Evolution of dispersal in closed advective environments

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We study a two-species competition model in a closed advective environment, where individuals are exposed to unidirectional flow (advection) but no individuals are lost through the boundary. The two species have the same growth and advection rates but different random dispersal rates. The linear stability analysis of the semi-trivial steady state suggests that, in contrast to the case without advection, slow dispersal is generally selected against in closed advective environments. We investigate the invasion exponent for various types of resource functions, and our analysis suggests that there might exist some intermediate dispersal rate that will be selected. When the diffusion and advection rates are small and comparable, we determine criteria for the existence and multiplicity of singular strategies and evolutionarily stable strategies. We further show that every singular strategy is convergent stable.

Keywords: evolution of dispersal; closed advective environments; invasion analysis; reaction–diffusion–advection

AMS Classification: 35K57; 92D25

1. Introduction

Hastings [25] showed that in a spatially varying but temporally constant environment, faster dispersal is always selected against if dispersal is completely random, see also [1,21]. However, organisms sometimes are forced to move in certain directions, for example, in advective environments such as rivers, water columns or the gut [4,26,30,40,43–46], or when environmental conditions shift, for example, movement of temperature isoclines caused by global climate change [6,37,41]. Active movement of organisms may also be biased in certain directions, for example, moving up a resource gradient [5,8,18,23,42], or a fitness gradient [10,12,17,19,27–29,35,39].

Evolution of biased movement along a resource gradient has received much attention recently [9,13,14,16]. Evolutionarily stable dispersal strategies are found to be those that have comparable dispersal and advection rates [2,11,24,33,34]. On the one hand, when individuals move upward along the gradient of a resource distribution, and the random dispersal rate is small relative to

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the advection rate, then individuals can become 'too good' at tracking favourable regions. They become overcrowded at only the best quality locations and miss other, reasonably beneficial areas [15,31,32,36]. Higher dispersal rates can help individuals utilize those resources as well. Therefore, slower dispersal is selected against. On the other hand, if random dispersal is large in comparison to resource tracking, the population will spread widely in the habitat so that it only utilizes some average quality of the resource. Therefore, fast dispersal is also selected against. Altogether, intermediate dispersal rates can evolve.

Much less is known about the evolution of dispersal in advective environments, where movement bias is caused by external forces such as river flow, gravity or climate. How should organisms disperse to better persist in advective environments? How should species disperse to avoid the invasion of a mutant with different movement strategies? We have recently attempted to address these questions in [38] in the framework of evolutionary game theory. We considered a two-species competition model in an open advective environment: individuals are exposed to unidirectional flow, with a net loss of individuals at the downstream end of the domain, for example, a river. We assumed that two species have the same growth dynamics and advection rates but different random dispersal rates. Among other things, we found that in such context of an open advective environment, unidirectional flow can put slow dispersers at a disadvantage and higher dispersal rates can evolve. In particular, the boundary conditions played an important role in the outcome of evolution. In [38], we derived several different boundary conditions and explained their biological significance in detail. Two contrasting results from [38] are as follows:

(1) In a homogeneous (i.e. constant intrinsic growth rate) advective environment with zero Neumann boundary conditions, a population with higher dispersal rate will always displace one with lower dispersal rate. In particular, larger dispersal rates evolve.
(2) In a homogeneous advective environment with zero Dirichlet boundary conditions, there seems to evolve a unique, intermediate dispersal rate, which is evolutionarily stable.

In this paper, we consider closed advective environments, where individuals cannot pass through the boundary. We had explicitly excluded this case in [38]. One biological scenario that results in such a closed advective environment is the community of microorganisms in the water column of a lake: most phytoplankton species have a higher density relative to water, so they tend to sink to the bottom of the water column. Besides that, water turbulence allows phytoplankton to mix randomly within the water column. These two processes of sinking and random mixing can be approximated by advection and diffusion, respectively. The upper boundary is the water surface, the lower boundary is the ground. Neither boundary allows individuals to pass through, so that we have a closed environment, which we model by imposing no-flux conditions at both ends. We refer to [22] and references therein.

Following the approach in [38], we study a system of reaction–diffusion equations for two logistically growing and competing species that differ only in their random diffusion rates:

$$u_t = d_1 u_{xx} - q u_x + u(r(x) - u - v), \quad 0 < x < L, \ t > 0,$$
$$v_t = d_2 v_{xx} - q v_x + v(r(x) - u - v), \quad 0 < x < L, \ t > 0, \qquad (1)$$
$$d_1 u_x - q u = d_2 v_x - q v = 0, \quad x = 0, L, \ t > 0.$$

Here u and v denote the densities of two species (e.g. phytoplankton species) at time t and location x in the bounded interval $[0, L]$. Function $r(x)$ accounts for the quality of the habitat; a rare single population can grow where $r > 0$ and will decline where $r < 0$. Diffusion rates are positive, that is, $d_i > 0$, and advection points towards larger x, that is, $q > 0$. In analogy with rivers, we call $x = 0$ the upstream end and $x = L$ the downstream end of the habitat.

The rest of the paper is organized as follows. In Section 2, we consider sufficient conditions for the existence of a single-species steady state and establish various a priori estimates of the

steady state. In Section 3, we perform a preliminary linear stability analysis of the semi-trivial steady state and find that small dispersal rates should generally be selected against. In Section 4, we investigate the selection gradient (see Lemma 4.1 for the definition) for various types of resource functions, and our analysis suggests that for a monotone increasing resource function, there might exist some intermediate dispersal rate that is convergent stable. In Sections 5–7, we focus on the case when the diffusion and advection rates are small and comparable. Section 5 is devoted to further analysis of the selection gradient and to the existence of singular strategies (see Section 5 for the definition); in Section 6, we give criteria for the existence of evolutionarily stable strategies; in Section 7, we show that every singular strategy is convergent stable. Finally, we conclude with some discussions in Section 8.

2. Persistence of a single species

In this section, we consider sufficient conditions for the existence of a single-species steady state $(u^*(x), 0)$ of system (1), where u^* is a positive solution of the equation

$$d_1 u_{xx} - q u_x + u(r(x) - u) = 0, \quad 0 < x < L,$$
$$d_1 u_x - q u = 0 \quad \text{at } x = 0, L. \tag{2}$$

It is known that existence and uniqueness of u^* is equivalent to the zero solution of Equation (2) being linearly unstable [7]. Hence, we study conditions for the dominant eigenvalue of

$$d_1 \phi_{xx} - q \phi_x + r(x)\phi = \lambda \phi, \quad 0 < x < L,$$
$$d_1 \phi_x - q \phi = 0 \quad \text{at } x = 0, L \tag{3}$$

to be positive.

In the following, we frequently use the identity

$$d_1 \phi_{xx} - q \phi_x = d_1 (e^{\alpha x}(e^{-\alpha x}\phi)_x)_x, \quad \text{where } \alpha = q/d_1. \tag{4}$$

All integrals are definite integrals over the interval $[0, L]$, unless otherwise specified.

LEMMA 2.1 *If $\int_0^L e^{q/d_1 x} r(x)\, dx \geq 0$, then the dominant eigenvalue of Equation (3) is positive. In particular, there exists a unique positive solution of Equation (2).*

Proof Using $\alpha = q/d_1$ and identity (4), we write the eigenvalue problem as

$$d_1 (e^{\alpha x}(e^{-\alpha x}\phi)_x)_x + r(x)\phi = \lambda \phi. \tag{5}$$

Now, we denote $\psi = e^{-\alpha x}\phi$ and divide the previous equation by ψ to obtain

$$\frac{d_1 (e^{\alpha x}\psi_x)_x}{\psi} + e^{\alpha x} r(x) = \lambda e^{\alpha x}. \tag{6}$$

Integration by parts yields

$$\int \frac{(e^{\alpha x}\psi_x)_x}{\psi}\, dx = \left. \frac{e^{\alpha x}\psi_x}{\psi} \right|_0^L + \int \frac{e^{\alpha x}\psi_x^2}{\psi^2}\, dx = \int \frac{e^{\alpha x}\psi_x^2}{\psi^2}\, dx, \tag{7}$$

where the second equality follows from the no-flux boundary conditions,

$$d_1 e^{\alpha x}\psi_x = d_1 \phi_x - q\phi = 0 \quad \text{for } x = 0, L. \tag{8}$$

Integrating Equation (6) by parts, we arrive at

$$d_1 \int \frac{\mathrm{e}^{\alpha x}(\psi_x)^2}{\psi^2}\,\mathrm{d}x + \int \mathrm{e}^{\alpha x} r(x)\,\mathrm{d}x = \lambda \int \mathrm{e}^{\alpha x}\,\mathrm{d}x. \qquad (9)$$

As $r(x)$ is non-constant, the first term in this equation is always positive (by Equation (7)); as the second term is non-negative, we deduce that $\lambda > 0$. $\blacksquare$

Remark 2.2 By Lemma 2.1, if $r > 0$ in $[0, L]$, then for any $d_1 > 0$ and $q \geq 0$, there exists a unique positive solution of Equation (2). For most of this paper, we consider the case when r is strictly positive in $[0, L]$ only.

Next, we establish some a priori estimates of u^*.

LEMMA 2.3   *Denote $\alpha := q/d_1$. For any $x \in [0, L]$, we have*

$$\mathrm{e}^{\alpha x} \min_{[0,L]}(r(x)\mathrm{e}^{-\alpha x}) \leq u^*(x) \leq \mathrm{e}^{\alpha x} \max_{[0,L]}(r(x)\mathrm{e}^{-\alpha x}). \qquad (10)$$

Proof   Set $w = \mathrm{e}^{-\alpha x} u^*$. Then, w satisfies

$$d_1 w_{xx} + q w_x + w(r - \mathrm{e}^{\alpha x} w) = 0, \quad 0 < x < L, \quad w_x(0) = w_x(L) = 0.$$

Let $w(x_0) = \max_{[0,L]} w(x)$ for some $x_0 \in [0, L]$. Hence, we have $w_{xx}(x_0) \leq 0$ and $w_x(x_0) = 0$. Therefore,

$$w(x_0) \leq r(x_0)\mathrm{e}^{-\alpha x_0} \leq \max_{[0,L]}(r(x)\mathrm{e}^{-\alpha x}),$$

which implies that

$$u^*(x) = \mathrm{e}^{\alpha x} w(x) \leq \mathrm{e}^{\alpha x} w(x_0) \leq \mathrm{e}^{\alpha x} \max_{[0,L]}(r(x)\mathrm{e}^{-\alpha x}).$$

Similarly, we can show that

$$u^*(x) \geq \mathrm{e}^{\alpha x} \min_{[0,L]}(r(x)\mathrm{e}^{-\alpha x}).$$

This proves Equation (10). $\blacksquare$

LEMMA 2.4   *Denote $\alpha := q/d_1$. Suppose that $r > 0$.*

(i) *If $\alpha \geq \max_{[0,L]} r_x/r$, then for any $x \in [0, L]$,*

$$u^*(x) > r(L)\mathrm{e}^{\alpha(x-L)}.$$

(ii) *If $\alpha \leq \min_{[0,L]} r_x/r$, then for any $x \in [0, L]$,*

$$u^*(x) < r(L)\mathrm{e}^{\alpha(x-L)}.$$

Proof   The proof follows directly from Lemma 2.3 and the monotonicity of $r(x)\mathrm{e}^{-\alpha x}$ in x when $\alpha < \min_{[0,L]} r_x/r$ or $\alpha > \max_{[0,L]} r_x/r$. $\blacksquare$

LEMMA 2.5 $\int u^*(x)\,\mathrm{d}x \to 0$ *as $q \to \infty$.*

Proof Integrating the steady state equation (2) and using the boundary conditions, we find

$$\int u^*(r - u^*) \, dx = 0. \tag{11}$$

From this, we obtain

$$\int (u^*)^2 \, dx \leq \sqrt{\int r^2 \, dx} \sqrt{\int (u^*)^2 \, dx}. \tag{12}$$

In particular, $\int (u^*)^2 \, dx$ is bounded, independently of q.

Now, we choose any function $g \in C^2[0, L]$ with $g_x(0) = g_x(L) = 0$. Multiplying the steady state equation (2) with g and integrating by parts, we obtain

$$-d_1 \int g_{xx} u^* \, dx - q \int g_x u^* \, dx + \int g u^*(r - u^*) \, dx = 0. \tag{13}$$

Dividing by q and letting $q \to \infty$, we see that $\int g_x u^* \, dx \to 0$. From this, we see that $\int u^*(x) \, dx \to 0$. ∎

3. Local stability of the semi-trivial state $(u^*, 0)$

We perform a preliminary linear stability analysis of the steady state $(u^*, 0)$. The linearized system at $(u^*, 0)$ decouples, so that it suffices to consider the eigenvalue problem

$$\begin{aligned}
d_2 \phi_{xx} - q \phi_x + \phi(r - u^*) &= \lambda \phi, \quad 0 < x < L, \\
d_2 \phi_x - q \phi &= 0 \quad \text{at } x = 0, L.
\end{aligned} \tag{14}$$

To determine the stability of the semi-trivial state $(u^*, 0)$, we study the sign of the dominant (i.e. the largest) eigenvalue of Equation (14), denoted by λ. We emphasize that $\lambda = \lambda(d_1, d_2)$, as in the following this form is used frequently.

LEMMA 3.1 *Suppose that $d_1 < d_2$. Then, for sufficiently small positive q, $(u^*, 0)$ is stable.*

Proof When $q = 0$, the equation and boundary conditions reduce to the case studied by Hastings [25]. Hence, we know that $\lambda < 0$ when $d_1 < d_2$ and $q = 0$. By continuous dependence of λ on parameters, we have $\lambda < 0$ for small enough values of q. ∎

Lemma 3.1 implies that a faster disperser cannot invade when rare by slightly increasing the advection rate of both species. An interesting open problem is to describe the changes of stability of $(u^*, 0)$ when $d_1 < d_2$ are fixed and q varies from small to large. See [3] for related effort.

We are particularly interested in situations where a faster disperser can invade when it is rare. To this end, we first consider the case when q and d_2 are sufficiently large.

THEOREM 3.2 *Suppose that $r > 0$ in $[0, L]$. Fix $d_1 > 0$. There exists some positive constant q^* such that if $q \geq q^*$ and $d_2 \geq (q^2 L)/(2 \int r)$, then $(u^*, 0)$ is unstable.*

Proof The transformation $\phi = e^{qx/(2d_2)}\psi$ gives

$$d_2\psi_{xx} + \psi\left(r - u^* - \frac{q^2}{4d_2}\right) = \lambda\psi, \quad 0 < x < L \tag{15}$$

with boundary conditions

$$d_2\psi_x - \frac{q}{2}\psi = 0 \quad \text{for } x = 0, L. \tag{16}$$

Hence, we obtain the dominant eigenvalue as

$$\lambda = \max_{\xi \in H^1: \|\xi\|_{L^2}=1}\left\{-d_2\int \xi_x^2\,dx + \int(r - u^*)\xi^2\,dx + \frac{q}{2}(\xi^2(L) - \xi^2(0))\right\} - \frac{q^2}{4d_2}. \tag{17}$$

Choosing the constant function $\xi(x) = 1/\sqrt{L}$ in Equation (17), we obtain the lower bound

$$\lambda \geq \frac{1}{L}\int[r(x) - u^*(x)]\,dx - \frac{q^2}{4d_2}. \tag{18}$$

By assumption $d_2 \geq q^2 L/(2\int r)$, we have

$$\lambda \geq \frac{1}{2L}\int r - \frac{1}{L}\int u^*. \tag{19}$$

By Lemma 2.5 and $\int r > 0$, we see that in the limit for large q, λ is positive. ∎

Theorem 3.2 implies that if the advection rate is large, a mutant can invade when rare as long as it disperses sufficiently fast. This is very different from the case of no advection or small advection, where a mutant cannot invade when rare if it disperses sufficiently fast.

THEOREM 3.3 *Suppose that $r > 0$ in $[0, L]$ and $q > 0$.*

(i) *If $q/d_1 \geq \max_{[0,L]} r_x/r$, then for sufficiently small d_2, $(u^*, 0)$ is stable.*
(ii) *If $q/d_1 \leq \min_{[0,L]} r_x/r$, then for sufficiently small d_2, $(u^*, 0)$ is unstable.*

Proof Set $\psi = e^{-(q/d_2)x}\phi$. Then, ψ satisfies

$$d_2\psi_{xx} + q\psi_x + \psi(r - u^*) = \lambda\psi, \quad 0 < x < L; \quad \psi_x = 0 \quad \text{at } x = 0, L. \tag{20}$$

By Theorem 2 of [16], as $q > 0$, we have

$$\lim_{d_2 \to 0+}\lambda = r(L) - u^*(L). \tag{21}$$

The rest of the proof follows from Equation (21) and Lemma 2.4. ∎

Part (i) of Theorem 3.3 implies that if d_1 is suitably small (relative to q) and d_2 is chosen smaller, then the species v cannot invade when rare. This means that slow dispersal is always selected against in such advection environments, in contrast with the case of no advection where fast dispersal is always selected against. Part (ii) implies that if the resident is a fast disperser (relative to q), a slow dispersing mutant can invade when rare, provided that, for example, the resource function is monotone increasing. These results suggest that when the resource function is monotone increasing, there might exist some intermediate dispersal rate (comparable to q) that will be selected. We will investigate this issue in later sections when both diffusion and advection rates are small.

4.   The selection gradient

Let λ be the dominant eigenvalue of Equation (14) with corresponding eigenfunction ϕ. When $d_1 = d_2$, $\lambda = 0$ and $\phi = u^*$. The selection gradient is given by $(\partial/\partial d_2)\lambda(d_1, d_1)$ [20]. If the selection gradient is positive, an invader with d_2 slightly larger than d_1 will invade, and thus evolution will proceed to larger diffusion. If the selection gradient is negative, then the reverse statement holds. The big advantage of calculating the selection gradient is that for $d_1 = d_2$, the eigenfunction ϕ in Equation (14) corresponding to the dominant eigenvalue $\lambda = 0$ is given by the equilibrium density u^* of a single species.

LEMMA 4.1   *The selection gradient of mutant invader v at the steady state $(u^*, 0)$ of Equation (1) is given by*

$$\frac{\partial}{\partial d_2}\lambda(d_1, d_1) = -\frac{\int (e^{-qx/d_1}u^*)_x u_x^* \, dx}{\int e^{-qx/d_1}(u^*)^2 \, dx}. \tag{22}$$

The calculations are exactly the same as in Lemma 4.1 of [38].

When $r(x) = r = $ const., we can show that an invader is successful exactly when its diffusion rate is higher than that of the resident.

LEMMA 4.2   *If r is constant, then the selection gradient is positive.*

Proof   Integrating the equation for u^* and using the boundary conditions, we find

$$\int u^*(r - u^*) \, dx = 0. \tag{23}$$

Therefore, $r - u^*$ has to have at least one sign change. We shall show that $u_x^* > 0$ in $[0, L]$ and therefore there is exactly one sign change, from positive to negative. First, the following claim follows directly from the defining equation of u^*.

CLAIM 4.3   (a) *If $u_{xx}^* \leq 0$ and $u_x^*(x') = 0$, then $u^*(x') \leq r$. In particular, there can be no interior maximum point in $\{x : u^*(x) > r\}$.*
(b) *If $u_{xx}^* \geq 0$ and $u_x^*(x') = 0$, then $u^*(x') \geq r$. In particular, there can be no interior minimum point in $\{x : u^*(x) < r\}$.*

It remains to show that $u_x^* \neq 0$ in $[0, L]$, as $u_x^*(0) = qu^*(0)/d_1 > 0$. Suppose now that $u_x^* = 0$ somewhere. Define

$$x_1 := \inf\{x \in [0, L] : u_x^*(y) > 0 \text{ for all } y \in [0, x]\}.$$

Then, $x_1 < L$ and $u_x^*(x_1) = 0$, by our assumption that $u^* = 0$ somewhere.

CLAIM 4.4 $u^*(x_1) = r$.

As $u_{xx}^*(x_1) \leq 0$ and $u_x^*(x_1) = 0$, Claim 4.3(a) says that $u^*(x_1) \leq r$. Suppose $u^*(x_1) < r$, then $u_{xx}^*(x_1) < 0 = u_x^*(x_1)$ by the defining equation of u^*. These, together with the fact that $u_x^*(L) = qu^*(L)/d_1 > 0$, imply that u^* attains a local minimum value strictly less than r in (x_1, L), which contradicts Claim 4.3(b). This establishes Claim 4.4.

Now $u^*(x_1) = r$, $u_x^*(x_1) = 0$. By the uniqueness of solution to ordinary differential equation, we deduce that $u^* \equiv r$ in $[0, L]$. This is in contradiction with the boundary condition satisfied by u^*. Hence, we conclude that $u_x^* \neq 0$ in $[0, L]$. This gives $u_x^* > 0$ in $[0, L]$.

Now we integrate the equation for u^* from 0 to x and use the boundary condition again:

$$d_1 u_x^*(x) - qu^*(x) = \int_0^x u^*(s)(u^*(s) - r)\,\mathrm{d}s. \tag{24}$$

The right-hand side (RHS) is zero at $x = 0, L$. It is decreasing when $u^* < r$ and increasing when $u^* > r$. Hence, it is always negative. Therefore, the flux on the left-hand side (LHS) is always negative. This implies that the term $(\mathrm{e}^{-\alpha x} u^*)_x$ in the selection gradient is negative. Since u_x^* is positive, this implies (by Equation (22)) that the selection gradient is positive. ∎

Based on Lemma 4.2, we conjecture that in a homogeneous advective environment with no-flux boundary conditions, populations with higher dispersal rate will always competitively exclude populations with lower dispersal rate.

The main result of this section, which includes the constant resource as a special case, can be stated as follows.

THEOREM 4.5 *Suppose that $r > 0$ and $r_x \geq 0$ in $[0, L]$.*

(i) *If $q/d < \min_{[0,L]} r_x/r$, then $(\partial/\partial d_2)\lambda(d, d) < 0$.*
(ii) *If $q/d > \max_{[0,L]} r_x/r$, then $(\partial/\partial d_2)\lambda(d, d) > 0$.*

Theorem 4.5 suggests that when the resource function is monotone increasing, there might exist some intermediate dispersal rate which is convergent stable (but may not be evolutionarily stable, as we will see in Section 6). It is interesting to enquire the corresponding scenario for the case of monotone decreasing resource functions.

Before we prove Theorem 4.5, we prove an auxiliary one-dimensional lemma.

LEMMA 4.6 *Let $\phi \in C^2([0, L])$ be a solution to*

$$\phi_{xx} + b(x)\phi_x + g(x, c(x) - \phi(x)) = 0 \quad in\ (0, L),$$
$$\phi_x \geq 0 \quad when\ x = 0, L, \tag{25}$$

where $\mathrm{sign}\,g(x, s) = \mathrm{sign}\,s$. *If $c_x \geq 0$ in $[0, L]$, then $\phi_x \geq 0$ in $[0, L]$. If in addition $c_x > 0$ in $(0, L)$, then $\phi_x > 0$ in $(0, L)$.*

COROLLARY 4.7 *Let u^* be the unique positive solution to*

$$du_{xx}^* - qu_x^* + u^*(r(x) - u^*) = 0 \quad in\ (0, L),$$
$$du_x^* - qu^* = 0 \quad at\ x = 0, L.$$

(i) *If $r_x \geq 0$ in $[0, L]$, then for all $d > 0$ and $q \geq 0$, $u_x^* \geq 0$ in $(0, L)$.*
(ii) *If $q/d < \min_{[0,L]} r_x/r$, then $(\mathrm{e}^{-qx/d} u^*)_x > 0$ in $(0, L)$.*
(iii) *If $q/d > \max_{[0,L]} r_x/r$, then $(\mathrm{e}^{-qx/d} u^*)_x < 0$ in $(0, L)$.*

Proof of Corollary 4.7 (i) follows from Lemma 4.6 immediately.
For (ii), we observe that $v := \mathrm{e}^{-qx/d} u^*$ satisfies

$$dv_{xx} + qv_x + \mathrm{e}^{qx/d} v[r\mathrm{e}^{-qx/d} - v] = 0 \quad in\ (0, L),$$
$$v_x = 0 \quad at\ x = 0, L.$$

In addition, the assumption $q/d < \min_{[0,L]} r_x/r$ implies that $(r\mathrm{e}^{-qx/d})_x > 0$ in $[0, L]$. Hence, Lemma 4.6 implies that $(\mathrm{e}^{-qx/d} u^*)_x > 0$ in $(0, L)$.

For (iii), set $w(x) := v(L - x)$, then w satisfies

$$dw_{xx} - qw_x + e^{q(L-x)/d}w[r(L - x)e^{-q(L-x)/d} - w] = 0 \quad \text{in } (0, L),$$
$$w_x = 0 \quad \text{at } x = 0, L.$$

In addition, the assumption $q/d > \max_{[0,L]} r_x/r$ implies that $(r(L - x)e^{-q(L-x)/d})_x > 0$ in $[0, L]$. This completes the proof. ∎

Now we give the proof of Lemma 4.6.

Proof of Lemma 4.6 First we claim that $\phi_x \geq 0$ in $[0, L]$. Suppose to the contrary that there exists $0 \leq x_1 < x_2 \leq L$ such that $\phi_x < 0$ in (x_1, x_2) and $\phi_x(x_1) = \phi_x(x_2) = 0$. Then, $\phi_{xx}(x_1) \leq 0 \leq \phi_{xx}(x_2)$, which implies by Equation (25) that $c(x_1) \geq \phi(x_1)$ and $c(x_2) \leq \phi(x_2)$. Combining with the strict monotonicity of ϕ in $[x_1, x_2]$, we have

$$c(x_1) \geq \phi(x_1) > \phi(x_2) \geq c(x_2),$$

which contradicts the monotonicity of c. This shows that $\phi_x \geq 0$ in $[0, L]$.

Next, under the assumption that $c_x > 0$ in $(0, L)$, we wish to show that $\phi_x > 0$ in $(0, L)$. Suppose to the contrary that $\phi_x(x_0) = 0$ for some $x_0 \in (0, L)$. Then, by the previous claim, x_0 is a local interior minimum of ϕ_x in $(0, L)$. Therefore, $\phi_{xx}(x_0) = 0$ and by Equation (25), we have $c(x_0) = \phi(x_0)$. Together with

$$(c - \phi)_x(x_0) = c_x(x_0) > 0,$$

we derive that $c - \phi > 0$ in $(x_0, x_0 + \delta)$ for some $\delta > 0$. But then

$$(e^{\int_0^x b(s)\,ds}\phi_x)_x = -e^{\int_0^x b(s)\,ds}g(x, c - \phi) < 0 \quad \text{and} \quad \phi_x(x_0) = 0.$$

Hence $\phi_x < 0$ in $(x_0, x_0 + \delta)$. This contradicts the fact that $\phi_x \geq 0$ in $(0, L)$, and completes the proof. ∎

Proof of Theorem 4.5 The theorem follows directly from Lemma 4.1 and Corollary 4.7. ∎

5. Singular strategies and the small advection case

When diffusion and advection rates are small, we can use the techniques developed in [33,34] to obtain a detailed description of the selection gradient and singular strategies. Recall that $\hat{d}$ is a singular strategy if the selection gradient vanishes at $\hat{d}$, that is,

$$\frac{\partial}{\partial d_2}\lambda(\hat{d}, \hat{d}) = 0.$$

We write the model as

$$u_t = \epsilon(d_1 u_{xx} - qu_x) + u(r(x) - u - v), \quad 0 < x < L,\ t > 0,$$
$$v_t = \epsilon(d_2 v_{xx} - qv_x) + v(r(x) - u - v), \quad 0 < x < L,\ t > 0, \qquad (26)$$
$$d_1 u_x - qu = d_2 v_x - qv = 0, \quad x = 0, L,\ t > 0.$$

From this point on, we adjust notation slightly and denote u^* as the positive steady state of the u equation in Equation (26) when $v = 0$. Here we need some estimates of u^*.

LEMMA 5.1 Convergence of u^* to $r(x)$ as $\epsilon \to 0$.   (i) *For each $K > 0$, there exist positive constants c, C such that whenever $q/d \in [0, K]$, then*

$$c \leq u^*(x) \leq C \quad in \ [0, L].$$

(ii) *For each $K > 1$, $u^* \to r$ in $L^\infty((0, L))$ uniformly for q, d satisfying $d \in [1/K, K]$ and $q \in [0, K]$.*

(iii) *For each $K > 0$, there exists C such that for all $\phi \in H^1((0, L))$, and for all q, d such that $q/d \in [0, K]$,*

$$\int_0^L |u_x^* - r_x|^2 \phi^2 \leq C \|u^* - r\|_{L^\infty((0,L))} \|\phi\|_{H^1((0,L))}^2.$$

Proof   (i) is similar to Lemma 2.3. For the rest, we refer to Lemmas 3.2 and 3.3 of [33].   ∎

LEMMA 5.2 $\partial u^*/\partial d_1 \to 0$ in $H^1([0, L])$, as $\epsilon \to 0$, *uniformly on compact subsets of $(0, \infty)$ in d_1.*

Proof   Denote $u' = \partial u^*/\partial d_1$, which satisfies

$$\begin{aligned}
\epsilon(d_1 u'_{xx} - q u'_x) + (r - 2u^*)u' &= -\epsilon u_{xx}^* \quad in \ (0, L), \\
d_1 u'_x - q u' &= -u_x^* \quad at \ x = 0, L.
\end{aligned} \tag{27}$$

Multiplying by $-e^{-qx/d_1} u'/\epsilon$, and integrating by parts, we have

$$d_1 \int e^{qx/d_1} (e^{-qx/d_1} u')_x^2 + \frac{1}{\epsilon} \int e^{-qx/d_1} (2u^* - r)(u')^2 = -\int u_x^* (e^{-qx/d_1} u')_x. \tag{28}$$

Since $u^* \to r$ in $L^\infty((0, L))$ (Lemma 5.1(ii)) and $r > 0$ in $[0, L]$, we may assume $2u^* - r \geq \min_{[0,L]} r/2$ and the second integral is non-negative for ϵ small. We obtain by Hölder's inequality that

$$d_1 \int e^{qx/d_1} (e^{-qx/d_1} u')_x^2 + \frac{\min_{[0,L]} r}{2\epsilon} \int e^{-qx/d_1} (u')^2 \leq \frac{d_1}{2} \int e^{qx/d_1} (e^{-qx/d_1} u')_x^2$$
$$+ \frac{1}{2d_1} \int e^{-qx/d_1} (u_x^*)^2$$

$$\frac{d_1}{2} \int e^{qx/d_1} (e^{-qx/d_1} u')_x^2 + \frac{\min_{[0,L]} r}{2\epsilon} \int e^{-qx/d_1} (u')^2 \leq \frac{1}{2d_1} \int e^{-qx/d_1} (u_x^*)^2.$$

Since the RHS is uniformly bounded (by Lemma 5.1), $\|u'\|_{L^2} \to 0$ and $\|u_x'\|_{L^2} = O(1)$. This proves that $u' \rightharpoonup 0$ (weakly) in H^1. This implies in particular that the RHS of Equation (28) goes to zero, and we deduce that $\|(e^{-qx/d_1} u')_x\|_{L^2} \to 0$. This, together with $\|u'\|_{L^2} \to 0$ yields $\|u'\|_{H^1} \to 0$.   ∎

Denote by λ the dominant eigenvalue of the linearization of the v equation at $(u^*, 0)$. Denote $\partial/\partial d_2$ by $'$ and set $\alpha = q/d_1$.

LEMMA 5.3   *The selection gradient satisfies*

$$\frac{1}{\epsilon} \frac{\partial}{\partial d_2} \lambda(d_1, d_1) = -\frac{\int u_x^* (e^{-\alpha x} u^*)_x}{\int e^{-\alpha x} (u^*)^2}. \tag{29}$$

Proof The stability of $(u^*, 0)$ of Equation (26) is determined by the dominant eigenvalue $\lambda = \lambda(d_1, d_2)$ of the following problem.

$$\epsilon(d_2\phi_{xx} - q\phi_x) + (r - u^*)\phi = \lambda\phi \quad \text{in } (0, L),$$
$$d_2\phi_x - q\phi = 0 \quad \text{at } x = 0, L. \tag{30}$$

We normalize the principal eigenfunction by $\int_0^L e^{-qx/d_1}\phi^2 = \int_0^L e^{-qx/d_1}(u^*)^2$, so that $\phi = u^*$ when $d_1 = d_2$. We can differentiate Equation (30) with respect to d_2, and obtain (denoting the derivative with respect to d_2 by $'$)

$$\epsilon(d_2\phi'_{xx} - q\phi'_x) + (r - u^*)\phi' + \epsilon\phi_{xx} = \lambda\phi' + \lambda'\phi \quad \text{in } (0, L),$$
$$d_2\phi'_x - q\phi' + \phi_x = 0 \quad \text{at } x = 0, L \quad \text{and} \quad \int_0^L e^{-qx/d_1}\phi\phi' = 0. \tag{31}$$

Set $d_2 = d_1$ and $\alpha = q/d_2$, then $\lambda = 0$ and $\phi = u^*$, so Equation (31) becomes

$$\epsilon(d_2\phi'_{xx} - q\phi'_x) + (r - u^*)\phi' + \epsilon u^*_{xx} = \lambda'u^* \quad \text{in } (0, L),$$
$$d_2\phi'_x - q\phi' + u^*_x = 0 \quad \text{at } x = 0, L \quad \text{and} \quad \int_0^L e^{-qx/d_1}u^*\phi' = 0. \tag{32}$$

Multiplying Equation (32) by $e^{-\alpha x}u^*$ and integrating by parts, we have

$$-\epsilon\int_0^L u^*_x(e^{-\alpha x}u^*)_x = \lambda'\int_0^L e^{-\alpha x}(u^*)^2,$$

which proves the lemma. ∎

LEMMA 5.4 *As $\epsilon \to 0$,*

$$\int_0^L u^*_x(e^{-\alpha x}u^*)_x \to \int_0^L r_x(e^{-\alpha x}r)_x \tag{33}$$

in $C^1_{loc}([0, \infty))$.

Proof By Lemma 5.1 (iii), $\int u^*_x(e^{-qx/d_1}u^*)_x \to \int r_x(e^{-qx/d_1}r)_x$ uniformly in compact subsets of $(0, \infty)$ in d_1. Now,

$$\frac{\partial}{\partial d_1}\int u^*_x(e^{-qx/d_1}u^*)_x$$
$$= \int (u^*)'(e^{-qx/d_1}u^*)_x + \int u^*_x(e^{-qx/d_1}(u^*)')_x + \int u^*_x\left(e^{-qx/d_1}\frac{qx}{d_1^2}u^*\right)_x$$
$$\to \int r_x\left(e^{-qx/d_1}\frac{qx}{d_1^2}r\right)_x \quad \text{as } \epsilon \to 0, \quad \text{by Lemma 5.2}$$
$$= \frac{\partial}{\partial d_1}\int r_x(e^{-qx/d_1}r)_x.$$

Since the above convergence is again uniform on compact subsets of $(0, \infty)$ in d_1, the lemma is proved. ∎

Define

$$F(\alpha) = \int_0^L r_x(e^{-\alpha x}r)_x \, dx.$$

DEFINITION 5.5   *We say that d_0 is a singular strategy in the limit if $F(q/d_0) = 0$.*

By Lemma 5.4, one can conclude the following about the original problem by inverse function theorem.

PROPOSITION 5.6   *If d_0 is a singular strategy in the limit, and $F'(q/d_0) \neq 0$, then for all ϵ sufficiently small, there exists $\hat{d} = \hat{d}(\epsilon)$ such that $\hat{d} \to d_0$ and*

$$\frac{\partial}{\partial d_2}\lambda(\hat{d}, \hat{d}) = -\epsilon \frac{\int_0^L u_x^*(e^{-qx/\hat{d}}u^*)_x \, dx}{\int_0^L e^{-qx/\hat{d}}(u^*)^2 \, dx} = 0.$$

Moreover, $\hat{d}$ is the unique singular strategy near d_0.

Example   Consider the linear growth rate $r(x) = r_0 + r_1 x$. We require $r(x) > 0$, in particular, $r_0 > 0$. By rescaling, we may assume $L = 1$. If $r_1 < 0$, then there is no positive singular strategy in the limit. If $r_1 > 0$, then there is a unique positive singular strategy, and it is given by

$$d = \frac{q}{\ln(1 + r_1/r_0)} = \frac{q}{\ln(\max r/\min r)}. \tag{34}$$

To see this, replace $r(x) = r_0 + r_1 x$ in the equation

$$\int_0^1 r_x(e^{-\alpha x}r)_x \, dx = 0 \tag{35}$$

and carry out the calculations. We can find that the integral equality is equivalent to $(r_0 + r_1)e^{-\alpha} = r_0$. This equation is solvable for positive $\alpha = q/d$ if and only if $r_1 > 0$.

The following two lemmas give sufficient condition for the existence of a unique singular strategy in the limit (i.e. for $F(\alpha)$ to have a unique root).

LEMMA 5.7   *$F(\alpha)$ has a unique root in either of the two following cases*:

 (i) $r_x(0), r_x(L) > 0$ *and* $r_{xx} \leq 0$.
(ii) $r_x(0) > 0$ *and* $r_{xx} \geq 0$.

Proof   Without loss we assume $L = 1$. Write

$$F(\alpha) = \int e^{-\alpha x}r_x^2 - \alpha \int e^{-\alpha x}rr_x, \tag{36}$$

where all integrals are over $[0, 1]$. It is easy to see that

$$F(0) = \int r_x^2 > 0, \quad F(\infty) = -r(0)r_x(0) < 0. \tag{37}$$

Hence, there is at least one root. The derivative of F is

$$F'(\alpha) = -\int e^{-\alpha x}xr_x^2 - \int e^{-\alpha x}rr_x + \alpha \int e^{-\alpha x}xrr_x. \tag{38}$$

Integrate the last term by parts and obtain

$$F'(\alpha) = -r(1)r_x(1)e^{-\alpha} + \int e^{-\alpha x}xrr_{xx} < 0, \tag{39}$$

where the final inequality follows from the assumption (i). Since F' is negative, the root is unique.

To prove the claim under the second assumption, we integrate by parts the second integral in expression (36). Assuming that α is a root of F, we find

$$F(\alpha) = \mathrm{e}^{-\alpha} r(1) r_x(1) - r(0) r_x(0) - \int \mathrm{e}^{-\alpha x} r r_{xx} = 0. \tag{40}$$

We use this expression to replace the boundary term in Equation (39) and find for any root α

$$F'(\alpha) = -r(0) r_x(0) - \int \mathrm{e}^{-\alpha x} (1 - x) r r_{xx}. \tag{41}$$

Under the second assumption, this final expression is negative since $x < 1$. Hence, $F'(\alpha) < 0$ for all roots α, therefore the root is unique. ∎

LEMMA 5.8   *If $r, r_x > 0$ in $[0, L]$ and r_x/r is monotone in $[0, L]$, then the function F has a unique root.*

Remark 5.9   The assumptions are equivalent to $r > 0$ in $[0, L]$, $r_x(0), r_x(L) > 0$ and r_x/r is monotone in $[0, L]$.

One can immediately conclude the following result regarding the original problem.

COROLLARY 5.10   *Suppose the assumptions of either Lemma 5.7 or Lemma 5.8 hold, then for all ϵ sufficiently small, there exists a unique singular strategy for the original problem. In fact, there exists $\hat{d} = \hat{d}(\epsilon) \in (q \min_{[0,L]} r/r_x, q \max_{[0,L]} r/r_x)$ such that*

$$\frac{\partial}{\partial d_2} \lambda(d, d) = \begin{cases} > 0 & when\ 0 < d < \hat{d}, \\ = 0 & when\ d = \hat{d}, \\ < 0 & when\ d > \hat{d}. \end{cases}$$

Moreover, $\lim_{\epsilon \to 0} \hat{d} = d_0$, where d_0 is the unique singular strategy in the limit guaranteed by either Lemma 5.7 or Lemma 5.8.

Proof of Corollary 5.10   By Theorem 4.5, the selection gradient $(\partial/\partial d_2)\lambda(d, d)$ changes sign at least once, from positive to negative. Moreover, any sign change has to take place in the interval $d \in [q \min_{[0,L]} r/r_x, q \max_{[0,L]} r/r_x]$. But then by Theorem 4.5 and Lemma 5.4, for sufficiently small ϵ, there is exactly one (non-degenerate) sign change of the selection gradient. ∎

Proof of Lemma 5.8   Let $r(x) = \mathrm{e}^{g(x)}$. Then,

$$F(\alpha) = \int \mathrm{e}^{-\alpha x + 2g} g_x (g_x - \alpha). \tag{42}$$

The assumption of the lemma says that $g_x > 0$ and g_{xx} does not change sign. We consider the two cases: (i) $g_{xx} \leq 0$; (ii) $g_{xx} \geq 0$. If $g_x \equiv$ constant, then the lemma is trivial. We henceforth assume that g_x is non-constant and monotone in $[0, L]$. It is clear then that $F(\alpha)$ changes sign at least once, and any root lies within the interval $(\min g_x, \max g_x)$.

Case (i): $g_{xx} \leq 0$. Suppose α_0 is a root, then

$$F'(\alpha_0) = -\int xe^{-\alpha_0 x + 2g} g_x (g_x - \alpha_0) - \int e^{-\alpha_0 x + 2g} g_x$$

$$< -\int xe^{-\alpha_0 x + 2g} g_x (g_x - \alpha_0)$$

$$= \int xe^{-\alpha_0 x + 2g} g_x (\alpha_0 - g_x)$$

$$< 0,$$

where the last strict inequality follows from the fact that $h(x) := e^{-\alpha_0 x + 2g} g_x (\alpha_0 - g_x)$ changes sign from negative to positive as x varies from 0 to L. More precisely, choose $x_0 \in (0, L)$ such that $h(x) < 0$ in $[0, x_0)$ and $h(x) \geq 0$ in $(x_0, L]$, then

$$\int_0^L xe^{-\alpha_0 x + 2g} g_x (\alpha_0 - g_x) = \int_0^{x_0} xh(x) + \int_{x_0}^L xh(x) < x_0 \int_0^L h(x) = x_0 F(\alpha_0) = 0.$$

This proves Case (i).

Case (ii): $g_{xx} \geq 0$. Then, $r_{xx} = e^g (g_{xx} + g_x^2) \geq 0$ and the result follows from Lemma 5.7(ii).
∎

Example 1   We consider the case of a piecewise linear growth function

$$r(x) = A + B|x - C|, \tag{43}$$

where parameters A, B, C are chosen such that $r > 0$ on the interval $\Omega = [0, 1]$. (We again assume $L = 1$ without loss of generality.) For $0 < C < 1$, this function is not differentiable in Ω. However, one can 'smooth' the corner at $x = C$ by altering the function r on an interval of arbitrarily small length around C and with a bounded derivative between -1 and 1. Hence, the integral in the selection gradient can be approximated arbitrarily closely by the piecewise integral

$$\int_0^C r_x (e^{-\alpha x} r)_x \, dx + \int_C^1 r_x (e^{-\alpha x} r)_x \, dx,$$

which is well defined. Explicit calculations lead to the expression

$$F(\alpha) = \int_0^1 r_x (e^{-\alpha x} r)_x \, dx = B[A + BC + (A + B(1 - C))e^{-\alpha} - 2Ae^{-\alpha C}]. \tag{44}$$

By setting $y = e^{-\alpha}$, we obtain the following equation for $y \in (0, 1]$:

$$K_1 + K_2 y = K_3 y^C, \tag{45}$$

where

$$K_1 = A + BC = r(0) > 0, \quad K_2 = A + B(1 - C) = r(1) > 0, \quad K_3 = 2A = 2r(C) > 0.$$

The LHS in Equation (45) is a straight line, the RHS a root-like function (monotone increasing, concave down). We observe the following.

(1) There is exactly one root of $F(\alpha) = 0$ (no double root) if $B < 0$. To see this, simply consider the condition that the straight line is below the root function at $y = 1$, or $K_1 + K_2 < K_3$.

Hence, when the resource function has a single hump, then there is precisely one singular strategy.

(2) Let $B > 0$. If $F(\alpha) = 0$ has a double root, then necessarily $C < \frac{1}{2}$. To see this, we notice that the straight line is tangent to the root function at $y^* = K_1/K_2(1/C - 1)$. The requirement $y^* \in (0, 1)$ gives the condition on C. Hence, the minimum of the growth function has to be upstream of the midpoint.

(3) For all $B > 0$, there exists $C^*(B) \in (0, \frac{1}{2})$ such that
  (i) If $C \in (0, C^*)$, then $F(\alpha)$ has exactly two roots.
  (ii) If $C = C^*$, then $F(\alpha)$ has a double root.
  (iii) If $C \in (C^*, 1)$, then $F(\alpha)$ has no roots.

   For existence, we first consider $C = 1$, then for all $B > 0$, $F(\alpha) = 0$ has no root. Now if we decrease C, then the linear function on the LHS is decreasing, while the concave function on the RHS is increasing. Moreover,

$$K_3 y^C|_{y=0} = 0 < (K_1 + K_2 y)|_{y=0},$$

and $\lim_{C \to 0^+} K_3 y^C = K_3 = 2A$ locally uniformly for $y \in (0, 1]$, hence for all $B > 0$, there are exactly two roots for all C sufficiently small. Finally, $C^*(B)$ belongs to $(0, \frac{1}{2})$ follows from the previous claim.

(4) There exists $\delta_0 > 0$ such that $F(\alpha) = 0$ has exactly two roots when $B, C \in (0, \delta_0)$.

6. Criteria for evolutionarily stable strategies (ESS)

In this section, we aim to find criteria for the existence of evolutionarily stable strategies, when the diffusion and advection rates are small. Recall that $' = \partial/\partial d_2$.

LEMMA 6.1 *At a singular strategy d, we have $\lambda = \lambda(d, d) = 0$, and $(\partial/\partial d_2)\lambda(d, d) = 0$. Then, the second derivative of λ is given by $(\alpha = q/d_1)$*

$$\frac{1}{\epsilon}\frac{\partial^2}{\partial d_2^2}\lambda(d, d) = -2\frac{\int \phi_x'(e^{-\alpha x}u^*)_x}{\int e^{-\alpha x}(u^*)^2}, \tag{46}$$

where ϕ' satisfies

$$\epsilon(d\phi_{xx}' - q\phi_x') + (r(x) - u^*)\phi' + \epsilon u_{xx}^* = 0 \quad in\ (0, L),$$

$$d\phi_x' - q\phi' + u_x^* = 0 \quad when\ x = 0, L, \quad \int e^{-qx/d}u^*\phi' = 0. \tag{47}$$

Proof Let d be chosen such that $\lambda'(d, d) = 0$. Differentiate Equation (31) with respect to d_2 and then set $d_2 = d_1 = d$, so that $\lambda = \lambda' = 0$, we obtain

$$\epsilon(d\phi_{xx}'' - q\phi_x'') + (r - u^*)\phi'' + 2\epsilon\phi_{xx}' = \lambda''u^* \quad in\ (0, L),$$

$$d\phi_x'' - q\phi'' + 2\phi_x' = 0 \quad at\ x = 0, L \quad and \tag{48}$$

$$\int_0^L e^{-qx/d}u^*\phi'' + \int_0^L e^{-qx/d}\phi'^2 = 0,$$

where ϕ' satisfies Equation (32). Multiplying the above by $e^{-qx/d}u^*$ and integrating by parts, we obtain

$$-2\epsilon \int \phi_x'(e^{-qx/d}u^*)_x = \lambda'' \int e^{-qx/d}(u^*)^2.$$

This proves the lemma. ∎

PROPOSITION 6.2 *Suppose for $\epsilon = \epsilon_k \to 0$, $\{d_k\}$ are a sequence of singular strategies such that $d_k \to d$ for some $d > 0$, then*

$$\int \phi'_x(\mathrm{e}^{-qx/d_k}u^*)_x \to \int \psi_x(\mathrm{e}^{-qx/d}r)_x,$$

where ψ satisfies

$$\begin{aligned}
(d\psi_{xx} - q\psi_x) - \frac{dr_{xx} - qr_x}{r}\psi &= -r_{xx} \quad in\ (0, L), \\
d\psi_x - q\psi - \frac{dr_x - qr}{r}\psi &= -r_x \quad at\ x = 0, L, \quad \int \mathrm{e}^{-qx/d}r\psi = 0.
\end{aligned} \tag{49}$$

Proof We refer to Lemma 4.5 of [33]. ∎

DEFINITION 6.3 *Suppose that d_0 is a singular strategy in the limit, that is, $\int_0^L r_x(\mathrm{e}^{-qx/d_0}r)_x = 0$. We say that d_0 is a local ESS in the limit if $\int \psi_x(\mathrm{e}^{-qx/d_0}r)_x > 0$.*

Our first main result of this section provides an explicit criterion for the existence of a local ESS in the limit.

THEOREM 6.4 *Suppose $r, r_x > 0$ in $[0, L]$ and*

$$2\min_{[0,L]}\frac{r_x}{r} > \max_{[0,L]}\frac{r_x}{r}. \tag{50}$$

If r_x/r is decreasing and non-constant, then the unique singular strategy d_0 in the limit, given by Lemma 5.8, is also a local ESS in the limit.

As an interesting complement of Theorem 6.4, our next result gives a sufficient condition on the non-existence of an ESS in the limit.

THEOREM 6.5 *Suppose $r, r_x > 0$ in $[0, L]$ and Equation (50) holds. If r_x/r is increasing and non-constant, then there are no ESSs in the limit.*

Under the assumption of either Theorem 6.4 or Theorem 6.5, for all ϵ sufficiently small, Equation (26) has a unique singular strategy $\hat{d} = \hat{d}(\epsilon)$ (by Lemmas 5.3, 5.4 and 5.8). Therefore, we have the following theorem regarding evolutionary stability of these singular strategies.

COROLLARY 6.6 *Suppose $r, r_x > 0$ in $[0, L]$, and Equation (50) holds.*

(i) *If r_x/r is decreasing and non-constant, then for all ϵ sufficiently small, the unique singular strategy $\hat{d}$ is also a local ESS; that is, there exists $\delta > 0$ such that*

$$\lambda(\hat{d}, d_2) < 0 \quad for\ all\ d_2 \in (\hat{d} - \delta, \hat{d} + \delta) \setminus \{\hat{d}\}.$$

(ii) *If r_x/x is increasing and non-constant, then for all ϵ sufficiently small, the unique singular strategy $\hat{d}$ is not an ESS. In particular, there are no ESSs for all ϵ sufficiently small.*

Remark 6.7 (i) By a different method, it is proved in [2] that when $r_x/r \equiv c_0$ for some positive constant c_0, then the unique singular strategy is given by $\hat{d} = q/c_0$, which is independent of $\epsilon > 0$. Moreover, $\hat{d} = q/c_0$ is an ESS. Our results here explores the stability of this result.

(ii) It is unclear biologically why the shape of the resource function plays such a critical role. It seems interesting to enquire whether the assumption (50) is purely technical or not.

We first prepare by proving a few lemmas.

LEMMA 6.8 *Suppose*

$$\int r_x(e^{-qx/d}r)_x = 0, \tag{51}$$

(if $r, r_x > 0$, then by Theorem 4.5 necessarily $q/d \in [\min_{[0,L]} r_x/r, \max_{[0,L]} r_x/r])$, then the following conditions are equivalent:

(i) $\int \psi_x(e^{-qx/d}r)_x > 0$ *(condition for $d > 0$ to be an ESS in the limit)*,
(ii) $d \int e^{-qx/d}r^2|y_x|^2 < \int (qx/d^2 - 2\ln r/d)r_x(e^{-qx/d}r)_x$,
(iii) $\int (y - 2\ln r/d + qx/d^2)r_x(e^{-qx/d}r)_x > 0$,

where ψ is given by Equation (49), and y is a solution to

$$d(r^2e^{-qx/d}y_x)_x = r_x(e^{-qx/d}r)_x \quad and \; y_x|_{x=0,L} = 0. \tag{52}$$

Proof Let $\psi = rz$, then by some elementary but tedious computations involving Equation (49), we have

$$drz_{xx} + (2dr_x - qr)z_x + r_{xx} = 0 \quad \text{in } (0, L),$$
$$z_x = -\frac{r_x}{dr} \quad \text{at } x = 0, L. \tag{53}$$

Now, let $y = z + \ln r/d$, then (adding an integral constraint for uniqueness)

$$dry_{xx} + (2dr_x - qr)y_x = r_x\left(\frac{r_x}{r} - \frac{q}{d}\right) \quad \text{in } (0, L),$$
$$y_x = 0 \quad \text{at } x = 0, L \quad \text{and} \quad \int y = 0. \tag{54}$$

Or equivalently,

$$d(e^{-qx/d}r^2y_x)_x = r_x(e^{-qx/d}r)_x \quad \text{in } (0, L),$$
$$y_x = 0 \quad \text{at } x = 0, L \quad \text{and} \quad \int y = 0. \tag{55}$$

It remains to show the following claim. Recall that ψ, y satisfies Equations (49) and (52), respectively.

CLAIM 6.9 $\quad \int \psi_x(e^{-qx/d}r)_x = \int (y - 2\ln r/d + qx/d^2)r_x(e^{-qx/d}r)_x.$

First, we show Claim 6.9:

$$\int \psi_x(e^{-qx/d}r)_x$$
$$= \int \left[r\left(y - \frac{\ln r}{d}\right)\right]_x (e^{-qx/d}r)_x$$

$$= \int r \left(y_x - \frac{r_x}{dr}\right) (\mathrm{e}^{-qx/d} r)_x + \int \left(y - \frac{\ln r}{d}\right) r_x (\mathrm{e}^{-qx/d} r)_x$$

$$= \int r y_x (\mathrm{e}^{-qx/d} r)_x + \int \left(y - \frac{\ln r}{d}\right) r_x (\mathrm{e}^{-qx/d} r)_x \quad \text{by Equation (51)}$$

$$= \int \mathrm{e}^{-qx/d} r^2 y_x \left(\frac{r_x - qr/d}{r}\right) + \int \left(y - \frac{\ln r}{d}\right) r_x (\mathrm{e}^{-qx/d} r)_x$$

$$= \int \mathrm{e}^{-qx/d} r^2 y_x \left(\ln r - \frac{qx}{d}\right)_x + \int \left(y - \frac{\ln r}{d}\right) r_x (\mathrm{e}^{-qx/d} r)_x$$

$$= -\frac{1}{d} \int d(\mathrm{e}^{-qx/d} r^2 y_x)_x \left(\ln r - \frac{qx}{d}\right) + \int \left(y - \frac{\ln r}{d}\right) r_x (\mathrm{e}^{-qx/d} r)_x$$

$$= -\frac{1}{d} \int r_x (\mathrm{e}^{-qx/d} r)_x \left(\ln r - \frac{qx}{d}\right) + \int \left(y - \frac{\ln r}{d}\right) r_x (\mathrm{e}^{-qx/d} r)_x \quad \text{by Equation (55)}$$

$$= \int \left(y - \frac{2 \ln r}{d} + \frac{qx}{d^2}\right) r_x (\mathrm{e}^{-qx/d} r)_x.$$

Second, we notice, by multiplying Equation (55) by y and integrating by parts,

$$-d \int \mathrm{e}^{-qx/d} r^2 |y_x|^2 = \int y r_x (\mathrm{e}^{-qx/d} r)_x. \tag{56}$$

Lemma 6.8 follows from Claim 6.9 and Equation (56). ∎

Proof of Theorem 6.5 By Lemma 6.8(ii), it remains to show that

$$\int \left(\frac{qx}{d} - 2 \ln r\right) r_x (\mathrm{e}^{-qx/d} r)_x < 0, \tag{57}$$

which implies that $\lim_{\epsilon \to 0} (\partial^2/\partial d_2^2) \lambda > 0$. First, by the fact that $\int r_x (\mathrm{e}^{-qx/d})_x = 0$ (singular strategy in limit) and that r_x/r increasing, the expression

$$r_x (\mathrm{e}^{-qx/d} r)_x = \mathrm{e}^{-qx/d} r_x r \left(\frac{r_x}{r} - \frac{q}{d}\right)$$

changes sign exactly once, from negative to positive (since r_x/r is assumed to be increasing, non-constant) and $\int r_x (\mathrm{e}^{-qx/d} r)_x = 0$ (singular strategy in the limit). Hence, there exists $x_0 \in (0, L)$ such that $r_x (\mathrm{e}^{-qx/d} r)_x$ is non-constant, and

$$r_x (\mathrm{e}^{-qx/d} r)_x = \begin{cases} \leq 0 & \text{when } x \in [0, x_0), \\ = 0 & \text{when } x = x_0, \\ \geq 0 & \text{when } x \in (x_0, L]. \end{cases} \tag{58}$$

Moreover, $(qx/d - 2 \ln r - qx_0/d + 2 \ln r(x_0))_x < 0$ by Equation (50), hence

$$\frac{qx}{d} - 2 \ln r - \frac{qx_0}{d} - 2 \ln r(x_0) = \frac{q(x - x_0)}{d} - 2 \ln \frac{r}{r(x_0)} = \begin{cases} > 0 & \text{for } x \in [0, x_0), \\ = 0 & \text{for } x = x_0, \\ < 0 & \text{for } x \in (x_0, L]. \end{cases} \tag{59}$$

Finally, Equations (58) and (59) imply

$$\int \left(\frac{qx}{d} - 2 \ln r - \frac{qx_0}{d} + 2 \ln r(x_0)\right) r_x (\mathrm{e}^{-qx/d} r)_x < 0. \tag{60}$$

which is equivalent to Equation (57), by $\int r_x (\mathrm{e}^{-qx/d} r)_x = 0$. ∎

Proof of Theorem 6.4   First we show the following calculus lemma.

LEMMA 6.10   *Suppose that $g(t) : [0, L] \to (0, \infty)$ is a decreasing function and it satisfies* $2 \min g > \max g$, *then*

$$g(x) \frac{g(x) - \eta}{2g(x) - \eta} < 2 g(y) - \eta \quad \text{for all } x, y \in [0, L], \quad \text{and } \eta \in [\min g, \max g].$$

Proof   By the monotonicity of LHS with respect to $g(x)$ and of RHS with respect to $g(y)$, it is equivalent to show

$$b \frac{b - \eta}{2b - \eta} < 2a - \eta \quad \text{for all } \eta \in [a, b], \tag{61}$$

where $b = \max g = g(0)$ and $a = \min g = g(L)$ as g is a decreasing function.

Next, define

$$h(\eta) = 2a - \eta - \frac{b(b - \eta)}{2b - \eta},$$

then

$$\frac{\partial}{\partial \eta} h(\eta) = \frac{b^2 - (2b - \eta)^2}{(2b - \eta)^2} = \begin{cases} > 0 & \text{when } \eta \in (b, 3b), \\ < 0 & \text{when } \eta \notin [b, 3b]. \end{cases}$$

In particular, for all $\eta \in [\min g, \max g] = [a, b]$, we have $h'(\eta) < 0$. Hence,

$$h(\eta) \geq h(b) = 2a - b > 0 \quad \text{for all } \eta \in [\min g, \max g] = [a, b].$$

This proves Equation (61) and completes the proof of the lemma.   ∎

To prove Theorem 6.4, it remains to show that

$$\int \left(y - \frac{2 \ln r}{d} + \frac{qx}{d^2} \right) r_x (e^{-qx/d} r)_x > 0. \tag{62}$$

By (i) $r, r_x > 0$, (ii) r_x/r non-constant and decreasing, and (iii) $\int r_x (e^{-qx/d} r)_x = 0$, we deduce

$$r_x (e^{-qx/d} r)_x \text{ changes sign exactly once, from positive to negative.} \tag{63}$$

Hence, Equation (62) holds provided we can show that

$$\left(y - \frac{2 \ln r}{d} + \frac{qx}{d^2} \right)_x < 0. \tag{64}$$

It is enough to show

$$d \max_{[0, L]} y_x < 2 \frac{r_x}{r} - \frac{q}{d}. \tag{65}$$

By Equations (55) and (63), $y_x > 0$ in $(0, L)$. Suppose, $\max_{[0, L]} y_x = y_x(x_0)$ for some $x_0 \in (0, L)$. ($x_0 \neq 0, L$ by the Neumann b.c.) Then by Equation (54),

$$dy_x(x_0) = \frac{r_x}{r} \frac{(r_x/r - q/d)}{(2r_x/r - q/d)} \bigg|_{x=x_0}.$$

But then by Lemma 6.10 (here we use Equation (50)), taking $g = r_x/r$, we deduce that for all $q/d \in [\min r_x/r, \max r_x/r]$,

$$d \max_{[0, L]} y_x = \frac{r_x}{r} \frac{(r_x/r - q/d)}{(2r_x/r - q/d)} \bigg|_{x=x_0} < 2 \min_{[0, L]} \frac{r_x}{r} - \frac{q}{d}.$$

This proves Equation (65) and finishes the proof of Theorem 6.4.   ∎

7. Every singular strategy is convergent stable

In this section, we show that every singular strategy is convergent stable, when both diffusion and advection rates are small. The main result can be stated as follows.

THEOREM 7.1   *Suppose as $\epsilon \to 0$, $\hat{d} = \hat{d}(\epsilon)$ are singular strategies such that $\hat{d} \to d_0$, then necessarily*

$$\liminf_{\epsilon \to 0} \frac{1}{\epsilon} \frac{\partial^2}{\partial d_1^2} \lambda(\hat{d}, \hat{d}) > 0.$$

If we assume in addition that $\limsup_{\epsilon \to 0} \partial/\partial t[(\partial \lambda/\partial d_2)(t, t)]|_{t=\hat{d}} < 0$, *then for all ϵ sufficiently small, there exist $\delta_0 > 0$ such that*

$$\lambda(d_1, d_2) > 0 \quad \text{if } \hat{d} - \delta_0 < d_1 < d_2 \leq \hat{d} \quad \text{or } \hat{d} \leq d_2 < d_1 < \hat{d} + \delta_0.$$

In particular, all assumptions of Theorem 7.1 can be verified under the assumption of Lemmas 5.7 and 5.8.

COROLLARY 7.2   *Under the assumption of either Lemma 5.7 or Lemma 5.8, for all ϵ sufficiently small, there exists $\delta_0 > 0$ such that*

$$\lambda(d_1, d_2) > 0 \quad \text{if } \hat{d} - \delta_0 < d_1 < d_2 \leq \hat{d} \quad \text{or } \hat{d} \leq d_2 < d_1 < \hat{d} + \delta_0,$$

where $\hat{d} = \hat{d}(\epsilon)$ is the unique singular strategy guaranteed by Corollary 5.10.

Proof   That $\limsup_{\epsilon \to 0} \partial/\partial t[(\partial \lambda/\partial d_2)(t, t)]|_{t=\hat{d}} < 0$ follows from the proofs of Lemmas 5.7 and 5.8 and by Corollary 5.10.   ∎

7.1. *Formulas for $\partial \lambda/\partial d_1$ and $\partial^2 \lambda/\partial d_1^2$*

Differentiating Equation (30) with respect to d_1 once, then we have

$$\epsilon \left(d_2 \left(\frac{\partial \phi}{\partial d_1}\right)_{xx} - q\left(\frac{\partial \phi}{\partial d_1}\right)_x\right) + (r - u^*)\frac{\partial \phi}{\partial d_1} - \lambda \frac{\partial \phi}{\partial d_1} = \frac{\partial \lambda}{\partial d_1}\phi + \frac{\partial u^*}{\partial d_1}\phi \quad \text{in } (0, L),$$

$$d_2 \left(\frac{\partial \phi}{\partial d_1}\right)_x - q\frac{\partial \phi}{\partial d_1} = 0 \quad \text{at } x = 0, L. \tag{66}$$

Multiplying Equation (66) by $\mathrm{e}^{-qx/d_2}\phi$ and integrating by parts, we have

$$\frac{\partial \lambda}{\partial d_1}(d_1, d_2) \int \mathrm{e}^{-qx/d_2}\phi^2 = -\int \mathrm{e}^{-qx/d_2}\frac{\partial u^*}{\partial d_1}\phi^2. \tag{67}$$

Differentiate Equation (67) with respect to d_1 again, and set $d_1 = d_2 = \hat{d}$ ($\hat{d}$ is a singular strategy) (hence $\phi = u^*$ and $\lambda = \partial \lambda/\partial d_1 = \partial \lambda/\partial d_2 = 0$), we have

$$\frac{1}{\epsilon}\frac{\partial^2 \lambda}{\partial d_1^2} \int \mathrm{e}^{-qx/\hat{d}}(u^*)^2 = -\frac{1}{\epsilon}\int \mathrm{e}^{-qx/\hat{d}}\frac{\partial^2 u^*}{\partial d_1^2}(u^*)^2 - \frac{2}{\epsilon}\int \mathrm{e}^{-qx/\hat{d}}u^*\frac{\partial u^*}{\partial d_1}\frac{\partial \phi}{\partial d_1}, \tag{68}$$

where $\partial \phi/\partial d_1 = (\partial \phi/\partial d_1)(\hat{d}, \hat{d})$ satisfies

$$\epsilon \left(\hat{d}\left(\frac{\partial \phi}{\partial d_1}\right)_{xx} - q\left(\frac{\partial \phi}{\partial d_1}\right)_x\right) + (r - u^*)\frac{\partial \phi}{\partial d_1} = \frac{\partial u^*}{\partial d_1}u^* \quad \text{in } (0, L),$$

$$\hat{d}\left(\frac{\partial \phi}{\partial d_1}\right)_x - q\frac{\partial \phi}{\partial d_1} = 0 \quad \text{at } x = 0, L. \tag{69}$$

7.2. *Asymptotic limit of $\partial^2\lambda/\partial d_1^2$*

In this section, we shall prove Theorem 7.1 in a few lemmas.

LEMMA 7.3 *Set $d_1 = d_2 = \hat{d}$, then as $\epsilon \to 0$, a subsequence $(\partial\phi/\partial d_1)(\hat{d}, \hat{d}) \rightharpoonup \phi'$ in $H^1((0, L))$, where ϕ' is a solution of*

$$
\begin{aligned}
d_0\phi'_{xx} - q\phi'_x - \frac{d_0 r_{xx} - q r_x}{r}\phi' = r_{xx} \quad in \ (0, L), \\
d_0\phi'_x - q\phi' - \frac{d_0 r_x - qr}{r}\phi' = r_x \quad at \ x = 0, L.
\end{aligned}
\tag{70}
$$

In particular, if we define

$$
\frac{\partial\phi}{\partial d_1}^{\perp} = \frac{\partial\phi}{\partial d_1} - \frac{\int e^{-qx/\hat{d}} \frac{\partial\phi}{\partial d_1} u^*}{\int e^{-qx/\hat{d}}(u^*)^2} u^*,
\tag{71}
$$

then $\partial\phi/\partial d_1^{\perp} \to \phi'^{\perp}$ weakly in $H^1((0, L))$, where $\phi'^{\perp}$ is the unique solution to

$$
d_0\phi'^{\perp}_{xx} - q\phi'^{\perp}_x - \frac{d_0 r_{xx} - q r_x}{r}\phi'^{\perp} = r_{xx} \quad in \ (0, L),
$$

$$
d_0\phi'^{\perp}_x - q\phi'^{\perp} - \frac{d_0 r_x - qr}{r}\phi'^{\perp} = r_x \quad at \ x = 0, L \quad and \quad \int e^{-qx/d_0}\phi'^{\perp} r = 0.
\tag{72}
$$

Proof From $\phi|_{d_1=d_2=d} = u^*|_{d_1=d}$, one can observe that

$$
\frac{\partial\phi}{\partial d_1}(\hat{d}, \hat{d}) + \frac{\partial\phi}{\partial d_2}(\hat{d}, \hat{d}) = \left.\frac{\partial u^*}{\partial d_1}\right|_{d_1=\hat{d}}.
$$

It follows that (since we know the equation for $\partial\phi/\partial d_2$ which is Equation (47)), by passing to a subsequence, $\partial\phi/\partial d_1)(\hat{d}, \hat{d}) \to \phi'$, which satisfies Equation (70). The rest follows from the fact that $r = \lim_{\epsilon\to 0} u^*$ is in the kernel, and normalization. ∎

LEMMA 7.4 *For any d and any q, $\limsup_{\epsilon\to 0}(1/\epsilon)\int e^{-qx/d}(u^*)^2\partial^2 u^*/\partial d_1^2 \leq 0$.*

Proof Denote $\partial u^*/\partial d_1 = u'$ and $\partial^2 u^*/\partial d_1^2 = u''$, we have

$$
\begin{aligned}
\epsilon(du''_{xx} - qu''_x) + (r - 2u^*)u'' = -2\epsilon u'_{xx} + 2(u')^2 \quad in \ (0, L), \\
du''_x - qu' = -2u'_x \quad at \ x = 0, L.
\end{aligned}
\tag{73}
$$

Multiply by $-1/\epsilon e^{-qx/d} u^*$ and integrate by parts, we have

$$
\begin{aligned}
\frac{1}{\epsilon}\int e^{-qx/d}(u^*)^2 u'' &= -2\int u'_x(e^{-qx/d}u^*)_x - \frac{2}{\epsilon}\int e^{-qx/d}u^*(u')^2 \\
&\leq -2\int u'_x(e^{-qx/d}u^*)_x.
\end{aligned}
$$

The last quantity is of order $o(1)$ as $u' \to 0$ in H^1 (Lemma 5.2) and u^* is bounded in H^1 (Lemma 5.1). ∎

LEMMA 7.5   *For each singular strategy $\hat{d}$, if $\hat{d} \to d_0 > 0$ as $\epsilon \to 0$, then*

$$\lim_{\epsilon \to 0} \frac{1}{\epsilon} \int e^{-qx/\hat{d}} u^* \frac{\partial \phi}{\partial d_1} \frac{\partial u^*}{\partial d_1} < 0.$$

Proof   Denote $\partial \phi / \partial d_1 = \phi'$ and $\partial u^* / \partial d_1 = u'$. Multiply Equation (69) by $e^{-qx/\hat{d}} \phi'$, then

$$\frac{1}{\epsilon} \int e^{-qx/\hat{d}} u^* u' \phi' = -\hat{d} \int e^{qx/\hat{d}} [(e^{-qx/\hat{d}} \phi')_x^2 - (m - u^*)(\phi')^2]$$

$$\leq -\frac{\lambda_2}{\epsilon} \int e^{-qx/\hat{d}} \left(\frac{\partial \phi}{\partial d_1}^{\perp} \right)^2$$

$$\to -\sigma_2 \int e^{-q/d_0} (\bar{\phi}'^{\perp})^2,$$

where the second last inequality follows from Poincaré's inequality and the definition of $\phi'^{\perp}$ in Equation (71). λ_2 is the first strictly negative eigenvalue of (which is Equation (14) with ϵ, $d_1 = d_2 = \hat{d}$ and $\lambda_1 = \lambda(\hat{d}, \hat{d}) = 0$)

$$\epsilon(\hat{d}\phi_{xx} - q\phi_x) + (m - u^*)\phi = \lambda\phi \text{ in } (0, L),$$

$$\hat{d}\phi_x - q\phi = 0 \text{ at } x = 0, L.$$

Since one can show (see, e.g. [33, Proposition 4.2]) that $\lambda_2/\epsilon \to \sigma_2$, which denotes the first negative eigenvalue of (assuming $\hat{d} \to d_0$)

$$d_0\phi_{xx} - q\phi_x - \frac{d_0 r_{xx} - q r_x}{r}\phi = \sigma\phi \quad \text{in } (0, L),$$

$$d_0\phi_x - q\phi - \frac{d_0 r_x - qr}{r}\phi = 0 \quad \text{at } x = 0, L,$$

we deduce that $\limsup_{\epsilon \to 0} \int e^{-qx/\hat{d}} u^* u' \phi' < 0$.   ∎

Proof of Theorem 7.1   When $d_1 = d_2 = \hat{d}$, Equation (68) is valid. Thus, the theorem follows from Lemmas 7.4 and 7.5.   ∎

8.   Discussion

The question of why individuals disperse has a long and distinguished history in ecology and evolutionary theory. While it is fairly straightforward to understand why dispersal is beneficial in a temporally varying environment, early results in temporally constant but spatially varying environments all point towards the benefit of slower dispersal. Simply put, random dispersal tends to move individuals away from higher quality regions to lower quality habitat and therefore slower dispersal should be beneficial. Ever since the work by Hastings [25], the challenge is to find ecological mechanisms – and mathematical proof – for intermediate or higher dispersal rates to evolve.

One such mechanism that has recently received much attention is that random dispersal can – and sometimes needs to – balance individual movement behaviour along a resource or fitness gradient. In the absence of strong enough diffusion, intrinsic movement bias towards better environmental conditions may trap individuals and lead to overcrowding. With too strong diffusion,

on the other hand, individuals underutilize regions of highest resource quality. Combining these two mechanisms, intermediate dispersal can emerge as an optimal strategy (e.g. [2,11,24,33,34]).

Here and in [38], we consider an extrinsic movement bias (advection) as a mechanism that may make higher diffusion rates beneficial. In an open environment, where advection may push individuals out of the domain, some minimal dispersal rate is required for a population to persist in the first place [40], so that the evolution of slower dispersal is impossible. In fact, when only advection causes boundary loss, then higher diffusion is always beneficial, whereas when diffusion may also cause boundary loss, an intermediate diffusion rate seems most beneficial [38]. In a closed environment that we studied here, advection pushes individuals in one direction but not out of the domain. Therefore, the population concentrates at the downstream boundary and, similar to the case of strong movement bias to better resources, higher diffusion can be beneficial. The detailed results depend subtly on the actual resource distribution, that is, the shape of the function $r(x)$.

The example of a piecewise linear resource function could lead to the guess that if the resource decreases in the direction of advection, then higher dispersal rates should evolve as a mechanism for individuals to remain in areas where resources are high. Whereas when resources increase in the direction of advection, then an intermediate optimal dispersal rate might exist. Some diffusion is necessary to get away from the boundary but too much diffusion spreads the population to upstream areas of low resource. However, the more detailed analysis reveals a condition involving the function r_x/r for the existence or non-existence of an ESS. Future work will investigate the cases where condition (50) is not satisfied and consider examples when r_x/r is not monotone.

The theory developed in this paper can also be extended to other models such as

$$u_t = [d_1 u_x - q\left(\frac{r_x}{r}\right) u]_x + u(r - u - v), \quad 0 < x < L,\ t > 0,$$

$$v_t = [d_2 v_x - q\left(\frac{r_x}{r}\right) v]_x + v(r - u - v), \quad 0 < x < L,\ t > 0, \quad (74)$$

$$d_1 u_x - q\left(\frac{r_x}{r}\right) u = d_2 v_x - q\left(\frac{r_x}{r}\right) v = 0, \quad x = 0, L,\ t > 0.$$

We refer to [2,11] for a detailed derivation of such models and related mathematical results.

It will also be of interest to consider more general ecological models such as

$$u_t = d_1 u_{xx} - q u_x + ru\left(1 - \frac{u+v}{K}\right), \quad 0 < x < L,\ t > 0,$$

$$v_t = d_2 v_{xx} - q v_x + rv\left(1 - \frac{u+v}{K}\right), \quad 0 < x < L,\ t > 0, \quad (75)$$

$$d_1 u_x - q u = d_2 v_x - q v = 0, \quad x = 0, L,\ t > 0.$$

Note that if $r(x) \equiv K(x)$, system (75) is reduced to system (1). We suspect that the theory of this paper can be extended to the model (75).

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