Multi-patch Laplace Dispersal across Biased Interfaces

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

Master of Science

In the Graduate Academic Unit of Mathematics and Statistics

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This thesis is accepted

Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

November, 2019

Abstract

In the study of the dispersal of species across a landscape, most previous models approximate heterogeneous landscapes by a set of homogeneous patches and allow for different demographic and dispersal rates within each patch. Some work has been done designing and analyzing models which also include a patch preference at the boundaries, which is commonly referred to as a degree of bias. Individuals dispersing across a patchy landscape can detect the changes in habitat at a neighbourhood of a patch boundary, and as a result, they might change the direction of their movement if they are approaching a bad patch. This thesis is devoted to the mathematical derivation of a generalization of the classic Laplace kernel, which includes different dispersal rates in each patch as well as different degrees of bias at the patch boundaries. The simple Laplace kernel and the truncated Laplace kernel most often used in classical work appear as special cases of this general kernel. The form of this general kernel is the sum of two different terms: the classic truncated Laplace kernel within each patch, and a correction accounting for the bias at patch boundaries.

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x	settlement point
y	release point
t	time, or generation in chapter 2
u	density of dispersers, during the dispersal phase
m	number of bounded patches
Ω_i	i^{th} patch
ν_i	diffusion coefficient within patch Ω_i
α_i	per capita settling rate within patch Ω_i
β_i	per capita death rate within patch Ω_i
μ_i	dispersal decay rate within patch Ω_i
a_i	patch boundary between Ω_i and Ω_{i+1}, (interface point)
z_i	bias at the interface point a_i
δ	Dirac delta function
η_i	measure of retention in Ω_i, $\eta_i = \dfrac{\mu_i(1-z_i)}{\mu_{i+1}(1+z_i)}$
ϵ_i	measure of patch-width in Ω_i, $\epsilon_i = e^{-\mu_i(a_i - a_{i-1})}$
k	dispersal kernel
k_L	Laplace kernel
K	dispersal kernel in matrix form
N	population density
F	growth function
I	identity matrix

Chapter 1

Introduction

Patchy landscapes are spatially heterogeneous regions where dispersers may encounter several habitat patches during their dispersal stage. In order to study the dispersal of individuals in a heterogeneous landscape, we approximate the region by considering it to be a union of homogeneous patches. That is, the region is assumed to be partitioned into homogeneous patches. Reproduction and dispersal are assumed to be uniform within each patch, but in a small neighbourhood of each interface between patches, a disperser can sense the presence of the two habitat types and will bias its movement toward the favoured habitat type [7].

The details of the movement behaviour of individuals upon encountering patch boundaries is a critical factor in the modelling the population dynamics of organisms across fragmented landscapes. For instance, the behaviour of two butterfly species at four edge types (ranging from low to high contrast) were studied to determine the extent to which habitat boundaries act as a barrier to dispersal [8]. A habitat specialist (*Speyeria idalia*) responded strongly to all edge types, both by turning to avoid crossing them and by returning to the patch if they had crossed the edge. In contrast, a habitat generalist (*Danaus plexippus*) responded strongly only to high-contrast (tree line) edges. It responded by seldom crossing edges, but rarely returned once it had crossed.

Our primary objective in this dissertation is to formulate a dispersal kernel for a general patchy landscape. The kernel has a nice matrix form which can be expressed as the addition of two terms: one represents the Laplace kernel for dispersal of individuals within each patch, and the other term represents the dispersal of those individuals who leave their birth patch and settle somewhere else. The latter term can be expressed as a product of matrix exponential functions of the birth and settlement locations. This separation of the kernel will be useful for studying the dispersal success function in the future. Moreover, the kernel can be used to study and predict the consequences of habitat fragmentation on populations.

1.1 The derivation of a dispersal kernel from a reaction-diffusion equation

Reaction-Diffusion (RD) models provide a way to translate local assumptions or data about the movement, mortality, and reproduction of individuals into global conclusion about the persistence or extinction of populations [2]. Each individual is expected to move in random patterns which we specify as a random walk. Random walks are based on the idea of taking successive steps of random length and random direction. Individuals confined initially in a small region of space diffuse symmetrically outward [1]. In this section, we discuss methods of deriving kernels by applying RD equations and show the dispersal kernel is the Green's function of a differential operator.

Suppose an individual is released at position y at time zero. If the individual performs an unbiased random walk, then the probability density of the individual's location

x, and at time t, denoted by $u(x, y, t)$, satisfies the heat equation

$$u_t = \nu u_{xx}, \tag{1.1}$$

with the initial condition $u(x, y, 0) = \delta(x - y)$ [1], where δ is the Dirac delta function. Since the individual is assumed to move independently of one another, this is the same as finding the distribution of the displacement of a single organism after a time t. The diffusion coefficient, ν, characterizes the rate individuals spread out from the origin. There is a relation between ν, the displacement and time. Berg [1] showed that it takes four times as long for populations to wander twice as far.

The solution of Equation (1.1) is

$$u(x, y, t) = \frac{1}{2\sqrt{\pi \nu t}} e^{-(x-y)^2/4\nu t}. \tag{1.2}$$

That is, if we assume that each individual settles at the exact same instant of time, the position of the individual is seen to be a normally distributed random variable [1]. In other words, the entire population of individuals disperses in synchrony and settles simultaneously at $t = t_s$. Then, the dispersal kernel is the Gaussian kernel

$$k(x, y) = \frac{1}{2\sqrt{\pi \nu t_s}} e^{-|x-y|^2/4\nu t_s}. \tag{1.3}$$

However, if we assume that individuals settle at the per capita rate α, then

$$u_t = \nu u_{xx} - \alpha u, \tag{1.4}$$

with the initial conditions

$$u(x, y, 0) = \delta(x - y). \tag{1.5}$$

In the simplest case, in which the settling rate α is constant, the dispersal kernel can be defined as

$$k(x, y) = \int_0^\infty \alpha u(x, y, t) dt. \tag{1.6}$$

The kernel, $k(x, y)$, can be applied in a landscape, in which the kernel depends on the distance, $|x - y|$, between the release point, y, and the settlement location, x. Integrating $u_t = \nu u_{xx} - \alpha u$ from $t = 0$ to $t = \infty$ gives us an ODE with the dispersal kernel, $k(x, y)$, as a solution of

$$\frac{\nu}{\alpha} k_{xx} - k = -\delta(x - y). \tag{1.7}$$

This solution is the Laplace distribution, which is defined by

$$k(x, y) = \frac{1}{2}\sqrt{\alpha/\nu}e^{-\sqrt{\alpha/\nu}|x-y|}. \tag{1.8}$$

By far the most commonly used models for dispersal are the Gaussian and Laplace kernels [4]. These two kernels are used in many models, such as for the larval dispersal of green crabs (*Carcinus maenas*) [3]. However, there are some essential differences between the Gaussian and Laplace kernels. An assumption of synchronous settling following a fixed dispersal period leads to a Gaussian distribution, whereas continuous settling at a constant per capita rate over a longer time results in a Laplace distribution. The Laplace distribution has a heavier tail compared to the Gaussian kernel, implying a greater tendency for long distance dispersal. Furthermore, the probability of finding dispersers around the origin in the Laplace kernel is higher than with the Gaussian kernel, Figure (1.1).

More generally, if we assume that in addition to settling at a per capita rate α, dispersing individuals die at a per capita rate β, then the time evolution of $u(x, y, t)$

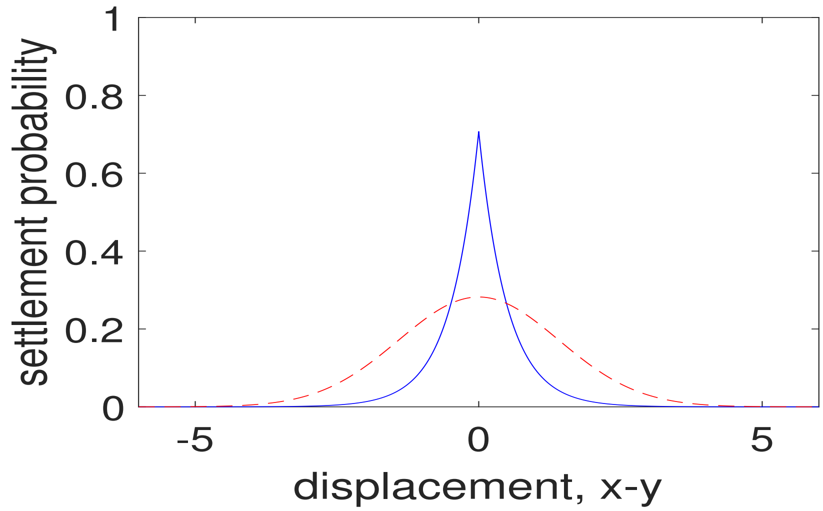

Figure 1.1: The most commonly used dispersal kernels are the Laplace distribution (1.8) (solid) and the Gaussian distribution (1.3) (dashed). Parameters in this plot are $\alpha = 2$, $\nu = 1$, at $t_s = 1$.

is governed by the following partial differential equation

$$\begin{cases} \frac{\partial}{\partial t} u(x,y,t) = \nu \frac{\partial^2}{\partial x^2} u(x,y,t) - (\alpha+\beta) u(x,y,t), \\ \\ u(x,y,0) = \delta(x-y). \end{cases} \tag{1.9}$$

Integrating $\frac{\partial}{\partial t} u(x,y,t) = \nu \frac{\partial^2}{\partial x^2} u(x,y,t) - (\alpha+\beta) u(x,y,t)$ from $t = 0$ to $t = \infty$ gives us the kernel

$$k_L(\zeta,\mu) = \frac{1}{2} \mu e^{-\mu|\zeta|}$$

as the Green's function of the operator

$$\mathcal{L} = \big(\nu/\alpha\big) \frac{\partial^2}{\partial x^2} - \frac{\alpha+\beta}{\alpha}, \tag{1.10}$$

where $\zeta = x - y$ is the position relative to release point, and $\mu = \sqrt{\frac{\alpha+\beta}{\nu}}$ is the decay rate of the displacement. This operator will be our main reference in the next chapter where we are going to derive the general kernel for the dispersal process in a patchy domain. Since we have included the death rate in model (1.9), some individuals die during the dispersal process, and

$$\int_{-\infty}^{\infty} k_L(x-y,\mu)dx \leq 1.$$

1.2 Patchy domain

Ovaskainen and Cornell [7] analyzed random walks with different types of biologically-motivated movement bias at patch boundaries in a one dimensional space. They assumed that in the neighbourhood of the boundary, an individual can perceive the presence of the two habitat types, and that it will bias its movement toward the preferred habitat type.

We first consider the case in which there is only one interface point at a_0, Figure (1.2), and then in the next chapter, we expand the idea to the case that there are any finite number of interface points on the whole real line. The habitat type to the left of a_0 differs from the habitat type to the right of a_0. If the individual is not located at a_0, the probabilities of making a move to the left or to the right are assumed to be equal. When the individual is located at a_0, there is a preference in movement direction. The probability of moving to the left is denoted by $(1-z)/2$ and the probability for moving to the right by $(1+z)/2$, where $-1 \leq z \leq 1$ measures the preference for the habitat.

All parameters may differ on the left and right hand sides of the interface point, a_0:

$$\alpha(x) = \begin{cases} \alpha_1, & x > a_0, \\ \alpha_0, & x < a_0; \end{cases} \qquad \beta(x) = \begin{cases} \beta_1, & x > a_0, \\ \beta_0, & x < a_0; \end{cases} \qquad \nu(x) = \begin{cases} \nu_1, & x > a_0, \\ \nu_0, & x < a_0. \end{cases} \tag{1.11}$$

The time evolution of the probability density $u(x, y, t)$ of an individual's location at

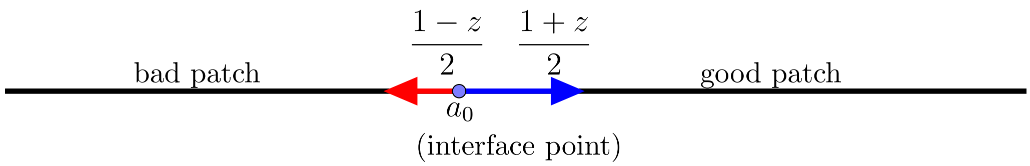

Figure 1.2: In an unbiased walk, the probability of moving to the left and to right side of an interface point are not equal. The diagram represents a one dimensional landscape with a single interface point, a_0, and a bias, z. If $z > 0$ then the probability of moving to the right is larger than to the left.

time t is approximated by the diffusion equation

$$\frac{\partial}{\partial t}u(x,y,t) = \begin{cases} \nu_0 \frac{\partial^2}{\partial^2 x}u(x,y,t) - (\alpha_0 + \beta_0)u(x,y,t) & x < a_0, \\ \\ \nu_1 \frac{\partial^2}{\partial^2 x}u(x,y,t) - (\alpha_1 + \beta_1)u(x,y,t) & x > a_0, \end{cases} \tag{1.12}$$

with the interface conditions

$$\nu_1(1-z)u(a_0^+, y, t) = \nu_0(1+z)u(a_0^-, y, t), \tag{1.13}$$

$$\nu_1 u_x(a_0^+, y, t) = \nu_0 u_x(a_0^-, y, t). \tag{1.14}$$

Interface condition (1.14) expresses the conservation of mass to the left, a_0^-, and right, a_0^+, at the interface, and ensures that no individuals are added or removed at the interface. Interface condition (1.13) represents the effect of the bias at the interface, and expresses that there is no conservation of the momentum at the patch boundaries. Ovaskainen and Cornell [7] showed that terms on the right and the left hand sides of Equation (1.13) are the order terms of a Taylor series in the time-step and step-size of the random walk. Equation (1.13) holds in a limit as those two quantities approach zero. Applying these interface conditions into (1.6) give us

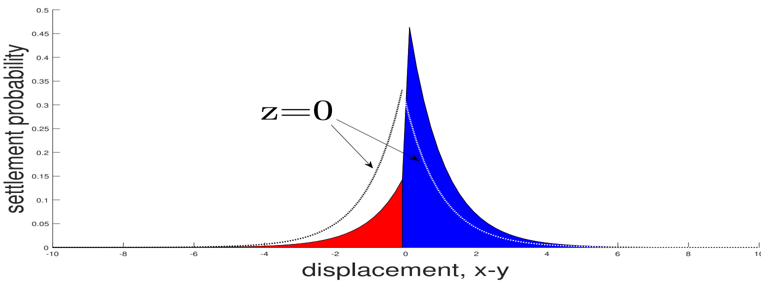

Figure 1.3: With $z > 0$, a fraction z of dispersers are reflected back across the interface (the second term in (1.19)), and will be added to the blue area (the second term in (1.20)). The dashed cure is the Laplace kernel in which the landscape is assumed to be homogeneous, and the walk is not biased. However, when we consider a positive bias, $z = 0.7$, to the walk at the origin, a positive term will be subtracted from the left side of the origin (the white area above the red area), and will be added to the right side.

similar interface conditions for the dispersal kernel,

$$\nu_0\alpha_1(1+z)k(a_0^-, y) = \nu_1\alpha_0(1-z)k(a_0^+, y), \tag{1.15}$$

$$\nu_0\alpha_1 k_x(a_0^-, y) = \nu_1\alpha_0 k_x(a_0^+, y). \tag{1.16}$$

Integrating (1.12) gives us a system of ODEs in terms of the dispersal kernel:

$$-\delta(x-y) = \frac{\nu_1}{\alpha_1}\frac{\partial^2}{\partial^2 x}k(x,y) - \frac{\alpha_1+\beta_1}{\alpha_1}k(x,y), \quad x > a_0 \tag{1.17}$$

$$0 = \frac{\nu_0}{\alpha_0}\frac{\partial^2}{\partial^2 x}k(x,y) - \frac{\alpha_0+\beta_0}{\alpha_0}k(x,y). \quad x < a_0 \tag{1.18}$$

In this case we assume that the kernel K is a matrix of four entries k_{00}, k_{01}, k_{10} and k_{11}, where k_{ij}, $i, j \in \{0, 1\}$, is the piece of the kernel when $x \in \Omega_i$ and $y \in \Omega_j$.

For example, suppose $a_0 = 0$, $z = 0$, and the parameters, α_i, β_i, and ν_i, are the same on the left and right hand side of the interface point. For clarity, we drop the subscripts on the parameters. For $y > 0$, the two pieces of the kernel are as follows:

$$k_{01} = \frac{\alpha}{\alpha+\beta}\Big(k_L(|x-y|,\mu) - zk_L(|x+y|,\mu)\Big), \tag{1.19}$$

$$k_{11} = \frac{\alpha}{\alpha+\beta}\Big(k_L(|x-y|,\mu) + zk_L(|x+y|,\mu)\Big), \tag{1.20}$$

where $k_L(|x+y|,\mu)$ is the probability density for a disperser travelling from y to $(-x)$ in absence of bias, Figure (1.3). With $z > 0$, a fraction z of dispersers are reflected back the interface.

1.3 Discussion

In this dissertation, the mechanistic derivation of dispersal kernels, as pioneered by Neubert et al. [6], in a homogeneous landscape has been chosen and we generalize it to patchy landscapes. We can include movement behaviour at interfaces between patches by employing results obtained by Ovaskainen and Cornell [7].

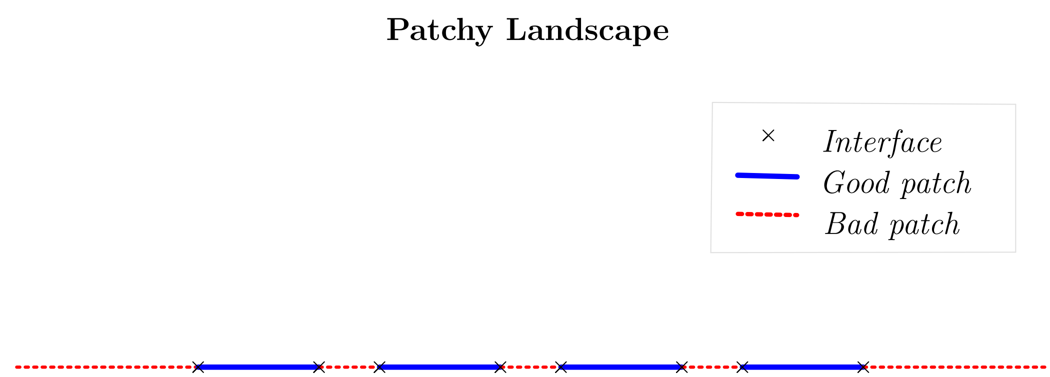

Figure 1.4: A patchy landscape consists of different homogeneous patches with different parameters. The landscape might be periodic, in which several good patches of equal size and quality are separated with equal-sized gaps, and are surrounded by two semi-infinite bad patches

Musgrave and Lutscher [5] studied persistence conditions on an infinite, periodic, patchy landscape in which an individual may encounter several habitat patches and corresponding interfaces during the dispersal stage in three different cases. They assumed the domain has several *good* patches of equal size with equal-sized gaps between them and the landscape is surrounded by two semi-infinite *bad* patches, Figure (1.4), while all good patches have the same quality.

In contrast, natural patches are generally not of equal size and quality. Parameters such as settling rate and death rate may differ from one patch to another. In this thesis, I consider a landscape including different parameters within different patches. The maximum value of the kernel occurs at the release point, and the dispersal kernel is discontinuous at patch boundaries, Figure (1.5).

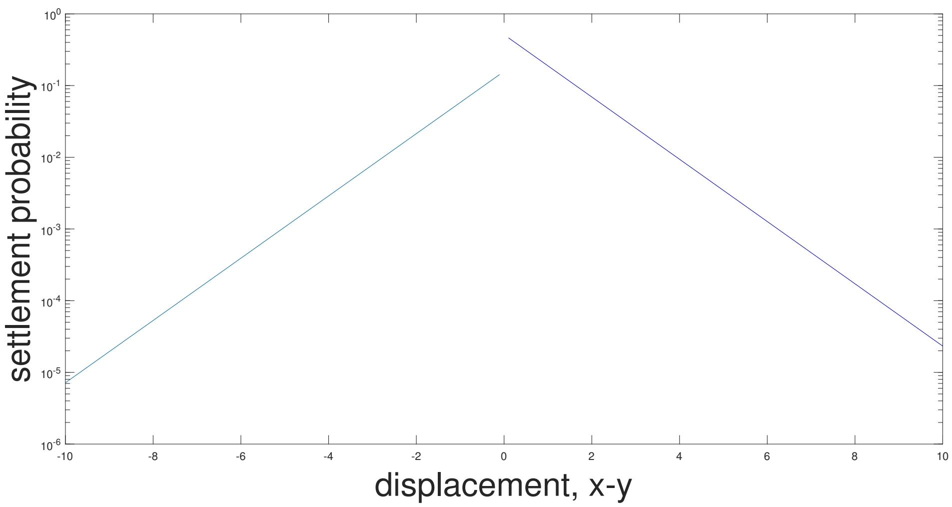

Figure 1.5: The interface conditions cause a discontinuity for the function k at the interface point when the parameters vary in patches. Since the kernel is a piecewise exponential function, its semi-log plot is linear. Parameters of the graph are $\alpha = 1, 2 \quad \beta = 2, 1 \quad \nu = 4, 2$ respectively, with $z = 0.8$.

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Chapter 2

An explicit formula for a dispersal kernel in a patchy landscape

2.1 Introduction

Integrodifference equations are often used to model the distribution of annual species with distinct growth and dispersal stages across a landscape. The general form of an integrodifference equation (IDE) modelling growth and dispersal is as follows:

$$N_{t+1}(x) = \int_{\Omega} k(x,y)F(N_t(y),y)dy. \tag{2.1}$$

Here $N_t(x)$ is the population density at a point $x \in \Omega$ at the end of the dispersal period in year t, the growth function, F, is the density of dispersers, or new recruits following the reproduction phase of year t, and the dispersal kernel, $k(x,y)$, is the probability a disperser originating at a point $y \in \Omega$ disperses to x [4]. Note that we do not assume all dispersers survive the dispersal phase. Hence, $\int_{\Omega} k(x,y)\,dy \leq 1$. The integral operator in (2.1) allows us to accommodate a wide variety of empirically determined dispersal patterns, such as random dispersion [4].

IDEs with a discontinuous population density have been recently analyzed in patchy landscapes equipped with discontinuous kernels [see e.g., 9]. Many of these studies restrict the analysis to the case with no bias at patch boundaries [see e.g., 2]. However, the degree of bias has direct effect on, for example, the speed of spread [5], and should be included in dispersal models. There is an explicit formula for a discontinuous dispersal kernel in case of periodic infinite patches with consideration of the habitat preference [8]. Yurk and Cobbold [14] presented a homogenization approach to the multi-scale problem of how individual behavioural responses to sharp transitions in landscape features, such as forest edges, affect population-dynamical outcomes. In their work, they treated the special case of a periodic environment consisting of two types of alternating patches, but the theory carries over to other periodic settings. We have obtained a general m-patch kernel including multiple patches with movement bias at the boundaries. The m-patch kernel extends several previous models for dispersal.

Many heterogeneous landscapes can be reasonably approximated by a mosaic of homogeneous patches, where individuals can respond to the boundaries by changing dispersal characteristics and by possibly immediately reversing direction to stay within the same patch. Musgrave [7] showed that a certain formulation of a random walk with bias at the boundaries on such landscapes leads to discontinuities in the dispersal kernel at the patch boundaries. Dispersal bias, while not necessary for persistence, can significantly increase chances of persistence [6]. More generally, there are many behaviours, especially in two or three dimensions involving responses to boundaries and movement along boundaries. For example, butterflies tended to prefer prairie at prairie-forest edges but tended to move faster in prairies than in open woods [12].

Here our aim is to derive a general dispersal kernel for the most straightforward one-dimensional case. We first focus on a heterogeneous landscape that can be approximated by homogeneous patches, then we partition the heterogeneous landscape into pieces with homogeneous dynamics on each piece. In our work, the landscape is not simply good and bad patches [as per 7], but now all sorts of different patches. Within each patch, individuals follow a simple random walk with a constant step size, mortality and settling rates [as per 10]. We obtain an explicit formula for the kernel as piecewise exponential function with coefficients and rates determined by the inverse of a unique matrix of model parameters. Each piece of the kernel is a linear combination of four exponential functions with coefficients representing the measure of retention at the boundaries. Moreover, the kernel can be expressed in terms of the distance between the settlement point and the reflections of the original point. We formulate the kernel with only one matrix of coefficients, which is independent of the location (x, y). As a result, the process of studying the effect of changing parameters on the model is simplified.

2.2 General dispersal kernel

2.2.1 Kernel derivation

We formulate the kernel, which depends on the parameters in every patch, to study the dispersal of species in a one-dimensional patchy domain. We assume that the real line is partitioned into different pieces such that there are non-equal probabilities for individuals at boundaries to move to the right or left side of the boundary. The domain $\mathbb{R}$ is partitioned by the $m+1$ interface points $\{a_0, \ldots, a_m\}$, and let $\Omega_i = (a_{i-1}, a_i),\ i \in \{1, \ldots, m\}$, denote the bounded patches, which are accompanied by two semi infinite patches, $\Omega_0 = (-\infty, a_0)$ and $\Omega_{m+1} = (a_m, \infty)$. For each patch Ω_i, the settling rate, the death rate, and the motility of individuals are denoted by α_i, β_i, and ν_i, respectively. The degree of bias, $-1 < z_i < 1$, at each interface determines two probabilities, $(1 - z_i)/2$ and $(1 + z_i)/2$, of moving to the left and to the right at boundary i, respectively. Ovaskainen and Cornell [10] showed that the dispersal kernel is the Green's function, $k(x, y)$, satisfying the differential equation

$$\frac{\partial^2}{\partial x^2}k(x,y) - \mu_i^2 k(x,y) = -\delta(x-y), \quad (x,y) \in \Omega_i \times \Omega_j, \quad (i,j) \in \{0,\dots,m+1\}^2, \tag{2.2}$$

where $\mu_i = \sqrt{\dfrac{\alpha_i + \beta_i}{\nu_i}}$ is the decay rate of the dispersal, and the following conditions:

$$k(y^-, y) = k(y^+, y), \tag{2.3}$$

$$k_x(y^-, y) - k_x(y^+, y) = \alpha_j/\nu_j, \tag{2.4}$$

$$\frac{\nu_i}{\alpha_i}(1+z_i)k(a_i^-, y) = \frac{\nu_{i+1}}{\alpha_{i+1}}(1-z_i)k(a_i^+, y), \tag{2.5}$$

$$\frac{\nu_i}{\alpha_i}k_x(a_i^-, y) = \frac{\nu_{i+1}}{\alpha_{i+1}}k_x(a_i^+, y), \tag{2.6}$$

where $i \in \{0, \dots, m\}$, $j \in \{0, \dots, m+1\}$, and $y \in \Omega_j$. Condition (2.3) ensures the kernel is continuous at $x = y$; Condition (2.4) arises from a matching condition [see 3]; Condition (2.5) is a jump condition; and finally, Condition (2.6) is the flux balance condition and represents continuity of the flux across the interface, so that no individuals are added or removed at the interface [7]. To ensure the kernel is bounded, we also add the conditions

$$k(\pm\infty, y) = 0. \tag{2.7}$$

We expect the kernel to be piecewise continuous with possible discontinuities along the lines $x = a_i$, $i \in \{0, \dots, m\}$, Figure (2.1). Let k_{ij} denote the portion of the kernel representing dispersal from patch Ω_j to patch Ω_i. That is, $k(x, y) = k_{ij}(x, y)$, for $(x, y) \in \Omega_i \times \Omega_j$, $(i, j) \in \{0, \dots, m+1\}^2$.

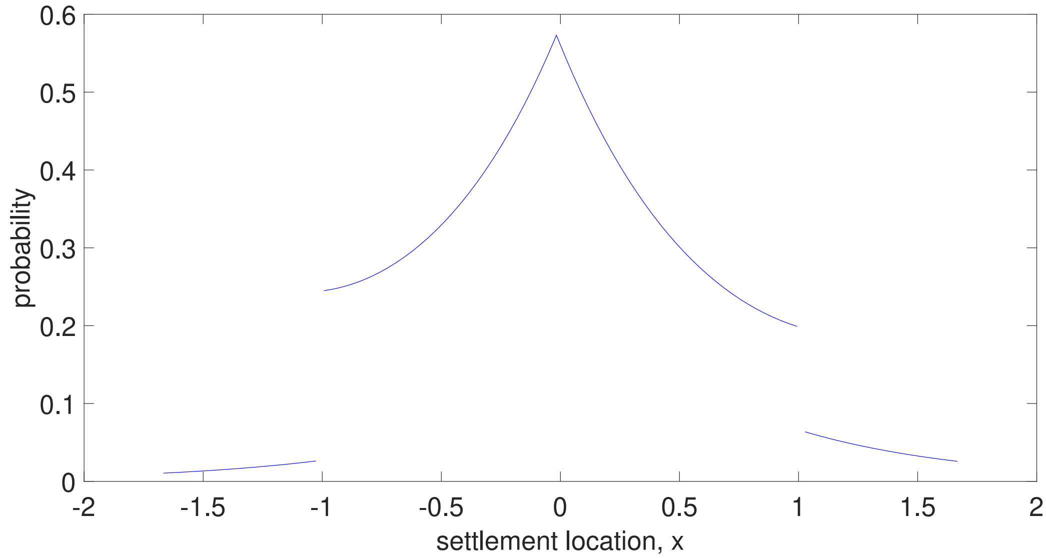

Figure 2.1: The kernel is a piecewise continuous exponential function, with discontinuities at patch boundaries, even when all parameters do not change except the degree of bias. The domain Ω includes three patches and two interfaces with $\Omega_0 = (-\infty, -1)$, $\Omega_1 = [-1, 1]$, and $\Omega_2 = (1, \infty)$. The parameters do not change in patches and are $\alpha = 3, \quad \beta = 1, \quad \nu = 2$, however the degree of bias is not zero, and varies in interfaces, with $z_0 = 0.8, z_1 = -0.5$.

Using E_i to denote the functions

$$E_i(x) = \begin{cases} e^{\mu_0(x-a_0)} & i = 0, \\ e^{\mu_i(x-a_{i-1})} & i \in \{1, \dots, m+1\}, \end{cases} \tag{2.8}$$

which are solutions to $k_{xx} - \mu_i^2 k = 0$, we can express each piece of the kernel in the form

$$k_{ij} = \begin{cases} \frac{\alpha_i}{2\mu_i\nu_i}\big((A_{ij} - C_j)E_i(x) + (B_{ij} - D_j)/E_i(x)\big) & i = j, x > y \\ \frac{\alpha_i}{2\mu_i\nu_i}\big(A_{ij}E_i(x) + B_{ij}/E_i(x)\big) & \text{otherwise.} \end{cases} \tag{2.9}$$

It follows immediately from Condition (2.7) that

$$A_{ij} = 0 \qquad i = m+1, \qquad j \in \{0, \dots, m\}, \tag{2.10}$$

$$A_{ij} = C_j \qquad i = m+1, \qquad j = m+1, \tag{2.11}$$

$$B_{ij} = 0 \qquad i = 0, \qquad j \in \{0, \dots, m+1\}. \tag{2.12}$$

From continuity at $x = y$ we have

$$C_j E_j(y) + D_j / E_j(y) = 0, \quad j \in \{0, \dots, m+1\},$$

and from the matching condition on k_x at $x = y$ we have

$$C_j E_j(y) - D_j / E_j(y) = 2, \quad j \in \{0, \dots, m+1\}.$$

These can be solved for C_j and D_j to obtain

$$C_j = \left(E_j(y)\right)^{-1} \tag{2.13}$$

$$D_j = -E_j(y) \tag{2.14}$$

Upon substituting the expression for C_{m+1} into Equation (2.11), we find that

$$A_{ii} = \left(E_i(y)\right)^{-1}, \quad i = m+1.$$

From Conditions (2.5) and (2.6), for $(i, j) \in \{0, \dots, m\} \times \{0, \dots, m+1\}$, we have the interface conditions

$$\begin{aligned} \mu_{i+1}(1 + z_i)\left((A_{ij} - \delta_{ij} C_j) E_i(a_i) + (B_{ij} - \delta_{ij} D_j)/E_i(a_i)\right) = \\ \mu_i(1 - z_i)\left(A_{i+1,j} + B_{i+1,j}\right), \end{aligned} \tag{2.15}$$

$$\left((A_{ij} - \delta_{ij} C_j) E_i(a_i) - (B_{ij} - \delta_{ij} D_j)/E_i(a_i)\right) = \left(A_{i+1,j} - B_{i+1,j}\right), \tag{2.16}$$

where δ_{ij} denotes the Kronecker delta.

Substituting Equations (2.13) and (2.14) into Equations (2.15) and (2.16) leads to the conditions

$$E_i(a_i)A_{ij} - \eta_i A_{i+1,j} + \tfrac{1}{E_i(a_i)} B_{ij} - \eta_i B_{i+1,j} = \delta_{ij}\big(\tfrac{E_i(a_i)}{E_j(y)} - \tfrac{E_j(y)}{E_i(a_i)}\big), \tag{2.17}$$

$$E_i(a_i)A_{ij} - A_{i+1,j} - \tfrac{1}{E_i(a_i)} B_{ij} + B_{i+1,j} = \delta_{ij}\big(\tfrac{E_i(a_i)}{E_j(y)} + \tfrac{E_j(y)}{E_i(a_i)}\big), \tag{2.18}$$

where

$$\eta_i = \frac{\mu_i(1 - z_i)}{\mu_{i+1}(1 + z_i)} \tag{2.19}$$

can be viewed as a measure of the retention at the interface.

Equations (2.17) and (2.18) along with Equations (2.10)-(2.12) are a linear system of $2(m+2)(m+2)$ equations for the coefficients A_{ij} and B_{ij} with $(i, j) \in \{0, \ldots, m+1\}^2$. Solving this system for the coefficients gives us a piecewise-defined form of the kernel as expressed by Equation (2.9)

2.2.2 Matrix form of the kernel

The system derived in the previous section is linear, implying that the kernel can be expressed in a compact matrix form. As we show next, this result can be exploited to greatly reduce the computations required to numerically compute the kernel. Furthermore, it emphasizes the similarity of the general kernel (2.9) with the simpler Laplace kernels and truncated Laplace kernels appearing in the literature [13].

Let $\epsilon_i = E_i(a_i)$, and let T and W denote the following blocked matrices of parameters:

$$T = \begin{pmatrix}
\epsilon_0 & -\eta_0 & & & 0 & \epsilon_0^{-1} & -\eta_0 & & & 0 \\
 & \epsilon_1 & -\eta_1 & & & & \epsilon_1^{-1} & -\eta_1 & & \\
 & & \ddots & \ddots & & & & \ddots & \ddots & \\
 & & & \epsilon_m & -\eta_m & & & & \epsilon_m^{-1} & -\eta_m \\
0 & & & & 1 & 0 & & & & 0 \\
\epsilon_0 & -1 & & & 0 & -\epsilon_0^{-1} & 1 & & & 0 \\
 & \epsilon_1 & -1 & & & & -\epsilon_1^{-1} & 1 & & \\
 & & \ddots & \ddots & & & & \ddots & \ddots & \\
 & & & \epsilon_m & -1 & & & & -\epsilon_m^{-1} & 1 \\
0 & & & & 0 & 1 & & & & 0
\end{pmatrix} \tag{2.20}$$

$$W = \begin{pmatrix} -\epsilon_0^{-1} & & 0 & \epsilon_0 & & 0 \\ & \ddots & & & \ddots & \\ & & -\epsilon_m^{-1} & & & \epsilon_m \\ 0 & & 0 & 0 & & 1 \\ \epsilon_0^{-1} & & 0 & \epsilon_0 & & 0 \\ & \ddots & & & \ddots & \\ & & \epsilon_m^{-1} & & & \epsilon_m \\ 0 & & 0 & 0 & & 0 \end{pmatrix} \tag{2.21}$$

If we let A and B denote the two $(m+2) \times (m+2)$ matrices of coefficients, and we define

$$E(y) = \begin{pmatrix} E_0(y) & & 0 \\ & \ddots & \\ 0 & & E_{m+1}(y) \end{pmatrix}, \tag{2.22}$$

we can write the system of equations from the previous section as

$$T \begin{bmatrix} A \\ B \end{bmatrix} = W \begin{bmatrix} E(y) \\ E^{-1}(y) \end{bmatrix}. \tag{2.23}$$

Consequently,

$$\begin{bmatrix} A \\ B \end{bmatrix} = T^{-1} W \begin{bmatrix} E(y) \\ E^{-1}(y) \end{bmatrix}. \tag{2.24}$$

Thus Equation (2.9) has the matrix form

$$K = P \begin{bmatrix} E(x) & E^{-1}(x) \end{bmatrix} \left(T^{-1} W + \mathcal{H}(x-y) \begin{bmatrix} 0 & -I \\ I & 0 \end{bmatrix} \right) \begin{bmatrix} E(y) \\ E^{-1}(y) \end{bmatrix} \tag{2.25}$$

where I is the identity matrix, P is a diagonal matrix with diagonal entries $\frac{1}{2} \cdot \frac{\mu_i \alpha_i}{\alpha_i + \beta_i}$, $i \in \{0, \ldots, m+1\}$, and $\mathcal{H}$ is the Heaviside step function, defined as

$$\mathcal{H}(x-y) \begin{cases} 0 & x < y, \\ 1 & x > y, \end{cases}$$

It is useful to rearrange Equation (2.25) to bring out a comparison between the general form of the kernel and the simple Laplace kernel. To this end, note that $1 - \mathcal{H}(x-y) = \mathcal{H}(y-x)$, and so

$$\begin{bmatrix} E(x) & E^{-1}(x) \end{bmatrix} \begin{bmatrix} 0 & (1-\mathcal{H}(x-y))\,I \\ \mathcal{H}(x-y)I & 0 \end{bmatrix} \begin{bmatrix} E(y) \\ E^{-1}(y) \end{bmatrix} = K_L, \tag{2.26}$$

where K_L represents the exponential pieces of the patchy-truncated Laplace kernel, defined as

$$K_L = \begin{pmatrix} e^{-\mu_0|x-y|} & & 0 \\ & \ddots & \\ 0 & & e^{-\mu_{m+1}|x-y|} \end{pmatrix}. \tag{2.27}$$

Hence,

$$K = P \begin{bmatrix} E(x) & E^{-1}(x) \end{bmatrix} \left(T^{-1}W - \begin{bmatrix} 0 & I \\ 0 & 0 \end{bmatrix} \right) \begin{bmatrix} E(y) \\ E^{-1}(y) \end{bmatrix} + PK_L. \tag{2.28}$$

The reciprocal of ϵ_i can be interpreted as a measure of patch-width. Specifically, if we define the homogeneous Laplace kernel by

$$k_L(x,\mu) = \tfrac{1}{2}\mu e^{-\mu|x|}, \tag{2.29}$$

then for $i \in \{1,\ldots,m\}$, $\epsilon_i^{-1} = \int_{a_i}^{\infty} k_L(x,\mu_i)\,dx / \int_{a_{i-1}}^{\infty} k_L(x,\mu_i)\,dx$, which is the probability a given individual settles beyond a_i given that they settle beyond a_{i-1}. Therefore, ϵ_i can be viewed as the fraction of dispersers reaching a_{i-1} that continue across a_i. Similarly, η_i, as a measure of the retention at the interface, is the ratio of the rescaled kernel across the interface. Note, however, that retention also depends on the entries of P, or more accurately on the jumps in motility, ν, and settling, α, across the interface, and the value of z_i.

The matrix form of the kernel implies that the functional form of each piece k_{ij} is a linear combination of the four functions

$$e^{+\mu_i x}e^{+\mu_j y},\quad e^{+\mu_i x}e^{-\mu_j y},\quad e^{-\mu_i x}e^{+\mu_j y},\ \text{and}\ e^{-\mu_i x}e^{-\mu_j y}. \tag{2.30}$$

Since the entries of $T^{-1}W$ depend on parameters in every patch through the two parameter groups, η and ϵ, the component of the kernel, k_{ij} representing settlement in patch i by dispersers originating in patch j, also depends in general on all parameters.

2.3 Special cases

2.3.1 Single interface

To illustrate the method, we first consider the simplest case where $m = 0$. That is, there is only a single interface point, with possibly different parameters on each side of the interface. From the definitions of T and W, and noting that $\epsilon_0 = 1$, we find that

$$\left(T^{-1}W - \begin{bmatrix} 0 & I \\ 0 & 0 \end{bmatrix}\right) = \begin{pmatrix} \frac{\eta_0-1}{(\eta_0+1)} & 0 & 0 & \frac{2\eta_0}{(\eta_0+1)} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \frac{2}{(\eta_0+1)} & 0 & 0 & \frac{-(\eta_0-1)}{(\eta_0+1)} \end{pmatrix} = \begin{pmatrix} 1-\phi_{21} & 0 & 0 & \phi_{12} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \phi_{21} & 0 & 0 & 1-\phi_{12} \end{pmatrix}, \tag{2.31}$$

with $\phi_{12} = \frac{2\eta_0}{(\eta_0+1)}$ and $\phi_{21} = \frac{2}{(\eta_0+1)}$, as the coefficients in front of the exponential functions. Hence, from Equation (2.28),

$$P^{-1}K = \begin{bmatrix} E(x) & E^{-1}(x) \end{bmatrix} \begin{pmatrix} 1-\phi_{21} & 0 & 0 & \phi_{12} \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \phi_{21} & 0 & 0 & 1-\phi_{12} \end{pmatrix} \begin{bmatrix} E(y) \\ E^{-1}(y) \end{bmatrix} + \begin{pmatrix} e^{-\mu_0|x-y|} & 0 \\ 0 & e^{-\mu_1|x-y|} \end{pmatrix}. \tag{2.32}$$

The k_{ij} entry of the matrix K involves only the $(i+1)$st row and $(j+1)$st column of the product of the right hand side. For example, k_{00} involves the first row and first column of the product, which involves the first row of $E(x)$ and $E^{-1}(x)$ and the first column of $E(y)$ and $E^{-1}(y)$. Since $E(x)$ is a diagonal matrix, this implies only the first and third rows and columns of $T^{-1}W$ are used in computing k_{00}. Similarly, k_{01} uses only the first and third rows and the second and fourth columns of $T^{-1}W$.

$$k_{00} = \tfrac{1}{2}\tfrac{\alpha_0\mu_0}{\alpha_0+\beta_0}\left((1-\phi_{21})e^{-\mu_0(a_0-x)}e^{-\mu_0(a_0-y)} + e^{-\mu_0|x-y|}\right) \tag{2.33}$$

$$k_{01} = \tfrac{1}{2}\tfrac{\alpha_0\mu_0}{\alpha_0+\beta_0}\phi_{12}e^{-\mu_0(a_0-x)}e^{-\mu_1(y-a_0)} \tag{2.34}$$

$$k_{10} = \tfrac{1}{2}\tfrac{\alpha_1\mu_1}{\alpha_1+\beta_1}\phi_{21}e^{-\mu_1(x-a_0)}e^{-\mu_0(a_0-y)} \tag{2.35}$$

$$k_{11} = \tfrac{1}{2}\tfrac{\alpha_1\mu_1}{\alpha_1+\beta_1}\left((1-\phi_{12})e^{-\mu_1(x-a_0)}e^{-\mu_1(y-a_0)} + e^{-\mu_1|x-y|}\right) \tag{2.36}$$

The pattern of zeros in $T^{-1}W$ after subtracting the identity matrix from the upper right block arises from the condition that the kernel remain bounded. For a fixed x, when $y \to \infty$ in Equation (2.34), the dispersal kernel goes to zero. We have the same limit for k, when $y \to -\infty$ in Equation (2.35).

For $m = 0$, we can, without loss of generality, assume $a_0 = 0$. If we further assume that the habitat quality is identical in both patches ($\mu = \mu_0 = \mu_1$, etc.), we have $\eta_0 = (1 - z_0)/(1 + z_0)$, and after dropping the unnecessary subscripts on the parameters the components of the kernel simplify to

$$k_{00} = \tfrac{\alpha}{\alpha+\beta}\Bigg(k_L(|x-y|,\mu) - zk_L(|x+y|,\mu)\Bigg) \tag{2.37}$$

$$k_{10} = \tfrac{\alpha}{\alpha+\beta}(1+z)k_L(|x-y|,\mu) \tag{2.38}$$

$$k_{01} = \tfrac{\alpha}{\alpha+\beta}(1-z)k_L(|x-y|,\mu) \tag{2.39}$$

$$k_{11} = \tfrac{\alpha}{\alpha+\beta}\Bigg(k_L(|x-y|,\mu) + zk_L(|x+y|,\mu)\Bigg) \tag{2.40}$$

The first term, $k_L(|x-y|,\mu)$ in k_{00} and k_{11} is the probability density for a disperser

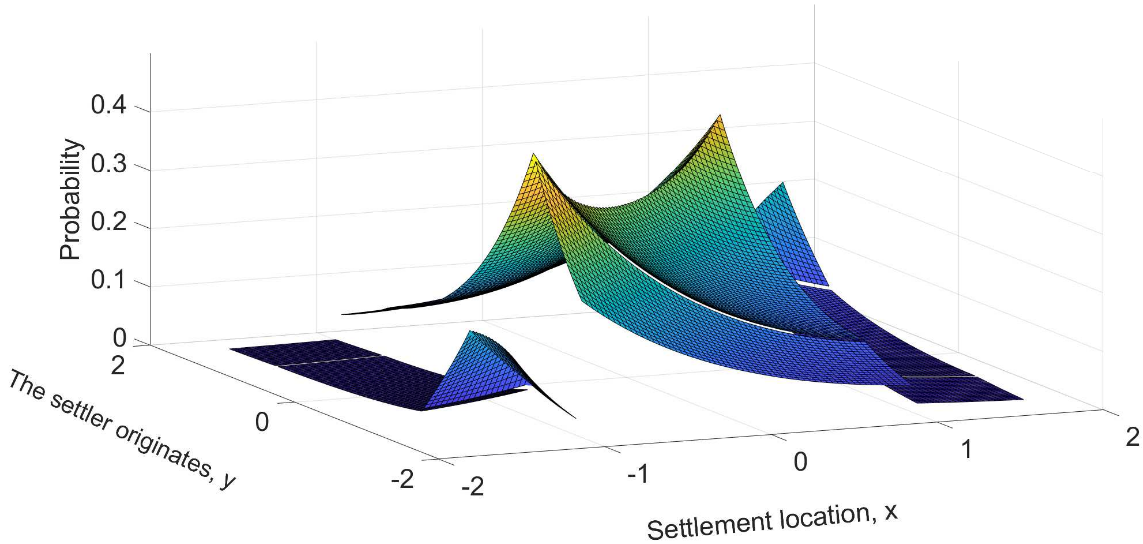

Figure 2.2: The kernel as a function of two variables x and y, is a discontinuous surface. The plot shows the nine pieces of the kernel, K in Equation (2.28), when there are two interface points, $a_0 = -1$ and $a_1 = 1$, with $z_0 = 0.8$, $z_1 = -0.5$, and $\mu = 1$ for all patches

following a homogeneous Laplace kernel dispersing a distance $|x - y|$, and the remaining term in each piece, $k_L(|x + y|, \mu)$, is the probability density for the same disperser travelling a net distance $|x + y|$. This second distance is the net distance travelled by a disperser settling at the reflection of x across the interface. With no bias, $z = 0$, each piece of the kernel reduces to the homogeneous Laplace kernel. With $z > 0$, a fraction z of dispersers are reflected back across the interface, thus the terms of k_{11} are the following probabilities, with x and y positive: $k_L(|x - y|, \mu)$ is the probability density for a disperser travelling from y to x; $k_L(|x + y|, \mu)$ is the probability density for a disperser travelling from y to $(-x)$ in absence of bias; with bias, a fraction z of these dispersers are reflected to (x); finally, a fraction $\beta/(\alpha + \beta)$ of all dispersers die before settling, leaving only a fraction $\alpha/(\alpha + \beta)$ that survive the dispersal process.

2.3.2 A single isolated patch

For the special case $m = 1$ the habitat consists of a single patch of finite length surrounded by two semi-infinite patches. This typically arises as either a single isolated patch of good habitat surrounded by poor habitat, or a large (i.e, infinite) good habitat fragmented by an unsuitable, or poor quality habitat represented by a finite interval. With $m = 1$, the dispersal kernel has 9 pieces, Figure (2.2), and $T^{-1}W$ is a 6×6 matrix. As with the previous case, the middle two rows and columns of $T^{-1}W$ after subtracting the identity matrix from the upper right block are zeros, leaving 16 nonzero entries.

$$\frac{1}{\phi}\begin{pmatrix} \phi_1 & -2\eta_0(1-\eta_1)\epsilon_1^{-2} & 0 & 0 & 2\eta_0(1+\eta_1) & 4\eta_0\eta_1\epsilon_1^{-1} \\ -2(1-\eta_1)\epsilon_1^{-2} & -(1+\eta_0)(1-\eta_1)\epsilon_1^{-2} & 0 & 0 & -(1-\eta_0)(1-\eta_1)\epsilon_1^{-2} & 2\eta_1(1+\eta_0)\epsilon_1^{-1} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 2(1+\eta_1) & -(1-\eta_0)(1-\eta_1)\epsilon_1^{-2} & 0 & 0 & (1-\eta_0)(1+\eta_1) & 2\eta_1(1-\eta_0)\epsilon_1^{-1} \\ 4\epsilon_1^{-1} & 2(1+\eta_0)\epsilon_1^{-1} & 0 & 0 & 2(1-\eta_0)\epsilon_1^{-1} & \phi_2 \end{pmatrix}, \tag{2.41}$$

where

$$\phi = (1+\eta_0)(1+\eta_1) + \epsilon_1^{-2}(1-\eta_0)(1-\eta_1), \tag{2.42}$$

$$\phi_1 = (1+\eta_0)(1-\eta_1)\epsilon_1^{-2} + (1-\eta_0)(1+\eta_1), \tag{2.43}$$

$$\phi_2 = (1-\eta_0)(1+\eta_1)\epsilon_1^{-2} + (1+\eta_0)(1-\eta_1). \tag{2.44}$$

Recalling that $\mu_i^2\nu_i = \alpha_i + \beta_i$, the first few pieces of the kernel are as follows:

$$k_{00} = \frac{\alpha_0\mu_0}{2(\alpha_0+\beta_0)}\Big(e^{-\mu_0|x-y|} - \frac{1}{\phi}\left((1-\eta_0)(1+\eta_1) + \epsilon_1^{-2}(1+\eta_0)(1-\eta_1)\right) e^{-\mu_0(a_0-x)}e^{-\mu_0(a_0-y)}\Big) \tag{2.45}$$

$$k_{01} = \frac{\eta_0\alpha_0\mu_0}{2\phi(\alpha_0+\beta_0)}e^{-\mu_0(a_0-x)}\left(-2\epsilon_1^{-2}(1-\eta_1)e^{\mu_1(y-a_0)} + 2(1+\eta_1)e^{-\mu_1(y-a_0)}\right) \tag{2.46}$$

$$k_{02} = \frac{\eta_0\eta_1\alpha_0\mu_0}{2\phi(\alpha_0+\beta_0)}\epsilon_1^{-1}e^{-\mu_0(a_0-x)}e^{-\mu_2(y-a_1)} \tag{2.47}$$

$$\begin{aligned} k_{11} = \frac{\alpha_1\mu_1}{2(\alpha_1+\beta_1)}e^{-\mu_1|x-y|} + \frac{\alpha_1\mu_1}{2\phi(\alpha_1+\beta_1)}\Big(&\epsilon_1^{-2}(1+\eta_0)(\eta_1-1)e^{\mu_1(x-a_0)}e^{\mu_1(y-a_0)} \\ &+ \epsilon_1^{-2}(1-\eta_0)(\eta_1-1)e^{\mu_1(x-a_0)}e^{-\mu_1(y-a_0)} \\ &+ \epsilon_1^{-2}(1-\eta_0)(\eta_1-1)e^{-\mu_1(x-a_0)}e^{\mu_1(y-a_0)} \\ &+ (1-\eta_0)(1+\eta_1)e^{-\mu_1(x-a_0)}e^{-\mu_1(y-a_0)}\Big) \end{aligned} \tag{2.48}$$

The first piece of the kernel can be expressed in terms of the homogeneous Laplace kernel and distances between the settling point, x, and the reflections y_0 and y_1 of the starting point, y, across the interfaces a_0 and a_1 respectively.

$$k_{00} = \frac{\alpha_0}{\alpha_0+\beta_0}\Big(k_L(|x-y|,\mu_0) + \phi_1 k_L(y_0-x,\mu_0) + e^{-2(\mu_1-\mu_0)(a_1-a_0)}\phi_2 k_L(y_1-x,\mu_0)\Big) \tag{2.49}$$

with $\phi_1 = -(1-\eta_0)(1+\eta_1)\phi^{-1}$ and $\phi_2 = (1+\eta_0)(1-\eta_1)\phi^{-1}$. It can be shown that $|\phi_1| < 1$ and $|\phi_2| < 1$, suggesting that they are fractions of dispersers reflected back into region Ω_0 by each interface.

There are several interesting special cases appearing in the literature where reproduction is zero outside the central patch and the IDE model only involves k_{11}. In these cases we have the following formulae for k_{11}.

Case 1: If the bias at the two interfaces is equal and opposite, $z_0 = -z_1 = z$, and the two outside patches are identical, $\nu_2 = \nu_0$, $\alpha_2 = \alpha_0$, and $\beta_2 = \beta_0$, then $\eta_0 = \dfrac{\mu_0(1-z)}{\mu_1(1+z)}$, and $\eta_1 = \dfrac{\mu_1(1+z)}{\mu_0(1-z)} = 1/\eta_0$. Hence,

$$\begin{aligned} k_{11} = \tfrac{\alpha_1}{2\mu_1\nu_1} e^{-\mu_1|x-y|} + \tfrac{\alpha_1}{2\mu_1\nu_1\hat{\phi}} \Big(& \epsilon_1^{-2}(1-\eta_0^2) e^{\mu_1(x-a_0)} e^{\mu_1(y-a_0)} \\ & + \epsilon_1^{-2}(1-\eta_0)^2 e^{\mu_1(x-a_0)} e^{-\mu_1(y-a_0)} \\ & + \epsilon_1^{-2}(1-\eta_0)^2 e^{-\mu_1(x-a_0)} e^{\mu_1(y-a_0)} \\ & + (1-\eta_0^2) e^{-\mu_1(x-a_0)} e^{-\mu_1(y-a_0)} \Big) \end{aligned} \tag{2.50}$$

where

$$\hat{\phi} = -\epsilon_1^{-2}(1-\eta_0)^2 + (1+\eta_0)^2 \tag{2.51}$$

Case 2: If the bias at the two interfaces is equal and opposite, $z_0 = -z_1 = z$, and dispersal within each patch is the same, $\mu_2 = \mu_1 = \mu_0$, $\alpha_2 = \alpha_1 = \alpha_0$, and $\beta_2 = \beta_1 = \beta_0$, then

$$\begin{aligned} k_{11} = \tfrac{\alpha_1}{2\mu_1\nu_1} e^{-\mu_1|x-y|} - \tfrac{\alpha_1\hat{\phi}}{2\mu_1\nu_1} \Big(& - z e^{-\mu_1(a_1-x)} e^{-\mu_1(a_1-y)} \\ & - z^2 \epsilon^{-1} e^{-\mu_1(a_1-x)} e^{-\mu_1(y-a_0)} \\ & - z^2 \epsilon^{-1} e^{-\mu_1(x-a_0)} e^{-\mu_1(a_1-y)} \\ & - z e^{-\mu_1(x-a_0)} e^{-\mu_1(y-a_0)} \Big) \end{aligned} \tag{2.52}$$

where

$$\hat{\phi} = \frac{1}{1 - z\epsilon^{-1}} \tag{2.53}$$

Case 3: If there is perfect reflection back in to the central patch, $z_0 = -z_1 = 1$, then $\eta_0 \to 0, \eta_1 \to \infty$, and

$$k_{11} = \tfrac{\alpha_1}{2\mu_1\nu_1}\Big(e^{-\mu_1|x-y|} + \epsilon_1^{-2}e^{\mu_1(x-a_0)}e^{\mu_1(y-a_0)} + \epsilon_1^{-2}e^{\mu_1(x-a_0)}e^{-\mu_1(y-a_0)} + \epsilon_1^{-2}e^{-\mu_1(x-a_0)}e^{\mu_1(y-a_0)} + e^{-\mu_1(x-a_0)}e^{-\mu_1(y-a_0)}\Big) \tag{2.54}$$

Case 4: If the bias at the boundaries perfectly balances the jump in kernel decay rates across the patch interfaces, $\eta_0 = \eta_1 = 1$, then k_{11} reduces to the truncated Laplace distribution.

which gives us

$$k_{11}(x, y) = \tfrac{\alpha}{2\mu\nu}e^{-\mu|x-y|}. \tag{2.55}$$

Case 5: Finally, we consider a case where the death rates in the exterior patches Ω_0 and Ω_2 are high, $\beta_2, \beta_0 \to \infty$ implying $\mu_2, \mu_0 \to \infty$ so that $\eta_0 \to \infty$, and $\eta_1 \to 0$.

$$k_{11} = \tfrac{\alpha_1\mu_1}{2(\alpha_1+\beta_1)}e^{-\mu_1|x-y|} + \tfrac{\alpha_1\mu_1}{2\phi(\alpha_1+\beta_1)}\Big(- \epsilon_1^{-2}e^{\mu_1(x-a_0)}e^{\mu_1(y-a_0)} + \epsilon_1^{-2}e^{\mu_1(x-a_0)}e^{-\mu_1(y-a_0)} + \epsilon_1^{-2}e^{-\mu_1(x-a_0)}e^{\mu_1(y-a_0)} - e^{-\mu_1(x-a_0)}e^{-\mu_1(y-a_0)}\Big) \tag{2.56}$$

with $\phi = 1 - \epsilon_1^{-2}$. Further, as expected, the other pieces of the kernel tend to zero as all indiduals leaving the central patch die before settling.

2.4 Discussion

In this study, we assumed that the real line, as a one-dimensional landscape, is partitioned into different pieces such that there are non-equal probabilities for individuals at boundaries to move to the right or left side of the boundary. During the dispersal phase, animals may respond to habitat quality and habitat edges and these responses may affect their distribution between habitats [1]. Ecologists who have incorporated detailed and realistic behaviour into the movement process have accomplished better fits to movement data [11]. This discussion will benefit from detailed studies on movement behaviour in combination with a study on the population outcome of this behaviour. We questioned if there is a straightforward method to formulate the dispersal kernel in non-homogeneous environments, that came from the random walk theory, governing the probability of successful dispersal.

The m-patch Laplace kernel is a piecewise exponential function of two variables, x and y. Each piece, k_{ij}, is a linear combination of four exponential functions (2.30) with coefficients representing the measure of retention at the boundaries. Moreover, k_{ij} can be expressed in terms of the distance between the settling point and the reflections of the starting point (2.37). We have investigated a method to formulate the kernel with only one matrix of coefficients, T, independent of the location y but dependent on the parameters in every patch through the two parameter groups η and ϵ in terms of the measure of retention at the boundaries. With this achievement, the process of studying the effect of changing parameters on the model is simplified. For example, when the degree of bias at the origin increases in (2.37), we see k_{10} increases and k_{01} decreases with z. As another example, for $m = 1$, setting $\eta_0 = \eta_1 = 1$ for the measure of retention can be viewed as balancing the bias with the ratio of the kernel decay rates across the patch interfaces.

The matrix form of the kernel will be useful for numerical simulations of IDEs, where it is necessary to integrate the product of the kernel and a reproduction function, particularly when the environment is heterogeneous. Since the integration is over y, where the dispersers originate, and several terms of the kernel are independent of y, only one part of the kernel is involved in the computation. Therefore, partitioning the whole real line into m patches does not complicate the simulation of an IDE.

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