### Abstract:

Theories of evolution of dispersal study how organisms living in heterogeneous landscapes should move to maximize their fitness. An evolutionarily stable strategy (ESS) is a movement strategy that cannot be invaded by any other strategy. Classical reaction-diffusion models assume that landscape quality varies continuously. Landscape ecologists consider landscapes as mosaics of patches where individuals can make movement decisions at sharp interfaces between patches of different quality. We use a recent formulation of reaction-diffusion systems in patchy landscapes to study the evolution of dispersal strategies via adaptive dynamics. Two independent analytical approaches allow us to explicitly calculate the optimal strategy. This ESS turns out to be the one that leads to the ideal-free distribution.

### Suggested Reviewers:
- Xinfu Chen
  xinfu@pitt.edu
- Richard Hambrock
  rhambrock@daltonstate.edu
- Junping Shi
  jxshix@wm.edu
- Xingfu Zou
  xzou@uwo.ca
Evolutionarily stable movement strategies in reaction-diffusion models with edge behavior

Gabriel Maciel
Chris Cosner† Robert Stephen Cantrell‡ Frithjof Lutscher§

April 10, 2018

Keywords: Evolution of dispersal, reaction-diffusion system, stability analysis, interface behavior

Abstract

Theories of evolution of dispersal study how organisms living in heterogeneous landscapes should move to maximize their fitness. An evolutionarily stable strategy (ESS) is a movement strategy that cannot be invaded by any other strategy. Classical reaction-diffusion models assume that landscape quality varies continuously. Landscape ecologists consider landscapes as mosaics of patches where individuals can make movement decisions at sharp interfaces between patches of different quality. We use a recent formulation of reaction-diffusion systems in patchy landscapes to study the evolution of dispersal strategies via adaptive dynamics. Two independent analytical approaches allow us to explicitly calculate the optimal strategy. This ESS turns out to be the one that leads to the ideal-free distribution.

1 Introduction

Organisms move in order to acquire resources and avoid dangers. In a given landscape with spatially varying habitat quality, what would be an ‘optimal’ strategy

*Department of Mathematics and Statistics, University of Ottawa, Ottawa, Canada. Current address: São Paulo State University (UNESP), Instituto de Física Teórica, São Paulo, Brazil
†Department of Mathematics, University of Miami, Miami, USA
‡Department of Mathematics, University of Miami, Miami, USA
§Department of Mathematics and Statistics, and Department of Biology, University of Ottawa, Ottawa, Canada
of movement? This question is, of course, much too general to have a meaningful
answer, in particular since the meaning of ‘optimal’ is not easily defined. One as-
pect of this question has, however, generated a fascinating body of literature on the
‘evolution of dispersal’ that has inspired and challenged mathematicians and evolu-
tionary biologists alike (McPeek and Holt, 1992; Lou, 2008; Cosner, 2014; Cantrell
et al., 2017; Clobert et al., 2001b,a). Here, we study the evolution of dispersal in
the relatively novel framework of reaction-diffusion equations in ‘patchy’ landscapes
(Maciej and Lutscher, 2013).

In the standard, adaptive-dynamics approach to the evolution of dispersal, one
considers the dynamics of two (or more) populations that differ only in their move-
ment strategy and asks whether one population can invade (i.e. grow from low den-
sity) and dynamically exclude the other (Geritz et al., 1998). The evolution of move-
ment strategies can then be studied by considering a succession of such competitive
interactions between an initially rare ‘invader’ (or ‘mutant’) population and a ‘resi-
dent’ population (Dockery et al., 1998; Cosner, 2014). The underlying assumption of
this approach is that ecological processes (e.g. competition) occur on a much faster
time scale than evolutionary changes. In the successive competition processes, more
advantageous traits substitute others until an ‘evolutionarily stable strategy’ (ESS)
is reached. By definition, a population that uses an ESS can not be invaded by any
other initially small population using a different strategy.

Reaction-diffusion equations have been instrumental in studying questions in the-
eoretical spatial ecology (Cantrell and Cosner, 2003). In the simplest case, they de-
scribe the temporal dynamics of the density, \( u(x, t) \), of a population from random
movement and growth by
\[
    u_t = du_{xx} + f(x, u),
\]  
(1)
where \( d \) denotes the diffusion rate and \( f \) the spatially dependent population growth
function. Hastings (1983) first studied the evolution of movement strategies (‘disper-
sal’) in this framework. He showed that a ‘mutant’ population can invade if and only
if it has a smaller diffusion rate than the ‘resident’. This conclusion that evolution
in a spatially varying but temporally constant habitat favors slow dispersal rates has
since been confirmed and strengthened in many respects (Dockery et al., 1998; Hut-
son et al., 2003; Altenberg, 2012). Intermediate or higher dispersal rates can evolve
under certain conditions when movement is more than simple, random diffusion. In
this case, diffusion could be space dependent and/or an additional advective or taxis
term can describe directed movement. For example, when habitat variability also
induces conditional dispersal, faster dispersal can be selected (McPeek and Holt,
1992). Faster dispersal can also be selected in advective environments (Lam et al.,
2014; Lou and Lutscher, 2014). Directed movement towards more favorable regions
has also been shown to confer competitive superiority in some situations (Cantrell et al., 2006).

While it can often be shown that an ESS exists, it can typically not be calculated analytically (unless it corresponds to zero movement). There is, however, growing evidence that dispersal strategies that generate an ideal-free distribution (IFD) are evolutionarily stable (Cosner, 2014). An IFD is a spatial distribution of the population in which organisms best exploit a resource by maximizing their ‘fitness’ (Fretwell and Lucas, 1969; Cantrell et al., 2008), defined as the per-capita growth rate \( i.e. f(x, u)/u \). Several empirical studies have shown that approximations of IFDs naturally occur in ecological populations (Parker and Sutherland, 1986; Doncaster et al., 1997; Diffendorfer, 1998; Morris et al., 2004). In the IFD it is assumed that fitness is spatially constant, otherwise individuals could move from lower fitness regions to regions of higher fitness. In addition, when an IFD is reached, net movement ceases as dispersal would break this distribution. It follows that at the IFD the fitness is zero, see Cosner (2014) for details.

Reaction-advection-diffusion equations with spatially varying coefficients are not only difficult to study mathematically, they are also difficult to parametrize empirically. Landscape ecologists typically view heterogeneous landscapes as collections of ‘patches’, i.e. regions that are relatively homogeneous within but substantially different from the adjacent region. This view has the empirical advantage that it requires only one set of parameters per patch, and it allows one to include habitat preference of organisms by studying movement behavior at (or near) an edge or interface between two patch types. There is ample empirical evidence that individuals of many taxa adjust their movement behavior to habitat conditions inside patches and preferentially chose one over the other habitat at interfaces (Schultz and Crone, 2001; Schtickzelle and Baguette, 2003; Crone and Schultz, 2008; Reeve et al., 2008).

Reaction-diffusion equations in patchy landscapes were first studied by Shigesada et al. (1986), but without consideration of movement behavior at edges or interfaces between patches. Appropriate matching conditions at these interfaces were introduced by Maciel and Lutscher (2013), based on work by Ovaskainen and Cornell (2003). In the simplest case, one considers only two patches, say \( \{ x > x_n \} \) for patch 1 and \( \{ x < x_n \} \) for patch 2 with an interface at \( x = x_n \). Population densities in patches 1 and 2 are denoted by \( u_1 \) and \( u_2 \), respectively. Then one has an equation of the form (1) on each patch with diffusion rates \( d_i \) and growth functions \( f_i = f_i(u_i) \) on patch \( i \). At the interface, the matching conditions are
\[ u_1(x_1^+, t) = k \ u_2(x_1^-, t) \]
\[ d_1 u_1(x_1^+, t) = d_2 u_2(x_1^-, t), \]

where \( k \) is a parameter that encapsulates individual movement behavior and patch preference at the interface. Superscripts \( \pm \) denote the one-sided limits from the right and left, respectively. We write \( \alpha \in (0, 1) \) for the probability that an individual at the interface chooses to move to patch 1 and \( 1 - \alpha \) for the probability that it moves to patch 2. Then we have the explicit expression (Ovaskainen and Cornell, 2003; Maciel and Lutscher, 2013)

\[ k = \frac{\alpha \ d_2}{1 - \alpha \ d_1}. \]

Thus, densities are discontinuous at interfaces in the presence of patch preference (i.e. \( \alpha \neq 0.5 \)) and/or when diffusion rates in the two patches are different. This discontinuity and its dependence on movement behavior turns out to be crucial to basic quantities such as population persistence conditions and spread rates in periodic environment in the absence (Maciel and Lutscher, 2013) or presence (Maciel and Lutscher, 2015) of Allee effects. More recently, Maciel and Lutscher (2018) showed how different movement strategies for competing species in patchy landscapes can lead to different outcomes of the competition. Here, we study how the outcome of competition feeds back to the evolution of movement strategies in patchy landscapes.

In this work, we consider a landscape of two patch types. We model movement and growth through reaction-diffusion equations in a patchy landscape and include interface conditions as above. A movement strategy is given by the diffusion rates in each patch type \( (d_i) \) as well as the patch preference \( (\alpha) \). We seek evolutionarily stable strategies using two distinct approaches. First, we consider an infinite periodic landscape in which patches of the two types alternate. Our analysis of this case is based on a recently derived homogenization technique for these type of models. In the limit of small-scale heterogeneity, this technique allows us to transform a spatial problem in heterogeneous space into a problem in homogeneous space where diffusion and growth are given by certain spatial averages. The standard framework of adaptive dynamics can then be applied to the homogenized model. Secondly, we consider a landscape of only two patches. We consider this scenario as one period of the infinite landscape. We study this case by deriving the ideal-free distribution (IFD) and determining its stability analytically. We find that both approaches lead to the same result that ideal-free strategies are indeed evolutionarily stable.
2 The model

We model population dynamics of a ‘resident’ and an ‘invader’ (‘mutant’) in a one-dimensional patchy landscape consisting of two types of patches, denoted by Ω_i, with i = 1, 2. On patch (type) i, we denote by u_i the density of the resident population and by u'_i the density of the invader/mutant. In patch type i, these populations have diffusion rates d_i, d'_i, respectively. For population dynamics, we assume logistic growth and Lotka-Volterra competition, and – as indicated above – we assume that resident and invader are identical with respect to these dynamics. Hence, our system of equations for x ∈ Ω_i is

\[ u_{it} = d_i u_{ixx} + r_i u_i (1 - (u_i + u'_i)/K_i), \]

\[ u'_{it} = d'_i u'_{ixx} + r_i u'_i (1 - (u'_i + u_i)/K_i). \]

Parameters \( r_i, K_i \) are assumed positive.

For interface behavior, we denote by \( \alpha (\alpha') \) the probability with which a resident (invader) moves into the patch of type 1 at an interface. Thus, at an interface point with patch type 1 on the right and type 2 on the left, we choose the conditions in (2)-(3) with \( k \) given by (4). At points where patch type 1 is to the left and type 2 to the right, the same conditions apply with the signs denoting the directions of the one-sided limits in (2)-(3) exchanged. The matching conditions for the invader have \( \alpha \) replaced by \( \alpha' \) and \( d_i \) by \( d'_i \).

For our first approach, we divide the real line into periodically alternating patches of type i with length \( l_i \) and period \( l = l_1 + l_2 \). Accordingly, type-1 patches may be taken as \( \Omega_1 = \{x ∈ (nl, nl + l_1)|n ∈ \mathbb{Z}\} \) and type-2 patches as \( \Omega_2 = \{x ∈ (nl + l_1, (n + 1)l)|n ∈ \mathbb{Z}\} \). The interface points \( x_m = nl \ (n ∈ \mathbb{Z}) \) have a type-1 patch to the right whereas the interface points \( x_m = nl + l_1 \ (n ∈ \mathbb{Z}) \) have a type-2 patch on the right.

For our second approach, we take \( \Omega_1 = (0, l_1) \) and \( \Omega_2 = (-l_2, 0) \). The interface \( x = 0 \) has the type-1 patch to the right. At the boundary points \( l_1 \) and \( -l_2 \), we impose no-flux conditions \( u_{1x}(l_1, t) = u_{2x}(-l_2, t) = 0 \). This set-up is equivalent to a periodic setting with patches of length 2\( l_1 \) and 2\( l_2 \).

Our main goal is to determine dispersal strategies, in terms of diffusion rates and patch preference, that are evolutionarily stable. Evolutionarily stable strategies are characterized by the property that a population using such a strategy cannot be invaded by any small population using a different strategy. We present some analytical preliminaries for the second approach in the next section. In Section 4, we begin with the infinite landscape and use the homogenization approach. In Section
5, we consider to the bounded landscape and present exact stability and invasion
conditions. We collect the proofs for the latter case in Section 6. We close with a
discussion of biological implications.

3 Analytical preliminaries

Before we turn to the exploration of trait evolution, we need to provide some an-
alytical results, such as a maximum and comparison principle, the existence of a
dominant eigenvalue as well as existence and uniqueness of solutions in appropriate
function spaces for our model. We begin with the following maximum principle.

Proposition 3.1 Suppose that smooth functions $u_i$ satisfy the inequalities
\begin{align}
 u_{1t} & \geq d_1 u_{1xx} + a_1(x,t) u_1, & 0 \leq x \leq l_1, \\
 u_{2t} & \geq d_2 u_{2xx} + a_2(x,t) u_2, & -l_2 \leq x \leq 0,
\end{align}
with smooth functions $a_i$ for $0 < t \leq T^*$ and with boundary and interface conditions
$$u_{2x}(-l_2,t) = 0 = u_{1x}(l_1,t), \quad u_{1}(0^+,t) = kw_2(0^-,t), \quad d_1 u_{1x}(0^+,t) = d_2 u_{2x}(0^-,t),$$
where $k > 0$. Suppose further that $u_i(x,0) \geq 0$. Then $u_i(x,t) \geq 0$ for $0 < t \leq T^*$. Furthermore, if $u_i(x,0) > 0$ for at least one $i$, then $u_i(x,t) > 0$ for $i = 1, 2$ and
$0 < t \leq T^*$.

We provide the proof in Section 6. From this proposition, we immediately obtain
the following comparison principle.

Proposition 3.2 Suppose that smooth functions $u_i, v_i$ satisfy the inequalities
\begin{align}
 u_{1t} & \geq d_1 u_{1xx} + f_1(x,u_1), & 0 \leq x \leq l_1, \\
 u_{2t} & \geq d_2 u_{2xx} + f_2(x,u_2), & -l_2 \leq x \leq 0,
\end{align}
and
\begin{align}
 v_{1t} & \leq d_1 v_{1xx} + f_1(x,v_1), & 0 \leq x \leq l_1, \\
 v_{2t} & \leq d_2 v_{2xx} + f_2(x,v_2), & -l_2 \leq x \leq 0,
\end{align}
for $0 < t \leq T$ with boundary and interface conditions (9) for both $u_i$ and $v_i$. Suppose
further that $u_i(x,0) \geq v_i(x,0)$. Then $u_i(x,t) \geq v_i(x,t)$ for $0 < t \leq T$. 

6
The proof of this proposition follows from Proposition 3.1 as in the classical case. We set \( w_i = u_i - v_i \). Then
\[
w_{it} \geq d_i w_{ixx} + f_i(x, u_i) - f_i(x, v_i) = d_i w_{ixx} + g_i(x) w_i,
\]
where \( g_i \) are functions that depend on \( u_i, v_i \) and \( \partial f_i / \partial u_i \). By Proposition 3.1 we have \( w_i \geq 0 \) for \( 0 < t \leq T \) since \( w_i(x, 0) \geq 0 \). \hfill \blacksquare

We now move to the time-independent problem
\[
\begin{align*}
-d_1 u_{1xx} + c_1 u_1 &= f_1, & 0 \leq x \leq l_1, \\
-d_2 u_{2xx} + c_2 u_2 &= f_2, & -l_2 \leq x \leq 0,
\end{align*}
\]
with \( d_1 u_1(0) = d_2 u_2(0), \ u_1(0) = k u_2(0), \ u_{1x}(l_1) = 0 = u_{2x}(-l_2). \) \( (16) \)

**Proposition 3.3** Suppose \( u_i \) solve \((14)-(16)\) with \( c_i > 0 \) and \( f_i \geq 0 \). Then \( u_i > 0 \).

We give the proof of this proposition in Section 6.

**Proposition 3.4** Suppose \( c_i > 0 \). Given \( f_1 \in C([0, l_1]) \) and \( f_2 \in C([-l_2, 0]) \), there is a unique solution \( u_1 \in C^2([0, l_1]) \) and \( u_2 \in C^2([-l_2, 0]) \) of \((14)-(16)\) with
\[
\|u_1\|_{C^2([0, l_1])} + \|u_2\|_{C^2([-l_2, 0])} \leq C \left( \|f_1\|_{C([0, l_1])} + \|f_2\|_{C([-l_2, 0])} \right). \]

The proof of this proposition can also be found in Section 6.

We are now ready to prove the existence of a principal eigenvalue that will be important in the analysis of trait evolution.

**Proposition 3.5** The operator defined by the left-hand sides of \((14)\) and \((15)\) and the boundary and interface conditions \((16)\) has a principal eigenvalue with positive eigenfunction.

The proof follows from the previous results. Assume at first that \( c_i(x) > 0 \). By Proposition 3.4, the solution operator of \((14)-(16)\) defines a continuous mapping from \( C([0, l_1]) \times C([-l_2, 0]) \) into \( C^2([0, l_1]) \times C^2([-l_2, 0]) \), which, when combined with the compact embedding of \( C^2 \) into \( C \) gives a compact mapping from \( C([0, l_1]) \times C([-l_2, 0]) \) into itself. By Proposition 3.3, this mapping is strongly positive. Hence, by the Krein-Rutman theorem (Du, 2006), the operator has a positive principal eigenvalue with positive eigenfunction.

If \( c_i \) are not positive, we pick a large enough constant \( q > 0 \) and solve instead the problem
\[
\begin{align*}
-d_1 u_{1xx} + (c_1 + q) u_1 &= (\lambda + q) u_1 = \tilde{\lambda} u_1, & 0 \leq x \leq l_1, \\
-d_2 u_{2xx} + (c_2 + q) u_2 &= (\lambda + q) u_2 = \tilde{\lambda} u_2, & -l_2 \leq x \leq 0,
\end{align*}
\]
with conditions \((16)\). When \( c_i + q > 0 \), the previous reasoning applies, and a principal eigenvalue \( \lambda > 0 \) exists. We find that \( \lambda = \tilde{\lambda} - q \) need not be positive. \hfill \blacksquare
4 Homogenization analysis

Our first approach to the problem is based on homogenization. We assume that the habitat consists of two types of patches that are alternating periodically in one-dimensional space. We then assume that the period is small and use an asymptotic expansion. To lowest order, we obtain a spatially homogeneous averaged model that can be analyzed with simple standard tools from the theory of adaptive dynamics (Geritz et al., 1998).

As described above, the two types of patches are arranged as

\[ \Omega_1 = \{ x \in [nl, nl + l_1] | n \in \mathbb{Z} \} \quad \text{and} \quad \Omega_2 = \{ x \in [nl + l_1, (n + 1)l] | n \in \mathbb{Z} \}. \]

The dynamic equations are given by (5)-(6) and the interface conditions are as explained in Section 2.

To simplify notation, it is convenient to define a function \( u(x, t) \) for \( x \in \mathbb{R} \) as \( u(x, t) = u_i(x, t) \) on \( \Omega_i \). Similarly, it is convenient to think of the diffusion coefficients as piecewise constant functions \( d = d(x) \) with values \( d(x) = d_i \) for \( x \in \Omega_i \). In the same way, we can write the reaction terms as \( f(x, u, u') \) according to the right hand terms in (5)-(6). Analogous definitions can be made for \( u'(x, t), d'(x) \) and \( f' \). Then formally, the densities satisfy the equations

\[
\begin{align*}
    u_t &= [d(x)u(x, t)]_{xx} + f(x, u, u'), \\
    u'_t &= [d'(x)u'(x, t)]_{xx} + f'(x, u, u'),
\end{align*}
\]

with the interface conditions to hold at the points of discontinuity of the coefficient functions.

The technique of homogenization (Othmer, 1983; Garlick et al., 2011) assumes that the spatial scale of observation is much larger than the scale of habitat heterogeneity. We choose \( l = \epsilon \ll 1 \) as the small parameter, and assume the existence of two distinct spatial scales, \( \xi = x \) and \( y = x/\epsilon \). Variable \( \xi \) is termed the “slow” and \( y \) the “fast” scale. Diffusion and growth are assumed to depend on the fast scale only, i.e. \( d = d(y) \) and \( f = f(y, u, u') \), while population density is a function of both scales, \( u = u(\xi, y, t) \).

The discontinuities in the coefficient functions prevent us from applying the classical homogenization theory (Othmer, 1983), but recent progress has extended the theory to the single-species version of the model in (20) with interface conditions (2)-(3), see Yurk and Cobbold (2018). Applications of this technique to competition and age-structured models show that these asymptotic methods work very well (Maciel and Lutscher, 2018; Alqawasmeh and Lutscher, submitted). We briefly explain the main steps of the method using only the equation for \( u \) in (20) and setting \( u' = 0 \). For details, please see Yurk and Cobbold (2018).
To obtain the homogenization equations, we write the population density as a series expansion in \( \epsilon \),

\[ u(\xi, y, t) = \sum \epsilon^i u^{(i)}(\xi, y, t) \]

Substituting this series into (20), we obtain equations for the different orders of \( \epsilon \), again satisfying corresponding matching conditions at interface points. The lowest-order term can be written as (Yurk and Cobbold, 2018)

\[
u^{(0)}(\xi, y, t) = \frac{w(\xi, t)}{h(y)}, \tag{21}\]

with

\[ h(y) = \begin{cases} 1 & \text{if } y \in \tilde{\Omega}_1 = \Omega_1/\epsilon, \\ k & \text{if } y \in \tilde{\Omega}_2 = \Omega_2/\epsilon. \end{cases} \tag{22}\]

The numerator, \( w(\xi, t) \), is a function of time and the slow scale only, so that it solves the equation

\[ w_t = \hat{l}^2 \langle d \rangle_H \hat{w} + \langle f \rangle_A, \tag{23}\]

where \( \hat{l} = (l_1 + l_2)/(l_1 + l_2/k) \) is a weighted average of the patch lengths, and \( \langle d \rangle_H \) and \( \langle f \rangle_A \) are the harmonic mean of diffusion and arithmetic mean of growth, explicitly given by

\[ \langle d \rangle_H = \left( \frac{l_1 + l_2/k}{\frac{l_1}{l_1} + \frac{l_2/k}{l_2/k}} \right), \quad \langle f \rangle_A = \left[ \frac{l_1 f_1(w) + l_2 f_2(w/k)}{l_1 + l_2/k} \right]. \tag{24}\]

Recall that \( f_i(u) = f(x, u) \), with \( x \in \Omega_i \), is the population growth function in \( \Omega_i \).

Thus, at small scale heterogeneity, the solution of the first equation in (20) is approximated by the leading term (21). Its time evolution is completely determined by \( w(\xi, t) \), which satisfies the “homogenized equation” (23).

The exact same procedure applies directly to the competition equations in (5)-(6). The resident \((u)\) leading term is given by (21), with \( w(\xi, t) \) and \( h(y) \) obtained from (23) and (22). The only modification arises in the average growth rate where the interaction term with the invader \((u')\) must be considered. We thus have

\[ \langle f \rangle_A = \left[ \frac{l_1 f_1(w, w') + l_2 f_2(w/k, w'/k')}{l_1 + l_2/k} \right], \tag{25}\]

where \( k' = d_{1,2}'' \alpha'/[d_1''(1 - \alpha')] \) is the composite parameter that defines the density jump of the invader at an interface. We obtain similar equations for the invader substituting \( w', k', f_1', f_2' \), and \( d_{1,2}'' \) for \( w, k, f_1, f_2 \) and \( d_{1,2} \). For a more detailed application of this homogenization method to systems of equations, please see Maciel and Lutscher (2018); Alqawasmeh and Lutscher (submitted).
This procedure applied to equations (5)-(6) leads to the following homogenized equations with the averaged growth and competition coefficients written explicitly in terms of the original model parameters.

\[
\begin{align*}
    w_t &= \hat{\epsilon}^2 \langle d \rangle_H w_{\xi \xi} + \left( \frac{r_1 l_1 + r_2 l_2 / k}{l_1 + l_2 / k} \right) w \left[ 1 - \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k^2 K_2)}{r_1 l_1 + r_2 l_2 / k} \right) w \right], \\
    w'_t &= \hat{\epsilon}^2 \langle d' \rangle_H w'_{\xi \xi} + \left( \frac{r_1 l_1 + r_2 l_2 / k'}{l_1 + l_2 / k'} \right) w' \left[ 1 - \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k'^2 K_2)}{r_1 l_1 + r_2 l_2 / k'} \right) w' \right].
\end{align*}
\]

This homogenized competition system contains no spatial variation. In the case of spatially homogeneous Lotka-Volterra competition systems for two competitors, if one of the competitors excludes the other in the model without diffusion, then the same is true for the corresponding model with diffusion on the real line. This follows from Theorem 4.4 of Weinberger et al. (2002) after a suitable change of coordinates. Hence, we study the non-spatial dynamics of the preceding model. It turns out that the analysis is simplified by the rescaling

\[
v = \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k^2 K_2)}{r_1 l_1 + r_2 l_2 / k} \right) w, \quad v' = \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k'^2 K_2)}{r_1 l_1 + r_2 l_2 / k'} \right) w',
\]

which leads to the system

\[
\begin{align*}
    \frac{dv}{dt} &= r \ v \ (1 - v - av') \\
    \frac{dv'}{dt} &= r' \ v' \ (1 - v' - a'v'),
\end{align*}
\]

with coefficients.
\[ r = \left( \frac{r_1 l_1 + r_2 l_2 / k}{l_1 + l_2 / k} \right), \quad r' = \left( \frac{r_1 l_1 + r_2 l_2 / k'}{l_1 + l_2 / k'} \right), \quad \text{(31)} \]

\[ a = \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k' k K_2)}{r_1 l_1 / K_1 + r_2 l_2 / (k'^2 K_2)} \right), \quad a' = \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k' k K_2)}{r_1 l_1 / K_1 + r_2 l_2 / (k'^2 K_2)} \right), \quad \text{(32)} \]

\[ a' = \left( \frac{r_1 l_1 / K_1 + r_2 l_2 / (k' k K_2)}{r_1 l_1 / K_1 + r_2 l_2 / (k'^2 K_2)} \right), \quad \text{(33)} \]

It is straightforward to analyze the rescaled system according to the procedures of adaptive dynamics (Geritz et al., 1998). The resident-only steady state is \( v = 1, v' = 0 \). The initial invasion dynamics of a small invader population \( v' \) are governed by

\[ \frac{dv'}{dt} = r' (1 - a') v', \quad \text{so that} \quad v' \propto e^{r'(1-a')t}. \quad \text{(34)} \]

We note that the competition between resident and invader depend only on the composite parameters \( k \) and \( k' \) and not on the preference and diffusion parameters individually. This fact simplifies our analysis considerably since the adaptive dynamics become a one-dimensional problem in the ‘trait value’ \( k \). The invasion exponent of a potential invader with trait \( k' \) at small density in an established resident with trait \( k \) is given by

\[ s(k, k') = r' (1 - a'). \quad \text{(35)} \]

The ‘canonical equation of adaptive dynamics’ (Geritz et al., 1998) describes the change of the trait \( k \) over evolutionary time \( (T) \) via the selection gradient as

\[ \frac{d}{dT} k = \frac{\partial s(k, k')}{\partial k'} \big|_{k'=k}. \]

The calculation of the selection gradient

\[ \frac{\partial s}{\partial k'} \big|_{k'=k} = \frac{dv'}{dk'} (1 - a') \big|_{k'=k} - r' \frac{\partial a'}{\partial k'} \big|_{k'=k} \]

is simplified by the fact that \( a'(k, k) = 1 \). Furthermore, after a somewhat tedious calculation, we find that the sign of the selection gradient is given by

\[ \text{sign} \left( \frac{\partial s}{\partial k'} \big|_{k'=k} \right) = -\text{sign} \left( \frac{\partial a'}{\partial k'} \big|_{k'=k} \right) = -\text{sign} \left( k - \frac{K_1}{K_2} \right). \]

Therefore, the evolutionarily singular strategy

\[ k = \frac{K_1}{K_2}. \quad \text{(35)} \]
where the selection gradient vanishes, is an evolutionarily stable strategy (ESS) that can invade its neighbors and to which the adaptive dynamics will converge.

With this expression for the ESS, we return to the non-spatial system (29)-(30). Species \( v \) can invade at \((0, 1)\) if and only if \( a < 1 \). Vice versa, \( v' \) can invade at \((1, 0)\) if and only if \( a' < 1 \). Stable coexistence is possible if and only if \( a, a' < 1 \). If species \( v \) uses the singular strategy (i.e., \( k = \bar{k} \)), one finds that \( a \leq 1 \) with equality only if \( k' = k \) as well. It is straightforward to see that \( a' = 1 \) if \( k = \bar{k} \). In that case, coexistence requires \( a = 1 \), i.e., \( k' = \bar{k} \), so that the two have to be identical. Hence, if \( v \) uses the ESS then it will invade all strategies that are different from the ESS and go to fixation, i.e., dynamically exclude the other strategy.

In summary, when the patches are small compared to the dispersal ability, averaging allows us to reduce the problem in the heterogeneous landscape to a homogeneous system, that, in turn, simplifies to an ODE problem for the question that we want to answer. The adaptive dynamics for the movement parameters \( d_i, \alpha \) reduces to the dynamics of the single trait value \( k \), the combined behavior at an interface. The result then predicts that \( k \) should evolve to \( \bar{k} \). In the next section, we explain how this value of \( k \) represents an ideal-free distribution (IFD) in the full model.

5 Steady-state analysis

We now move to the steady-state analysis of the model in a heterogeneous landscape. We first identify the IFD for a single species in this case and then study its stability. Since the landscape is periodic, we study the problem on a single period only. Hence, we denote \( \Omega_1 = [0, l_1], \Omega_2 = [-l_2, 0] \). We have the equations

\[
\begin{align*}
\frac{d_1}{dt} u_1 &= d_1 u_{1xx} + r_1 u_1 (1 - u_1 / K_1), \quad \text{in } \Omega_1, \\
\frac{d_2}{dt} u_2 &= d_2 u_{2xx} + r_2 u_2 (1 - u_2 / K_2), \quad \text{in } \Omega_2,
\end{align*}
\]

(36) (37)

together with the boundary conditions

\[
\begin{align*}
u_1(0^+, t) &= k u_2(0^-, t), & d_1 u_{1x}(0^+, t) &= d_2 u_{2x}(0^-, t), \\
u_1(l_1^-, t) &= k u_2(-l_2^+, t), & u_{1x}(l_1^-, t) &= 0 = u_{2x}(-l_2^+, t).
\end{align*}
\]

(38) (39)

We provide a proof for the global existence of unique solutions to this system (in fact, to the system with the two competing populations) in the appendix.
We denote a candidate for an IFD by $u_{1,2}$. As individual fitness must be zero at the IFD (see introduction), the only candidate for (36) and (37) is the piecewise constant function $u_i = K_i$ for $x \in \Omega_i$.

Consequently, at an IFD the population matches the carrying capacity in each habitat patch. The piecewise constant equilibrium $u_{1,2}$ must also satisfy boundary conditions (38)-(39). Values of the composite parameter $k$ for which this is possible may be termed the ‘ideal-free dispersal strategies’. The only possible choice is

$$
\bar{k} = \frac{K_1}{K_2}.
$$

(40)

Hence, the ideal-free dispersal strategies are exactly the same as the ones that emerged from the adaptive dynamics approach in the previous section.

In the following we investigate whether $\bar{k}$ is an ESS for the non-homogenized equations as well. First, we show that a population using this strategy cannot coexist at steady state with any other population using a different strategy. Second, we will show that a population using the ideal-free strategy will be able to invade from low density any population using a different strategy.

The steady-state densities of a resident $\phi_{1,2}(x)$ and a mutant $\phi'_{1,2}(x)$ of equations (5)-(6) satisfy the equations

$$
d_1 \phi_{1,2,xx} + r_1 \phi_{1,2} (1 - (\phi_{1,2} + \phi'_{1,2})/K_1) = 0
$$

(41)

$$
d_1 \phi'_{1,2,xx} + r_1 \phi'_{1,2} (1 - (\phi'_{1,2} + \phi_{1,2})/K_1) = 0 \text{ in } \Omega_1
$$

(42)

and

$$
d_2 \phi_{2,xx} + r_1 \phi_2 (1 - (\phi_2 + \phi'_{2})/K_2) = 0
$$

(43)

$$
d_2 \phi'_{2,xx} + r_1 \phi'_{2} (1 - (\phi'_{2} + \phi_2)/K_2) = 0 \text{ in } \Omega_2,
$$

(44)

together with the periodic boundary conditions (38)-(39), with $k$ and $d_{1,2}$ substituted by $k'$ and $d'_{1,2}$ in the mutant’s equations.

**Theorem 5.1** Let $\phi_{1,2}(x)$ and $\phi'_{1,2}(x)$ be positive solutions of (41)-(44) with boundary conditions as described and parameters $k, k'$, respectively. If $k = \bar{k} = K_1/K_2$, $\phi_i$ and $\phi'_i$ are constant on $\Omega_i$ and $k' = \bar{k}$.

13
Proof. Dividing (41) and (43) by \( \phi_1/K_1 \) and \( \phi_2/K_2 \), respectively, and integrating over space, we get

\[
\int_0^{l_1} \left[ d_1 K_1 \frac{\phi_{1xx}}{\phi_1} + r_1 K_1 \left( 1 - \frac{\phi_1 + \phi_1'}{K_1} \right) \right] dx \\
+ \int_{-l_2}^{0} \left[ d_2 K_2 \frac{\phi_{2xx}}{\phi_2} + r_2 K_2 \left( 1 - \frac{\phi_2 + \phi_2'}{K_2} \right) \right] dx = \\
\int_0^{l_1} \left[ d_1 K_1 \frac{\phi_{1x}^2}{\phi_1^2} + r_1 K_1 \left( 1 - \frac{\phi_1 + \phi_1'}{K_1} \right) \right] dx \\
+ \int_{-l_2}^{0} \left[ d_2 K_2 \frac{\phi_{2x}^2}{\phi_2^2} + r_2 K_2 \left( 1 - \frac{\phi_2 + \phi_2'}{K_2} \right) \right] dx = 0, \quad (45)
\]

where we have integrated by parts and used boundary conditions, with \( k = \overline{k} \).

Integrating equations (41) and (43) directly, we obtain

\[
\int_0^{l_1} d_1 \phi_{1xx} + r_1 \phi_1 \left( 1 - \frac{\phi_1 + \phi_1'}{K_1} \right) dx + \int_{-l_2}^{0} d_2 \phi_{2xx} + r_2 \phi_2 \left( 1 - \frac{\phi_2 + \phi_2'}{K_2} \right) dx = \\
\int_0^{l_1} r_1 \phi_1 \left( 1 - \frac{\phi_1 + \phi_1'}{K_1} \right) dx + \int_{-l_2}^{0} r_2 \phi_2 \left( 1 - \frac{\phi_2 + \phi_2'}{K_2} \right) dx = 0. \quad (46)
\]

Similarly, the integrals of (42) and (44) result in

\[
\int_0^{l_1} r_1 \phi_1' \left( 1 - \frac{\phi_1 + \phi_1'}{K_1} \right) dx + \int_{-l_2}^{0} r_2 \phi_2' \left( 1 - \frac{\phi_2 + \phi_2'}{K_2} \right) dx = 0. \quad (47)
\]

We now subtract (46) and (47) from (45) to derive the expression

\[
\int_0^{l_1} d_1 K_1 \frac{\phi_{1x}^2}{\phi_1^2} dx + \int_0^{l_1} r_1 K_1 \left( 1 - \frac{\phi_1 + \phi_1'}{K_1} \right)^2 dx \\
+ \int_{-l_2}^{0} D_2 K_2 \frac{(\phi_{2x})^2}{\phi_2^2} dx + \int_{-l_2}^{0} r_2 K_2 \left( 1 - \frac{\phi_2 + \phi_2'}{K_2} \right)^2 dx = 0. \quad (48)
\]

Since all integrand functions are positive, they must cancel individually. We thus have

\[
\phi_{ix} = 0, \quad \phi_i + \phi_i' = K_i \quad \text{in} \quad \Omega_i, \quad i = 1, 2. \quad (49)
\]

In particular, \( \phi_i, \phi_i' \) are constant on \( \Omega_i \).

Then we can write \( \phi_1 = s \) and \( \phi_2 = s/\overline{k} = sK_2/K_1 \). Conditions (49) then give

\[
\phi_1' = K_1 - s \quad \text{and} \quad \phi_2' = K_2(K_1 - s)/K_1. \quad \text{Hence,} \quad k' = \phi_1'/\phi_2' = K_1/K_2 = \overline{k}. \quad \text{Thus, we}
\]
have shown that if the resident employs the ideal-free movement strategy \( k = \overline{k} \), a nontrivial coexistence steady state with a mutant occurs only if the mutant uses the same strategy \( k' = \overline{k} \). ■

We consider now the invasibility problem of a rare population using the ideal-free movement strategy on an established population using a different strategy. We write \( \phi'_{1,2}(x) \) for the steady-state density of the established population and \( k' \) for its strategy as above. It satisfies equations (42) and (44) with \( \phi_1 = 0 \). The growth rate of a rare population in the presence of \( \phi'_{1,2} \) is determined from the eigenvalue problem (Cantrell and Cosner, 2003)

\[
\begin{align*}
d_1u_{1xx} + r_1(1 - \phi_1'/K_1)u_1 &= \sigma u_1 \quad \text{in } \Omega_1, \\
d_2u_{2xx} + r_2(1 - \phi_2'/K_2)u_2 &= \sigma u_2 \quad \text{in } \Omega_2,
\end{align*}
\]

with periodic boundary conditions as in (38)-(39) and parameter \( k = \overline{k} \).

**Theorem 5.2** Under the above assumptions and conditions, we have \( \sigma > 0 \).

**Proof.** Dividing (50) and (51) respectively by \( u_1/K_1 \) and \( u_2/K_2 \), and integrating over space, we have

\[
\begin{align*}
\int_0^{l_1} \left[ d_1K_1 \frac{u_{1xx}}{u_1} + r_1K_1 \left(1 - \frac{\phi_1'}{K_1}\right) \right] dx &= l_1K_1\sigma, \\
\int_{-l_2}^{0} \left[ d_2K_2 \frac{u_{2xx}}{u_2} + r_2K_2 \left(1 - \frac{\phi_2'}{K_2}\right) \right] dx &= l_2K_2\sigma.
\end{align*}
\]

Integrating by parts and using boundary conditions (38) and (39), with \( k = \overline{k} = K_1/K_2 \), we find

\[
\begin{align*}
\int_0^{l_1} d_1K_1 \frac{(u_{1x})^2}{u_1} dx + \int_0^{l_1} r_1K_1 \left(1 - \frac{\phi_1'}{K_1}\right) dx \\
+ \int_{-l_2}^{0} d_2K_2 \frac{(u_{2x})^2}{u_2} dx + \int_{-l_2}^{0} r_2K_2 \left(1 - \frac{\phi_2'}{K_2}\right) dx &= (l_1K_1 + l_2K_2)\sigma.
\end{align*}
\]

The steady steady \( \phi'_{1,2}(x) \), in turn, is determined from the system

\[
\begin{align*}
d_1\phi_{1xx} + r_1\phi_1'(1 - \phi_1'/K_1) &= 0, \quad \text{in } \Omega_1, \\
d_2\phi_{2xx} + r_2\phi_2'(1 - \phi_2'/K_2) &= 0, \quad \text{in } \Omega_2.
\end{align*}
\]
Integrating and summing the equations, we get
\[
\int_0^{l_1} r_1 \phi'_1 \left( 1 - \frac{\phi'_1}{K_1} \right) \, dx + \int_0^{l_2} r_2 \phi'_2 \left( 1 - \frac{\phi'_2}{K_2} \right) \, dx = 0. \tag{57}
\]

Finally, we subtract (57) from (54) and obtain
\[
\sigma = \frac{1}{l_1 K_1 + l_2 K_2} \left[ \int_0^{l_1} d_1 K_1 \left( \frac{u_{1x}}{u_1} \right)^2 \, dx + \int_0^{l_1} r_1 K_1 \left( 1 - \frac{\phi'_1}{K_1} \right)^2 \, dx 
+ \int_{-l_2}^0 D_2 K_2 \left( \frac{u_{2x}}{u_2} \right)^2 \, dx + \int_{-l_2}^0 r_2 K_2 \left( 1 - \frac{\phi'_2}{K_2} \right)^2 \, dx \right] \geq 0. \tag{58}
\]

The inequality is strict if at least one of the integrals is not zero. If the established population \( \phi'_i \) does not use the ideal-free strategy, then at least one of the integrals involving \( \phi'_i \) must be positive. Thus, a rare population using the ideal-free movement strategy can always invade a population using any other movement strategy at steady state. \( \blacksquare\)

6 Proofs

In this section, we provide the proofs of the analytical preliminaries from Section 3.

6.1 Proof of Proposition 3.1

First we note that, as in the classical maximum principle, we can assume functions \( a_i \) to be of any sign. The new variables \( \tilde{u}_i = e^{\gamma t} u_i \) satisfy the same equations as \( u_i \) with \( a_i \) replaced by \( a_i + \gamma \) and the same boundary and interface conditions.

Secondly, for \( \varepsilon > 0 \) we define
\[
v_1 = u_1 + k \varepsilon e^t, \quad v_2 = u_2 + \varepsilon e^t.
\]

Then \( v_i(x, 0) > 0 \) and \( v_i \) satisfy (7)-(8) with strict inequalities, as well as the boundary and interface conditions (9).

Now suppose that \( v_i(x, t) \leq 0 \) for some \( i \), some \( x \in [-l_2, 0] \cup [0, l_1] \) and \( t \leq T \), and define
\[
t_0 = \sup \{ 0 < t \leq T : v_i(x, t) > 0, \, x \in [-l_2, 0] \cup [0, l_1], \, i = 1, 2 \} > 0.
\]

Then there exists some \( x_0 \in [-l_2, 0] \cup [0, l_1] \) with \( v_1(x_0, t_0) = 0 \) or \( v_2(x_0, t_0) = 0 \) and \( v_i \geq 0 \) for \( t \leq t_0, \, x \in [-l_2, 0] \cup [0, l_1] \). We distinguish two cases.
If \( x_0 \in (-l_2, 0) \) or \( x \in (0, l_1) \), then \( v_{it}(x_0, t_0) \leq 0 \) and \( v_{ixx}(x_0, t_0) \geq 0 \) but \( v_{it}(x_0, t_0) - v_{ixx}(x_0, t_0) > 0 \) by assumption. Hence, we have a contradiction as in the classical maximum principle.

If \( x_0 = 0 \), then \( v_i(0, t_0) = kv_2(0, t_0) = 0 \). However, since \( v_i \geq 0 \), for \( x \in (-l_2, 0) \cup (0, l_1) \), we have \( v_{1x}(0, t_0) \geq 0 \) and \( v_{2x}(0, t_0) \leq 0 \). By the interface condition, we find \( v_{1x}(0, t_0) = 0 = v_{2x}(0, t_0) \).

Now, if \( v_1(x, t_0) > 0 \) on some interval \((0, \delta)\) then \( v_{1x}(0, t_0) > 0 \), and similarly if \( v_2(x, t_0) > 0 \) on some interval \((-\delta, 0)\) then \( v_{2x}(0, t_0) < 0 \), which is a contradiction.

Hence, we must have \( v_1(x, t_0) = 0 \) somewhere in \((0, l_1)\) and also \( v_2(x, t_0) = 0 \) somewhere in \((-l_2, 0)\). But then by the classical maximum principle, we have \( v_1 = v_2 = 0 \) for \( 0 < t \leq t_0 \). This is another contradiction.

The remaining two cases \( x_0 = -l_2 \) and \( x_0 = l_1 \) are treated in the same way. Hence, we must have \( u_i > 0 \) for all \( \varepsilon > 0 \), we find \( u_i \geq 0 \) for \( i = 1, 2 \), \( x \in [-l_2, 0] \cup [0, l_1] \) and \( 0 < t \leq T \).

Finally, assume that \( u_i \neq 0 \) for \( t = 0 \) but \( u_i(x_0, t_0) = 0 \) for some \( i = 1, 2 \), \( x_0 \in [-l_2, 0] \cup [0, l_1] \) and \( 0 < t \leq T \). Then, by the strong maximum principle \( u_i \equiv 0 \) for \( 0 < t \leq t_0 \), which is a contradiction. Hence, we must have \( u_i > 0 \) for all \( i = 1, 2 \), \( x \in [-l_2, 0] \cup [0, l_1] \) and \( 0 < t \leq T \).

6.2 Proof of Proposition 3.3

If \( u_1 \) has a negative minimum on \([0, l_1]\) or \( u_2 \) on \([-l_2, 0]\) then it must occur at \(-l_2, 0\) or \( l_1 \) by the classical maximum principle. Suppose that a negative minimum occurs at \(-l_2\). Then either \( u_2 \equiv \text{const} < 0 \) or \( u_{2x}(-l_2) > 0 \). By the boundary condition, we exclude the latter. But with the former, we find the contradiction \( 0 > c_2 u_2 = f_2 \geq 0 \).

The same argument applies for a negative minimum at \( l_1 \).

Suppose now that the minimum occurs at \( x = 0 \). Then either \( u_2 \equiv \text{const} < 0 \) or \( u_{2x}(0) < 0 \). The former case cannot occur by the same argument as above; therefore the latter holds. By the interface condition, we then find \( u_{1x}(0) < 0 \). But this means that the minimum of \( u_1 \) must occur in \((0, l_1)\), which is impossible by the previous argument. Therefore, \( u_i \geq 0 \).

Now suppose that \( f_2 \geq 0 \) and \( f_2 \neq 0 \). Then \( u_2 > 0 \) by the strong maximum principle. This implies \( u_2(0) > 0 \), so that \( u_1(0) > 0 \) as well. But then \( u_1 > 0 \) by the strong maximum principle, again.
6.3 Proof of Proposition 3.4

We begin with the time-independent problems (14) and (15) together with Neumann boundary conditions on each interval. The two problems decouple, so that each problem becomes an independent, regular Sturm–Liouville problem. Hence, we obtain solutions of

\[-d_i \ddot{u}_{i xx} + c_i \dot{u}_i = f_i\]

with Neumann boundary conditions on \([0, l_1]\) and \([-l_2, 0]\), respectively, for continuous functions \(f_i\). By the maximum principle, we have \(\min f_i < \tilde{u}_i < \max f_i\) so that \(\|\tilde{u}_i\|_\infty \leq \|f_i\|_\infty\). From the equation, we then find \(\|\tilde{u}_{ixx}\|_\infty \leq C\|f_i\|_\infty\). We can bound the first derivative from the bound of the second derivative so that we obtain the estimates

\[\|\tilde{u}_1\|_{C^2([0, l_1])} \leq C\|f_i\|_{C([0, l_1])}\quad \text{and} \quad \|\tilde{u}_2\|_{C^2([-l_2, 0])} \leq C\|f_2\|_{C([-l_2, 0])}\]

Secondly, we define \(y_1\) to be the solution of

\[-d_1 y_{1 xx} + c_1 y_1 = 0, \quad 0 \leq x \leq l_1,\]

with conditions \(y_1(l_1) = 1\), and \(y_{1 x}(l_1) = 0\). Then we have \(d_1 y_{1 xx}(l_1) = c_1(l_1) > 0\) by the differential equation, which leads to \(y_{1 x}(l_1) < 0\). Hence, near \(l_1\) we have \(y_{1 x}(x) < 0\) and \(y_1(x) > 1\). Suppose that \(y_{1 x}(x) = 0\) somewhere in \([0, l_1]\) and denote \(x_0\) as the supremum of all such \(x\). Then for \(x > x_0\), we have \(y_{1 x}(x) < 0\) and \(y_1(x) > 1\). Therefore, we find \(y_{1 xx}(x_0) \leq 0\). However, by the differential equation, \(d_1 y_{1 xx}(x_0) = c_1(x_0)y_1(x_0) > c_1(x_0) > 0\). Hence, we have a contradiction and conclude that \(y_{1 x}(0) < 0\) and \(y_1(0) > 0\).

The same argument goes to show that \(y_2\) defined as the solution of

\[-d_2 y_{2 xx} + c_2 y_2 = 0, \quad -l_2 \leq x \leq 0,\]

with conditions \(y_2(-l_2) = 1\), and \(y_{2 x}(-l_2) = 0\) satisfies \(y_2(0) > 0\) and \(y_{2 x}(0) > 0\).

Now we define

\[u_1 = \tilde{u}_1 + a_1 y_1, \quad u_2 = \tilde{u}_2 + a_2 y_2\]

for parameters \(a_i\). Then \(u_i\) satisfy the equations (14) and (15). Furthermore, we have \(u_{1 x}(l_1) = 0\) and \(u_{2 x}(-l_2) = 0\). We claim that we can choose the parameters in such a way as to satisfy the interface conditions in (16). The conditions can be written as

\[d_1 y_{1 x}(0)a_1 - d_2 y_{2 x}(0)a_2 = 0, \quad \quad y_1(0)a_1 - ky_2(0)a_2 = k\tilde{u}_2(0) - \tilde{u}_1(0)\]
The determinant of the coefficient matrix on the left-hand side is
\[ -kd_1y_1(0)y_2(0) + d_2y_1(0)y_2(0) > 0. \]
In particular, there is a unique solution \( u_i \) that depends on \( d_i, c_i, k \) but not on \( f_i \). Therefore the solution \( u_i \) satisfies the estimate in the statement of the proposition. ■

7 Discussion

Habitat heterogeneity is ubiquitous in nature, and organisms respond to habitat variation by adjusting their movement behavior. For instance, populations can develop conditional dispersal and exhibit patch specific movement rates as well as attraction towards more favorable regions. It is critical to the persistence of the population that individuals choose 'good' movement strategies. These strategies are therefore traits subject to selection and evolution (Clobert et al., 2001b,a). The theoretical study of the evolution of dispersal is well established by now (Johnson and Gaines, 1990; McPeek and Holt, 1992; Cosner, 2014), and models based on reaction-diffusion equations in particular, have generated interesting biological results as well as challenging mathematical problems (Cantrell et al., 2006; Lou, 2008; Lou and Lutscher, 2014). Our work continues this line of inquiry by using a relatively recently established reaction-diffusion model for population dynamics in a 'patchy' landscape.

Our model reflects a landscape-ecology point of view that separates a heterogeneous landscape into patches. Within a patch, conditions are homogeneous, at interfaces between patches, they change abruptly. Individual movement behavior depends on patch quality and may include patch preference. Our model is both, easier and more difficult than previous models. It is easier to parametrize than models with continuous variation in habitat quality and movement behavior, and it allows the straightforward inclusion of empirical results on patch preference. It is more difficult because the population density is discontinuous at an interface with a prescribed jump condition so that the classical results on existence and uniqueness of solutions cannot be applied directly. We provided a proof of the well-posedness of the equations, as well as extensions of the classical maximum- and comparison principles, and the existence of a dominant eigenvalue.

We studied the evolution of dispersal in our model within an adaptive dynamics framework (Geritz et al., 1998). We used two different approaches, one via homogenization and one via steady-state analysis. Somewhat surprisingly, both approaches gave the exact same results. The three movement parameters (habitat-specific movement rates and habitat preference) combine to a single effective preference parameter.
that governs the density matching at an interface and is based on a mechanistic derivation (Ovaskainen and Cornell, 2003; Maciel and Lutscher, 2013, 2015). The adaptive dynamics identifies the optimal value $\bar{k} = K_1/K_2$ as the ESS of the system: We showed that a population with this strategy cannot be invaded by any other strategy but can invade every other strategy. It turns out that the ESS is also an IFD. This result fits into a growing awareness of a general principle (Cosner, 2014). It is somewhat remarkable that the optimal strategy $\bar{k}$ does not depend on patch sizes. This observation explains why the homogenization, which is accurate for very small patch sizes, yields the same result as the non-homogenized steady-state analysis.

Because of the mechanistic interpretation of trait $k$, we can interpret special cases of our result. If diffusivities are equal, the evolutionarily stable habitat preference is given by $\bar{\alpha} = K_1/(K_1 + K_2)$. This intermediate preference allows the population to optimally make use of space, preventing the invasion of mutant traits. On the other hand, when there is no habitat preference, i.e. $\alpha = 0.5$, the evolutionarily stable ratio of diffusion rates is $d_2/d_1 = K_1/K_2$. Selected diffusion rates in a patch are then inversely proportional to the carrying capacity in that patch. Since the inverse of the diffusion rate is proportional to the ‘residence index’ (McNair, 1982; Turchin, 1998), our result says that the time that an individual spends in a certain patch should be proportional to the carrying capacity of that patch.

Although we have assumed an explicit expression for $k$ based on specific movement characteristics, our analysis is quite general and is valid when other assumptions on movement are made. Potapov et al. (2014) derived a family of diffusion models by modelling random walks with transition probabilities, from one location to the next, that depend on conditions at the starting point, at the end point or at some position in between. In this formulation, transition probabilities from $x$ to $x \pm \Delta x$ are then written as $p = p(x \pm \theta \Delta x)$, with $\theta \in [0, 1]$. Fokker-Plank (FP), $u_t = (du)_{xx}$, and Fickian, $u_t = (du_x)_x$, diffusion equations are obtained when $\theta = 0$ and $\theta = 0.5$, respectively. When $\theta = 1$ one gets the diffusion equation $u_t = (d^2(u/dx)_x)$, which has been termed attractive dispersal (AD). In the absence of habitat preference, FP, Fickian and AD diffusion equations lead to $k = d_2/d_1$, $k = 1$ and $k = d_1/d_2$, respectively. The first case corresponds exactly to the equations we have considered (when $\alpha = 0.5$). AD results in an ESS $d_1/d_2 = K_1/K_2$, where diffusion is proportional to the carrying capacity in a patch. Yet for Fickian diffusion, an IFD can not be achieved as, unless $K_1 = K_2$, we always have $k \neq K_1/K_2$. Potapov et al. (2014) numerically determined that FP and AD are two candidates for ESS’s within this family of diffusion models, FP being selected when diffusion is decreasing with fitness and AD being selected when diffusion increases with fitness. The FP equation is
often considered to provide the best description of ecological diffusion as it agregates individuals where movement is slow (Turchin, 1998).

Acknowledgements
GAM is thankful for a postdoctoral grant from CNPq - Brazil. CC and RSC would like to acknowledge funding through the National Science Foundation of the United States (grant DMS-1514752). FL gratefully acknowledges funding from the Natural Sciences and Engineering Research Council of Canada through an individual Discovery Grant (RGPIN-2016-04759) and a Discovery Accelerator Supplement (RGPAS-2016-492872).

Appendix
In this appendix, we show the existence and uniqueness and global boundedness of solutions to our model equations on the intervals \([-l_2,0] \cup [0,l_1]\). Our proof is based on semi-group theory and closely follows the proof in Cosner (1987).

We consider the reaction-diffusion system

\[
\begin{align*}
\frac{d}{dt}u_i &= d_i u_{i xx} + (e_i - f_i u_i - g_i v_i) u_i = d_i u_{i xx} + h_i(u_i, v_i), \\
\frac{d}{dt}v_i &= D_i v_{i xx} + (E_i - F_i u_i - G_i v_i) v_i = D_i v_{i xx} + H_i(u_i, v_i),
\end{align*}
\]

for \(t \geq 0\) and

\[
x \in \begin{cases} 
[0,l_1], & i = 1, \\
[-l_2,0], & i = 2,
\end{cases} \quad (63)
\]

together with boundary and interface conditions

\[
\begin{align*}
&u_{1x}(l_1,t) = 0 = u_{2x}(-l_2,t), \quad u_1(0,t) = k v_2(0,t), \quad d_{1x}u_1(0,t) = d_{2x}u_2(0,t), \\
&v_{1x}(l_1,t) = 0 = v_{2x}(-l_2,t), \quad v_1(0,t) = K v_2(0,t), \quad D_{1x}v_1(0,t) = D_{2x}v_2(0,t).
\end{align*}
\]

All parameters are assumed positive. We begin by defining the appropriate function spaces.

Set-up of the problem
We cast the problem into the form of an abstract evolution equation

\[
\frac{d}{dt}w + Aw = F(w),
\]

(66)
where \( w = (u, v)^T \) and \( u = (u_1, u_2)^T \) and \( v = (v_1, v_2)^T \). We define operators

\[
A_u \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} -d_1 u_{1xx} \\ -d_2 u_{2xx} \end{pmatrix} \quad \text{and} \quad A_v \begin{pmatrix} v_1 \\ v_2 \end{pmatrix} = \begin{pmatrix} -D_1 v_{1xx} \\ -D_2 v_{2xx} \end{pmatrix}.
\]

Then we can write

\[
Aw = \begin{pmatrix} A_u + I \\ 0 \\ A_v + I \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} = \begin{pmatrix} -d_1 u_{1xx} + u_1 \\ -d_2 u_{2xx} + u_2 \\ -D_1 v_{1xx} + v_1 \\ -D_2 v_{2xx} + v_2 \end{pmatrix}
\]

and \( F(w) = (F_u, F_v)^T \), where

\[
F(w) = \begin{pmatrix} F_u(w) \\ F_v(w) \end{pmatrix} = \begin{pmatrix} h_1(u_1, v_1) + u_1 \\ h_2(u_2, v_2) + u_2 \\ H_1(u_1, v_1) + v_1 \\ H_2(u_2, v_2) + v_2 \end{pmatrix}.
\]

We define the following function spaces.

\[
Y_u = Y_v = L^2([0, l_1]) \times L^2([-l_2, 0]), \quad \text{and} \quad Y = Y_u \times Y_v.
\]

\[
W_u = W_v = W_{2,2}^2([0, l_1]) \times W_{2,2}^2([-l_2, 0]), \quad \text{and} \quad W = W_u \times W_v.
\]

Since we are in one space dimension, we have \( W_{2,2}^2 \leftrightarrow C^1 \). Hence, a function \( u \in W_u \) is continuously differentiable, so that we can impose the boundary and interface conditions that we want. We therefore set \( X = X_u \times X_v \) with

\[
X_u = \{ (u_1, u_2) \in W_u \mid u \text{ satisfies (64)} \}
\]

and accordingly for \( X_v \) with (64) replaced by (65).

On \( Y_u \) we define the inner product

\[
\langle u, z \rangle_{Y_u} = \langle u_1, z_1 \rangle_{L^2([0,l_1])} + k \langle u_2, z_2 \rangle_{L^2([-l_2,0])}
\]

and obtain the norm

\[
\| u \|_{Y_u}^2 = \| u_1 \|_{L^2([0,l_1])}^2 + k \| u_2 \|_{L^2([-l_2,0])}^2
\]

and similarly on \( Y_v \) with \( k \) replaced by \( K \). Finally, we have

\[
\| w \|_{Y}^2 = \| u \|_{Y_u}^2 + \| v \|_{Y_v}^2.
\]
The linear problem

**Proposition 7.1** The linear operator $A$ defines an analytic semigroup on $Y$.

**Proof.** We will show that $A$ is invertible and that the closure of the numerical range is contained in $[1, \infty)$. Then Lemma 2 in Cosner (1987) (which is a special case of Theorem V.3.2 in Kato (1966)) states that the conditions for the generation of an analytic semigroup from Part 2, Section 2 in Friedman (1969) are satisfied.

We note that since the operator $A$ is diagonal and since $A_1$ and $A_2$ are essentially identical, it is sufficient to show the two properties for $A_1$.

We begin by calculating the numerical range of $A_1$.

$$
\langle A_1u, u \rangle_{Y_u} = \int_0^{l_1} (-d_1 u_1xx + u_1) \bar{u}_1 dx + k \int_{-l_2}^0 (-d_2 u_2xx + u_2) \bar{u}_2 dx
$$

$$
= -d_1 u_1xx \bar{u}_1|_{l_1} + \int_0^{l_1} d_1 u_1xx \bar{u}_1 dx - k d_2 u_2xx \bar{u}_2|_{-l_2} + \int_{-l_2}^0 k d_2 u_2xx \bar{u}_2 dx + \langle u, u \rangle_{Y_u}.
$$

(Note that $\bar{u}$ denotes the complex conjugate of the function $u$.)

By the boundary and interface conditions (64), the first and third term cancel. The two integral terms are non-negative, and therefore, we find

$$
\langle A_1u, u \rangle_{Y_u} = \int_0^{l_1} d_1 u_1xx \bar{u}_1 dx + \int_{-l_2}^0 k d_2 u_2xx \bar{u}_2 dx + \langle u, u \rangle_{Y_u}
$$

$$
\geq \langle u, u \rangle_{Y_u}.
$$

Hence, the numerical range

$$
\theta(A_1) = \{ \langle A_1u, u \rangle_{Y_u} \mid \|u\|_{Y_u} = 1 \} \quad (76)
$$

is contained in $[1, \infty)$ and so is its closure. The same is true for $A_2$ and therefore also for $A$.

Secondly, we show that $A_1$ has a bounded inverse. Consider $(f_1, f_2) \in Y_u$. There exist unique functions $\tilde{u}_{1,2}$ that satisfy

$$
-d_1 \tilde{u}_{1xx} + \tilde{u}_1 = f_1, \quad x \in [0, l_1],
$$

$$
-d_2 \tilde{u}_{2xx} + \tilde{u}_2 = f_2, \quad x \in [-l_2, 0],
$$

with Neumann conditions at all boundaries, i.e. $\tilde{u}_{1x}(l_1) = \tilde{u}_{1x}(0) = \tilde{u}_{2x}(0) = \tilde{u}_{2x}(-l_2) = 0$. The reason is as follows. We notice that with these boundary conditions, the two
equations decouple. Then each problem is an inhomogeneous boundary value problem, a special case of a regular Sturm–Liouville problem. A unique solution exists by classical methods (e.g., an explicit calculation of the Green’s function). We need to estimate the norm. Classical results (e.g., Theorem 9.27 in Renardy and Rogers (2004)) give the estimate in \( W^{1,2} \)

\[
\|\tilde{u}_1\|_{W^{1,2}([0,l_1])} \leq C\|f_1\|_{L^2([0,l_1])}, \quad \|\tilde{u}_2\|_{W^{1,2}([-l_2,0])} \leq C\|f_2\|_{L^2([-l_2,0])}.
\]  

(77)

However, we need an estimate in \( W^{2,2} \). We can write the equations as

\[
\tilde{u}_{i,xx} = \frac{1}{d_i}(\tilde{u}_i - f_i)
\]

and take norms on both sides to get

\[
\|\tilde{u}_{i,xx}\|_{L^2} \leq \tilde{C}(\|\tilde{u}_i\|_{L^2} + \|f_i\|_{L^2}).
\]

By the previous estimate, the right hand side can be bounded by some multiple of the \( L^2 \)-norm of the data \( f_i \) alone so that we obtain the overall estimate

\[
\|\tilde{u}_1\|_{W^{2,2}([0,l_1])} \leq C\|f_1\|_{L^2([0,l_1])}, \quad \|\tilde{u}_2\|_{W^{2,2}([-l_2,0])} \leq C\|f_2\|_{L^2([-l_2,0])}.
\]  

(78)

We now use the same construction of functions \( y_{1,2} \) in the proof of the existence of the dominant eigenvalue to obtain functions

\[
u_i = \tilde{u}_i + y_i
\]

(79)

that satisfy the differential equations and the same norm estimates as \( \tilde{u}_i \) with potentially different constants.

The same construction works for \( A_v \) and therefore we have shown that \( A \) is invertible with bounded inverse. Lemma 2 in Cosner (1987) (which is a special case of Theorem V.3.2 in Kato (1966)) now states that \( \mathbb{C}\setminus[1,\infty) \) is contained in the resolvent set of \( A \) and

\[
\|(\lambda - A)^{-1}\| \leq \frac{1}{\text{dist}(\lambda, \theta(A))}
\]  

(80)

for all \( \lambda \) in the resolvent set.

Denote the distance by \( d = \text{dist}(\lambda, \theta(A)) \). We want to show that there exists a constant \( C \) such that

\[
d \geq \frac{1 + |\lambda|}{C}
\]
for $\Re \lambda \leq 0$, so that from (80) we get the required estimate
\[
\|(\lambda - A)^{-1}\| \leq \frac{C}{1 + |\lambda|}.
\] (81)

On the semicircle $|\lambda|$ with $\Re \lambda \leq 0$, the function $d$ assumes its minimum when $\lambda$ is purely imaginary. Hence, it is enough to show the inequality on the imaginary line. Hence, we need to show the existence of a constant $C$ such that
\[\sqrt{1 + z^2} \geq \frac{1 + z}{C}, \quad z \geq 0.\]

The function $z \mapsto \frac{1 + z^2}{(1 + z)^2}$ is positive, continuous, and bounded with $f(0) = f(\infty) = 1$. Its maximum is 1 and its minimum occurs at $x = 1$. We can take $C$ to be the inverse of the minimum of this function.

With this, we see that $A$ satisfies the characterization to generate an analytic semigroup according to the theory developed in Friedman (1969), Part 2, Section 2. The statement is also available in Theorem 36.2 in Sell and You (2002) or in the book Pazy (1983). ■

The nonlinear problem

We now return to the nonlinear problem (66) and prove local existence of solutions. We use the following (notation adapted) time-independent version of Lemma 3 in Cosner (1987).

**Proposition 7.2** Let $A$ be a closed linear operator on a Banach space $Y$ such that (81) holds. Suppose that $F$ is a function on $Y$ such that for some $0 < \beta < 1$ and for any $R > 0$, there exists a constant $C(R)$ such that
\[
\|F(A^{-\beta}p_1) - F(A^{-\beta}p_2)\|_Y \leq C(R)\|p_1 - p_2\|_Y
\] (82)
for all $p_1, p_2 \in Y$ with $\|p_1\|_Y < R$. Then for any $p_0 \in D(A)$ and each $R > \|A^{-\beta}p_0\|_Y$ there exists a $t^* > 0$ such that problem (66) has a unique solution in $[0, t^*]$.

From the previous section, we know that $A$ is a closed linear operator on $Y$ and that the norm estimate for the resolvent holds. To find an appropriate choice of $\beta$, we begin with the statement of Lemma 37.8 in Sell and You (2002).

**Lemma 7.3** Let $A$ be a positive, sectorial operator on $L^q(\Omega, \mathbb{R}^n)$ with domain $D(A) \hookrightarrow W^{m,q}$ for some $m \geq 1$. Let $0 < \beta \leq 1$. Then $D(A^\beta) \hookrightarrow W^{k,p}$ if $p \geq q$, $k \geq 0$ and $k - n/p < m\beta - n/q$. 25
We apply this lemma with \( n = 1, q = p = 2 \) and \( m = 2 \). Then we get that \( D(A^\beta) \hookrightarrow W^{1,2} \) for all \( 1/2 < \beta \leq 1 \). We now fix some \( \beta \in (1/2, 1) \).

We pick functions \( p_{1,2} \in Y \) and set \( q_i = A^{-\beta}p_i \). Since \( A^{-\beta} \) maps into \( D(A^\beta) \) and since by the previous lemma and our choice of \( \beta \), we have the embedding into \( W^{1,2} \) in each component, we see that \( q_i \) are continuous and there is a constant \( C_1(R) \) such that \( \|q_i\|_\infty \leq C_1(R)\|q_i\|_{W^{1,2}} \leq C_1(R)\|A^{-\beta}\|\|p_i\|_Y \).

For \( \nu \in [0,1] \) we define \( u(\nu) = q_2 + \nu(q_1 - q_2) \). The function \( \nu \mapsto F(u(\nu)) \) satisfies \( F(u(1)) = F(q_1) \) and \( F(u(0)) = F(q_2) \). We apply the fundamental theorem of calculus and the chain rule to write

\[
\begin{align*}
\|F(A^{-\beta}p_1) - F(A^{-\beta}p_2)\|_Y &= \|F(q_1) - F(q_2)\|_Y \\
&= \|F(u(1)) - F(u(0))\|_Y \\
&= \|\int_0^1 DF(u(\nu)) \frac{d}{d\nu} u(\nu) d\nu\|_Y.
\end{align*}
\]

(83)

(84)

(85)

Clearly, the derivative of \( u \) is \( \frac{d}{d\nu} u(\nu) = q_1 - q_2 \). Furthermore, the nonlinearity of \( F \) consists of polynomials of degree at most 2 in each component. In particular, \( DF \) consists of at most linear combinations of the functions in \( q_i \). Since \( q_i \) are bounded by the above reasoning, there is an \( L^\infty \)-bound \( C_2 = C_2(R) \) on \( DF \) for \( \|p_i\| \leq R \).

Hence, we get the estimate

\[
\|F(A^{-\beta}p_1) - F(A^{-\beta}p_2)\|_Y \leq C_2(R)\|q_1 - q_2\|_Y
\]

(86)

Therefore, the proposition applies and we obtain local existence of solutions.

**Proposition 7.4** Let \( p_0 \in D(A) \) and denote by \( w(t) \) the unique local solution of (66) and \( w(0) = p_0 \). Then \( w(t) \in D(A) \) for all \( t \in [0, t^*] \) and \( w \) as well as \( dw/dt \) are strongly continuous in \( [0, t^*] \). Furthermore, \( d^2w/dt^2 \) exists and is strongly continuous. Finally, if the initial condition as a function of \( x \) is non-negative and appropriately bounded, then so is the solution.

**Proof.**

The analytic semigroup generated by \( A \) maps \( Y \) into \( D(A^\beta) \) for all \( \beta \geq 0 \) (Theorem 37.5 in Sell and You (2002)). Therefore, the solution is in \( D(A) \), see also Theorem 2, in Friedman (1965). Continuity of \( w \) with respect to time follows from Theorem 2 in Friedman (1965). Higher regularity of solutions follows from the considerations following that theorem. Specifically, if the (Fréchet) derivative of \( F(A^{-\beta}p) \) exists
and is Lipschitz continuous, then the solution has strong first and second derivatives and they all belong to \( D(A^2) \). Since \( F \) consists of quadratic terms, the derivative consists of linear terms and is therefore Lipschitz continuous.

To show positivity of solutions with non-negative, non-zero initial data, we apply the comparison principle (Proposition 3.2). To show the upper bounds, we proceed as follows. Function \( h_i \) is negative for \( u_i > e_i/f_i \), independently of \( v_i \). Hence, it is sufficient to show an upper bound for solutions of the \( u_i \)-equations alone.

If \( ke_1/f_1 \geq e_2/f_2 \), we set \( u_1(x, t) = e_1/f_1 \) and \( u_2(x, t) = ku_1 \). If \( ke_1/f_1 < e_2/f_2 \), we set \( u_2(x, t) = e_2/f_2 \) and \( u_1(x, t) = u_2/k > e_1/f_1 \). In either case, we find \( h_i(u_i, 0) \leq 0 \). Hence, we have found an upper solution and can apply the comparison principle again.

**Proposition 7.5** The local solutions obtained above are global solutions, i.e. they exist for \( t \in [0, \infty) \).

**Proof.** We pick \( T_0 > 0 \). As in the proof of Lemma 3 in Cosner (1987) and in the proof of Theorem 1 in Bell and Cosner (1981), we need to show that for every local solution \( w \) on \([0, T_1]\) with \( T_1 \leq T_0 \), there exists a constant \( R' \) such that \( \|Aw\| < R' \).

Then we can choose \( R > R' \) and apply the local existence result successively on \([0, t^*], [t^*, 2t^*] \), and so on until \( T_0 \). Since \( T_0 \) was arbitrary, we have global existence.

To show the existence of the constant \( R' \), we note that \( Aw = -w_t + F(w) \). Hence, we aim to estimate

\[
\| -w_t + F(w) \|_Y.
\]

We set

\[
E(t) = \frac{1}{2}(\|u\|_Y^2 + \|w_t\|_Y^2) = \frac{1}{2}(\|u\|_{Y_u}^2 + \|v\|_{Y_v}^2 + \|u_t\|_{Y_u}^2 + \|v_t\|_{Y_v}^2)
\]

and calculate \( E'(t) \).

The first term in (87) gives

\[
\frac{d}{dt} \frac{1}{2} \|u\|_{Y_u}^2 = -\langle u, A_u u \rangle_{Y_u} + \langle u, F_u(u, v) \rangle_{Y_v}.
\]

We estimate the first of these terms as we did in the calculation of the numerical range of the operator \( A \), see Proposition 7.1. We obtain

\[
-\langle u, A_u u \rangle_{Y_u} \leq -\langle u, u \rangle_{Y_u} \leq 0.
\]
To estimate the second of these terms, we note that by the maximum principle, non-negative solutions \((u, v)\) are \(L^\infty\) bounded independent of time (see previous proposition), so that the terms \(e_i - f_i u_i - g_i v_i\) are also \(L^\infty\) bounded independent of time. Then we can estimate

\[
\langle u, F_u(u, v) \rangle_{Y_u} = \int_0^{t_1} u_1(e_1 - f_1 u_1 - g_1 v_1)u_1 dx + k \int_{-t_2}^0 u_2(e_2 - f_2 u_2 - g_2 v_2)u_2 dx \leq C_1 \langle u, u \rangle_{Y_u}.
\]

The second term in (87) is estimated in the exact same way.

The third term in (87) consists of three terms, namely

\[
\frac{d}{dt} \frac{1}{2} \|u_t\|^2_{Y_u} = -\langle u_t, A_u u_t \rangle_{Y_u} + \langle u_t, D_u F_u(u, v)u_t \rangle_{Y_u} + \langle u_t, D_v F_u(u, v)u_t \rangle_{Y_u}.
\]

The first of these three terms satisfies the same estimate as the corresponding term above, i.e.

\[-\langle u_t, A_u u_t \rangle_{Y_u} \leq -\langle u_t, u_t \rangle_{Y_u} \leq 0.
\]

The second term can be estimated in a similar way as the second term above since \(D_u F_u\) consists of linear polynomials. Hence, we find

\[
\langle u_t, D_u F_u(u, v)u_t \rangle_{Y_u} \leq C_2 \langle u_t, u_t \rangle_{Y_u}.
\]

The third term is slightly different. It is given by

\[
\langle u_t, D_v F_u(u, v)u_t \rangle_{Y_u} = \int_0^{t_1} u_{1t}(-g_1 u_1)v_{1t} dx + k \int_{-t_2}^0 u_{2t}(-g_2 u_2)v_{2t} dx
\]

\[
\leq C_3 \left( \int_0^{t_1} u_{1t}v_{1t} dx + k \int_{-t_2}^0 u_{2t}v_{2t} dx \right)
\]

\[
\leq C_3 \left( \int_0^{t_1} (u_{1t}^2 + v_{1t}^2) dx + k \int_{-t_2}^0 (u_{2t}^2 + v_{2t}^2) dx \right)
\]

\[
\leq C_4 \left( \langle u_t, u_t \rangle_{Y_u} + \langle v_t, v_t \rangle_{Y_u} \right).
\]

A similar estimate holds for the \(v\)-component.

Altogether, we obtain the estimate \(E'(t) \leq \hat{C} E(t)\). In particular, \(E\) can grow at most exponentially in time. In particular, \(\|w\|\) and \(\|w_t\|\) remain bounded for any finite time. The bound on \(F(w)\) is obvious by the \(L^\infty\)-bound of \(w\). Hence, we have shown that a constant \(R'\) exists as required.
References


