tag{3.8}$$

and $v_3(\cdot;\epsilon)$ is some function which is uniformly bounded in the $C^2(\bar{\Omega})$ norm for all small ϵ.

The stability of $(0, v^*)$ is determined by the sign of the principal eigenvalue, denoted by λ^*, of the problem

$$\begin{cases} \nabla \cdot [\nabla \varphi - \varphi \nabla(\ln m)] + (m - v^*)\varphi = -\lambda\varphi \quad \text{in } \Omega, \\ [\nabla \varphi - \varphi \nabla(\ln m)] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{3.9}$$

As v^* is a smooth function of ϵ, λ^* is also a smooth function of ϵ. It is clear to see that $\lambda^* = 0$ when $\epsilon = 0$. Hence, we may expand λ^* as $\lambda^* = \epsilon\lambda_1 + \epsilon^2\lambda_2 + O(\epsilon^3)$. Also, after suitable normalization we may expand the principal eigenfunction φ^* as ([4]) $\varphi^* = m + \epsilon\varphi_1 + \epsilon^2\varphi_2 + \epsilon^3\varphi_3$, where φ_1 satisfies

$$\begin{cases} \nabla \cdot [\nabla \varphi_1 - \varphi_1 \nabla(\ln m)] - v_1 m = -\lambda_1 m \quad \text{in } \Omega, \\ [\nabla \varphi_1 - \varphi_1 \nabla(\ln m)] \cdot n|_{\partial\Omega} = 0 \end{cases}$$

and φ_2 satisfies

$$\begin{cases} \nabla \cdot [\nabla \varphi_2 - \varphi_2 \nabla(\ln m)] - v_2 m - v_1\varphi_1 = -\lambda_2 m \quad \text{in } \Omega, \\ [\nabla \varphi_2 - \varphi_2 \nabla(\ln m)] \cdot n|_{\partial\Omega} = 0, \end{cases}$$

and $\varphi_3(\cdot;\epsilon)$ is some function that is uniformly bounded in $C^2(\bar{\Omega})$ norm for all small ϵ.

Integrating the equation of v_1 in Ω, we have $\int_\Omega v_1 m = 0$. Integrating the equation of φ_1 in Ω, we have $\int_\Omega v_1 m = \lambda_1 \int_\Omega m$. Hence, $\lambda_1 = 0$. Similarly, from the equations of v_2 and φ_2 we have

$$-\lambda_2 \int_\Omega m = -\int_\Omega m v_2 - \int_\Omega v_1\varphi_1 = \int_\Omega v_1^2 - \int_\Omega v_1\varphi_1.$$

As $\lambda_1 = 0$, φ_1 satisfies

$$\begin{cases} \nabla \cdot [\nabla \varphi_1 - \varphi_1 \nabla(\ln m)] - v_1 m = 0 \quad \text{in } \Omega, \\ [\nabla \varphi_1 - \varphi_1 \nabla(\ln m)] \cdot n|_{\partial\Omega} = 0. \end{cases}$$

Subtracting the preceding equation from the equation of v_1 we have

$$\begin{cases} \nabla \cdot [\nabla (v_1 - \varphi_1) - (v_1 - \varphi_1) \nabla(\ln m) - m\nabla R] = 0 \quad \text{in } \Omega, \\ [\nabla (v_1 - \varphi_1) - (v_1 - \varphi_1) \nabla(\ln m) - m\nabla R] \cdot n|_{\partial\Omega} = 0. \end{cases}$$

We can rewrite this equation as

$$\begin{cases} \nabla \cdot \left[m\nabla \left(\frac{v_1 - \varphi_1}{m} - R \right) \right] = 0 & \text{in } \Omega, \\ \nabla \left(\frac{v_1 - \varphi_1}{m} - R \right) \cdot n|_{\partial\Omega} = 0. \end{cases}$$

Hence, $(v_1 - \varphi_1)/m - R = C$ for some constant C. Therefore,

$$-\lambda_2 \int_\Omega m = \int_\Omega v_1(v_1 - \varphi_1) = \int_\Omega v_1(Cm + mR) = \int_\Omega v_1 mR,$$

where the last equality follows from $\int_\Omega v_1 m = 0$.

Set $w = (v_1/m) - R$. Then w satisfies

$$\begin{cases} \nabla \cdot [m\nabla w] - v_1 m = 0 & \text{in } \Omega, \\ \nabla w \cdot n|_{\partial\Omega} = 0. \end{cases}$$

Multiplying the equation of w by R and integrating in Ω, we have

$$\int_\Omega v_1 mR = -\int_\Omega m\nabla w \cdot \nabla R.$$

Note that w satisfies (2.3). Hence, by Lemma 2.2 we have $\int_\Omega m\nabla w \cdot \nabla R < 0$. Therefore, $\int_\Omega v_1 mR > 0$, which implies that $\lambda_2 < 0$. Hence, $\lambda^* < 0$ for $0 < |\epsilon| \ll 1$; i.e., $(0, v^*)$ is unstable for $0 < |\epsilon| \ll 1$. □

Lemma 3.3. *Suppose that $P(x) - \ln m$ is non-constant. Then there exists some $R \in C^2(\bar{\Omega})$ such that for $Q(x) = P(x) + \epsilon R(x)$, $(u^*, 0)$ is unstable for $0 < |\epsilon| \ll 1$.*

Proof. The stability of $(u^*, 0)$ is determined by the sign of the principal eigenvalue, denoted as λ^*, of the problem

$$\begin{cases} \nabla \cdot [\nabla\psi - \psi\nabla(P + \epsilon R)] + (m - u^*)\psi = -\lambda\psi & \text{in } \Omega, \\ [\nabla\psi - \psi\nabla(P + \epsilon R)] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{3.10}$$

As u^* is a smooth function of ϵ, λ^* is also a smooth function of ϵ. It is easy to see that $\lambda^* = 0$ when $\epsilon = 0$ and its corresponding eigenfunction can be chosen as u^* after suitable normalization. Hence, we may expand λ^* as $\lambda^* = \epsilon\lambda_1 + O(\epsilon^2)$. Also, after suitable normalization we may expand the principal eigenfunction ψ^* as $\psi^* = u^* + \epsilon\psi_1 + \epsilon^2\psi_2$, where ψ_1 satisfies

$$\begin{cases} \nabla \cdot \left[e^P \nabla \left(\psi_1/e^P \right) - u^*\nabla R \right] + (m - u^*)\psi_1 = -\lambda_1 u^* & \text{in } \Omega, \\ \left[\nabla \left(\psi_1/e^P \right) - u^*\nabla R \right] \cdot n|_{\partial\Omega} = 0, \end{cases} \tag{3.11}$$

and ψ_2 is some function which is uniformly bounded in $C^2(\bar{\Omega})$ norm for all small ϵ.

Rewrite the equation of u^* as

$$\begin{cases} \nabla \cdot \left[e^P \nabla \left(u^*/e^P \right) \right] + (m - u^*)u^* = 0 & \text{in } \Omega, \\ \nabla \left(u^*/e^P \right) \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{3.12}$$

Multiplying (3.11) by u^*/e^P and (3.12) by ψ_1/e^P, subtracting them and integrating in Ω, we have

$$\lambda_1 \int_\Omega \frac{(u^*)^2}{e^P} = \int_\Omega R\nabla \cdot \left[u^* \nabla \left(u^*/e^P \right) \right]. \tag{3.13}$$

We claim that $\nabla \cdot \left[u^*\nabla\left(u^*/e^P\right)\right] \not\equiv 0$ in Ω. To establish this assertion, we argue by contradiction and suppose that $\nabla \cdot \left[u^*\nabla\left(u^*/e^P\right)\right] = 0$ in Ω. As $\nabla(u^*/e^P)\cdot n = 0$ on $\partial\Omega$, we see that $u^*/e^P = C$ for some constant C. This along with the equation of u^* implies that $u^* = m$ in Ω; i.e., $P - \ln m$ is equal to some constant, which contradicts our assumption. Hence, we can choose $R \in C^2(\bar{\Omega})$ such that $\int_\Omega R \cdot \nabla\left[u^*\nabla\left(u^*/e^P\right)\right] < 0$. For such a choice of $Q = P + \epsilon R$, by (3.13) we have $\lambda_1 < 0$; i.e., $(u^*, 0)$ is unstable for all $0 < |\epsilon| \ll 1$. □

4. **Lyapunov-Schmidt procedure:** $\mu = \nu$. Again, as we focus on the case $\mu = \nu$, without loss of generality we assume that $\mu = \nu = 1$. The main goal of this section is to classify positive solutions of the system

$$\begin{cases} \nabla \cdot [\nabla u - u\nabla(\ln m + \alpha R)] + u(m - u - v) = 0 \quad \text{in } \Omega, \\ \nabla \cdot [\nabla v - v\nabla(\ln m + \beta R)] + v(m - u - v) = 0 \quad \text{in } \Omega, \\ [\nabla u - u\nabla(\ln m + \alpha R)] \cdot n = [\nabla v - v\nabla(\ln m + \beta R)] \cdot n = 0 \quad \text{on } \partial\Omega, \end{cases} \tag{4.1}$$

where α, β are real numbers, and $m, R \in C^2(\bar{\Omega})$.

Set $U = u/(me^{\alpha R})$ and $V = v/(me^{\beta R})$. Then U and V satisfy

$$\begin{cases} \nabla \cdot [me^{\alpha R}\nabla U] + m^2 e^{\alpha R} U(1 - e^{\alpha R}U - e^{\beta R}V) = 0 \quad \text{in } \Omega, \\ \nabla \cdot [me^{\beta R}\nabla V] + m^2 e^{\beta R} V(1 - e^{\alpha R}U - e^{\beta R}V) = 0 \quad \text{in } \Omega, \\ \dfrac{\partial U}{\partial n} = \dfrac{\partial V}{\partial n} = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{4.2}$$

As we are only concerned with the situation when α, β are close, for the rest of this section we assume that

$$\alpha = \alpha_0 + \gamma, \quad \beta = \alpha_0 + \epsilon,$$

where $\alpha_0 \in \mathbf{R}^1$ and $|\gamma|, |\epsilon| \ll 1$.

If $m > 0$ in $\bar{\Omega}$ and $m \in C^2(\bar{\Omega})$, then

$$\begin{cases} \nabla \cdot [me^{\alpha_0 R}\nabla\theta] + m^2 e^{2\alpha_0 R}\theta(e^{-\alpha_0 R} - \theta) = 0 \quad \text{in } \Omega, \\ \dfrac{\partial\theta}{\partial n}|_{\partial\Omega} = 0 \end{cases}$$

has a unique positive solution in $C^2(\bar{\Omega})$, denoted by θ. Note that when $\alpha_0 = 0$, $\theta \equiv 1$ in Ω.

When $\gamma = \epsilon = 0$, the set of positive solutions of (4.2) is given by $\Sigma = \{(s\theta, (1-s)\theta) : s \in [0,1]\}$. We first show that the set of position solutions of (4.2) is close to Σ for sufficiently small γ and ϵ.

Lemma 4.1. *Let (U, V) denote any positive solution of (4.2). Then, after passing to some subsequence if necessary, we have $(U, V) \to (s\theta, (1-s)\theta)$ in $C^2(\bar{\Omega})$ for some $s \in [0,1]$ as $(\gamma, \epsilon) \to (0,0)$.*

Proof. By the maximum principle [34] it is easy to show that $\|U\|_\infty \le \|e^{-\alpha R}\|_\infty$ and $\|V\|_\infty \le \|e^{-\beta R}\|_\infty$. This implies that both U and V are uniformly bounded for small γ and ϵ. By elliptic regularity and Sobolev embedding theorems [22] we see that both U and V are uniformly bounded in $C^{2,\tau}(\bar{\Omega})$ for some $\tau \in (0,1)$ and for all small γ and ϵ. Hence, passing to some subsequence if necessary, we may assume that $U \to U^*$ and $V \to V^*$ in $C^2(\bar{\Omega})$, and U^*, V^* satisfy

$$\begin{cases} \nabla \cdot [me^{\alpha_0 R}\nabla U^*] + m^2 e^{2\alpha_0 R} U^*(e^{-\alpha_0 R} - U^* - V^*) = 0 & \text{in } \Omega, \\ \nabla \cdot [me^{\alpha_0 R}\nabla V^*] + m^2 e^{2\alpha_0 R} V^*(e^{-\alpha_0 R} - U^* - V^*) = 0 & \text{in } \Omega, \\ \dfrac{\partial U^*}{\partial n} = \dfrac{\partial V^*}{\partial n} = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{4.3}$$

Since U, V are positive, we have $U^* \geq 0$ and $V^* \geq 0$. We claim that $(U^*, V^*) \neq (0,0)$. If not, we may assume that $U, V \to (0,0)$ in $L^\infty(\Omega)$. This implies that $e^{-\alpha_0 R} - e^{\gamma R}U - e^{\epsilon R}V \to e^{-\alpha_0 R}$ in $L^\infty(\Omega)$ as $\gamma, \epsilon \to 0$. In particular, for small γ and ϵ we have $e^{-\alpha_0 R} - e^{\gamma R}U - e^{\epsilon R}V > 0$ in Ω. However, integrating the equation of U in Ω we find that

$$\int_\Omega m^2 e^{\alpha R} e^{\alpha_0 R} U(e^{-\alpha_0 R} - e^{\gamma R}U - e^{\epsilon R}V) = 0,$$

which implies that $e^{-\alpha_0 R} - e^{\gamma R}U - e^{\epsilon R}V$ must change sign in Ω, which is a contradiction. Therefore, we have either $U^* \neq 0$ or $V^* \neq 0$; i.e., $U^* + V^* \geq 0$ and $U^* + V^* \neq 0$. Adding the equations of U^* and V^* we see that $U^* + V^*$ satisfies the same equation as θ does. By the uniqueness of θ, we have $U^* + V^* \equiv \theta$. Hence, U^* and V^* satisfy

$$\begin{cases} \nabla \cdot [me^{\alpha_0 R}\nabla U^*] + m^2 e^{2\alpha_0 R} U^*(e^{-\alpha_0 R} - \theta) = 0 & \text{in } \Omega, \\ \nabla \cdot [me^{\alpha_0 R}\nabla V^*] + m^2 e^{2\alpha_0 R} V^*(e^{-\alpha_0 R} - \theta) = 0 & \text{in } \Omega, \\ \dfrac{\partial U^*}{\partial n} = \dfrac{\partial V^*}{\partial n} = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{4.4}$$

Moreover, by the equation of θ we see that 0 is the largest eigenvalue of the operator $\nabla \cdot [me^{\alpha_0 R}\nabla] + m^2 e^{2\alpha_0 R}(e^{-\alpha_0 R} - \theta)$ with zero Neumann boundary condition, and with θ as the corresponding principal eigenfunction. Hence, $U^* = s\theta$ and $V^* = \tilde{s}\theta$ for some $s, \tilde{s} \geq 0$. As $U^* + V^* = \theta$, we see that $s + \tilde{s} = 1$. This implies that $(U^*, V^*) = (s\theta, (1-s)\theta)$ for some $s \in [0,1]$. □

Next, we apply the Lyapunov-Schmidt procedure to determine the structure of the solution set of system (4.2) for $|\gamma|, |\epsilon| \ll 1$.

Set $X = W_n^{2,p}(\Omega) \times W_n^{2,p}(\Omega)$ with $p > N$, $Y = L^p(\Omega) \times L^p(\Omega)$, where $W_n^{2,p}(\Omega) = \{u \in W^{2,p}(\Omega) : \frac{\partial u}{\partial n}|_{\partial\Omega} = 0\}$. We rewrite solutions (U, V) of (4.2) as $(U, V) = (s(\theta + y), (1-s)(\theta + z))$, where $s \in R$ and

$$(y, z) \in X_1 := \left\{(y, z) \in X : \int_\Omega (y - z)\theta = 0\right\}.$$

For $\delta > 0$, define mapping $F : X_1 \times (-\delta, \delta) \times (-\delta, \delta) \times (-\delta, 1+\delta) \to Y$ by

$$F(y, z, \gamma, \epsilon, s) = L_s \begin{pmatrix} y \\ z \end{pmatrix} + \begin{pmatrix} f \\ g \end{pmatrix},$$

where

$$L_s \begin{pmatrix} y \\ z \end{pmatrix} = \begin{pmatrix} \nabla \cdot [me^{\alpha_0 R}\nabla y] + m^2 e^{2\alpha_0 R}\theta[-sy - (1-s)z] + m^2 e^{\alpha_0 R} y(1 - e^{\alpha_0 R}\theta) \\ \nabla \cdot [me^{\alpha_0 R}\nabla z] + m^2 e^{2\alpha_0 R}\theta[-sy - (1-s)z] + m^2 e^{\alpha_0 R} z(1 - e^{\alpha_0 R}\theta) \end{pmatrix},$$

and

$$\begin{aligned} f =& \gamma m e^{\alpha_0 R}\nabla R \cdot \nabla(\theta + y) + m^2 e^{2\alpha_0 R}[-sy^2 - (1-s)yz \\ &+ s(1 - e^{\gamma R})(\theta + y)^2 + (1-s)(1 - e^{\epsilon R})(\theta + y)(\theta + z)], \end{aligned}$$

and

$$g = \epsilon m e^{\alpha_0 R}\nabla R\cdot\nabla(\theta+z) + m^2 e^{2\alpha_0 R}[-syz-(1-s)z^2 + s(1-e^{\gamma R})(\theta+y)(\theta+z) + (1-s)(1-e^{\epsilon R})(\theta+z)^2].$$

Define operator P_s by

$$P_s(y,z) = \frac{\int_\Omega (y-z)\theta}{\int_\Omega \theta^2}\begin{pmatrix}(1-s)\theta\\ -s\theta\end{pmatrix}.$$

It is easy to check that $P_s^2 = P_s$, and that the range of P_s is spanned by $((1-s)\theta, -s\theta)$. Moreover, by using the definition of P_s and the equation of θ, we have $P_sL_s = 0$.

Following the Lyapunov-Schmidt procedure, we need to solve

$$P_sF(y,z,\gamma,\epsilon,s) = 0 \tag{4.5}$$

and

$$(I-P_s)F(y,z,\gamma,\epsilon,s) = 0. \tag{4.6}$$

Since $D_{(y,z)}F(0,0,0,0,s) = L_s$ and $P_sL_s = 0$, we see that

$$D_{(y,z)}(I-P_s)F(0,0,0,0,s) = (I-P_s)L_s = L_s.$$

As the kernel of L_s is spanned by $((1-s)\theta, -s\theta)$, we see that $Ker(L_s)\cap X_1 = \{(0,0)\}$. This implies that $D_{(y,z)}(I-P_s)F(0,0,0,0,s) : X_1 \to Y$ is invertible. By the implicit function theorem, there exist a neighborhood V_0 of $(0,0)$ in X_1, and $\delta_1 > 0$ and functions $y(\gamma,\epsilon,s), z(\gamma,\epsilon,s)$ with $(y(0,0,s), z(0,0,s)) = (0,0)$ such that $F(y,z,\gamma,\epsilon,s) = 0$ for $(y,z,\gamma,\epsilon,s) \in V_0\times(-\delta_1,\delta_1)\times(-\delta_1,\delta_1)\times(-\delta_1, 1+\delta_1)$ if and only if $(y,z) = (y(\gamma,\epsilon,s), z(\gamma,\epsilon,s))$ solves (4.5).

Define $\chi(\gamma,\epsilon,s)$ by

$$P_sF(y(\gamma,\epsilon,s), z(\gamma,\epsilon,s),\gamma,\epsilon,s) = \chi(\gamma,\epsilon,s)\begin{pmatrix}(1-s)\theta\\ -s\theta\end{pmatrix}.$$

To determine non-trivial solutions of (4.5), we need to find the roots of $\chi(\gamma,\epsilon,s) = 0$ with $s\in(0,1)$ for small γ and ϵ. It is straightforward to check that

Lemma 4.2. *For $s\in(0,1)$ and sufficiently small γ, ϵ, $\chi(\gamma,\epsilon,s)$ can be expressed as*

$$\begin{aligned}\chi(\gamma,\epsilon,s) &= \frac{1}{\int_\Omega\theta^2}\int_\Omega \theta m e^{\alpha_0 R}\Big\{\gamma\nabla R\cdot\nabla(\theta+y) - \epsilon\nabla R\cdot\nabla(\theta+z) + m e^{\alpha_0 R}(y-z)\cdot \\ &\quad \big[-sy-(1-s)z + s(1-e^{\gamma R})(\theta+y) + (1-s)(1-e^{\epsilon R})(\theta+z)\big]\Big\},\end{aligned} \tag{4.7}$$

where $(y,z) = (y(\gamma,\epsilon,s), z(\gamma,\epsilon,s))$.

4.1. The case $\alpha_0 \neq 0$.

In this subsection we consider the case $\alpha_0 \neq 0$ and $|\gamma|, |\epsilon| \ll 1$. As $y(0,0,s) = z(0,0,s) = 0$, by formula (4.7) we see that

$$\chi(\gamma,\epsilon,s) = \frac{1}{\int_\Omega\theta^2}\left[(\gamma-\epsilon)\int_\Omega \theta m e^{\alpha_0 R}(\nabla R\cdot\nabla\theta) + O(\gamma^2+\epsilon^2)\right]. \tag{4.8}$$

Next we show that $\chi(\epsilon,\epsilon,s)\equiv 0$ for $|\epsilon|\ll 1$ and $s\in[-\delta_1,1+\delta_1]$. Let θ_ϵ be the unique positive solution of

$$\begin{cases}\nabla\cdot\left[me^{(\alpha_0+\epsilon)R}\nabla\theta_\epsilon\right]+m^2e^{(\alpha_0+\epsilon)R}\theta_\epsilon\left[1-e^{(\alpha_0+\epsilon)R}\theta_\epsilon\right]=0 & \text{in } \Omega,\\ \nabla\theta_\epsilon\cdot n|_{\partial\Omega}=0.\end{cases}$$

Set $y^*=\theta_\epsilon-\theta$ and $z^*=\theta_\epsilon-\theta$. Then one can check that $(I-P)F(y^*,z^*,\epsilon,\epsilon,s)=0$ and $(y^*,z^*)\in V_0$ for $|\epsilon|\ll 1$. By the uniqueness of the solution of $(I-P)F(y,z,\gamma,\epsilon,s)=0$ in $V_0\times(-\delta_1,\delta_1)\times(-\delta_1,\delta_1)\times(-\delta_1,1+\delta_1)$ we see that $(y(\epsilon,\epsilon,s),z(\epsilon,\epsilon,s))=(y^*,z^*)$ for $|\epsilon|\ll 1$ and $s\in[-\delta_1,1+\delta_1]$. This along with formula (4.7) implies that $\chi(\epsilon,\epsilon,s)\equiv 0$ for $|\epsilon|\ll 1$ and $s\in[-\delta_1,1+\delta_1]$. Hence, we can rewrite (4.8) as

$$\chi(\gamma,\epsilon,s)=\frac{\gamma-\epsilon}{\int_\Omega\theta^2}\left[\int_\Omega\theta me^{\alpha_0R}(\nabla R\cdot\nabla\theta)+O(|\gamma|+|\epsilon|)\right]. \tag{4.9}$$

The following is the main result of this subsection:

Proposition 2. *Suppose that $\mu=\nu$, $P=\ln m+\alpha R$, and $Q=\ln m+\beta R$ in (1.5). Further assume that $\Omega=(0,1)$, $m>0$ and $R_x\neq 0$ in $[0,1]$. Given any $\alpha_0\neq 0$, there exists some $\kappa>0$ small such that if either $\alpha_0-\kappa<\alpha<\beta<\alpha_0+\kappa<0$ or $0<\alpha_0-\kappa<\beta<\alpha<\alpha_0+\kappa$, $(0,v^*)$ is globally asymptotically stable.*

Proof. Set $\alpha=\alpha_0+\gamma$ and $\beta=\alpha_0+\epsilon$. By assumption, either $R_x>0$ for every $x\in[0,1]$ or $R_x<0$ for every $x\in[0,1]$. We first consider the case $R_x>0$ in $[0,1]$. If $\alpha_0<0$, by Lemma 2.1 we have $\theta_x>0$ in $(0,1)$, which implies that

$$\int_0^1\theta me^{\alpha_0R}R_x\cdot\theta_x\neq 0. \tag{4.10}$$

If $\alpha_0>0$, by Lemma 2.1 we have $\theta_x<0$ in $(0,1)$, which implies that (4.10) still holds. This together with (4.8) ensures that if $0<|\gamma|,|\epsilon|\ll 1$ and $\gamma\neq\epsilon$, $\chi(\gamma,\epsilon,s)\neq 0$ for any $s\in(-\delta_1,1+\delta_1)$. Hence, by Lemma 4.1 we see that there exists some $\kappa>0$ such that system (1.5) has no coexistence states provided either $\alpha_0-\kappa<\alpha<\beta<\alpha_0+\kappa<0$ or $0<\alpha_0-\kappa<\beta<\alpha<\alpha_0+\kappa$. Since the system is strongly monotone (Theorem 3), the global asymptotic stability of $(0,v^*)$ follows from the nonexistence of coexistence states, Theorem 4, and the local stability of semi-trivial steady states (Lemma 3.1). The proof of the case $R_x<0$ is similar and is thus omitted. □

4.2. The case $\alpha_0=0$.

In this subsection, we consider system (4.2) with $\alpha_0=0$ and $|\gamma|,|\epsilon|\ll 1$; i.e., we study system (1.5) with $P=\ln m+\gamma R$, $Q=\ln m+\epsilon R$. The following is the main result of this subsection.

Proposition 3. *Suppose that $\mu=\nu$, $P=\ln m+\alpha R$, $Q=\ln m+\beta R$, $\alpha\neq\beta$ and R is non-constant. Then there exists some constant $\kappa>0$ such that if $0\le\alpha,\beta\le\kappa$ or $-\kappa\le\alpha,\beta\le 0$, system (1.5) has no coexistence states.*

Proof. Following the Lyapunov-Schmidt procedure as in the beginning of this section, since $\theta \equiv 1$ when $\alpha_0 = 0$, we see that

$$\begin{aligned}\chi(\gamma, \epsilon, s) =& \frac{1}{|\Omega|} \int_\Omega m\Big\{\gamma \nabla R \cdot \nabla y - \epsilon \nabla R \cdot \nabla z + m(y-z)[-sy - (1-s)z \\ &+ s(1-e^{\gamma R})(1+y) + (1-s)(1-e^{\epsilon R})(1+z)]\Big\},\end{aligned} \tag{4.11}$$

where $(y, z) = (y(\gamma, \epsilon, s), z(\gamma, \epsilon, s))$. By $y(0,0,s) = z(0,0,s) = 0$ we have $\chi(0,0,s) = \chi_\gamma(0,0,s) = \chi_\epsilon(0,0,s) = 0$. Set $y_\gamma = y_\gamma(0,0,s)$, $y_\epsilon = y_\epsilon(0,0,s)$, $z_\gamma = z_\gamma(0,0,s)$, and $z_\epsilon = z_\epsilon(0,0,s)$. By differentiating $(I - P_s)F(y(\gamma,\epsilon,s), z(\gamma,\epsilon,s), \gamma, \epsilon, s) = 0$ with respect to γ and evaluating at $\gamma = \epsilon = 0$, using $\chi_\gamma(0,0,s) = 0$ we see that y_γ, z_γ satisfy

$$\begin{cases} \nabla \cdot [m \nabla y_\gamma] - sm^2 y_\gamma - (1-s)m^2 z_\gamma - sm^2 R = 0 & \text{in } \Omega, \\ \nabla \cdot [m \nabla z_\gamma] - sm^2 y_\gamma - (1-s)m^2 z_\gamma - sm^2 R = 0 & \text{in } \Omega, \\ \dfrac{\partial y_\gamma}{\partial n} = \dfrac{\partial z_\gamma}{\partial n} = 0 \quad \text{on } \partial\Omega. \end{cases}$$

Therefore, $\nabla \cdot [m \nabla (y_\gamma - z_\gamma)] = 0$ and $\partial(y_\gamma - z_\gamma)/\partial n = 0$ on $\partial\Omega$. Since $\int_\Omega (y_\gamma - z_\gamma) = 0$, we see that $y_\gamma = z_\gamma$, from which it follows that $y_\gamma = z_\gamma = sw$, where w is the unique solution of (2.3). Similarly, we have $y_\epsilon = z_\epsilon = (1-s)w$.

By using $y_\gamma = z_\gamma = sw$ and $y_\epsilon = z_\epsilon = (1-s)w$ we have

$$\begin{aligned} \frac{\partial^2 \chi}{\partial \gamma^2}(0,0,s) &= \frac{2s}{|\Omega|} \int_\Omega m \nabla R \cdot \nabla w, \\ \frac{\partial^2 \chi}{\partial \gamma \partial \epsilon}(0,0,s) &= \frac{(1-2s)}{|\Omega|} \int_\Omega m \nabla R \cdot \nabla w, \\ \frac{\partial^2 \chi}{\partial \epsilon^2}(0,0,s) &= -\frac{2(1-s)}{|\Omega|} \int_\Omega m \nabla R \cdot \nabla w. \end{aligned}$$

Since $\chi(\epsilon, s)$ are smooth functions of ϵ and s, by $\chi(0,0,s) = \chi_\gamma(0,0,s) = \chi_\epsilon(0,0,s) = 0$ we see that

$$\chi(\gamma, \epsilon, s) = \frac{\int_\Omega m \nabla R \cdot \nabla w}{|\Omega|} \Big\{(\gamma - \epsilon)[s\gamma + (1-s)\epsilon] + \chi_0(\gamma, \epsilon, s)\Big\}, \tag{4.12}$$

where $\chi_0(\gamma, \epsilon, s) = O(|\gamma|^3 + |\epsilon|^3)$ uniformly for $s \in [-\delta_1, 1 + \delta_1]$ as $\gamma, \epsilon \to 0$. As $\chi(\epsilon, \epsilon, s) \equiv 0$ (this corresponds to the case when $y(\epsilon, \epsilon, s) = z(\epsilon, \epsilon, s)$ as discussed in previous subsection), we have

$$\chi_0(\gamma, \epsilon, s) = (\gamma - \epsilon)\chi_1(\gamma, \epsilon, s),$$

where $\chi_1(\gamma, \epsilon, s) = O(|\gamma|^2 + |\epsilon|^2)$ uniformly for $s \in [-\delta_1, 1 + \delta_1]$ for small γ, ϵ. Hence,

$$\chi(\gamma, \epsilon, s) = \frac{\int_\Omega m \nabla R \cdot \nabla w}{|\Omega|} (\gamma - \epsilon)\Big[s\gamma + (1-s)\epsilon + \chi_1(\gamma, \epsilon, s)\Big]. \tag{4.13}$$

We claim that $\chi(0, \epsilon, 1) = 0$ and $\chi(\gamma, 0, 0) = 0$. To show that $\chi(0, \epsilon, 1) = 0$, we first prove that $y(0, \epsilon, 1) = 0$. Set $y^* := y(0, \epsilon, 1)$ and $z^* = z(0, \epsilon, 1)$. We observe that $y^* = 0$ as this case corresponds to $(U, V) = (1, 0)$. Another way to see this is that y^* satisfies

$$\begin{cases} \nabla \cdot [m \nabla y] - m^2 y - m^2 y^2 = 0 & \text{in } \Omega, \\ \nabla y \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases}$$

Note that $y = 0$ is an isolated solution of the above equation, i.e., $y = 0$ is the unique solution in a small neighborhood of $y = 0$. Since (y^*, z^*) lies in a small neighborhood V_0 of $(0,0)$ in X_1, by shrinking V_0 if necessary we have $y^* = 0$.

Hence, by (4.11) we see that $\chi(0, \epsilon, 1)$ satisfies

$$\chi(0, \epsilon, 1) = -\frac{\epsilon}{|\Omega|} \int_\Omega m \nabla R \cdot \nabla z^*. \tag{4.14}$$

From (4.6) we see that z^* satisfies

$$\begin{cases} \nabla \cdot [m \nabla z^*] + \epsilon m \nabla R \cdot \nabla z^* - \dfrac{\epsilon}{|\Omega|} \displaystyle\int_\Omega m \nabla R \cdot \nabla z^* = 0 & \text{in } \Omega, \\ \nabla z^* \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases}$$

Multiplying the equation of z^* by $e^{\epsilon R}$, we see that z^* also satisfies

$$\begin{cases} \nabla \cdot [m e^{\epsilon R} \nabla z^*] - \dfrac{\epsilon e^{\epsilon R}}{|\Omega|} \displaystyle\int_\Omega m \nabla R \cdot \nabla z^* = 0 & \text{in } \Omega, \\ \nabla z^* \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases}$$

Integrating the above equation in Ω, we see that

$$\int_\Omega e^{\epsilon R} \cdot \int_\Omega m \nabla R \cdot \nabla z^* = 0,$$

which implies that

$$\int_\Omega m \nabla R \cdot \nabla z^* = 0.$$

Hence, by (4.14) we have $\chi(0, \epsilon, 1) = 0$. Similarly, we can show that $\chi(\gamma, 0, 0) = 0$ (corresponding to the case $s = 0$, i.e. $(U, V) = (0, v^*)$).

From (4.12), $\chi(0, \epsilon, 1) = 0$ and $\chi(\gamma, 0, 0) = 0$, we see that $\chi_1(0, \epsilon, 1) = \chi_1(\gamma, 0, 0) = 0$. Next, we claim that $\chi_1(\gamma, \epsilon, s)$ can be expressed by

$$\chi_1(\gamma, \epsilon, s) = s\gamma\chi_2(\gamma, \epsilon, s) + (1 - s)\epsilon\chi_3(\gamma, \epsilon, s) \tag{4.15}$$

for some smooth functions χ_i ($i = 2, 3$) that satisfy $\chi_i(\gamma, \epsilon, s) = O(|\gamma| + |\epsilon|)$ uniformly for $s \in [-\delta_1, 1 + \delta_1]$. To establish our assertion, since $\chi_1(0, \epsilon, 1) = \chi_1(\gamma, 0, 0) = 0$, we have

$$\chi_1(\gamma, \epsilon, s) = s[\chi_1(\gamma, \epsilon, s) - \chi_1(0, \epsilon, 1)] + (1 - s)[\chi_1(\gamma, \epsilon, s) - \chi_1(\gamma, 0, 0)]. \tag{4.16}$$

Since $\chi_1(0, \epsilon, s) = O(\epsilon^2)$, we have

$$\begin{aligned} \chi_1(\gamma, \epsilon, s) - \chi_1(0, \epsilon, 1) &= [\chi_1(\gamma, \epsilon, s) - \chi_1(0, \epsilon, s)] + [\chi_1(0, \epsilon, s) - \chi_1(0, \epsilon, 1)] \\ &= \gamma\chi_4(\gamma, \epsilon, s) + (1 - s)\epsilon\chi_5(\epsilon, s), \end{aligned} \tag{4.17}$$

where χ_4 and χ_5 are smooth functions that satisfy $\chi_4(\gamma, \epsilon, s) = O(|\gamma| + |\epsilon|)$ and $\chi_5(\epsilon, s) = O(|\epsilon|)$. Similarly, we have

$$\chi_1(\gamma, \epsilon, s) - \chi_1(\gamma, 0, 0) = \epsilon\chi_6(\gamma, \epsilon, s) + s\gamma\chi_7(\gamma, s), \tag{4.18}$$

where χ_6 and χ_7 are smooth functions that satisfy $\chi_6(\gamma, \epsilon, s) = O(|\gamma| + |\epsilon|)$ and $\chi_7(\gamma, s) = O(|\gamma|)$. Hence, (4.15) follows from (4.16), (4.17) and (4.18).

Therefore, by (4.13) and (4.15) we have

$$\chi(\gamma, \epsilon, s) = \frac{\int_\Omega m \nabla R \cdot \nabla w}{|\Omega|} (\gamma - \epsilon) \left[s\gamma(1 + \chi_2) + (1 - s)\epsilon(1 + \chi_3) \right]. \tag{4.19}$$

Hence, by Lemma 2.2 and assumption $\alpha \neq \beta$ (i.e., $\gamma \neq \epsilon$), the solutions of $\chi(\gamma, \epsilon, s) = 0$ for small γ, ϵ are given by the solutions of

$$H(\gamma, \epsilon, s) := s\gamma(1 + \chi_2) + (1 - s)\epsilon(1 + \chi_3) = 0.$$

We claim that there exists some $\kappa_1 > 0$ such that if either $0 < \gamma, \epsilon \leq \kappa_1$ or $-\kappa_1 \leq \gamma, \epsilon < 0$, then $H = 0$ has no root $s \in [0, 1]$. We shall only consider the case $\gamma, \epsilon > 0$: for this case, since $\chi_2, \chi_3 = O(|\gamma| + |\epsilon|)$, we see that for small γ and ϵ,

$$H(\gamma, \epsilon, s) \geq \frac{s}{2}\gamma + \frac{1-s}{2}\epsilon \geq \min\left\{\frac{\gamma}{2}, \frac{\epsilon}{2}\right\} > 0.$$

The case $\gamma, \epsilon < 0$ is similar. Hence, there exists some $\kappa_1 > 0$ such that if $0 < \gamma, \epsilon \leq \kappa_1$ or $-\kappa_1 \leq \gamma, \epsilon < 0$, then H has no root $s \in [0, 1]$.

The other cases can be similarly treated. For example, for the case $\gamma = 0$ and $0 < |\epsilon| \ll 1$, it follows from (4.19) that

$$\chi(0, \epsilon, s) = -\frac{(1-s)\epsilon^2}{|\Omega|}\left[\int_\Omega m\nabla R \cdot \nabla w + \chi_3(\epsilon, s)\right], \tag{4.20}$$

where $\chi_3(\epsilon, s) \to 0$ uniformly for $s \in [-\delta_1, 1 + \delta_1]$ as $\epsilon \to 0$. By Lemma 2.2 and (4.20), there exists some $\kappa_2 > 0$ such that if $0 < |\epsilon| < \kappa_2$, the only solution of $\chi(0, \epsilon, s) = 0$ with $s \in [-\delta_1, 1 + \delta_1]$ is given by $s = 1$, which corresponds to the semi-trivial solution $(0, v^*)$.

Set $\kappa_0 = \min\{\kappa_1, \kappa_2\}$. Hence, if R is non-constant, $\alpha \neq \beta$ and either $0 \leq \alpha, \beta \leq \kappa_0$ or $-\kappa_0 \leq \alpha, \beta \leq 0$, system (1.5) with $P = \ln m + \alpha R$ and $Q = \ln m + \beta R$ has no coexistence states. □

Proof of Theorem 1. As $\chi(0, \epsilon, s) = 0$ has no roots of $s \in (0, 1)$ for $0 < |\epsilon| \ll 1$, this along with Lemma 4.1 implies that system (4.2) with $\alpha_0 = 0$ and $\gamma = 0$ has no positive solutions for $0 < |\epsilon| \ll 1$, provided that R is non-constant. That is, system (1.5) with $P = \ln m$, $Q = \ln m + \epsilon R$ has no coexistence states for $0 < |\epsilon| \ll 1$, provided that R is non-constant. Furthermore, by Lemma 3.2, $(0, v^*)$ is unstable for $0 < |\epsilon| \ll 1$. It then follows from Theorem 4 that $(u^*, 0)$ is globally asymptotically stable for $0 < |\epsilon| \ll 1$. This establishes part (a) of Theorem 1. Part (b) follows from Lemma 3.3. □

Proof of Theorem 2. Given any $\eta > 0$, we first consider $-\eta \leq \alpha < \beta \leq 0$. It follows from part (a) of Lemma 3.1 that $(u^*, 0)$ is unstable and from part (b) of Lemma 3.1 that $(0, v^*)$ is stable. By Propositions 2 and 3 we see that for any $\tau \in [-\eta, 0]$, there exists some $\epsilon_\tau > 0$ such that if $\alpha, \beta \in (\tau - \epsilon_\tau, \tau + \epsilon_\tau) \cap [-\eta, 0]$ and $\alpha < \beta$, then $(0, v^*)$ is globally asymptotically stable. Since $[-\eta, 0] \subset \cup_{-\eta \leq \tau \leq 0}(\tau - \epsilon_\tau/2, \tau + \epsilon_\tau/2)$, we can find a finite number of $\tau_i \in [-\eta, 0]$ and $\epsilon_i := \epsilon_{\tau_i} > 0$, $1 \leq i \leq k$, such that $[-\eta, 0] \subset \cup_{i=1}^k(\tau_i - \epsilon_i/2, \tau_i + \epsilon_i/2)$. Define $\epsilon^* = \min_{1 \leq i \leq k} \epsilon_i/2$. We now proceed to show that if $-\eta \leq \alpha, \beta \leq 0$ and $0 < \beta - \alpha < \epsilon^*$, then $(0, v^*)$ is globally asymptotically stable. Since $\alpha \in [-\eta, 0)$, there exists some i such that $\alpha \in (\tau_i - \epsilon_i/2, \tau_i + \epsilon_i/2)$. Therefore, $|\beta - \tau_i| \leq |\beta - \alpha| + |\alpha - \tau_i| < \epsilon^* + \epsilon_i/2 \leq \epsilon_i$. Hence, by our choice of ϵ_i and Propositions 2 and 3 we see that $(0, v^*)$ is globally asymptotically stable. This completes the proof of part (a). For the proof of (b), it follows from Lemma 3.1 that both $(u^*, 0)$ and $(0, v^*)$ are unstable if either $\alpha < 0 < \beta$ or $\alpha > 0 > \beta$. Since system (1.5) is monotone (Theorem 3), it follows from Theorem 4 and the instability of $(u^*, 0)$ and $(0, v^*)$ that system (1.5) has at least one stable coexistence state. This completes the proof of Theorem 2. □

5. Discussion. There are various reasons to expect that directed movement can influence population dynamics and hence that evolutionary selection can act on the nature of directed movement that is present in the dispersal strategies of populations [1, 2, 11, 36, 37]. The analysis in this paper shows that in the framework of logistic reaction-advection-diffusion models with spatially varying local growth rate $m(x)$, constant carrying capacity, and simple diffusion, the ideal free dispersal strategy arising from advection upward along the gradient of $\ln m$, that is, $\nabla m/m$, is locally an evolutionarily stable strategy. Furthermore, in the case of a one-dimensional habitat and monotone $m(x)$, it is globally convergent stable. On the other hand, the analysis also shows that strategies with advective terms that deviate from the ideal free strategy in opposite directions (that is, strategies where the advection is along the gradients of $\ln m + \alpha R$ and $\ln m + \beta R$ where α and β have opposite signs) can coexist. We expect that stronger and more general versions of these results are valid, partly because related results have been obtained in rather different modeling contexts [5, 14, 30, 32].

A key idea behind these phenomena is that ideal free dispersal allows a population to distribute itself in a way that perfectly matches the availability of resources as described by the local population growth rate, so that once such a population is established it reduces the level of available resources to zero, so that no other population can invade it. On the other hand, populations using strategies that leave resources available in some locations typically can be invaded by other populations that disperse so as to exploit those resources more effectively. If dispersal strategies are sufficiently asymmetric, this can allow coexistence. It is interesting to compare the effects of advection in response to $\nabla m/m$ and advection in response to constant multiples of ∇m, as studied in [3, 6, 7, 9, 10, 13, 23]. In the latter case there is no strategy that is ideal free, so no population can completely exploit the available resources. Thus, whether any given strategy confers an advantage relative to any other strategy seems to depend on details of the two strategies and even the geometry of the underlying spatial domain in delicate and complicated ways.

We plan to explore the idea of ideal free dispersal and its connections to evolutionary stability further by extending the ideas and results of this paper and by considering the effects of other mechanisms for ideal free dispersal, including those described in [8, 12], among other possibilities.

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