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On several conjectures from evolution of dispersal

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We address several conjectures raised in Cantrell *et al.* [*Evolution of dispersal and ideal free distribution*, Math. Biosci. Eng. 7 (2010), pp. 17–36 [9]] concerning the dynamics of a diffusion–advection–competition model for two competing species. A conditional dispersal strategy, which results in the ideal free distribution of a single population at equilibrium, was found in Cantrell *et al.* [9]. It was shown in [9] that this special dispersal strategy is a local evolutionarily stable strategy (ESS) when the random diffusion rates of the two species are equal, and here we show that it is a global ESS for arbitrary random diffusion rates. The conditions in [9] for the coexistence of two species are substantially improved. Finally, we show that this special dispersal strategy is not globally convergent stable for certain resource functions, in contrast with the result from [9], which roughly says that this dispersal strategy is globally convergent stable for any monotone resource function.

Keywords: evolution of dispersal; ideal free distribution; evolutionarily stable strategy; reaction–diffusion–advection

AMS Classification: 35K57; 92D25

1. Introduction

Within the broad scope of theoretical ecology, the notion of dispersal is indispensable in determining the distribution, dynamics, and persistence of a species within its habitat. More specifically, one can ask how the spread and movement of a population evolves over time. Recent studies have identified several mechanisms which play significant roles in this evolution [18], one of which is temporal and spatial variability in the environment. Hastings [23] focused on spatial variation in the environment, utilizing a reaction–diffusion model to study its effect on the evolution of passive dispersal (see also [19,30]). Following Hastings' work, Belgacem and Cosner [1] added an advection term to the well-known logistic reaction–diffusion model, realizing that in a spatially variable environment, a population may move towards regions that are more favourable. The endeavour to understand the evolution of this combination of passive and biased dispersal, via a reaction–diffusion–advection model in a spatially inhomogeneous environment, prompted the work of Cosner and Lou [13], Cantrell *et al.* [4,6,8,9], Chen and Lou [10], Chen *et al.* [11], Hambrook and Lou [22], Bezuglyy and Lou [2], Lam [34,35], and Lam and Ni [36].

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Our paper emerges from the above context with the aim of addressing several conjectures raised in Cantrell *et al.* [9] concerning the dynamics of the two species diffusion–advection–competition model

$$u_t = \mu\nabla \cdot [\nabla u - u\nabla P(x)] + u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$

$$v_t = \nu\nabla \cdot [\nabla v - v\nabla Q(x)] + v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - u\nabla P] \cdot n = [\nabla v - v\nabla Q] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty), \tag{1}$$

where $u(x, t)$ and $v(x, t)$ represent the densities of two competing species, μ and ν are their random diffusion coefficients, $P, Q, m \in C^2(\bar{\Omega})$, and $m(x)$ is the intrinsic growth rate of both species. Throughout this paper we will always assume that $m > 0$ in $\bar{\Omega}$, where Ω is a bounded domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$, n is the outward unit normal vector on $\partial\Omega$, and the boundary condition in Equation (1) says that there is no flux across the boundary.

To motivate our discussion, we first consider the dynamics of Equation (1) when $v(x, t) \equiv 0$, i.e. only species u is present. For such a situation, Equation (1) is reduced to the single species reaction–diffusion–advection model

$$u_t = \mu\nabla \cdot [\nabla u - u\nabla P] + u(m - u) \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - u\nabla P] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty). \tag{2}$$

It is known that if $m > 0$ in Ω, then Equation (2) has a unique positive steady state, denoted by u^*, which is globally asymptotically stable among non-negative non-trivial initial data, and u^* solves

$$\mu\nabla \cdot [\nabla u^* - u^*\nabla P] + u^*(m - u^*) = 0 \quad \text{in } \Omega,$$

$$[\nabla u^* - u^*\nabla P] \cdot n = 0 \quad \text{on } \partial\Omega. \tag{3}$$

Integrating the equation of u^* and applying the divergence theorem, we have

$$\int_\Omega u^*(m - u^*)\,dx = 0.$$

Since $u^* > 0$ in Ω, either $m - u^*$ changes sign in Ω or $m - u^* \equiv 0$ in Ω. If we regard $m - u^*$ as the fitness of the species u at equilibrium, $m - u^*$ changes sign means that there is some mismatch between the species density and its resource distribution. On the other hand, $m - u^* \equiv 0$ means that the population matches the environmental quality perfectly and the fitness of the population is the same everywhere in the habitat. Furthermore, if $m - u^* \equiv 0$, then $\nabla \cdot [\nabla u^* - u^*\nabla P] \equiv 0$ in Ω, i.e. zero net movement of individuals. Hence, if the scenario $m - u^* \equiv 0$ occurs, then the species' equilibrium density with dispersal present is the same as that with dispersal absent. Such rather peculiar spatial distribution of species is usually referred to as the ideal free distribution [5].

A natural question is: for what kind of functions $P(x)$ can it happen that $m - u^* \equiv 0$? It was found [9] that $m - u^* \equiv 0$ if and only if $P(x) - \ln m(x)$ is equal to some constant. Since $\nabla(P + C) = \nabla P$ for any constant C, we may simply restrict our discussion to the case $P(x) = \ln m(x)$ instead of $P(x) = \ln m(x) + C$. It is known that population models with nonlinear diffusion can support or approximate ideal free dispersal strategies (see [7,12]). It is quite interesting that even biased movement of a species along its resource gradient alone can also produce ideal free distributions of populations at equilibrium.

A steady state $(\tilde{u}, \tilde{v})$ of Equation (1) with both components being positive is called a coexistence state; $(\tilde{u}, \tilde{v})$ is a semi-trivial steady state if one component is positive and the other is the zero function. It is known that if $m > 0$, Equation (1) has exactly two semi-trivial steady states, denoted as $(u^*, 0)$ and $(0, v^*)$, where u^* is the unique positive solution of Equation (3) and v^* can be defined similarly.

The first result of Cantrell *et al.* [9] can be stated as follows.

THEOREM 1.1 [9, Theorem 1]   *Suppose that $\mu = \nu$, $m \in C^2(\bar{\Omega})$, and $m > 0$ in $\bar{\Omega}$.*

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

An important idea in adaptive dynamics [15–17,20] is the idea of evolutionarily stable strategies (ESS). A strategy is said to be evolutionarily stable if a population using it cannot be invaded by any small population using a different strategy. Part (a) of Theorem 1.1 shows that $P = \ln m$ is a local ESS and part (b) shows that no other strategy can be a local ESS. It was conjectured in [9] that $P = \ln m$ is a global ESS, i.e. part (a) of Theorem 1.1 holds for any $\epsilon \neq 0$. Our first result is to answer this conjecture positively.

THEOREM 1.2   *Given any μ, $\nu > 0$. Suppose that $P(x) = \ln m$, and $Q(x) - \ln m$ is not a constant function. Then, the semi-trivial steady state $(u^*, 0)$ is globally asymptotically stable.*

Remark 1.1   This theorem proves the conjecture that $P(x) = \ln m$ is a global ESS. In fact, we also allow μ, ν to be arbitrary here. The condition on $Q(x)$ is also necessary: if $Q(m) - \ln m$ is also a constant function, Equation (1) has a continuum family of positive steady states, all of them are of the form $(sm(x), (1 - s)m(x))$, where $s \in (0, 1)$.

Remark 1.2   Note that $u^* \equiv m$ when $P(x) = \ln m(x)$. It is easy to see that the semi-trivial steady state $(m, 0)$ is neutrally stable. Thus, even the local asymptotic stability of $(m, 0)$ is non-trivial and is of independent interest.

The second main result in [9] concerns the coexistence of two competing species and it can be stated as the following.

THEOREM 1.3 [9, Theorem 2, part (b)]   *Suppose that $\mu = \nu$, $P(x) = \ln m + \alpha R$, $Q(x) = \ln m + \beta R$, $m > 0$. We further assume that $\Omega = (0, 1)$ and $R_x \neq 0$ in $[0, 1]$. If $\alpha \beta < 0$, then both $(u^*, 0)$ and $(0, v^*)$ are unstable, and system (1) has at least one stable positive steady state.*

Theorem 1.3 implies that the two species can coexist provided that their dispersal strategies lie on two 'opposite sides' of the optimal strategy $\ln m$. Our second result is to sharpen Theorem 1.3 as follows.

THEOREM 1.4   *Suppose that $P(x) = \ln m + \alpha R$, $Q(x) = \ln m + \beta R$, and $R \in C^2(\bar{\Omega})$ is non-constant. If $\alpha \beta < 0$, then both $(u^*, 0)$ and $(0, v^*)$ are unstable, and system (1) has at least one stable positive steady state.*

The third main result of [9] concerns whether $\ln m$ is a convergent stable strategy (CSS) of system (1). A strategy is convergent stable if selection favours strategies that are closer to it over strategies that are further away. More precisely, the following result is established in [9].

THEOREM 1.5 [9, Theorem 2, part (a)]   *Suppose that $\mu = \nu$, $P(x) = \ln m + \alpha R$, $Q(x) = \ln m + \beta R$, $\Omega = (0, 1)$, and $R_x \neq 0$ in $[0, 1]$. If $\alpha < \beta < 0$ or $0 < \beta < \alpha$, then $(u^*, 0)$ is unstable and $(0, v^*)$ is stable. Moreover, given any $\eta > 0$, there exists $\kappa > 0$ such that if either*

(i) $\alpha, \beta \in [-\eta, 0]$ *and* $0 < \beta - \alpha < \kappa$ *or* (ii) $\alpha, \beta \in [0, \eta]$ *and* $-\kappa < \beta - \alpha < 0$, *then* $(0, v^*)$ *is globally asymptotically stable.*

It is natural to inquire whether the assumption R_x non-vanishing in Ω is essential for Theorem 1.5 to hold. A little surprisingly, it turns out to be possible to construct non-monotone functions $R(x)$ such that for $P(x) = \ln m + \alpha R(x)$ and $Q(x) = \ln m + \beta R(x)$, both $(u^*, 0)$ and $(0, v^*)$ are unstable for suitably chosen positive constants α, β, μ, ν. To this end, we first give a description of such non-monotone functions $R(x)$. Given any function $m > 0$ in $\bar{\Omega}$, we assume that $R(x)$ satisfies the following.

(A) There exists some $x_0 \in \bar{\Omega}$ such that x_0 is a local maximum of $R(x)$ and

$$R(x_0) < \frac{\int_\Omega m^2 R}{\int_\Omega m^2}.$$

It is not difficult to see that for any positive function m (even if m is a positive constant), there exist functions $R \in C^2(\bar{\Omega})$ which satisfy assumption (A). If we perturb R slightly, we may further assume that all critical points of R are non-degenerate. Clearly, any function $R(x)$ which satisfies assumption (A) will have at least two local maxima and thus cannot be monotone. To see this, let x^* be any global maximum point of $R(x)$, then we have

$$R(x_0) < \frac{\int_\Omega m^2 R}{\int_\Omega m^2} < R(x^*) = \max_{\bar{\Omega}} R.$$

In other words, for any local maximum point x_0 of R satisfying assumption (A), x_0 cannot be a global maximum point of R.

Our main goal is to show that under assumption (A), $(u^*, 0)$ is unstable for suitably chosen parameters $\alpha, \beta, \mu, \nu > 0$. The key ingredient is to find $\alpha > 0$ and $\mu > 0$ such that $u^*(x_0) < m(x_0)$, i.e. the species u at equilibrium undermatches its resource at some local maximum point of R. Once this is done, we can choose β sufficiently large, i.e. the species v has a strong tendency to concentrate near the local maxima of R, such that small populations of v can invade in a neighbourhood of x_0 since the effective growth rate for v is $m(x) - u(x)$, which is positive for x close to x_0. The precise statement of our result is as follows.

THEOREM 1.6 *Suppose that $R(x)$ satisfies assumption* (A) *and all critical points of R are non-degenerate. Assume that $P(x) = \ln m + \alpha R$ and $Q(x) = \ln m + \beta R$ in Equation* (1). *Then there exists some $\alpha_0 > 0$ such that for every $\alpha \in (0, \alpha_0)$, we can find some $\mu_0 > 0$ such that if $\mu > \mu_0$, then given any $\nu > 0$, both $(u^*, 0)$ and $(0, v^*)$ are unstable for sufficiently large $\beta > 0$. Furthermore, system* (1) *has at least a stable positive steady state.*

Note that ν can be arbitrarily chosen, so we allow $\mu = \nu$ in our constructions. This immediately gives a counterexample to some conjecture raised in part (c), Remark 1.1 of [9].

Theorem 1.6 suggests that there is some $\alpha^* > \alpha_0 > 0$ such that the strategy $P(x) = \ln m(x) + \alpha^* R(x)$ may be a local ESS and/or CSS. At first look this appears to contradict part (b) of Theorem 1.1, which says that no other strategy can be a local ESS except $P = \ln m$. Actually they are consistent with each other since part (b) of Theorem 1.1 allows R to vary arbitrarily, while here we are fixing m and R and only allow the parameters α, β to vary. In other words, if we only consider the evolution of a single trait α, β, then system (1) may have other local ESS and/or CSS besides $P = \ln m$. Hence, while the global ESS exists and is unique, this global ESS may not be a global CSS, and there may exist multiple local ESS and/or CSS for system (1) if we only allow one single trait to evolve.

This paper is organized as follows. In Section 2, we give some preliminary results on monotone dynamical systems and criteria on the local stability of semi-trivial steady states. Sections 3–5 are devoted to proofs of Theorems 1.2, 1.4, and 1.6, respectively. Some discussions of the results are given in Section 6.

2. Preliminary results

In this section, we summarize some statements regarding solutions of system (1) and the stability of its steady states, which will be useful in later sections. By the maximum principle for cooperative systems [40] and the standard theory for parabolic equations [25], if the initial conditions of Equation (1) are non-negative and not identically zero, system (1) has a unique positive smooth solution which exists for all time and it defines a smooth dynamical system on $C(\bar{\Omega}) \times C(\bar{\Omega})$ [3,26,41]. The stability of steady states of Equation (1) is understood with respect to the topology of $C(\bar{\Omega}) \times C(\bar{\Omega})$. The following result is a consequence of the maximum principle and the structure of Equation (1) (see [9, Theorem 3]).

THEOREM 2.1 *The system* (1) *is a strongly monotone dynamical system, i.e.*

(a) $u_1(x, 0) \geq u_2(x, 0)$ *and* $v_1(x, 0) \leq v_2(x, 0)$ *for all* $x \in \Omega$ *and*
(b) $(u_1(x, 0), u_2(x, 0)) \not\equiv (u_2(x, 0), v_2(x, 0))$ *implies* $u_1(x, t) > u_2(x, t)$ *and* $v_1(x, t) < v_2(x, t)$ *for all* $x \in \bar{\Omega}$ *and* $t > 0$.

The following result is a consequence of Theorem 2.1 and the monotone dynamical system theory [26,41].

THEOREM 2.2 *If system* (1) *has no coexistence state, then one of the semi-trivial steady states is unstable and the other one is globally asymptotically stable* [29]; *if both semi-trivial steady states are unstable, then Equation* (1) *has at least one stable coexistence state* [14,37].

The following result concerns the linear stability of semi-trivial steady states of Equation (1) (see, e.g. [11, Lemma 5.5]).

LEMMA 2.1 *The steady state* $(u^*, 0)$ *is linearly stable/unstable if and only if the following eigenvalue problem, for* $(\lambda, \psi) \in \mathbb{R} \times C^2(\bar{\Omega})$, *has a positive/negative eigenvalue*:

$$\nu \nabla \cdot [\nabla \psi - \psi \nabla (\ln m + \beta R)] + (m - u^*)\psi = -\lambda \psi \quad \text{in } \Omega,$$

$$[\nabla \psi - \psi \nabla (\ln m + \beta R)] \cdot n = 0 \quad \text{on } \partial\Omega.$$

The criterion for the linearized stability of the semi-trivial steady state $(0, v^*)$ *is analogous.*

3. Proof of Theorem 2

In this section, we focus on the case when $P(x) = \ln m$, i.e. the following model:

$$u_t = \mu \nabla \cdot [\nabla u - u \nabla (\ln m)] + u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$

$$v_t = \nu \nabla \cdot [\nabla v - v \nabla Q(x)] + v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - u \nabla (\ln m)] \cdot n = [\nu \nabla v - v \nabla Q(x)] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty). \tag{4}$$

THEOREM 3.1   *Given any $\mu, \nu > 0$. Suppose that $Q(x) - \ln m$ is not a constant function. Then, the semi-trivial steady state $(u^*, 0)$ is globally asymptotically stable.*

Proof   Step 1. We show that Equation (4) has no positive steady states. To this end, we argue by contradiction. Suppose that u, v are positive steady states of Equation (4), i.e. they satisfy

$$\mu \nabla \cdot [\nabla u - u\nabla(\ln m)] + u[m(x) - u - v] = 0 \quad \text{in } \Omega,$$
$$\nu \nabla \cdot [\nabla v - v\nabla Q(x)] + v[m(x) - u - v] = 0 \quad \text{in } \Omega,$$
$$[\nabla u - u\nabla(\ln m)] \cdot n = [\nabla v - v\nabla Q(x)] \cdot n = 0 \quad \text{on } \partial\Omega. \tag{5}$$

Set $w = u/m$. Then w satisfies

$$\mu \nabla \cdot [m\nabla w] + mw(m - u - v) = 0 \quad \text{in } \Omega, \quad \left.\frac{\partial w}{\partial n}\right|_{\partial\Omega} = 0.$$

Since $w > 0$, dividing the equation of w by w and integrating in Ω, we have

$$\mu \int_\Omega m\frac{|\nabla w|^2}{w^2} + \int_\Omega m(m - u - v) = 0. \tag{6}$$

Integrating the equations of u and v, we have

$$\int_\Omega u(m - u - v) = 0 \tag{7}$$

and

$$\int_\Omega v(m - u - v) = 0, \tag{8}$$

respectively.

Adding up Equations (7) and (8), we have

$$\int_\Omega (u + v)(m - u - v) = 0. \tag{9}$$

Subtracting Equation (9) from Equation (6), we obtain

$$\mu \int_\Omega m\frac{|\nabla w|^2}{w^2} + \int_\Omega (m - u - v)^2 = 0,$$

which implies that $m - u - v \equiv 0$ and $w = s$ for some positive constant $s > 0$; i.e. $u/m = s$ for some constant s. Since $u > 0$ and $v > 0$, from $m - u - v = 0$, we see that $s \in (0, 1)$ and $v = (1 - s)m$. Substituting $(u, v) = (sm, (1 - s)m)$ into the equation of v and dividing the result by $(1 - s)$, we see that

$$\nu \nabla \cdot [m\nabla(\ln m - Q(x))] = 0 \quad \text{in } \Omega, \quad \nabla(\ln m - Q(x)) \cdot n|_{\partial\Omega} = 0. \tag{10}$$

By the maximum principle [40], $Q(x) - \ln m$ must be equal to some constant, which contradicts our assumption. This proves that Equation (4) has no positive steady states.

Step 2. We show that $(0, v^*)$ is unstable. By Lemma 2.1, it suffices to show the smallest eigenvalue, denoted by λ_1, of the linear eigenvalue problem

$$\mu \nabla \cdot [\nabla \varphi - \varphi \nabla (\ln m)] + (m - v^*)\varphi = -\lambda \varphi \quad \text{in } \Omega,$$

$$[\nabla \varphi - \varphi \nabla (\ln m)] \cdot n = 0 \quad \text{on } \partial \Omega$$

satisfies $\lambda_1 < 0$. Let φ_1 denote the positive eigenfunction of λ_1 uniquely determined by $\max_{\bar{\Omega}} \varphi_1 = 1$. Set $\psi = \varphi_1/m$. Then the previous equation can be written as

$$\mu \nabla \cdot [m \nabla \psi] + m(m - v^*)\psi = -\lambda_1 m \psi, \quad \nabla \psi \cdot n|_{\partial \Omega} = 0.$$

Dividing the equation of ψ by ψ and integrating the result in Ω, we have

$$\mu \int_\Omega m \frac{|\nabla \psi|^2}{\psi^2} + \int_\Omega m(m - v^*) = -\lambda_1 \int_\Omega m. \tag{11}$$

Integrating the equation of v^*, we have

$$\int_\Omega v^*(m - v^*) = 0. \tag{12}$$

Subtracting Equation (12) from Equation (11), we find that

$$\mu \int_\Omega m \frac{|\nabla \psi|^2}{\psi^2} + \int_\Omega (m - v^*)^2 = -\lambda_1 \int_\Omega m.$$

Hence, $\lambda_1 < 0$ as long as $v^* \not\equiv m$. To this end, we argue by contradiction and suppose that $v^* \equiv m$. Then by the equation of v^*, we see that Equation (10) holds, which implies that $Q(x) - \ln m$ is constant and we reach a contradiction. Hence, $v^* \not\equiv m$ and thus $\lambda_1 < 0$.

Step 3. We show that the semi-trivial steady state $(u^*, 0)$ is globally asymptotically stable. This follows from Theorem 2.2, system (4) has no positive steady state (Step 1), and the semi-trivial steady state $(0, v^*)$ is unstable (Step 2). ∎

4. Proof of Theorem 4

In this section, we generalize previous results in Cantrell *et al.* [9] on the coexistence of two competing species. In particular, we focus on the case where $P(x) = \ln m + \alpha R$ and $Q(x) = \ln m + \beta R$, i.e. we consider

$$u_t = \mu \nabla \cdot [\nabla u - u \nabla (\ln m + \alpha R)] + u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$

$$v_t = \nu \nabla \cdot [\nabla v - v \nabla (\ln m + \beta R)] + v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty),$$

$$[\nabla u - u \nabla (\ln m + \alpha R)] \cdot n = [\nabla v - v \nabla (\ln m + \beta R)] \cdot n = 0 \quad \text{on } \partial \Omega \times (0, \infty). \tag{13}$$

THEOREM 4.1 *Suppose that $\alpha \beta < 0$ and $R \in C^2(\bar{\Omega})$ is non-constant. Then, both semi-trivial steady states $(u^*, 0)$ and $(0, v^*)$ are unstable, and system (13) has at least one stable positive steady state.*

Proof Step 1. We show that $(0, v^*)$ is unstable. Let λ_1 denotes the smallest eigenvalue of the following linear problem

$$\mu\nabla \cdot [\nabla\varphi - \varphi\nabla(\ln m + \alpha R)] + \varphi(m - v^*) = -\lambda\varphi \quad \text{in } \Omega,$$
$$[\nabla\varphi - \varphi\nabla(\ln m + \alpha R)] \cdot n = 0 \quad \text{on } \partial\Omega, \tag{14}$$

and let φ_1 denote the unique positive eigenfunction of λ_1 which satisfies $\max_{\bar{\Omega}} \varphi_1 = 1$. Set $\psi = \varphi_1/(me^{\alpha R})$. Then, ψ satisfies

$$\mu\nabla \cdot [me^{\alpha R}\nabla\psi] + \psi me^{\alpha R}(m - v^*) = -\lambda_1 me^{\alpha R}\psi \quad \text{in } \Omega, \quad \nabla\psi \cdot n|_{\partial\Omega} = 0. \tag{15}$$

Dividing the equation of ψ by ψ and integrating in Ω, we have

$$-\lambda_1 \int_\Omega me^{\alpha R} = \mu \int_\Omega me^{\alpha R}\frac{|\nabla\psi|^2}{\psi^2} + \int_\Omega me^{\alpha R}(m - v^*). \tag{16}$$

Recall that v^* satisfies

$$\nu\nabla \cdot [\nabla v^* - v^*\nabla(\ln m + \beta R)] + v^*[m(x) - v^*] = 0,$$
$$[\nabla v^* - v^*\nabla(\ln m + \beta R)] \cdot n = 0 \quad \text{on } \partial\Omega. \tag{17}$$

Set $w = v^*/(me^{\beta R})$. Then w satisfies

$$\nu\nabla \cdot [me^{\beta R}\nabla w] + v^*(m - v^*) = 0 \quad \text{in } \Omega, \quad \nabla w \cdot n|_{\partial\Omega} = 0.$$

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

$$\nu l \int_\Omega me^{\beta R}w^{l-1}|\nabla w|^2 - \int_\Omega \frac{(v^*)^{l+1}}{m^l e^{l\beta R}}(m - v^*) = 0, \tag{18}$$

where $l > 0$ is to be chosen later.

By Equations (16) and (18) we have

$$-\lambda_1 \int_\Omega me^{\alpha R} = \mu \int_\Omega me^{\alpha R}\frac{|\nabla\psi|^2}{\psi^2} + \nu l \int_\Omega me^{\beta R}w^{l-1}|\nabla w|^2$$
$$+ \int_\Omega \frac{m^{l+1}e^{(\alpha+l\beta)R} - (v^*)^{l+1}}{m^l e^{l\beta R}}(m - v^*).$$

Choose

$$l = -\frac{\alpha}{\beta}.$$

By our assumption $\alpha\beta < 0$, we have $l > 0$. Hence,

$$-\lambda_1 \int_\Omega me^{\alpha R} \geq \int_\Omega \frac{m^{l+1} - (v^*)^{l+1}}{m^l e^{l\beta R}}(m - v^*),$$

where the equality holds if and only if ψ and w are both equal to constants. Since $l > 0$, we see that

$$(m^{l+1} - (v^*)^{l+1})(m - v^*) \geq 0$$

in Ω, where the equality holds if and only if $m = v^*$. Therefore, $\lambda_1 \leq 0$, and $\lambda_1 = 0$ if and only if $m - v^* \equiv 0$. To complete the proof, it suffices to rule out the possibility $m \equiv v^*$. To this end, we see that if $m \equiv v^*$, v^* satisfies

$$\nu \nabla \cdot [\nabla v^* - v^* \nabla (\ln m + \beta R)] = 0 \quad \text{in } \Omega,$$
$$[\nabla v^* - v^* \nabla (\ln m + \beta R)] \cdot n = 0 \quad \text{on } \partial \Omega. \tag{19}$$

By the maximum principle [40] we see that $v^*/(me^{\beta R})$ is equal to some constant. This together with $m \equiv v^*$ implies that $e^{\beta R}$ must be equal to some constant. Since $\beta \neq 0$, we see that R must be equal to some constant, which contradicts our assumption. Hence, $\lambda_1 < 0$, which together with Lemma 2.1 implies that $(0, v^*)$ is unstable.

Step 2. Similarly, by symmetry we see that if $\alpha \beta < 0$, $(u^*, 0)$ is unstable. Since the system (13) is a strongly monotone dynamical system, by Theorem 2.2 we see that system (13) has at least a stable positive steady state. ∎

5. Proof of Theorem 1.6

This section is devoted to the case when both α and β are positive. It is shown in Cantrell *et al.* [9] that if Ω is an interval and $R_x > 0$ in $\bar{\Omega}$, $0 < \alpha < \beta$, then $(u^*, 0)$ is stable and $(0, v^*)$ is unstable. A natural question is whether the monotonicity of $R(x)$ is essential. In this section, we will construct non-monotone functions $R(x)$ such that for $P(x) = \ln m + \alpha R(x)$ and $Q(x) = \ln m + \beta R(x)$, both $(u^*, 0)$ and $(0, v^*)$ are unstable for suitably chosen positive constants α, β, μ, ν.

LEMMA 5.1 *Let x_0 be a local maximum of R which satisfies assumption* (A). *There exists some $\alpha_0 > 0$ such that for every $\alpha \in (0, \alpha_0)$,*

$$e^{\alpha R(x_0)} < \frac{\int_\Omega m^2 e^{2\alpha R}}{\int_\Omega m^2 e^{\alpha R}}.$$

Proof For sufficiently small α,

$$\frac{\int_\Omega m^2 e^{2\alpha R}}{\int_\Omega m^2 e^{\alpha R}} - e^{\alpha R(x_0)} = \left[1 + \alpha \frac{\int_\Omega m^2 R}{\int_\Omega m^2} + O(\alpha^2)\right] - [1 + \alpha R(x_0) + O(\alpha^2)]$$

$$= \alpha \left[\frac{\int_\Omega m^2 R}{\int_\Omega m^2} - R(x_0)\right] + O(\alpha^2) > 0.$$

∎

LEMMA 5.2 *Let x_0 be a local maximum of R which satisfies assumption* (A). *Then there exists some μ_0 such that if $\mu > \mu_0$, $u^*(x_0) < m(x_0)$.*

Proof Set $w = u^*/(me^{\alpha R})$. Then w satisfies

$$\mu \nabla \cdot [me^{\alpha R} \nabla w] + u^*(m - u^*) = 0 \quad \text{in } \Omega, \quad \nabla w \cdot n|_{\partial \Omega} = 0.$$

By the maximum principle [40], w and u^* are both uniformly bounded for all $\mu \geq 1$. By L^p theory for second-order elliptic operators (see [21]), for any $p > 1$, $\|w\|_{W^{2,p}(\Omega)}$ is uniformly bounded for all $\mu \geq 1$. By the Sobolev embedding theorem, $\|w\|_{C^{1,\tau}(\bar{\Omega})}$ is uniformly bounded for some

$\tau \in (0, 1)$. Passing to a subsequence if necessary, w converges to some function $\bar{w} \in C^1(\bar{\Omega})$. Multiplying the equation of w by w and integrating the result in Ω, we have

$$\mu \int_\Omega e^{\alpha R} m |\nabla w|^2 + \int_\Omega w u^* (m - u^*) = 0.$$

By letting $\mu \to +\infty$, we see that $\bar{w}$ satisfies

$$\int_\Omega e^{\alpha R} m |\nabla \bar{w}|^2 = 0,$$

i.e. $\bar{w}$ is a constant. To determine $\bar{w}$, by integrating the equation of u^* in Ω we find

$$\int_\Omega u^* (m - u^*)\, dx = 0. \tag{20}$$

If $\bar{w} = 0$, i.e. $w \to 0$ in $C^1(\bar{\Omega})$, then $u^* \to 0$ in $L^\infty(\Omega)$ as $\mu \to \infty$. Since $m > 0$ in Ω, $m - u^* > 0$ in Ω for large μ. This implies that $u^*(m - u^*) > 0$ in Ω for large μ, which contradicts Equation (20). Hence $\bar{w}$ must be a positive constant. This together with Equation (20) implies that

$$\bar{w} = \frac{\int_\Omega m^2 e^{\alpha R}}{\int_\Omega m^2 e^{2\alpha R}}.$$

Since $\bar{w}$ is uniquely determined, the convergence of w to $\bar{w}$ is independent of the subsequence. Hence,

$$\frac{u^*}{m} \longrightarrow \frac{\int_\Omega m^2 e^{\alpha R}}{\int_\Omega m^2 e^{2\alpha R}} e^{\alpha R}$$

uniformly in $\bar{\Omega}$ as $\mu \to \infty$. In particular, this, together with Lemma 5.1, implies that for every $\alpha \in (0, \alpha_0)$, $u^*(x_0) < m(x_0)$ for sufficiently large μ. ∎

LEMMA 5.3 *Suppose that R satisfies assumption* (A) *and all critical points of R are non-degenerate. Then for $\alpha \in (0, \alpha_0)$, $\mu > \mu_0$, $\nu > 0$, the semi-trivial steady state $(u^*, 0)$ is unstable for sufficiently large $\beta > 0$.*

Proof By Lemma 2.1, it suffices to show the least eigenvalue, denoted by λ_1, of the eigenvalue problem

$$\nu \nabla \cdot [\nabla \varphi - \varphi \nabla (\ln m + \beta R)] + (m - u^*)\varphi = -\lambda \varphi \quad \text{in } \Omega,$$

$$[\nabla \varphi - \varphi \nabla (\ln m + \beta R)] \cdot n = 0 \quad \text{on } \partial\Omega$$

satisfies $\lambda_1 < 0$. Set $\psi = \varphi/(me^{\beta R})$. Then ψ satisfies

$$\nu \nabla \cdot [me^{\beta R} \nabla \psi] + (m - u^*) me^{\beta R} \psi = -\lambda m e^{\beta R} \psi \quad \text{in } \Omega, \quad \nabla \psi \cdot n|_{\partial\Omega} = 0.$$

By the variational characterization, λ_1 is determined by

$$\lambda_1 = \inf_{\psi \in W^{1,2}(\Omega)} \left\{ \frac{\int_\Omega [\nu m e^{\beta R} |\nabla \psi|^2 - m(m - u^*) e^{\beta R} \psi^2]}{\int_\Omega m e^{\beta R} \psi^2} \right\}.$$

Hence, to show $\lambda_1 < 0$, we need to find ψ such that

$$\int_\Omega [\nu m e^{\beta R} |\nabla \psi|^2 - m(m - u^*) e^{\beta R} \psi^2] < 0.$$

Let $\max_{\bar{\Omega}} m$ denote the maximum of m. It suffices to find ψ such that

$$\int_{\Omega} \left[\nu \left(\max_{\bar{\Omega}} m \right) \cdot e^{\beta R} |\nabla \psi|^2 - m(m - u^*) e^{\beta R} \psi^2 \right] < 0. \tag{21}$$

To establish Equation (21), consider another linear eigenvalue problem

$$\nu \left(\max_{\bar{\Omega}} m \right) \nabla \cdot [e^{\beta R} \nabla \psi] + (m - u^*) m e^{\beta R} \psi = -\lambda e^{\beta R} \psi, \quad \nabla \psi \cdot n|_{\partial \Omega} = 0. \tag{22}$$

Let λ^* denote the principal eigenvalue of Equation (22). Rewrite Equation (22) as

$$-\nu \left(\max_{\bar{\Omega}} m \right) \Delta \psi - \nu \left(\max_{\bar{\Omega}} m \right) \beta \nabla R \cdot \nabla \psi + m(u^* - m) \psi = \lambda \psi, \quad \nabla \psi \cdot n|_{\partial \Omega} = 0. \tag{23}$$

Hence, by Theorem 1 of [10] we have

$$\lim_{\beta \to \infty} \lambda^* = \min_{\mathcal{R}} [m(u^* - m)],$$

where $\mathcal{R}$ denotes the set of local maxima of R. Note that

$$\min_{\mathcal{R}} [m(u^* - m)] \leq m(x_0)(u^*(x_0) - m(x_0)) < 0,$$

where the last inequality follows from Lemma 5.2, provided that $\alpha \in (0, \alpha_0)$ and $\mu > \mu_0$. This implies that $\lambda^* < 0$. Let $\psi^* > 0$ denote an eigenfunction of λ^*. Note that λ^* can be characterized as

$$\lambda^* = \inf_{\psi \in W^{1,2}(\Omega)} \left\{ \frac{\int_{\Omega} \left[\nu \left(\max_{\bar{\Omega}} m \right) e^{\beta R} |\nabla \psi|^2 - m(m - u^*) e^{\beta R} \psi^2 \right]}{\int_{\Omega} m e^{\beta R} \psi^2} \right\}, \tag{24}$$

which is attained by ψ^*. It then follows from $\lambda^* < 0$ and Equation (24) that Equation (21) holds for $\psi = \psi^*$. This shows that $\lambda_1 < 0$. ∎

The proof of the following result is identical to that of Theorem 3.5 in Cantrell *et al.* [6], so we omit the details.

LEMMA 5.4 *Suppose that the set of critical points of $R(x)$ has Lebesgue measure zero and v^* is given by Equation (17). Then $v^* \to 0$ in $L^2(\Omega)$ as $\beta \to \infty$.*

LEMMA 5.5 *Suppose that the set of critical points of $R(x)$ has measure zero. Given any $\mu > 0$, $\nu > 0$, and $\alpha > 0$. If β is sufficiently large, then $(0, v^*)$ is unstable.*

Proof By Lemma 2.1 it suffices to show the principal eigenvalue, denoted by λ_1, of the eigenvalue problem

$$\mu \nabla \cdot [\nabla \varphi - \varphi \nabla (\ln m + \alpha R)] + (m - v^*)\varphi = -\lambda \varphi \quad \text{in } \Omega,$$

$$[\nabla \varphi - \varphi \nabla (\ln m + \alpha R)] \cdot n = 0 \quad \text{on } \partial \Omega,$$

is negative. Let φ_1 be the positive eigenfunction of λ_1 uniquely determined by $\max_{\bar{\Omega}} \varphi_1 = 1$. Set $\psi = \varphi_1/(m e^{\alpha R})$. Then $\psi > 0$ satisfies

$$\mu \nabla \cdot [m e^{\alpha R} \nabla \psi] + (m - v^*) m e^{\alpha R} \psi = -\lambda_1 m e^{\alpha R} \psi \quad \text{in } \Omega, \quad \nabla \psi \cdot n|_{\partial \Omega} = 0.$$

Dividing the above equation by ψ and integrating the result in Ω, we have

$$-\lambda_1 \int_\Omega m\mathrm{e}^{\alpha R} = \mu \int_\Omega \frac{m\mathrm{e}^{\alpha R}|\nabla\psi|^2}{\psi^2} + \int_\Omega m\mathrm{e}^{\alpha R}(m - v^*) \geq \int_\Omega m^2\mathrm{e}^{\alpha R} - \|m\mathrm{e}^{\alpha R}\|_{L^\infty} \int_\Omega v^* > 0,$$

where the last inequality follows from Lemma 5.4, provided that β is sufficiently large.   ∎

Proof of Theorem 1.6   It follows from Lemmas 5.3 and 5.5 and Theorem 2.2.   ∎

6.   Discussion

In this paper, we addressed several conjectures raised in Cantrell *et al.* [9] concerning the dynamics of some diffusion–advection–competition model for two competing species. Both species are assumed to have the same population dynamics but different dispersal strategies: they both disperse by random diffusion and advection along certain gradients, but possibly do so with different rates and/or gradients. A conditional dispersal strategy, which results in the ideal free distribution of a single population at equilibrium, was found in [9]. It was shown in [9] that this special dispersal strategy is a local ESS when random diffusion rates of two species are equal, and we show that it is actually a global ESS for arbitrary random diffusion rates. The conditions in [9] for the coexistence of two species are also substantially improved. Finally, we construct some examples to show that this special strategy may not be a globally CSS for certain resource functions with two or more local maxima, in strong contrast with the result from [9], which roughly says that this dispersal strategy is always a globally CSS for any monotone resource function. Our results seem to suggest that for resource functions with two or more local maxima, there may exist some other local ESS and/or CSS, besides the obvious candidate – the special conditional dispersal strategy found in [9]. The biological intuition behind this is that if resource functions have two or more local maxima, the resident species at equilibrium may undermatch its resource at some local maximum of the resource, which makes it vulnerable to invasion by other species near such local maxima.

Some ideas from this work might be useful in studying the evolutionary stability of dispersal strategies in reaction–diffusion models [19,24,42,43], patch models [5,27,28,33,38,39], non-local dispersal models [31,32,44], or metapopulation models [23,45]. These findings will be reported in some forthcoming paper(s).

We conjecture that the special dispersal strategy $P = \ln m$ is a globally CSS when the function R has a unique local maximum (and thus it must be the global maximum). For such functions R, the construction of the counterexample in Theorem 1.6 breaks down since one always has $u^*(x_0) \geq m(x_0)$ for any global maximum x_0; i.e. the population at equilibrium always overmatches its resource at the global maximum of R. To see this, following the proofs of Theorem 1.3 in [7] or Lemma 5.2 in [11], if $\alpha \geq 0$, we have the following inequality:

$$u^*(x) \geq m(x)\mathrm{e}^{\alpha[R(x) - \max_{\bar\Omega} R]}$$

for every $x \in \bar\Omega$. In particular, $u^*(x_0) \geq m(x_0)$ for any global maximum x_0 of R. We further refer to [34–36] for recent important development on the qualitative profiles of u^* and also steady-state solutions of two species competition model with one sufficiently large advection coefficient.

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References

[1] F. Belgacem and C. Cosner, *The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment*, Can. Appl. Math. Q. 3 (1995), pp. 379–397.

[2] A. Bezuglyy and Y. Lou, *Reaction-diffusion models with large advection coefficients*, Appl. Anal. 89 (2010), pp. 983–1004.

[3] R.S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.

[4] R.S. Cantrell, C. Cosner, and Y. Lou, *Movement towards better environments and the evolution of rapid diffusion*, Math. Biosci. 204 (2006), pp. 199–214.

[5] R.S. Cantrell, C. Cosner, D.L. DeAngelis, and V. Padrón, *The ideal free distribution as an evolutionarily stable strategy*, J. Biol. Dyn. 1 (2007), pp. 249–271.

[6] R.S. Cantrell, C. Cosner, and Y. Lou, *Advection mediated coexistence of competing species*, Proc. R. Soc. Edinb. 137A (2007), pp. 497–518.

[7] R.S. Cantrell, C. Cosner, and Y. Lou, *Approximating the ideal free distribution via reaction-diffusion-advection equations*, J. Diff. Eqs 245 (2008), pp. 3687–3703.

[8] R.S. Cantrell, C. Cosner, and Y. Lou, *Evolution of dispersal in heterogeneous landscape, Spatial Ecology, Spatial Ecology Mathematical and Computational Biology Series*, R.S. Cantrell, C. Cosner and S. Ruan, eds, Chapman Hall/CRC Press, Boca Raton, FL, 2009, pp. 213–229.

[9] R.S. Cantrell, C. Cosner, and Y. Lou, *Evolution of dispersal and ideal free distribution*, Math. Biosci. Eng. 7 (2010), pp. 17–36.

[10] X.F. Chen and Y. Lou, *Principal eigenvalue and eigenfunction of elliptic operator with large convection and its application to a competition model*, Indiana Univ. Math. J. 57 (2008), pp. 627–658.

[11] X.F. Chen, R. Hambrock, and Y. Lou, *Evolution of conditional dispersal: A reaction-diffusion-advection model*, J. Math. Biol. 57 (2008), pp. 361–386.

[12] C. Cosner, *A dynamic model for the ideal-free distribution as a partial differential equation*, Theor. Popul. Biol. 67 (2005), pp. 101–108.

[13] C. Cosner and Y. Lou, *Does movement toward better environments always benefit a population?* J. Math. Anal. Appl. 277 (2003), pp. 489–503.

[14] E.N. Dancer, *Positivity of maps and applications*, in *Topological Nonlinear Analysis*, M. Matzeu and A. Vignoli, eds, Birkhauser, Boston, 1995, pp. 303–340. Prog. Nonlinear Diff. Eqs Appl. 15.

[15] U. Dieckmann, *Can adaptive dynamics invade?* Trends Ecol. Evol.12 (1997), pp. 128–131.

[16] O. Diekmann, *A beginner's guide to adaptive dynamics*, Banach Cent. Publ. 63 (2003), pp. 47–86.

[17] U. Dieckmann and R. Law, *The dynamical theory of coevolution: A derivation from stochastic ecological processes*, J. Math. Biol. 34 (1996), pp. 579–612.

[18] U. Dieckmann, B. O'Hara, and W. Weisser, *The evolutionary ecology of dispersal*, Trends Ecol. Evol. 14 (1999), pp. 88–90.

[19] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, *The evolution of slow dispersal rates: A reaction-diffusion model*, J. Math. Biol. 37 (1998), pp. 61–83.

[20] S.A.H. Geritz, E. Kisdi, G. Meszena, and J.A.J. Metz, *Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree*, Evol. Ecol. 12 (1998), pp. 35–57.

[21] D. Gilbarg and N. Trudinger, *Elliptic Partial Differential Equation of Second Order*, 2nd ed., Springer-Verlag, Berlin, 1983.

[22] R. Hambrock and Y. Lou, *The evolution of conditional dispersal strategy in spatially heterogeneous habitats*, Bull. Math. Biol. 71 (2009), pp. 1793–1817.

[23] I. Hanski, *Metapopulation Ecology*, Oxford University Press, Oxford, 1999.

[24] A. Hastings, *Can spatial variation alone lead to selection for dispersal?* Theor. Popul. Biol. 24 (1983), pp. 244–251.

[25] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Mathematics, Vol. 840, Springer, Berlin, 1981.

[26] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman Research Notes Mathematics Series 247, Longman Scientific & Technical, John Wiley & Sons, New York, 1991.

[27] R.D. Holt, *Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution*, Theor. Popul. Biol. 28 (1985), pp. 181–208.

[28] R.D. Holt and M.A. McPeek, *Chaotic population dynamics favors the evolution of dispersal*, Am. Nat. 148 (1996), pp. 709–718.

[29] S. Hsu, H. Smith, and P. Waltman, *Competitive exclusion and coexistence for competitive systems on ordered Banach spaces*, Trans. Am. Math. Soc. 348 (1996), pp. 4083–4094.

[30] V. Hutson, K. Mischaikow, and P. Poláčik, *The evolution of dispersal rates in a heterogeneous time-periodic environment*, J. Math. Biol. 43 (2001), pp. 501–533.

[31] V. Hutson, S. Martinez, K. Mischaikow, and G.T. Vickers, *The evolution of dispersal*, J. Math. Biol. 47 (2003), 483–517.

[32] C.Y. Kao, Y. Lou, and W.X. Shen, *Random dispersal vs non-local dispersal*, Discrete Contin. Dyn. Syst. Ser. A 26 (2010), pp. 551–596.

[33] S. Kirkland, C.-K. Li, and S.J. Schreiber, *On the evolution of dispersal in patchy environments*, SIAM J. Appl. Math. 66 (2006), pp. 1366–1382.

[34] K.Y. Lam, *Concentration phenomena of a semilinear elliptic equation with large advection in an ecological model*, J. Diff. Eqs. 250 (2011), pp. 161–181.

[35] K.Y. Lam, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics II*, preprint.

[36] K.Y. Lam and W.M. Ni, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics*, Discrete Contin. Dyn. Syst. Ser. A 28 (2010), pp. 1051–1067.

[37] H. Matano, *Existence of nontrivial unstable sets for equilibriums of strongly order-preserving systems*, J. Fac. Sci. Univ. Tokyo 30 (1984), pp. 645–673.

[38] M.A. McPeek and R.D. Holt, *The evolution of dispersal in spatially and temporally varying environments*, Am. Nat. 140 (1992), pp. 1010–1027.

[39] V. Padrón and M.C. Trevisan, *Environmentally induced dispersal under heterogeneous logistic growth*, Math. Biosci. 199 (2006), pp. 160–174.

[40] M.H. Protter and H.F. Weinberger, *Maximum Principles in Differential Equations*, 2nd ed., Springer-Verlag, Berlin, 1984.

[41] H. Smith, *Monotone Dynamical Systems*, Mathematical Surveys and Monographs 41, American Mathematical Society, Providence, RI, 1995.

[42] X.F. Wang, *Qualitative behavior of solutions of chemotactic diffusion systems: Effects of motility and chemotaxis and dynamics*, SIAM J. Math. Anal. 31 (2000), pp. 535–560.

[43] X.F. Wang and Y.P. Wu, *Qualitative analysis on a chemotactic diffusion model for two species competing for a limited resource*, Q. Appl. Math. LX (2002), pp. 505–531.

[44] C. Cosner, J. Davila, and S. Martinez, *Evolutionary stability of ideal free nonlocal dispersal*, J. Biol. Dyn., submitted.

[45] D. Xu and Z. Feng, *A metapopulation model with local competitions*, Discrete Contin. Dyn. Syst. Ser. B 12 (2009) pp. 495–510.