Journal of Mathematical Biology (2021) 82:36
https://doi.org/10.1007/s00285-021-01579-1

Mathematical Biology

Evolution of anisotropic diffusion in two-dimensional heterogeneous environments

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Received: 24 February 2020 / Revised: 22 January 2021 / Accepted: 14 February 2021 /

Abstract

We consider a system of two competing populations in two-dimensional heterogeneous environments. The populations are assumed to move horizontally and vertically with different probabilities, but are otherwise identical. We regard these probabilities as dispersal strategies. We show that the evolutionarily stable strategies are to move in one direction only. Our results predict that it is more beneficial for the species to choose the direction with smaller variation in the resource distribution. This finding seems to be in agreement with the classical results of Hastings (1983) and Dockery et al. (1998) for the evolution of slow dispersal, *i.e.* random diffusion is selected against in spatially heterogeneous environments. These conclusions also suggest that broader dispersal strategies should be considered regarding the movement in heterogeneous habitats.

Keywords Dispersal evolution · Selection · Reaction-diffusion systems

Mathematics Subject Classification 35K57 · 92D15 · 92D25

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1 Introduction

1.1 Background and motivation

In this paper, we consider populations of individuals that disperse in a bounded two-dimensional habitat, where the resources are distributed heterogeneously across the landscape. A natural question (see Fretwell and Lucas Jr (1969) or Clobert et al. (2001) for instance) is: how organisms should distribute themselves in space to better match the available resources, and, accordingly, what kind of dispersal strategies organisms should adopt to reach such distributions? Most of the previous studies on the evolution of dispersal assume that individuals move in two orthogonal directions with the same probability, which we refer to as random dispersal (see Hastings (1983) for instance). For spatially varying but temporally constant environments, Hastings considered a scenario in which the resident is randomly dispersing and reaches the equilibrium; some rare mutant, which is also randomly dispersing but differs from the resident only in the diffusion rate, is introduced to the habitat. He found that slower rates of dispersal will be selected, as the mixing of populations tends to reduce the growth (Altenberg 1984, 2012). Dockery et al. (1998) considered a system of two randomly diffusing competing populations in spatially varying but temporally constant environments, the two being identical except for their dispersal rates. They showed that the population with the smaller dispersal rate always drives the population with the larger dispersal rate to extinction, irrelevant of the initial data. This phenomenon is often termed as the evolution of slow dispersal, as any population with a positive dispersal rate will be replaced by a mutant with a smaller dispersal rate.

If we assume that individuals move, *e.g.,* horizontally and vertically with two different probabilities (with the sum of probabilities equal to one) and regard these probabilities as dispersal strategies, what kind of strategies will be evolutionarily stable? Here, we are referring to the situation where the population moves east or west with probability $p/2$, and north or south with probability $(1-p)/2$, respectively, with p being chosen in $[0, 1]$. Intuitively, random dispersal strategies, *i.e.* $p = 1/2$, might not be evolutionarily stable as the distribution of resources is generally not the same in the horizontal and vertical directions, so that it could be more advantageous for the population to have a higher probability moving in one direction than the other. This is indeed the case, and one might attempt to conjecture that some mixed strategy p^* in $(0, 1)$, allowing the population to move in horizontal and vertical directions with different probabilities, would emerge as an evolutionarily stable dispersal strategy in this particular setting. A bit surprisingly, our results suggest that the only evolutionarily stable dispersal strategies are $p^* = 0$ and/or $p^* = 1$, *i.e.* it is more advantageous for the population to move in only one direction.

More specifically, we consider a system of two competing populations in two-dimensional heterogeneous environments. The populations are assumed to move horizontally and vertically with different probabilities, but are otherwise identical. We introduce a function F of the dispersal probability, which measures the difference between the spatial variations of the population distribution at equilibrium in horizontal and vertical directions: when it is positive, the species has more variations in the horizontal direction; when it is negative, it has more variations in the vertical direction. We show that it is monotone decreasing and that the evolutionarily stable dispersal strategies are to maximize the function when it is positive and to minimize it when it is negative, *i.e.* the evolutionarily stable strategies are to move in one direction. As the population distribution is often positively correlated with the resource distribution, the function F indirectly measures the difference between the resource variations in horizontal and vertical directions. Therefore, our results seem to predict that it is more favorable for a species to choose the direction with smaller variation in the resource distribution.

To explain these findings intuitively, consider a peculiar scenario in which the underlying habitat is a rectangular region and the resources are distributed inhomogeneously in the horizontal direction but homogeneously in the vertical one. For such case, as there are only spatial variations in the horizontal direction, the results of Hastings (1983) and Dockery et al. (1998) for the evolution of slow dispersal suggest that it might be better for the population not to move horizontally, which is in agreement with our findings in the present paper. These considerations also suggest that we should probably consider a broader set of dispersal strategies, *e.g.,* strategies which allow for condition-dependent movement (Cantrell et al. 2010; Cosner 2014; Gyllenberg et al. 2016; Kisdi et al. 2012; Lam and Lou 2014a, b; Potapov et al. 2014).

1.2 Organization of the paper

Section 2 contains the formal derivations of the mathematical models at stage and the main results. We present numerical simulations in Sect. 3 to complement the analytical results and to provide some intuition and insights. In Sect. 4, we discuss the stability of semi-trivial equilibria and investigate properties of the invasion fitness. In Sect. 5, we further study the stability of the semi-trivial equilibria and identify all evolutionarily stable strategies. Section 6 is devoted to the classification of the global dynamics of the two-species competition model introduced in Sect. 2. In Sect. 7, we summarize our conclusions, and discuss possible extensions of the present work. Finally, some technical materials are given in the Appendix.

2 The models and analytical results

2.1 Formal derivation from random walks

In this section, we will closely follow the approach in (Slover 2019). Let the habitat be the discrete lattices of steps Δx and Δy in the full two-dimensional space $\mathbb{R}^2$. Assume that each individual moves horizontally to the left and to the right with probability $\frac{\theta}{2}$ and vertically up and down with probability $\frac{1-\theta}{2}$, with θ in $(0, 1)$. Let $N(t, x, y)$ denote the number of individuals of the population at time t and location (x, y) in $\mathbb{R}^2$.

Then

$$\begin{aligned}N(t+\Delta t,x,y) =&\frac{\theta}{2}\left[N(t,x+\Delta x,y)+N(t,x-\Delta x,y)\right]\\&+\frac{1-\theta}{2}[N(t,x,y+\Delta y)+N(t,x,y-\Delta y)].\end{aligned}$$

Using Taylor series expansions, we have

$$\begin{aligned}\frac{N(t+\Delta t,x,y)-N(t,x,y)}{\Delta t} =&\frac{(\Delta x)^2}{2\Delta t}\theta N_{xx}+\frac{(\Delta y)^2}{2\Delta t}(1-\theta)N_{yy}\\&+\frac{(\Delta x)^2}{\Delta t}\cdot O(\Delta x)+\frac{(\Delta y)^2}{\Delta t}\cdot O(\Delta y),\end{aligned}$$

where $O(\Delta x)$ and $O(\Delta y)$ denote terms which are bounded with respect to Δx and Δy, respectively. Assuming that both $\frac{(\Delta x)^2}{2\Delta t}$ and $\frac{(\Delta y)^2}{2\Delta t}$ tend to some positive constant $\overline{D}$ as the lengths of the time step Δt and of the space steps Δx and Δy tend to 0, we obtain, passing to the limit in the relation above,

$$N_t=\overline{D}\left[\theta N_{xx}+(1-\theta)N_{yy}\right], \tag{2.1}$$

which is the type of anisotropic diffusion operator to be considered in the present article.

The parameter θ can be regarded as a dispersal strategy. Namely, when $\theta=0$, the whole population will either move north or south with probability 1/2. Similarly, when $\theta=1$, the population will only move east or west. Most of previous studies assume that individuals are randomly diffusing, *i.e.* they move in two orthogonal directions with the same probability ($\theta=1/2$). Given arbitrarily distributed resources, is there some particular strategy θ in [0, 1] which can convey a competitive advantage? The main goal of the present article is to address this question.

2.2 The single-species model

We are given two orthogonal space directions $e_1=(1,0)$ and $e_2=(0,1)$, so that (x,y) are the Cartesian coordinates in this basis. Incorporating the population dynamics into Eq. (2.1), we arrive at the following reaction-diffusion equation:

$$\begin{cases}N_t=D(\theta)N_{xx}+D(1-\theta)N_{yy}+(a-N)N \text{ in } \Omega,\ t>0,\\ D(\theta)N_x\nu_x+D(1-\theta)N_y\nu_y=0 \text{ on } \partial\Omega,\ t>0,\\ N(0,\cdot,\cdot)=N_0\gneqq 0 \text{ in } \Omega.\end{cases} \tag{2.2}$$

Here, the domain Ω is a smooth open bounded subset of $\mathbb{R}^2$, and we denote its boundary by $\partial\Omega$. We assume without any further notice that $\overline{\Omega}$ is strictly convex and $\partial\Omega$ is of class C^1. The unit outward normal vector to $\partial\Omega$ is denoted by $\nu=(\nu_x,\nu_y)$. Thus, the map ν is one-to-one and continuous from $\partial\Omega$ to $\mathbb{S}^1$. The free growth rate

a is an heterogeneous function of the space variables x and y, that is assumed to be positive, Hölder continuous and non-constant in $\overline{\Omega}$.

For any θ in $[0, 1]$, the function D is defined by

$$D(\theta) := \underline{D} + (\overline{D} - \underline{D})\theta, \qquad \theta \in [0, 1].$$

Note that if $\underline{D} = 0$, $D(\theta) = \overline{D}\theta$ is reduced to the form of diffusion considered in equation (2.1), which is degenerate when $\theta = 0$. To avoid such degeneracy, we assume in the remainder of the paper that $\overline{D}$ and $\underline{D}$ are positive constants satisfying

$$0 < \underline{D} < \overline{D}.$$

The equation is complemented with zero flux boundary conditions, so that the number of individuals that enter the domain is equal to the number that leave. The model is not mass conservative since individuals may reproduce according to monostable non-linearities.

By standard regularity theory for parabolic equations and a comparison argument (see for instance (Cantrell and Cosner 2003)), it can be shown that N is positive in $\overline{\Omega}$ at all times and that $N(t, \cdot, \cdot)$ tends to N_θ uniformly in $\overline{\Omega}$ as t tends to infinity, where N_θ, the equilibrium distribution of the population, is the unique positive steady state of system (2.2), i.e. N_θ satisfies

$$\begin{cases} D(\theta)(N_\theta)_{xx} + D(1-\theta)(N_\theta)_{yy} + (a - N_\theta)N_\theta = 0 \text{ in } \Omega, \\ (D(\theta)(N_\theta)_x, D(1-\theta)(N_\theta)_y) \cdot \nu = 0 \text{ on } \partial\Omega. \end{cases} \tag{2.3}$$

Note that if the free growth rate a is non-constant, so is the steady state N_θ.

Clearly, the parameter θ has a strong influence on N_θ. As θ increases, the single species has a tendency to move more horizontally than vertically, which may reduce the spatial variations of the population distribution in the horizontal direction and increase the variations in the vertical direction. In this connection, we have the following result.

Theorem 2.1 *Define, for θ in* $[0, 1]$, *the function*

$$F(\theta) := \int_\Omega \left[((N_\theta)_x)^2 - \left((N_\theta)_y\right)^2 \right] dx\, dy. \tag{2.4}$$

Then $F'(\theta) < 0$ for θ in $(0, 1)$. *In particular, F is either strictly positive, strictly negative or sign-changing exactly once in* $(0, 1)$.

The function F, which plays a critical role in later analysis, can be regarded as a measurement of the difference between the variations of the population distribution in horizontal and vertical directions: when F is positive, we envision that the species at equilibrium has more spatial variations horizontally; when F is negative, it has more variations in the vertical direction. Theorem 2.1 implies that as the species increases the horizontal diffusion and reduces the vertical diffusion, then it tends to have more variations in the vertical direction than in the horizontal direction.

As the population distribution is often positively correlated with the resource distribution, the function F can also be viewed as an indirect measurement of the difference between the resource variations in the horizontal and vertical directions. Numerical results on the shape of the function F are presented in the next section (see Fig. 1).

2.3 The two-species competition model

Given arbitrarily distributed resources across the habitat, we may regard the parameter θ as a dispersal strategy and ask whether there is some value of the parameter which is evolutionarily stable. To address this question, we now move to the situation where two populations are competing for the same resources but adopt different dispersal strategies. We thus consider the following reaction-diffusion system for two competing species:

$$\begin{cases} U_t = D(p)U_{xx} + D(1-p)U_{yy} + (a - U - V)U \text{ in } \Omega,\ t > 0, \\ V_t = D(q)V_{xx} + D(1-q)V_{yy} + (a - U - V)V \text{ in } \Omega,\ t > 0, \\ (D(p)U_x, D(1-p)U_y) \cdot \nu = 0 \text{ on } \partial\Omega,\ t > 0, \\ (D(q)V_x, D(1-q)V_y) \cdot \nu = 0 \text{ on } \partial\Omega,\ t > 0, \\ U(0,\cdot,\cdot) = U_0 \gneqq 0,\ V(0,\cdot,\cdot) = V_0 \gneqq 0 \text{ in } \Omega, \end{cases} \tag{2.5}$$

in which the functions U and V represent the respective population densities of two competing species. By standard regularity theory and the maximum principle for parabolic equations, it can be shown that U and V are positive in $\overline{\Omega}$ at all times. The competition for resources is neutral and independent of the dispersal strategy of the individuals, so that the death rate is given by $U + V$ for both populations.

We may emphasise that, since we are given two orthogonal space directions e_1 and e_2, the problem is not rotationally invariant. As such, the two populations disperse with their own dispersal strategies, assimilated to the respective probabilities p and q to move in the direction e_1, with p and q chosen in $[0, 1]$. As formally explained in Subsection 2.1, this way of dispersing results in a diffusion coefficient given by $D(p)$ (resp. $D(q)$) in the direction e_1 and $D(1-p)$ (resp. $D(1-q)$) in the direction e_2 for the first (resp. second) density.

We will adopt a viewpoint from the theory of adaptive dynamics, in which an important concept is that of *evolutionarily stable strategies* (ESS). A strategy is said to be evolutionarily stable if a population using it cannot be invaded by any small population using a different strategy. In system (2.5), p and q represent strategies for the two populations. In terms of adaptive dynamics, we say that p in $[0, 1]$ is an ESS if the semi-trivial steady state $(N_p, 0)$ is locally asymptotically stable for $q \neq p$, with q in $[0, 1]$ and q close to p (note here that N_p is a function of x and y only).

The following result characterizes the local stability of $(N_p, 0)$ for p and q in $[0, 1]$.

Theorem 2.2 *There exists some continuous function $q = q^*(p)$, defined in* $[0, 1]$, *satisfying* $0 \le q^*(p) \le 1$ *and such that the following statements hold.*

- *(i) If F is positive in $[0, 1]$, then $q^*(p) > p$ for p in $(0, 1)$ and $q^*(p) \equiv 1$ for p close to 1 such that $(N_p, 0)$ is stable for $p < q < q^*(p)$, unstable when either $q > q^*(p)$ or $q < p$ holds. In particular, if $q^*(p) \equiv 1$, then $(N_p, 0)$ is stable for $q > p$, unstable for $q < p$.*
- *(ii) If F has a unique root θ^* in $(0, 1)$, then $q^*(p) > p$ for p in $[0, \theta^*)$ and $q^*(p) < p$ for p in $(\theta^*, 1]$, such that $(N_p, 0)$ is stable for $\min\{q^*(p), p\} < q < \max\{q^*(p), p\}$, unstable when either $q > \max\{q^*(p), p\}$ or $q < \min\{q^*(p), p\}$ holds.*
- *(iii) If F is negative in $[0, 1]$, then $q^*(p) < p$ for p in $(0, 1)$ and $q^*(p) \equiv 0$ for p close to 0 such that $(N_p, 0)$ is stable for $q^*(p) < q < p$, and unstable when either $q < q^*(p)$ or $q > p$ holds. In particular, if $q^*(p) \equiv 0$, then $(N_p, 0)$ is stable for $q < p$ and unstable for $q > p$.*

This result follows from Theorems 5.2, 5.4, and 5.6. In the next section, numerical simulations shed some insight into the stability of $(N_p, 0)$ and illustrate the conclusions of Theorem 2.2 (see Fig. 5). Some biological intuition can also be gained from this result, as it provides a criterion for finding the ESS of system (2.5).

Corollary 2.3 *The following conclusions hold.*

- *(i) If F is positive in $[0, 1]$, then $p = 0$ is the only ESS.*
- *(ii) If F has exactly one root θ^* in $(0, 1)$ so that F is positive in $[0, \theta^*)$ and negative in $(\theta^*, 1]$, then both $p = 0$ and $p = 1$ are ESS, and θ^* is not evolutionarily stable.*
- *(iii) If F is negative in $[0, 1]$, then $p = 1$ is the only ESS.*

Our remaining goals include understanding the global dynamics of system (2.5). This system possesses two semi-trivial steady states, given by $(N_p, 0)$ and $(0, N_q)$, respectively. Theorem 2.2 addresses the local stability of $(N_p, 0)$ for arbitrary values of p and q, and the stability of $(0, N_q)$ can be similarly determined. Furthermore, we shall show that there are only three alternatives for the global dynamics of system (2.5):

- (i) the state $(N_p, 0)$ is globally stable;
- (ii) the state $(0, N_q)$ is globally stable;
- (iii) the states $(N_p, 0)$ and $(0, N_q)$ are both unstable, and there exists a unique positive steady state which is globally stable.

We refer to the statements of Theorems 6.4, 6.5 and 6.6 for further details on the characterizations of the global dynamics of system (2.5). These analytical results on the dynamics of system (2.5), complemented by numerical simulations in the next section for a free growth rate of the form $a(x, y) = \lambda A(x) + (1 - \lambda)A(y)$, with λ in $[0, 1]$, will help provide a more clear picture on the dynamics of system (2.5).

3 Numerical simulations

All the simulations presented here were achieved using the free and open-source software FREEFEM (Hecht 2012). The numerical approximation of the large-time solution to system (2.2) is based on a variational form of the problem and achieved using a spatial discretisation based on the finite element method, with P_1 Lagrange elements, combined with an implicit-explicit (IMEX) Euler scheme (see (Asher et al. 1995) for instance) for the time-integration of the resulting ordinary differential equations. The linear terms in the reaction-diffusion equation are then treated implicitly in time, while the non-linear reaction term is dealt with explicitly, in order to enforce the stability of the scheme.

The mesh used to discretise the domain Ω realised as a disk of radius 2 was comprised of 3916 triangles and the length of the time step used was 0.01. The chosen initial state N_0 is the constant one, with value 0.5. Once the stationarity of the approximate solution was obtained in relative L^2-norm within a prescribed tolerance of 1e−15, the approximate steady state was used to compute an approximate value of $F(p)$ and also for a finite element discretisation of the linear eigenvalue problem (4.1). The computation of an approximation of the smallest eigenvalue of (4.1), denoted by $\Lambda(p, q)$, was done with the ARPACK package. Representations of an approximation to the nodal set of $\Lambda(p, q)$ for different values of λ were then obtained by repeating the computation for numerous values of the parameters p and q taken in a discrete grid of the interval $[0, 1]$.

Note that the state $(N_p, 0)$ is linearly stable when $\Lambda(p, q)$ is positive, and unstable when $\Lambda(p, q)$ is negative. Furthermore, $\Lambda(p, q)$ vanishes whenever $p = q$, *i.e.* the nodal set of $\Lambda(p, q)$ always contains the diagonal line $p = q$ in the (p, q) plane.

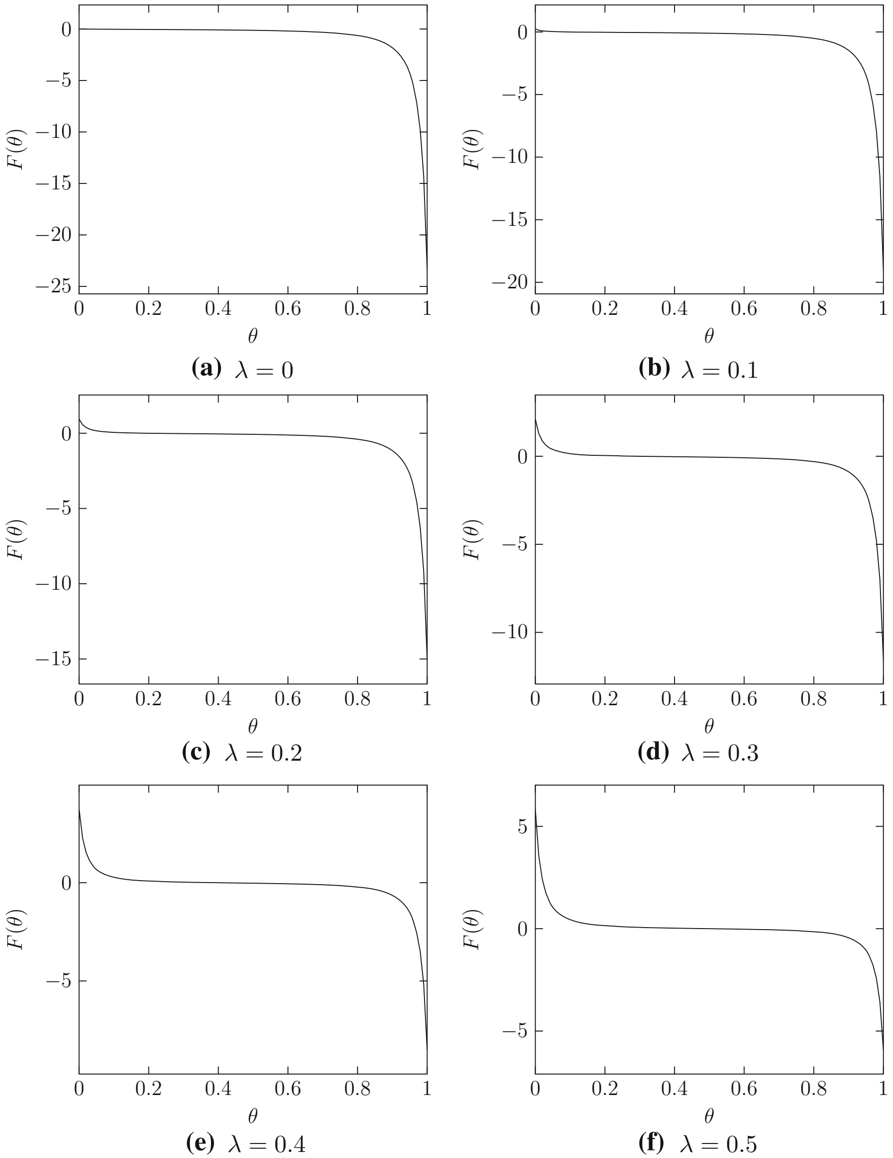
3.1 The function *F*

Numerical approximations of the graph of the function F in the case of a free growth rate of the form $a(x, y) = \lambda A(x) + (1 - \lambda)A(y)$ are provided in Fig. 1. For the simulations, we considered a disk of radius 2 centered at the origin for the domain Ω, anisotropic diffusion parameters $\underline{D}$ and $\overline{D}$ respectively equal to 0.1 and 10, and the function $A(x) = 2 - \sin(\pi x)$.

It is easily seen that, for all λ in $[0, 1]$ and all θ in $[0, 1]$, the value $F(\theta)$ for λ is equal to the value of $-F(1-\theta)$ for $1-\lambda$. Due to the symmetry in the function F with respect to λ, we only plot the graph of F for different values of λ between 0 and 0.5, illustrating how the function goes from strictly negative, to sign-changing once, and to strictly positive as λ varies. As shown in Fig. 1, the function F is strictly decreasing in θ, as predicted by Theorem 2.1.

Figures 2 and 3 present the numerical approximations of the free growth rate a and of the steady state N_θ for various values of θ in $[0, 1]$ and λ respectively equal to 0.4 and 0.6, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, and $A(x) = 2 - \sin(\pi x)$. For such values of λ, the function does not appear more biased in the horizontal direction than in the vertical one. Yet, one can see clearly that the steady state shows very little variation in vertical direction for $\theta = 0$, but changes as the value of the parameter θ grows to end with very little variation in the horizontal direction for $\theta = 1$. This illustrates how the function F goes from being negative to positive as θ varies.

For the simulations in Fig. 4, we considered a disk of radius 2 centered at the origin for the domain Ω, anisotropic diffusion parameters $\underline{D}$ and $\overline{D}$ respectively equal to 0.1

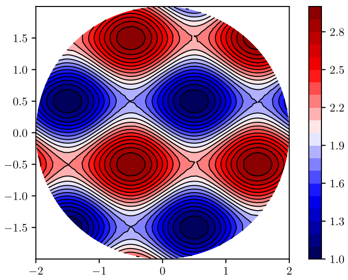


(a) $\lambda = 0$ **(b)** $\lambda = 0.1$

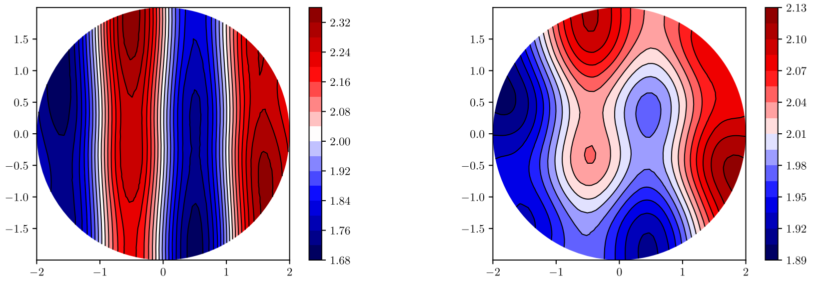
(c) $\lambda = 0.2$ **(d)** $\lambda = 0.3$

(e) $\lambda = 0.4$ **(f)** $\lambda = 0.5$

Fig. 1 Numerical approximations of the graphs of the function F for λ taking the values 0, 0.1, 0.2, 0.3, 0.4, and 0.5, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, and $A(x) = 2 - \sin(\pi x)$

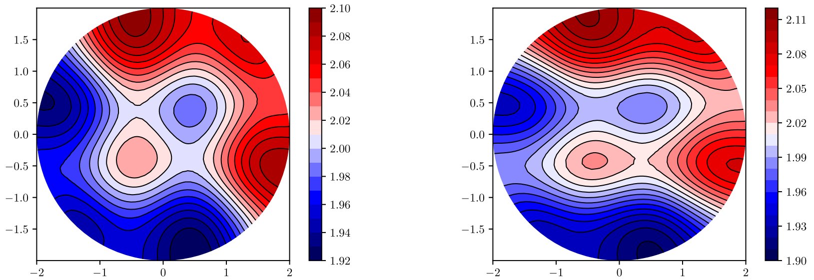


(a) The function a.



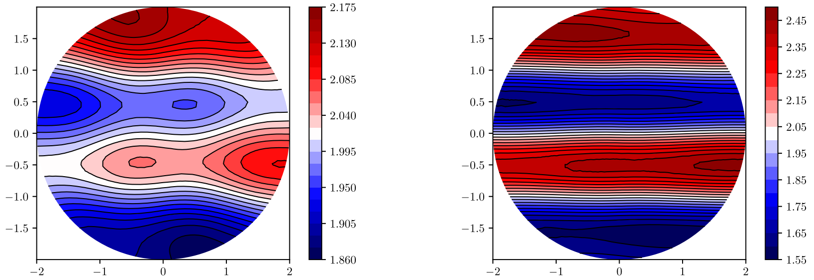
(b) The steady state for $\theta = 0$.

(c) The steady state for $\theta = 0.2$.



(d) The steady state for $\theta = 0.4$.

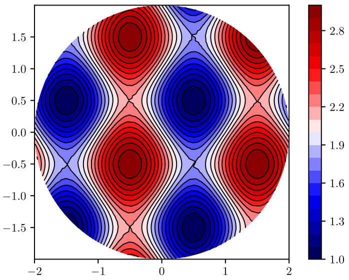
(e) The steady state for $\theta = 0.6$.



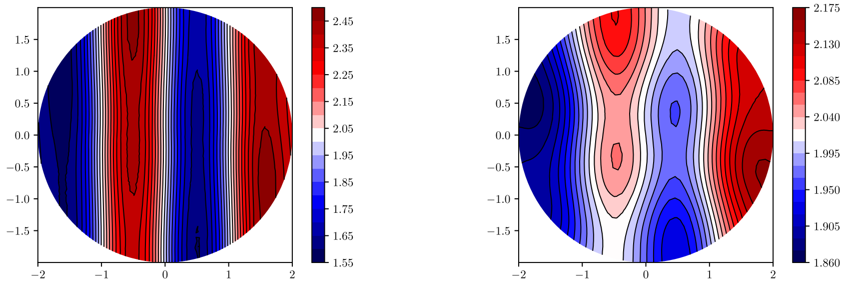
(f) The steady state for $\theta = 0.8$.

(g) The steady state for $\theta = 1$.

Fig. 2 Isolines for numerical approximations of the free growth rate a and of the steady state N_θ for θ taking the values 0, 0.2, 0.4, 0.6, 0.8, and 1, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, $\lambda = 0.4$, and $A(x) = 2 - \sin(\pi x)$

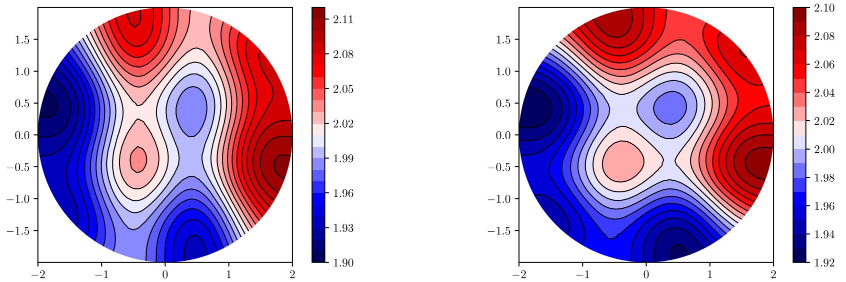


(a) The function a.



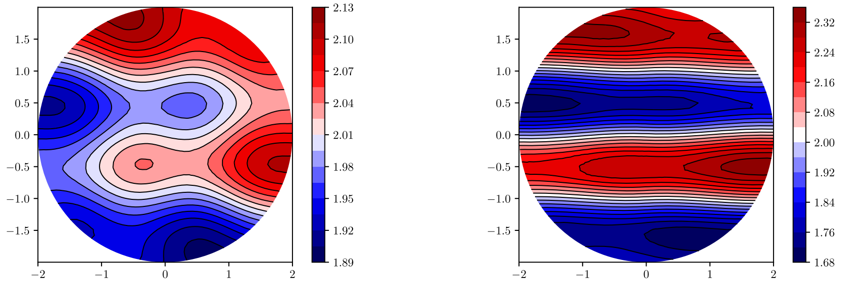
(b) The steady state for $\theta = 0$.

(c) The steady state for $\theta = 0.2$.



(d) The steady state for $\theta = 0.4$.

(e) The steady state for $\theta = 0.6$.



(f) The steady state for $\theta = 0.8$.

(g) The steady state for $\theta = 1$.

Fig. 3 Isolines for numerical approximations of the free growth rate a and of the steady state N_θ for θ taking the values 0, 0.2, 0.4, 0.6, 0.8, and 1, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, $\lambda = 0.6$, and $A(x) = 2 - \sin(\pi x)$

and 10, and the function $A(x) = 4 - \frac{1}{4}x^2$. Fixing values of θ, we observe that $F(\theta)$, seen as a function of λ, is not necessarily monotone.

3.2 Local stability of $(N_p, 0)$

Figure 5 presents numerical approximations of the nodal sets of $\Lambda(p, q)$ for a free growth function of the form $a(x, y) = \lambda A(x) + (1-\lambda)A(y)$, the choice of the problem parameters being the same as for the graphs of F in Fig. 1.

Here, $\Lambda(p, q)$ is positive if and only if $(N_p, 0)$ is linearly stable and $\Lambda(p, q) < 0$ if and only if $(0, N_q)$ is linearly unstable. Again, for all λ in $[0, 1]$ and all (p, q) in $[0, 1]^2$, the value of $\Lambda(p, q)$ for λ is equal to the value of $\Lambda(1 - p, 1 - q)$ for $1 - \lambda$. Due to the symmetry of $\Lambda(p, q)$ with respect to λ, we only plot the nodal sets for values of λ between 0 and 0.5, providing a graphical illustration of how the nodal set of $\Lambda(p, q)$ changes as λ varies, in connection with the results of Theorem 2.2 or, more broadly, the conclusions of Theorems 5.2, 5.4, and 5.6.

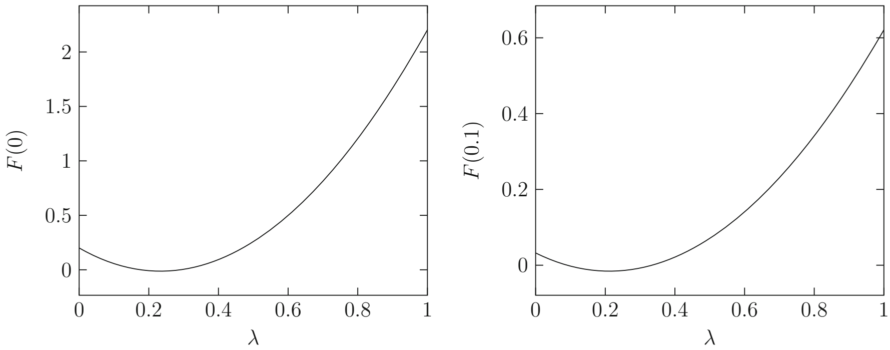
Subfigure 5(a) corresponds to statement (iii) of Theorem 2.2 with $q^*(p) \equiv 0$, which shows that $(N_p, 0)$ is stable for $p > q$ and unstable for $p < q$. In particular, $p = 1$ is the only ESS. In this case, the nodal set of $\Lambda(p, q)$ consists precisely of the diagonal line $q = p$. These conclusions are consistent with Subfigure 1(a), in which F is strictly negative.

Subfigures 5(b) to 5(f) correspond to statement (ii) of Theorem 2.2, which shows that $(N_p, 0)$ is stable for $\min\{q^*(p), p\} < q < \max\{q^*(p), p\}$, unstable when either $\max\{q^*(p), p\} < q$ or $q < \min\{q^*(p), p\}$ holds, and the nodal set of $\Lambda(p, q)$ consists of the curve $q = q^*(p)$ and the diagonal line $q = p$. Hence, both $p = 0$ and $p = 1$ are the only ESS. These conclusions are in accordance with Subfigures 1(b) to 1(f), in which F changes sign exactly once in $(0, 1)$, from positive to negative.

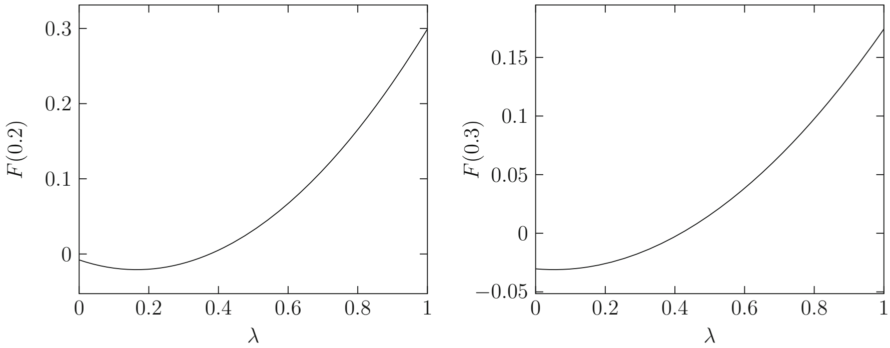
3.3 Global dynamics

Figure 6 presents numerical approximations of the nodal sets of $\Lambda(p, q)$ and $\Lambda(q, p)$ for a free growth rate of the form $a(x, y) = \lambda A(x) + (1 - \lambda)A(y)$, which correspond to the stability of semi-trivial steady states $(N_p, 0)$ and $(0, N_q)$, respectively. The domain Ω is again a disk of radius 2 centered at the origin, the anisotropic diffusion parameters $\underline{D}$ and $\overline{D}$ are respectively equal to 0.1 and 10, but the function A is now $A(x) = 4 - \frac{1}{4}x^2$. Due to a symmetry of $\Lambda(p, q)$ and $\Lambda(q, p)$ with respect to λ, we only plot the nodal sets for values of λ between 0 and 0.5.

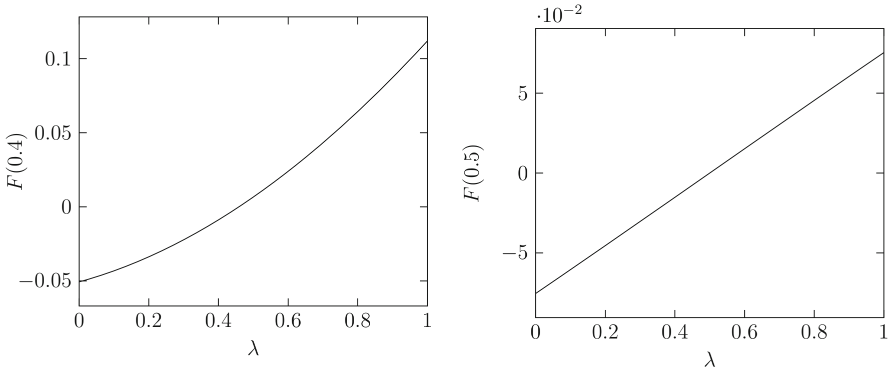
For Fig. 6, in the green colored region, $(N_p, 0)$ is stable and $(0, N_q)$ is unstable. By Theorems 6.4, 6.5 and 6.6, $(N_p, 0)$ is globally stable for (p, q) in the green region. Similarly, the one colored in red is the one in which $(0, N_q)$ is globally stable. The white region is where both $(N_p, 0)$ and $(0, N_q)$ are unstable, and there is a unique positive steady state which is globally stable. The white regions for $\lambda = 0.4$ and $\lambda = 0.5$ are substantially greater than those for smaller values of λ. Biologically, this suggests that if the spatial variations of the resource distribution in the vertical and horizontal directions become more comparable, the chances for coexistence of the two competing populations could be greater.



(a) $\theta = 0$ **(b)** $\theta = 0.1$

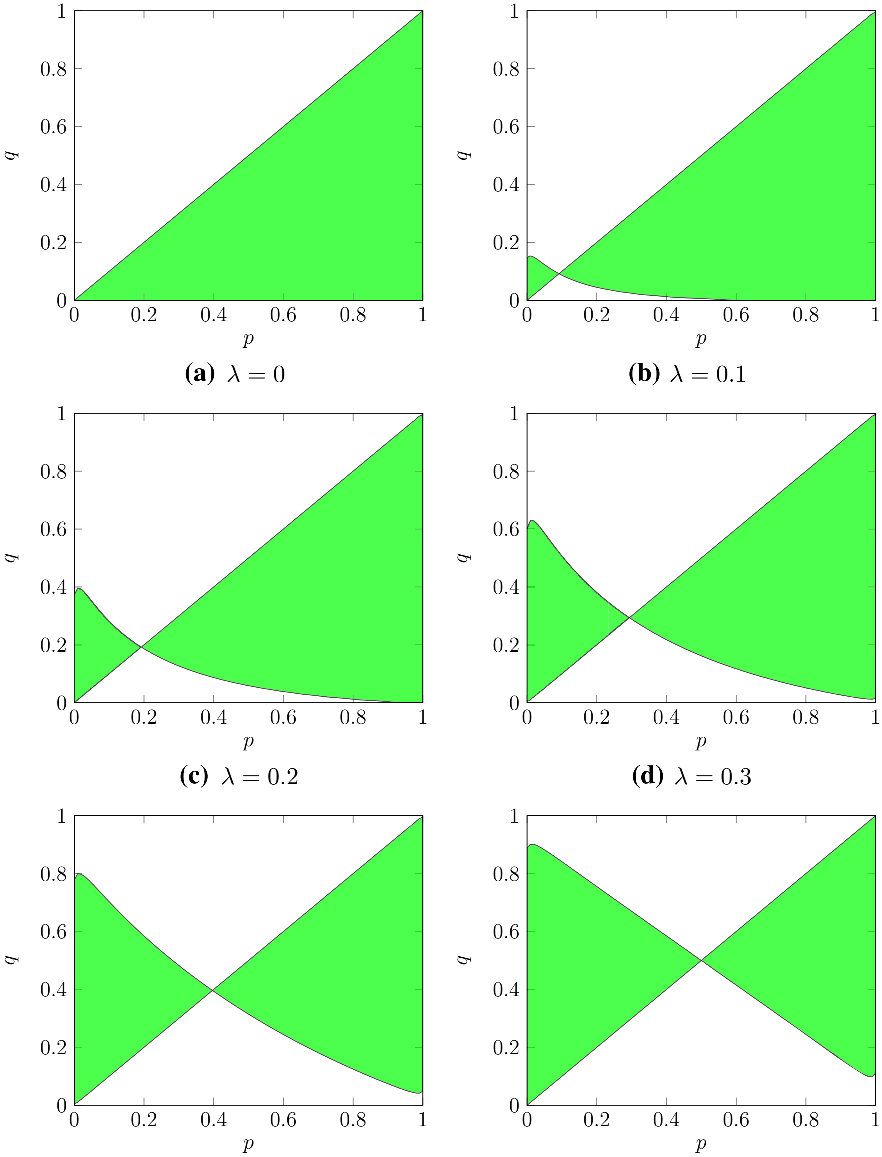


(c) $\theta = 0.2$ **(d)** $\theta = 0.3$



(e) $\theta = 0.4$ **(f)** $\theta = 0.5$

Fig. 4 Numerical approximations of the graphs of $F(\theta)$ as a function of λ for θ taking the values 0, 0.1, 0.2, 0.3, 0.4, and 0.5, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, and $A(x) = 4 - \frac{1}{4}x^2$

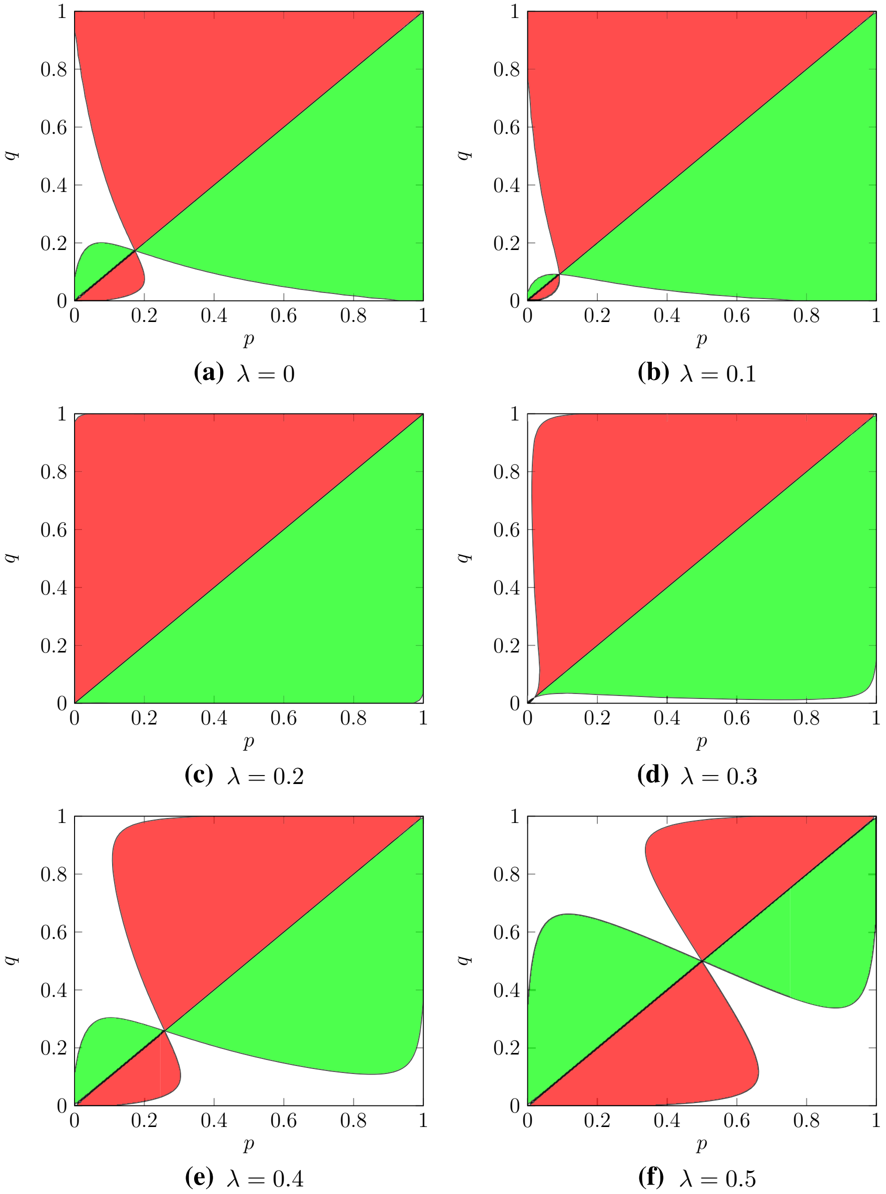


(a) $\lambda = 0$ **(b)** $\lambda = 0.1$

(c) $\lambda = 0.2$ **(d)** $\lambda = 0.3$

(e) $\lambda = 0.4$ **(f)** $\lambda = 0.5$

Fig. 5 Numerical approximations of the nodal sets of $\Lambda(p, q)$ for λ taking the values 0, 0.1, 0.2, 0.3, 0.4, and 0.5, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, and $A(x) = 2 - \sin(\pi x)$. The subset colored in green is the one in which $\Lambda(p, q) > 0$, that is in which the steady state $(N_p, 0)$ is linearly stable (colour figure online)



(a) $\lambda = 0$ **(b)** $\lambda = 0.1$

(c) $\lambda = 0.2$ **(d)** $\lambda = 0.3$

(e) $\lambda = 0.4$ **(f)** $\lambda = 0.5$

Fig. 6 Numerical approximations of the nodal sets of $\Lambda(p, q)$ and $\Lambda(q, p)$ for λ taking the values 0, 0.1, 0.2, 0.3, 0.4, and 0.5, in the case where Ω is a disk of radius 2 centered at the origin, $\underline{D} = 0.1$, $\overline{D} = 10$, and $A(x) = 4 - \frac{1}{4}x^2$. The subset colored in green is the one in which $\Lambda(p, q) > 0 > \Lambda(q, p)$, i.e. in which $(N_p, 0)$ is stable, while that colored in red is the one in which $\Lambda(q, p) > 0 > \Lambda(q, p)$, i.e. in which $(0, N_q)$ is stable. The white region is where both $(N_p, 0)$ and $(0, N_q)$ are unstable

4 Invasion fitness

In this section, we consider the stability of $(N_p, 0)$, study some properties of the invasion fitness and establish Theorem 2.1.

By the spectral theorem for compact self-adjoint operators, it can be shown that for the linear eigenvalue problem

$$\begin{cases} D(q)\varphi_{xx} + D(1-q)\varphi_{yy} + (a - N_p)\varphi + \lambda\varphi = 0 \text{ in } \Omega, \\ (D(q)\varphi_x, D(1-q)\varphi_y) \cdot \nu = 0 \text{ on } \partial\Omega, \end{cases} \tag{4.1}$$

all of the eigenvalues are real and can be arranged in increasing order. Furthermore, the smallest eigenvalue of (4.1) is simple (i.e., the eigenspace is a one-dimensional vector space) and its corresponding eigenfunctions can be chosen positive in Ω (see (Cantrell and Cosner 2003) and references therein). As N_p is smooth with respect to p and $D(q)$ is smooth in q, it follows from the implicit function theorem and the simplicity of the smallest eigenvalue that the corresponding eigenfunctions are also smooth with respect to p and q (see (Belgacem and Cosner 1995)).

Let $\Lambda := \Lambda(p, q)$ denote the smallest eigenvalue of (4.1). The linear stability of $(N_p, 0)$ is determined by the sign of Λ, as seen in the following result.

Lemma 4.1 *The semi-trivial equilibrium* $(N_p, 0)$ *is linearly stable if* $\Lambda(p, q)$ *is positive and unstable if* $\Lambda(p, q)$ *is negative. Similarly, the semi-trivial equilibrium* $(0, N_q)$ *is linearly stable if* $\Lambda(q, p)$ *is positive and unstable if* $\Lambda(q, p)$ *is negative.*

The proof of Lemma 4.1 is the same as that of Lemma 5.5 in (Chen et al. 2008) and is thus omitted.

In the theory of adaptive dynamics (Dieckmann and Law 1996; Diekmann 2003; Geritz et al. 1998), $\Lambda(p, q)$ is termed as the *invasion fitness* or *invasion exponent*, which can be regarded as the payoff function for the mutant phenotype with trait q, when the resident phenotype with trait p is at the equilibrium. Namely, if $\Lambda(p, q)$ is positive, the mutant with trait q can invade when rare; on the contrary, when $\Lambda(p, q)$ is negative, the mutant with trait q cannot invade when rare. We shall now give some properties of the map $(p, q) \mapsto \Lambda(p, q)$ that will be used later to describe more precisely the stability of both semi-trivial steady states.

From now on, for notational ease, we will drop the $dxdy$ in the integrals.

4.1 The selection gradient

If $p = q$, that is when both phenotypes are identical, $\Lambda(p, p) = 0$ for any p in $[0, 1]$, both semi-trivial steady states $(N_p, 0)$ and $(0, N_q)$ are neutrally stable. In this section, we consider the stability of $(N_p, 0)$ for p and q sufficiently close to each other. The following result provides a criterion in determining the sign of $\Lambda(p, q)$ in such case (see also (Slover 2019)).

Lemma 4.2 *There holds*

$$\frac{\partial \Lambda}{\partial q}\bigg|_{q=p} = \frac{(\overline{D}-\underline{D})}{\int_\Omega (N_p)^2} F(p),$$

where F is the function defined by (2.4).

Proof As the eigenspace corresponding to $\Lambda(p,q)$ is one-dimensional, we can normalize the positive eigenfunction φ associated with $\Lambda(p,q)$ by imposing that $\int_\Omega \varphi^2 = \int_\Omega (N_p)^2$, so that it is uniquely determined. As indicated earlier, φ is a smooth function of p and q, and, for simplicity of notation, we denote $\frac{\partial\varphi}{\partial q}$ by φ'. Differentiating system (4.1) with respect to q, we obtain

$$\begin{cases} D(q)\varphi'_{xx} + D(1-q)\varphi'_{yy} + (a-N_p)\varphi' + \Lambda(p,q)\varphi' + \dfrac{\partial\Lambda}{\partial q}(p,q)\varphi \\ \qquad\qquad\qquad\qquad + (\overline{D}-\underline{D})(\varphi_{xx}-\varphi_{yy}) = 0 \text{ in } \Omega, \\ (D(q)\varphi'_x + (\overline{D}-\underline{D})\varphi_x, D(1-q)\varphi'_y - (\overline{D}-\underline{D})\varphi_y)\cdot\nu = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.2}$$

Multiplying the first equation in system (4.1) by φ', integrating by parts the result over Ω and using the second equation in system (4.1), we have

$$-\int_\Omega (D(q)\varphi_x\varphi'_x + D(1-q)\varphi_y\varphi'_y) + \int_\Omega (a-N_p)\varphi\varphi' + \Lambda(p,q)\int_\Omega \varphi\varphi' = 0.$$

Similarly, multiplying the first equation in system (4.2) by φ, integrating by parts the result over Ω and using the second equation in system (4.2), we obtain

$$\begin{aligned} &-\int_\Omega (D(q)\varphi'_x\varphi_x + D(1-q)\varphi'_y\varphi_y) \\ &+\int_\Omega (a-N_p)\varphi'\varphi - (\overline{D}-\underline{D})\int_\Omega ((\varphi_x)^2-(\varphi_y)^2) \\ &+\Lambda(p,q)\int_\Omega \varphi'\varphi + \frac{\partial\Lambda}{\partial q}(p,q)\int_\Omega \varphi^2 = 0. \end{aligned}$$

Subtracting the above two equalities then yields

$$\frac{\partial\Lambda}{\partial q}(p,q)\int_\Omega \varphi^2 = (\overline{D}-\underline{D})\int_\Omega ((\varphi_x)^2-(\varphi_y)^2). \tag{4.3}$$

Since $\Lambda(p,p) = 0$, it follows from the normalization of φ that $\varphi_{|_{q=p}} = N_p$, which completes the proof. □

In view of Lemma 4.2, it is critical to understand the sign of function F. The following result establishes Theorem 2.1.

Lemma 4.3 *For any θ in* $[0,1]$, *one has* $F'(\theta) < 0$.

Proof For simplicity of notation, we denote $\frac{\partial N_\theta}{\partial \theta}$ by N'_θ. Integrating by parts, one gets

$$\begin{aligned} F'(\theta) &= 2\int_\Omega ((N_\theta)_x (N'_\theta)_x - (N_\theta)_y (N'_\theta)_y) \\ &= 2\int_{\partial\Omega} N'_\theta ((N_\theta)_x, -(N_\theta)_y)\cdot\nu - 2\int_\Omega N'_\theta((N_\theta)_{xx} - (N_\theta)_{yy}). \end{aligned}$$

Differentiating system in (2.3) for N_θ with respect to θ, we obtain

$$\begin{cases} D(\theta)(N'_\theta)_{xx} + D(1-\theta)(N'_\theta)_{yy} + (a - 2N_\theta)N'_\theta \\ \quad + (\overline{D} - \underline{D})((N_\theta)_{xx} - (N_\theta)_{yy}) = 0 \text{ in } \Omega, \\ (D(\theta)(N'_\theta)_x + (\overline{D} - \underline{D})(N_\theta)_x, D(1-\theta)(N'_\theta)_y - (\overline{D} - \underline{D})(N_\theta)_y)\cdot\nu = 0 \text{ on } \partial\Omega. \end{cases}$$

Multiplying the first of the above equations by N'_θ and integrating the result over Ω, we find that

$$\begin{aligned} &(\overline{D} - \underline{D})\int_\Omega N'_\theta((N_\theta)_{xx} - (N_\theta)_{yy}) \\ &\quad = -\int_\Omega N'_\theta\left[D(\theta)(N'_\theta)_{xx} + D(1-\theta)(N'_\theta)_{yy} + (a-2N_\theta)N'_\theta\right] \\ &\quad = -\int_{\partial\Omega} N'_\theta(D(\theta)(N'_\theta)_x, D(1-\theta)(N'_\theta)_y)\cdot\nu \\ &\qquad + \int_\Omega [D(\theta)((N'_\theta)_x)^2 + D(1-\theta)((N'_\theta)_y)^2 - (a-2N_\theta)(N'_\theta)^2] \\ &\quad = (\overline{D} - \underline{D})\int_{\partial\Omega} N'_\theta((N_\theta)_x, -(N_\theta)_y)\cdot\nu \\ &\qquad + \int_\Omega [D(\theta)((N'_\theta)_x)^2 + D(1-\theta)((N'_\theta)_y)^2 - (a-2N_\theta)(N'_\theta)^2], \end{aligned}$$

where the last equality follows from the boundary condition satisfied by N'_θ. We therefore have

$$F'(\theta) = -\frac{2}{\overline{D} - \underline{D}}\int_\Omega [D(\theta)((N'_\theta)_x)^2 + D(1-\theta)((N'_\theta)_y)^2 - (a-2N_\theta)(N'_\theta)^2].$$

Let λ_1 denote the smallest eigenvalue of the linear problem

$$\begin{cases} D(\theta)\varphi_{xx} + D(1-\theta)\varphi_{yy} + (a - N_\theta)\varphi + \lambda\varphi = 0 \text{ in } \Omega, \\ (D(\theta)\varphi_x, D(1-\theta)\varphi_y)\cdot\nu = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.4}$$

It is well-known that λ_1 can be characterized by the variational formula (see, e.g., (Courant and Hilbert 1953)[Sect. 1, Chap. VI])

$$\lambda_1 = \inf_{\varphi\in H^1(\Omega),\ \varphi\neq 0} \frac{\int_\Omega [D(\theta)(\varphi_x)^2 + D(1-\theta)(\varphi_y)^2 - (a-N_\theta)\varphi^2]}{\int_\Omega \varphi^2}. \tag{4.5}$$

Using system (2.3) for N_θ, we see that 0 is an eigenvalue of (4.4) with eigenfunction N_θ. As λ_1 is the only eigenvalue of (4.4) such that its corresponding eigenfunction does not change sign in Ω, it follows that $\lambda_1 = 0$ and that its corresponding principal eigenfunction is a scalar multiple of N_θ. In particular, by choosing the test function $\varphi = N'_\theta$ in (4.5), we have that

$$\int_\Omega [D(\theta)((N'_\theta)_x)^2 + D(1-\theta)((N'_\theta)_y)^2 - (a - N_\theta)(N'_\theta)^2] \geq 0,$$

which yields

$$F'(\theta) \leq -\frac{2}{\overline{D} - \underline{D}} \int_\Omega N_\theta (N'_\theta)^2 \leq 0.$$

This gives $F' \leq 0$, with the equality if and only if $N'_\theta \equiv 0$ in Ω.

Finally, if $N'_\theta \equiv 0$ for some θ, then N_θ satisfies

$$\begin{cases} (N_\theta)_{xx} - (N_\theta)_{yy} = 0 \text{ in } \Omega, \\ ((N_\theta)_x, -(N_\theta)_y) \cdot \nu = 0 \text{ on } \partial\Omega. \end{cases}$$

This, together with the boundary condition satisfied by N_θ, implies that

$$(N_\theta)_x \nu_x = (N_\theta)_y \nu_y = 0 \text{ on } \partial\Omega.$$

According to Lemma 8.1 in the Appendix, N_θ is then a positive constant function, and it follows from the first equation in (2.3) that the free growth rate a is also constant, contradicting an assumption made on this function. Consequently, one has $F' < 0$ in $[0, 1]$. □

Remark 1 If we allow Lipschitz domains with flat parts on the boundary, it is possible to construct domains such that $F \equiv 0$ (and thus $F' \equiv 0$) in $[0, 1]$ (see Subsection 8.2 in the Appendix for further details).

4.2 Concavity of $\Lambda(p, q)$

The following result concerns the concavity of $\Lambda(p, q)$ with respect to q. For notational ease, we write $\frac{\partial \Lambda}{\partial q}$ and $\frac{\partial^2 \Lambda}{\partial q^2}$ as Λ_q, Λ_{qq}, respectively.

Lemma 4.4 *For any p in $[0, 1]$, the function $q \mapsto \Lambda(p, q)$ is concave in $[0, 1]$. Moreover, if $\Lambda_q(p^*, q^*) = 0$ for some couple (p^*, q^*), then $\Lambda_{qq}(p^*, q^*) < 0$.*

Proof Let us fix p in $[0, 1]$. The concavity of $q \mapsto \Lambda(p, q)$ follows from a standard argument based on the variational characterization of $\Lambda(p, q)$, see (Ni 2011). Nevertheless, we include here a proof of this result in order to facilitate the proof of the second statement of the Lemma.

Consider the positive eigenfunction φ associated with $\Lambda(p,q)$ normalised by $\int_\Omega \varphi^2 = \int_\Omega (N_p)^2$. Differentiating (4.3) with respect to q yields

$$\Lambda_{qq}(p,q)\int_\Omega \varphi^2 + 2\Lambda_q(p,q)\int_\Omega \varphi'\varphi = 2(\overline{D}-\underline{D})\int_\Omega (\varphi_x'\varphi_x - \varphi_y'\varphi_y),$$

with the notations $\varphi' = \frac{\partial\varphi}{\partial q}$, $\varphi_x' = \frac{\partial\varphi_x}{\partial q}$, and $\varphi_y' = \frac{\partial\varphi_y}{\partial q}$. Note that the second term in the left-hand side vanishes due to the above normalisation condition on φ, which implies that $\int_\Omega \varphi'\varphi = 0$.

Multiplying the first equation in system (4.2) by φ' and integrating by parts the result over Ω then gives

$$\begin{aligned}
&(\overline{D}-\underline{D})\int_\Omega (\varphi_x\varphi_x' - \varphi_y\varphi_y') \\
&\quad = -\int_\Omega \Big[D(q)(\varphi_x')^2 + D(1-q)(\varphi_y')^2 - (a-N_p)(\varphi')^2 - \Lambda(p,q)(\varphi')^2\Big] \\
&\quad \le 0,
\end{aligned}$$

where we have used the second equation in system (4.2) and the fact that $\int_\Omega \varphi'\varphi = 0$, the inequality following from the variational characterization of $\Lambda(p,q)$,

$$\Lambda(p,q) = \inf_{\varphi\in H^1(\Omega),\ \varphi\neq 0} \frac{\int_\Omega \left[D(q)(\varphi_x)^2 + D(1-q)(\varphi_y)^2 - (a-N_p)\varphi^2\right]}{\int_\Omega \varphi^2}.$$

It then holds that $\Lambda_{qq}(p,q) \le 0$, where the equality holds if and only if the function φ' is a scalar multiple of φ. Since φ is positive in Ω, this implies that $\varphi' \equiv 0$ in Ω.

Thus, if $\Lambda_q(p,q) = \Lambda_{qq}(p,q) = 0$, system (4.2) reduces to

$$\varphi_{xx} - \varphi_{yy} = 0 \text{ in } \Omega \text{ and } (\varphi_x, -\varphi_y)\cdot\nu = 0 \text{ on } \partial\Omega.$$

Due to the boundary condition for φ in system (4.1), we further have $\varphi_x\nu_x = \varphi_y\nu_y = 0$ on $\partial\Omega$. As a consequence of Lemma 8.1, the function φ is constant, which implies, using the first equation in system (4.1), that the function $a - N_p$ is also constant. Integrating over Ω the main equation in system (2.3) with $\theta = p$, we then obtain

$$\int_\Omega (a-N_p)N_p = 0,$$

which ensures that $a - N_p = 0$ in Ω, so that system (2.3) for N_p reduces to

$$\begin{aligned}
&D(p)(N_p)_{xx} + D(1-p)(N_p)_{yy} = 0 \text{ in } \Omega, \\
&(D(p)(N_p)_x, D(1-p)(N_p)_y)\cdot\nu = 0 \text{ on } \partial\Omega.
\end{aligned}$$

Finally, it follows from the maximum principle that the function N_p is constant. This contradicts the assumption of the function a being non-constant. □

Lemma 4.5 *If* $\Lambda(\tilde{p},\tilde{q})=0$ *for some couple* $(\tilde{p},\tilde{q})$ *such that* $\tilde{p}\neq\tilde{q}$*, then* $\Lambda_q(\tilde{p},\tilde{q})\neq 0$.

Proof We argue by contradiction. Suppose that there exists a couple $(\tilde{p},\tilde{q})$ such that $\tilde{p}\neq\tilde{q}$ for which $\Lambda(\tilde{p},\tilde{q})=\Lambda_q(\tilde{p},\tilde{q})=0$. By Lemma 4.4, one has $\Lambda_{qq}(\tilde{p},\tilde{q})<0$, which implies that the function $q\mapsto\Lambda(\tilde{p},q)$ has a local maximum point at $q=\tilde{q}$. This contradicts the fact that $\Lambda(\tilde{p},\tilde{p})=0$ and the concavity of $\Lambda(p,q)$ with respect to q. ☐

A consequence of Lemma 4.5 is that the nodal set of $\Lambda(p,q)$ within the region $\{(p,q)\ :\ 0\leq p,q\leq 1\}$ can be parameterized by a function $q=\tilde{q}(p)$. However, we caution the reader that the domain of this function can be either [0, 1] or a strict subset of it.

5 Local stability for (p,q) in $[0,1]^2$: nodal set of invasion fitness

We have previously considered the stability of the semi-trivial steady state $(N_p,0)$ for p and q close to each other. In this section, we study the local stability of $(N_p,0)$ for general p and q in [0, 1]. This is equivalent to giving a description of the nodal set of $\Lambda(p,q)$ for p and q in [0, 1], and as well the sets where $\Lambda(p,q)$ is positive or negative.

By Lemma 4.3, the function F is strictly decreasing in [0, 1], so it suffices to consider three generic cases: $F(\theta)>0$ for all θ in [0, 1], F changes sign exactly once in (0, 1), and $F(\theta)<0$ for all θ in [0, 1].

5.1 Stability when $F(\theta)>0$

First, we consider the case for which the function F is positive in [0, 1).

Lemma 5.1 *Suppose that* $F(\theta)>0$ *for all* θ *in* [0, 1)*. If* $0\leq p<q\leq 1$*, then the steady state* $(0,N_q)$ *is unstable. Conversely, if* $0\leq q<p\leq 1$*, then the steady state* $(N_p,0)$ *is unstable.*

Proof We first consider the situation $0\leq p<q<1$. The stability of the steady state $(0,N_q)$ is determined by the sign of the smallest eigenvalue, denoted by $\Lambda(q,p)$, of the linear eigenproblem

$$\begin{cases} D(p)\varphi_{xx}+D(1-p)\varphi_{yy}+(a-N_q)\varphi+\lambda\varphi=0 \text{ in } \Omega,\\ (D(p)\varphi_x, D(1-p)\varphi_y)\cdot\nu=0 \text{ on } \partial\Omega. \end{cases}$$

By the variational characterization of $\Lambda(q,p)$ we have

$$\begin{aligned}\Lambda(q,p)&=\inf_{\varphi\in H^1(\Omega),\ \varphi\neq 0}\frac{\int_\Omega\left[D(p)\varphi_x^2+D(1-p)\varphi_y^2-(a-N_q)\varphi^2\right]}{\int_\Omega\varphi^2}\\ &\leq\frac{\int_\Omega[D(p)((N_q)_x)^2+D(1-p)((N_q)_y)^2-(a-N_q)(N_q)^2]}{\int_\Omega(N_q)^2}\end{aligned}$$

Multiplying the main equation in system (2.3) with $\theta = q$ by N_q and integrating by parts the result over Ω yields

$$\int_\Omega \left[D(q)\left((N_q)_x\right)^2 + D(1-q)\left((N_q)_y\right)^2 - (a - N_q)(N_q)^2\right] = 0.$$

Therefore, we have, using the assumptions that $p < q$ and $F > 0$ in $[0, 1]$,

$$\begin{aligned}\Lambda(q, p) &\le \frac{[D(p) - D(q)]\int_\Omega((N_q)_x)^2 + [D(1-p) - D(1-q)]\int_\Omega((N_q)_y)^2}{\int_\Omega(N_q)^2}\\ &= (\overline{D} - \underline{D})(p-q)\frac{\int_\Omega((N_q)_x)^2 - \int_\Omega((N_q)_y)^2}{\int_\Omega(N_q)^2}\\ &= (\overline{D} - \underline{D})(p-q)\frac{F(q)}{\int_\Omega(N_q)^2} < 0.\end{aligned}$$

If $q = 1$, we note that, as $\Lambda(p, q) < 0$ for $0 \le p < q < 1$, $\Lambda(p, 1) \le 0$. Since $\Lambda(1, 1) = 0$, we see by Lemma 4.5 that $\Lambda(p, 1) < 0$ for all $0 \le p < 1$. Hence, the steady state $(0, N_q)$ is unstable for $0 \le q < p \le 1$.

Similarly, we can show that if $0 \le q < p \le 1$, then $(N_p, 0)$ is unstable. □

The first main result of this section is the following.

Theorem 5.2 *Suppose that the function F is positive in $[0, 1]$. Then, there exists some positive, continuous function $q = q^*(p)$, defined in $[0, 1]$, satisfying $p < q^*(p) \le 1$ for all p in $[0, 1]$ and $q^*(p) \equiv 1$ for p close to 1, such that*

(i) $\Lambda(p, q) > 0$ for $0 \le p < q < q^*(p)$,
(ii) $\Lambda(p, q) < 0$ when either $q^*(p) < q \le 1$ or $0 \le q < p \le 1$ holds.

In particular, if $q^*(p) \equiv 1$, then $\Lambda(p, q) > 0$ for $p < q \le 1$ and $\Lambda(p, q) < 0$ for $0 \le q < p$.

Proof Since $\Lambda(p, p) = 0$ for all p in $[0, 1]$ and F is positive in $[0, 1]$, there exists some positive real number δ such that $\Lambda(p, q) > 0$ for p and q in $[0, 1]$ with $0 < q - p < \delta$.

Given any p in $[0, 1]$, if $\Lambda(p, 1) < 0$, by Lemma 4.4 and the positivity of $\Lambda(p, q)$ in the strip $0 < q - p < \delta$, there exists a unique $q^* = q^*(p)$ in $(p, 1)$ such that $\Lambda(p, q^*) = 0$, $\Lambda(p, q) > 0$ for $p < q < q^*$ and $\Lambda(p, q) < 0$ for $q > q^*$. If $\Lambda(p, 1) \ge 0$, we define $q^*(p) = 1$. Again by Lemma 4.4, $\Lambda(p, q) > 0$ holds for $p < q < q^* = 1$. This establishes statements (i) and (ii).

To show that $q = q^*(p)$ is a continuous curve, suppose that $\Lambda(\tilde{p}, \tilde{q}) = 0$ for some $\tilde{p} < \tilde{q} < 1$. By Lemma 4.5, there exists a smooth curve $q = q^{**}(p)$ passing through $(\tilde{p}, \tilde{q})$ and such that $\Lambda(p, q^{**}(p)) = 0$, which can be extended to the left and to right until it reaches either $p = 0$ or $q = 1$, as, by the choice of δ, $q = q^{**}(p)$ and its extension can never enter the strip $0 < q - p < \delta$. For each p, there exists at most one $q > p$ such that $\Lambda(p, q) = 0$.

Hence, $q^{**} \equiv q^*$ as long as these functions are strictly less than 1. Therefore, q^* defines a continuous curve on $[0, 1]$. By the choice of δ, we see that $q^*(p) \equiv 1$ for p close to 1. □

Similarly to Theorem 5.2, the local stability of the semi-trivial steady state $(0, N_q)$ can be determined as follows.

Theorem 5.3 *Suppose that the function F is positive in $[0, 1]$. Then, there exists some positive, continuous function $p = p^*(q)$, defined in $[0, 1]$, satisfying $q < p^*(q) \leq 1$ for q in $[0, 1]$ and $p^*(q) \equiv 1$ for q close to 1, such that $\Lambda(q, p) > 0$ for $q < p < p^*(q)$ and $\Lambda(q, p) < 0$ when either $p^*(q) < p \leq 1$ or $q < p$ holds.*

The proof being the same as that for Theorem 5.2, we omit it.

5.2 Stability when $F(\theta) < 0$

Next, we consider the case for which the function F is negative in $[0, 1]$. This case is similar to the previous one, so that we may state the following results without proof.

Theorem 5.4 *Suppose that the function F is negative in $[0, 1]$. Then, there exists a positive continuous function $q = q^*(p)$, defined in $[0, 1]$, satisfying $0 \leq q^*(p) < p$ for p in $[0, 1]$ and $q^*(p) \equiv 0$ for p close to 0 such that*

(i) $\Lambda(p, q) > 0$ for $q^*(p) < q < p \leq 1$,
(ii) $\Lambda(p, q) < 0$ for when either $0 \leq q < q^*(p)$ or $0 \leq p < q \leq 1$ holds.

In particular, if $q^*(p) \equiv 0$, then $\Lambda(p, q) > 0$ for $q < p$ and $\Lambda(p, q) < 0$ for $q > p$.

Theorem 5.5 *Suppose that the function F is negative in $[0, 1]$. Then, there exists a positive continuous function $p = p^*(q)$, defined in $[0, 1]$, satisfying $p^*(q) < q$ for q in $[0, 1]$ and $p^*(q) \equiv 0$ for q close to 0, such that $\Lambda(q, p) > 0$ for $p^*(q) < p < q$ and $\Lambda(q, p) < 0$ when either $0 \leq p < p^*(q)$ or $q < p$ holds.*

5.3 Stability when *F* changes sign once

We finally consider the case for which the function F possesses a unique root in $(0, 1)$, denoted by θ^*. This function being decreasing, this implies that it is positive in $[0, \theta^*)$ and negative in $(\theta^*, 1]$.

Theorem 5.6 *Suppose that the function F has a unique root θ^* in $(0, 1)$. Then, there exists a positive continuous function $q = q^*(p)$, defined in $[0, 1]$, satisfying $p < q^*(p) \leq 1$ for p in $[0, \theta^*)$ and $0 \leq q^*(p) < p$ for p in $(\theta^*, 1]$, such that*

(i) $\Lambda(p, q) > 0$ for p in $[0, 1]$ and $\min\{q^*(p), p\} < q < \max\{q^*(p), p\}$,
(ii) $\Lambda(p, q) < 0$ for p in $[0, 1]$ and either $\max\{q^*(p), p\} < q \leq 1$ or $0 \leq q < \min\{q^*(p), p\}$ holds.

Proof Since $\Lambda(p, p) = 0$ for all p in $[0, 1]$ and F changes sign exactly once at some θ^* in $(0, 1)$, it follows from Lemma 4.4 and the implicit function theorem that there exist both a smooth curve $q = q^*(p)$, which passes through (θ^*, θ^*), such that $q^*(p) > p$ for p less than and close to θ^*, and $q^*(p) < p$ for p greater than and close to θ^*, and a positive real number δ, such that $\Lambda(p, q) = 0$ in the stripe $|q - p| < \delta$ if and only if either $q = p$ or $q = q^*(p)$.

Using Lemma 4.5, we can extend the curve $q = q^*(p)$ to the left until it reaches either $p = 0$ or $q = 1$. Note that we can choose δ so small that this extension can never re-enter the strip $0 < q - p < \delta$ once it leaves it. If it first reaches $q = 1$ at some $p = \hat{p}$ in $(0, \theta^*)$, one can proceed as in the proof of Theorem 5.2 to define $q^*(p)$ for p in $[0, \theta^*)$ and show that $q = q^*(p)$ is a continuous curve. If it never attains $q = 1$, note that it can only intersect the line $q = p$ at $q = p = \theta^*$, thus it can be defined at $p = 0$ in such a way that $p < q^*(p) < 1$ for p in $(0, \theta^*)$. From Lemma 4.5 and the implicit function theorem, the curve $q = q^*(p)$ is smooth in this scenario. Similarly, one can extend $q^*(p)$ to $[\theta^*, 1]$ as a continuous curve.

These arguments also show that the nodal set of $\Lambda(p, q)$ is contained in the line $q = p$ and the curve $q = q^*(p)$, so that the conclusions in (i) and (ii) hold. □

Similarly to Theorem 5.6, the local stability of $(0, N_q)$ can be determined as follows.

Theorem 5.7 *Suppose that the equation* $F = 0$ *has a unique root, denoted by* θ^**, in* $(0, 1)$. *Then, there exists some positive, continuous function* $p = p^*(q)$*, defined in* $[0, 1]$*, satisfying* $q < p^*(q) \le 1$ *for* $qin[0, \theta^*)$ *and* $0 \le p^*(q) < q$ *for* q *in* $(\theta^*, 1]$*, such that*

- *(i)* $\Lambda(q, p) > 0$ *for* q *in* $[0, 1]$ *and* $\min\{p^*(q), q\} < p < \max\{p^*(q), q\}$,
- *(ii)* $\Lambda(q, p) < 0$ *for* q *in* $[0, 1]$, *and either* $\max\{p^*(q), q\} < p \le 1$ *or* $0 \le p < \min\{p^*(q), q\}$ *holds.*

The proof being the same as that for Theorem 5.6, we omit it.

5.4 Proofs of Theorem 2.2 and Corollary 2.3

We are now in a position to prove some of the main results of the paper. Theorem 2.2 follows from Theorems 5.2, 5.4, and 5.6.

Proof of Corollary 2.3 If the function F is positive in $[0, 1]$, statement (i) follows from Theorem 5.2. If $F > 0$ in $[0, 1)$ with $F(1) = 0$, we can apply Lemma 5.1 to conclude that $p = 1$ is an evolutionarily singular strategy but not an evolutionarily stable one, and $p = 0$ is thus the only ESS. Statement (ii) can be proved similarly. Finally, statement (iii) is a direct consequence of Theorem 5.6. □

Remark 2 While the function F plays a critical role in the analysis provided in the current section, it appears that it only captures some partial information on $\Lambda(p, q)$ and cannot possibly determine entirely the nodal set of $\Lambda(p, q)$. For instance, even the sign of $\Lambda(0, 1)$ cannot be resolved using only the function F, as it depends on a, $\underline{D}$ and $\overline{D}$ in delicate manners. As an example, assume that $a(x, y) = \lambda A(x) + (1 - \lambda)A(y)$, where λ belongs to $[0, 1)$ and A attains a strict global maximum. Then, for large $\overline{D}$, choosing $\underline{D}$ sufficiently small, $\Lambda(0, 1) < 0$. However, for such choices of a, $\underline{D}$ and $\overline{D}$, the function F changes from negative to sign-changing and to positive as λ varies from 0 to 1. We refer the interested readers to the online supplement for further discussions.

6 Full dynamics of the two-species model

6.1 Local stability of semi-trivial steady states

In this subsection, we investigate further the local stability of both semi-trivial steady states $(N_p, 0)$ and $(0, N_q)$, for general p and q in $[0, 1]$.

The next result shows that the states $(N_p, 0)$ and $(0, N_q)$ cannot be simultaneously stable, *i.e.* bistability cannot occur.

Lemma 6.1 *The following assertions hold for any* p *and* q *in* $[0, 1]$.

(i) If $\Lambda(p, q) > 0$, *then* $\Lambda(q, p) < 0$.
(ii) If $\Lambda(p, q) = 0$, *then either* $p = q$ *or* $\Lambda(q, p) < 0$.

Proof It follows from the variational characterization of $\Lambda(p, q)$ that

$$\begin{aligned}\Lambda(p,q) &= \inf_{\varphi\in H^1(\Omega),\ \varphi\neq 0} \frac{\int_\Omega \left[D(q)(\varphi_x)^2 + D(1-q)(\varphi_y)^2 - (a-N_p)\varphi^2\right]}{\int_\Omega \varphi^2}\\ &\le \frac{\int_\Omega [D(q)((N_q)_x)^2 + D(1-q)((N_q)_y)^2 - (a-N_p)(N_q)^2]}{\int_\Omega (N_p)^2}\\ &= \frac{\int_\Omega (N_p - N_q)(N_q)^2}{\int_\Omega (N_p)^2},\end{aligned}$$

where the last equality follows from the equation of N_q. If $\Lambda(p, q) > 0$, then

$$\int_\Omega (N_q)^3 < \int_\Omega N_p (N_q)^2 \le \left(\int_\Omega (N_p)^3\right)^{1/3} \left(\int_\Omega (N_q)^3\right)^{2/3},$$

which implies that

$$\int_\Omega (N_q)^3 < \int_\Omega (N_p)^3.$$

If we assume that $\Lambda(q, p) \ge 0$, we have, by the same argument as above,

$$\int_\Omega (N_p)^3 \le \int_\Omega (N_p)^2 N_q \le \left(\int_\Omega (N_p)^3\right)^{2/3} \left(\int_\Omega (N_q)^3\right)^{1/3},$$

from which we get

$$\int_\Omega (N_p)^3 \le \int_\Omega (N_q)^3,$$

which is a contradiction. Hence, statement (i) holds.

If $\Lambda(p, q) = 0$, following the same argument as above, we see that $\Lambda(q, p) \le 0$. If $\Lambda(q, p) = 0$, the only possibility is that $N_p \equiv N_q$, that is $p = q$, which proves (ii). □

To describe the global dynamics of the two-species model, we first introduce the sets

$$\Gamma_1 := \{(p, q) \in [0, 1]^2 : \Lambda(p, q) = 0\},$$
$$\Gamma_2 := \{(p, q) \in [0, 1]^2 : \Lambda(q, p) = 0\}.$$

Clearly, Γ_1 and Γ_2 correspond respectively to the situations when $(N_p, 0)$ and $(0, N_q)$ are neutrally stable. Therefore, we have, by Theorems 5.2 to 5.7,

$$\Gamma_1 = \{(p, q) \in [0, 1]^2 : q = p \text{ or } q = q^*(p)\},$$
$$\Gamma_2 = \{(p, q) \in [0, 1]^2 : p = q \text{ or } p = p^*(q)\}.$$

Next, we define the sets

$$\Sigma_1 := \{(p, q) \in [0, 1]^2 : \Lambda(p, q) > 0 > \Lambda(q, p)\},$$
$$\Sigma_2 := \{(p, q) \in [0, 1]^2 : \Lambda(p, q) < 0 < \Lambda(q, p)\},$$
$$\Sigma_3 := \{(p, q) \in [0, 1]^2 : \Lambda(p, q) < 0,\ \Lambda(q, p) < 0\}.$$

The sets Σ_i $(i = 1, 2, 3)$ are disjoint and

$$\Sigma_1 \cup \Sigma_2 \cup \Sigma_3 = [0, 1] \times [0, 1]/(\Gamma_1 \cup \Gamma_2 \cup \Gamma_3).$$

Theorem 6.2 *The following characterizations hold:*

$$\Sigma_1 = \{(p, q) \in [0, 1] \times [0, 1] : (q - q^*(p))(q - p) < 0\},$$
$$\Sigma_2 = \{(p, q) \in [0, 1] \times [0, 1] : (p - p^*(q))(p - q) < 0\},$$
$$\Sigma_3 = \{(p, q) \in [0, 1] \times [0, 1] : (q - q^*(p))(p - p^*(q)) < 0\}.$$

Proof By Lemma 6.1, one has

$$\Sigma_1 = \{(p, q) \in [0, 1] \times [0, 1] : \Lambda(p, q) > 0\}.$$

It then follows from Theorems 5.2, 5.3 and 5.4 that Σ_1 is determined by $(q - q^*(p))(q - p) < 0$. The proof for the characterization of Σ_2 is similar and thus skipped. From the new characterizations for Σ_1 and Σ_2, it follows that (p, q) belongs to Σ_3 if and only if $(q - q^*)(q - p) > 0$ and $(p - p^*)(p - q) > 0$, which amounts to $(q - q^*(p))(p - p^*(q)) < 0$. □

6.2 Stability of positive steady states of system (2.5)

The following result shows that any positive steady state of system (2.5) is asymptotically stable. It is essentially due to He and Ni (2016). For the sake of completeness, we have included here a slightly different demonstration of this result.

Lemma 6.3 *Suppose that the free growth rate a is non-constant and that p is not equal to q. Then, any positive steady state of system (2.5) is linearly stable and thus locally asymptotically stable.*

Proof Let (U, V) denote any positive steady state of system (2.5), *i.e.*

$$\begin{cases} D(p)U_{xx} + D(1-p)U_{yy} + (a - U - V)U = 0 & \text{in } \Omega, \\ D(q)V_{xx} + D(1-q)V_{yy} + (a - U - V)V = 0 & \text{in } \Omega, \\ (D(p)U_x, D(1-p)U_y) \cdot \nu = (D(q)V_x, D(1-q)V_y) \cdot \nu = 0 \text{ on } \partial\Omega. \end{cases}$$

The linear stability of this state is determined by the sign of the principal eigenvalue λ_1 of the linear problem

$$\begin{cases} D(p)\varphi_{xx} + D(1-p)\varphi_{yy} + (a - 2U - V)\varphi - \psi V + \lambda_1\varphi = 0 \text{ in } \Omega, \\ D(q)\psi_{xx} + D(1-q)\psi_{yy} - U\varphi + (a - U - 2V)\psi + \lambda_1\psi = 0 \text{ in } \Omega, \\ (D(p)\varphi_x, D(1-p)\varphi_y) \cdot \nu = 0 \text{ on } \partial\Omega, \\ (D(q)\psi_x, D(1-q)\psi_y) \cdot \nu = 0 \text{ on } \partial\Omega. \end{cases}$$

It is known (Cantrell and Cosner 2003; Smith 1995) that we may choose $\varphi > 0$ and $\psi < 0$ in $\overline{\Omega}$. Set $W = \varphi/U$ and $Z = -\psi/V$ so that W and Z are both positive in $\overline{\Omega}$ and satisfy

$$\begin{cases} D(p)(U^2W_x)_x + D(1-p)(U^2W_y)_y - U^3W + U^2VZ + \lambda_1U^2W = 0 \text{ in } \Omega, \\ D(q)(V^2Z_x)_x + D(1-q)(V^2Z_y)_y + UV^2W - V^3Z + \lambda_1V^2Z = 0 \text{ in } \Omega, \\ (D(p)W_x, D(1-p)W_y) \cdot \nu = (D(q)Z_x, D(1-q)Z_y) \cdot \nu = 0 \text{ on } \partial\Omega. \end{cases}$$

Multiplying the first line of this system by W^2 and integrating the result over Ω yields

$$\int_\Omega \left[D(p)U^2W(W_x)^2 + D(1-p)U^2W(W_y)^2 + (UW)^3 - (UW)^2(VZ) - \lambda_1U^2W^3\right] = 0.$$

Similarly, multiplying the second line of the system by Z^2 and integrating the result over Ω, we find that

$$\int_\Omega \left[D(q)V^2Z_x(Z^2)_x + D(1-q)V^2Z_y(Z^2)_y + (VZ)^3 - (UW)(VZ)^2 - \lambda_1V^2Z^3\right] = 0.$$

It suffices to show $\lambda_1 > 0$. We argue by contradiction by assuming that $\lambda_1 \le 0$. Then, one has

$$\int_\Omega (UW)^3 \le \int_\Omega (UW)^2(VZ), \tag{6.1}$$

and the equality in (6.1) holds if and only if $\lambda_1 = 0$, W is a positive constant, and UW is a positive scalar multiple of VZ. Similarly, if $\lambda_1 \le 0$, one has

$$\int_\Omega (VZ)^3 \le \int_\Omega (UW)(VZ)^2, \tag{6.2}$$

and the equality in (6.2) holds if and only if $\lambda_1 = 0$, Z is a positive constant, and UW is a positive scalar multiple of VZ. Finally, it follows from the Hölder inequality that

$$\int_\Omega (UW)^3 \le \left(\int_\Omega (UW)^3\right)^{2/3} \left(\int_\Omega (VZ)^3\right)^{1/3} \tag{6.3}$$

and

$$\int_\Omega (VZ)^3 \le \left(\int_\Omega (VZ)^3\right)^{2/3} \left(\int_\Omega (UW)^3\right)^{1/3}, \tag{6.4}$$

from which we see that inequalities (6.1), (6.2), (6.3) and (6.4) must all be equalities. As a consequence, λ_1 is zero, both W and Z are positive constants, and UW is a positive scalar multiple of VZ, i.e. $U = cV$ for some positive constant c. Therefore, U satisfies

$$\begin{cases} D(p)U_{xx} + D(1-p)U_{yy} + (a - (c+1)U)U = 0 & \text{in } \Omega, \\ D(q)U_{xx} + D(1-q)U_{yy} + (a - (c+1)U)U = 0 & \text{in } \Omega, \\ (D(p)U_x, D(1-p)U_y) \cdot \nu = (D(q)U_x, D(1-q)U_y) \cdot \nu = 0 \text{ on } \partial\Omega. \end{cases}$$

Hence, we find that $U \equiv N_p/(c+1)$ and $U \equiv N_q/(c+1)$, which implies that $N_p \equiv N_q$. As the function a is non-constant, so is N_p. Since $p \neq q$, by subtracting the equations of the systems respectively satisfied by N_p and N_q, we see that N_p is a solution to system (8.1) and is therefore a non-constant function, which contradicts the assumption. □

6.3 Global dynamics of system (2.5)

As the two-species competition model (2.5) is strongly monotone, its global dynamics can be fully determined by the local stability of its equilibria in some cases (see (Hess 1991, Chapter IV) for instance). Let us recall below some known facts.

(a) If there is no positive steady state, then one of the semi-trivial equilibria is unstable and the other is globally asymptotically stable among non-negative and non-identically zero initial data.
(b) If there is a unique positive steady state and it is stable, then it is globally asymptotically stable.
(c) If all positive steady states are asymptotically stable, then there is at most one of them. In particular, either (a) or (b) applies.

We are now ready to infer on the global stability of steady states.

Theorem 6.4 *Suppose that the function F is positive in* $[0, 1]$ *and let p^* and q^* be the functions introduced in Theorems 5.2 and 5.3, respectively. Then, one of the following statements holds.*

(i) If $p < q < q^*$, then the steady state $(N_p, 0)$ is globally asymptotically stable.
(ii) If $q < p < p^*$, then the steady state $(0, N_q)$ is globally asymptotically stable.
(iii) If either $q^* < q \le 1$ or $p^* < p \le 1$ holds, then system (2.5) has a unique positive steady state, which is also globally asymptotically stable among non-negative and not identically zero initial data.

Proof We first establish statement (i). By Theorem 6.2, we see that under assumption that $p\, belongs\, to$ $[0, 1]$ and $p < q < q^*$, $\Lambda(p, q) > 0 > \Lambda(q, p)$. Hence, $(N_p, 0)$ is stable and $(0, N_q)$ is unstable. As system (2.5) is strongly monotone, by Lemma 6.3 and statements (a) and (c), $(N_p, 0)$ is globally stable.

The proof of statement (ii) is similar to that of statement (i) and thus omitted.

For statement (iii), $\Lambda(p, q) < 0$ and $\Lambda(q, p) < 0$. Hence, both states $(N_p, 0)$ and $(0, N_q)$ are unstable. As system (2.5) is strongly monotone, by Lemma 6.3 and statements (b) and (c) recalled above, there is a unique positive steady state which is globally asymptotically stable. □

Note that $p^* \equiv 1$ if and only if $q^* \equiv 1$. For such a scenario, alternative (iii) in Theorem 6.4 does not occur, the state $(N_p, 0)$ is globally stable when $q > p$ and the state $(0, N_q)$ is globally stable when $q < p$.

Similar to Theorem 6.4, if $F < 0$ in $[0, 1]$, the global dynamics of system (2.5) can be characterized as follows.

Theorem 6.5 *Suppose that the function F is negative in* $[0, 1]$ *and let p^* and q^* be the functions introduced in Theorems 5.4 and 5.5, respectively. Then, one of the following statements holds.*

(i) If $q^* < q < p$, then the steady state $(N_p, 0)$ is globally asymptotically stable.
(ii) If $p^* < p < q$, then the steady state $(0, N_q)$ is globally asymptotically stable.
(iii) If either $0 \le q < q^*(p)$ or $0 \le p < p^*(q)$ holds, then system (2.5) has a unique positive steady state, which is also globally asymptotically stable among non-negative and not identically zero initial data.

If the function F changes sign in $(0, 1)$, the global dynamics of system (2.5) is given by the following result.

Theorem 6.6 *Suppose that the function F changes sign in* $(0, 1)$ *and let $p = p^*(q)$ and $q = q^*(p)$ be the functions given in Theorems 5.6 and 5.7. Then, one of the following alternatives holds.*

(i) If $(q - q^*)(p - p^*) < 0$, then system (2.5) has a unique positive steady state, which is also globally asymptotically stable among non-negative and not identically zero initial data.
(ii) If $(q - q^*)(q - p) < 0$, then the steady state $(N_p, 0)$ is globally asymptotically stable.
(iii) If $(q - q^*)(q - p) < 0$, then the steady state $(0, N_q)$ is globally asymptotically stable.

The proof of Theorem 6.6 is the same as that of Theorem 6.4 and follows from Theorem 6.2 and Lemma 6.3.

7 Discussion

In this paper, we considered a reaction-diffusion model for two competing populations, which disperse in a bounded two dimensional habitat by moving horizontally and vertically with different probabilities but are otherwise identical. We regard these probabilities as dispersal strategies and ask what strategies are evolutionarily stable.

Our main finding is that the only evolutionarily stable dispersal strategies are to move in one direction. In particular, when the resources are distributed inhomogeneously only in one direction, *e.g.,* horizontally, our result implies that the evolutionarily stable strategy could simply be to move in the vertical direction, in which the resources are homogeneously distributed.

We introduced a function F of the dispersal probability, which measures the difference between the spatial variations of the population equilibrium distributions in horizontal and vertical directions: when it is positive, the species has more variations in the horizontal direction; when it is negative, it has more variations in the vertical direction. We show that function F is monotone decreasing and that the evolutionarily stable dispersal strategies are to maximize the function F when it is positive and to minimize it when it is negative. As the population distribution at equilibrium is often positively correlated with the resource distribution, function F also indirectly measures the difference between the resource variations in horizontal and vertical directions. Therefore, our results seem to predict that it is more favorable for the species to choose the direction with smaller spatial variations in resource distributions.

This finding seems to be in agreement with the classical results of Hastings (1983) and Dockery et al. (1998) for the evolution of slow dispersal, *i.e.*, random diffusion is selected against in spatially heterogeneous and temporally constant environments.

We further investigated the local and global dynamics of the two-species system and determined the dynamics of system (2.5) for three different cases of the selection gradient. We used numerical simulations to illustrate how the shapes of function F, the local stability of the semi-trivial steady states and the global dynamics of the system sequentially change with respect to a certain parameter which measures the difference between the resource variations in the horizontal and vertical directions. Our numerical results suggest that if the spatial variations of resource distributions in vertical and horizontal directions become more comparable, the chances for coexistence of two competing populations could be greater.

While our findings support that smaller diffusion rate is favoured in spatially varying but temporally constant environment, our study also reveals that, in the context of anisotropic diffusion, random diffusion, which is often adopted in the older studies and assumes that the transition probabilities in all directions are equal, is not an ESS. Instead, the ESS are to move either vertically or horizontally in two dimensional habitats. Biologically, our results seem to suggest that if organisms are forced to move, anisotropic diffusion could provide more options than random diffusion for the populations to better match the available resources and coexistence is also more likely. To be more specific, when the resource variations in the horizontal and vertical directions are quite different, then the preferred strategy is to solely move in the direction with less variation in resource distribution. In contrast, if the resource variations in both directions are comparable, anisotropic diffusion provides an interesting mechanism for the coexistence of two competing populations, with one population moving in the horizontal direction and the other in the vertical direction.

There has been little use of anisotropic diffusion in mathematical models in ecology. A well studied natural system with anisotropic diffusion is the movement of wolves in areas of Canada where seismic lines are found (Dickie et al. 2017; Hillen and Painter 2013; McKenzie et al. 2012). However, there, the wolves benefit from using the seismic lines to diffuse faster than they could otherwise, allowing them to search larger areas to find prey. The observed behaviour is thus in a sense opposite to the conclusions of the present paper. This is not entirely surprising because search for mobile prey is different from exploitation of static resources, which is the setting we considered in this paper. It will be of interest and importance to incorporate the resource dynamics and reexamine the evolution of anisotropic diffusion in such more biologically realistic settings.

Some of our future works are to extend the mathematical modelling and analysis to any dimensional habitats, to continuous trait models, and to the following reaction-diffusion equation in divergence form:

$$\begin{cases} N_t = \nabla \cdot (\mathbb{D}\nabla N) + (a - N)N \text{ in } \Omega, \ t > 0, \\ \nu \cdot (\mathbb{D}\nabla N) = 0 \text{ on } \partial\Omega, \ t > 0, \\ N(0, \cdot, \cdot) = N_0 \gneqq 0 \text{ in } \Omega, \end{cases}$$

where $\mathbb{D}$ is a symmetric tensor.

Another future work will be to include a temporal variation of the environment and ask how it affects the evolution of horizontal and vertical movement. For example, if we choose $a(t, x, y) = \lambda A(x) + (1 - \lambda)B(t, y)$, a natural question is when vertical movement will be selected as in (Hutson et al. 2001).

Acknowledgements We thank Professor Yoshikazu Giga for the helpful discussions which motivated the study of anisotropic diffusion. We sincerely thank the referees for their suggestions which helped to improve the manuscript. We are also very grateful to Maxime Chupin for his assistance with the post-processing of the numerical simulations.

8 Appendix

8.1 Some remarks on solutions to a wave equation

In the proofs of Lemmas 4.3 and 4.4, the following result, which seems to be of self interest, plays an important role in eliminating the degeneracy of the function F and in establishing the strict concavity of the function $\Lambda(p, q)$ with respect to q.

Lemma 8.1 *Let W in $C^2(\Omega) \cap C^1(\overline{\Omega})$ be a solution to the system*

$$\begin{cases} W_{xx} - W_{yy} = 0 \text{ in } \Omega, \\ W_x \nu_x = W_y \nu_y = 0 \text{ on } \partial\Omega. \end{cases} \tag{8.1}$$

Then, the function W is constant.

Proof By the strict convexity assumption on the domain, the components ν_x and ν_y of the outward normal vector ν are non-zero on the boundary $\partial\Omega$, except possibly over a set of measure zero. Hence, W_x and W_y both vanish almost everywhere on $\partial\Omega$. Since W belongs to $C^1(\overline{\Omega})$, the gradient ∇W vanishes on $\partial\Omega$.

Set $\eta = x + y$, $\zeta = x - y$ and $Z(\eta, \zeta) := W(x, y)$. The function Z then satisfies

$$Z_{\eta\zeta} = 0 \text{ in } \Omega' \quad \text{and} \quad (Z_\eta, Z_\zeta) = (0, 0) \text{ on } \partial\Omega',$$

where Ω' is the image of Ω under the map $(x, y) \mapsto (\eta, \zeta)$. It follows from the first relation that $Z(\eta, \zeta) = f(\eta) + g(\zeta)$ for some functions f and g, and the second one then implies that both f and g have to be constant functions. As a consequence, Z is a constant function, and so is W. □

It is possible to construct domains such that problem (8.1) admits *non-constant* solutions, if we allow Lipschitz domains with flat parts on their boundaries.

Example 1 Consider $\Omega = (0, 1) \times (0, 1)$ and let f be an even and 2-periodic function in $\mathbb{R}$. Set $W(x, y) = f(x + y) + f(x - y)$, which then clearly satisfies problem (8.1), and is a positive non-constant function if f is taken positive and non-constant.

On the other hand, the type of domain given in the above example seems to be non-generic, as illustrated by the following result.

Lemma 8.2 *Suppose that $\Omega = (0, L_1) \times (0, L_2)$ for some positive numbers L_1 and L_2. If L_1/L_2 is not a rational number, then problem* (8.1) *has only constant solutions.*

Proof For any W satisfying problem (8.1), we have $W(x, y) = f(x + y) + f(x - y)$ for some scalar function f and then $W_x = f'(x+y) + f'(x-y)$. Since $W_x(0, y) = 0$, we have $f'(y) = -f'(-y)$, i.e. f' is an odd function. Since $W_x(L_1, y) = 0$, we have $f'(y + L_1) = -f'(L_1 - y) = f'(y - L_1)$, i.e. f' is $2L_1$-periodic.

Similarly, one has $W_y = f'(x + y) - f'(x - y)$. Note that $W_y(x, 0) = 0$ automatically holds. By $W_y(x, L_2) = 0$, we have $f'(x + L_2) = f'(x - L_2)$, that is f' is also $2L_2$-periodic. Hence, if L_1/L_2 is not rational, then f' must be a constant function. Since f' is an odd function, then $f' = 0$, that is W is a constant function. □

8.2 A remark about a possible degeneracy induced by the domain Ω

Throughout the paper, we have assumed that Ω is a strictly convex domain. We now comment on this point, showing with a very basic example that a domain with flat parts on its boundary may lead to a degeneracy of the function F.

Consider $\Omega = (0, 1) \times (0, 1)$ and let f and D be given as in Example 1. Setting

$$a := -(\overline{D} + \underline{D})\frac{W_{xx}}{W} + W,$$

it is easy to check that, for each θ in $[0, 1]$, W also solves (2.3), that is $N_\theta \equiv W$ for each θ in $[0, 1]$. Since the function W is non-constant, the free growth rate a is also non-constant. Furthermore, for each value of p and q in $[0, 1]$, problem (2.5) has a continuum of positive steady states of the form $(U, V) = (sW, (1-s)W)$, with s in $(0, 1)$. Moreover, in this case, $F \equiv 0$ in $[0, 1]$, even though the function a is not constant. Indeed, since f is even, we have $W(x, y) = W(y, x)$, which implies that $F \equiv 0$ in $[0, 1]$.

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