EVOLUTIONARILY STABLE DISPERSSAL STRATEGIES IN A TWO-PATCH ADVECTIVE ENVIRONMENT

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(Communicated by Yuan Lou)

Abstract. Two-patch models are used to mimic the unidirectional movement of organisms in continuous, advective environments. We assume that species can move between two patches, with patch 1 as the upper stream patch and patch 2 as the downstream patch. Species disperse between two patches with the same rate, and species in patch 1 is transported to patch 2 by drift, but not vice versa. We also mimic no-flux boundary conditions at the upstream and zero Dirichlet boundary conditions at the downstream. The criteria for the persistence of a single species is established. For two competing species model, we show that there is an intermediate dispersal rate which is evolutionarily stable. These results support the conjecture in [6], initially proposed for reaction-diffusion models with continuous advective environments.

1. Introduction. Dispersal is an important life history trait that can considerably affect the population dynamics of single and multiple interacting species. It influences the persistence of single populations, the distribution and the abundance of interacting species and community [1]. Meanwhile, understanding the mechanism for the evolution of dispersal has been an active research topic over the last few decades in empirical as well as theoretical studies [2].

A useful tool to study the evolution of dispersal is the adaptive dynamics theory [3]. A core concept in adaptive dynamics is the evolutionarily stable strategy (abbreviated as ESS henceforth), and it serves as a starting point to explore the realm of frequency-dependent selection. ESS was firstly introduced in a game-theoretical context [12]: A strategy is said to be an ESS if it cannot be invaded by any other strategy when established. ESS can be thought to be the fixed point of evolution: it stops when an ESS becomes established. In [4] Hastings considered the evolution of unconditional dispersal in temporally constant but spatially variable environments.

2010 Mathematics Subject Classification. Primary: 37X75; Secondary: 92D40.

Key words and phrases. Evolution of dispersal, patch model, advective environment, evolutionarily stable strategy.

Jing-jing Xiang is partially supported by the Research Foundation of Education Bureau of Shaanxi Province (15JK1433), “The mathematical modeling and analysis of disease spreading in media”. Yihao Fang is partially supported by the National Natural Science Foundation of China (11571364).

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He showed that between two phenotypes with identical population dynamics but different dispersal rates, the slower dispersal rate is always selected, which suggests that zero diffusion rate is an ESS for the evolution of dispersal in such scenario. However, the dispersals of organisms often depend upon environmental conditions and are thus conditional: e.g., they sometimes disperse in specific directions, for instance in advective environments such as river, water columns or veins [13].

Recently there has been increasing interest in modeling and understanding the spatial population dynamics in advective environments, i.e. environments where individuals are exposed to unidirectional flow [9, 10, 14, 15]. Lou and Lutscher [6] applied reaction-diffusion equations to analyze the evolution of dispersal in open advective environments. They showed that larger dispersal rates will evolve in a homogeneous (i.e. constant intrinsic growth rate) advective environment with free flow boundary conditions at the downstream end. Moreover, based on numerical results they conjectured that there seemed to be a unique, intermediate dispersal rate in a homogeneous advective environment with zero Dirichlet boundary conditions at the downstream end, which is an ESS. In addition, Lam et al. [5] established sufficient criteria for the existence and multiplicity of ESS in closed, advective and heterogeneous environments subject to zero Dirichlet boundary conditions at the downstream end. Our goal is to show that there is a unique dispersal rate which is evolutionarily stable for two patch models, which will support the conjecture in [6] on the existence and uniqueness of ESS, originally proposed for reaction-diffusion models with zero Dirichlet boundary conditions at the downstream end.

We first propose the following model for a single species:

\[
\begin{align*}
\frac{du_1}{dt} &= d(u_2 - u_1) - qu_1 + u_1(1 - u_1) \\
\frac{du_2}{dt} &= d(u_1 - 2u_2) + qu_1 - qu_2 + u_2(1 - u_2)
\end{align*}
\] (1)

Here \(u_i\) is the population size in patch \(i\), \(i = 1, 2\). \(d\) is the diffusion rate of the population and \(q\) denotes the speed of flow. Both \(d\) and \(q\) are assumed to be positive constants.

To derive (1), we envision that there are four patches at the beginning, with population size \(u_i\) in patch \(i\), \(i = 0, 1, 2, 3\). In particular, the dynamics of \(u_1\) and \(u_2\) are given by, respectively,

\[
\begin{align*}
\frac{du_1}{dt} &= d(u_2 - 2u_1 + u_0) + q(u_0 - u_1) + u_1(1 - u_1) \\
\frac{du_2}{dt} &= d(u_1 - 2u_2 + u_3) + q(u_1 - u_2) + u_2(1 - u_2),
\end{align*}
\] (2)

where we assume that populations in any patch can disperse to neighboring patches with rate \(d\), and the species in patch \(i\) is transported to patch \(i + 1\) by drift with rate \(q\); \(i = 0, 1, 2\). The flux from patch 0 to patch 1 is given by \(d(u_0 - u_1) + qu_0\), which we assume to be zero in this paper, i.e.

\[
u_1 = \frac{d + q}{d} u_0.
\] (3)

Then the first equation of (2) is reduced to the first equation of (1). This implies that the first equation of (1) mimics no-flux boundary conditions at the upstream patch.

For the second equation of (2), if we assume that

\[
u_3 = 0,
\] (4)
then it is reduced to the second equation of (1). This implies that the first equation of (1) mimics zero Dirichlet boundary conditions at the downstream patch. Patches 0 and 3 do not appear in (1) and they are refereed as “ghost” patches in some literature. As it is clear from previous discussions, the roles of patches 0 and 3 are to assign proper boundary conditions for our two patch models. Once \( u_1 \) and \( u_2 \) are determined, \( u_0 \) and \( u_3 \) can be determined by (3) and (4), respectively.

Now we can straightforwardly extend the single species model (1) to the following model for two competing species in two patches:

\[
\begin{align*}
\frac{du_1}{dt} &= d(u_2 - u_1) - qu_1 + u_1(1 - u_1 - v_1), \\
\frac{du_2}{dt} &= d(u_1 - 2u_2) + qu_1 - qu_2 + u_2(1 - u_2 - v_2), \\
\frac{dv_1}{dt} &= D(v_2 - v_1) - qv_1 + v_1(1 - u_1 - v_1), \\
\frac{dv_2}{dt} &= D(v_1 - 2v_2) + qv_1 - qv_2 + v_2(1 - u_2 - v_2).
\end{align*}
\]  

(5)

Here we denote \( u_i \) as the size of the resident population and \( v_i \) is the size of mutant population in patch-i, \( i = 1, 2 \), respectively. \( d \) is the diffusion rate of the resident population and \( D \) is the diffusion rate of the mutant population; \( q \) denotes the speed of flow, which is assumed to be the same for both populations. The competition between two populations is of the Lotka-Volterra type. We assume that the two populations are identical except for their diffusion rate, i.e. \( d \neq D \).

This paper is organized as follows: In Section 2 we study the persistence of a single species in the two-patch model. In Section 3 we study the two species competition model and prove the existence and uniqueness of ESS. Finally in section 4 we discuss briefly the implications of our results to ecology and evolutionary theory and propose some questions for further studies.

2. Persistence of a single species. In this section we consider the single species model

\[
\begin{align*}
\frac{du_1}{dt} &= d(u_2 - u_1) - qu_1 + u_1(1 - u_1), \\
\frac{du_2}{dt} &= d(u_1 - 2u_2) + qu_1 - qu_2 + u_2(1 - u_2), \\
u_1(0) > 0, \quad u_2(0) > 0.
\end{align*}
\]  

(6)

We aim to find necessary and sufficient conditions for the persistence of the single species. For the species to persist, a precise range of diffusion rate \( d \) and speed \( q \) of the flow is determined in the following result:

**Theorem 2.1.** If \( 0 < d < \frac{3 + \sqrt{5}}{2} \), \( 0 \leq q < 1 - d + \sqrt{d} \), then (6) has a unique positive equilibrium which is globally asymptotically stable among all positive initial data; If \( q > 1 - d + \sqrt{d} \), or \( d > \frac{3 + \sqrt{5}}{2} \) then the zero equilibrium is globally asymptotically stable.

**Proof.** Obviously, (6) always has a zero equilibrium. From the theory of monotone dynamical systems [11], (6) has a unique positive equilibrium, which is also globally asymptotically stable, is equivalent to the instability of the zero equilibrium. To determine the linear stability of \((0,0)\), it suffices to consider the Jacobian matrix

\[
H = \begin{pmatrix}
1 - d - q & d \\
\frac{d}{d + q} & 1 - 2d - q
\end{pmatrix}
\]
As the dominant eigenvalue of matrix $H$ can be written as $\lambda = -\frac{3}{2}d - q + 1 + \frac{1}{2}\sqrt{5d^2 + 4dq}$, the condition for the single species to persist is $\lambda > 0$.

Hence $0 < d < \frac{1 + \sqrt{5}}{2}$, $0 < q < 1 - d + \sqrt{d}$.

As a consequence of Lemma 2.1 and direct computations we have

**Corollary 1.** For any $d > 0$, (6) has a positive equilibrium if and only $0 \leq q < 1 - d + \sqrt{d}$. Furthermore, the maximum of $1 - d + \sqrt{d}$ is $\frac{9}{4}$, attained at $d = \frac{1}{4}$.

i) if $0 \leq q < 1$, (6) has a positive equilibrium if and only $0 \leq d < \frac{3 - 2q + \sqrt{5 - 4q}}{2}$;

ii) if $1 \leq q < 5/4$, (6) has a positive equilibrium if and only if $\frac{3 - 2q - \sqrt{5 - 4q}}{2} < d < \frac{3 - 2q + \sqrt{5 - 4q}}{2}$.

From now on we shall denote $(u_1^*, u_2^*)$ the unique positive equilibrium of (6), whenever it exists, and use $(d_{\text{min}}, d_{\text{max}})$ to represent the interval of $d$ in (i) and (ii), i.e.

$$d_{\text{min}} = \begin{cases} 0, & 0 \leq q \leq 1 \\ \frac{3 - 2q - \sqrt{5 - 4q}}{2}, & 1 \leq q < \frac{5}{4} \end{cases}$$

and

$$d_{\text{max}} = \frac{3 - 2q + \sqrt{5 - 4q}}{2}.$$

**Corollary 2.** For $0 \leq q < 1$, $0 = d_{\text{min}} \leq d < d_{\text{max}}$, the Jacobian matrix at $(0,0)$

$$\begin{pmatrix} 1 - d - q & d \\ d + q & 1 - 2d - q \end{pmatrix}$$

has a positive dominant eigenvalue, and the Jacobian matrix at $(u_1^*, u_2^*)$

$$\begin{pmatrix} 1 - d - q - 2u_1^* & d \\ d + q & 1 - 2d - q - 2u_2^* \end{pmatrix}$$

has a negative dominant eigenvalue. For $d = d_{\text{max}}$, both matrices have zero as their dominant eigenvalues.

For $1 \leq q < 5/4$ and $d_{\text{min}} < d < d_{\text{max}}$, the Jacobian matrix at $(0,0)$ has a positive dominant eigenvalue, and the Jacobian matrix at $(u_1^*, u_2^*)$ has a negative dominant eigenvalue. For $d = d_{\text{max}}, d_{\text{min}}$, both matrices have zero as their dominant eigenvalues.

These results have some interesting ecological interpretations. For a species to persist in advective environments, both diffusion rate and speed of flow should be in a proper range. In particular, for small flow speed, the diffusion rate can vary from zero to a positive threshold value. If $q$ falls into some intermediate range, the dispersal rate $d$ has to be between two positive threshold values. And the species will go to extinction if the speed $q$ is too large, irrelevant of the diffusion rate. These results serve as our preparations for finding an ESS.
3. Two competing species. In this section we consider

\[
\begin{align*}
\frac{du_1}{dt} &= d(u_2 - u_1) - q u_1 + u_1(1 - u_1 - v_1) \\
\frac{du_2}{dt} &= d(u_1 - 2u_2) + q u_1 - q u_2 + u_2(1 - u_2 - v_2) \\
\frac{dv_1}{dt} &= D(v_2 - v_1) - qv_1 + v_1(1 - u_1 - v_1) \\
\frac{dv_2}{dt} &= D(v_1 - 2v_2) + qv_1 - qv_2 + v_2(1 - u_2 - v_2) \\
\end{align*}
\]

(7)

Recall that (6) has at most one positive equilibrium, denoted by \((u_1^*, u_2^*)\). When \((u_1^*, u_2^*)\) exists, (7) has a semi-trivial steady state \((u_1^*, u_2^*, 0, 0)\). \(d^* > 0\) is an ESS for \(d = d^*\) and \(D \neq d^*\), the semi-trivial steady state \((u_1^*, u_2^*, 0, 0)\) is always stable. The main goal of this section is to establish the existence and uniqueness of such \(d^*\).

We first derive a necessary condition for the existence of the ESS in the following result:

**Theorem 3.1.** If \(d^* > 0\) is an ESS, then \(d^*\) be the fixed of \(f(d) := -d - 2q - 2u_1^* - u_2^* + 3\), \(d_{\text{min}} \leq d \leq d_{\text{max}}\).

**Proof.** As \((u_1^*, u_2^*)\) is the unique positive equilibrium of (6), \((u_1^*, u_2^*)\) satisfies

\[
\begin{pmatrix}
1 - u_1^* - d - q \\
d + q \\
1 - u_2^* - 2d - q
\end{pmatrix}
\begin{pmatrix}
u_1^* \\
u_2^*
\end{pmatrix}
= \begin{pmatrix}0 \\
0
\end{pmatrix}.
\]

Hence,

\[
\begin{vmatrix}
1 - u_1^* - d - q \\
d + q \\
1 - u_2^* - 2d - q
\end{vmatrix}
= 0,
\]

which yields the following relation of \(d, q, u_1^*, u_2^*:\)

\[
(q + d)^2 + u_1^* u_2^* + (2d + q - 1)u_1^* + (d + q - 1)u_2^* - 3d - 2q + 1 = 0. \tag{8}
\]

Back to two species model (7), consider the linear stability of \((u_1^*, u_2^*, 0, 0)\), the corresponding Jacobian matrix is given by

\[
J = \begin{pmatrix}
-d - q + (1 - 2u_1^*) & d & -u_1^* & 0 \\
-d - q + (1 - 2u_2^*) & 0 & 0 & -u_2^* \\
0 & -D - q + 1 - u_1^* & D + q & -u_2^* \\
0 & 0 & -D - q + (1 - u_2^*) & D + q
\end{pmatrix}
\]

A necessary condition of the dominant eigenvalue being equal to zero is that the determinant of the matrix is zero. Observe that \(|J| = |J_1||J_2|\), where

\[
J_1 = \begin{pmatrix}
-d - q + 1 - 2u_1^* & d \\
-d - q + 1 - 2u_2^*
\end{pmatrix}
\]

and

\[
J_2 = \begin{pmatrix}
-D - q + 1 - u_1^* & D \\
-D - q + 1 - u_2^*
\end{pmatrix}
\]

From Corollary 2.3 we know that the eigenvalues of \(J_1\) are both negative, hence \(|J| = 0\) is equivalent to \(|J_2| = 0\), where

\[
|J_2| = (q + D)^2 + u_1^* u_2^* + (2D + q - 1)u_1^* + (D + q - 1)u_2^* - 3D - 2q + 1 = 0. \tag{9}
\]

Subtract (8) from (9), we have

\[
(D - d)(D + d + 2q + 2u_1^* + u_2^* - 3) = 0, \tag{10}
\]

|J| = 0 is equivalent to |J_2| = 0, where

|J_2| = (q + D)^2 + u_1^* u_2^* + (2D + q - 1)u_1^* + (D + q - 1)u_2^* - 3D - 2q + 1 = 0. (9)

Subtract (8) from (9), we have

\[
(D - d)(D + d + 2q + 2u_1^* + u_2^* - 3) = 0, \tag{10}
\]
which implies that
\[
D - d = 0
\] (11)
or
\[
D + d + 2q + 2u_1^* + u_2^* - 3 = 0. \tag{12}
\]
Note that both \((u_1^*, u_2^*)\) are functions of \((d, q)\). Fix \(q\), \(D = -d - 2q - 2u_1^* - u_2^* + 3\) can be written as \(D = f(d)\) which is a curve in \(d - D\) plane. By the definition of \(d^*\), we see that \(d^*\) is an intersection of \(D = d\) and the curve \(D = f(d)\).

For the rest of this paper we define
\[
f(d) := -d - 2q - 2u_1^* - u_2^* + 3, \quad d_{\text{min}} \leq d \leq d_{\text{max}}.
\]
Note that for \(0 \leq q < 5/4\), \(f(d)\) is well defined.

Next we prove the existence and uniqueness of \(d^*\).

**Theorem 3.2.** There exists at least one \(d^* > 0\) such that line \(D = d\) and curve \(D = -d - 2q - 2u_1^* - u_2^* + 3\) intersect at \((d^*, d^*)\) for every \(0 < q < \frac{5}{4}\).

**Proof.** Define \(g(d) = D - d = -2d - 2q - 2u_1^* - u_2^* + 3\). It suffices to find \(d^* > 0\) such that \(g(d^*) = 0\). From Theorem 2.1, we restrict the domain of \(q\) to \(0 \leq q < 5/4\). For \(0 \leq q < 1\), we have \(0 \leq d < d_{\text{max}}\). Let \(d = 0\), we have \(u_1^* = 1 - q\) and
\[
u_2^* = \frac{1}{2} \left[1 - q + \sqrt{(1 - q)^2 + 4q(1 - q)}\right].
\]
Hence \(g(0) = 1 - u_2^* \geq 0\) (equality holds only when \(q = 0\)). Let \(d = d_{\text{max}}\), we have \(u_1^* = u_2^* = 0\) and \(g(d_{\text{max}}) = -\sqrt{5 - 4q} < 0\). Using the intermediate value theorem, we get the existence of \(d^*\) such that \(g(d^*) = 0\).

For \(1 \leq q < 5/4\), we have \(d_{\text{min}} < d < d_{\text{max}}\). Similarly, \(g(d_{\text{min}}) = \sqrt{5 - 4q} > 0\) and \(g(d_{\text{max}}) = -\sqrt{5 - 4q} < 0\). Using the intermediate value theorem again, we obtain the existence of \(d^* > 0\) such that \(g(d^*) = 0\).

**Theorem 3.3.** There exists a unique \(d^* > 0\) such that line \(D = d\) and curve \(D = f(d)\) intersect at \((d^*, d^*)\) for every \(0 < q < \frac{5}{4}\).

**Proof.** From Theorem 3.1, for every fixed \(0 < q < \frac{5}{4}\), \(d^*\) satisfies
\[
\begin{aligned}
&d^*(u_2^* - u_1^*) - qu_1^* + u_1^*(1 - u_1^*) = 0 \\
d^*(u_1^* - 2u_2^*) + qu_1^* - qu_2^* + u_2^*(1 - u_2^*) = 0 \\
&-2d^* - 2q - 2u_1^* - u_2^* + 3 = 0.
\end{aligned}
\]
(13)

We substitute \(u_2^*\) by \(u_2^* = -2d^* - 2q - 2u_1^* + 3\) into the first equation to get
\[
u_1^* = \frac{1 - 3d^* - q + \sqrt{(q - 1)^2 + d^*(d^* + 6 - 2q)}}{2},
\]
and thus
\[
u_2^* = 2 + d^* - q - \sqrt{(q - 1)^2 + d^*(d^* + 6 - 2q)}.
\]
Substitute these expressions into the second equation, we have
\[
(9d^* - q + 6)\sqrt{d^*2 + 6d^* + 1 - 2d^*q - 2q + q^2 - (11d^*2 + 25d^* - 6d^*q + q^2 - 7q + 6)} = 0,
\]
which can be simplified as
\[
d^*[10(d^*)^3 + 12(d^*)^2q - 15(d^*)q^2 + 2q^3 - 11(d^*)^2 + 11(d^*)q - 10q^2 - 2d^* - 11q - 6] = 0
\]
Dropping $d^*$ in the above equation, we obtain the following cubic equation for $d^*$:

$$10(d^*)^3 + 12(d^*)^2q - 15(d^*)q^2 + 11(d^*)^2 - 10q^2 - 2d^* - 11q - 6 = 0,$$

and its discrimination is given by

$$\Delta = -233928q^6 - 726408q^5 + 2589474q^3 + 1887753q^2 + 627120q + 456300.$$

Note that

$$-233928q^6 - 726408q^5 + 2589474q^3 > -233928(5/4)^3 - 726408(5/4)^2 + 2589474 > 0$$

in the domain $0 \leq q \leq 5/4$, as

$$-233928q^3 - 726408q^2 + 2589474 = q^3(-233928q^3 - 726408q^2 + 2589474) \geq 0$$

in the domain $0 \leq q \leq 5/4$. Hence, $\Delta > 0$ always holds. Therefore, the cubic equation has only one real root and two complex conjugate roots. The uniqueness of $d^*$ is proved.

To prove that $d^*$ is an ESS, we need a few preliminary results for later analysis.

**Lemma 3.4.** For any matrix $A$ of the form

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

with $b, c > 0$, if we reduce the value on diagonal, like $B$

$$\begin{pmatrix} a - u & b \\ c & d - v \end{pmatrix}$$

the dominant eigenvalue $\lambda$ will decrease if $u, v > 0$.

*Proof.* The dominant eigenvalue of matrix $B$ is given by

$$\lambda = \frac{1}{2} \left[ a + d - u - v + \sqrt{(a - u - d + v)^2 + 4bc} \right].$$

It is easy to check $\partial \lambda / \partial u < 0$ and $\partial \lambda / \partial v < 0$ when $b > 0, c > 0$.

**Lemma 3.5.** Let $A$ be a $2 \times 2$ matrix and its off-diagonal elements are non-negative. If the eigenvalues of $A$ are all zero, then $A$ must be one of the following forms:

$$\begin{pmatrix} 0 & b \\ 0 & 0 \end{pmatrix}, \quad \begin{pmatrix} 0 & 0 \\ c & 0 \end{pmatrix}.$$

*Proof.* If the eigenvalues of $A$ are all zero, the trace and determinant of $A$ must be zero. Since the off-diagonal elements are non-negative, both diagonal elements must be 0 and at least one of the off-diagonal elements is zero.

**Lemma 3.6.** Set $f(d) := -d - 2q - 2u_1^* - u_2^* + 3$, where $d \in [0, d_{max}]$. Suppose that $0 < q < 1$. Then the followings hold:

i) $0 \leq f(d) < d_{max}$ for $0 \leq d \leq d_{max}$;

ii) The curve $D = f(d)$ is tangent to the line $D = 0$ exactly at $(d, D) = (q, 0)$;

iii) $\lambda_1 = 0$ if and only if $D = d$ with $d \in [0, d_{max}]$ and $D = f(d)$ for $d \in [0, q]$.
Proof. From Theorem 2.1, for any fixed \( q > 0 \), the domain of \( d \) for the persistence of a single species is given by \((d_{\min}, d_{\max})\), with \( d_{\min} = 0 \). Similarly, \((d_{\min}, d_{\max})\) is the domain of \( D \). Hence \([0, d_{\max}] \times [0, d_{\max}]\) is the domain under consideration.

Firstly, we prove that \( 0 \leq f(d) < d_{\max} \) for any \( 0 \leq d \leq d_{\max} \).

If \( D = f(d) = 0 \), we have

\[
|J_2| = \begin{vmatrix} q + 1 - u_1^* & 0 \\ q & -q + 1 - u_2^* \end{vmatrix} = 0.
\]

Hence, \((q + 1 - u_1^*)(q + 1 - u_2^*) = 0\), i.e. either \( u_1^* = 1 - q \) or \( u_2^* = 1 - q \). If \( u_1^* = 1 - q \), from the equation of \( u_1^* \) we have \( u_2^* = 1 - q \). Hence, \( u_2^* = 1 - q \) always holds.

If \( u_2^* = 1 - q \), from the equation \( f(d) = 0 \) we obtain \( u_1^* = (2 - d - q)/2 \) and \( u_2^* = 1 - q \) into the equation of \( u_2^* \), i.e.

\[
d(u_1^* - 2u_2^*) + qu_1^* - qu_2^* + u_2^*(1 - u_2^*) = 0.
\]

After simplifications we obtain

\[
d^2 + q^2 - 2dq + 2d - 2q = 0,
\]

from which it follows that \( d = q \). Hence \( f(d) \geq 0 \) for any \( 0 \leq d \leq d_{\max} \). Moreover, the curve \( D = f(d) \) is tangent to the boundary \( D = 0 \) only at \((d, D) = (q, 0)\).

Similarly, if \( D = f(d) = d_{\max} \),

\[
|J_2| = \begin{vmatrix} -d_{\max} - q + 1 - u_1^* & d_{\max} \\ d_{\max} + q & -2d_{\max} - q + 1 - u_2^* \end{vmatrix} = 0.
\]

From Theorem 2.1,

\[
\begin{vmatrix} -d_{\max} - q + 1 - u_1^* & d_{\max} \\ d_{\max} + q & -2d_{\max} - q + 1 - u_2^* \end{vmatrix} = 0.
\]

Subtracting the above two equations we have

\[
-u_1^*(1 - 2d_{\max} - q) - u_2^*(1 - d_{\max} - q) + u_1^*u_2^* = 0.
\]

Since \( 1 - d_{\max} - q = -\frac{1 + \sqrt{5 - 4q}}{2} < 0 \), the only possibility is \( u_1^* = u_2^* = 0 \), which is a contradiction. This contradiction shows that \( f(d) < d_{\max} \) for \( 0 \leq d \leq d_{\max} \).

Secondly, we characterize the set of \((d, D)\) such that \( \lambda_1 = 0 \). Let \( \lambda_1, \lambda_2 \) be eigenvalues of matrix \( J_2 \) with \( \lambda_1 \geq \lambda_2 \). By calculation,

\[
\lambda_1 = -\frac{3}{2}D - q - u_1^*/2 - u_2^*/2 + 1 + \frac{1}{2}\sqrt{5D^2 + 4Dq - 2Du_1^* + 2Du_2^* + u_1^{*2} - 2u_1^*u_2^* + u_2^{*2}},
\]

\[
\lambda_2 = -\frac{3}{2}D - q - u_1^*/2 - u_2^*/2 + 1 - \frac{1}{2}\sqrt{5D^2 + 4Dq - 2Du_1^* + 2Du_2^* + u_1^{*2} - 2u_1^*u_2^* + u_2^{*2}}.
\]

Hence \( \lambda_1, \lambda_2 \) are both continuous in \( d, D \).

Applying Lemma 3.5 to \( J_2 \), where

\[
J_2 = \begin{pmatrix} -D - q + 1 - u_1^* & D \\ D + q & -2D - q + (1 - u_2^*) \end{pmatrix},
\]

we see that \( \lambda_1 = \lambda_2 = 0 \) hold if and only if \( D = 0 \) and \( u_1^* = u_2^* = 1 - q \), i.e. \( d = q \). Hence \( \lambda_1 = \lambda_2 = 0 \) only holds at \((d, D) = (q, 0)\) for \((d, D) \in [0, d_{\max}] \times [0, d_{\max}]\).

By direct calculation we have \( 0 = \lambda_1 > \lambda_2 \) at \((d, D) = (0, f(0))\) and \( \lambda_1 > \lambda_2 = 0 \) at \((d, D) = (d_{\max}, f(d_{\max}))\). Hence, \( \lambda_1 = 0 \) holds if and only if \( D = f(d) \) for \( d \in [0, q] \) and \( D = d \) for \( d \in [0, d_{\max}] \).

\( \square \)
Let \( P \) be the point \((0, f(0))\), \( Q \) be the point \((q, 0)\), and \( R \) be the point \((d_{\max}, f(d_{\max}))\), and denote the curve \( D = f(d) \) connecting \( P \) and \( Q \) by \( PQ \), and the curve \( D = f(d) \) connecting \( Q \) and \( R \) by \( QR \). The curve \( PQ \) is given by \( D = f(d) \) with \( d \in [0, q] \), and the curve \( QR \) is given by \( D = f(d) \) with \( d \in [q, d_{\max}] \). However, \( \lambda_1 > \lambda_2 = 0 \) holds on the curve \( QR \). The curve \( PQ \) and the line \( D = d \) are precisely where the dominant eigenvalue \( \lambda_1 \) vanishes, and \( \lambda_1 > 0 \) or \( \lambda_1 < 0 \) hold in other areas. An illustration is given in Fig. 1.

**Figure 1.** Illustration of Lemma 3.6 for \( 0 \leq q < 1 \)

**Lemma 3.7.** Set \( f(d) := -d - 2q - 2u_1^* - u_2^* + 3 \). If \( 1 \leq q < 5/4 \), then the followings hold:

i) \( d_{\min} \leq f(d) \leq d_{\max} \) for \( d_{\min} \leq d \leq d_{\max} \);

ii) \( f(d) = d_{\max} \) if and only if \( d = d_{\min} \), and \( f(d) = d_{\min} \) if and only if \( d = d_{\max} \);

iii) \( \lambda_1 = 0 \) if and only if \( D = d \) or \( D = f(d) \) for \( d_{\min} \leq d \leq d_{\max} \).

**Proof.** From Theorem 2.1 we see that if \( q \in [1, 5/4] \), then the domain for the persistence of a single species is given by \((d_{\min}, d_{\max})\), where \( d_{\min} > 0 \). Hence, \([d_{\min}, d_{\max}] \times [d_{\min}, d_{\max}]\) is the domain under consideration.

One can check that for \( 1 \leq q < 5/4 \), \( f(d_{\min}) = d_{\max} \) and \( f(d_{\max}) = d_{\min} \) hold. Furthermore, using the same method as in Lemma 3.6 we can show that \( d_{\min} \leq f(d) \leq d_{\max} \) if and only if \( d = d_{\min} \), and \( f(d) = d_{\min} \) if and only if \( d = d_{\max} \).

If \( q \geq 1 \), we have \(-D - q + 1 - u_2^* < 0 \) and \(-2D - q + 1 - u_2^* < 0 \). Hence, \( \lambda_1 = \lambda_2 = 0 \) can not hold in \([d_{\min}, d_{\max}] \times [d_{\min}, d_{\max}]\). By calculation, \( \lambda_1 = 0 \) at \((d, D) = (d_{\min}, d_{\max}) \times (d_{\max}, d_{\min})\), respectively. Hence \( \lambda_1 = 0 \) on the curve \( D = f(d) \) for \( d \in [d_{\min}, d_{\max}] \). Hence, \( \lambda_1 = 0 \) if and only \( D = f(d) \) and \( D = d \), for \( d \in [d_{\min}, d_{\max}] \). \( \square \)

Let \( M \) be the point \((d_{\min}, d_{\max})\) and \( N \) be the point \((d_{\max}, d_{\min})\), and denote the curve \( D = f(d) \) connecting \( M \) and \( N \) by \( MN \). The curve \( MN \) and the line \( D = d \) are precisely where the dominant eigenvalue \( \lambda_1 \) vanishes, and \( \lambda_1 > 0 \) or \( \lambda_1 < 0 \) hold in other areas. An illustration is given in Figure 2.

Finally, we prove that \( d^* \) is an ESS in both cases \( 0 < q < 1 \) and \( 1 \leq q < 5/4 \).

**Theorem 3.8.** For \( 0 < q < 1 \), \((u_1^*, u_2^*, 0, 0)\) is asymptotically stable for \( d = d^* \) and \( D \neq d^* \). Hence, \( d^* \) is an ESS.
Proof. By Lemma 3.6 we see that \( \lambda_1 > 0 \) or \( \lambda_1 < 0 \) hold in the domain \([0, d_{\text{max}}] \times [0, d_{\text{max}}] \) except \( \overline{PQ} \) and \( D = d \). The whole domain is divided into four regions by \( D = d \) and \( \overline{PQ} \). Now we determine the sign of \( \lambda_1 \) in all regions, which can be derived from the sign of \( \lambda_1 \) on boundaries of \([0, d_{\text{max}}] \times [0, d_{\text{max}}] \).

By direct calculations we have

\[
\frac{\partial \lambda_1}{\partial D} = -\frac{3}{2} + \frac{1}{2} \frac{5D + 2q - u_1^* + u_2^*}{\sqrt{5D^2 + 4Dq - 2D u_1^* + 2D u_2^* + (u_2^* - u_1^*)^2}}.
\]

Let \( O \) be the origin \((0,0)\), \( \lambda_1 = 0 \) holds at \( O \). At \( O(0,0) \), \( u_1^* \) and \( u_2^* \) are given by

\[
\begin{align*}
u_1^* &= 1 - q, \quad u_2^* = \frac{1}{2} \left[ 1 - q + \sqrt{(1-q)^2 + 4q(1-q)} \right].
\end{align*}
\]

After some calculations we find that \( \frac{\partial \lambda_1}{\partial D} > 0 \) at \((d,D) = (0,0)\). Thus \( \lambda_1 > 0 \) holds on \( \overline{OF} \) (expect two endpoints \( O \) and \( P \)). By the continuity of \( \lambda_1 \), \( \lambda_1 > 0 \) holds on region I of Fig. 3.

Since \( \frac{\partial \lambda_1}{\partial D} = - \frac{\partial \lambda_1}{\partial q} < 0 \) holds at \((d,D) = (0,0)\), we see that \( \lambda_1 < 0 \) holds on \( \overline{OQ} \) (expect two endpoints \( O \) and \( Q \)). Therefore, \( \lambda_1 < 0 \) holds on region II of Fig. 3.

Note that \( \lambda_1 = 0 \) holds at \((d_{\text{max}}, d_{\text{max}})\). On the line \( d = d_{\text{max}} \) we have \( u_1^* = u_2^* = 0 \), so that species \( v \) can always invade. Hence, \( \lambda_1 > 0 \) on the line \( d = d_{\text{max}} \) except \((d_{\text{max}}, d_{\text{max}})\). By the continuity of \( \lambda_1 \), \( \lambda_1 > 0 \) holds on region IV. Similarly at the line \( D = d_{\text{max}} \), species \( v \) always goes extinction. Hence \( \lambda_1 < 0 \) holds on the line \( D = d_{\text{max}} \) (expect two endpoints). Again by the continuity of \( \lambda_1 \), we see that \( \lambda_1 < 0 \) holds on region III.

Furthermore, because of the uniqueness of \( d^* \) and \( f(0) > 0 \), the angle of \( \overline{PQ} \) intersecting \( D = d \) at \((d^*, d^*)\) is no greater than 90 degrees. Hence we get Fig. 3.

Plotting a vertical line through \((d^*, d^*)\), from the above analysis we find that \( \lambda_1 < 0 \) when \( d = d^* \) and \( D \neq d^* \). This proves that \( d^* \) is an ESS when \( 0 < q < 1 \).

**Theorem 3.9.** For \( 1 \leq q < 5/4 \), \((u_1^*, u_2^*, 0,0)\) is stable for \( d = ds, D \neq d^* \). In particular, \( d^* \) is an ESS.

Proof. By Lemma 3.7 we see that \( \lambda_1 > 0 \) or \( \lambda_1 < 0 \) hold in the whole domain except \( MN \) and \( D = d \). The domain is divided into four regions by \( D = d \) and \( MN \). Now we determine the sign of \( \lambda_1 \) in all regions.
Since $\lambda_1 = \lambda_2 = 0$ does not hold in the domain, $\lambda_1 = 0, \lambda_2 < 0$ holds on $\overline{MN}$ and $D = d$. Because of the continuity of $\lambda_2$, $\lambda_2 < 0$ holds for all $(d, D)$. Since $|J_2| = \lambda_1 \lambda_2$, $\text{sign}(\lambda_1) = -\text{sign}(|J_2|)$ holds for the whole domain.

In region I we have $D > d, D < f(d)$. Since $|J_2| = (D - d)(D - f(d))$, we see that $|J_2| < 0$ in region I, i.e. $\lambda_1 > 0$ holds in region I. Similarly we can determine the sign of $\lambda_1$ in other regions.

Furthermore, the angle of $\overline{MN}$ intersecting $D = d$ at $(d^*, d^*)$ is no greater than 90 degrees. This is illustrated in Fig. 4.

From the above analysis we see that $\lambda_1 < 0$ for $d = d^*$ and $D \neq d^*$. Hence, $d^*$ is an ESS for $1 \leq q < 5/4$.

Discussion. We introduce some two-patch models to mimic the unidirectional movement of organisms in continuous, advective environments, where populations can move between two patches, with patch 1 as the upper stream patch and patch 2 as the downstream patch. Species disperse between two patches with the same rate, and species in patch 1 is transported to patch 2 by drift, but not vice versa. We also mimic no-flux boundary conditions at the upstream and zero Dirichlet boundary condition at the downstream. The criteria for the persistence of a single species is
established. For two competing species model we show that there is an intermediate dispersal rate which is evolutionarily stable.

For two-patch models in homogeneous environments, we conjecture that the unique ESS $d^*$ is also convergent stable, namely, if $D < d \leq d^*$ or $d^* \leq d < D$, then $(u_1^*, u_2^*, 0, 0)$ is globally asymptotically stable. It will also be of interest to consider general boundary conditions at the downstream patch and different drift rates for two populations, connecting with previous results for reaction-diffusion-advection models in homogeneous advective environments [7, 8, 16, 17]. It might be mathematically challenging to extend current results to N-patch models in homogeneous environments for $N \geq 3$, with zero Dirichlet boundary condition at the downstream patch. We expect that for N-patch models, there exists some intermediate dispersal rate which is evolutionarily stable and convergent stable.

Acknowledgments. Jing-jing Xiang is partially supported by the Research Foundation of Education Bureau of Shaanxi Province (15JK1433) and the National Natural Science Foundation of China (11601412). Yihao Fang is partially supported by the National Natural Science Foundation of China (11571364). The authors thank Yuan Lou, King-Yeung Lam, R.S. Cantrell and the anonymous referee for their generous help.

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Received December 2017; revised March 2018.

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