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Evolution of movement strategies in patchy landscapes

Lin Wang [a], King-Yeung Lam [b], Frithjof Lutscher [c,*]

[a] *School of Science, Jimei University, Xiamen, Fujian, 361021, China*
[b] *Department of Mathematics, The Ohio State University, Columbus, OH, 43210, USA*
[c] *Department of Mathematics and Statistics, and Department of Biology, University of Ottawa, Ottawa, ON, K1N6N5, Canada*

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Abstract

How individuals move across a landscape determines their opportunities to gather resources and their risk to adverse conditions. Studying how their movement evolves in response to landscape quality is therefore paramount to understanding the fate of populations. We consider a landscape consisting of several adjacent patches where landscape quality differs between patches but is constant within each patch. The movement strategy of individuals consists of random dispersal within each patch and some patch preference to move between patches. Accordingly, our model consists of a system of reaction-diffusion equations for the population density on each patch together with matching conditions for the population density and flux at boundaries between patches. In the linear form of our model, we study the principal eigenvalue, its existence and its dependence on movement parameters. In the nonlinear form of our model, we study steady states, their existence and their stability with respect to invasion by a population with a different movement strategy. We find that lower random dispersal rates evolve when patch preferences are fixed; that the evolution of patch preferences depends on the arrangement of habitat quality in the landscape when dispersal rates are fixed; and that simultaneous evolution of both can lead to the so-called Ideal Free Distribution, which is a well-established concept in movement ecology. These findings provide theoretical insight into how dispersal and habitat selection coevolve in heterogeneous landscapes.

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* Corresponding author.
E-mail address: flutsche@uottawa.ca (F. Lutscher).

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1. Introduction

The evolution of movement strategies in spatially heterogeneous landscapes is a fundamental question in theoretical ecology and evolutionary biology. It concerns how organisms should optimally move across a landscape whose local habitat quality varies spatially. The movement decisions that individuals make in order to exploit resources and avoid dangers can profoundly influence their ability to persist in a given landscape. Hence, studying optimal movement behavior is particularly relevant as human activity often leads to increasing landscape fragmentation, which, in turn, triggers a decline in population abundance and diversity.

Reaction-diffusion models have long served as a theoretical framework for describing spatiotemporal population dynamics [6]. In the context of strictly random movement strategies, a fundamental and fairly general result is that in temporally constant environments with a spatial optimum, there is selection against random dispersal [10,17,22,27]; whereas there is selection for dispersal if there is no spatially optimal location [4,51]. Selection for dispersal is also possible when individuals move with a combination of directional and random movement strategy. Examples of nonrandom movement include movements conditional on habitat quality such as gradient sensing (see [3] and references therein), or when individuals are pushed in one direction by external forces such as wind or water flow [30,33]. These results hold across different modeling frameworks, for example in so-called patch models (see [28,53] and references therein). In those models, a landscape is divided into discrete patches and the population densities on the patches as well as their movement between patches are described by systems of ordinary differential equations.

A more recent modeling approach combines continuous and discrete landscape structure in so-called patchy reaction-diffusion equations [36]. This approach is inspired by landscape ecology, which conceptualizes landscapes as consisting of multiple spatial regions ("patches"), each of which is relatively homogeneous within but differs from the adjacent patches. Differences may result from natural sources of environmental heterogeneity, such as variations in topography, soil, or vegetation, or they may arise due to anthropogenic disturbances, including agricultural development and urban expansion, which lead to habitat fragmentation. This piecewise constant landscape is represented in patchy reaction-diffusion equations for population dynamics by piecewise constant parameter functions, for example diffusion coefficients and growth rates. In addition, patchy reaction-diffusion models require matching conditions for the density and flux of a population across a boundary or interface between two patches. These conditions encapsulate movement behavior and patch preference of individuals [40], which were treated too simplistically in early patch models [19,41,45]. With mechanistically derived matching conditions that allow modeling of asymmetric boundary movement and habitat selection behavior, the framework became much more biologically realistic and widely applicable [34,36,37,46,52], and also generated novel analytical investigations [21,48]. Compared to reaction-diffusion equations with smooth parameter functions, patchy reaction-diffusion equations require fewer and possibly more easily accessible parameters. Compared to patch models based on ordinary differential equations, patchy reaction-diffusion equations give more insight into the spatial distribution of a population within each patch.

Despite the recent surge in ecological applications of patchy reaction-diffusion equations, there are only relatively few studies that consider evolutionary aspects, some for processes of spatial spread on unbounded domains [44], others for steady states on bounded domains [35], which we consider here. Specifically, Maciel and coworkers considered a two-patch model with interface conditions as described above and studied the evolution of movement behavior at an interface [35]. They determined the ideal free dispersal (IFD) strategy in this case and showed that it is an evolutionarily steady state (ESS). An ideal free dispersal strategy is one that leads to individuals being distributed proportional to the available resource [20]. An ESS represents a movement strategy such that a population using an ESS cannot be invaded by a population using any other strategy [38]. Most existing work has, however, focused on two patches (or two periodically alternating patch types in the case of an unbounded landscape), although there is related work using patchy reaction-diffusion equations with three patches of identical quality in a river network [50]. When there are three or more patches, there can be different network geometries and different orientations of up/downstream [23], therefore the arguments for two-patch case do not lend for easy generalization to multiple patches. More general questions of how behavioral traits such as dispersal and patch preference evolve in three and more patches or patch types require further investigation.

We consider a population residing in a landscape consisting of multiple patches in a one-dimensional spatial domain. While we state and prove many of our results in the case of three patches, we add remarks indicating how these proofs can be generalized to any number of adjacent patches. The dispersal rates and growth rates of individuals vary from patch to patch, and movement between patches is characterized by location-dependent preferences. Dispersal rates and patch preferences are the evolvable traits that we consider. In the study of our model, the principal eigenvalue of a linearized model is crucial for many of the relevant biological questions such as the invasion or persistence of a species. We therefore devote large sections to the analysis of the eigenvalue problem, in particular to the question of how the principal eigenvalue depends on model parameters. We then study the nonlinear model in the framework of adaptive dynamics [16], i.e., we determine the IFD strategy and show that it is not only an ESS, which means that other strategies are unsuccessful against it (see above), but also a neighborhood invader strategy (NIS), which means that it is successful in the presence of other strategies [2].

We describe our model in detail in Section 2 and give the necessary analytical results on existence and uniqueness of solutions in Section 3, where we also introduce the notions of sub- and supersolutions that are relevant in subsequent sections. The bulk of our work is in Section 4, where we study the properties of the principal eigenvalue of the linearized model. The analysis of various aspects of the nonlinear model is in Section 5. We end with a discussion of possible applications, as well as similarities and differences with the existing literature.

2. Model description

We describe the movement and demography of a population in a patchy landscape by using reaction-diffusion equations on each patch and appropriate interface matching conditions to connect patches. The model with three patches extends recently studied models on two patches (or two patch types periodically arranged); see [34,36]. We number patches from left to right with lengths L_i, $i = 1, 2, 3$ and set $L = L_1 + L_2 + L_3$ (see Fig. 1), and denote the patches as

$$P_1 = (0, L_1), \quad P_2 = (L_1, L_1 + L_2), \quad \text{and} \quad P_3 = (L_1 + L_2, L). \tag{2.1}$$

On patch i, the density of the species is denoted by $u_i(x, t)$. It satisfies the reaction-diffusion equation

$$u_{i,t} = d_i u_{i,xx} + r_i u_i \left(1 - \frac{u_i}{K_i}\right), \quad x \in P_i, \quad t > 0, \tag{2.2}$$

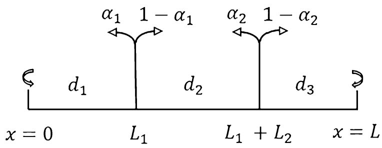


Fig. 1. Arrangement of three adjacent patches with lengths L_i. The probabilities of moving left at interface between patches P_j, P_{j+1} are denoted by α_j, $j=1,2$. The return arrows at $x=0$ and $x=L$ indicate no-flux boundary conditions at those ends.

where d_i is the diffusion coefficient, r_i is the growth rate of the species in patch i, and K_i represents the carrying capacity of patch i. All parameters are assumed positive. Individuals can move between adjacent patches but cannot leave the set of patches. Accordingly, we impose no-flux boundary conditions at 0 and L, i.e.,

$$u_{1,x}(0,t)=0 \quad \text{and} \quad u_{3,x}(L,t)=0. \tag{2.3}$$

Movement between patches conserves the density of individuals leading to the *flux-matching conditions*

$$d_1u_{1,x}(L_1,t)=d_2u_{2,x}(L_1,t) \quad \text{and} \quad d_2u_{2,x}(L_1+L_2,t)=d_3u_{3,x}(L_1+L_2,t). \tag{2.4}$$

At the interface between patches 1 and 2 (and 2 and 3), individuals may have a preference for moving to one or the other. We denote by α_1 (resp. α_2) the probability that an individual at L_1 (resp. L_1+L_2) moves to the left and by $1-\alpha_1$ (resp. $1-\alpha_2$) the probability that an individual moves to the right. This leads to the *density matching conditions* [36]:

$$(1-\alpha_1)d_1u_1(L_1,t)=\alpha_1d_2u_2(L_1,t), \tag{2.5}$$

$$(1-\alpha_2)d_2u_2(L_1+L_2,t)=\alpha_2d_3u_3(L_1+L_2,t). \tag{2.6}$$

It is sometimes useful to consider the triple of functions (u_1,u_2,u_3) as one function u on $[0,L]$, while keeping in mind that this function is multi-valued at L_1 and L_1+L_2.

The quality of the i-th patch is expressed in terms of the population dynamics parameters r_i and K_i, which depend on the species in question. Higher values of r_i and K_i indicate higher landscape quality. The diffusion coefficient describes the movement response of individuals to local patch quality. It may therefore depend on patch quality. For example, we expect that individuals move slowest when quality is high and fastest when it is low. Similarly, patch preferences may depend on the relative quality of the two adjacent patches. In general, we expect that individuals at the interface between two patches preferentially choose to move into the patch of higher quality.

Eventually, we are interested in the evolution of movement behavior. One way to look at this is through the (random) dispersal ability. To deal with the three (potentially different) dispersal parameters, we write the individual parameters as multiples of an overall dispersal propensity (d) and a scaling factor that depends on the environment ($\tilde{d}_i$), i.e., $d_i=d\tilde{d}_i$. This allows us to study certain limiting cases ($d\to\infty$ or $d\to 0$) while keeping the ratios between the d_i constant. In particular, varying d does not affect the interface matching conditions since they only depend on those ratios.

Similarly, we might want to look at limiting cases of the directed movement behavior as encapsulated by the patch preferences α_j. These only appear in the interface conditions. We form the ratios $z_j = \alpha_j/(1-\alpha_j)$, which range from 0 to ∞. The limit $z_j \to 0$ means that all individuals move to the right, while $z_j \to \infty$ means that all individuals move to the left.

Since our model is not just a standard reaction-diffusion equation, we present basic preliminary results on existence and various related topics in the next section.

3. Preliminaries

We present some basic analytical results for equations (2.2) with boundary and matching conditions (2.3)–(2.6) in this section. In particular, we prove that the maximum principle holds, that certain a priori estimates are available, and that a dominant eigenvalue exists. These results are inspired by corresponding results for the two-patch model in [35]; see also [21].

Consider the following problem

$$\begin{cases} \mathcal{L}_i u_i = f_i(x), \quad x \in P_i, \\ u_{1x}(0) = u_{3x}(L) = 0, \\ d_1 u_{1x}(L_1) = d_2 u_{2x}(L_1),\ u_1(L_1) = k_1 u_2(L_1), \\ d_2 u_{2x}(L_1+L_2) = d_3 u_{3x}(L_1+L_2),\ u_2(L_1+L_2) = k_2 u_3(L_1+L_2), \end{cases} \tag{3.1}$$

where $\mathcal{L}_i = -d_i \frac{d^2}{dx^2} - c_i(x)$, $i = 1, 2, 3$ and

$$k_1 = \frac{\alpha_1}{1-\alpha_1}\frac{d_2}{d_1}, \quad \text{and} \quad k_2 = \frac{\alpha_2}{1-\alpha_2}\frac{d_3}{d_2}. \tag{3.2}$$

To simplify notation, we sometimes write $\mathcal{L} = (\mathcal{L}_1, \mathcal{L}_2, \mathcal{L}_3)$.

Proposition 3.1. *Suppose that u_i solve (3.1) with $c_i(x) \le 0$ and $f_i(x) \ge 0, \not\equiv 0$. Then $u_i > 0$ on $\bar{P}_i$.*

Proof. It follows from the classical maximum principle and the Hopf boundary lemma that a negative minimum cannot occur at the interior of any of the P_i and not at the boundary points 0 and L either. Therefore, it can only occur at the interfaces, given by $x = L_1$ or $x = L_1 + L_2$. Suppose that the minimum occurs at $x = L_1$. Then $u_{1x}(L_1) < 0$, by applying the Hopf boundary lemma in the subinterval $[0, L_1]$. According to the matching conditions, we have $u_{2x}(L_1) < 0$. This means that the minimum of u_2 must be attained either in $(L_1, L_1 + L_2)$ or at $x = L_1 + L_2$. In the first case, then $u_2 \equiv \text{const} < 0$. But from the equation for u_2, we have that $0 \ge -c_2(x)u_2 = f_2(x) \ge 0, \not\equiv 0$, which is a contradiction. In case the minimum of u_2 is attained at $x = L_1 + L_2$, then we repeat the same argument to deduce that u_3 must attain an internal minimum in $(L_1 + L_2, L_3)$ (since $x = L_3$ is not possible thanks to the Hopf boundary lemma). But then $u_3 \equiv \text{const} < 0$ and we have a contradiction as before. Hence, $u_i \ge 0$ on $\bar{P}_i$.

Now suppose that $f_1(x) \ge 0, \not\equiv 0$. Then $u_1 > 0$ on $\bar{P}_1$ by the strong maximum principle. Based on the matching conditions, we have $u_2(L_1) > 0$, so that $u_2 > 0$ on $\bar{P}_2$ by the strong maximum principle. Similarly, we can obtain $u_3 > 0$ on $\bar{P}_3$. □

Proposition 3.2. *Suppose that $c_i(x) \le 0$. Given $f_i(x) \in \mathcal{C}(\bar{P}_i)$, there is a unique solution $u_i \in \mathcal{C}^2(\bar{P}_i)$ of (3.1) with*

$$\|u_1\|_{\mathcal{C}^2(\bar{P}_1)} + \|u_2\|_{\mathcal{C}^2(\bar{P}_2)} + \|u_3\|_{\mathcal{C}^2(\bar{P}_3)} \le C(\|f_1\|_{\mathcal{C}(\bar{P}_1)} + \|f_2\|_{\mathcal{C}(\bar{P}_2)} + \|f_3\|_{\mathcal{C}(\bar{P}_3)}). \tag{3.3}$$

Proof. First, we consider the following decoupled problems,

$$-d_i\tilde{u}_{i,xx} - c_i\tilde{u}_i = f_i, \quad x \in P_i,$$

with Neumann boundary conditions on each P_i. By the maximum principle, we get the estimates

$$\|\tilde{u}_i\|_{\mathcal{C}^2(\bar{P}_i)} \le C\|f_i\|_{\mathcal{C}(\bar{P}_i)} \tag{3.4}$$

on each patch.

Next, we define y_1 to be the solution of

$$-d_1y_{1,xx} - c_1(x)y_1 = 0, \ x \in P_1, \ \text{ and } \ y_1(0) = 1, \ y_{1x}(0) = 0.$$

By similar arguments as in [35, Proposition 3.4], we obtain $y_{1x}(L_1) > 0$. The same reasoning shows that y_3, defined as the solution of

$$-d_3y_{3,xx} - c_3(x)y_3 = 0, \ x \in P_3, \text{ and } y_3(L) = 1, \ y_{3x}(L) = 0,$$

satisfies $y_{3x}(L_1 + L_2) < 0$. On P_2, we define two functions, y_2 and y_4, as the solutions of

$$-d_2y_{l,xx} - c_2(x)y_l = 0, \ x \in P_2$$

with boundary conditions $y_2(L_1 + L_2) = 1$, $y_{2x}(L_1 + L_2) = 0$ and $y_4(L_1) = 1$, $y_{4x}(L_1) = 0$, respectively. By the same reasoning as above, these satisfy $y_{2x}(L_1) < 0$ and $y_{4x}(L_1 + L_2) > 0$.

Finally, we define

$$u_1 = \tilde{u}_1 + a_1y_1, \ \ u_2 = \tilde{u}_2 + a_2y_2 + a_4y_4, \ \ u_3 = \tilde{u}_3 + a_3y_3,$$

for parameters $(a_1, \dots, a_4)$. These functions u_i satisfy the differential equations and the boundary conditions in (3.1). To satisfy the interface matching conditions in (3.1), we must have

$$\begin{aligned}
d_1y_{1x}(L_1)a_1 - d_2y_{2x}(L_1)a_2 &= 0,\\
y_1(L_1)a_1 - k_1y_2(L_1)a_2 - k_1a_4 &= k_1\tilde{u}_2(L_1) - \tilde{u}_1(L_1),\\
d_3y_{3x}(L_1 + L_2)a_3 - d_2y_{4x}(L_1 + L_2)a_4 &= 0,\\
a_2 - k_2y_3(L_1 + L_2)a_3 + y_4(L_1 + L_2)a_4 &= k_2\tilde{u}_3(L_1 + L_2) - \tilde{u}_2(L_1 + L_2).
\end{aligned}$$

The equations are linear in $(a_1, \dots, a_4)$ and hence can be written in matrix form. The determinant of the resulting matrix is

$$d_1 y_{1x}(L_1)[k_1 d_3 y_{3x}(L_1+L_2)(1-y_2(L_1)y_4(L_1+L_2))$$
$$+k_1k_2d_2y_2(L_1)y_3(L_1+L_2)y_{4x}(L_1+L_2)]+d_2y_{2x}(L_1)[d_3y_1(L_1)y_{3x}(L_1+L_2)y_4(L_1+L_2)$$
$$-k_2d_2y_1(L_1)y_3(L_1+L_2)y_{4x}(L_1+L_2)]>0.$$

Hence, there is a unique solution for $(a_1,\dots,a_4)$ that depends on d_i, c_i and k_j, but not on f_i, where $i=1,2,3,\ j=1,2$. Therefore, the solution u_i satisfies the estimate in the statement of the proposition. □

By similar arguments as in Proposition 3.2, we obtain the following result.

Proposition 3.3. *Suppose that $c_i(x)\le 0$. Given $f_i(x)\in L^2(\bar P_i)$, there is a unique solution $u_i\in W^{2,2}(\bar P_i)$ of (3.1) with*

$$\|u_1\|_{W^{2,2}(\bar P_1)}+\|u_2\|_{W^{2,2}(\bar P_2)}+\|u_3\|_{W^{2,2}(\bar P_3)}\le C(\|f_1\|_{L^2(\bar P_1)}+\|f_2\|_{L^2(\bar P_2)}+\|f_3\|_{L^2(\bar P_3)}).$$

Next, we consider the eigenvalue problem corresponding to the operator $\mathcal{L}$ from (3.1), i.e.,

$$\begin{cases}\mathcal{L}_i\varphi_i=\lambda\varphi_i, \quad x\in P_i,\\ \varphi_{1x}(0)=\varphi_{3x}(L)=0,\\ d_1\varphi_{1x}(L_1)=d_2\varphi_{2x}(L_1),\ \varphi_1(L_1)=k_1\varphi_2(L_1),\\ d_2\varphi_{2x}(L_1+L_2)=d_3\varphi_{3x}(L_1+L_2),\ \varphi_2(L_1+L_2)=k_2\varphi_3(L_1+L_2).\end{cases} \tag{3.5}$$

Using Propositions 3.1-3.3, we obtain the existence of the principal eigenvalue for (3.5) from the Krein-Rutman theorem [49]. We denote this eigenvalue by $\lambda_1(\mathcal{L})$, which is simple and has a positive eigenfunction $\varphi=(\varphi_i)$. We shall normalize (φ_i) by $\max_i \sup_{x\in\bar P_i}\varphi_i=1$.

We define super- and sub-solutions of $\mathcal{L}\varphi=0$ associated with the interface and boundary conditions in (3.5). To simplify notation, we let $\mathrm{X}=\mathcal{C}^2(\bar P_1)\times\mathcal{C}^2(\bar P_2)\times\mathcal{C}^2(\bar P_3)$.

Definition 3.1. A function $\bar\varphi=(\bar\varphi_i)\in\mathrm{X}$ is called a supersolution of $\mathcal{L}$ with the interface and boundary conditions in (3.5), if $\bar\varphi$ satisfies

$$\begin{cases}\mathcal{L}_i\bar\varphi_i\ge 0, \quad x\in P_i,\\ \bar\varphi_{1x}(0)\le 0, \quad \bar\varphi_{3x}(L)\ge 0,\\ \bar\varphi_1(L_1)=k_1\bar\varphi_2(L_1),\ \ d_1\bar\varphi_{1x}(L_1)^-\ge d_2\bar\varphi_{2x}(L_1)^+,\\ \bar\varphi_2(L_1+L_2)=k_2\bar\varphi_3(L_1+L_2),\ d_2\bar\varphi_{2x}(L_1+L_2)^-\ge d_3\bar\varphi_{3x}(L_1+L_2)^+.\end{cases} \tag{3.6}$$

The supersolution $\bar\varphi$ is called a strict supersolution if it is not a solution of (3.6) with all inequality signs replaced by equality signs. A subsolution is defined in a similar way with all the inequality signs above reversed.

Lemma 3.4. *If $\bar\varphi=(\bar\varphi_i)$ is a supersolution of $\mathcal{L}$ and it is nonnegative, then either $\bar\varphi\equiv 0$, or $\bar\varphi_i>0$ in $\bar P_i$ for all i.*

Proof. Assume $\bar{\varphi} \not\equiv 0$ and we shall prove that $\bar{\varphi}_i > 0$ in $\bar{P}_i$ for all i. Suppose that the assertion is false. Then there exists some point $x_0 \in \bar{P}_i$ such that $\bar{\varphi}_i(x_0) = 0$ for some i. If $x_0 \in \partial P_i$, then there are two subcases to consider: (i) $\bar{\varphi}_1(0) = \bar{\varphi}_3(L) = 0$, then by the Hopf boundary lemma, we have $\bar{\varphi}_{1x}(0) > 0$, and $\bar{\varphi}_{3x}(L) < 0$, a contradiction to $\bar{\varphi}_{1x}(0) \le 0,\ \bar{\varphi}_{3x}(L) \ge 0$. (ii) $\bar{\varphi}_1(L_1) = \bar{\varphi}_2(L_1 + L_2) = 0$, then $\bar{\varphi}_2(L_1) = 0$ and $\bar{\varphi}_3(L_1 + L_2) = 0$ via the matching conditions. From Definition 3.1, it follows that $d_2\bar{\varphi}_{2x}(L_1)^+ \le d_1\bar{\varphi}_{1x}(L_1)^- < 0$, and $d_3\bar{\varphi}_{3x}(L_1 + L_2)^+ \le d_2\bar{\varphi}_{2x}(L_1 + L_2)^- < 0$. This contradicts the assumption that $\bar{\varphi}_i \ge 0$. Hence, $\bar{\varphi}_i > 0$ on ∂P_i. If $x_0 \in P_i$, then $\bar{\varphi}_i$ attains its minimum in the interior point x_0, and so it follows from the classical maximum principle that $\bar{\varphi}_i \equiv 0$ on $\bar{P}_i$. Furthermore, by the matching conditions and the classical maximum principle, it can be deduced that $\bar{\varphi} \equiv 0$, which contradicts our assumption that $\bar{\varphi} \not\equiv 0$. Thus, we conclude that $\bar{\varphi}_i > 0$ in $\bar{P}_i$ for all i. □

Definition 3.2. We say that $\mathcal{L}$ admits the maximum principle if any supersolution $\varphi = (\varphi_i) \in \mathrm{X}$ of $\mathcal{L}$ is nonnegative.[1]

Theorem 3.5. *The following statements are equivalent:*

(i) *$\mathcal{L}$ admits the maximum principle;*
(ii) $\lambda_1(\mathcal{L}) > 0$*;*
(iii) *$\mathcal{L}$ has a strict supersolution $\bar{\varphi} = (\bar{\varphi}_i)$, which is nonnegative and not identically zero.*

Proof. (i) ⇒ (ii). Suppose that $\lambda_1(\mathcal{L}) \le 0$. Then for the corresponding principal eigenfunction $\varphi_i > 0$ in P_i, we have

$$\begin{cases} \mathcal{L}_i(-\varphi_i) = \lambda_1(\mathcal{L})(-\varphi_i) \ge 0, \quad x \in P_i, \\ (-\varphi_1)_x(0) = (-\varphi_3)_x(L) = 0, \\ (-\varphi_1)(L_1) = k_1(-\varphi_2)(L_1),\ d_1(-\varphi_1)_x(L_1) = d_2(-\varphi_2)_x(L_1), \\ (-\varphi_2)(L_1 + L_2) = k_2(-\varphi_3)(L_1 + L_2),\ d_2(-\varphi_2)_x(L_1 + L_2) = d_3(-\varphi_3)_x(L_1 + L_2). \end{cases} \tag{3.7}$$

By applying the maximum principle to $-\varphi_i$, we derive that $-\varphi_i \ge 0$ in P_i, a contradiction with the positivity of φ_i.

(ii) ⇒ (iii). Obviously, the corresponding principal eigenfunction $\varphi_i > 0$ is a strict supersolution of $\mathcal{L}$.

(iii) ⇒ (i). For any given supersolution φ of $\mathcal{L}$, if $\varphi \ge 0$, then there is nothing to prove. Assume for contradiction that $\inf_{P_i} \varphi_i < 0$ for some i.

Let $\bar{\varphi}$ be a strict supersolution of $\mathcal{L}$, then $\bar{\varphi} \not\equiv 0$ and $\inf_{P_i} \bar{\varphi}_i > 0$ for all i by Lemma 3.4. Then consider $\psi = \varphi + k\bar{\varphi}$, where $k > 0$ is chosen such that $\min_i \left(\inf_{P_i} \psi_i\right) = 0$. Then by Lemma 3.4 again, we deduce that $\psi \equiv 0$. However, this implies that $\varphi = -k\bar{\varphi}$. So it φ is simultaneously a supersolution and a strict subsolution, which is a contradiction. □

Here, we give two comparison lemmas for the principal eigenvalue of (3.5). These principles are extensions of the corresponding results for scalar equations in [26, Lemmas 1.3.12–1.3.13].

[1] Different authors have proposed different formulations of a maximum principle or a strong maximum principle. Our definition follows Gilbarg and Trudinger's book but differs slightly from that in [18].

Lemma 3.6. *Suppose there exists a function* $w = (w_i) \in \mathrm{X}$ *and a constant* $\underline{\lambda}$ *such that* $w_i > 0$ *in* $\bar{P}_i$ *is a supersolution of* (3.5) *in the sense that*

$$\begin{cases} \mathcal{L}_i w_i \geq \underline{\lambda} w_i, \quad x \in P_i, \\ w_{1x}(0) \leq 0, \quad w_{3x}(L) \geq 0, \\ w_1(L_1) = k_1 w_2(L_1), \ d_1 w_{1x}(L_1)^- \geq d_2 w_{2x}(L_1)^+, \\ w_2(L_1+L_2) = k_2 w_3(L_1+L_2), \ d_2 w_{2x}(L_1+L_2)^- \geq d_3 w_{3x}(L_1+L_2)^+. \end{cases} \tag{3.8}$$

Then $\lambda_1(\mathcal{L}) \geq \underline{\lambda}$*, and equality holds iff* w_i *is the corresponding eigenfunction.*

Proof. If all the inequalities in (3.8) are equalities, then w_i is a solution and it follows that $\lambda_1(\mathcal{L}) = \underline{\lambda}$. Otherwise, w_i is a strict supersolution, then we may apply Theorem 3.5 to the operator $\tilde{\mathcal{L}} = \mathcal{L} - \underline{\lambda}$ to conclude that $\lambda_1(\mathcal{L}) > \underline{\lambda}$. □

Lemma 3.7. *Suppose there exists a function* $w = (w_i) \in \mathrm{X}$ *and a constant* $\bar{\lambda}$ *such that* w_i *is a nonnegative subsolution of* (3.5) *in the sense that*

$$\begin{cases} \mathcal{L}_i w_i \leq \bar{\lambda} w_i, \quad x \in P_i, \\ w_{1x}(0) \geq 0, \quad w_{3x}(L) \leq 0, \\ w_1(L_1) = k_1 w_2(L_1), \ d_1 w_{1x}(L_1)^- \leq d_2 w_{2x}(L_1)^+, \\ w_2(L_1+L_2) = k_2 w_3(L_1+L_2), \ d_2 w_{2x}(L_1+L_2)^- \leq d_3 w_{3x}(L_1+L_2)^+. \end{cases}$$

Then $\lambda_1(\mathcal{L}) \leq \bar{\lambda}$*, and equality holds iff* w_i *is the corresponding eigenfunction.*

Proof. The proof is analogous to Lemma 3.6 and is omitted. □

4. Analysis of the eigenvalue problem

In this section, we study how the principal eigenvalue depends on the movement-related parameters, i.e., on the diffusion coefficients (d_i) and the preference probabilities at the interfaces (α_j); see Section 2.

The eigenvalue problem consists of the three equations

$$d_i \varphi_{i,xx} + c_i(x)\varphi_i + \lambda \varphi_i = 0, \quad x \in P_i, \qquad i = 1,2,3, \tag{4.1}$$

together with the boundary and interface matching conditions

$$\varphi_{1x}(0) = 0, \tag{4.2a}$$

$$d_1 \varphi_{1x}(L_1) = d_2 \varphi_{2x}(L_1), \varphi_1(L_1) = k_1 \varphi_2(L_1), \tag{4.2b}$$

$$d_2 \varphi_{2x}(L_1+L_2) = d_3 \varphi_{3x}(L_1+L_2), \varphi_2(L_1+L_2) = k_2 \varphi_3(L_1+L_2), \tag{4.2c}$$

$$\varphi_{3x}(L) = 0, \tag{4.2d}$$

where k_j are as in (3.2). As in the preceding section, we shall assume throughout that the eigenfunction is positive and normalized to $\max_i \sup_{\bar{P}_i} \varphi_i = 1$.

As indicated in the introduction, we write the diffusion coefficient in each patch as the product of a patch-dependent rate ($\tilde{d}_i$) and an overall diffusion propensity parameter (d). Hence, we set $d_i = d\tilde{d}_i$. Consequently, the dimensionless parameters k_j depend only on $\tilde{d}_i$ and are independent of d. As parameters α_j denote probabilities, they range in [0, 1], whereas d_i and k_j can assume any positive value.

We begin with a general upper and lower bound of the principal eigenvalue λ_1.

Lemma 4.1. *The principal eigenvalue* λ_1 *of* (4.1)–(4.2) *satisfies*

$$\min_{i=1,2,3}\{-\max_{x\in\bar{P}_i} c_i(x)\} \le \lambda_1 \le \max_{i=1,2,3}\{-\min_{x\in\bar{P}_i} c_i(x)\}. \tag{4.3}$$

Proof. We integrate the equations in (4.1) over their respective interval $\bar{P}_i$ and add the results. The boundary and interface matching conditions ensure that all the terms containing φ_{ix} disappear. We obtain

$$\begin{aligned}
&\lambda_1\left[\int_0^{L_1}\varphi_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2}\varphi_2 \mathrm{d}x + \int_{L_1+L_2}^{L}\varphi_3 \mathrm{d}x\right]\\
&= -\int_0^{L_1} c_1(x)\varphi_1 \mathrm{d}x - \int_{L_1}^{L_1+L_2} c_2(x)\varphi_2 \mathrm{d}x - \int_{L_1+L_2}^{L} c_3(x)\varphi_3 \mathrm{d}x\\
&\ge -\max_{x\in\bar{P}_1} c_1(x)\int_0^{L_1}\varphi_1 \mathrm{d}x - \max_{x\in\bar{P}_2} c_2(x)\int_{L_1}^{L_1+L_2}\varphi_2 \mathrm{d}x - \max_{x\in\bar{P}_3} c_3(x)\int_{L_1+L_2}^{L}\varphi_3 \mathrm{d}x\\
&\ge \min\{-\max_{x\in\bar{P}_1} c_1(x), -\max_{x\in\bar{P}_2} c_2(x), -\max_{x\in\bar{P}_3} c_3(x)\}\left[\int_0^{L_1}\varphi_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2}\varphi_2 \mathrm{d}x + \int_{L_1+L_2}^{L}\varphi_3 \mathrm{d}x\right].
\end{aligned}$$

Hence,

$$\lambda_1 \ge \min\{-\max_{x\in\bar{P}_1} c_1(x), -\max_{x\in\bar{P}_2} c_2(x), -\max_{x\in\bar{P}_3} c_3(x)\}. \tag{4.4}$$

The upper bound follows from similar considerations. □

When $c_i(x)$ is constant, the eigenfunction $\varphi_i(x)$ exhibits monotonicity with respect to the spatial variable x in some special cases.

Lemma 4.2. *Let* $c_i(x) = c_i$ *be constants. Then we have the following statements.*

(i) *If* $c_3 \ge c_2 \ge c_1$ *with at most one equality, then* $\varphi_{1x}(x) > 0$ *in* $(0, L_1]$, $\varphi_{3x}(x) > 0$ *in* $[L_1 + L_2, L)$, *and* $\varphi_{2x}(L_1) > 0$, $\varphi_{2x}(L_1 + L_2) > 0$;

(ii) *If* $c_3 \le c_2 \le c_1$ *with at most one equality, then* $\varphi_{1x}(x) < 0$ *in* $(0, L_1]$, $\varphi_{3x}(x) < 0$ *in* $[L_1 + L_2, L)$, *and* $\varphi_{2x}(L_1) < 0$, $\varphi_{2x}(L_1 + L_2) < 0$.

Proof. Let us consider case (i). Integrating the first equation of (4.1) over $(0, x)$, $x \le L_1$, we have

$$d_1\varphi_{1x}(x) = -(c_1+\lambda_1)\int_0^x \varphi_1 ds.$$

Similarly, we have

$$d_2\varphi_{2x}(y) - d_2\varphi_{2x}(x) = -(c_2+\lambda_1)\int_x^y \varphi_2 ds, \quad L_1 \le x < y \le L_1+L_2,$$

$$d_3\varphi_{3x}(y) = (c_3+\lambda_1)\int_y^L \varphi_3 ds, \quad L_1+L_2 \le y < L.$$

When $x = L_1$, $y = L_1 + L_2$, we can obtain that

$$\begin{aligned} 0 &= (c_1+\lambda_1)\int_0^{L_1}\varphi_1 \mathrm{d}x + (c_2+\lambda_1)\int_{L_1}^{L_1+L_2}\varphi_2\mathrm{d}x + (c_3+\lambda_1)\int_{L_1+L_2}^{L}\varphi_3\mathrm{d}x \\ &> (c_1+\lambda_1)\left[\int_0^{L_1}\varphi_1\mathrm{d}x + \int_{L_1}^{L_1+L_2}\varphi_2\mathrm{d}x + \int_{L_1+L_2}^{L}\varphi_3\mathrm{d}x\right]. \end{aligned}$$

Hence, $c_1+\lambda_1 < 0$. Similarly, we have $c_3+\lambda_1 > 0$. Therefore, $\varphi_{1x}(x) > 0$ in $(0, L_1]$, $\varphi_{3x}(x) > 0$ in $[L_1+L_2, L)$. Moreover, we have $\varphi_{2x}(L_1) > 0$ and $\varphi_{2x}(L_1+L_2) > 0$ based on the interface conditions. □

4.1. The properties of the principal eigenvalue with respect to diffusion

The question of how the principal eigenvalue depends on the movement behavior of the population has been studied in many contexts [6,10,24,26,39,51]. It can give important insights into optimal movement rates for population persistence or the evolution of dispersal ability. We study this question for our patch model. To indicate the parameter dependence, we denote the principal eigenvalue by $\lambda_1 = \lambda_1(d)$ and by $'$ the derivative with respect to this parameter d.

Lemma 4.3. *Let $\lambda_1 = \lambda_1(d)$ be the principal eigenvalue of* (4.1)–(4.2)*. Then $\lambda_1'(d) \ge 0$. Moreover, $\lambda_1'(d) > 0$ for all $d > 0$ unless there is a constant k_0 such that $c_i(x) = k_0$ in P_i for all i. In the latter case, we have $\lambda_1(d) \equiv k_0$ for all $d > 0$.*

Remark 4.4. In the jargon of population dynamics, this lemma establishes the *reduction principle* [1]. In the next section, we state as a consequence of this lemma the evolution of slow dispersal (Theorem 5.9).

Proof. We differentiate equations (4.1)-(4.2) with respect to d (denoted by $'$) and obtain

$$\tilde{d}_i \varphi_{i,xx} + d\tilde{d}_i \varphi'_{i,xx} + c_i(x)\varphi'_i + \lambda_1 \varphi'_i = -\lambda'_1(d)\varphi_i, \quad x \in P_i, \tag{4.5}$$

with boundary and matching conditions

$$\begin{cases} \varphi'_{1x}(0) = \varphi'_{3x}(L) = 0, \\ \tilde{d}_1 \varphi'_{1x}(L_1) = \tilde{d}_2 \varphi'_{2x}(L_1), \varphi'_1(L_1) = k_1 \varphi'_2(L_1), \\ \tilde{d}_2 \varphi'_{2x}(L_1+L_2) = \tilde{d}_3 \varphi'_{3x}(L_1+L_2), \varphi'_2(L_1+L_2) = k_2 \varphi'_3(L_1+L_2). \end{cases} \tag{4.6}$$

Multiplying the equations of (4.5) by φ_1, $k_1\varphi_2$ and $k_1k_2\varphi_3$, respectively, integrating the equations over $[0, L_1]$, $[L_1, L_1+L_2]$, and $[L_1+L_2, L]$, respectively, and adding the results, we obtain

$$\begin{aligned} &-\lambda'_1(d)\left[\int_0^{L_1} \varphi_1^2 \mathrm{d}x + \int_{L_1}^{L_1+L_2} k_1 \varphi_2^2 \mathrm{d}x + \int_{L_1+L_2}^{L} k_1 k_2 \varphi_3^2 \mathrm{d}x\right] \\ &= \int_0^{L_1} \tilde{d}_1 \varphi_{1,xx}\varphi_1 + d\tilde{d}_1 \varphi'_{1,xx}\varphi_1 + c_1(x)\varphi'_1\varphi_1 + \lambda_1\varphi'_1\varphi_1 \mathrm{d}x \\ &+ k_1 \int_{L_1}^{L_1+L_2} \tilde{d}_2 \varphi_{2,xx}\varphi_2 + d\tilde{d}_2 \varphi'_{2,xx}\varphi_2 + c_2(x)\varphi'_2\varphi_2 + \lambda_1\varphi'_2\varphi_2 \mathrm{d}x \\ &+ k_1k_2 \int_{L_1+L_2}^{L} \tilde{d}_3 \varphi_{3,xx}\varphi_3 + d\tilde{d}_3 \varphi'_{3,xx}\varphi_3 + c_3(x)\varphi'_3\varphi_3 + \lambda_1\varphi'_3\varphi_3 \mathrm{d}x. \end{aligned} \tag{4.7}$$

By using the boundary and matching conditions (4.6), we obtain

$$\begin{aligned} &\int_0^{L_1} d\tilde{d}_1 \varphi'_{1,xx}\varphi_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2} k_1 d\tilde{d}_2 \varphi'_{2,xx}\varphi_2 \mathrm{d}x + \int_{L_1+L_2}^{L} k_1k_2 d\tilde{d}_3 \varphi'_{3,xx}\varphi_3 \mathrm{d}x \\ &= \int_0^{L_1} d\tilde{d}_1 \varphi_{1,xx}\varphi'_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2} k_1 d\tilde{d}_2 \varphi_{2,xx}\varphi'_2 \mathrm{d}x + \int_{L_1+L_2}^{L} k_1k_2 d\tilde{d}_3 \varphi_{3,xx}\varphi'_3 \mathrm{d}x. \end{aligned} \tag{4.8}$$

Substituting (4.8) into (4.7), we have

$$
\begin{aligned}
&-\lambda_1'(d)\left[\int_0^{L_1}\varphi_1^2\mathrm{d}x+\int_{L_1}^{L_1+L_2}k_1\varphi_2^2\mathrm{d}x+\int_{L_1+L_2}^{L}k_1k_2\varphi_3^2\mathrm{d}x\right]\\
&=\int_0^{L_1}\tilde d_1\varphi_{1,xx}\varphi_1+\int_0^{L_1}(d\tilde d_1\varphi_{1,xx}+c_1(x)\varphi_1+\lambda_1\varphi_1)\varphi_1'\mathrm{d}x\\
&+\int_{L_1}^{L_1+L_2}k_1\tilde d_2\varphi_{2,xx}\varphi_2+\int_{L_1}^{L_1+L_2}k_1(d\tilde d_2\varphi_{2,xx}+c_2(x)\varphi_2+\lambda_1\varphi_2)\varphi_2'\mathrm{d}x\\
&+\int_{L_1+L_2}^{L}k_1k_2\tilde d_3\varphi_{3,xx}\varphi_3+\int_{L_1+L_2}^{L}k_1k_2(d\tilde d_3\varphi_{3,xx}+c_3(x)\varphi_3+\lambda_1\varphi_3)\varphi_3'\mathrm{d}x\\
&=\int_0^{L_1}\tilde d_1\varphi_{1,xx}\varphi_1+\int_{L_1}^{L_1+L_2}k_1\tilde d_2\varphi_{2,xx}\varphi_2+\int_{L_1+L_2}^{L}k_1k_2\tilde d_3\varphi_{3,xx}\varphi_3\\
&=-\int_0^{L_1}\tilde d_1\varphi_{1,x}^2-\int_{L_1}^{L_1+L_2}k_1\tilde d_2\varphi_{2,x}^2-\int_{L_1+L_2}^{L}k_1k_2\tilde d_3\varphi_{3,x}^2\le 0.
\end{aligned}
\tag{4.9}
$$

Hence, $\lambda_1'(d)\ge 0$ for all d, i.e., $\lambda_1(d)$ is non-decreasing in $d>0$.

Suppose $\lambda_1'(d)=0$ for some $d>0$, then it follows that $\varphi_{i,x}=0$ in P_i for all i i.e., $\varphi_i\equiv c_i$ in P_i for some constant c_i. This happens if and only if

$$c_i(x)\equiv\lambda_1(d)\quad\text{ for } i=1,2,3.$$

Hence, we deduce that if $c_i(x)\equiv k_0$ for some constant k_0 independent of i, then $\lambda_1(d)\equiv k_0$ for all $d>0$. Otherwise, we have $\lambda_1'(d)>0$ for all $d>0$. □

Lemma 4.5. *In the limit of large diffusion, we obtain*

$$\lim_{d\to\infty}\lambda_1(d)=-\frac{\int_0^{L_1}c_1(x)\mathrm{d}x+\frac{1}{k_1}\int_{L_1}^{L_1+L_2}c_2(x)\mathrm{d}x+\frac{1}{k_1k_2}\int_{L_1+L_2}^{L}c_3(x)\mathrm{d}x}{L_1+\frac{1}{k_1}L_2+\frac{1}{k_1k_2}L_3}. \tag{4.10}$$

Proof. Dividing (4.1)–(4.2) by d, we find

$$\begin{cases}\tilde d_i\varphi_{i,xx}+\frac{1}{d}(c_i(x)+\lambda_1(d))\varphi_i=0,\ x\in P_i,\\ \varphi_{1x}(0)=\varphi_{3x}(L)=0,\\ \tilde d_1\varphi_{1x}(L_1)=\tilde d_2\varphi_{2x}(L_1),\varphi_1(L_1)=k_1\varphi_2(L_1),\\ \tilde d_2\varphi_{2x}(L_1+L_2)=\tilde d_3\varphi_{3x}(L_1+L_2),\varphi_2(L_1+L_2)=k_2\varphi_3(L_1+L_2).\end{cases}$$

We now let $d\to\infty$. As $\lambda_1(d)$ is bounded, so is the term multiplying φ_i in the differential equation. Hence, by standard L^p estimates for elliptic equations, we obtain a (sub-)sequence of corresponding eigenfunctions that converge weakly in $W^{2,p}(\bar{P}_i)$. By a suitable Sobolev embedding, this gives us a strongly convergent sequence in $\mathcal{C}^1(\bar{P}_i)$. Hence, we have $(\varphi_i) \to (\varphi_{i\infty})$, where $\varphi_{i\infty}$ satisfies

$$\begin{cases} \tilde{d}_i \varphi_{i\infty,xx} = 0, \ x \in P_i, \\ \varphi_{1\infty,x}(0) = \varphi_{3\infty,x}(L) = 0, \\ \tilde{d}_1 \varphi_{1\infty,x}(L_1) = \tilde{d}_2 \varphi_{2\infty,x}(L_1), \varphi_{1\infty}(L_1) = k_1 \varphi_{2\infty}(L_1), \\ \tilde{d}_2 \varphi_{2\infty,x}(L_1+L_2) = \tilde{d}_3 \varphi_{3\infty,x}(L_1+L_2), \varphi_{2\infty}(L_1+L_2) = k_2 \varphi_{3\infty}(L_1+L_2). \end{cases}$$

Hence, $\varphi_{i\infty}$ is constant on each patch. By the interface matching conditions, we have $\varphi_{1\infty} = c$, $\varphi_{2\infty} = \frac{c}{k_1}$ and $\varphi_{3\infty} = \frac{c}{k_1 k_2}$, for some positive constant c. The constant c is chosen such that $c = \min\{1, k_1, k_1 k_2\}$, ensuring that $\max_i \sup_{\bar{P}_i} \varphi_{i\infty} = 1$.

Integrating the equations of (4.1) over $[0, L_1]$, $[L_1, L_1+L_2]$, $[L_1+L_2, L]$, respectively, and adding the results, we have

$$\lambda_1(d)\left[\int_0^{L_1} \varphi_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2} \varphi_2 \mathrm{d}x + \int_{L_1+L_2}^{L} \varphi_3 \mathrm{d}x\right]$$
$$= -\int_0^{L_1} d_1\varphi_{1,xx} + c_1(x)\varphi_1 \mathrm{d}x - \int_{L_1}^{L_1+L_2} d_2\varphi_{2,xx} + c_2(x)\varphi_2 \mathrm{d}x - \int_{L_1+L_2}^{L} d_3\varphi_{3,xx} + c_3(x)\varphi_3 \mathrm{d}x.$$

According to the boundary and matching conditions, we have

$$\int_0^{L_1} d_1\varphi_{1,xx} + \int_{L_1}^{L_1+L_2} d_2\varphi_{2,xx} + \int_{L_1+L_2}^{L} d_3\varphi_{3,xx} = 0.$$

Letting $d \to \infty$, we obtain the desired result

$$\lim_{d\to\infty} \lambda_1(d) = -\frac{\int_0^{L_1} c_1(x)\varphi_{1\infty}\mathrm{d}x + \int_{L_1}^{L_1+L_2} c_2(x)\varphi_{2\infty}\mathrm{d}x + \int_{L_1+L_2}^{L} c_3(x)\varphi_{3\infty}\mathrm{d}x}{\int_0^{L_1} \varphi_{1\infty}\mathrm{d}x + \int_{L_1}^{L_1+L_2} \varphi_{2\infty}\mathrm{d}x + \int_{L_1+L_2}^{L} \varphi_{3\infty}\mathrm{d}x}$$
$$= -\frac{\int_0^{L_1} c_1(x)\mathrm{d}x + \frac{1}{k_1}\int_{L_1}^{L_1+L_2} c_2(x)\mathrm{d}x + \frac{1}{k_1k_2}\int_{L_1+L_2}^{L} c_3(x)\mathrm{d}x}{L_1 + \frac{1}{k_1}L_2 + \frac{1}{k_1k_2}L_3}. \quad \square$$

Lemma 4.6. *In the limit of small diffusion, we find*

$$\lim_{d\to 0} \lambda_1(d) = \min\{-\max_{x\in\bar{P}_1} c_1(x), -\max_{x\in\bar{P}_2} c_2(x), -\max_{x\in\bar{P}_3} c_3(x)\}. \tag{4.11}$$

Proof. According to (4.4), we have

$$\lambda_1(d) \geq \min\{-\max_{x\in\bar{P}_1} c_1(x), -\max_{x\in\bar{P}_2} c_2(x), -\max_{x\in\bar{P}_3} c_3(x)\}$$

for all $d > 0$.

Next, we prove

$$\limsup_{d\to 0} \lambda_1(d) \le \min\{-\max_{x\in \bar{P}_1} c_1(x), -\max_{x\in \bar{P}_2} c_2(x), -\max_{x\in \bar{P}_3} c_3(x)\}, \tag{4.12}$$

which is equivalent to proving

$$\limsup_{d\to 0} \lambda_1(d) \le -\max_{x\in \bar{P}_i} c_i(x), \qquad i = 1, 2, 3.$$

For any $x_0 \in P_1$, fix $0 < r < \mathrm{dist}(x_0, \partial P_1)$, and let μ_1 and ϕ_1 be the principal eigenvalue and eigenfunction of the problem

$$\phi_{1,xx} + \mu_1 \phi_1 = 0 \ \text{ in } B_r(x_0), \ \phi_1 = 0 \ \text{ on } \partial B_r(x_0).$$

Noting that $\varphi_1 > 0$ in $\bar{B}_r(x_0)$ and $\phi_1 = 0$ on $\partial B_r(x_0)$, up to multiplication of ϕ_1 by a positive constant, one may assume that $\varphi_1 \ge \phi_1$ in $B_r(x_0)$ and $\varphi_1(x_0') = \phi_1(x_0') > 0$ for some $x_0' \in B_r(x_0)$. Hence, by the maximum principle, we have $\varphi_{1,xx}(x_0') \ge \phi_{1,xx}(x_0')$. Then,

$$d\tilde{d}_1 \mu_1 \phi_1(x_0') = -d\tilde{d}_1 \phi_{1,xx}(x_0') \ge -d\tilde{d}_1 \varphi_{1,xx}(x_0') = c_1(x_0')\phi_1(x_0') + \lambda_1(d)\phi_1(x_0').$$

Dividing by $\phi_1(x_0')$, we have

$$\lambda_1(d) \le d\tilde{d}_1 \mu_1 - c_1(x_0') \le d\tilde{d}_1 \mu_1 - \inf_{B_r(x_0)} c_1(x).$$

Taking the limsup as $d \to 0$ and letting $r \to 0$, we obtain

$$\limsup_{d\to 0} \lambda_1(d) \le -c_1(x_0), \ \text{ for } x_0 \in P_1.$$

Since x_0 is arbitrary, we have

$$\limsup_{d\to 0} \lambda_1(d_i) \le -\max_{x\in \bar{P}_1} c_1(x).$$

Similar considerations apply to the two other patches. Therefore, (4.12) holds. Combining (4.4) with (4.12), (4.11) follows. □

4.2. The properties of the principal eigenvalue with respect to patch preference

The question of how the principal eigenvalue depends on the patch preference parameters has not been studied before. This question is, however, somewhat related to the question of how the principal eigenvalue depends on directed movement ("advection"), which has been studied in a variety of contexts; see [3,12,25,30]. To indicate the parameter dependence, we denote the principal eigenvalue by $\lambda_1 = \lambda_1(\alpha_1, \alpha_2)$.

Lemma 4.7. *The total differential of the principal eigenvalue of* (4.1)–(4.2) *is given by*

$$\mathbf{d}\lambda_1(\alpha_1,\alpha_2)=\partial_{\alpha_1}\lambda_1(\alpha_1,\alpha_2)\mathbf{d}\alpha_1+\partial_{\alpha_2}\lambda_1(\alpha_1,\alpha_2)\mathbf{d}\alpha_2, \tag{4.13}$$

where $\partial_{\alpha_1}\lambda_1(\alpha_1,\alpha_2)$ *and* $\partial_{\alpha_2}\lambda_1(\alpha_1,\alpha_2)$ *are given by*

$$\partial_{\alpha_1}\lambda_1(\alpha_1,\alpha_2)=\frac{\frac{1}{(1-\alpha_1)^2}d_2\varphi_2(L_1)\varphi_{1x}(L_1)}{\int_0^{L_1}\varphi_1^2\mathrm{d}x+\int_{L_1}^{L_1+L_2}k_1\varphi_2^2\mathrm{d}x+\int_{L_1+L_2}^{L}k_1k_2\varphi_3^2\mathrm{d}x} \tag{4.14}$$

and

$$\partial_{\alpha_2}\lambda_1(\alpha_1,\alpha_2)=\frac{\frac{k_1}{(1-\alpha_2)^2}d_3\varphi_3(L_1+L_2)\varphi_{2x}(L_1+L_2)}{\int_0^{L_1}\varphi_1^2\mathrm{d}x+\int_{L_1}^{L_1+L_2}k_1\varphi_2^2\mathrm{d}x+\int_{L_1+L_2}^{L}k_1k_2\varphi_3^2\mathrm{d}x}. \tag{4.15}$$

Proof. Differentiating both sides of (4.1)-(4.2) with respect to α_1, and denoting $\frac{\partial}{\partial\alpha_1}=\dot{}$, we obtain

$$d_i\dot{\varphi}_{i,xx}+c_i(x)\dot{\varphi}_i+\lambda_1(\alpha_1,\alpha_2)\dot{\varphi}_i=-\dot{\lambda}_1(\alpha_1,\alpha_2)\varphi_i,\quad x\in P_i, \tag{4.16}$$

with boundary and matching conditions

$$\begin{cases}\dot{\varphi}_{1x}(0)=\dot{\varphi}_{3x}(L)=0,\\ d_1\dot{\varphi}_{1x}(L_1)=d_2\dot{\varphi}_{2x}(L_1),\dot{\varphi}_1(L_1)=\frac{d_2}{d_1(1-\alpha_1)^2}\varphi_2(L_1)+k_1\dot{\varphi}_2(L_1),\\ d_2\dot{\varphi}_{2x}(L_1+L_2)=d_3\dot{\varphi}_{3x}(L_1+L_2),\dot{\varphi}_2(L_1+L_2)=k_2\dot{\varphi}_3(L_1+L_2).\end{cases} \tag{4.17}$$

Multiplying the equations of (4.16) by φ_1, $k_1\varphi_2$ and $k_1k_2\varphi_3$, respectively, and integrating the results over $[0,L_1]$, $[L_1,L_1+L_2]$, and $[L_1+L_2,L]$, respectively, and adding the results, we obtain

$$\begin{aligned}-\dot{\lambda}_1(\alpha_1,\alpha_2)&\left[\int_0^{L_1}\varphi_1^2\mathrm{d}x+\int_{L_1}^{L_1+L_2}k_1\varphi_2^2\mathrm{d}x+\int_{L_1+L_2}^{L}k_1k_2\varphi_3^2\mathrm{d}x\right]\\&=\int_0^{L_1}d_1\dot{\varphi}_{1,xx}\varphi_1+c_1(x)\dot{\varphi}_1\varphi_1+\lambda_1(\alpha_1,\alpha_2)\dot{\varphi}_1\varphi_1\mathrm{d}x\\&+k_1\int_{L_1}^{L_1+L_2}d_2\dot{\varphi}_{2,xx}\varphi_2+c_2(x)\dot{\varphi}_2\varphi_2+\lambda_1(\alpha_1,\alpha_2)\dot{\varphi}_2\varphi_2\mathrm{d}x\\&+k_1k_2\int_{L_1+L_2}^{L}d_3\dot{\varphi}_{3,xx}\varphi_3+c_3(x)\dot{\varphi}_3\varphi_3+\lambda_1(\alpha_1,\alpha_2)\dot{\varphi}_3\varphi_3\mathrm{d}x.\end{aligned} \tag{4.18}$$

By using the boundary and matching conditions (4.17), we obtain

$$\begin{aligned}
&\int_0^{L_1} d_1\dot{\varphi}_{1,xx}\varphi_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2} k_1 d_2\dot{\varphi}_{2,xx}\varphi_2 \mathrm{d}x + \int_{L_1+L_2}^{L} k_1k_2d_3\dot{\varphi}_{3,xx}\varphi_3 \mathrm{d}x \\
&= -\frac{1}{(1-\alpha_1)^2} d_2\varphi_2(L_1)\varphi_{1x}(L_1) \\
&+ \int_0^{L_1} d_1\varphi_{1,xx}\dot{\varphi}_1 \mathrm{d}x + \int_{L_1}^{L_1+L_2} k_1 d_2\varphi_{2,xx}\dot{\varphi}_2 \mathrm{d}x + \int_{L_1+L_2}^{L} k_1k_2d_3\varphi_{3,xx}\dot{\varphi}_3 \mathrm{d}x.
\end{aligned} \tag{4.19}$$

Substituting (4.19) into (4.18), we have

$$\begin{aligned}
&-\dot{\lambda}_1(\alpha_1,\alpha_2)\left[\int_0^{L_1} \varphi_1^2 \mathrm{d}x + \int_{L_1}^{L_1+L_2} k_1\varphi_2^2 \mathrm{d}x + \int_{L_1+L_2}^{L} k_1k_2\varphi_3^2 \mathrm{d}x\right] \\
&= -\frac{1}{(1-\alpha)^2} d_2\varphi_2(L_1)\varphi_{1x}(L_1) + \int_0^{L_1} (d_1\varphi_{1,xx} + c_1(x)\varphi_1 + \lambda_1(\alpha_1,\alpha_2)\varphi_1)\dot{\varphi}_1 \mathrm{d}x \\
&+ \int_{L_1}^{L_1+L_2} k_1(d_2\varphi_{2,xx} + c_2(x)\varphi_2 + \lambda_1(\alpha_1,\alpha_2)\varphi_2)\dot{\varphi}_2 \mathrm{d}x \\
&+ \int_{L_1+L_2}^{L} k_1k_2(d_3\varphi_{3,xx} + c_3(x)\varphi_3 + \lambda_1(\alpha_1,\alpha_2)\varphi_3)\dot{\varphi}_3 \mathrm{d}x \\
&= -\frac{1}{(1-\alpha_1)^2} d_2\varphi_2(L_1)\varphi_{1x}(L_1).
\end{aligned} \tag{4.20}$$

Hence, (4.14) follows. The derivation of (4.15) follows the same ideas. □

Our next goal is to investigate the asymptotic behavior of the principal eigenvalue as the patch preferences α_j tend to 0 or 1. The biological interpretation is that when $\alpha_1 \to 0$, individuals at the interface between patches 1 and 2 have a strong preference for patch 2, whereas when $\alpha_1 \to 1$, they have a strong preference for patch 1 (see Fig. 1). In the limiting cases, all individuals leave the patch or no individuals leave the patch, depending on which side of the interface we consider. For that reason, we can expect that the matching conditions at the interface will decouple and become hostile or reflecting conditions accordingly. Therefore, it will be useful to consider subproblems to our problem, namely eigenvalue problems that are defined on only one of the three patches or on two adjacent of the three patches. With this in mind, we introduce the following notation.

Notation. We consider the eigenvalue problem on a single patch

$$d_i \psi_{i,xx} + c_i(x)\psi + \lambda_i \psi_i = 0, \quad x \in P_i, \tag{4.21}$$

with several combinations of reflecting (Neumann) and hostile (Dirichlet) boundary conditions. We denote by $\lambda_i^{\mathcal{ND}}$ the principal eigenvalue of the elliptic eigenvalue problem (4.21) with Neumann boundary conditions at the left endpoint and Dirichlet conditions at the right endpoint of P_i. Similarly, we define $\lambda_i^{\mathcal{NN}}$, $\lambda_i^{\mathcal{DN}}$, and $\lambda_i^{\mathcal{DD}}$. In the same way, we may consider the eigenvalue problem on two adjacent patches, say patches 1 and 2, with Neumann conditions at the left endpoint of P_1 and Dirichlet conditions at the right endpoint of P_2 and the usual interface matching conditions at the boundary point between P_1 and P_2. We denote the corresponding principal eigenvalue by $\lambda_{1,2}^{\mathcal{ND}}$.

Lemma 4.8. *The principal eigenvalue $\lambda_1(\alpha_1, \alpha_2)$ of (4.1)–(4.2) satisfies*

$$\lim_{\alpha_1,\alpha_2 \to 0} \lambda_1(\alpha_1, \alpha_2) = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\}. \tag{4.22}$$

Moreover, the limiting cases of the corresponding eigenfunctions are as follows

(i) *if $\lambda_1^{\mathcal{ND}} < \min\{\lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (\psi_1^{\mathcal{ND}}, \breve{\psi}_2, \breve{\psi}_3)$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

(ii) *if $\lambda_2^{\mathcal{ND}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\} < \lambda_3^{\mathcal{NN}}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (0, \psi_2^{\mathcal{ND}}, \hat{\psi}_3)$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

(iii) *if $\lambda_3^{\mathcal{NN}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (0, 0, \psi_3^{\mathcal{NN}})$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

where $\psi_1^{\mathcal{ND}}$, $\psi_2^{\mathcal{ND}}$ and $\psi_3^{\mathcal{NN}}$ are eigenfunctions corresponding to $\lambda_1^{\mathcal{ND}}$, $\lambda_2^{\mathcal{ND}}$ and $\lambda_3^{\mathcal{NN}}$, respectively, while $\breve{\psi}_2$, $\breve{\psi}_3$, and $\hat{\psi}_3$ are the positive solution of the following corresponding problems:

$$d_2 \breve{\psi}_{2,xx} + c_2(x)\breve{\psi}_2 + \lambda_1^{\mathcal{ND}} \breve{\psi}_2 = 0, \ x \in P_2, \ \ d_2 \breve{\psi}_{2x}(L_1) = d_1 \psi_{1x}^{\mathcal{ND}}(L_1) < 0, \ \breve{\psi}_2(L_1 + L_2) = 0; \tag{4.23}$$

$$\begin{aligned} &d_3 \breve{\psi}_{3,xx} + c_3(x)\breve{\psi}_3 + \lambda_1^{\mathcal{ND}} \breve{\psi}_3 = 0, \ x \in P_3, \\ &d_3 \breve{\psi}_{3x}(L_1 + L_2) = d_2 \breve{\psi}_{2x}(L_1 + L_2) < 0, \ \breve{\psi}_{3x}(L) = 0; \end{aligned} \tag{4.24}$$

$$\begin{aligned} &d_3 \hat{\psi}_{3,xx} + c_3(x)\hat{\psi}_3 + \lambda_2^{\mathcal{ND}} \hat{\psi}_3 = 0, \ x \in P_3, \\ &d_3 \hat{\psi}_{3x}(L_1 + L_2) = d_2 \psi_{2x}^{\mathcal{ND}}(L_1 + L_2) < 0, \ \hat{\psi}_{3x}(L) = 0. \end{aligned} \tag{4.25}$$

Proof. We first prove that there is a constant M, independent of $\alpha_{1,2}$, such that $\|\varphi_i\|_{\mathcal{C}^2(\bar{P}_i)} \le M$ for $i = 1, 2, 3$. This uniform bound will then ensure that the limit in (4.22) exists.

For φ_1, we rewrite equation (4.1) as

$$\varphi_{1,xx} = -\frac{1}{d_1}(c_1(x) + \lambda_1(\alpha_1, \alpha_2))\varphi_1.$$

Since φ_1 is bounded by 1 by construction and λ_1 is bounded by Lemma 4.1, so is $\varphi_{1,xx}$. Integrating the first equation of (4.1) over $(0, x)$, $x \le L_1$, we have

$$\varphi_{1x}(x) = -\frac{1}{d_1}\int_0^x (c_1(x) + \lambda_1(\alpha_1, \alpha_2))\varphi_1 \mathrm{d}x.$$

As before, from the bounds of φ_1 and λ_1 it follows that $\varphi_{1,x}$ is bounded. Since the bounds of φ_1 and λ_1 are independent of $\{\alpha_i\}_{i=1}$, there exists a constant $M > 0$ independent of $\{\alpha_i\}_{i=1}$ such that $\|\varphi_1\|_{C^2(\bar{P}_1)} \le M$. The same reasoning leads to corresponding bounds for $\|\varphi_2\|_{C^2(\bar{P}_2)}$ and $\|\varphi_3\|_{C^2(\bar{P}_3)}$.

Before we pass to the limit, we observe that

$$\lambda_1(\alpha_1, \alpha_2) \le \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \lambda_{1,2}^{\mathcal{N}\mathcal{D}}\}, \tag{4.26}$$

where $\lambda_1^{\mathcal{N}\mathcal{D}}$ and $\lambda_{1,2}^{\mathcal{N}\mathcal{D}}$ are the principal eigenvalues of the subproblems on patch 1 and patches 1 and 2, respectively, with Neumann conditions on the left and Dirichlet conditions on the right, see (4.21). We obtain this inequality from eigenvalue comparison: The eigenfunction φ_1 of $\lambda_1(\alpha_1, \alpha_2)$ is a strict supersolution of the eigenvalue problem of $\lambda_1^{\mathcal{N}\mathcal{D}}$. Similarly, the pair (φ_1, φ_2) is a strict supersolution of the eigenvalue problem of $\lambda_{1,2}^{\mathcal{N}\mathcal{D}}$. Hence, $\lambda_1(\alpha_1, \alpha_2)$ is bounded by either of those eigenvalues.

Note that the principal eigenfunction of $\lambda_{1,2}^{\mathcal{N}\mathcal{D}}$ depends on α_1 (but not on α_2) because α_1 determines the interface matching conditions between patches 1 and 2. We can assume that this principal eigenfunction (φ_1', φ_2') is normalized such that $\|\varphi_1'\|_\infty + \|\varphi_2'\|_\infty = 1$. By the same reasoning as above, we can also assume that it is uniformly bounded in C^2.

Finally, we consider the limit as $\alpha_i \to 0$. By the Arzelà-Ascoli theorem, we can pass to a subsequence, such that along this subsequence, $\lambda_1(\alpha_1, \alpha_2) \to \bar{\lambda}$ and $\varphi_i \to \bar{\varphi}_i \ge 0$ in $\mathcal{C}^1(\bar{P}_i)$. Hence, the limiting functions $\bar{\varphi}_i$ satisfy

$$d_i\bar{\varphi}_{i,xx} + c_i(x)\bar{\varphi}_i + \bar{\lambda}\bar{\varphi}_i = 0,\ x \in P_i, \tag{4.27a}$$

$$\bar{\varphi}_{1x}(0) = 0,\ \bar{\varphi}_1(L_1) = 0, \tag{4.27b}$$

$$d_1\bar{\varphi}_{1x}(L_1)^- = d_2\bar{\varphi}_{2x}(L_1)^+,\ \bar{\varphi}_2(L_1 + L_2) = 0, \tag{4.27c}$$

$$d_2\bar{\varphi}_{2x}(L_1 + L_2)^- = d_3\bar{\varphi}_{3x}(L_1 + L_2)^+,\ \bar{\varphi}_{3x}(L) = 0, \tag{4.27d}$$

$$\bar{\varphi}_i \ge 0 \quad \text{and} \quad \max_i \sup_{x\in\bar{P}_i} \bar{\varphi}_i = 1. \tag{4.27e}$$

By passing to a further subsequence, one can also assume that the principal eigenvalue $\lambda_{1,2}^{\mathcal{N}\mathcal{D}}$ and its eigenfunction (φ_1', φ_2') also converge to some limit $\bar{\lambda}_{1,2}^{\mathcal{N}\mathcal{D}}$ and $(\bar{\varphi}_1', \bar{\varphi}_2')$, and they satisfy a limiting system of two equations satisfying the conditions (4.27a)-(4.27c). In particular, (4.26) then implies that

$$\bar{\lambda} \le \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \bar{\lambda}_{1,2}^{\mathcal{N}\mathcal{D}}\}. \tag{4.28}$$

Note that the limiting system decouples in the following sense: the equation for $\bar{\varphi}_1$ is independent of the other two equations but influences the equation for $\bar{\varphi}_2$. The equations for $\bar{\varphi}_1$ and

$\bar{\varphi}_2$ combined are independent of the equation for $\bar{\varphi}_3$ but they influence the equation for $\bar{\varphi}_3$. This mathematical observation (which we exploit in the proof below) nicely corresponds to the biological interpretation of the limit $\alpha_j = 0$: individuals from patch 1 enter patch 2 but not vice versa; therefore the dynamics on patch 1 are independent of those on patch 2 but influence those on patch 2. The same consideration applies to the interface between patches 2 and 3.

Next, we prove that the limiting value $\bar{\lambda}$ is bounded above by the minimum in (4.22). From (4.28), we already have that $\bar{\lambda} \le \lambda_1^{\mathcal{N}\mathcal{D}}$. Then we note that $\bar{\varphi}_3 \not\equiv 0$, since, if $\bar{\varphi}_3 \equiv 0$, then, by the matching conditions at $L_1 + L_2$, we also have $\bar{\varphi}_2 \equiv 0$, which, in turn, implies that $\bar{\varphi}_1 \equiv 0$, again by the matching conditions. But not all functions $\bar{\varphi}_i$ can equal zero since their maximum must equal 1. Since $\bar{\varphi}_3 \not\equiv 0$, it is a supersolution to the eigenvalue problem of $\lambda_3^{\mathcal{N}\mathcal{N}}$; see (4.21). It follows by eigenvalue comparison that

$$\bar{\lambda} \le \lambda_3^{\mathcal{N}\mathcal{N}}. \tag{4.29}$$

To prove the missing inequality that $\bar{\lambda} \le \lambda_2^{\mathcal{N}\mathcal{D}}$, we first note that from (4.28) we already have $\bar{\lambda} \le \bar{\lambda}_{1,2}^{\mathcal{N}\mathcal{D}}$. Then we argue for patch 2 in the subproblem of two patches in the same way as we just did for patch 3 in the full problem on all three patches: we must have $\bar{\varphi}_2' \not\equiv 0$, because if it was zero, then $\bar{\varphi}_1'$ would be zero as well, which is impossible. Since $\bar{\varphi}_2'$ is not identically zero, it is a supersolution to the eigenvalue problem of $\lambda_2^{\mathcal{N}\mathcal{D}}$. Therefore, by eigenvalue comparison, we have

$$\bar{\lambda}_{1,2}^{\mathcal{N}\mathcal{D}} \le \lambda_2^{\mathcal{N}\mathcal{D}}. \tag{4.30}$$

Hence, we have proved that

$$\bar{\lambda} = \lim_{\alpha_1,\alpha_2 \to 0} \lambda_1(\alpha_1, \alpha_2) \le \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \lambda_2^{\mathcal{N}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\}. \tag{4.31}$$

To show the equality (4.22) and the particular form of the eigenfunctions in the limiting cases, we consider several cases.

Case (i). If $\bar{\varphi}_1 \not\equiv 0$ on P_1, then, $\bar{\varphi}_1$ is a solution of the eigenvalue problem on P_1 with Neumann and Dirichlet boundary conditions on the left and right, respectively. In particular, $\bar{\lambda} = \lambda_1^{\mathcal{N}\mathcal{D}}$, $\bar{\varphi}_1 = \psi_1^{\mathcal{N}\mathcal{D}}$ on P_1. By (4.31), we have $\lambda_1^{\mathcal{N}\mathcal{D}} = \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \lambda_2^{\mathcal{N}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\}$. Since $\bar{\varphi}_1 \not\equiv 0$, the interface conditions ensure that $\bar{\varphi}_2, \bar{\varphi}_3 \not\equiv 0$ and that they are positive, strict supersolutions to $\lambda_2^{\mathcal{N}\mathcal{D}}$ and $\lambda_3^{\mathcal{N}\mathcal{N}}$, respectively. This implies that $\lambda_1^{\mathcal{N}\mathcal{D}} < \min\{\lambda_2^{\mathcal{N}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\}$, and, by applying the Fredholm alternative theorem, that (4.23) (resp. (4.24)) has a unique solution $\breve{\psi}_2$ (resp. $\breve{\psi}_3$). By uniqueness, we have $(\bar{\varphi}_2, \bar{\varphi}_3) = (\breve{\psi}_2, \breve{\psi}_3)$. Hence, we conclude that

$$\bar{\lambda} = \lambda_1^{\mathcal{N}\mathcal{D}} < \min\{\lambda_2^{\mathcal{N}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\} \quad \text{and} \quad (\bar{\varphi}_1, \bar{\varphi}_2, \bar{\varphi}_3) = (\psi_1^{\mathcal{N}\mathcal{D}}, \breve{\psi}_2, \breve{\psi}_3). \tag{4.32}$$

Case (ii). If $\bar{\varphi}_1 \equiv 0$ on P_1 but $\bar{\varphi}_2 \not\equiv 0$ on P_2, then, $\bar{\varphi}_2$ is a solution of the eigenvalue problem on P_2 with Neuman and Dirichlet boundary conditions on the left and right endpoints, respectively. In particular, $\bar{\lambda} = \lambda_2^{\mathcal{N}\mathcal{D}}$, $\bar{\varphi}_2 = \psi_2^{\mathcal{N}\mathcal{D}}$ on P_2. Arguing as in case (i), we deduce that on patch three, $\bar{\varphi}_3 > 0$ is a positive strict supersolution to $\lambda_3^{\mathcal{N}\mathcal{N}}$, so that $\lambda_2^{\mathcal{N}\mathcal{D}} = \bar{\lambda} < \lambda_3^{\mathcal{N}\mathcal{N}}$. Therefore, (4.25) has a unique solution, denoted by $\hat{\psi}_3$. Again, uniqueness lets us conclude that

$$\bar{\lambda} = \lambda_2^{\mathcal{ND}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\} < \lambda_3^{\mathcal{NN}} \quad \text{and} \quad (\bar{\varphi}_1, \bar{\varphi}_2, \bar{\varphi}_3) = (0, \psi_2^{\mathcal{ND}}, \hat{\psi}_3). \tag{4.33}$$

Case (iii). If $\bar{\varphi}_1 \equiv 0$ on P_1, and $\bar{\varphi}_2 \equiv 0$ on P_2, then necessarily $\bar{\varphi}_3 \not\equiv 0$ on P_3. In that case, $\bar{\varphi}_3$ is a solution of the eigenvalue problem on P_3 with Neumann boundary conditions at both endpoints. In particular, $\bar{\lambda} = \lambda_3^{\mathcal{NN}}$ and $\bar{\varphi}_3 = \psi_3^{\mathcal{NN}}$ on P_3. Hence,

$$\bar{\lambda} = \lambda_3^{\mathcal{NN}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\} \quad \text{and} \quad (\bar{\varphi}_1, \bar{\varphi}_2, \bar{\varphi}_3) = (0, 0, \psi_3^{\mathcal{NN}}). \tag{4.34}$$

Finally, by examining the inequalities in (4.32), (4.33) and (4.34), one can observe that if the minimum value of $\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{ND}}, \lambda_3^{\mathcal{NN}}\}$ is achieved by λ_3^{NN} (which includes the case when two or all of them are equal), then case (iii) must hold. If the minimum is achieved by λ_2^{ND} but not by λ_3^{NN}, then case (ii) must hold. If the minimum is achieved neither by λ_2^{ND} nor by λ_3^{NN}, then case (i) must hold. This completes the proof. □

Remark 4.9. As noted in the preceding proof, the limiting case of $\alpha_j = 0$ induces directionality into the system. The dynamics on patches to the left are independent of the dynamics on patches to the right, but the dynamics on patches to the right are influenced by the dynamics on patches to the left. The situation is reminiscent of a stream or river where information flows downstream (to the right) but not upstream (to the left). What we learned intuitively from the predecing proof is that when we have a (sub-)system of two adjacent patches with flow from upstream to downstream, then the eigenvalue of the limiting case is bounded above by the minimum of the decoupled eigenvalue problems on each patch with appropriately chosen boundary conditions at the interface: Dirichlet conditions at the downstream end of the upstream patch and Neumann conditions at the upstream end of the downstream patch.

With this insight, the proof of the above lemma can be generalized to any finite number of linearly arranged patches with interfaces and corresponding movement probabilities between them. From any given patch, one can trace upstream to find a unique "top" patch. If the limiting function is identically zero on some patch, then it is necessarily zero on all "upstream" patches; if the limiting function is not zero on some patch, then it is necessarily positive on all "downstream" patches as well. This property allows us to generalize to, say, N linearly arranged patches where movement at the interfaces is, say, to the right. We obtain eigenvalue estimates corresponding to (4.28) and (4.29) for the first (most upstream) and the last (most downstream) patch and the set of the top $N - 1$ patches. Then we proceed by induction.

As the mirror symmetric case of the preceding lemma, if we change the limit from $\alpha_j \to 0$ to $\alpha_j \to 1$, we simply switch the direction of the influence or hierarchy. The "river" now flows to the left, and the following analogous result holds.

Lemma 4.10. *The principal eigenvalue $\lambda_1(\alpha_1, \alpha_2)$ of (4.1)–(4.2) satisfies*

$$\lim_{\alpha_1, \alpha_2 \to 1} \lambda_1(\alpha_1, \alpha_2) = \min\{\lambda_1^{\mathcal{NN}}, \lambda_2^{\mathcal{DN}}, \lambda_3^{\mathcal{DN}}\}. \tag{4.35}$$

Moreover, the limiting cases of the corresponding eigenfunctions are as follows

(i) *if $\lambda_1^{\mathcal{NN}} = \min\{\lambda_1^{\mathcal{NN}}, \lambda_2^{\mathcal{DN}}, \lambda_3^{\mathcal{DN}}\}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (\psi_1^{\mathcal{NN}}, 0, 0)$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

(ii) *if* $\lambda_2^{\mathcal{DN}} = \min\{\lambda_1^{\mathcal{NN}}, \lambda_2^{\mathcal{DN}}, \lambda_3^{\mathcal{DN}}\} < \lambda_1^{\mathcal{NN}}$, *then* $(\varphi_1, \varphi_2, \varphi_3) \to (\hat{\psi}_1, \psi_2^{\mathcal{DN}}, 0)$ *in* $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$*;*

(iii) *if* $\lambda_3^{\mathcal{DN}} < \min\{\lambda_1^{\mathcal{NN}}, \lambda_2^{\mathcal{DN}}\}$, *then* $(\varphi_1, \varphi_2, \varphi_3) \to (\check{\psi}_1, \check{\psi}_2, \psi_3^{\mathcal{DN}})$ *in* $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$*;*

where $\psi_1^{\mathcal{NN}}$, $\psi_2^{\mathcal{DN}}$ *and* $\psi_3^{\mathcal{DN}}$ *are eigenfunctions corresponding to* $\lambda_1^{\mathcal{NN}}$, $\lambda_2^{\mathcal{DN}}$ *and* $\lambda_3^{\mathcal{DN}}$, *respectively;* $\hat{\psi}_1$, $\check{\psi}_1$, *and* $\check{\psi}_2$ *are the positive solution of the following corresponding problems:*

$$d_1\hat{\psi}_{1,xx} + c_1(x)\hat{\psi}_1 + \lambda_2^{\mathcal{DN}}\hat{\psi}_1 = 0,\ x \in P_1,\ \ \hat{\psi}_{1x}(0) = 0,\ d_1\hat{\psi}_{1x}(L_1) = d_2\psi_{2x}^{\mathcal{DN}}(L_1) > 0;$$
$$d_1\check{\psi}_{1,xx} + c_1(x)\check{\psi}_1 + \lambda_3^{\mathcal{DN}}\check{\psi}_1 = 0,\ x \in P_1,\ \ \check{\psi}_{1x}(0) = 0,\ d_1\check{\psi}_{1x}(L_1) = d_2\check{\psi}_{2x}(L_1) > 0;$$
$$\begin{aligned} &d_2\check{\psi}_{2,xx} + c_2(x)\check{\psi}_2 + \lambda_3^{\mathcal{DN}}\check{\psi}_2 = 0,\ x \in P_2,\ \ \check{\psi}_2(L_1) = 0,\\ &d_2\check{\psi}_{2x}(L_1 + L_2) = d_3\psi_{3x}^{\mathcal{DN}}(L_1 + L_2) > 0. \end{aligned}$$

The previous two lemmas dealt with the case that all individuals move to the left (Lemma 4.10) or all move to the right (Lemma 4.8) at *both* interfaces. Now, we turn to the mixed cases, where α_1 and α_2 tend to different limits, i.e., individuals move to the left at one interface and to the right at the other. There are two cases. We start with the case $(\alpha_1, \alpha_2) \to (0, 1)$, when individuals move to the middle patch (which then is "downstream" of both, patch 1 and 3). Later, we treat the remaining case $(\alpha_1, \alpha_2) \to (1, 0)$, when individuals move to the outer patches (so that the middle patch us "upstream" of both patch 1 and 3).

Lemma 4.11. *The principal eigenvalue* $\lambda_1(\alpha_1, \alpha_2)$ *of* (4.1)–(4.2) *satisfies*

$$\lim_{(\alpha_1,\alpha_2)\to(0,1)} \lambda_1(\alpha_1, \alpha_2) = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{NN}}, \lambda_3^{\mathcal{DN}}\}. \tag{4.36}$$

Moreover, the limiting cases of the corresponding eigenfunctions are as follows

(i) *if* $\lambda_1^{\mathcal{ND}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{NN}}, \lambda_3^{\mathcal{DN}}\} < \lambda_2^{\mathcal{NN}}$, *then* $(\varphi_1, \varphi_2, \varphi_3) \to (\psi_1^{\mathcal{ND}}, \tilde{\psi}_2, 0)$ *in* $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$*;*

(ii) *if* $\lambda_2^{\mathcal{NN}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{NN}}, \lambda_3^{\mathcal{DN}}\}$, *then* $(\varphi_1, \varphi_2, \varphi_3) \to (0, \psi_2^{\mathcal{NN}}, 0)$ *in* $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$*;*

(iii) *if* $\lambda_3^{\mathcal{DN}} = \min\{\lambda_1^{\mathcal{ND}}, \lambda_2^{\mathcal{NN}}, \lambda_3^{\mathcal{DN}}\} < \lambda_2^{\mathcal{NN}}$, *then* $(\varphi_1, \varphi_2, \varphi_3) \to (0, \hat{\psi}_2, \psi_3^{\mathcal{DN}})$ *in* $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$*;*

where $\psi_1^{\mathcal{ND}}$, $\psi_2^{\mathcal{NN}}$ *and* $\psi_3^{\mathcal{DN}}$ *are eigenfunctions corresponding to* $\lambda_1^{\mathcal{ND}}$, $\lambda_2^{\mathcal{NN}}$ *and* $\lambda_3^{\mathcal{DN}}$, *respectively, while* $\tilde{\psi}_2$ *and* $\hat{\psi}_2$ *are the positive solution of the following problems, respectively,*

$$d_2\tilde{\psi}_{2,xx} + c_2(x)\tilde{\psi}_2 + \lambda_1^{\mathcal{ND}}\tilde{\psi}_2 = 0,\ x \in P_2,\ \ d_2\tilde{\psi}_{2x}(L_1) = d_1\psi_{1x}^{\mathcal{ND}}(L_1) < 0,\ \tilde{\psi}_{2x}(L_1 + L_2) = 0. \tag{4.37}$$

$$\begin{aligned} &d_2\hat{\psi}_{2,xx} + c_2(x)\hat{\psi}_2 + \lambda_3^{\mathcal{DN}}\hat{\psi}_2 = 0,\ x \in P_2,\quad \hat{\psi}_{2x}(L_1) = 0,\\ &d_2\hat{\psi}_{2x}(L_1 + L_2) = d_3\psi_{3x}^{\mathcal{DN}}(L_1 + L_2) > 0. \end{aligned} \tag{4.38}$$

Proof. We only outline the proof since the details are similar to the proof of Lemma 4.8 and the more general insights that resulted from it. By eigenvalue comparison, we have $\lambda_1(\alpha_1, \alpha_2) \leq \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \lambda_3^{\mathcal{D}\mathcal{N}}\}$. Passing to the limit, we obtain

$$\bar{\lambda} = \lim_{(\alpha_1,\alpha_2)\to(0,1)} \lambda_1(\alpha_1, \alpha_2) \leq \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \lambda_3^{\mathcal{D}\mathcal{N}}\}.$$

Now, since patch 2 is the downstream patch, we deduce that the corresponding part of the eigenfunction satisfies $\bar{\varphi}_2 \not\equiv 0$. Therefore, it is a supersolution to the eigenvalue problem corresponding to $\lambda_2^{\mathcal{N}\mathcal{N}}$. Hence, we have $\bar{\lambda} \leq \lambda_2^{\mathcal{N}\mathcal{N}}$. In summary, we proved

$$\bar{\lambda} \leq \min\{\lambda_1^{\mathcal{N}\mathcal{D}}, \lambda_2^{\mathcal{N}\mathcal{N}}, \lambda_3^{\mathcal{D}\mathcal{N}}\}. \tag{4.39}$$

Now, to see that the above inequality is an equality, it suffices to observe that exactly one of the following alternatives holds: (i) $\bar{\varphi}_1 \not\equiv 0$ or $\bar{\varphi}_3 \not\equiv 0$; (ii) $\bar{\varphi}_1 \equiv \bar{\varphi}_3 \equiv 0$ and $\bar{\varphi}_2 \not\equiv 0$. In case (i), we find that $\bar{\lambda} = \lambda_1^{\mathcal{N}\mathcal{D}}$ or $\lambda_3^{\mathcal{D}\mathcal{N}}$, whereas in case (ii), we have $\bar{\lambda} = \lambda_2^{\mathcal{N}\mathcal{N}}$. □

Finally, we look at the case where individuals move to the left at the left interface and to the right at the right interface. In other words, individuals move from the center to the boundary patches.

Lemma 4.12. *The principal eigenvalue $\lambda_1(\alpha_1, \alpha_2)$ of (4.1)–(4.2) satisfies*

$$\lim_{(\alpha_1,\alpha_2)\to(1,0)} \lambda_1(\alpha_1, \alpha_2) = \min\{\lambda_1^{\mathcal{N}\mathcal{N}}, \lambda_2^{\mathcal{D}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\}. \tag{4.40}$$

Moreover, the limiting cases of the corresponding eigenfunctions are as follows

(i) *if $\lambda_2^{\mathcal{D}\mathcal{D}} < \min\{\lambda_1^{\mathcal{N}\mathcal{N}}, \lambda_3^{\mathcal{N}\mathcal{N}}\}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (\tilde{\psi}_1, \psi_2^{\mathcal{D}\mathcal{D}}, \tilde{\psi}_3)$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

(ii) *if $\lambda_1^{\mathcal{N}\mathcal{N}} = \min\{\lambda_1^{\mathcal{N}\mathcal{N}}, \lambda_2^{\mathcal{D}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\} < \lambda_3^{\mathcal{N}\mathcal{N}}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (\psi_1^{\mathcal{N}\mathcal{N}}, 0, 0)$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

(iii) *if $\lambda_3^{\mathcal{N}\mathcal{N}} = \min\{\lambda_1^{\mathcal{N}\mathcal{N}}, \lambda_2^{\mathcal{D}\mathcal{D}}, \lambda_3^{\mathcal{N}\mathcal{N}}\} < \lambda_1^{\mathcal{N}\mathcal{N}}$, then $(\varphi_1, \varphi_2, \varphi_3) \to (0, 0, \psi_3^{\mathcal{N}\mathcal{N}})$ in $\mathcal{C}^1(\bar{P}_1) \times \mathcal{C}^1(\bar{P}_2) \times \mathcal{C}^1(\bar{P}_3)$;*

where $\psi_1^{\mathcal{N}\mathcal{N}}$, $\psi_2^{\mathcal{D}\mathcal{D}}$ and $\psi_3^{\mathcal{N}\mathcal{N}}$ are eigenfunctions corresponding to $\lambda_1^{\mathcal{N}\mathcal{N}}$, $\lambda_2^{\mathcal{D}\mathcal{D}}$ and $\lambda_3^{\mathcal{N}\mathcal{N}}$, respectively; $\tilde{\psi}_1$ and $\tilde{\psi}_3$ are the positive solution of the following problems, respectively,

$$d_1\tilde{\psi}_{1,xx} + c_1(x)\tilde{\psi}_1 + \lambda_2^{\mathcal{D}\mathcal{D}}\tilde{\psi}_1 = 0,\ x \in P_1,\ \ \tilde{\psi}_{1x}(0) = 0,\ d_1\tilde{\psi}_{1x}(L_1) = d_2\psi_{2x}^{\mathcal{D}\mathcal{D}}(L_1) > 0. \tag{4.41}$$

$$\begin{aligned} &d_3\tilde{\psi}_{3,xx} + c_3(x)\tilde{\psi}_3 + \lambda_2^{\mathcal{D}\mathcal{D}}\tilde{\psi}_3 = 0,\ x \in P_3, \\ &d_3\tilde{\psi}_{3x}(L_1 + L_2) = d_2\psi_{2x}^{\mathcal{D}\mathcal{D}}(L_1 + L_2) < 0,\ \tilde{\psi}_{3x}(L) = 0. \end{aligned} \tag{4.42}$$

Proof. Again, we only outline the proof, using the insights from the proof of Lemma 4.8 and subsequent remark. By eigenvalue comparison, we have $\lambda_1(\alpha_1, \alpha_2) \leq \min\{\lambda_2^{\mathcal{D}\mathcal{D}}, \lambda_{1,2}^{\mathcal{N}\mathcal{D}}, \lambda_{2,3}^{\mathcal{D}\mathcal{N}}\}$, where the elements in the set are defined as in (4.21) and "Notation". By passing to the limit, we obtain the upper bound

$$\bar{\lambda} = \lim_{(\alpha_1,\alpha_2)\to(1,0)} \lambda_1(\alpha_1,\alpha_2) \le \min\{\lambda_2^{\mathcal{DD}}, \bar{\lambda}_{1,2}^{\mathcal{ND}}, \bar{\lambda}_{2,3}^{\mathcal{DN}}\}. \tag{4.43}$$

Now, since patch 1 (resp. patch 3) is the downstream patch in the limiting system of $\bar{\lambda}_{1,2}^{\mathcal{ND}}$ (resp. $\bar{\lambda}_{2,3}^{\mathcal{DN}}$), we argue (in a similar fashion as in (4.30) and the corresponding remark) that

$$\bar{\lambda}_{1,2}^{\mathcal{ND}} \le \lambda_1^{\mathcal{NN}} \quad \text{and} \quad \bar{\lambda}_{2,3}^{\mathcal{DN}} \le \lambda_3^{\mathcal{NN}}. \tag{4.44}$$

Combining (4.43) and (4.44), we have again proved

$$\bar{\lambda} \le \min\{\lambda_1^{\mathcal{NN}}, \lambda_2^{\mathcal{DD}}, \lambda_3^{\mathcal{NN}}\}. \tag{4.45}$$

Finally, to see that the equality holds in (4.45), we divide into the following cases: (i) $\bar{\varphi}_2 \not\equiv 0$; (ii) $\bar{\varphi}_2 \equiv 0$. In the first case, $\bar{\lambda} = \lambda_2^{\mathcal{DD}}$. In the latter case, $\bar{\varphi}_1 \not\equiv 0$ or $\bar{\varphi}_3 \not\equiv 0$, whence $\bar{\lambda} = \lambda_1^{\mathcal{NN}}$ or $\bar{\lambda} = \lambda_1^{\mathcal{NN}}$. □

5. Analysis of the positive steady state

In this section, we analyze evolutionarily stable dispersal strategies by studying the positive steady states of a three-patch model. We begin by examining the existence and qualitative properties of positive steady states for a single species. This is followed by an invasion analysis in a two-species system, where dispersal rates and patch preferences are treated as evolutionary traits. The section concludes with a discussion of the ideal free distribution under specific conditions.

5.1. Existence and qualitative properties of the steady state

The population density u_i on the patch P_i satisfies the following equations; see (2.2):

$$\begin{cases} u_{it} = d_i u_{i,xx} + r_i u_i (1 - \frac{u_i}{K_i}), \quad x \in P_i, \quad t > 0, \\ u_{1x}(0,t) = u_{3x}(L,t) = 0, \\ d_1 u_{1x}(L_1,t) = d_2 u_{2x}(L_1,t), \ u_1(L_1,t) = k_1 u_2(L_1,t), \\ d_2 u_{2x}(L_1+L_2,t) = d_3 u_{3x}(L_1+L_2,t), \ u_2(L_1+L_2,t) = k_2 u_3(L_1+L_2,t). \end{cases} \tag{5.1}$$

We first prove the existence and uniqueness of the positive steady-state solution for model (5.1). Then, we classify the possible qualitative shapes of this positive steady-state solution. Finally, based on this classification, we discuss the relationship between the total population abundance at steady state and the total carrying capacity.

Theorem 5.1. *There exists a unique positive steady-state of* (5.1)*, denoted by* u_i^**, which is globally asymptotically stable.*

Proof. Since the single equation for u_i in (5.1) is monotone and of logistic type, the existence and uniqueness of a positive steady state for (5.1) is equivalent to the trivial steady state being linearly unstable (see [6, Propositions 3.2-3.3] and [26, Appendix C]).

Let (η_1, ϕ_i) be the principal eigenpair of

$$\begin{cases} d_i\phi_{i,xx} + r_i\phi_i + \eta_1\phi_i = 0, \quad x \in P_i, \\ \phi_{1x}(0) = \phi_{3x}(L) = 0, \\ d_1\phi_{1x}(L_1) = d_2\phi_{2x}(L_1), \phi_1(L_1) = k_1\phi_2(L_1), \\ d_2\phi_{2x}(L_1+L_2) = d_3\phi_{3x}(L_1+L_2), \phi_2(L_1+L_2) = k_2\phi_3(L_1+L_2). \end{cases} \tag{5.2}$$

Multiplying the equations of (5.2) by $\frac{1}{\phi_1}$, $\frac{1}{k_1\phi_2}$ and $\frac{1}{k_1k_2\phi_3}$, respectively, and integrating the results over $[0, L_1]$, $[L_1, L_1+L_2]$, and $[L_1+L_2, L]$, respectively, and adding the results, we obtain

$$\eta_1 = -\frac{\int_0^{L_1} d_1\frac{\phi_{1x}^2}{\phi_1{}^2} + r_1 \mathrm{d}x + \frac{1}{k_1}\int_{L_1}^{L_1+L_2} d_2\frac{\phi_{2x}^2}{\phi_2{}^2} + r_2\mathrm{d}x + \frac{1}{k_1k_2}\int_{L_1+L_2}^{L} d_3\frac{\phi_{3x}^2}{\phi_3{}^2} + r_3\mathrm{d}x}{L_1 + \frac{1}{k_1}L_2 + \frac{1}{k_1k_2}L_3} < 0.$$

Hence, the trivial steady state is unstable, and there is a unique positive steady-state solution, denoted by u_i^*. By the monotone dynamical system theory [47], u_i^* is globally asymptotically stable. □

Next, we investigate how model parameters affect the shape of the positive steady-state solution of the system (5.1). We begin by proving that it has to be monotone on the first and third patch and that it cannot change slope more than onces on the middle patch.

Lemma 5.2. *The positive steady state on the first patch, u_1^* of (5.1) satisfies one of the following alternatives:*

(i) *u_1^* is strictly increasing on P_1 and $u_1^*(0) > K_1$;*
(ii) *u_1^* is strictly decreasing on P_1 and $u_1^*(0) < K_1$;*
(iii) *u_1^* is identically constant on P_1 and $u_1^*(0) = K_1$.*

Corresponding statements hold for u_3^* with $> K_1$ ($< K_1$) replaced by $< K_3$ ($> K_3$). On the interior of the second patch, u_2^* cannot have more than one local extremum.

Proof. The steady-state u_i^* of (5.1) satisfies the equation

$$d_iu_{i,xx} + r_iu_i\left(1 - \frac{u_i}{K_i}\right) = 0, \quad x \in P_i, \tag{5.3}$$

together with the boundary and matching conditions in (5.1).

We note that $u_{1x}(L_1)$ fall into exactly one of the following three cases: $u_{1x}(L_1) > 0$, $u_{1x}(L_1) = 0$, or $u_{1x}(L_1) < 0$. First, we assume $u_{1x}(L_1) > 0$, and prove that $u_1(x)$ must be strictly increasing on P_1. Suppose, for contradiction that $u_1(x)$ is not strictly increasing, which means that there exists at least one internal critical point $x_1 \in P_1$, where $u_{1x}(x_1) = 0$. Dividing the equation of $u_1(x)$ by $\frac{u_1}{K_1}$ and integrating it over $[0, x_1]$, we obtain

$$\int_0^{x_1} d_1 K_1 \frac{u_{1,x}^2}{u_1^2} + r_1 K_1 \left(1 - \frac{u_1}{K_1}\right) \mathrm{d}x = 0. \tag{5.4}$$

Integrating the equation of $u_1(x)$ directly, we get

$$\int_0^{x_1} r_1 u_1 \left(1 - \frac{u_1}{K_1}\right) \mathrm{d}x = 0. \tag{5.5}$$

Subtracting (5.5) from (5.4) yields,

$$\int_0^{x_1} d_1 K_1 \frac{u_{1,x}^2}{u_1^2} + \frac{r_1}{K_1}(K_1 - u_1)^2 \mathrm{d}x = 0. \tag{5.6}$$

Therefore, we have $u_1 = K_1$ on $[0, x_1]$. By the uniqueness of the solution, this would imply $u_1 = K_1$ on P_1, which contradicts the condition $u_{1x}(L_1) > 0$. Consequently, $u_1(x)$ is strictly increasing on P_1. We now show that $u_1(0) > K_1$. Otherwise, if $u_1(0) = K_1$, then by uniqueness, we have $u_1(x) = K_1$ on P_1, contradicting the strictly increasing property of $u_1(x)$. If instead $u_1(0) < K_1$, then by continuity, there exists a small $\epsilon_0 > 0$ such that $u_1(x) < K_1$ on $[0, \epsilon_0)$. Since $u_{1x}(0) = 0$ and $u_{1,xx}(x) < 0$ for $x \in (0, \epsilon_0)$ by equation (5.3), it follows that $u_{1x}(x) < 0$ for $x \in (0, \epsilon_0)$, again contradicting the strictly increasing property of $u_1(x)$. Thus, we conclude that $u_1(0) > K_1$, and by monotonicity, $u_1(x) > K_1$ for all $x \in P_1$. The arguments in the other cases for u_1^* and u_3^* are similar.

To see the claim for u_2^*, we note that, by equation (5.3), a local maximum necessarily satisfies $u_2^* \le K_2$ while a local minimum necessarily satisfies $u_2^* \ge K_2$. Hence, at most local extremum is possible in the interior of P_2. □

Theorem 5.3. *The positive steady state u_i^* of (5.1) has the following profiles.*

(i) *$u_i^* = K_i$ on each P_i, provided that $K_1 = k_1 K_2$ and $K_2 = k_2 K_3$.*
(ii) *u_i^* is strictly increasing on each P_i with $u_1^* > K_1$, $u_3^* < K_3$, provided that $K_1 \le k_1 K_2$ and $K_2 \le k_2 K_3$ and at least one of these two inequalities is strict.*
(iii) *u_i^* is strictly decreasing on each P_i with $u_1^* < K_1$, $u_3^* > K_3$, provided that $K_1 \ge k_1 K_2$ and $K_2 \ge k_2 K_3$ and at least one of these two inequalities is strict.*

Proof. It suffices to prove cases (i) and (ii) as part (iii) follows from similar arguments as (ii).

(i) Under the conditions on the parameters, one can check that the constant functions $u_i^* = K_i$ on each P_i are a solution of the steady-state equations. Since the solution is unique, the claim follows.

(ii) According to Definition 3.1, $(k_1 k_2 K_3, k_2 K_3, K_3)$ and $(K_1, \frac{K_1}{k_1}, \frac{K_1}{k_1 k_2})$ are super- and sub-solutions of (5.3), respectively. Therefore, we have $u_1(x) \ge K_1$ on P_1, and $u_3(x) \le K_3$ on P_3. From the equation of $u_1(x)$, it follows that $u_{1,xx}(x) \ge 0$, and that $u_{1x}(x) \ge 0$ on P_1. Lemma 5.2 yields either $u_{1x}(x) > 0$ or $u_1(x) \equiv K_1$ on P_1. Next, we show that $u_1(x) \not\equiv K_1$. If $u_1(x) \equiv K_1$, then, by the matching conditions and $K_1 \le k_1 K_2$, we obtain $u_{2x}(L_1) = 0$ and $u_2(L_1) \le K_2$. If $u_2(L_1) = K_2$, then uniqueness yields $u_2(x) \equiv K_2$ on P_2. Repeating the same argument for P_3, we deduce that $u_3(x) \equiv K_3$ on P_3. However, this contradicts our assumption that at least one of the inequalities must be strict. Thus, $u_2(L_1) < K_2$, and by continuity, there exists a small $\varepsilon_1 > 0$ such that $u_2(x) < K_2$ on $[L_1, L_1 + \varepsilon_1)$, and by the equation of $u_2(x)$, we obtain $u_{2,xx}(x) < 0$ on this interval. From the maximum principle, it follows that $u_{2x}(L_1 + L_2) < 0$. Similarly, based on the matching conditions and $K_2 \leq k_2 K_3$, we can obtain $u_{3x}(L_1+L_2) < 0$ and $u_3(L_1+L_2) < K_3$. By the maximum principle again, we have $u_{3x}(L) < 0$, which is a contradiction to $u_{3x}(L) = 0$. Therefore, $u_{1x}(x) > 0$ on P_1 with $u_1(x) > K_1$. Similarly, we can prove that $u_{3x}(x) > 0$ on P_3 with $u_3(x) < K_3$.

Now, we only need to show that $u_2(x)$ is increasing on P_2. Let $w = u_{2x}(x)$. Then w satisfies

$$\begin{cases} d_2 w_{xx} + r_2(1 - \frac{2u_2}{K_2})w = 0, & x \in (L_1, L_1 + L_2), \\ w(L_1) > 0, & w(L_1 + L_2) > 0. \end{cases} \tag{5.7}$$

Since $d_2 u_{2,xx} + r_2 \left(1 - \frac{u_2}{K_2}\right) u_2 = 0$, and the inequality

$$0 = d_2 w_{xx} + r_2 \left(1 - \frac{u_2}{K_2}\right) w > d_2 w_{xx} + r_2 \left(1 - \frac{2u_2}{K_2}\right) w, \quad x \in (L_1, L_1 + L_2),$$

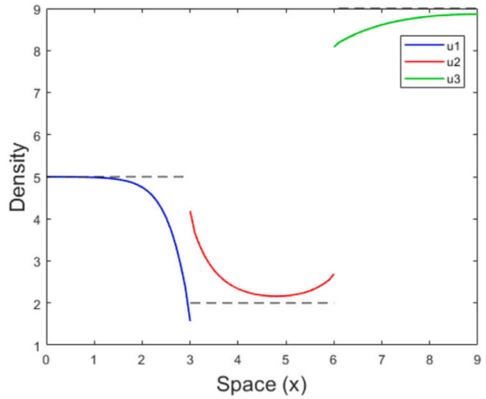
holds when $w = u_2$, then $w = u_2$ is a positive strict supersolution of (5.7). Therefore, according to Theorem 3.5, the maximum principle holds, and it is derived that $w > 0$ on P_2, i.e., $u_2(x)$ is increasing on P_2. □

Remark 5.4. Theorem 5.3 shows that under some conditions, steady-state solutions in the three-patch model are monotone. Previous work showed that steady-state solutions are always monotone in a corresponding two-patch model [19,52]. With the addition of a third patch that we are studying here, steady states can become non-monotone if the conditions of Theorem 5.3 are not satisfied, namely in the 'mixed' scenario, when $K_1 < k_1 K_2$ and $K_2 > k_2 K_3$ or $K_1 > k_1 K_2$ and $K_2 < k_2 K_3$. In that case, solutions can exhibit a local maximum or local minimum in the middle patch, but there is no simple characterization of when this occurs in terms of model parameters.

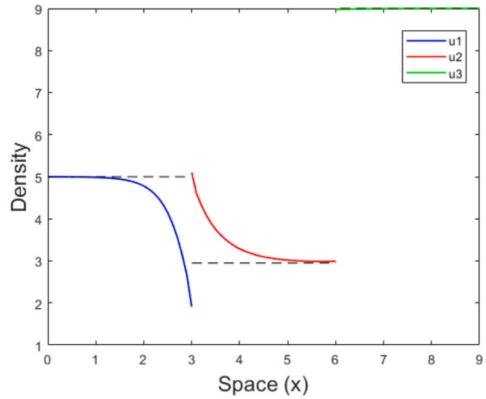
Using Lemma 5.2, we can characterize the shape of the positive steady state in terms of the values of u^* on the boundary as follows: If the differences $u_1^*(0) - K_1$ and $u_3^*(L) - K_3$ have opposite signs, then the corresponding steady-state solution is monotone; if they have the same sign, then there is a local extremum in the middle patch. Of course, the boundary values are determined by all model parameters in a nonlinear (and non-obvious) way.

We illustrate two transitions between monotone and non-monotone states by computing the steady state numerically as the parameter K_2 varies while all other parameters are fixed. We note that the boundary values $u_1^*(0)$ and $u_3^*(L)$ are increasing with K_2. In fact, if u^* and u^{**} are steady-state solutions with K_2^* and K_2^{**} while all other parameters are the same, and if $K_2^* < K_2^{**}$ then $u^* < u^{**}$. Our simulations show that as K_2 increases, the corresponding steady-state solution can change from having a local minimum in the middle patch to being monotone to having a local maximum in the middle patch; see Fig. 2. At the transitions from monotone to non-monotone, the solution is constant on one of the boundary patches; see panels (b) and (e) in Fig. 2. This corresponds to a degenerate case where the three-patch system effectively reduces to a two-patch configuration, in which the solution remains monotone across the remaining two patches.

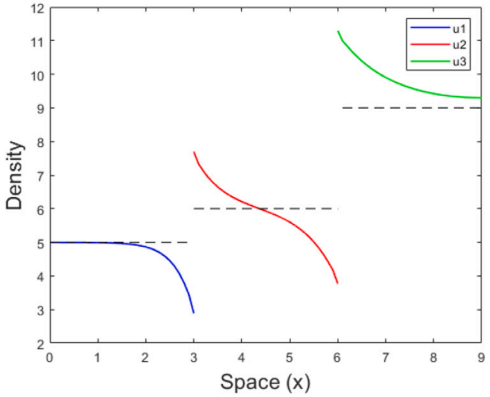
We now turn to the relation between total population abundance and total carrying capacity.



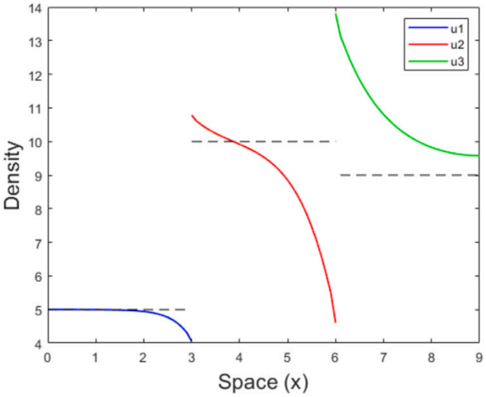
(a) $K_1 > k_1 K_2,\ \ K_2 < k_2 K_3$



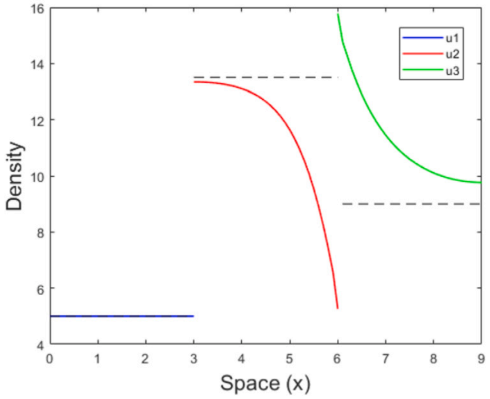
(b) $K_1 > k_1 K_2,\ \ K_2 < k_2 K_3$



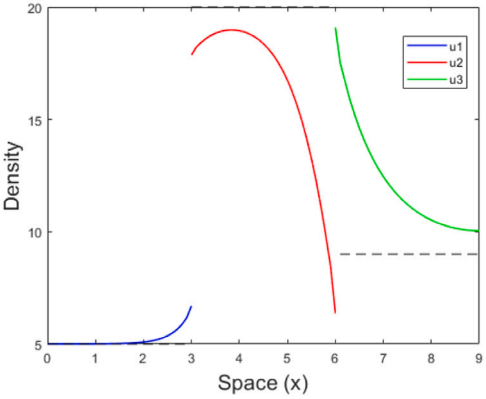
(c) $K_1 > k_1 K_2,\ \ K_2 > k_2 K_3$



(d) $K_1 > k_1 K_2,\ \ K_2 > k_2 K_3$



(e) $K_1 < k_1 K_2,\ \ K_2 > k_2 K_3$



(f) $K_1 < k_1 K_2,\ \ K_2 > k_2 K_3$

Fig. 2. Transitions in steady-state profiles as K_2 increases, where (a) $K_2 = 2$; (b) $K_2 = 2.95$; (c) $K_2 = 6$; (d) $K_2 = 10$; (e) $K_2 = 13.5$; (f) $K_2 = 20$. Other parameters are: $K_1 = 5$, $K_3 = 9$, $d_1 = 2$, $d_2 = 3$, $d_3 = 4$, $r_1 = 12$, $r_2 = 8$, $r_3 = 3$, $\alpha_1 = \alpha_2 = 0.2$ and $L_i = 3$ for $i = 1, 2, 3$. The dashed lines correspond to the respective carrying capacities. With our choice of parameters, the inequalities $K_1 \geq k_1 K_2$ and $K_2 \geq k_2 K_3$ become $3 \leq K_2 \leq 40/3 \approx 13.3$. They are satisfied in panels (c) and (d).

Theorem 5.5. *If*

$$d_1 \frac{u_{1x}^*(L_1)}{u_1^*(L_1)} \left[\frac{K_1}{r_1} - k_1 \frac{K_2}{r_2} \right] + d_2 \frac{u_{2x}^*(L_1+L_2)}{u_2^*(L_1+L_2)} \left[\frac{K_2}{r_2} - k_2 \frac{K_3}{r_3} \right] > 0, \tag{5.8}$$

then the positive steady state u_i^* of (5.1) satisfies

$$\int_0^{L_1} (u_1^*(x) - K_1)dx + \int_{L_1}^{L_1+L_2} (u_2^*(x) - K_2)dx + \int_{L_1+L_2}^{L} (u_3^*(x) - K_3)dx > 0, \tag{5.9}$$

i.e., the total population abundance at steady state is higher than the total carrying capacity.

Proof. Dividing (5.3) by $\frac{r_i u_i}{K_i}$, and integrating over P_i, and summing with respect to i, we obtain

$$\begin{aligned} &\int_0^{L_1} (u_1(x) - K_1)dx + \int_{L_1}^{L_1+L_2} (u_2(x) - K_2)dx + \int_{L_1+L_2}^{L} (u_3(x) - K_3)dx \\ &= \frac{d_1 K_1}{r_1} \int_0^{L_1} \frac{u_{1x}^2}{u_1^2} dx + \frac{d_2 K_2}{r_2} \int_{L_1}^{L_1+L_2} \frac{u_{2x}^2}{u_2^2} dx + \frac{d_3 K_3}{r_3} \int_{L_1+L_2}^{L} \frac{u_{3x}^2}{u_3^2} dx \\ &+ \frac{d_1 K_1}{r_1} \frac{u_{1x}(L_1)}{u_1(L_1)} + \frac{d_2 K_2}{r_2} \left[\frac{u_{2x}(L_1+L_2)}{u_2(L_1+L_2)} - \frac{u_{2x}(L_1)}{u_2(L_1)} \right] - \frac{d_3 K_3}{r_3} \frac{u_{3x}(L_1+L_2)}{u_3(L_1+L_2)}. \end{aligned} \tag{5.10}$$

By using the matching conditions, we have

$$\begin{aligned} &\frac{d_1 K_1}{r_1} \frac{u_{1x}(L_1)}{u_1(L_1)} + \frac{d_2 K_2}{r_2} \left[\frac{u_{2x}(L_1+L_2)}{u_2(L_1+L_2)} - \frac{u_{2x}(L_1)}{u_2(L_1)} \right] - \frac{d_3 K_3}{r_3} \frac{u_{3x}(L_1+L_2)}{u_3(L_1+L_2)} \\ &= d_1 \frac{u_{1x}(L_1)}{u_1(L_1)} \left[\frac{K_1}{r_1} - k_1 \frac{K_2}{r_2} \right] + d_2 \frac{u_{2x}(L_1+L_2)}{u_2(L_1+L_2)} \left[\frac{K_2}{r_2} - k_2 \frac{K_3}{r_3} \right]. \end{aligned} \tag{5.11}$$

Hence, when (5.8) holds, (5.9) follows. □

Corollary 5.6. *If the two chains of inequalities,*

$$1 < k_1 \frac{K_2}{K_1} < \frac{r_2}{r_1}, \quad \text{and} \quad 1 < k_2 \frac{K_3}{K_2} < \frac{r_3}{r_2}, \tag{5.12}$$

are satisfied, then (5.9) holds, i.e., the total population density at steady state exceeds the total carrying capacity. Similarly, if all inequalities are reversed, then (5.9) holds.

Proof. In each of the two chains of inequalities, the first one ensures that the steady-state solution is monotone increasing; see Theorem 5.3 (ii). Hence, the derivative terms in (5.8) are positive. Likewise, the second inequality in each chain ensures that the terms in square brackets in (5.8) are positive. Hence, the entire expression is positive. The case with reversed inequalities follows in the same way. □

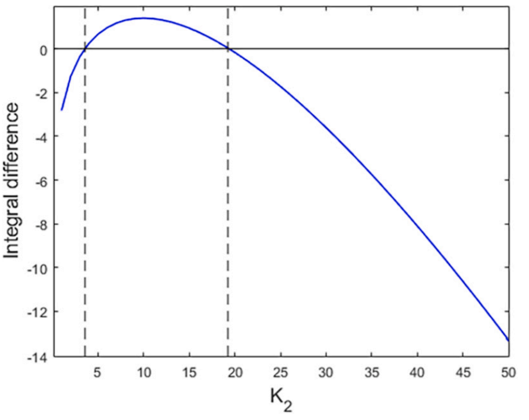


Fig. 3. The integral difference $\sum_i \int_{P_i} (u_i^*(x) - K_i)dx$ with respect to K_2, where positive values correspond to the total abundance exceeding the total carrying capacity. Other parameters are as in Fig. 2.

It is interesting to note that we can find simple sufficient conditions on parameters that ensure that the steady-state solution is monotone and that do not include the growth parameters r_i (see Theorem 5.3). Yet, even if the steady-state solution is monotone, we need additional conditions on the growth rates to ensure that the total density at steady state exceeds the total carrying capacity, i.e., that (5.9) holds. Importantly, these conditions are sufficient but not necessary, as demonstrated by our numerical results (see Fig. 3). While the strict inequalities in (5.12) guarantee a positive integral difference, we observe that the total abundance can exceed the carrying capacity even when these conditions are only partially met or not satisfied at all. Specifically, the first chain of inequalities in (5.12) holds for $\frac{80}{9} < K_2 < \frac{40}{3}$, whereas the second chain requires $3 < K_2 < 8$. Notably, Fig. 3 reveals that the integral difference remains positive across a wider range of K_2 (approximately $3 \leq K_2 \leq 19$), including cases where both chains fail (e.g. $14 \leq K_2 \leq 19$) or only a subset of conditions holds. This confirms that multiple scenarios can lead to abundance exceeding the carrying capacity.

This observation is consistent with findings from several related studies. (i) Lou showed that in heterogeneous environments, dispersal can lead to a total population size that exceeds the spatially averaged carrying capacity [29]. This occurs because individuals spill over from high-quality regions to nearby regions, highlighting the crucial role of spatial heterogeneity; (ii) DeAngelis and coworkers extended this insight to continuous-space logistic models with spatially varying growth rates and carrying capacities, showing that the analogue of (5.9) holds when carrying capacity and growth rate are positively correlated, provided the diffusion rate is either sufficiently small or large [14,15]. Our result does not depend on the absolute magnitude of diffusion, but rather on the ratio of diffusion coefficients between patches through the composite parameters k_j; (iii) Zaker et al. studied a two-patch model and proved that all steady states are monotone. Moreover, a sufficient condition for the analogue of (5.9) to hold required exactly the first chain of inequalities in (5.12) (see [52]).

For the non-monotone steady-state solutions that we described above (and that do not occur on a two-patch model), we can also give sufficient conditions for (5.9) to hold. However, just like in Remark 5.4, these conditions are not purely based on model parameters but on the steady-state density at the endpoints of the domain.

Corollary 5.7. *If*

1. $u_1^*(0) > K_1$ *and* $u_3^*(L) > K_3$*; and*
2. $k_1 \frac{K_2}{K_1} < \frac{r_2}{r_1}$ *and* $k_2 \frac{K_3}{K_2} > \frac{r_3}{r_2}$

then (5.9) is satisfied. Similarly, if all inequalities are reversed, (5.9) holds.

Proof. The first two conditions ensure that $u_{1x}(x) > 0$ while $u_{3x}(x) < 0$. The second condition guarantees that the first square bracket in (5.8) is positive while the second is negative. Hence, both terms on the left in (5.8) are positive and the desired inequality holds. □

5.2. Invasion analysis

We now analyze the evolutionary dynamics with respect to dispersal and patch preference in a spatially structured environment using the framework of adaptive dynamics [16]. Specifically, we investigate whether rare mutants with modified dispersal strategies or patch preferences can successfully invade a monomorphic resident population at equilibrium.

The model for the so-called wild type (or resident) and mutant (or invader) populations is the canonical extension of the single-species model (5.1) to two types. We consider the diffusion coefficients (d_i) and the patch preference coefficients (α_j) as the traits of interest. The population dynamics of the resident (u_i) and the mutant type (v_i) on patch i are described by the following coupled equations:

$$\begin{cases} u_{it} = d_i u_{i,xx} + r_i u_i (1 - \frac{u_i + v_i}{K_i}), & x \in P_i, \quad t > 0, \\ v_{it} = D_i v_{i,xx} + r_i v_i (1 - \frac{v_i + u_i}{K_i}), & x \in P_i, \quad t > 0. \end{cases} \tag{5.13}$$

The boundary and interface matching conditions are the same as (5.1), with d_i and k_j substituted by D_i and $\hat{k}_j$ in the equations for the mutant, where

$$\hat{k}_1 = \frac{\beta_1}{1-\beta_1} \frac{D_2}{D_1}, \quad \hat{k}_2 = \frac{\beta_2}{1-\beta_2} \frac{D_3}{D_2}. \tag{5.14}$$

Clearly, system (5.13) has the semi-trivial steady-state solutions $E_1 = (u_i^*, \mathbf{0})$ and $E_2 = (\mathbf{0}, v_i^*)$ since the system of equations reduces to the single-species equation (5.1) for one population when the other is absent. To determine how the above-mentioned traits of interest evolve, we analyze the stability of the resident equilibrium E_1 by linearization. Since the linearized equations for v_i are decoupled (see [11, Lemma 5.5]), we only need to consider the principal eigenvalue (Λ) of the linear eigenvalue problem

$$\begin{cases} D_i \phi_{i,xx} + r_i (1 - \frac{u_i^*}{K_i}) \phi_i = \Lambda \phi_i, & x \in P_i, \\ \phi_{1x}(0) = \phi_{3x}(L) = 0, \\ D_1 \phi_{1x}(L_1) = D_2 \phi_{2x}(L_1), \phi_1(L_1) = \hat{k}_1 \phi_2(L_1), \\ D_2 \phi_{2x}(L_1 + L_2) = D_3 \phi_{3x}(L_1 + L_2), \phi_2(L_1 + L_2) = \hat{k}_2 \phi_3(L_1 + L_2). \end{cases} \tag{5.15}$$

In the theory of adaptive dynamics, Λ is known as the invasion fitness or invasion exponent [16]. It can be viewed as the payoff of the mutant with its trait(s) in the presence of the resident at steady state with its respective trait(s). Specifically, if Λ is positive, the mutant can grow when rare in the presence of the resident, whereas when Λ is negative, it cannot. In the first case, we say that the mutant invades, whereas in the second, it does not. Typically, we cannot directly determine the sign of Λ, but can instead calculate the selection gradient, i.e., the derivative of Λ with respect to the traits under consideration, evaluated at the resident's trait value(s). This selection gradient determines the direction of evolutionary change (see [30] for details).

We begin with the case of the diffusion coefficients. To reduce the number of parameters, we will again write the diffusion coefficients in each patch as the product of an overall diffusion propensity parameter and a patch-specific diffusion rate, $d_i = d\tilde{d}_i$ for the resident population; see Section 4. To study the evolution of the overall diffusion propensity, we write $D_i = D\tilde{d}_i$ for the mutant population. Note that the ratios of the diffusion coefficients between the resident and the invaders are the same. We indicate the dependence of the principal eigenvalue in (5.15) as $\Lambda = \Lambda(d, D)$.

Lemma 5.8. *The selection gradient with respect to diffusion propensity is given by*

$$\frac{\partial \Lambda(d,D)}{\partial D}\Big|_{D=d} = -\frac{\int_0^{L_1} \tilde{d}_1 (u_1^*)_x^2 \mathrm{d}x + k_1 \int_{L_1}^{L_1+L_2} \tilde{d}_2 (u_2^*)_x^2 \mathrm{d}x + k_1 k_2 \int_{L_1+L_2}^{L} \tilde{d}_3 (u_3^*)_x^2 \mathrm{d}x}{\int_0^{L_1} (u_1^*)^2 \mathrm{d}x + k_1 \int_{L_1}^{L_1+L_2} (u_2^*)^2 \mathrm{d}x + k_1 k_2 \int_{L_1+L_2}^{L} (u_3^*)^2 \mathrm{d}x}. \tag{5.16}$$

Proof. The calculations are almost identical to those in Lemma 4.3. Note that Λ in (5.15) and λ in (4.1) have opposite signs. Note also that since the relative diffusion coefficients between patches are the same for the resident and the invader, we have $k_j = \hat{k}_j$. Finally, when $D = d$, then $\phi_i = u_i^*$ □

Since the selection gradient in (5.16) is negative, smaller overall diffusion propensity will evolve. In fact, we show below that zero diffusion is convergence stable.

Theorem 5.9. *Let $(\tilde{d}_i)_{i=1}^3 \in (0,\infty)^3$ be fixed, and let $d_i = d\tilde{d}_i$ and $D_i = D\tilde{d}_i$ for some $0 < d < D$. If the two species have the same patch preferences (i.e., $k_j = \hat{k}_j$ for $j = 1, 2$), then, for any positive solution of* (5.13)*, we have*

$$(u_1, u_2, u_3, v_1, v_2, v_3) \to (u_1^*, u_2^*, u_3^*, 0, 0, 0) \quad \text{as} \quad t \to \infty,$$

where (u_1^*, u_2^*, u_3^*) is the unique positive steady state of (5.1) *as given in Theorem 5.1.*

Proof. Once the monotonicity in d of the eigenvalue is established (Lemma 5.8), one can follow the strategy of proving [17, Lemma 4.1]. We omit the details. See also [26, Sect. 7.3.1]. □

Next, we assume that resident and invader differ only in their probabilities of moving left and right at an interface; α_j for the resident and β_j for the invader. Then the principal eigenvalue in (5.15) depends on four parameters, namely $\Lambda = \Lambda(\alpha_1, \alpha_2, \beta_1, \beta_2)$.

Lemma 5.10. *The selection gradient with respect to patch preferences is given by*

$$\nabla_\beta \Lambda_{|\beta_j=\alpha_j} = -\left(\frac{d_2 u_2^*(L_1) u_{1x}^*(L_1)}{(1-\alpha_1)^2 I}, \frac{k_1 d_3 u_3^*(L_1+L_2) u_{2x}^*(L_1+L_2)}{(1-\alpha_2)^2 I} \right), \tag{5.17}$$

with

$$I = \int_0^{L_1} (u_1^*)^2 \mathrm{d}x + k_1 \int_{L_1}^{L_1+L_2} (u_2^*)^2 \mathrm{d}x + k_1 k_2 \int_{L_1+L_2}^{L} (u_3^*)^2 \mathrm{d}x > 0. \tag{5.18}$$

Proof. The expression for the selection gradient in two and more traits was given in [16]. The calculations of the partial derivatives are similar to those in Lemma 4.7. Substituting $\beta_j = \alpha_j$ gives $\hat{k}_j = k_j$ and $\phi_i = u_i^*$ as in the preceding lemma. □

Remark 5.11. The selection gradient gives the direction of highest selection pressure. The actual path of evolution can be further constrained if the different traits are linked, i.e., if their covariance is not zero; see for example the discussion in [16]. We consider the direction of evolution according to (5.17) under the assumption that the two traits are independent variables. In that case, if the density at an interface is increasing (i.e., $u_x^* > 0$ at that interface), then the corresponding entry in the selection gradient is negative and hence the probability of moving to the left at that interface (α_j) decreases. Conversely, if the density at an interface is decreasing, then the corresponding entry is positive and the probability of moving left increases.

For example, when $K_1 \le k_1 K_2$, $K_2 \le k_2 K_3$, and at least one of these two inequalities is strict, Theorem 5.3(ii) implies that $u_{1x}^*(L_1) > 0$ and $u_{2x}^*(L_1 + L_2) > 0$. Hence, evolution acts to decrease the probability of moving to the left at both interfaces. Since k_j is an increasing function of α_j, decreasing α_j also leads to smaller values of k_j. This implies that evolution will eventually turn the inequalities $K_1 \le k_1 K_2$, $K_2 \le k_2 K_3$ into equalities. At that point, part (i) of Theorem 5.3 ensures that the corresponding steady-state solution u_i^* is constant on each patch. But that, in turn, implies that the selection gradient in (5.17) vanishes and, hence, that the evolution of α_j stops. The system has reached a 'singular strategy'. We study this singular strategy from a different point of view in the next section.

5.3. Ideal free distribution

The ideal free distribution (IFD) is a theoretical concept that describes how individuals distribute themselves across their habitat in an optimal way in the sense that individual fitnesses are equal at all locations [20]. Mathematical models have shown that movement strategies that lead to an IFD often can resist invasion by other, nearby strategies (i.e., they function as evolutionarily stable strategies, ESS) and populations adopting such IFD-producing strategies may often invade other similar but distinct strategies (i.e., they are neighborhood invader strategies, NIS) [7–9]. In this section, we show that both of these implications hold in our model, generalizing the corresponding results for two patches [35].

For a single species to exhibit the IFD, its local individual fitness must equal zero everywhere in the domain. We denote the species density in patch i at the IFD by $\bar{u}_i$. From the first equation in (5.1), we must have $\bar{u}_i = K_i$ on patch P_i for $i = 1, 2, 3$. To satisfy the interface matching conditions, the parameters associated with the IFD must satisfy

$$\bar{k}_1 = \frac{K_1}{K_2}, \quad \bar{k}_2 = \frac{K_2}{K_3}. \tag{5.19}$$

Since the $\bar{k}_j$ are (nondimensional) combinations of the movement-related parameters d_i, and α_j, they represent the dispersal strategy that leads to the IFD. In the following, we show that $(\bar{k}_1, \bar{k}_2)$ constitutes and ESS and NIS. The first step is to show that a population using the IFD cannot coexist at a positive steady state with a population using any other strategy.

Proposition 5.12. *Let $u_i(x)$ and $v_i(x)$ be the positive steady state of (5.13). If $k_1 = \bar{k}_1$ and $k_2 = \bar{k}_2$, then u_i and v_i are constant on P_i, and $\hat{k}_1 = \bar{k}_1$ and $\hat{k}_2 = \bar{k}_2$.*

Proof. The proof generalizes the one for two patches; see [35, Theorem 5.1]. The steady-state solution of (5.13) satisfies the equation

$$\begin{cases} d_i u_{i,xx} + r_i u_i (1 - \frac{u_i + v_i}{K_i}) = 0, & x \in P_i, \\ D_i v_{i,xx} + r_i v_i (1 - \frac{v_i + u_i}{K_i}) = 0, & x \in P_i, \end{cases} \tag{5.20}$$

with the boundary and matching conditions in (5.1), with d_i and k_j substituted by D_i and $\hat{k}_j$ in the corresponding equations for v_i.

Dividing the equations for the resident in (5.20) by $\frac{u_i}{K_i}$, and integrating over P_i, we obtain

$$\sum_i \int_{P_i} d_i K_i \frac{u_{i,x}^2}{u_i^2} + r_i K_i (1 - \frac{u_i + v_i}{K_i}) \mathrm{d}x = 0, \tag{5.21}$$

where we used the boundary and matching conditions and $k_1 = \bar{k}_1$, $k_2 = \bar{k}_2$.

Integrating the equations for the resident of (5.20) directly, we get

$$\sum_i \int_{P_i} r_i u_i (1 - \frac{u_i + v_i}{K_i}) \mathrm{d}x = 0. \tag{5.22}$$

Similarly, integrating the equations for the mutant of (5.20) directly, we have

$$\sum_i \int_{P_i} r_i v_i (1 - \frac{v_i + u_i}{K_i}) \mathrm{d}x = 0. \tag{5.23}$$

Subtracting (5.22) and (5.23) from (5.21) yields,

$$\sum_i \int_{P_i} d_i K_i \frac{u_{i,x}^2}{u_i^2} + \frac{r_i}{K_i} (K_i - u_i - v_i)^2 \mathrm{d}x = 0. \tag{5.24}$$

Therefore, we have $u_{i,x} = 0$ and $u_i + v_i = K_i$ on P_i. In particular, u_i and v_i are constant on P_i.

Let $u_1 = c$. Then it follows from the matching conditions of u_i and $k_1 = \bar{k}_1$, $k_2 = \bar{k}_2$ that $u_2 = c\frac{K_2}{K_1}$, $u_3 = c\frac{K_3}{K_1}$. Hence, we have $v_1 = K_1 - c$, $v_2 = K_2(1 - \frac{c}{K_1})$, $v_3 = K_3(1 - \frac{c}{K_1})$. Using the matching conditions of v_i, we conclude that $\hat{k}_1 = \frac{K_1}{K_2}$, $\hat{k}_2 = \frac{K_2}{K_3}$. □

Next, we show that a rare population that adopts the ideal-free movement strategy ($i.e.$, $\hat{k}_1 = \bar{k}_1,\ \hat{k}_2 = \bar{k}_2$) will be able to invade a resident population that adopts a different movement strategy.

Theorem 5.13 *(IFD implies NIS). Let Λ be the principal eigenvalue of (5.15). If*

$$(\hat{k}_1, \hat{k}_2) = (\bar{k}_1, \bar{k}_2) \quad \text{and} \quad (k_1, k_2) \neq (\bar{k}_1, \bar{k}_2)$$

then we have $\Lambda > 0$, i.e. the species v with IFD-strategy can invade resident species u without such a strategy when rare.

Proof. Again, the proof is a generalization of the case of two patches; see [35, Theorem 5.2]. Dividing the equations of (5.15) by $\frac{\phi_i}{K_i}$, and integrating over P_i, we obtain

$$\sum_i \int_{P_i} D_i K_i \frac{\phi_{i,x}^2}{\phi_i^2} + r_i K_i \left(1 - \frac{u_i}{K_i}\right) \mathrm{d}x = \Lambda(K_1 L_1 + K_2 L_2 + K_3 L_3), \tag{5.25}$$

where we used the boundary and matching conditions and the fact that $\hat{k}_i = \bar{k}_i$.

Integrating the equations for the resident of (5.13) directly, we get

$$\sum_i \int_{P_i} r_i u_i \left(1 - \frac{u_i}{K_i}\right) \mathrm{d}x = 0. \tag{5.26}$$

Subtracting (5.26) from (5.25) yields,

$$\sum_i \int_{P_i} D_i K_i \frac{\phi_{i,x}^2}{\phi_i^2} + r_i K_i \left(1 - \frac{u_i}{K_i}\right)^2 \mathrm{d}x = \Lambda(K_1 L_1 + K_2 L_2 + K_3 L_3). \tag{5.27}$$

Hence, $\Lambda \geq 0$. Note that $(k_1, k_2) \neq (\bar{k}_1, \bar{k}_2)$ (i.e. the resident population does not adopt the ideal-free strategy), so at least one integral term of (5.27) becomes positive, leading to $\Lambda > 0$. This indicates that a rare population employing the ideal-free strategy can successfully invade a resident population using any other movement strategy. □

Theorem 5.13 shows that the IFD is a NIS. In combination with Proposition 5.12, we see that the IFD is also an ESS.

Theorem 5.14 *(IFD implies ESS). Suppose $(v_1, v_2, v_3)\big|_{t=0}$ is nonnegative and nontrivial, and suppose*

$$(\hat{k}_1, \hat{k}_2) = (\bar{k}_1, \bar{k}_2) \quad \text{and} \quad (k_1, k_2) \neq (\bar{k}_1, \bar{k}_2).$$

Then $(u_1, u_2, u_3, v_1, v_2, v_3) \to (0, 0, 0, K_1, K_2, K_3)$ as $t \to \infty$.

Proof. Observe that the system (5.13) with the interface matching conditions generates a compact semiflow that satisfies the axioms of competition system (see, e.g. [26, Appendix E]). This can be proved by arguments similar as in [26, Lemma 7.1.3]. Therefore we can invoke [26, Theorem E.2.13] to conclude a trichotomy result. Namely, exactly one of the following holds:

(i) $(u_1, u_2, u_3, v_1, v_2, v_3) \to (u_1^*, u_2^*, u_3^*, 0, 0, 0)$ as $t \to \infty$;
(ii) $(u_1, u_2, u_3, v_1, v_2, v_3) \to (0, 0, 0, K_1, K_2, K_3)$ as $t \to \infty$;
(iii) there exists a positive coexistence equilibrium where all entries are strictly positive.

Now, (iii) is impossible thanks to Proposition 5.12, while (i) is ruled out thanks to Theorem 5.13. It follows that (ii) holds. □

6. Conclusions

We study a model for the dynamics of a population living in a habitat of three different, adjacent patches, where individuals move randomly within each patch and may have preferences when moving from one patch to another. Mathematically, our model consists of three reaction-diffusion equations, coupled through matching conditions for the density and the flux at each interface. Our model is a generalization of the two-patch model studied in [35], and our present arguments can be generalized to address any finite number of adjacent patches (see also [21,48]). After obtaining basic existence and uniqueness results, which are largely straightforward extensions of the work in [35], we studied how the principal eigenvalue of the linear form of our model depends on parameters (Section 4). This question was not addressed in [35] but is highly relevant to ecological applications; see related work on single-patch models in [6,12,13,26,30,39,42,51]. Finally, we studied the existence, qualitative shape, and evolutionary stability of positive steady states of our model (Section 5). In contrast to the two-patch model, we found a larger variety of possible shapes of the steady state (e.g., non-monotone states), and determined their stability with respect to invasion by another species.

While our model set-up seems highly artificial when compared to natural landscapes, it corresponds very well to certain laboratory experiments where micro-organisms are grown on substrate plates, which constitute indeed a piecewise constant landscape. For example, a so-called MEGA plate was used to study the evolution of resistance to antibiotics [5]. A smaller landscape of six adjacent plates was used to study the evolution of dispersal of nematode worms under various conditions [4]. A corresponding discrete-patch model of coupled ordinary differential equations was derived and analyzed there, but we believe that our approach of patchy reaction-diffusion equations would reveal more detailed spatial patterns. Expanding our model to six patches and estimating model parameters from the experiments is a challenging future task.

We showed that the principal eigenvalue is increasing with the diffusion rate (more precisely, the overall diffusion capacity of the species; see Lemma 4.3). Ecologically, this indicates that a lower diffusion rate is advantageous for the species, as it leads to a higher growth rate at low density. In this sense, our work continues the long tradition of studying the evolution of dispersal and finding that lower random dispersal rates are advantageous if the environment is spatially varying but temporally constant [1,10,17,22,27]. What makes our contribution surprising is that it holds also when there is some form of directed movement, namely at the interfaces between patches. Previous models that included directed movement, either through unidirectional flow or through resource sensing, found that intermediate or even high random dispersal rates can be evolutionarily advantageous [28,30–32,53]. Mathematically, this difference is reflected in the fact that the movement operator in our model is self-adjoint, independently of the choices of patch preferences, whereas in a simple advection model, it is not.

We showed also that the response of the principal eigenvalue to changes in patch preferences depends on the shape of the eigenfunction at an interface; see Lemma 4.7. For example, if the coefficients c_i are all constants (i.e., $c_i(x) \equiv c_i$) and ordered (e.g., $c_1 > c_2 > c_3$), then the eigenfunction is nonincreasing. In particular, its derivatives at the interfaces are nonpositive. According to the formulas in (4.13), the partial derivatives of the principal eigenvalue with respect to α_j are both nonpositive. Hence, the overall population growth rate increases when individuals preferentially move to the left. The condition $c_1 > c_2 > c_3$ indicates that the habitat quality is highest on the left and lowest on the right. Hence, it seems reasonable that movement preference to the left should be beneficial since population growth is higher there.

A different and somewhat complementary approach to studying population dynamics on three (or more) adjacent patches can be found in [48]. The authors consider a linear system of reaction-diffusion equations with matching conditions at the interfaces that include our conditions as a special case. The authors derive an implicit equation for the principal eigenvalue and corresponding eigenfunction. In particular, they find conditions that determine the qualitative shape of the eigenfunction (e.g., increasing, decreasing, hump-shaped,...) on each patch, given parameters. While they do not study how the principal eigenvalue depends on model parameters, in particular on movement ability and patch preference, their method could be used to evaluate and visualize those relationships numerically if parameters are available for a specific system. Their method can also be used to calculate properties of the slope of eigenfunctions, given parameters, to which our theoretical results in Lemma 4.7 can then be applied to find which patch preference is evolutionarily advantageous.

We studied how the principal eigenvalue behaves when patch preferences become very strong. In that case, the overall population growth rate is given by the highest growth rate on an individual patch with appropriate boundary conditions (Dirichlet or Neumann). Moreover, the corresponding eigenfunction is determined by the eigenfunction on that patch of highest growth rate, and it is positive in other patches only if individuals prefer those patches. This leads to a source-sink situation [43]: the patch with the highest growth rate acts as a source; other patches are sinks with a population, if individuals prefer those patches, and empty if they do not.

Our study of the positive steady state of the system revealed some interesting commonalities and some differences with the two-patch case. Most importantly, whereas the steady state in a two-patch landscape is monotone in each patch [52], we observe steady-state densities that can have local extrema on the middle patch in the three-patch landscape (see Fig. 2). It is clear that this result generalizes to any finite number of patches: the steady-state solution is monotone on the first and last patch but not necessarily on the patches in between. While it seems obvious that real populations could exhibit such local aggregations depending on habitat quality and movement pattern, there are no simple parameter conditions that guarantee such locally peaked solutions in our model. The situation is different for a linear model where the shape of the principal eigenfunction can be obtained from model parameters, albeit in a non-obvious way [48]. It is a formidable future challenge to obtain explicit parameter conditions for monotone and non-monotone profiles of the positive steady state. If it could be accomplished, we could also answer with precision whether the total steady-state density exceeds the total carrying capacity (Theorem 5.5) and how evolution acts on patch preferences (Lemma 5.10). As in the two-patch case, we determined that the ideal-free distribution (IFD) is an evolutionarily stable strategy and a neighborhood invader strategy (Theorems 5.13 and 5.14), but it is still an open question whether it is also convergent stable. In other words, we would like to know whether a mutant strategy that is "closer" to the IFD can invade a resident strategy that is "farther" from the IFD. The first step in this future analytical challenge is to properly define "closer" and "farther" in the two-dimensional trait space of k_1 and k_2. More generally, while some of our results clearly generalize to more than three patches, the generalization of others offers multiple highly rewarding future projects.

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Data availability

No data was used for the research described in the article.

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