Noname manuscript No.
(will be inserted by the editor)

Evolution of Conditional Dispersal: Evolutionarily Stable Strategies in Spatial Models

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Received: date / Accepted: date

Abstract We consider a two-species competition model in which the species have the same population dynamics but different dispersal strategies. Both species disperse by a combination of random diffusion and advection along environmental gradients, with the same random dispersal rates but different advection coefficients. Regarding these advection coefficients as movement strategies of the species, we investigate their course of evolution. By applying invasion analysis we find that if the spatial environmental variation is less than a critical value, there is a unique evolutionarily singular strategy, which is also evolutionarily stable. If the spatial environmental variation exceeds the critical value, there can be at least three evolutionarily singular strategies, one of which is not evolutionarily stable. Our results suggest that the evolution of conditional dispersal of organisms depends upon the spatial heterogeneity of the environment in a subtle way.

Keywords Evolutionarily stable strategy · Adaptive dynamics · Evolution of dispersal · Reaction-diffusion-advection

Mathematics Subject Classification (2000) 35K57 · 92D25

1 Background

The dispersal of organisms plays a fundamental role in their life histories. Despite its importance, understanding the evolution and ecological impact of dispersal remains a challenging issue [7, 8, 16, 38, 39, 41, 42]. In recent years there have been extensive studies on the ecological effect of dispersal in heterogeneous environments; see [4, 5, 28, 34, 35] and references therein. Much less is known about the evolution of dispersal. For instance, a question that has attracted considerable

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attention in recent years is whether conditional dispersal can evolve in a spatially varying but temporally constant environment [1,2,11,12,24,37].

To study the evolution of dispersal, a popular and powerful approach is that of Adaptive Dynamics [17,18,21,22], which connects the selection of a particular trait with the underlying population dynamical processes that drives selection. An important concept in Adaptive Dynamics is that of *Evolutionarily Stable Strategy* (ESS), introduced earlier by Maynard Smith and Price in [36]. A strategy is said to be evolutionarily stable if a population using it cannot be invaded by any small population using a different strategy. We shall frame our analysis within this paper in terms of Adaptive Dynamics. We will adopt the standard abbreviation ESS for "Evolutionarily Stable Strategy".

Our line of research begins with Hastings [25], who considered the outcome of the competition when a small number of invaders using a novel dispersal strategy are introduced into a resident population with a different strategy; see also [32]. It is shown [25] that in a spatially varying but temporally constant environment, an exotic species can invade when rare if and only if it has the smaller random dispersal rate. It is later shown in [19] that an invader with a smaller random dispersal rate always replace the resident species. Hence, unconditional dispersal is selected against in a spatially varying but temporally constant environment. It should be noted that in spatially and temporally varying environments faster random dispersal rates may sometimes be selected [27,33,37].

Unconditional dispersal alone, however, does not usually explain well the movement of many organisms. Following the modeling approach in [19], by replacing unconditional dispersal with a combination of unconditional dispersal and directed movement, the following reaction-diffusion-advection system is introduced in [12]:

$$\begin{cases} u_t = \mu\nabla\cdot(\nabla u - u\nabla P) + u(m-u-v) & \text{in } \Omega\times(0,\infty), \\ v_t = \nu\nabla\cdot(\nabla v - v\nabla Q) + v(m-u-v) & \text{in } \Omega\times(0,\infty), \\ \frac{\partial u}{\partial n} - u\frac{\partial P}{\partial n} = \frac{\partial v}{\partial n} - v\frac{\partial Q}{\partial n} = 0 & \text{on } \partial\Omega\times(0,\infty), \\ u(x,0)=u_0(x), \quad v(x,0)=v_0(x) & \text{in } \Omega, \end{cases} \tag{1}$$

where u and v denote the population densities of two species in a habitat Ω, which is a bounded domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$; $\frac{\partial}{\partial n}$ is the outward normal derivative on $\partial\Omega$, and the boundary conditions in (1) mean that there is no net flux across the boundary of the habitat for either of the two species; P and Q are two non-constant functions of the spatial variable x. The advection terms $-u\nabla P$ and $-v\nabla Q$ represent the directed movement upward along the gradients of P and Q, respectively. Throughout this paper, we assume

(M) $m \in C^2(\bar{\Omega})$, and it is non-constant and positive in $\bar{\Omega}$.

It is observed in [12] that if $P = \ln m$, then $(m,0)$ is a semi-trivial steady state of (1). Moreover, if $\mu=\nu$ and $Q = \ln m + \epsilon R$ for some non-constant $R \in C^2(\bar{\Omega})$, then $(m,0)$ is globally asymptotically stable for all $\epsilon > 0$ sufficiently small. In terms of adaptive dynamics, the strategy $P = \ln m$ is a local ESS. Subsequently, it is established in [2] that $P = \ln m$ is a global ESS in the following sense:

Theorem 1.1 ([2]). *Given any $\mu,\nu > 0$. Suppose that $P = \ln m$ and $Q - \ln m$ is non-constant. Then, the steady state $(m,0)$ is globally asymptotically stable among non-negative, not identically zero initial data.*

These results are closely connected to the fact that when $P = \ln m$, at equilibrium the population density of u *perfectly matches* the local carrying capacity m. That is, the strategy $P = \ln m$ is capable of producing an ideal free distribution (IFD) [20], a verbal concept in the ecology literature believed to be a sufficient condition for evolutionary stability. We refer to [12] for further discussions about the connections between ideal free distributions and evolution of dispersal.

As illustrated above, strategies which can produce ideal free distributions are obvious candidates of ESS. What if one is restricted to the situation where an ideal free distribution is not possible? This is the case if we consider the following system proposed in [9, 13]:

$$\begin{cases} u_t = \mu\nabla\cdot(\nabla u - \eta u \nabla m) + u(m-u-v) & \text{in } \Omega\times(0,\infty),\\ v_t = \nu\nabla\cdot(\nabla v - \xi v \nabla m) + v(m-u-v) & \text{in } \Omega\times(0,\infty),\\ \frac{\partial u}{\partial n} - \eta u \frac{\partial m}{\partial n} = \frac{\partial v}{\partial n} - \xi v \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega\times(0,\infty),\\ u(x,0)=u_0(x), \quad v(x,0)=v_0(x) & \text{in } \Omega, \end{cases} \tag{2}$$

where η, ξ are non-negative parameters which represent the "strategies" of u and v, and measure the ability of u and v to move upward along the gradient of m.

Different from the case when $P = \ln m$ or $Q = \ln m$, it can be shown that for any η, ξ, neither species u nor species v in system (2) can reach an ideal free distribution at equilibrium. In this situation, is there still a strategy (e.g., parametrized by η) which is an ESS? If so, is it unique? In this paper, we are going to give a partial answer to these questions when the diffusion rates are equal and sufficiently small. As we shall see in the next section, *the existence and uniqueness of an ESS depend crucially on the spatial environmental variation, characterized by the ratio* $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}$. We shall show that if the spatial environmental variation is less than a critical value, there is a unique evolutionarily singular strategy, which is also evolutionarily stable. If the spatial environmental variation exceeds the critical value, there might be three or more evolutionarily singular strategies, one of which is not evolutionarily stable.

Much work has been devoted to the understanding of positive steady states of system (2) when $\eta \to \infty$ and $\xi = 0$; see [6, 10, 13–15, 29–31]. In particular, it is proved in [31] in one dimension and subsequently in [30] in higher dimensions that if $\xi = 0$ and $\eta \to \infty$, then (2) always possesses a stable positive steady state which concentrates on a selected subset of the local maximum points of m. Different from all of the previous works on system (2), in this paper we are able to for the first time determine the existence and uniqueness of ESS for system (2).

2 Statement of Main Results

For the rest of this paper we assume that $\mu = \nu$. Then, (2) becomes

$$\begin{cases} u_t = \mu\nabla\cdot(\nabla u - \eta u \nabla m) + u(m-u-v) & \text{in } \Omega\times(0,\infty),\\ v_t = \mu\nabla\cdot(\nabla v - \xi v \nabla m) + v(m-u-v) & \text{in } \Omega\times(0,\infty),\\ \frac{\partial u}{\partial n} - \eta u \frac{\partial m}{\partial n} = \frac{\partial v}{\partial n} - \xi v \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega\times(0,\infty),\\ u(x,0)=u_0(x), \quad v(x,0)=v_0(x) & \text{in } \Omega. \end{cases} \tag{3}$$

We first prepare with some definitions. Let $\tilde{u} = \tilde{u}(\mu, \eta)$ be the unique positive solution of the single species equation

$$\begin{cases} \mu\nabla \cdot (\nabla\tilde{u} - \eta\tilde{u}\nabla m) + \tilde{u}(m - \tilde{u}) = 0 & \text{in } \Omega, \\ \frac{\partial\tilde{u}}{\partial n} - \eta\tilde{u}\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{4}$$

If assumption (M) is satisfied, then it is proved in [3] that $\tilde{u}$ exists for all $\eta \geq 0$; see also [15]. It is well known ([13]) that the stability of the steady state $(\tilde{u}, 0)$ of (3) is determined by the principal eigenvalue $\lambda = \lambda(\eta, \xi; \mu)$ of the following problem:

$$\begin{cases} \mu\nabla \cdot (\nabla\varphi - \xi\varphi\nabla m) + \varphi(m - \tilde{u}) + \lambda\varphi = 0 & \text{in } \Omega, \\ \frac{\partial\varphi}{\partial n} - \xi\varphi\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega, \end{cases} \tag{5}$$

where we denote the (positive) principal eigenfunction by φ, which is normalized by

$$\int_\Omega e^{-\eta m}\varphi^2(\eta, \xi; \mu) = \int_\Omega e^{-\eta m}\tilde{u}^2(\mu, \eta). \tag{6}$$

Notice that for all $\mu > 0$, if $\xi = \eta$, then $\varphi = \tilde{u}$, and $\lambda(\eta, \eta; \mu) = 0$ for any η. By Taylor's theorem,

$$\lambda = \frac{\partial\lambda}{\partial\xi}(\xi - \eta) + O(|\xi - \eta|^2).$$

Hence if $\frac{\partial\lambda}{\partial\xi}(\eta, \eta; \mu)$ is positive (resp. negative), then a rare mutant v with strategy ξ slightly less than (resp. greater than) η can invade the resident u with strategy η successfully. We first seek the existence and multiplicity of *evolutionarily singular strategies*, defined as follows:

Definition 2.1. *Fix $\mu > 0$. We say that η^* is an evolutionarily singular strategy if*

$$\frac{\partial\lambda}{\partial\xi}(\eta^*, \eta^*; \mu) = 0.$$

For the sake of simplicity we shall abbreviate $\frac{\partial\lambda}{\partial\xi}$ as λ_ξ. Our first main result states that if the spatial variation of the inhomogeneous environment is suitably small, then for sufficiently small migration rates, there is precisely one evolutionarily singular strategy.

Theorem 2.2. *Suppose that $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq 3 + 2\sqrt{2}$. Given any $\Lambda > 0$, for all small positive μ, there is exactly one evolutionarily singular strategy, denoted as $\hat{\eta} = \hat{\eta}(\mu)$, in $[0, \Lambda]$. Furthermore, $\hat{\eta} \to \eta_0$ as $\mu \to 0$, where η_0 is the unique positive root of*

$$g_0(\eta) := \int_\Omega m\nabla m \cdot \nabla(e^{-\eta m}m), \qquad 0 \leq \eta < \infty. \tag{7}$$

In fact, it holds that

$$\lambda_\xi(\eta, \eta; \mu) = \begin{cases} -, & \eta \in [0, \hat{\eta}); \\ 0, & \eta = \hat{\eta}; \\ +, & \eta \in (\hat{\eta}, \Lambda]. \end{cases} \tag{8}$$

If the underlying domain is one-dimensional, then we have a better result.

Corollary 2.3. *Suppose that $\Omega = (a, b)$, $m, m_x > 0$ in $\bar{\Omega}$, and $\frac{m(b)}{m(a)} \le 3 + 2\sqrt{2}$. Then for all small positive μ, there is exactly one evolutionarily singular strategy in $[0, \infty)$.*

A natural and important question is whether the singular strategy $\hat{\eta}$ is a Nash equilibrium, or evolutionarily stable. For the sake of completeness we first recall the definition of local ESS.

Definition 2.4. *Fix $\mu > 0$. A strategy η^* is a local ESS if there exists $\delta > 0$ such that $\lambda(\eta^*, \xi; \mu) > 0$ for all $\xi \in (\eta^* - \delta, \eta^* + \delta) \setminus \{\eta^*\}$.*

We say that η^* is a local Nash equilibrium if there exists $\delta > 0$ such that $\lambda(\eta^*, \xi; \mu) \ge 0$ for all $\xi \in (\eta^* - \delta, \eta^* + \delta)$. Hence, an ESS is a strict Nash equilibrium.

Our next result implies that $\hat{\eta}$ is indeed a local ESS under some further restrictions on Ω and m.

Theorem 2.5. *Suppose that Ω is convex with diameter d and $d\|\nabla \ln m\|_{L^\infty(\Omega)} \le \alpha_0$, where $\alpha_0 \approx 0.814$ is the unique positive root of the function $t \mapsto 4t + e^{-t} + 2\ln t - 1 - 2\ln \pi$. Then for $\mu > 0$ sufficiently small, $\hat{\eta}$ given in Theorem 2.2 is a local ESS.*

The assumptions of Theorem 2.5 are more restrictive than that of Theorem 2.2, as can be seen from the following:

$$\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \le e^{d\|\nabla \ln m\|_{L^\infty}} \le e^{\alpha_0} \approx 2.257 < 3 + 2\sqrt{2}.$$

Finally, we show that the critical constant $3 + 2\sqrt{2}$ in Theorem 2.2 is sharp, and that Theorem 2.5 fails for general m.

Theorem 2.6. *Let $\Omega = (a, b)$. For any $L > 3 + 2\sqrt{2}$, there exists $m \in C^2(\bar{\Omega})$ with $m, m_x > 0$ and $\frac{m(b)}{m(a)} = L$ such that for all $\mu > 0$ small,*

(i) *there are at least three evolutionarily singular strategies;*
(ii) *there exists one evolutionarily singular strategy, denoted as $\bar{\eta}$, which is not a local ESS. In fact, we can find some $\delta > 0$ so that $(\tilde{u}, 0)$ is unstable for all $\xi \in (\bar{\eta} - \delta, \bar{\eta} + \delta) \setminus \{\bar{\eta}\}$.*

We suspect that two of these singular strategies found in Theorem 2.6 are local ESS. A bit surprisingly, the function m constructed in Theorem 2.6 is monotone. On the other hand, we will show that if Ω is an interval and m is a linear function, then for sufficiently small μ, there is exactly one evolutionarily singular strategy. These results suggest that even if Ω is an interval, the exact multiplicity of singular strategies is a subtle issue and the answer depends upon the shape of function m.

This paper is organized as follows. Section 3 is devoted to the study of evolutionarily singular strategy and Theorem 2.2 will be established. In Section 4 we determine whether the evolutionarily singular strategy from Theorem 2.2 is also evolutionarily stable and prove Theorem 2.5. Finally in Section 5 we establish Theorem 2.6.

3 Evolutionarily singular strategies

In this section we investigate the existence and uniqueness of evolutionarily singular strategies.We first derive the formula of $\lambda_\xi(\eta, \eta; \mu)$ in Subsect. 3.1. Subsect. 3.2 is devoted to the study of asymptotic behaviors of $\tilde{u}$ for sufficiently small μ. The results from these two subsections enable us to obtain a limiting expression for $\lambda_\xi(\eta, \eta; \mu)$ as $\mu \to 0$. This limiting expression is investigated in Subsect. 3.3, which, together with results from previous subsections, will yield the proof of Theorem 2.2 and Corollary 2.3 in Subsect. 3.4.

3.1 Formula for λ_ξ

Taking derivative with respect to ξ in (5), denoting $\frac{\partial \varphi}{\partial \xi} = \varphi_\xi$ and $\frac{\partial \lambda}{\partial \xi} = \lambda_\xi$, we see that φ_ξ is the unique solution to

$$\begin{cases} \mu \nabla \cdot (\nabla \varphi_\xi - \xi \varphi_\xi \nabla m) + \varphi_\xi (m - \tilde{u}) + \lambda \varphi_\xi = \mu \nabla \cdot (\varphi \nabla m) - \lambda_\xi \varphi & \text{in } \Omega, \\ \frac{\partial \varphi_\xi}{\partial n} - \xi \varphi_\xi \frac{\partial m}{\partial n} = \varphi \frac{\partial m}{\partial n} \quad \text{on } \partial\Omega, \quad \int e^{-\eta m} \varphi_\xi \varphi = 0. \end{cases} \tag{9}$$

Multiplying (9) by $e^{-\xi m}\varphi$ and integrating by parts, we have

$$\lambda_\xi \int e^{-\xi m} \varphi^2 = -\mu \int \varphi \nabla m \cdot \nabla (e^{-\xi m} \varphi). \tag{10}$$

Since $\varphi = \tilde{u}$ when $\xi = \eta$, we obtain

Lemma 3.1. *For any $\mu > 0$ and $\eta \geq 0$, the following holds:*

$$\frac{\lambda_\xi(\eta, \eta; \mu)}{\mu} \int e^{-\eta m} \tilde{u}^2 = -\int \tilde{u} \nabla m \cdot \nabla (e^{-\eta m} \tilde{u}). \tag{11}$$

3.2 Estimates

First we consider the limiting behavior of $\tilde{u}$ as $\mu \to 0$.

Lemma 3.2. *For any $\Lambda > 0$, there exists positive constants c_Λ, C_Λ such that for all $\mu > 0$ and $\eta \in [0, \Lambda]$,*

$$c_\Lambda \leq \tilde{u}(x) \leq C_\Lambda \quad \text{in } \Omega. \tag{12}$$

Moreover, as $\mu \to 0$, $\|\tilde{u} - m\|_{L^\infty(\Omega)} \to 0$ uniformly for $\eta \in [0, \Lambda]$.

Proof. Set $\omega = e^{-\eta m}\tilde{u}$, then ω satisfies

$$\begin{cases} \mu \nabla \cdot (e^{\eta m} \nabla \omega) + (m - e^{\eta m} \omega) e^{\eta m} \omega = 0 & \text{in } \Omega, \\ \frac{\partial \omega}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{13}$$

By the maximum principle, if $\omega(x_1) = \max_{\bar{\Omega}} \omega$, then

$$\omega(x) \leq e^{-\eta m(x_1)} m(x_1) \leq \max_{\bar{\Omega}} \left(e^{-\eta m} m \right) \quad \text{for all } x \in \Omega.$$

Similarly, $\omega(x) \geq \min_{\bar{\Omega}} \left(e^{-\eta m} m\right)$ for all $x \in \Omega$. Therefore, if we take

$$c_\Lambda = \min_{\bar{\Omega}} \left(e^{-\Lambda m} m\right) \quad \text{and} \quad C_\Lambda = \max_{\bar{\Omega}} \left(e^{\Lambda m} m\right),$$

then (12) holds.

Lastly, $\|\tilde{u} - m\|_{L^\infty(\Omega)} \to 0$ as $\mu \to 0$ follows by applying the arguments in the Appendix of [26] to (13). □

Lemma 3.3. *There exists $C > 0$ such that for all $\phi \in H^1(\Omega)$,*

$$\int |\nabla \tilde{u} - \nabla m|^2 \phi^2 \leq C \|\tilde{u} - m\|_{L^\infty(\Omega)} \|\phi\|^2_{H^1(\Omega)},$$

where $C = C(\eta)$ is independent of μ, ϕ, and is uniformly bounded on compact subsets of $[0, \infty)$ in η.

Proof. Write (4) as

$$-\mu \nabla \cdot \{e^{\eta m} \nabla [e^{-\eta m}(m - \tilde{u})]\} + \tilde{u}(m - \tilde{u}) = -\mu \nabla \cdot [e^{\eta m} \nabla (e^{-\eta m} m)].$$

Multiply the above by $e^{-\eta m}(m - \tilde{u})\phi^2$, where ϕ is any given function in $H^1(\Omega)$, and integrate by parts (applying the boundary conditions of $\tilde{u}$), we deduce

$$\begin{aligned} &\mu \int e^{\eta m} |\nabla [e^{-\eta m}(m - \tilde{u})]|^2 \phi^2 + 2\mu \int \phi (m - \tilde{u}) \nabla [e^{-\eta m}(m - \tilde{u})] \cdot \nabla \phi \\ &\quad \leq \mu \int_{\partial \Omega} \frac{\partial}{\partial n} [e^{-\eta m} m](m - \tilde{u}) \phi^2 - \mu \int \nabla \cdot [e^{\eta m} \nabla (e^{-\eta m} m)] e^{-\eta m} (m - \tilde{u}) \phi^2. \end{aligned}$$

And hence by Hölder's inequality and the Trace theorem for Sobolev spaces (see, e.g. [23]),

$$\begin{aligned} &\int e^{\eta m} |\nabla [e^{-\eta m}(m - \tilde{u})]|^2 \phi^2 \\ &\leq C \left[\int e^{-\eta m} |\nabla \phi|^2 (m - \tilde{u})^2 + \int \phi^2 |m - \tilde{u}| + \int_{\partial \Omega} \phi^2 |m - \tilde{u}| \right] \\ &\leq C \|m - \tilde{u}\|_{L^\infty(\Omega)} \|\phi\|^2_{H^1(\Omega)}. \end{aligned}$$

This completes the proof. □

For later purposes, we state the following corollary, which follows from Lemmas 3.2 and 3.3.

Corollary 3.4. *For all $\phi_i \in H^1(\Omega)$, $i = 1, 2$,*

$$\int |\nabla \tilde{u} - \nabla m|^2 \frac{\phi_1 \phi_2}{\tilde{u}^2} \leq C \|\tilde{u} - m\|_{L^\infty(\Omega)} \left(\|\phi_1\|^2_{H^1(\Omega)} + \|\phi_2\|^2_{H^1(\Omega)} \right),$$

where $C = C(\eta)$ is independent of μ and uniformly bounded on compact subsets of $[0, \infty)$ in η.

Next, we prove a result on $\frac{\partial \tilde{u}}{\partial \eta}$.

Lemma 3.5. *As $\mu \to 0$, $\frac{\partial \tilde{u}}{\partial \eta} \to 0$ (strongly) in $H^1(\Omega)$ on compact subsets of $[0, \infty)$ in η.*

Proof. Denote $\frac{\partial \tilde{u}}{\partial \eta} = \tilde{u}'$ and differentiate (4) with respect to η, we have

$$\begin{cases} \mu\nabla\cdot(\nabla\tilde{u}' - \eta\tilde{u}'\nabla m) - (m-2\tilde{u})\tilde{u}' = \mu\nabla\cdot(\tilde{u}\nabla m) & \text{in } \Omega, \\ n\cdot(\nabla\tilde{u}' - \eta\tilde{u}'\nabla m) = n\cdot(\tilde{u}\nabla m) & \text{on } \partial\Omega. \end{cases} \tag{14}$$

Multiply (14) by $e^{-\eta m}\tilde{u}'$ and integrate by parts, we find

$$\mu\int e^{\eta m}|\nabla(e^{-\eta m}\tilde{u}')|^2 + \int(2\tilde{u}-m)e^{-\eta m}(\tilde{u}')^2 = \mu\int \tilde{u}\nabla m\cdot\nabla(e^{-\eta m}\tilde{u}'). \tag{15}$$

By Hölder's inequality and Lemma 3.2, we see that for each η, $\int|\nabla(e^{-\eta m}\tilde{u}')|^2 = O(1)$ and $\int(e^{-\eta m}\tilde{u}')^2 = O(\mu)$. Hence $e^{-\eta m}\tilde{u}' \rightharpoonup 0$ (weakly) in $H^1(\Omega)$. Upon considering (15) again, $e^{-\eta m}\tilde{u}' \to 0$ in $H^1(\Omega)$. □

Next, we show the following lemma.

Lemma 3.6. *As* $\mu \to 0$,

$$\frac{d}{d\eta}\left(\int \tilde{u}\nabla m\cdot\nabla(e^{-\eta m}\tilde{u})\right) \to -\int m\nabla m\cdot\nabla(e^{-\eta m}m^2),$$

uniformly on compact subsets of $[0,\infty)$ *in* η.

Proof. By Lemma 3.5, as $\mu \to 0$,

$$\begin{aligned} &\frac{d}{d\eta}\left(\int \tilde{u}\nabla m\cdot(e^{-\eta m}\tilde{u})\right) \\ &= \int \frac{\partial\tilde{u}}{\partial\eta}\nabla m\cdot\nabla(e^{-\eta m}\tilde{u}) - \int \tilde{u}\nabla m\cdot\nabla(e^{-\eta m}m\tilde{u}) + \int \tilde{u}\nabla m\cdot\nabla\left(e^{-\eta m}\frac{\partial\tilde{u}}{\partial\eta}\right) \\ &\to -\int m\nabla m\cdot\nabla(e^{-\eta m}m^2). \end{aligned}$$

This completes the proof. □

By Lemmas 3.3 and 3.6, we have the following result.

Corollary 3.7. *As* $\mu \to 0$,

$$\int \tilde{u}\nabla m\cdot\nabla(e^{-\eta m}\tilde{u}) \to g_0(\eta) := \int m\nabla m\cdot\nabla(e^{-\eta m}m) \quad \text{in } C^1_{loc}([0,\infty)). \tag{16}$$

Rewriting (7) as $g_0(\eta) = \int e^{-\eta m}m|\nabla m|^2(1-\eta m)$, we have

$$g_0(\eta) > 0 \text{ for } \eta \in \left[0, \frac{1}{\max_{\bar{\Omega}} m}\right] \text{ and } g_0(\eta) < 0 \text{ for } \eta \in \left[\frac{1}{\min_{\bar{\Omega}} m}, \infty\right). \tag{17}$$

And we see that for μ small, the roots of $\lambda_\xi(\eta,\eta;\mu) = 0$ and the roots of g_0 are in one-to-one correspondence, provided that the latter roots are non-degenerate.

3.3 Limit Problem for λ_ξ

By Lemma 3.1 and Corollary 3.7, the first step in establishing the existence of singular strategies is to study the roots of $g_0(\eta) = \int m\nabla m \cdot \nabla(e^{-\eta m} m)$. In this connection we have

Proposition 3.8. *Let $\Omega \subset \mathbb{R}^N$. Suppose that $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \le 3 + 2\sqrt{2}$. Then there exists $\eta_0 > 0$ such that* (i) *$g_0(\eta) > 0$ if $\eta \in [0, \eta_0)$;* (ii) *$g_0(\eta) = 0$ if $\eta = \eta_0$;* (iii) *$g_0(\eta) < 0$ if $\eta \in (\eta_0, \infty)$. Moreover, $g_0'(\eta_0) < 0$.*

Proof. By (17) it suffices to focus on $\eta \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$. We first consider the case $L := \frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} < 3 + 2\sqrt{2}$. Since

$$\frac{d}{d\eta} g_0(\eta) = \int |\nabla m|^2 m^2 (\eta m - 2) e^{-\eta m},$$

$g_0(\eta)$ is strictly decreasing in $\left[\frac{1}{\max_{\bar\Omega} m}, \frac{2}{\max_{\bar\Omega} m}\right]$. And we are done if $\frac{1}{\min_{\bar\Omega} m} \le \frac{2}{\max_{\bar\Omega} m}$. Therefore, in the following we assume $L \in (2, 3 + 2\sqrt{2})$. It remains to show that for all $\eta_1 \in [\frac{2}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}]$, there exists $p \in \mathbb{R}$ such that $\eta^p g_0(\eta)$ is strictly decreasing in some interval $[a, b]$ containing η_1. First we compute

$$\begin{aligned}\frac{d}{d\eta}\left(\eta^p g_0(\eta)\right) &= \frac{d}{d\eta}\left(\int |\nabla m|^2 m \eta^p (1 - \eta m) e^{-\eta m}\right)\\ &= \int |\nabla m|^2 m \eta^{p-1}[(\eta m)^2 - (p+2)\eta m + p].\end{aligned}$$

So

$$\eta^p g_0(\eta) \text{ is strictly decreasing if } \eta \in \left[\frac{p + 2 - \sqrt{p^2+4}}{2\min_{\bar\Omega} m}, \ \frac{p + 2 + \sqrt{p^2+4}}{2\max_{\bar\Omega} m}\right]. \tag{18}$$

Define $x_0 = 2$, $x_1 = 1 + \left(1 - \frac{2}{L}\right)^{-1}$ and $p_1 = \frac{2(2L-2)}{L(L-2)}$. In general, if $x_{i-1} \ge L$, we stop; else if $x_{i-1} < L$, we define

$$x_i = 1 + \left(1 - \frac{x_{i-1}}{L}\right)^{-1} \quad \text{and} \quad p_i = \frac{x_{i-1}(2L - x_{i-1})}{L(L - x_{i-1})} = \frac{\frac{x_{i-1}}{L}(2 - \frac{x_{i-1}}{L})}{1 - \frac{x_{i-1}}{L}}.$$

Claim 3.9. *For any $i \ge 1$ such that x_i, p_i are defined as above, $\eta^{p_i} g_0(\eta)$ is strictly decreasing in $\left[\frac{x_{i-1}}{\max_{\bar\Omega} m}, \frac{x_i}{\max_{\bar\Omega} m}\right]$.*

The claim follows from (18) by observing that for each i,

$$\frac{x_{i-1}}{L} = \frac{p_i + 2 - \sqrt{p_i^2 + 4}}{2} \quad \text{and} \quad x_i = \frac{p_i + 2 + \sqrt{p_i^2+4}}{2}, \tag{19}$$

which are consequences of the definitions of p_i and x_i respectively.

Next, we observe that $x_1 = 1 + \left(1 - \frac{2}{L}\right)^{-1} > x_0$, so by the identity

$$x_{i+1} - x_i = \frac{L(x_i - x_{i-1})}{(L - x_i)(L - x_{i-1})},$$

one can conclude that $\{x_i\}$ is strictly increasing in i.

Claim 3.10. *If $2 < L < 3+2\sqrt{2}$, then there exists i_0 such that $x_{i_0} \geq L$. That is, $\{x_i\}$ is a finite sequence.*

Suppose not, then $\{x_i\}_{i=0}^{\infty}$ is an increasing infinite sequence such that $x_i < L$ for all i. Then $s = \lim_{i\to\infty} x_i \leq L$ exists, and hence

$$s = 1 + \left(1 - \frac{s}{L}\right)^{-1} \qquad \text{for some } s.$$

This is equivalent to $-s^2 + (1+L)s - 2L = 0$ being solvable, i.e.,

$$(1+L)^2 - 8L \geq 0.$$

But this implies that $L \leq 3 - 2\sqrt{2}$ or $L \geq 3+2\sqrt{2}$. This is a contradiction.

Hence, by Claim 3.9, for each $i = 1, ..., i_0$, $\eta^{p_i} g_0(\eta)$ is strictly decreasing in $\left[\frac{x_{i-1}}{\max_{\bar\Omega} m}, \frac{x_i}{\max_{\bar\Omega} m}\right]$ with $x_{i_0} \geq L = \frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}$. This proves the Proposition for the case $L < 3+2\sqrt{2}$.

Now we take up the remaining case $L = 3+2\sqrt{2}$. By the same method above, one can show that $\{x_i\}$ forms an infinite increasing sequence such that $x_i \nearrow 2+\sqrt{2}$. Here $x_i < 2+\sqrt{2}$, since $x_1 < 2+\sqrt{2}$ and

$$\begin{aligned} x_{i+1} - (2+\sqrt{2}) &= \left(1 + \frac{1}{1 - \frac{x_i}{3+2\sqrt{2}}}\right) - \left(1 + \frac{1}{1 - \frac{2+\sqrt{2}}{3+2\sqrt{2}}}\right) \\ &= \frac{x_i - (2+\sqrt{2})}{(3+2\sqrt{2})\left(1 - \frac{x_i}{3+2\sqrt{2}}\right)\left(1 - \frac{2+\sqrt{2}}{3+2\sqrt{2}}\right)}. \end{aligned}$$

Then one may similarly show that for all $\eta_1 \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{2+\sqrt{2}}{\max_{\bar\Omega} m}\right)$, there exists i such that $\eta_1 \in \left[\frac{x_{i-1}}{\max_{\bar\Omega} m}, \frac{x_i}{\max_{\bar\Omega} m}\right]$ and that $\frac{d}{d\eta}[\eta^{p_i} g_0(\eta)] < 0$ in $\left[\frac{x_{i-1}}{\max_{\bar\Omega} m}, \frac{x_i}{\max_{\bar\Omega} m}\right]$.

Also, if one set $y_0 = 3+2\sqrt{2}$ and $y_{i+1} = (3+2\sqrt{2})\left(1 + \frac{1}{1-y_i}\right)$ and $q_i = \frac{y_{i-1}(2-y_{i-1})}{1-y_{i-1}}$, then one can prove similarly that $y_i \searrow 2+\sqrt{2}$ and that for all $\eta_2 \in \left(\frac{2+\sqrt{2}}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$, there exists i such that $\eta_2 \in \left[\frac{y_i}{\max_{\bar\Omega} m}, \frac{y_{i-1}}{\max_{\bar\Omega} m}\right]$ and that $\frac{d}{d\eta}[\eta^{q_i} g_0(\eta)] < 0$ in $\left[\frac{y_i}{\max_{\bar\Omega} m}, \frac{y_{i-1}}{\max_{\bar\Omega} m}\right]$.

This shows that even if $L = 3+2\sqrt{2}$, function $g_0(\eta)$ has a unique root $\eta_0 \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$. Moreover, $g_0'(\eta_0) < 0$ if $\eta_0 \neq \frac{2+\sqrt{2}}{\max_{\bar\Omega} m}$.

Lastly, we are going to argue that η_0 is also non-degenerate for the remaining case $\eta_0 = \frac{2+\sqrt{2}}{\max_{\bar\Omega} m}$. One can compute that

$$\frac{d}{d\eta}[\eta^2 g_0(\eta)] = \int |\nabla m|^2 [(\eta m)^3 - 4(\eta m)^2 + 2(\eta m)].$$

Setting $\eta = \eta_0 = \frac{2+\sqrt{2}}{\max_{\bar\Omega} m}$, then $\eta_0 m(x) \in [2-\sqrt{2}, 2+\sqrt{2}]$ in Ω and hence

$$\eta_0^2 g_0'(\eta_0) = \frac{d}{d\eta}[\eta^2 g_0(\eta)]\bigg|_{\eta=\eta_0} = \int |\nabla m|^2 [(\eta_0 m)^3 - 4(\eta_0 m)^2 + 2(\eta_0 m)] < 0.$$

This completes the proof. □

Remark 3.11. *The above proposition remains true if* $g_0(\eta) = \int_\Omega K(1-\eta m)e^{-\eta m}$ *for any non-negative function* $K \in L^1(\Omega)$.

3.4 Proofs of Theorem 2.2 and Corollary 2.3

Proof of Theorem 2.2. By Proposition 3.8, $g_0(\eta) = \int m\nabla m \cdot \nabla(e^{-\eta m}m)$ has a unique, non-degenerate root in $[0,\infty)$. Since

$$\int \tilde{u}\nabla m \cdot \nabla(e^{-\eta m}\tilde{u}) \to \int m\nabla m \cdot \nabla(e^{-\eta m}m)$$

in $C^1_{loc}([0,\infty))$ as $\mu \to 0$, we see that for any (large) $\Lambda > 0$, $\int \tilde{u}\nabla m \cdot \nabla(e^{-\eta m}\tilde{u})$ has a unique positive root in $[0,\Lambda]$ for all μ sufficiently small. By Lemma 3.1,

$$\frac{1}{\mu}\lambda_\xi(\eta,\eta;\mu) = -\frac{\int \tilde{u}\nabla m \cdot \nabla(e^{-\eta m}\tilde{u})}{\int e^{-\eta m}\tilde{u}^2}.$$

Therefore, given any $\Lambda > 0$, for sufficiently small μ, λ_ξ also changes sign exactly once in $[0,\Lambda]$. Moreover, denoting the unique root by $\hat{\eta}$, we see that $\hat{\eta} \to \eta_0$ as $\mu \to 0$, where η_0 is the unique positive root of $g_0(\eta)$. □

Finally, Corollary 2.3 follows from Theorem 2.2 and the following result:

Lemma 3.12 (Lemma 6.4 in [24])**.** *Let* $\Omega = (0,1)$. *Suppose that* $m, m_x > 0$ *in* $[0,1]$ *and* $\eta > 1/\min_{\bar{\Omega}} m$. *Then* $(e^{-\eta m}\tilde{u})_x < 0$ *for all* $x \in (0,1)$.

Proof of Corollary 2.3. Without loss of generality, assume $\Omega = (0,1)$. In view of Lemma 3.1 and Theorem 2.2, it suffices to show that

$$\lambda_\xi \int e^{-\eta m}\tilde{u}^2 = -\int \tilde{u}m_x(e^{-\eta m}\tilde{u})_x > 0 \qquad \text{for all } \eta > 1/\min_{\bar{\Omega}} m.$$

But this follows from the monotonicity of m and Lemma 3.12. □

4 Evolutionarily stable strategies

In this section we determine whether the singular strategy established in Theorem 2.2 is also evolutionarily stable. We first derive the formula of $\lambda_{\xi\xi}(\eta,\eta;\mu)$ in Subsect. 4.1. Subsect. 4.2 is devoted to various estimates of eigenfunctions for sufficiently small μ. The results from these two subsections enable us to obtain the limit of $\lambda_{\xi\xi}(\hat{\eta},\hat{\eta};\mu)/\mu$ as $\mu \to 0$. The sign of this limit is then determined in Subsect. 4.3, which plays the essential role in completing the proof of Theorem 2.5.

4.1 Formula for $\lambda_{\xi\xi}$

Differentiate (9) with respect to ξ, denoting $\frac{\partial^2\varphi}{\partial\xi^2} = \varphi_{\xi\xi}$ and $\frac{\partial^2\lambda}{\partial\xi^2} = \lambda_{\xi\xi}$, we have

$$\begin{cases} \mu\nabla\cdot(\nabla\varphi_{\xi\xi} - \xi\varphi_{\xi\xi}\nabla m) + \varphi_{\xi\xi}(m-\tilde{u}) + \lambda\varphi_{\xi\xi} \\ \qquad\qquad = 2\mu\nabla\cdot(\varphi_\xi\nabla m) - 2\lambda_\xi\varphi_\xi - \lambda_{\xi\xi}\varphi & \text{in } \Omega, \\ \frac{\partial\varphi_{\xi\xi}}{\partial n} - \xi\varphi_{\xi\xi}\frac{\partial m}{\partial n} = 2\varphi_\xi\frac{\partial m}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{20}$$

Set $\xi = \eta$, we have $\lambda = 0$, $\varphi = \tilde{u}$ and

$$\begin{cases} \mu\nabla\cdot(\nabla\varphi_{\xi\xi} - \eta\varphi_{\xi\xi}\nabla m) + \varphi_{\xi\xi}(m-\tilde{u}) = 2\mu\nabla\cdot(\varphi_\xi\nabla m) - 2\lambda_\xi\varphi_\xi - \lambda_{\xi\xi}\tilde{u} & \text{in } \Omega, \\ \frac{\partial\varphi_{\xi\xi}}{\partial n} - \eta\varphi_{\xi\xi}\frac{\partial m}{\partial n} = 2\varphi_\xi\frac{\partial m}{\partial n} & \text{on } \partial\Omega. \end{cases} \tag{21}$$

Multiplying (21) by $e^{-\eta m}\tilde{u}$, we obtain

$$\frac{\lambda_{\xi\xi}(\eta,\eta;\mu)}{\mu}\int e^{-\eta m}\tilde{u}^2 = -2\int \varphi_\xi\nabla m\cdot\nabla(e^{-\eta m}\tilde{u}) - 2\frac{\lambda_\xi}{\mu}\int e^{-\eta m}\varphi_\xi\tilde{u}, \tag{22}$$

where $\varphi_\xi = \varphi_\xi(\eta,\eta;\mu)$ is the unique solution to

$$\begin{cases} \mu\nabla\cdot(\nabla\varphi_\xi - \eta\varphi_\xi\nabla m) + \varphi_\xi(m-\tilde{u}) = \mu\nabla\cdot(\tilde{u}\nabla m) - \lambda_\xi\tilde{u} & \text{in } \Omega, \\ \frac{\partial\varphi_\xi}{\partial n} - \eta\varphi_\xi\frac{\partial m}{\partial n} = \tilde{u}\frac{\partial m}{\partial n} \quad \text{on } \partial\Omega, & \int e^{-\eta m}\varphi_\xi\tilde{u} = 0. \end{cases} \tag{23}$$

Hence, we have the following formula for $\lambda_{\xi\xi}$:

Lemma 4.1. *Suppose that η is a singular strategy, i.e., $\lambda_\xi(\eta,\eta;\mu) = 0$. Then*

$$\frac{\lambda_{\xi\xi}(\eta,\eta;\mu)}{\mu}\int e^{-\eta m}\tilde{u}^2 = -2\int \varphi_\xi\nabla m\cdot\nabla(e^{-\eta m}\tilde{u}), \tag{24}$$

where $\varphi_\xi = \varphi_\xi(\eta,\eta;\mu)$ is the unique solution to

$$\begin{cases} \mu\nabla\cdot(\nabla\varphi_\xi - \eta\varphi_\xi\nabla m) + \varphi_\xi(m-\tilde{u}) = \mu\nabla\cdot(\tilde{u}\nabla m) & \text{in } \Omega, \\ \frac{\partial\varphi_\xi}{\partial n} - \eta\varphi_\xi\frac{\partial m}{\partial n} = \tilde{u}\frac{\partial m}{\partial n} \quad \text{on } \partial\Omega, & \int e^{-\eta m}\varphi_\xi\tilde{u} = 0. \end{cases} \tag{25}$$

4.2 Estimates

Let (λ_k, φ_k) be the eigenpairs of (5) with $\xi = \eta$ and $\lambda_1 < \lambda_2 \le \lambda_3 \le \dots$. By the transformation $\phi = e^{-\eta m}\varphi$ and (4), (5) becomes

$$\begin{cases} \nabla\cdot(e^{\eta m}\nabla\phi) - \frac{\nabla\cdot[\nabla\tilde{u} - \eta\tilde{u}\nabla m]}{\tilde{u}}e^{\eta m}\phi + \frac{\lambda}{\mu}e^{\eta m}\phi = 0 & \text{in } \Omega, \\ n\cdot\nabla\phi = 0 & \text{on } \partial\Omega. \end{cases} \tag{26}$$

Then λ_k/μ is the k-th eigenvalue of (26). The following result determines the asymptotic behavior of λ_k as $\mu \to 0$.

Proposition 4.2. *As $\mu \to 0$, $\frac{\lambda_k}{\mu} \to \sigma_k$ locally uniformly in η, where $\lambda_k = \lambda_k(\eta,\eta;\mu)$ is the k-th eigenvalue of* (5) *when $\eta = \xi$, and $\sigma_k = \sigma_k(\eta)$ is the* k-th *eigenvalue of*

$$\begin{cases} \nabla\cdot(e^{\eta m}\nabla\phi) - \frac{\nabla\cdot[(1-\eta m)\nabla m]}{m}e^{\eta m}\phi + \sigma e^{\eta m}\phi = 0 & \text{in } \Omega, \\ n\cdot(\nabla\phi - \frac{(1-\eta m)\nabla m}{m}\phi) = 0 & \text{on } \partial\Omega, \end{cases} \tag{27}$$

satisfying $\sigma_1 < \sigma_2 \le \sigma_3 \le \dots$.

Remark 4.3. One can check that all σ_k are real, $\sigma_1 = 0$, and $me^{-\eta m}$ is an eigenfunction corresponding to σ_1. In particular, $\sigma_k > 0$ for $k \geq 2$.

Proof of Proposition 4.2. Let $\left(\frac{\lambda_k}{\mu}, \phi_k\right)$ denote the k-th eigenpair of (26), with ϕ_k normalized by $\int e^{\eta m}\phi_k^2 = 1$. Let

$$\begin{aligned} J_\mu(\phi) &= \frac{\int e^{\eta m}|\nabla\phi|^2 - \int e^{\eta m}\nabla(e^{-\eta m}\tilde{u})\cdot\nabla\left(\frac{\phi^2}{e^{-\eta m}\tilde{u}}\right)}{\int e^{\eta m}\phi^2} \\ &= \frac{\int e^{\eta m}|\nabla\phi|^2 + \int e^{\eta m}\frac{|\nabla(e^{-\eta m}\tilde{u})|^2}{(e^{-\eta m}\tilde{u})^2}\phi^2 - 2\int e^{\eta m}\frac{\nabla(e^{-\eta m}\tilde{u})}{e^{-\eta m}\tilde{u}}\phi\nabla\phi}{\int e^{\eta m}\phi^2}. \end{aligned}$$

Then by variational characterization,

$$\frac{\lambda_k}{\mu} = \inf J_\mu(\phi) = \inf\max J_\mu(\phi) \tag{28}$$

where the first infimum is taken over all $\phi \in C^1(\bar{\Omega})$ such that $\int e^{\eta m}\phi\phi_i = 0$ for all $i = 1, ..., k-1$. Whereas on the right hand side of the last equality, the maximum is taken over a given subspace $X_k \subset C^1(\bar{\Omega})$ of dimension k, and the infimum is taken over all such k-dimensional subspaces of $C^1(\bar{\Omega})$. In particular, $\frac{\lambda_k}{\mu} \geq 0$ as $J_\mu(\phi) \geq 0$ for all $\phi \in C^1(\bar{\Omega})$.

Similarly, let

$$J_0(\phi) = \frac{\int e^{\eta m}|\nabla\phi|^2 + \int e^{\eta m}\frac{|\nabla(e^{-\eta m}m)|^2}{(e^{-\eta m}m)^2}\phi^2 - 2\int e^{\eta m}\frac{\nabla(e^{-\eta m}m)}{e^{-\eta m}m}\phi\nabla\phi}{\int e^{\eta m}\phi^2}.$$

Then the k-th eigenvalue of (27) satisfies

$$\sigma_k = \inf\max J_0(\phi), \tag{29}$$

where the maximum is taken over a given k-dimensional subspace of $C^1(\bar{\Omega})$ and the infimum is taken over all such subspaces.

For any (fixed) $\phi \in C^1(\bar{\Omega})$, one can show by Lemma 3.3 that $J_\mu(\phi) \to J_0(\phi)$ as $\mu \to 0$. Hence for all k,

$$\limsup_{\mu\to 0}\frac{\lambda_k}{\mu} \leq \sigma_k. \tag{30}$$

In particular, for any k, $\frac{\lambda_k}{\mu}$ is uniformly bounded for all small μ. Since we have normalized the eigenfunction ϕ_k by $\int e^{\eta m}\phi_k^2 = 1$, then by (28), $\|\phi_k\|_{H^1(\Omega)}$ is bounded uniformly for all small μ. And we may assume, along a (diagonal) subsequence $\mu = \mu_j \to 0$, that for all k, $\frac{\lambda_k}{\mu} \to \liminf_{\mu\to 0}\frac{\lambda_k}{\mu}$ and ϕ_k converges weakly in $H^1(\Omega)$ to some non-zero $\bar{\phi}_k$.

On the other hand, multiply the equation of ϕ_k by a test function $\rho \in C^\infty(\bar{\Omega})$ and consider the weak formulation of (26):

$$-\int e^{\eta m}\nabla\phi_k\cdot\nabla\rho + \int(\nabla\tilde{u} - \eta\tilde{u}\nabla m)\cdot\nabla\left(\frac{e^{\eta m}\phi_k\rho}{\tilde{u}}\right) + \frac{\lambda_k}{\mu}\int e^{\eta m}\phi_k\rho = 0. \tag{31}$$

Claim 4.4. *For each $k \geq 1$, letting $\mu = \mu_j \to 0$, we have*

$$-\int e^{\eta m}\nabla\bar{\phi}_k \cdot \nabla\rho + \int [(1-\eta m)\nabla m] \cdot \nabla\left(\frac{e^{\eta m}\bar{\phi}_k\rho}{\tilde{u}}\right) + \left(\liminf_{\mu\to 0}\frac{\lambda_k}{\mu}\right)\int e^{\eta m}\bar{\phi}_k\rho = 0. \tag{32}$$

Firstly, by Lemma 3.3 it is easy to see that the first and third terms of (31) converge to the corresponding limits in (32).

$$-\int e^{\eta m}\nabla\phi_k\cdot\nabla\rho \to -\int e^{\eta m}\nabla\bar{\phi}_k\cdot\nabla\rho, \quad \frac{\lambda_k}{\mu}\int e^{\eta m}\phi_k\rho \to \left(\liminf_{\mu\to 0}\frac{\lambda_k}{\mu}\right)\int e^{\eta m}\bar{\phi}_k\rho.$$

Next, we rewrite the second term of (31) in the following way.

$$\int(\nabla\tilde{u} - \eta\tilde{u}\nabla m)\cdot\frac{\nabla(e^{\eta m}\phi_k\rho)}{\tilde{u}} + \int \eta\tilde{u}\nabla m\cdot\left(\frac{e^{\eta m}\phi_k\rho}{\tilde{u}^2}\nabla\tilde{u}\right) - \int|\nabla\tilde{u}|^2\frac{e^{\eta m}\phi_k\rho}{\tilde{u}^2}.$$

Then by Lemmas 3.2 and 3.3, the entire expression minus the last term converges.

$$\begin{aligned}&\int(\nabla\tilde{u} - \eta\tilde{u}\nabla m)\cdot\nabla\left(\frac{e^{\eta m}\phi_k\rho}{\tilde{u}}\right) + \int|\nabla\tilde{u}|^2\frac{e^{\eta m}\phi_k\rho}{\tilde{u}^2}\\ &\qquad \to \int(1-\eta m)\nabla m\cdot\nabla\left(\frac{e^{\eta m}\bar{\phi}_k\rho}{m}\right) + \int|\nabla m|^2\frac{e^{\eta m}\bar{\phi}_k\rho}{m^2}.\end{aligned}$$

It therefore remains to show that

$$\int|\nabla\tilde{u}|^2\frac{e^{\eta m}\phi_k\rho}{\tilde{u}^2} \to \int|\nabla m|^2\frac{e^{\eta m}\bar{\phi}_k\rho}{m^2},$$

which follows readily from

$$\begin{aligned}&\left|\int|\nabla\tilde{u}|^2\frac{e^{\eta m}\phi_k\rho}{\tilde{u}^2} - \int|\nabla m|^2\frac{e^{\eta m}\bar{\phi}_k\rho}{m^2}\right|\\ &\leq \left|\int(|\nabla\tilde{u}|^2 - |\nabla m|^2)\frac{e^{\eta m}\phi_k\rho}{\tilde{u}^2}\right| + \int|\nabla m|^2 e^{\eta m}\rho\left|\frac{\phi_k}{\tilde{u}^2} - \frac{\bar{\phi}_k}{m^2}\right|\\ &\leq C\left(|\tilde{u} - m|_{L^\infty(\Omega)} + |\phi_k - \bar{\phi}_k|_{L^2(\Omega)}\right) \to 0.\end{aligned}$$

Here we applied Corollary 3.4 to yield the last inequality. This proves Claim 4.4. As a consequence, $\bar{\phi}_1$ is the principal eigenfunction of (27) corresponding to σ_1. Hence (regardless of subsequence), $\lim_{\mu\to 0}\frac{\lambda_1}{\mu} = \sigma_1$. Next, for $k = 2$, we observe similarly that $\bar{\phi}_2$ is an eigenfunction of (27) with eigenvalue $\liminf_{\mu\to 0}\frac{\lambda_2}{\mu}$ satisfying $\int e^{\eta m}\bar{\phi}_2\bar{\phi}_1 = 0$. So $\liminf_{\mu\to 0}\frac{\lambda_2}{\mu} \geq \sigma_2$. Upon combining with (30), $\lim_{\mu\to 0}\frac{\lambda_2}{\mu} = \sigma_2$. Similarly, one can prove that $\lim_{\mu\to 0}\frac{\lambda_k}{\mu} = \sigma_k$ for all $k \geq 3$. This completes the proof. □

Next, we study the asymptotic behavior of $\varphi_\xi(\eta,\eta;\mu)$ as $\mu \to 0$. Recall that $\varphi_\xi(\eta,\eta;\mu)$ is the unique solution of (25). We shall assume that $\eta = \eta(\mu)$ is a singular strategy (i.e., $\lambda_\xi(\eta,\eta;\mu) = 0$) and $\eta \to \eta^*$ as $\mu \to 0$. Note that if $\frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} \leq 3 + 2\sqrt{2}$, then $\eta = \hat{\eta}(\mu)$ is the unique singular strategy as determined in Theorem 2.2, and $\eta^* = \eta_0$ is the unique positive root of $g_0(\eta) = \int m\nabla m\cdot\nabla(e^{-\eta m}m)$ as determined in Proposition 3.8.

Lemma 4.5. *Suppose that $\eta = \eta(\mu)$ is a singular strategy and $\eta \to \eta^*$ as $\mu \to 0$. By passing to a subsequence, $\varphi_\xi(\eta, \eta; \mu) \rightharpoonup \varphi'$ as $\mu \to 0$, where φ' is the unique solution to*

$$\begin{cases} \nabla \cdot (\nabla \varphi' - \eta^* \varphi' \nabla m) - \frac{\nabla \cdot [(1-\eta^* m)\nabla m]}{m} \varphi' = \nabla \cdot (m \nabla m) & \text{in } \Omega, \\ \frac{\partial \varphi'}{\partial n} - \frac{\varphi'}{m}\frac{\partial m}{\partial n} = m \frac{\partial m}{\partial n} & \text{on } \partial\Omega, \quad \int e^{-\eta^* m} \varphi' m = 0. \end{cases} \tag{33}$$

Proof. First we estimate $\|\nabla \varphi_\xi\|_{L^2(\Omega)}$ in terms of $\|\varphi_\xi\|_{L^2(\Omega)}$. To this end, multiply (25) by $e^{-\eta m}\varphi_\xi$ and integrate by parts, we obtain

$$\int e^{\eta m} |\nabla (e^{-\eta m} \varphi_\xi)|^2 - \int e^{\eta m} \nabla (e^{-\eta m} \tilde{u}) \cdot \nabla \left[\frac{(e^{-\eta m}\varphi_\xi)^2}{e^{-\eta m}\tilde{u}} \right] = \int \tilde{u} \nabla m \cdot \nabla (e^{-\eta m} \varphi_\xi) \tag{34}$$

which can be rewritten as

$$\begin{aligned} &\int e^{\eta m} |\nabla (e^{-\eta m} \varphi_\xi)|^2 + \int e^{\eta m} \frac{|\nabla (e^{-\eta m}\tilde{u})|^2}{(e^{-\eta m}\tilde{u})^2} (e^{-\eta m}\varphi_\xi)^2 \\ &= 2 \int e^{\eta m} \frac{\nabla (e^{-\eta m}\tilde{u}) \cdot \nabla (e^{-\eta m}\varphi_\xi)}{e^{-\eta m}\tilde{u}} e^{-\eta m}\varphi_\xi + \int \tilde{u} \nabla m \cdot \nabla (e^{-\eta m}\varphi_\xi). \end{aligned} \tag{35}$$

By Hölder's inequality, this yields

$$\begin{aligned} &\frac{1}{3} \int e^{\eta m} |\nabla (e^{-\eta m}\varphi_\xi)|^2 \\ &\le 2 \int e^{\eta m} \frac{|\nabla (e^{-\eta m}\tilde{u})|^2}{(e^{-\eta m}\tilde{u})^2} (e^{-\eta m}\varphi_\xi)^2 + \frac{3}{4} \int e^{-\eta m} \tilde{u}^2 |\nabla m|^2 \\ &\le C \left(\int |\nabla \tilde{u}|^2 (e^{-\eta m}\varphi_\xi)^2 + \int (e^{-\eta m}\varphi_\xi)^2 + 1 \right) \\ &\le C \int \left[|\nabla m|^2 + |\nabla \tilde{u} - \nabla m|^2 + 1 \right] (e^{-\eta m}\varphi_\xi)^2 + C \\ &\le C \left(\int (e^{-\eta m}\varphi_\xi)^2 + \|\tilde{u} - m\|_{L^\infty(\Omega)} \|e^{-\eta m}\varphi_\xi\|^2_{H^1(\Omega)} + 1 \right). \end{aligned}$$

The second and last inequalities follow from Lemmas 3.2 and 3.3 respectively. Hence, there is some constant C independent of μ small (and bounded locally uniformly in $\eta \ge 0$) such that

$$\int |\nabla \varphi_\xi|^2 \le C \left(\int (\varphi_\xi)^2 + 1 \right). \tag{36}$$

Next, we show that $\|\varphi_\xi\|_{L^2(\Omega)}$ is bounded uniformly as $\mu \to 0$. By applying the Poincaré's inequality and (34), we have

$$\begin{aligned} \frac{\lambda_2}{\mu} \int e^{-\eta m} (\varphi_\xi)^2 &\le \int e^{\eta m} |\nabla (e^{-\eta m}\varphi_\xi)|^2 - \int e^{\eta m} \nabla (e^{-\eta m}\tilde{u}) \cdot \nabla \left(\frac{e^{-\eta m}(\varphi_\xi)^2}{\tilde{u}} \right) \\ &= \int \tilde{u} \nabla m \cdot \nabla (e^{-\eta m}\varphi_\xi) \\ &\le C \left(\|\varphi_\xi\|_{H^1(\Omega)} + 1 \right). \end{aligned}$$

Combining with (36), we deduce that

$$\frac{\lambda_2}{\mu}\|\varphi_\xi\|^2_{L^2(\Omega)} \leq C\left(\|\varphi_\xi\|_{L^2(\Omega)} + 1\right).$$

By Proposition 4.2, $\frac{\lambda_2}{\mu} \to \sigma_2$ as $\mu \to 0$. Observe that $\sigma_1 = 0$ and it is simple, one can deduce that $\sigma_2 > 0$; see also Remark 4.3. So $\|\varphi_\xi\|_{L^2(\Omega)}$ is bounded independent of μ small. By this and (36), φ_ξ converges weakly in $H^1(\Omega)$ to some $\varphi_0 \in H^1(\Omega)$ satisfying $\int e^{-\eta^* m}\varphi_0 m = 0$. Passing to the limit using the weak formulation of (25), we see that $\varphi_0 = \varphi'$ by uniqueness. This proves the lemma. □

The following result is a direct consequence of Lemmas 4.1 and 4.5.

Corollary 4.6. *Suppose that $\eta = \eta(\mu)$ is a singular strategy and $\eta \to \eta^*$ as $\mu \to 0$. Then*

$$\lim_{\mu\to 0}\frac{\lambda_{\xi\xi}(\eta,\eta;\mu)}{\mu} = -\frac{2}{\int e^{-\eta^* m}m^2}\int_\Omega \varphi'\nabla m\cdot\nabla(e^{-\eta^* m}m), \tag{37}$$

where φ' is the unique solution of (33).

4.3 Limit problem for $\lambda_{\xi\xi}$

In this subsection we study, for sufficiently small μ, the sign of $\lambda_{\xi\xi}(\hat\eta,\hat\eta;\mu)$ when $\hat\eta$ is the unique singular strategy determined in Theorem 2.2. By Corollary 4.6, it suffices to study the sign of $\int \varphi'\nabla m\cdot(e^{-\eta_0 m}m)$, where φ' is the unique solution of (33) with $\eta^* = \eta_0$, where η_0 is a positive root of $g_0(\eta)$. A sufficient condition for the uniqueness of η_0 is given in Proposition 3.8. The main result of this subsection is

Proposition 4.7. *Suppose Ω is convex with diameter d. If m is non-constant and $d\|\nabla \ln m\|_{L^\infty(\Omega)} \leq \alpha_0$, then $\int \varphi'\nabla m\cdot\nabla(e^{-\eta_0 m}m) < 0$, where φ' is the unique solution to* (33) *(with $\eta^* = \eta_0$), $\alpha_0 \approx 0.814$ is the unique positive root of $t \mapsto 4t + e^{-t} + 2\ln t - 1 - 2\ln\pi$, and η_0 is given in Proposition* 3.8.

Remark 4.8. For a convex domain Ω with diameter d,

$$\ln\left(\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}\right) \leq d\|\nabla \ln m\|_{L^\infty(\Omega)}.$$

We do not expect a better result than $d\|\nabla \ln m\|_{L^\infty(\Omega)} \leq \ln(3+2\sqrt{2}) \approx 1.763$, as we shall see in later section that for any $L > 3 + 2\sqrt{2}$, there exist some m and $\bar\eta$ such that $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} = L$, $g_0(\bar\eta) = 0$ but $g_0'(\bar\eta) > 0$. This will imply that $\int \varphi'\nabla m\cdot\nabla(e^{-\eta m}) > 0$, by Lemma 4.11.

Let w denote the unique solution to

$$\begin{cases} \nabla\cdot(\nabla w - \eta w\nabla m) - \frac{\nabla\cdot[(1-\eta m)\nabla m]}{m} w = \nabla\cdot(m\nabla m) & \text{in } \Omega,\\ \frac{\partial w}{\partial n} - \frac{w}{m}\frac{\partial m}{\partial n} = m\frac{\partial m}{\partial n} \quad \text{on } \partial\Omega, & \int_\Omega m e^{-\eta m} w = 0. \end{cases} \tag{38}$$

It is clear that Proposition 4.7 follows from the following result:

Lemma 4.9. *Suppose that Ω is convex with diameter d. If m is non-constant, $\eta > 0$ satisfies $g_0(\eta) = 0$ and $d\|\nabla \ln m\|_{L^\infty(\Omega)} \leq \alpha_0$, then*

$$\int w\nabla m \cdot \nabla(e^{-\eta m} m) < 0.$$

Proof. First we note that by (17), necessarily $\eta \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$. Set $w = m(z + m)$. After some tedious but direct calculations we see that z satisfies

$$\begin{cases} \nabla \cdot [e^{-\eta m} m^2 \nabla z] + m e^{-\eta m} |\nabla m|^2 (1 - \eta m) = 0 & \text{in } \Omega, \\ \frac{\partial z}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{39}$$

Multiplying by z and integrate by parts, we have

$$\int e^{-\eta m} m^2 |\nabla z|^2 = \int z m e^{-\eta m} |\nabla m|^2 (1 - \eta m). \tag{40}$$

By (40) one can deduce

$$\int w\nabla m \cdot \nabla(e^{-\eta m} m) = \int e^{-\eta m} m^2 |\nabla z|^2 + \int m^2 |\nabla m|^2 e^{-\eta m} (1 - \eta m). \tag{41}$$

Now let $(\gamma_k, \phi_k)_{k=1}^\infty$ be the eigenpairs of the following problem:

$$\begin{cases} \nabla \cdot [m^2 e^{-\eta m} \nabla \phi] + \gamma m e^{-\eta m} \phi = 0 & \text{in } \Omega, \\ \frac{\partial \phi}{\partial n} = 0 & \text{on } \partial\Omega, \end{cases}$$

where $\gamma_1 < \gamma_2 \leq \gamma_3 \leq \dots$. Note that we have the orthogonality condition

$$\int m e^{-\eta m} \phi_k \phi_l = \delta_{kl}.$$

We may expand $z = \sum_{k=1}^\infty a_k \phi_k$. Then as $\gamma_1 = 0$,

$$-\nabla \cdot (m^2 e^{-\eta m} \nabla z) = \sum_{k=1}^\infty a_k \gamma_k m e^{-\eta m} \phi_k = m e^{-\eta m} \sum_{k=2}^\infty a_k \gamma_k \phi_k.$$

Similarly, we may expand $(1 - \eta m)|\nabla m|^2 = \sum_{k=1}^\infty b_k \phi_k$. Note that $b_1 = 0$ since $\phi_1 = 1$ and $g_0(\eta) = \int (1 - \eta m)|\nabla m|^2 m e^{-\eta m} = 0$. Hence,

$$(1 - \eta m)|\nabla m|^2 = \sum_{k=2}^\infty b_k \phi_k.$$

So by (39), $a_k\gamma_k = b_k$ for $k \geq 2$. Therefore, by (39),

$$\begin{aligned}
\int e^{-\eta m} m^2 |\nabla z|^2 &= -\int z \nabla \cdot (m^2 e^{-\eta m} \nabla z) \\
&= \int \left(\sum_{k=2}^{\infty} \frac{b_k}{\gamma_k} \phi_k \right) m e^{-\eta m} \left(\sum_{k=2}^{\infty} b_k \phi_k \right) \\
&= \int m e^{-\eta m} \sum_{k=2}^{\infty} \frac{b_k^2}{\gamma_k} \phi_k^2 \\
&\leq \frac{1}{\gamma_2} \int m e^{-\eta m} \sum_{k=2}^{\infty} b_k^2 \phi_k^2 \\
&= \frac{1}{\gamma_2} \int m e^{-\eta m} (1-\eta m)^2 |\nabla m|^4 \\
&\leq \frac{\|\nabla m\|^2_{L^\infty(\Omega)}}{\gamma_2} \int m e^{-\eta m} (\eta m - 1)^2 |\nabla m|^2 \\
&= \frac{\|\nabla (\eta m)\|^2_{L^\infty(\Omega)}}{\eta\gamma_2} \int m^2 e^{-\eta m} (\eta m - 1) |\nabla m|^2,
\end{aligned}$$

where we used $\int m e^{-\eta m} |\nabla m|^2 (\eta m - 1) = 0$ in the last equality. By (41) it suffices to obtain a sufficient condition for $\frac{\|\nabla(\eta m)\|^2_{L^\infty(\Omega)}}{\eta\gamma_2} < 1$. Notice that $\hat{\gamma}_2 := \eta\gamma_2$ is the second eigenvalue of

$$\begin{cases} \nabla \cdot [f_2(\eta m)\nabla\phi] + \hat{\gamma} f_1(\eta m)\phi = 0 & \text{in } \Omega, \\ \frac{\partial \phi}{\partial n} = 0 & \text{on } \partial\Omega, \end{cases}$$

where $f_1(t) = te^{-t}$ and $f_2(t) := t^2 e^{-t}$. Since $f_2(t)$ satisfies

$$f_2'(t) > 0 \quad \text{in } [0,2) \quad \text{and} \quad f_2'(t) < 0 \quad \text{in } (2,\infty),$$

we deduce that for each $t \geq 1$, $f_2(s) \geq \min\{f_2(t), f_2(t^{-1})\}$ for all $s \in [t^{-1}, t]$. In fact, for each $t \in [1, 3+2\sqrt{2}]$,

$$f_2(s) \geq f_2(t^{-1}) \qquad \text{for all } s \in [t^{-1}, t].$$

Hence $f_2(\eta m) \geq f_2\left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m}\right)$ in Ω provided $\eta \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$ and $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \leq 3+\sqrt{2}$ (see discussion after Theorem 2.5). We also have $f_1(\eta m) \leq e^{-1}$ in Ω. Therefore, by eigenvalue comparison,

$$\hat{\gamma}_2 = \eta\gamma_2 > \mu_2^N e f_2\left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m}\right) \geq \frac{\pi^2}{d^2} e f_2 \left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m}\right),$$

where μ_2^N denotes the second Neumann eigenvalue of the Laplacian of Ω. The last inequality follows from the following optimal estimate of μ_2^N for convex domains due to Payne and Weinberger.

Theorem 4.10 ([40]). *Suppose that Ω is a convex domain in $\mathbb{R}^N$ with diameter d, then*

$$\mu_2^N \geq \frac{\pi^2}{d^2}.$$

It remains to show

$$\frac{\pi^2}{d^2} e f_2 \left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m} \right) \geq \|\nabla \eta m\|^2_{L^\infty(\Omega)} \quad \text{for any } \eta \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m} \right]. \tag{42}$$

Let $s = \|\nabla \ln m\|_{L^\infty(\Omega)}$, then by the mean value theorem,

$$\ln(\max_{\bar\Omega} m) - \ln(\min_{\bar\Omega} m) \leq d \|\nabla \ln m\|_{L^\infty(\Omega)},$$

which is equivalent to

$$\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m} \geq e^{-d\|\nabla \ln m\|_{L^\infty(\Omega)}} = e^{-ds}. \tag{43}$$

Now, if $ds \leq \alpha_0$, then $4(ds) + e^{-ds} + 2\ln(ds) - 1 - 2\ln \pi \leq 0$ and this gives

$$\frac{\pi^2}{d^2} e^{-4ds} e^{1-e^{-ds}} \geq s^2.$$

By (43) and the monotonicity of $t \mapsto t^4 e^{1-t}$ in $[0,1]$,

$$\frac{\pi^2}{d^2} \left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m} \right)^4 e^{1-\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m}} \geq \|\nabla \ln m\|^2_{L^\infty(\Omega)} = \left\| \frac{\nabla m}{m} \right\|^2_{L^\infty(\Omega)}.$$

Divide both sides by $\left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m} \right)^2$, we have

$$\frac{\pi^2}{d^2} \left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m} \right)^2 e^{1-\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m}} \geq \left\| \frac{\nabla m}{m} \right\|^2_{L^\infty(\Omega)} \left(\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \right)^2$$

and hence

$$\frac{\pi^2}{d^2} e f_2 \left(\frac{\min_{\bar\Omega} m}{\max_{\bar\Omega} m} \right) \geq \|\nabla (\eta m)\|^2_{L^\infty(\Omega)} \quad \text{for any } \eta \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m} \right].$$

This proves (42) and concludes the proof of the lemma. □

The following result will be needed later in Sect. 5.

Lemma 4.11. *Let w denote the unique solution of* (38)*. Suppose that $g_0'(\eta) > 0$, then $\int w \nabla m \cdot \nabla (e^{-\eta m} m) > 0$.*

Proof. By (39), z can be characterized as a global minimizer of the functional

$$J(\tilde z) = \frac{1}{2} \int e^{-\eta m} m^2 |\nabla \tilde z|^2 + \int e^{-\eta m} m \tilde z |\nabla m|^2 (\eta m - 1).$$

By (40), we have $J(z) = -\frac{1}{2} \int e^{-\eta m} m^2 |\nabla z|^2$. Hence

$$\begin{aligned} -\frac{1}{2} \int e^{-\eta m} m^2 |\nabla z|^2 = J(z) \leq J(-m) &= \frac{1}{2} \int e^{-\eta m} m^2 |\nabla m|^2 (3 - 2\eta m) \\ &< \frac{1}{2} \int e^{-\eta m} m^2 |\nabla m|^2 (1 - \eta m), \end{aligned}$$

where we used assumption $g_0'(\eta) > 0$ in the last inequality. By (41), this is equivalent to $\int w \nabla m \cdot \nabla (e^{-\eta m} m) > 0$. □

4.4 Evolutionarily Stable Strategy

Proof of Theorem 2.5. By the assumptions,

$$\ln\left(\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m}\right) \le d\|\nabla \ln m\|_{L^\infty(\Omega)} \le \alpha_0 < \ln(3+2\sqrt{2}).$$

Hence $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \le 3+2\sqrt{2}$. By Theorem 2.2, for all μ sufficiently small, there exists a unique singular strategy, denoted by $\hat\eta = \hat\eta(\mu) \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$. Moreover, $\hat\eta \to \eta_0$ as $\mu \to 0$, where η_0 is the unique positive root of $g_0(\eta)$. Then, by Corollary 4.6 and Proposition 4.7, we have

$$\lim_{\mu\to 0} \frac{1}{\mu}\lambda_{\xi\xi}(\hat\eta,\hat\eta;\mu) = -\frac{2\int \varphi'\nabla m\cdot\nabla(e^{-\eta_0 m}m)}{\int e^{-\eta_0 m}m^2} > 0. \tag{44}$$

Therefore, since $\lambda(\hat\eta,\hat\eta;\mu) = \lambda_\xi(\hat\eta,\hat\eta;\mu) = 0$, for all μ small there exists $\delta = \delta(\mu) > 0$ such that $\lambda(\hat\eta,\xi;\mu) > 0$ if $\xi \in (\hat\eta-\delta,\hat\eta+\delta)\setminus\{\hat\eta\}$. Thus, the strategy $\eta = \hat\eta(\mu)$ is an ESS. □

5 Counterexample for $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} > 3+2\sqrt{2}$

To study the multiplicity of singular strategies when μ is small, by (17) it suffices to consider the number of roots of $g_0(\eta)$ for $\eta \in \left[\frac{1}{\max_{\bar\Omega} m}, \frac{1}{\min_{\bar\Omega} m}\right]$.

Suppose that $\Omega = (0,1)$ and m is non-decreasing (i.e. $m' \ge 0$), then by making the substitution $s = \eta m(x)$,

$$\eta^2 g_0(\eta) = \int_0^1 \eta |m'|^2(\eta m)(1-\eta m)e^{-\eta m}\,dx = \int_{\eta m(0)}^{\eta m(1)} m'(x)h(s)\,ds, \tag{45}$$

where $h(s) = s(1-s)e^{-s}$.

Proposition 5.1. *If $\Omega = (0,1)$ and $m(x) = a + (b-a)x$ for some $0 < a < b$, then $g_0(\eta)$ has exactly one root in $[0,\infty)$.*

Proof. Since $g_0(\eta) > 0$ in $[0, 1/b]$ and $g_0(\eta) < 0$ in $[1/a, \infty]$, it suffices to consider $\eta \in \left[\frac{1}{b}, \frac{1}{a}\right]$. Now $m'(x) \equiv (b-a)$. By (45),

$$\begin{aligned}\frac{d}{d\eta}\left(\frac{\eta^2}{b-a}g_0(\eta)\right) &= \frac{d}{d\eta}\left(\int_{\eta a}^{\eta b} h(s)\,ds\right)\\ &= h(\eta b)b - h(\eta a)a\\ &= \eta b(1-\eta b)e^{-\eta b}b - \eta a(1-\eta a)e^{-\eta a}a\\ &< 0\end{aligned}$$

for all $\eta \in \left[\frac{1}{b}, \frac{1}{a}\right]$. Hence $\eta^2 g_0(\eta)$ is strictly decreasing in $\left[\frac{1}{b}, \frac{1}{a}\right]$ and has exactly one root. □

Proposition 5.2. *For any $L > 3+2\sqrt{2}$, there exists $m \in C^2([0,1])$ satisfying $m, m' > 0$ in $[0,1]$, $\frac{m(1)}{m(0)} = L$ such that $g_0(\eta)$ has at least three positive roots.*

Proof. Since $g_0(1/\max_{\bar{\Omega}} m) > 0$ and $g_0(1/\min_{\bar{\Omega}} m) < 0$, it suffices to construct m such that

$$g_0(\eta_*) = 0 \quad \text{and} \quad \frac{d}{d\eta}\left(\eta^2 g_0(\eta)\right)\Big|_{\eta=\eta_*} > 0 \tag{46}$$

for some $\eta_* \in \left(\frac{1}{\max_{\bar{\Omega}} m}, \frac{1}{\min_{\bar{\Omega}} m}\right)$. To this end, first fix $L > 3+2\sqrt{2}$. Set $\min_{\bar{\Omega}} m = a = 1$ and $\max_{\bar{\Omega}} m = b = L$. Choose $\eta_* \in (1/L, 1)$ such that $\eta_* a < 2 - \sqrt{2}$ and $\eta_* b > 2+\sqrt{2}$. Such η_* exists as $L > 3+2\sqrt{2}$. Note that $sh'(s)+h(s) > 0$ if and only if $s < 2-\sqrt{2}$ or $s > 2+\sqrt{2}$. Hence, by our choice of η_*, $(\eta_* a)h'(\eta_* a) + h(\eta_* a) > 0$ and $(\eta_* b)h'(\eta_* b) + h(\eta_* b) > 0$. Furthermore, as $\eta_* a < 1 < \eta_* b$, we have $h(\eta_* a) > 0 > h(\eta_* b)$.

Let $m(x)$ be the piecewise linear function given by $m(0) = a$, $m(1) = b$, and

$$m'(x) = \begin{cases} L_1 & x \in \left[0, \frac{\epsilon}{L_1}\right] \\ L_2 & x \in \left[1 - \frac{\epsilon}{L_2}, 1\right] \\ L_3 := \frac{(b-\epsilon)-(a+\epsilon)}{1-\frac{\epsilon}{L_1}-\frac{\epsilon}{L_2}} & x \in \left(\frac{\epsilon}{L_1}, 1 - \frac{\epsilon}{L_2}\right), \end{cases}$$

where $\epsilon > 0$ is to be chosen small, and L_1, L_2 are to be chosen positive and large. Note that $L_3 \to b - a$ remains uniformly bounded for small ϵ and $L_1, L_2 \geq 1$. By the choices of m and η_*, we see that η_* satisfies $\eta_* \in \left(\frac{1}{\max_{\bar{\Omega}} m}, \frac{1}{\min_{\bar{\Omega}} m}\right)$. Then

$$\begin{aligned} \eta^2 g_0(\eta) &= L_1 \int_{\eta a}^{\eta(a+\epsilon)} h(s)\,ds + L_2 \int_{\eta(b-\epsilon)}^{\eta b} h(s)\,ds + L_3 \int_{\eta(a+\epsilon)}^{\eta(b-\epsilon)} h(s)\,ds \\ &:= L_1 I_1 + L_2 I_2 + L_3 I_3. \end{aligned}$$

Both $|I_3|$ and $|\frac{d}{d\eta} I_3|$ are uniformly bounded for $\epsilon > 0$ small:

$$\begin{aligned} I_3 &= H(\eta(b-\epsilon)) - H(\eta(a+\epsilon)), \quad H(s) = e^{-s}(s^2+s+1), \\ \frac{d}{d\eta} I_3 &= h(\eta(b-\epsilon))(b-\epsilon) - h(\eta(a+\epsilon))(a+\epsilon). \end{aligned}$$

It is easy to see that for sufficiently small ϵ,

$$I_1(\eta_*, \epsilon) \approx \epsilon h(\eta_* a) > 0 \quad \text{and } I_2(\eta_*, \epsilon) \approx \epsilon h(\eta_* b) < 0.$$

Therefore, for any $L_1 > 0$ large, there exists $L_2 > 0$ large such that $g_0(\eta_*) = 0$.

It remains to show that for sufficiently small $\epsilon > 0$

$$\frac{d}{d\eta} I_1\Big|_{\eta=\eta_*} > 0 \quad \text{and} \quad \frac{d}{d\eta} I_2\Big|_{\eta=\eta_*} > 0.$$

Firstly we compute $\frac{d}{d\eta} I_1$.

$$\begin{aligned} \frac{d}{d\eta} I_1 &= h(\eta(a+\epsilon))(a+\epsilon) - h(\eta(a))a \\ &= a[h(\eta(a+\epsilon)) - h(\eta a)] + \epsilon h(\eta a) \\ &= \epsilon[\eta a h'(\theta_1) + h(\eta(a+\epsilon))] \end{aligned}$$

where $\theta_1 \in (\eta a, \eta(a+\epsilon))$, and $\lim_{\epsilon\to 0}\left[\eta a h'(\theta_1) + h(\eta(a+\epsilon))\right] = \eta a h'(\eta a) + h(\eta a)$. Since $(\eta_* a)h'(\eta_* a) + h(\eta_* a) > 0$, we see that for sufficiently small $\epsilon > 0$ $\frac{d}{d\eta} I_1|_{\eta=\eta_*} > 0$.

Similarly,

$$\frac{d}{d\eta} I_2 = \epsilon[\eta b h'(\theta_2) + h(\eta(b-\epsilon))],$$

where $\theta_2 \in (\eta(b-\epsilon), \eta b)$ and $\lim_{\epsilon\to 0}\left[\eta b h'(\theta_2) + h(\eta(b-\epsilon))\right] = \eta b h'(\eta b) + h(\eta b)$. Since $(\eta_* b)h'(\eta_* b) + h(\eta_* b) > 0$, we see that for sufficiently small $\epsilon > 0$ $\frac{d}{d\eta} I_2|_{\eta=\eta_*} > 0$.

In conclusion, we have found a piecewise C^1 function m and some $\eta_* > 0$ such that (46) holds. Although the m constructed is only piecewise C^1, one can approximate it by $C^2(\bar{\Omega})$ functions $\tilde{m}$ such that $\frac{\max_{\bar{\Omega}} \tilde{m}}{\min_{\bar{\Omega}} \tilde{m}} = \frac{\max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m}$ and $\tilde{m} \to m$ in $W^{1,\infty}(\Omega)$. □

Remark 5.3. Let $\eta a = c$ and $\eta b = d$, it actually suffices to choose $0 < c < 1$ and $d > 1$ so that

$$dh'(d)h(c) > ch'(c)h(d) \quad \Leftrightarrow \quad h(c)(dh'(d) + th(d)) < h(d)(ch'(c) + th(c))$$

for some $t > 0$ that minimizes the ratio $\frac{d}{c} = \frac{\eta b}{\eta a} = \frac{b}{a}$. This reduces to minimizing the ratio of the roots of $s \mapsto sh'(s) + th(s)$ for various t and the optimal choice is $t = 1$, which is done above and gives the optimal ratio $\frac{2+\sqrt{2}}{2-\sqrt{2}} = 3 + 2\sqrt{2} \approx 5.828$.

Proof of Theorem 2.6. For each $L > 3 + 2\sqrt{2}$, let $\Omega = (0,1)$ and m be the monotone increasing function constructed in Proposition 5.2. By the proof of Proposition 5.2, there exists some η_* such that $g_0(\eta_*) = 0$ and $g_0'(\eta_*) > 0$. Then by Corollary 3.7 and Lemma 3.1, for sufficiently small μ, $\lambda_\xi(\eta, \eta; \mu) = 0$ has at least three positive roots. Furthermore, there exists some $\bar{\eta} = \bar{\eta}(\mu)$ such that $\lambda_\xi(\bar{\eta}, \bar{\eta}; \mu) = 0$ and $\bar{\eta} \to \eta_*$ as $\mu \to 0$. It follows from Lemma 4.11, Corollary 4.6, and $g_0'(\eta_*) > 0$ that for sufficiently small μ, $\lambda_{\xi\xi}(\bar{\eta}, \bar{\eta}; \mu) < 0$. In particular, for each sufficiently small μ, there exists some $\delta > 0$ such that $\lambda(\xi, \bar{\eta}; \mu) < 0$ for any ξ satisfying $0 < |\xi - \bar{\eta}| < \delta$. □

6 Discussion

We studied a two-species competition model in which the species have the same population dynamics but different dispersal strategies. Both species disperse by a combination of random diffusion and advection along environmental gradients, with the same random dispersal rate but different advection coefficients. We regard these advection coefficients as movement strategies of the species and ask how they will evolve. Results from previous works [10, 13, 24] on this model show that both small and large advection rates are selected against, which suggests that intermediate advection will be selected. In this work we show that the evolution of intermediate advection depends upon the spatial heterogeneity of the environment in a subtle way. To be more specific, we find that if the spatial environmental variation is less than a critical value, there exists an evolutionarily singular strategy, which is also unique and evolutionarily stable under suitable assumptions. If the spatial environmental variation exceeds the critical value, there can be at least three evolutionarily singularly strategies, one of which is not evolutionarily stable. We conjecture that there are two or more evolutionarily stable strategies for the later case.

In this paper the intrinsic growth rate m is assumed to be strictly positive everywhere. This means that, in the absence of interspecific and intraspecific competition, the birth rate is higher than the death rate in all regions. If we allow m to change sign, i.e., to incorporate unfavorable regions for the population, our proofs break down as they strongly rely on the positivity of m. It will be interesting to see whether comparable results can be obtained when m changes sign.

Acknowledgements The authors wish to thank the anonymous referees for their careful reading of the manuscript and helpful suggestions. This research was partially supported by the NSF grant DMS-1021179 and has been supported in part by the Mathematical Biosciences Institute and the National Science Foundation under grant DMS-0931642.

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