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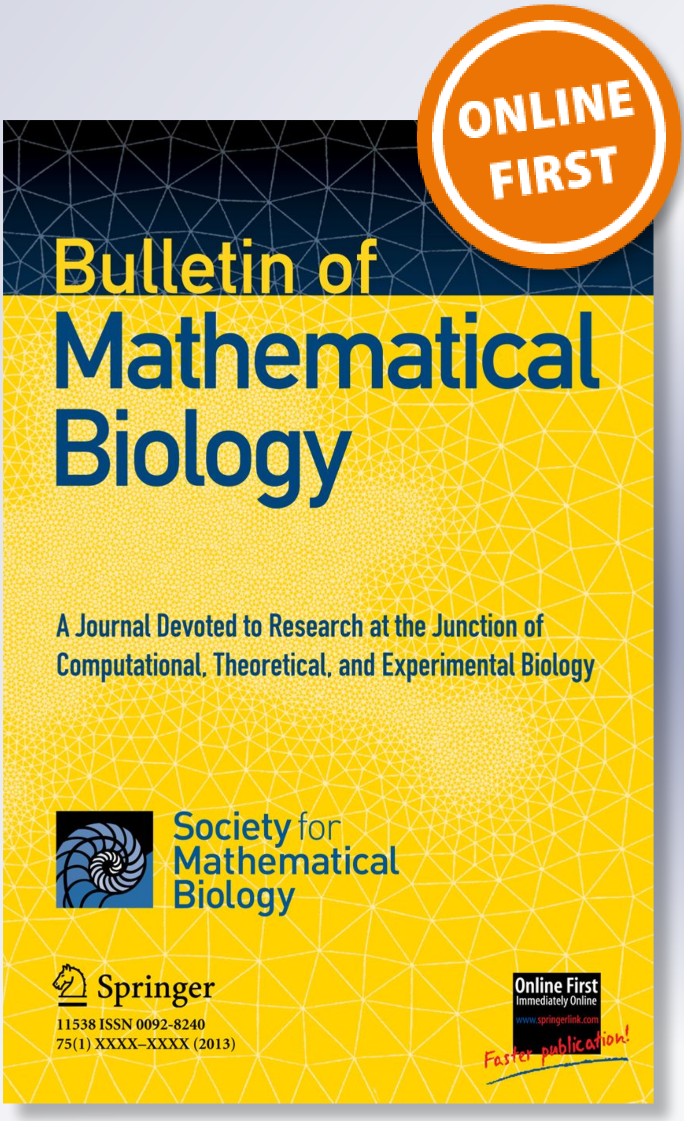

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ORIGINAL ARTICLE

Dimorphism by Singularity Theory in a Model for River Ecology

Martin Golubitsky[1] · **Wenrui Hao**[2] · **King-Yeung Lam**[1] · **Yuan Lou**[1,3]

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Abstract Geritz, Gyllenberg, Jacobs, and Parvinen show that two similar species can coexist only if their strategies are in a sector of parameter space near a nondegenerate evolutionarily singular strategy. We show that the dimorphism region can be more general by using the unfolding theory of Wang and Golubitsky near a degenerate evolutionarily singular strategy. Specifically, we use a PDE model of river species as an example of this approach. Our finding shows that the dimorphism region can exhibit various different forms that are strikingly different from previously known results in adaptive dynamics.

Keywords Adaptive dynamics · Singularity theory · Reaction–diffusion equation · River ecology

Mathematics Subject Classification 92D15 · 92D40 · 58K05 · 35K57

✉ King-Yeung Lam
lam.184@math.ohio-state.edu

Martin Golubitsky
golubitsky.4@osu.edu

Wenrui Hao
wxh64@psu.edu

Yuan Lou
lou@math.ohio-state.edu

[1] Department of Mathematics, The Ohio State University, Columbus, OH 43210, USA

[2] Department of Mathematics, Pennsylvania State University, State College, PA 16802, USA

[3] Institute for Mathematical Sciences, Renmin University of China, Beijing, China

1 Introduction

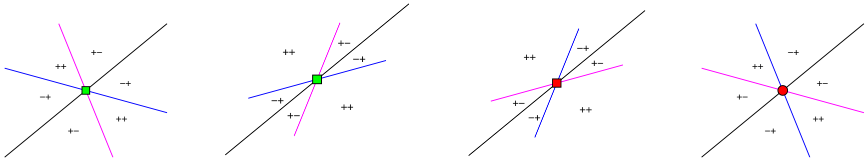
The niche concept is fundamental in ecology (Hutchinson 1957; Schoener 2009). Hutchinson (1957) states that a *fundamental niche* is a volume in which "every point …corresponds to a state of the environment that would permit the species …to exist indefinitely." A natural question is to determine how a fundamental niche of a particular species depends on its phenotypic trait, or *strategy*. We consider a family of species parametrized by a single real-valued strategy.

In general, the niches of two similar species playing nearby strategies tend to overlap, so that competition usually results in extinction of one of the species (Cantrell et al. 2017; Geritz et al. 2002). This fact has been studied using the framework of adaptive dynamics (Diekmann 2003). It is shown there that two similar species may coexist only if they are close to an evolutionarily singular strategy, which refers to the strategies at which the selection gradient vanishes.

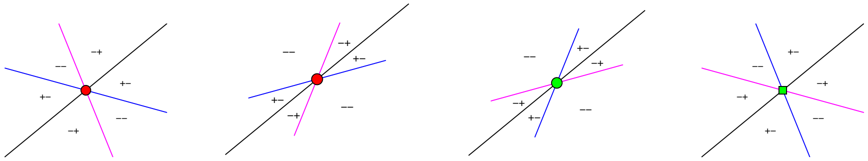
In this paper, we study the coexistence of two competing species in a PDE model of a river habitat with a spatially inhomogeneous environment. The diffusion rates of the two species are denoted by μ and ν; in evolutionary game theory these rates are considered to be strategies. The fitness function of this game, $\Lambda(\mu, \nu)$, is a smooth real-valued function that measures the advantage to the invader species playing strategy ν over the resident population playing strategy μ. In this formulation, the fitness function depends on the choice of environment (for example, resource distribution). Thus Λ is in fact a family of fitness functions, parametrized by environmental parameters. Our mathematical approach is to search for environmental parameters exhibiting unusual regions in strategy space of coexistence or dimorphism. Our analysis proceeds in two stages. First, we simplify the PDE by passing to the small dispersal limit, due to Averill et al. (2017). Second, we use the singularity and unfolding theories of fitness functions (Vutha and Golubitsky 2015; Wang and Golubitsky 2016) combined with numerical computation of derivatives of the fitness function at a degenerate singularity (Hao et al. 2012, 2013) to discover the surprising fundamental niches.

The PDE model is described in Sect. 2 (see (1)), as is the fitness function of the small dispersal limit (Proposition 3). The singularity theory of general fitness functions, studied in Wang and Golubitsky (2016), is described in Sect. 3. The formulae for the fitness function of the limiting system, together with its derivatives, in terms of parameters of the PDE model, are derived in Sect. 4. Finally, the numerical computation of fitness function derivatives is described in Sect. 5.

Our results are summarized by *mutual invasibility plots* (MIPs). The MIP associated with a fitness function Λ consists of two pieces of information. First, MIPs contain the union $\mathcal{V}$ of the zero sets of $\Lambda(\mu, \nu)$ and $\Lambda(\nu, \mu)$ (which always includes the diagonal since $\Lambda(\mu, \mu) = 0$ for all μ). Second, MIPs contain on each connected component of the complement of $\mathcal{V}$ a pair of signs, $\operatorname{sgn}(\Lambda(\nu, \mu))$ and $\operatorname{sgn}(\Lambda(\mu, \nu))$. By definition of the fitness function, two species playing strategies (μ_0, ν_0) coexist if and only if (μ_0, ν_0) belongs to the regions with $++$ signs. These regions are called *dimorphism regions*. The dimorphism regions are contained in the fundamental niche of each species.



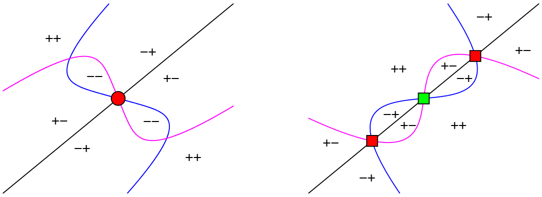
(a) $\tau = 1,\ \rho < -1$ **(b)** $\tau = 1,\ -1 < \rho < 0$ **(c)** $\tau = 1,\ 0 < \rho < 1$ **(d)** $\tau = 1,\ \rho > 1$



(e) $\tau = -1,\ \rho < -1$ **(f)** $\tau = -1,\ -1 < \rho < 0$ **(g)** $\tau = -1,\ 0 < \rho < 1$ **(h)** $\tau = -1,\ \rho > 1$

Fig. 1 The MIPs of the normal form fitness function $\Lambda(\mu, \nu) = \tau[\mu - \nu - \rho(\mu + \nu)](\mu - \nu)$ at $\mu = \nu = 0$ for $\rho \neq -1, 0, 1$ and $\tau = \pm 1$. Note that the diagonal $\mu = \nu$ is in *black*, the curve $\Lambda(\mu, \nu) = 0$ is in *pink*, and the curve $\Lambda(\nu, \mu) = 0$ is in *blue*. The pair of signs refer to those of $\Lambda(\nu, \mu)$ and $\Lambda(\mu, \nu)$. See Wang and Golubitsky (2016) (Color figure online)

Fig. 2 Interesting MIPs regions in the $\mu\nu$ plane obtained by a singularity theory analysis. The MIP on the left is Fig. 3c with $\tau = -1, \delta = 1$, while the MIP on the right is the right panel of Fig. 4 (Color figure online)



For the case when Λ has a singularity at a point (μ_0, μ_0) on the diagonal such that the Hessian of Λ at (μ_0, μ_0) is nondegenerate, the MIPs can be classified (Geritz et al. 1998; Wang and Golubitsky 2016). See Fig. 1.

Note that the region of mutual invasibility (++), when it exists, is shaped as a pair of sectors centered at the singular strategy (μ_0, μ_0) on the diagonal, i.e., coexistence of two strategies μ, ν close to an evolutionary strategy is possible provided that the ratio $(\mu - \mu_0)/(\nu - \mu_0)$ satisfies some restrictions. From a singularity theory point of view, the MIPs in Fig. 1 are the singularities of topological codimension zero (Wang and Golubitsky 2016). We show the existence of MIPs in the ecological river model that have the dimorphism regions indicated in Fig. 2. These MIPs are in the unfoldings of singularities of topological codimension one and two and do not exist only as sectors that touch the singularity. They are found by varying environmental parameters in order to identify the associated singularities. This search requires a combination of theory and numerics.

Observe that the dimorphism region in the left hand MIP in Fig. 2 is not a sector and is bounded away from the singularity. Also observe that the dimorphism region in the right hand MIP abuts on three different codimension zero singularities and is also not simply a sector.

Our approach is based on a new equivalence relation called *dimorphism equivalence*, from which a classification of mutual invasibility plots near an evolutionarily singular strategy is carried out for all singularities of topological codimension zero, one, and two (see Wang and Golubitsky 2016). The classification results are performed under minimal assumptions on the invasion fitness.

For each ecological situation, the invasion fitness is constrained by the biological details, which includes the environmental (biotic/abiotic) parameters that influence the population dynamics. It is interesting to see which classes of MIPs (and hence which dimorphism regions) are possible under these constraints.

Most previous efforts focused on determining the PIPs or MIPs for a set of given environmental conditions. Here we ask the reverse question: Up to dimorphism equivalence, which MIPs are possible in the context of evolution of dispersal?

2 A Reaction–Diffusion-Advection Model in Ecology

The following reaction–diffusion–advection system (1) was considered in Lam et al. (2014). The system models the population dynamics of two competing species in a river habitat represented by an interval $I = (0, 1)$.

$$\begin{array}{ll}
U_t = (\mu U_x - \alpha U)_x + U(r(x) - U - V) & \text{for } x \in (0,1), t \in (0,\infty) \\
V_t = (\nu V_x - \beta V)_x + V(r(x) - U - V) & \text{for } x \in (0,1), t \in (0,\infty) \\
\mu U_x - \alpha U = \nu V_x - \beta V = 0 & \text{for } x = 0, \text{ and } t \in (0,\infty) \\
\mu U_x - \alpha U = -q_1 U, \quad \nu V_x - \beta V = -q_2 V & \text{for } x = 1, \text{ and } t \in (0,\infty) \\
U(x,0) = U_0(x), \quad V(x,0) = V_0(x) & \text{for } x \in (0,1).
\end{array} \tag{1}$$

The species with density $U(x,t)$ (resp. $V(x,t)$) has diffusion rate μ (resp. ν) and is subject to a downstream (in the direction of increasing x) drift with rate α (resp. β); the function $r(x)$ represents the quality of the environment at spatial location x. No-flux boundary condition is imposed at the upstream end ($x = 0$) so that there is no net movement across the upstream boundary for either species. At the downstream end, the population $U(x,t)$ (resp. $V(x,t)$) is subject to a boundary loss with rate q_1 (resp. q_2).

There have been many studies of population dynamics in rivers using reaction–diffusion–advection models, such as the persistence of single species (Lutscher et al. 2006; Pachepsky et al. 2005; Speirs and Gurney 2001; Vasilyeva and Lutscher 2011), the range of species (Lam et al. 2016; Lutscher et al. 2007), and the coexistence of competing species (Vasilyeva and Lutscher 2012a, b). In recent years, there has been increased interest in the evolution of dispersal in rivers. For example, faster dispersal can evolve in advective homogeneous environments (Lou and Lutscher 2014; Lou and Zhou 2015). By contrast, much less is known about the evolution of dispersal in advective heterogeneous environments (Lam et al. 2014; Zhao and Zhou 2016).

Adaptive dynamics is used in Lam et al. (2014) to study heterogeneous river environments. Therein the existence and multiplicity of singular strategies and evolutionarily stable strategies in (1) are established. The dynamics of (1) (for example, the shapes of dimorphism regions in parameter space) remains a mystery. In this paper we use the unfolding theory of Wang and Golubitsky (2016) near a degenerate evolutionarily singular strategy, to show that dimorphism regions can exhibit various forms that are strikingly different from previous results in adaptive dynamics. We expect the general approach, demonstrated in this paper for a specific reaction–diffusion model, to be applicable for a range of models in mathematical ecology where the fitness function $\Lambda(\mu,\nu)$ can be calculated explicitly.

In this paper we consider for simplicity the special case $\alpha=\beta$; that is, the river imposes the same downward drift to the two species, whose strategies are parametrized by the diffusion rates. Moreover, we impose no-flux boundary condition for each of the species, which for instance models a river terminating at a hydroelectric dam with fish traps that keep the fish from going through the turbines. Other biological scenarios include phytoplankton species in a water column in a lake with different turbulent diffusion rates and the same downward gravity. In this case (1) becomes

$$\begin{array}{ll} U_t=(\mu U_x-\alpha U)_x+U(r(x)-U-V) & \text{for } x\in(0,1), t\in(0,\infty) \\ V_t=(\nu V_x-\alpha V)_x+V(r(x)-U-V) & \text{for } x\in(0,1), t\in(0,\infty) \\ \mu U_x-\alpha U=\nu V_x-\alpha V=0 & \text{for } x=0,1, \text{ and } t\in(0,\infty) \\ U(x,0)=U_0(x), \quad V(x,0)=V_0(x) & \text{for } x\in(0,1). \end{array} \tag{2}$$

System (2) has a trivial steady state $(0,0)$, as well as two steady states $(\theta_{\mu,\alpha},0)$ and $(0,\theta_{\nu,\beta})$ where only one species is present. Here, for each $\mu>0$ and $\alpha\geq 0$, $\theta_{\mu,\alpha}$ is the unique positive solution to the following equation:

$$\begin{array}{ll} (\mu\theta_x-\alpha\theta)_x+\theta(r(x)-\theta)=0 & \text{for } x\in(0,1) \\ \mu\theta_x-\alpha\theta=0 & \text{for } x=0,1 \end{array} \tag{3}$$

Note that $\theta_{\mu,\alpha}$ exists provided that, for example, $r(x)$ is Hölder continuous in $[0,1]$ and

$$\int_0^1 e^{(\alpha/\mu)x} r(x)\,\mathrm{d}x>0; \tag{4}$$

See, e.g., Cantrell and Cosner (2003). In this paper, we will consider the case that $r(x)>0$ so that (4) always holds.

For each choice of *habitat quality function* $r(x)$, there is a corresponding fitness function $\Lambda(\mu,\nu)$ which in turn determines a unique MIP. (Sometimes $r(x)$ is also called the *resource distribution function*.) By varying $r(x)$, we ask which kind of MIPs can be found, up to dimorphism equivalence? More generally, can one quantify in some way the dependence of MIPs on $r(x)$? It will be ecologically meaningful to focus on the ++ region of the MIP, which gives the parameter region in strategy space where both species coexist. In this paper, we apply adaptive dynamics and singularity theory to tackle the above questions.

The framework of adaptive dynamics anticipates the outcome when a resident population with density $U(x,t)$, adopting a given strategy μ at ecological equilibrium, is facing invasion by a rare mutant with density $V(x,t)$, adopting a different strategy ν. Mathematically, the outcome of the invasion is determined by the fitness function $\Lambda(\mu,\nu)$, which is given by the principal eigenvalue of the following problem:

$$\begin{cases} (\nu\varphi_x - \alpha\varphi)_x + (r(x) - \theta_{\mu,\alpha})\varphi = \Lambda\varphi & \text{for } x \in (0,1) \\ \nu\varphi_x - \alpha\varphi = 0 & \text{for } x = 0, 1 \end{cases} \tag{5}$$

The fitness function $\Lambda(\mu, \nu)$ is a smooth function that is implicitly defined in terms of the strategies μ, ν, as well as the environment $r(x)$. Roughly speaking, the invasion fitness $\Lambda(\mu, \nu)$ gives the initial exponential growth/decay rate of the mutant with density $V(x, t)$ as it invades a resident population adopting strategy μ, i.e., when $\Lambda(\mu, \nu) > 0$, the rare mutant with density $v(x, t)$ grows exponentially. When $\Lambda(\mu, \nu) < 0$, the rare mutant decays exponentially. It is therefore of interest to determine the zero set of $\Lambda(\mu, \nu)$, which divides the parameter space into where the (mutual) invasion is a success or a failure.

In which circumstance can two similar species coexist? A necessary condition is given by the following result by Cantrell et al. (2017), which generalizes the work of Geritz et al. (2002) on a system of two ODEs modeling two competing species.

Theorem 1 *(Cantrell et al. 2017) If $\partial_\nu\Lambda(\nu_0, \nu_0) > 0$ for some ν_0, then there exists $\delta > 0$ such that for any μ, ν satisfying $\nu_0 - \delta < \mu < \nu < \nu_0 + \delta$, $(0, \theta_{\nu,\alpha})$ is globally asymptotically stable among all nonnegative, nontrivial solutions of* (2).

A similar conclusion holds for $\partial_\nu\Lambda(\nu_0, \nu_0) < 0$. Therefore, coexistence of two nearby strategies is only possible near such ν_0 at which $\partial_\nu\Lambda(\nu_0, \nu_0) = 0$. Following conventions in adaptive dynamics, we call such a strategy an *evolutionarily singular strategy*.

The invasion fitness function $\Lambda(\mu, \nu)$ also classifies the region of mutual invasibility, which is sufficient to guarantee the persistence of both species.

Proposition 2 (Hsu et al. (1996)) *If $\Lambda(\mu, \nu) > 0$ and $\Lambda(\nu, \mu) > 0$, then there exists $\delta_0 > 0$ so that for any solution (U, V) of* (2) *such that the initial conditions satisfy $U_0 \not\equiv 0$ and $V_0 \not\equiv 0$,*

$$\liminf_{t\to\infty} U(x,t) \geq \delta_0 \quad \text{and} \quad \liminf V(x,t) \geq \delta_0.$$

Moreover, (2) has at least one stable coexistence steady state.

2.1 Limiting Problem

As already mentioned, the fitness function $\Lambda(\mu, \nu)$ is defined implicitly in terms of μ, ν and $r(x)$ and is in general difficult to compute. In this subsection, we shall pass to a limit problem by following the analytical framework of [Averill et al. (2017), Sect. 3.2.2], which yields a limiting fitness function that depends more explicitly on parameters. This allows for more direct numerical computations to be carried out. Specifically, let $\varepsilon > 0$ be a parameter and set

$$\alpha = \varepsilon, \quad \mu = \varepsilon\eta, \quad \nu = \varepsilon\xi.$$

We consider the regime of small dispersal, and let $\varepsilon \to 0$. The resulting limit of $\Lambda(\mu, \nu)$ as $\varepsilon \to 0$, which determines the limit MIPs, can be characterized as follows. This is based on arguments in [Averill et al. (2017), Sect. 3.2.2].

Proposition 3 *As* $\varepsilon \to 0$, $\varepsilon^{-1}\Lambda(\varepsilon\eta, \varepsilon\xi) \to \lambda(\eta, \xi)$ *locally uniformly in* $\mathbb{R}^2_+$, *where* $\lambda(\eta, \xi)$ *is the principal eigenvalue of*

$$\begin{aligned} \xi\phi_{xx} + \phi_x - \tfrac{1}{r(x)}[\eta r_x(x) - r(x)]_x\phi &= \lambda\phi \textit{ for } x \in (0, 1) \\ \xi\phi_x - \tfrac{1}{r(x)}[\eta r_x(x) - r(x)]\phi &= 0 \quad \textit{for } x = 0, 1 \end{aligned} \tag{6}$$

Moreover, the positive eigenfunction ϕ *can be uniquely determined by the normalizing condition*

$$\int_0^1 e^{2x/(\xi+\eta)}\phi^2\,dx = \int_0^1 e^{-2x/(\xi+\eta)}r^2\,dx.$$

Remark 4 The eigenvalue λ is a smooth function of the strategies η, ξ. Note that $\lambda = 0$ when $\eta = \xi$ and the normalized principal eigenfunction is $\phi(x) = e^{-x/\eta}r(x)$.

Proof By the fact that $r(x) > 0$ and [Lam et al. (2014), Lemma 5.1], the unique positive solution $\theta_{\mu,\alpha}$ (with $\mu = \varepsilon\eta$ and $\alpha = \varepsilon$) satisfies, as $\varepsilon \to 0$,

$$\theta_{\mu,\alpha} \to r \quad \text{in } C([0, 1]) \cap H^1((0, 1)). \tag{7}$$

Write $\theta = \theta_{\mu,\alpha} = \theta_{\eta\varepsilon,\varepsilon}$, and rewrite the eigenvalue problem (5) as

$$\begin{aligned} \xi\varphi_{xx} - \varphi_x + \tfrac{r-\theta}{\varepsilon}\varphi &= \tfrac{\Lambda}{\varepsilon}\varphi \quad \text{for } 0 < x < 1, \\ \xi\varphi_x - \varphi &= 0 \quad\;\; \text{for } x = 0, 1. \end{aligned}$$

Let $\phi = e^{-x/\xi}\varphi$, and by the Eq. (3), we have

$$\begin{aligned} \xi\phi_{xx} + \phi_x - \tfrac{(\eta\theta_x - \theta)_x}{\theta}\phi &= \tfrac{\Lambda}{\varepsilon}\phi \quad \text{for } 0 < x < 1, \\ \phi_x &= 0 \quad\;\; \text{for } x = 0, 1. \end{aligned} \tag{8}$$

By variational characterization,

$$\frac{\Lambda(\varepsilon\eta, \varepsilon\xi)}{\varepsilon} = \sup_{\psi \in H^1((0,1))} \frac{\int_0^1 \left[-\xi e^{x/\xi}|\psi_x|^2 + (\eta\theta_x - \theta)\left(\frac{e^{x/\xi}\psi^2}{\theta}\right)_x\right] \mathrm{d}x}{\int_0^1 e^{x/\xi}\psi^2\,\mathrm{d}x}. \tag{9}$$

Letting $\varepsilon \to 0$ and using (7), we deduce that $\Lambda(\varepsilon\eta, \varepsilon\xi)/\varepsilon \to \lambda(\eta, \xi)$, where

$$\lambda(\eta, \xi) = \sup_{\psi \in H^1((0,1))} \frac{\int_0^1 \left[-\xi e^{x/\xi}|\psi_x|^2 + (\eta r_x - r)\left(\frac{e^{x/\xi}\psi^2}{r}\right)_x\right] \mathrm{d}x}{\int_0^1 e^{x/\xi}\psi^2\,\mathrm{d}x}.$$

Finally, it is straight forward to verify that the eigenvalue problem satisfied by $\lambda = \lambda(\eta, \xi)$ is given by (6). □

By Proposition 3, for $0 < \varepsilon \ll 1$ the MIP of $\Lambda(\mu, \nu)$ is qualitatively equivalent to that of $\lambda(\eta, \xi)$. In other words, each type of MIP for the limiting fitness function $\lambda(\eta, \xi)$ can indeed be realized as MIP for the fitness function $\Lambda(\mu, \nu)$ of the original problem. With this in mind, we will focus in the remainder of this paper on the limiting fitness function $\lambda(\eta, \xi)$.

3 Singularity Theory of Adaptive Game Theory

A fitness function in a two-player single trait game is a function $\lambda : \mathbf{R}^2 \to \mathbf{R}$ (denoted $\lambda(\xi, \eta)$) that satisfies $\lambda(\xi, \xi) = 0$ for all ξ. Such functions have a *singularity* if $\lambda_\xi = \lambda_\eta = 0$. Along the diagonal $\eta = \xi$ a singularity occurs if $\lambda_\xi(\xi, \xi) = 0$. *Mutual invasibility plots* (MIPs) provide the vehicle for the application of singularity theory to adaptive dynamics. We now describe MIPs.

The MIP corresponding to a fitness function λ is a diagram in the $\eta\xi$-plane consisting of three curves and pairs of signs ($+$ or $-$) in each connected component of the complement of the union of the three curves. The curves are $\lambda(\eta, \xi) = 0$, $\lambda(\xi, \eta) = 0$, and the diagonal $\xi = \eta$. Note that the second curve is just the reflection of the first curve across the principal diagonal. The pair of signs are $\operatorname{sign}(\lambda(\xi, \eta))$ and $\operatorname{sign}(\lambda(\eta, \xi))$, and these signs are constant on the aforementioned connected components. These signs are important because regions whose signs are $++$ lead to the possibility of dimorphism pairs in adaptive dynamics and the coexistence of two species.

Wang and Golubitsky (2016), building on Vutha and Golubitsky (2015), introduce the notion of *dimorphism equivalence* and show that two dimorphism equivalent fitness functions have the same singularity and unfolding structures, and their MIPs are qualitatively the same. Thus, we can use singularity theory to detect complicated behavior in MIPs by searching for degenerate singularities in λ and applying unfolding theory.

The defining conditions and universal unfoldings with respect to dimorphism equivalence for all singularities of fitness functions through topological codimension two are determined in Wang and Golubitsky (2016). The MIPS of the well-known codimension zero singularities are shown in Fig. 1. The singularity theory of Wang and Golubitsky (2016) presents a way of finding all small perturbations of a fitness function singularity.

It is shown in Wang and Golubitsky (2016) that fitness functions can be written in the form

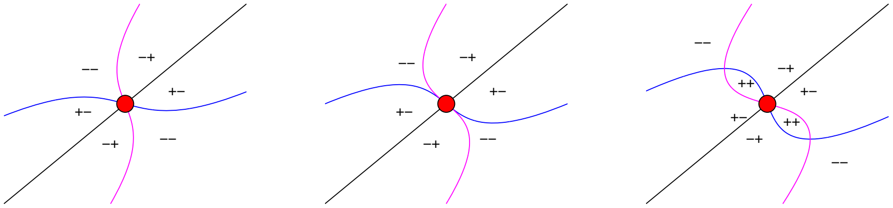
$$\lambda(\eta, \xi) = p(u, w)w + q(u, w)v,$$

where $u = \xi + \eta$, $v = \xi - \eta$, and $w = v^2$. In these coordinates, the diagonal $\eta = \xi$ occurs at $v = 0$ and a singularity occurs when $q(u, 0) = 0$.

We recall two singularities, one of codimension one and one of topological codimension two.

3.1 A Codimension One Singularity

Perhaps the most interesting codimension one singularity appears in Fig. 3. Using the notation in [Wang and Golubitsky (2016), Table 3], this singularity is called (d) and is defined by



(a) $a < 0$ **(b)** $a = 0$ **(c)** $a > 0$

Fig. 3 MIPs of $\lambda = \tau\Big[\Big(a + \delta v^2\Big)v^2 + uv\Big]$ in (13) where $\tau = \delta = +1$ (Color figure online)

$$p = q = 0 \tag{10}$$

along with the nondegeneracy conditions

$$q_u \neq 0 \quad \text{and} \quad p_w q_u - p_u q_w \neq 0. \tag{11}$$

Theorem 5 *Assume the defining conditions* (10) *and the nondegeneracy conditions* (11)*. Then* $\lambda(u, v)$ *is dimorphism equivalent to*

$$\tau\left(\delta w^2 + uv\right) \tag{12}$$

where $\tau = \operatorname{sgn}(q_u)$ *and* $\delta = \operatorname{sgn}(p_w q_u - p_u q_w)$*. A universal unfolding of (12) is*

$$\tau\left((a + \delta w)w + uv\right) \tag{13}$$

where a *is the universal unfolding parameter.*

Regions of coexistence emerge from the perturbation of a singular fitness function λ. The MIP of λ is the middle plot of Fig. 3, and we see no region of coexistence $(++)$. If we perturb the parameter to $a > 0$ (as in the right plot), the strategy function has two regions of coexistence; whereas, when $a < 0$ (as in the left plot), the strategy function has no region of coexistence. We can think of this singular strategy as creating regions of coexistence. Note that $-\lambda$ also leads to interesting MIPs and it is this codimension one singularity that occurs in our ecological model. See Fig. 5.

3.2 A Topological Codimension Two Singularity

The defining conditions of one of the three types of codimension two singularities in Wang and Golubitsky (2016) at a point on the line $v = 0$ of the uv-plane are:

$$q = q_u = q_{uu} = 0 \tag{14}$$

See (Wang and Golubitsky 2016, Table 4g).

Theorem 6 (Wang and Golubitsky (2016)) *Assume the defining conditions* (14) *and certain nondegeneracy conditions. Then* $\lambda(u, v)$ *is dimorphism equivalent to*

$$\tau\left(w + \left(\delta u^3 + \mu u^5\right) v\right) \tag{15}$$

where $\tau = \pm 1$ *and* $\delta = \pm 1$. *Up to dimorphism equivalence, the normal form for the universal unfolding of* (15) *is*

$$\tau\left(w + \left(\delta u^3 + \mu u^5\right)v + (a + bu)v\right) \tag{16}$$

where a, b *are universal unfolding parameters and* μ *is a modal parameter.*

Remark 7 Modal parameters are parameters μ that cannot be eliminated by dimorphism equivalence, but do not affect (over open sets of its values) the MIPs in a universal unfolding. Such parameters are standard in singularity theory. The modal parameter μ in (15) and (16) does not change MIPs over all of its values.

As is typical in universal unfolding theory, there are regions near the origin in the *ab* parameter plane that have qualitatively similar MIPs. More precisely, there exists a *transition variety* in the *ab*-plane across which MIPs change, and structural stability of MIPs hold in connected components of the complement of the transition variety. The transition varieties (left) and their structurally stable perturbations (right) for the universal unfoldings listed in Theorem 6 are shown in Fig. 4.

There are four singularities in (15) distinguished by the signs of τ and δ. Observe that changing the sign of τ just transforms λ to $-\lambda$. It follows that all signs in the MIPs are reversed (+ to − and − to +). In (14) changing the signs of τ, δ, a, b, μ transforms $\lambda(\xi, \eta)$ to $\lambda(\eta, \xi)$. So the transformed MIPs are obtained by either changing all of the signs or by reflecting across the principal diagonal or by a combination of both transformations.

3.3 Derivatives of *p*, *q* in Terms of Fitness Function

In order to compute the defining conditions in (10) and (14), we need to compute the derivatives of p and q in terms of λ. The relevant derivatives are

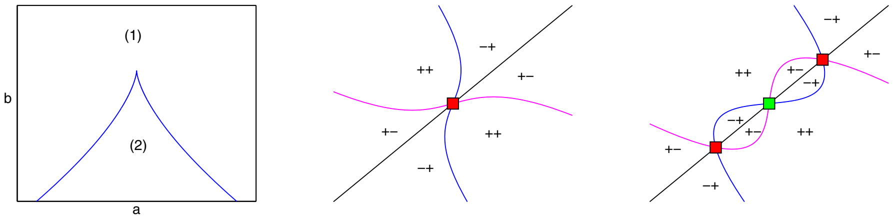


Fig. 4 When $\mu = 0$, the transition variety of (15) with $\tau = \delta = 1$ is $27a^2 + 4b^3 = 0$. The structurally stable MIPs are given by (1) $27a^2 + 4b^3 > 0$ and (2) $27a^2 + 4b^3 < 0$ (Color figure online)

$$\begin{aligned} q(u,0) &= \lambda_v(u,0) \\ p(u,0) &= \frac{1}{2}\lambda_{vv}(u,0) \\ q_u(u,0) &= \lambda_{uv}(u,0) \\ q_{uu}(u,0) &= \lambda_{uuv}(u,0) \end{aligned} \tag{17}$$

Proof Write $\lambda = p(u, v^2)v^2 + q(u, v^2)v$. The odd powers of v in λ are in $q(u, v^2)v$, and the even powers are in $p(u, v^2)v^2$. We can write the Taylor series of qv to cubic order in v as

$$q(u, v^2)v = q(u,0)v + q_w(u,0)v^3 + \cdots$$

In particular,

$$\lambda_v(u,0) = q(u,0), \quad \lambda_{uv}(u,0) = q_u(u,0), \text{ and } \lambda_{vuu}(u,0) = q_{uu}(u,0),$$

as claimed in (17). Similarly, we can write the Taylor series of pv^2 to fourth order in v as

$$p(u, v^2)v^2 = p(u,0)v^2 + p_w(u,0)v^4 + \cdots$$

In particular, $\lambda_{vv}(u,0)/2 = p(u,0)$, as claimed in (17). □

Due to (17), the two sets of defining conditions (10) and (14) can now be stated in terms of derivatives of λ, as follows.

Theorem 8 *In terms of derivatives of λ, the defining conditions of the normal form* (12) *are*

$$\lambda_v(u,0) = \lambda_{vv}(u,0) = 0 \tag{18}$$

and the defining conditions of the normal form (15) *are*

$$\lambda_v(u,0) = \lambda_{vu}(u,0) = \lambda_{vuu}(u,0) = 0. \tag{19}$$

4 Formulae for Derivatives of the Limiting Fitness Function λ in (17)

Let $\xi = (u+v)/2$ and $\eta = (u-v)/2$, then (6) may be written as

$$\begin{aligned} L(u,v)[\phi] &:= (u+v)\phi_{xx} + 2\phi_x - \tfrac{1}{r}[(u-v)r_x - 2r]_x\phi = 2\lambda\phi \quad \text{for } x \in (0,1) \\ B(u,v)[\phi] &:= (u+v)\phi_x - \tfrac{1}{r}[(u-v)r_x - 2r]\phi \qquad = \quad 0 \quad \text{at } x = 0,1 \end{aligned} \tag{20}$$

where $\int_0^1 e^{2x/u}\phi^2\,\mathrm{d}x = \int_0^1 e^{-2x/u}r^2\,\mathrm{d}x$.

We obtain the following formulae which enable us to compute the defining conditions for the singularities (12) and (15):

Proposition 9 *Let* $(\lambda(u,v),\phi)$ *be the principal eigenpair of the problem* (20).

(i) $\lambda_v(u,0)=0$ *if and only if*

$$\int_0^1 r_x(e^{-2x/u}r)_x\,dx=0.$$

(ii) *Assume* $\lambda_v(u,0)=0$. *Then* $\lambda_{vu}(u,0)=0$ *if and only if*

$$\int_0^1 r_x(e^{-2x/u}xr)_x\,dx=0.$$

(iii) *Assume* $\lambda_v(u,0)=\lambda_{vu}(u,0)=0$. *Then* $\lambda_{vuu}(u,0)=0$ *if and only if*

$$\int_0^1 r_x(e^{-2x/u}x^2r)_x\,dx=0.$$

(iv) *If* $\lambda_v(u,0)=0$, *then* $\lambda_{vv}(u,0)=0$ *if and only if*

$$\int_0^1 r_x(\phi_v)_x\,dx=0$$

where ϕ_v *is determined by*

$$\begin{aligned} L(u,0)[\phi_v]&=-\left((e^{-2x/u}r)_{xx}+r_{xx}e^{-2x/u}\right)\\ B(u,0)[\phi_v]&=-\left((e^{-2x/u}r)_x+r_xe^{-2x/u}\right)\end{aligned}\tag{21}$$

and the constraint $\int_0^1\phi_v r\,dx=0$.

Proof Differentiate (20) with respect to v, and denote $\phi'=\phi_v$, then we have

$$\begin{aligned} &(u+v)\phi'_{xx}+\phi_{xx}+2\phi'_x-\tfrac{[(u-v)r_x-2r]_x}{r}\phi'+\tfrac{r_{xx}}{r}\phi=2(\lambda\phi'+\lambda_v\phi) && \text{for } x\in(0,1)\\ &(u+v)\phi'_x+\phi_x-\tfrac{(u-v)r_x-2r}{r}\phi'+\tfrac{r_x}{r}\phi\qquad\qquad\quad=0 && \text{at } x=0,1\end{aligned}\tag{22}$$

where $\int_0^1 e^{2x/u}\phi'\phi\,\mathrm{d}x=0$. Setting $v=0$, so that $\lambda=0$ and $\phi=e^{-2x/u}r$. Rewrite (22) as

$$\begin{aligned} u(e^{2x/u}\phi'_x)_x-u\frac{\left[e^{2x/u}(e^{-2x/u}r)_x\right]_x}{e^{-2x/u}r}\phi'&=-e^{2x/u}(e^{-2x/u}r)_{xx}-r_{xx}+2\lambda_v r\\ ue^{2x/u}\phi'_x-u\frac{e^{2x/u}(e^{2x/u}r)_x}{e^{-2x/u}r}\phi'&=-e^{2x/u}(e^{-2x/u}r)_x-r_x\quad\text{at } x=0,1.\end{aligned}$$

Multiplying by $e^{-2x/u}r(x)$ and integrating by parts, we arrive at

$$2\lambda_v(u,0)\int_0^1 e^{-2x/u}r^2\,\mathrm{d}x = -2\int_0^1 r_x(e^{-2x/u}r)_x\,\mathrm{d}x. \tag{23}$$

This proves (i).

Differentiate (23) with respect to u, we obtain

$$\begin{aligned}\lambda_{vu}\int_0^1 e^{-2x/u}r^2\,\mathrm{d}x + \frac{2}{u^2}\lambda_v(u,0)\int_0^1 e^{-2x/u}xr^2\,\mathrm{d}x\\ = -\frac{2}{u^2}\int_0^1 r_x(e^{-2/u}xr)_x\,\mathrm{d}x\end{aligned} \tag{24}$$

where $\lambda_{vu} = \lambda_{vu}(u,0)$. This proves (ii). (iii) can be obtained by differentiating (24) with respect to u.

For (iv), differentiate (22) with respect to v to yield (denote $\phi'' = \phi_{vv}$)

$$\begin{array}{ll} L(u,v)[\phi''] + 2\phi'_{xx} + 2\frac{r_{xx}}{r}\phi' = 2(\lambda\phi'' + 2\lambda_v\phi' + \lambda_{vv}\phi) & \text{for } x \in (0,1),\\ B(u,v)[\phi''] + 2\phi'_x + 2\frac{r_x}{r}\phi' = 0 & \text{for } x = 0, 1 \end{array}$$

Setting $v = 0$, so that $\lambda = \lambda_v = 0$ and $\phi = e^{-2x/u}r$, we have

$$\begin{array}{ll} L(u,0)[\phi''] + 2\phi'_{xx} + 2\frac{r_{xx}}{r}\phi' = 2\lambda_{vv}e^{-2x/u}r & \text{for } x \in (0,1),\\ B(u,0)[\phi''] + 2\phi'_x + 2\frac{r_x}{r}\phi' = 0 & \text{for } x = 0, 1. \end{array}$$

Multiplying the above by $r(x)$ and integrating by parts similarly as part (i), we obtain

$$2\lambda_{vv}\int_0^1 e^{-2x/u}r^2\,\mathrm{d}x = -4\int_0^1 r_x\phi'_x,$$

and (iv) is proved. □

5 Numerical Results

In this section, we numerically identify special choices of the habitat quality function $r(x)$ corresponding to the singularities with defining conditions (10) and (14). Then we apply a homotopy method to compute the transition variety near each singularity (which is a consequence of unfolding theory). Finally, for each component of the complement of the transition variety, a representative MIP is plotted numerically. We remark that $r(x) > 0$ holds in all the numerical examples, which is consistent with the persistence criterion (4) as well as the limiting arguments in Proposition 3.

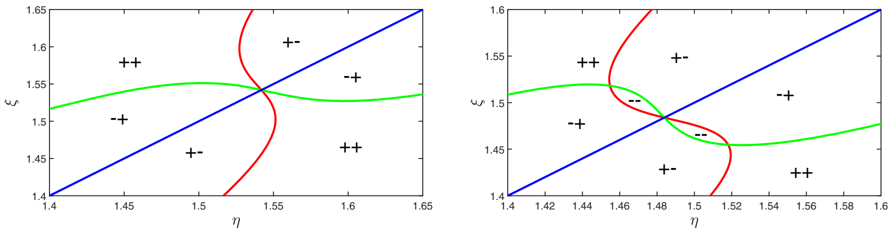


Fig. 5 Numerically computed MIPs showing the existence of the codimension one singularity (12) in river model: (*Left*) $c = -0.065$; (*Right*) $c = -0.05$. The *red curve* is the nondiagonal portion of the zero set of $\lambda(\eta, \xi)$, and the *green curve* is the nondiagonal portion of the zero set of $\lambda(\xi, \eta)$. The signs in the figures are $\text{sgn}(\lambda(\xi, \eta))\text{sgn}(\lambda(\eta, \xi))$ (Color figure online)

5.1 A Singularity of Codimension One

Let the habitat quality function be given by

$$r(x) = 1 + x + cx^3,$$

where c is a parameter. By varying c, we search for a singularity $(u, 0)$ satisfying the defining conditions (10) of the normal form (12). By Theorem 8 and Proposition 9 (i,iv), this search is equivalent to solving

$$\begin{pmatrix} \int_0^1 r_x (e^{-2x/u} r)_x \, \mathrm{d}x \\ \int_0^1 r_x (\phi_v)_x \, \mathrm{d}x \end{pmatrix} = 0 \tag{25}$$

where ϕ_v is given by (21). Using Newton's method, we find a root to (25); namely,

$$(u_s, c_s) = (2.975468, -0.058082).$$

We pick two representative parameter values $c = -0.065$ and $c = -0.05$ belonging to distinct regions in the transition variety. The MIPs corresponding to these two cases are shown in Fig. 5 (cf. Fig. 3).

5.2 A Singularity of Topological Codimension Two

Let

$$r(x) = 1 + x + bx^2 + cx^3,$$

where b, c are parameters. We search for b, c so that the corresponding MIP has a singularity satisfying the defining condition of (14). By Theorem 8 (ii) and Proposition 9 (i,ii,iii), it is equivalent to solving

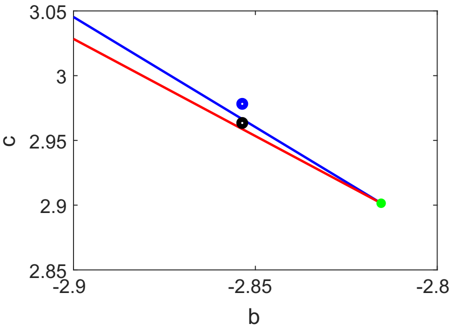


Fig. 6 Numerically computed transition variety showing the existence of normal form (15) in the river model: the cusp point is $(b_s, c_s) = (-7.176831, 9.166792)$ (Color figure online)

$$\begin{pmatrix} \int_0^1 r_x(e^{-2x/u}r)_x \,\mathrm{d}x \\ \int_0^1 r_x(e^{-2x/u}xr)_x \,\mathrm{d}x \\ \int_0^1 r_x(e^{-2x/u}x^2r)_x \,\mathrm{d}x \end{pmatrix} = 0 \tag{26}$$

for unknowns u, b, c. By using Newton's method with the initial guess $(u_0, b_0, c_0) = (0.1, 0.1, 0.1)$, we find a singularity of (26) at

$$(u_s, b_s, c_s) = (0.340778, -7.176831, 9.166792).$$

Next, we obtain the transition variety in the bc-plane. This yields a description of the structural change in MIPs in terms of the environmental function $r(x)$. Numerically, this can be achieved by solving the first two Equations in (26) for unknowns b, c in terms of the parameter u, which varies from 0.2 to 0.34. The transition variety in the bc-plane is shown in Fig. 6, where the red and blue curves are tracked from the singularity point (b_s, c_s) by employing a homotopy continuation method (Hao et al. 2012, 2013). Next, we pick two points in different regions of the complement of the transition variety: $(-8, 10.8)$ and $(-8, 12)$, which are the black and blue dots in Fig. 6. The MIPs corresponding to these two points are shown in Fig. 7 (cf. Fig. 4).

6 Conclusions and Discussions

The reaction–diffusion–advection model considered in this paper and the small dispersal limit was investigated in Lam et al. (2014). From the point of view of conservation and management, it is of interest to explore the influence of environmental parameters on the evolutionary dynamics of river organisms. Specifically, how does the habitat quality function $r(x)$ influence MIPs? Previous work has answered this question in situations leading to codimension zero singularities.

If r_x/r equals the constant c (that is, $r(x) = e^{cx}$), then the species with strategy $\mu = \alpha/c$ matches the resource distribution perfectly at the equilibrium $\theta_{\mu,\alpha}(x) \equiv r(x)$. The ideal free dispersal strategy is an evolutionarily stable strategy (Cantrell et al. 2007, 2010; Fretwell and Lucas 1970; Krivan et al. 2008). What about dispersal strategies that do not give rise to ideal free distributions, that is, when r_x/r is nonconstant?

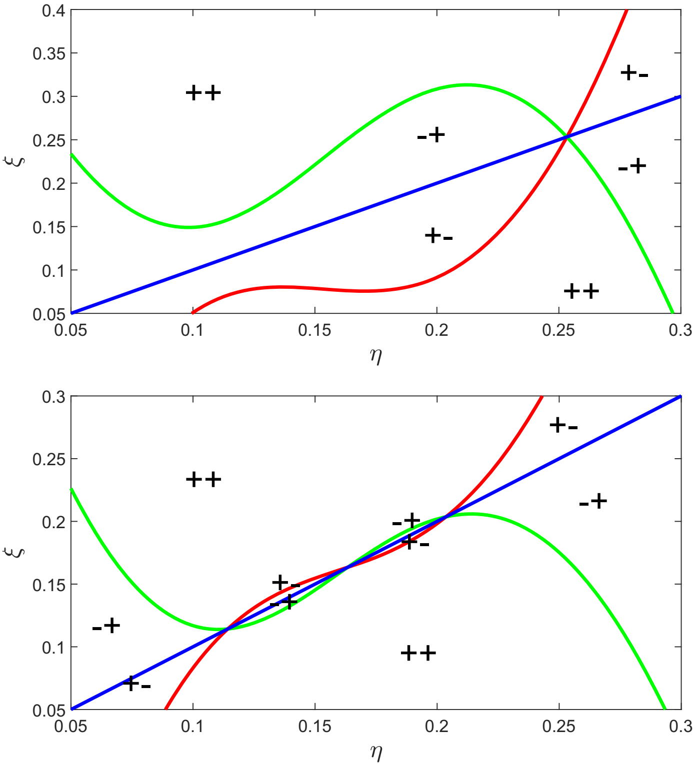


Fig. 7 Numerically computed MIPs in different connected components of the complement of the transition variety in Fig. 6. For the top panel, $(b, c) = (-8, 12)$; for the lower panel, $(b, c) = (-8, 10.8)$. Compare with Fig. 4. The *red curve* is the nondiagonal portion of the zero set of $\lambda(\eta, \xi)$ and the *green curve* is the nondiagonal portion of the zero set of $\lambda(\xi, \eta)$. The signs in the figures are $\text{sgn}(\lambda(\xi, \eta))\text{sgn}(\lambda(\eta, \xi))$ (Color figure online)

Let $\lambda(\eta, \xi)$ be the fitness function determined by (6) and assume $r(x) > 0$ and $r_x(x) > 0$ for all x. We recall the following results in Lam et al. (2014):

- If r_x/r is monotone, then there is a unique singular strategy $\hat{\eta}$ for the fitness function λ.
- If r_x/r is monotone decreasing, then $\lambda(\hat{\eta}, \xi) < 0$ for all ξ near $\hat{\eta}$ with $\xi \neq \hat{\eta}$. That is, the unique singular strategy $\hat{\eta}$ is locally an *evolutionarily stable strategy* (ESS). See the codimension zero MIP in Fig. 1e.
- If r_x/r is monotone increasing, then $\lambda(\hat{\eta}, \xi) > 0$ for all ξ near $\hat{\eta}$ with $\xi \neq \hat{\eta}$. That is, the unique singular strategy $\hat{\eta}$ is an *evolutionarily branching point* (BP). See the codimension zero MIP in Fig. 1f.

Note that the transition between ESS and BP does not lead to qualitatively different MIPs. However, the transition between other codimension zero MIPs do lead to qualitative changes in MIPs and it is this singularity theory fact that we use to discover new MIPs in the river model.

The bulleted results give sufficient conditions on $r(x)$ for two different configurations of MIPs, where the convexity of $\log r(x)$ determines whether the unique singular strategy $\hat{\eta}$ is an ESS or a BP. Roughly speaking, there is less spatial heterogeneity when r_x/r is decreasing; the river behaves like a single patch and there is an ESS $\hat{\eta}$ that can prevent the invasion of all nearby strategies. On the other hand, the river behaves like a two-patch model (upstream, downstream) when r_x/r is increasing: There is no single strategy that can defend itself against invasion by all different strategies. Following this line of reasoning, general $r(x)$ will likely divide the river into yet more patches, resulting in yet more complex MIPs.

With minimal assumption on the strategy function, namely $\lambda(\xi, \eta)$ vanishes on the diagonal, the singularity theory classification of strategy functions by codimension developed in Wang and Golubitsky (2016) offers a menu of MIPs that are likely to occur near a singular strategy. In applications, however, details of the specific ecological situation further constrain the number of potential MIPs. For example, in the river model (2), the resident and invader species compete for resources that is heterogeneous distributed according to the function $r(x)$. Although we have demonstrated that various MIPs can indeed be obtained by varying $r(x)$, what is perhaps also important is to determine the kinds of MIPs that can never be realized no matter how $r(x)$ is chosen. The family of MIPs that can/cannot be realized thus provides a signature of the kind of ecological interaction under investigation. Indeed, a singular strategy of a fitness function with a nondegenerate Hessian corresponds to one of 8 possible singularities of codimension zero (Diekmann 2003, p. 19). It is, however, proved in Lam and Lou (2014b) that for the limit fitness function λ of a closely related model, every ESS is necessarily convergent stable as well. Thus, at least one of these 8 MIPs (namely Fig. 1f) is never realized for the model. In this sense, the range of possible MIPs provides important information concerning of the ecology that is independent of parameters in the model.

By varying the habitat quality function $r(x)$, we searched for two singularities from the classification in Wang and Golubitsky (2016), one of codimension one and one of codimension two, whose unfoldings give five different kinds of MIPs, up to dimorphism equivalence. The two MIPs obtained from the unfolding of the codimension one singularity show two different shapes of the dimorphism region near an ESS $\hat{\eta}$. The MIP of Fig. 5 (left) is qualitatively similar to the codimension zero case where the dimorphism region is a sector that abuts the diagonal of the strategy plane. The MIP of Fig. 5 (right) shows that a dimorphism region may appear close to the diagonal, but be disconnected from that diagonal.

From the unfolding of the codimension two singularity, one MIP contains three singular strategies, none of which is an ESS. This partially answers the question regarding evolutionary stability raised in Lam and Lou (2014a) for a related model where the multiplicity of singular strategies was explored. Based on the available analytical and numerical results, we conjecture that, for any number N, there exists $r(x)$ which satisfies

$$\int_0^1 r_x (e^{-x/u} x^j r)_x = 0 \qquad \text{for } j = 0, \ldots, N-1.$$

Such a singularity will be of topological codimension $N-1$, and the universal unfolding of which contains a MIP with exactly N singular strategies locally.

Furthermore, the absence of ESS suggests that disruptive selection (Bolnick 2004; Dieckmann and Doebeli 1999) is likely; that is, the resident population splits into two coexisting species playing different strategies. In this case, the dimorphism regions (++) found in MIPs provide the parameter range in which the evolutionary dynamics of the dimorphic population takes place. What will be the evolutionary endpoint for the co-evolution of two resident species? Is there a coalition of two strategies that can defend themselves against invasion by any third strategy (for example, see Gejji et al. 2012)? These are questions for future discussion.

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