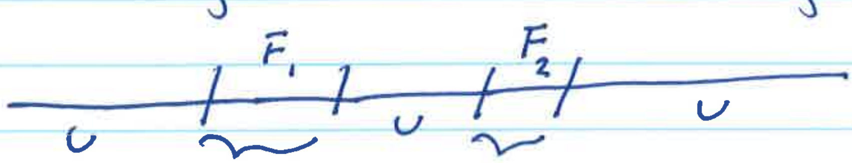
Lecture 11

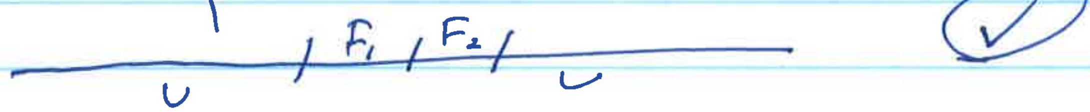
A problem in transitioning from spatial to landscape ecology: perspectives from several modeling formulations

- work that has been in progress for some time; joint with Chris Cosner and William F. Fagan of the University of Maryland

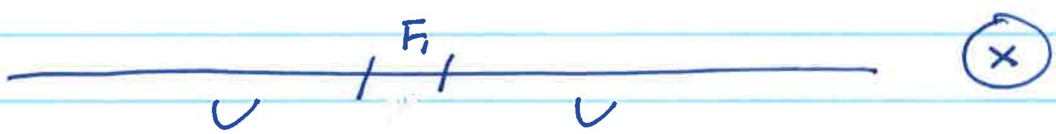
- idea: Consider a one-dimensional universe of infinite extent (i.e., a line). Assume there are two patches (i.e., intervals) along the line that are favorable to reproduction in some given species. These patches are separated in between by a patch unfavorable to reproduction and also have environment unfavorable to reproduction on the left and right of the left and right patches.



Let F_1 and F_2 represent the lengths of the patches. Assume that a single favorable patch of length $F_1 + F_2$ is sufficient to the sustaining of the species in question in this one-dimensional universe when the patch of length $F_1 + F_2$ is surrounded by unfavorable habitat.



On the other hand, assume that a single patch of length F_1 or F_2 is insufficient by itself to sustain the species in question



A natural expectation is that in the original setting if the patches with lengths F_1 and F_2 are not too far apart the two patches should act in concert to sustain the species, whereas if the two patches are far enough apart, the species should go extinct.

Questions:

(1) What do linear level models tell us about this situation?

(2) Are there differences among model predictions? In particular, how well can spatially implicit models approximate the conclusions from spatially explicit models?

A. Reaction-diffusion formulation

Consider the linear problem

(1) $$u_t = d u_{xx} + m(x) u \qquad \text{on } \mathbb{R} \times (0, \infty)$$

where

(2) $$m(x) = \begin{cases} -1 & , x < 0 \\ r^2 > 0 & , 0 < x < L \\ -1 & , L < x < L + D \\ r^2 & , L + D < x < L + D + \ell \\ -1 & , x > L + D + \ell \end{cases}$$

(wlog $\ell \leq L$)

subject to the constraint

(3) $$u \to 0 \qquad \text{as} \qquad x \to \pm\infty$$

When the associated eigenvalue problem

(4) $$du_{xx} + m(x)u = \sigma u \qquad \text{on } \mathbb{R}$$

$$u \to 0 \qquad \text{as } x \to \pm\infty$$

$$u > 0 \qquad \text{on } \mathbb{R}$$

is such that $\sigma > 0$, we have a linear level prediction of growth (and hence a presumption of persistence). If, on the other hand, $\sigma < 0$, we have a linear level prediction of extinction.

The predictions of (4) regarding persistence vs. extinction can be determined by considering an alternate version of a steady-state eigenvalue problem, namely:

(5)
$$
\begin{aligned}
&u_{xx} + \lambda m(x) u = 0 && \text{on } \mathbb{R} \\
&u \to 0 && \text{as } x \to \pm\infty \\
&u > 0 && \text{on } \mathbb{R}
\end{aligned}
$$

where $d = 1/\lambda$ $\quad (\lambda = 1/d)$

Our assumptions on $m(x)$ (namely that it is positive on the two intervals of lengths L and ℓ but is equal to -1 outside $[0, L+D+\ell]$) guarantee that (5) has a unique – necessarily positive –

eigenvalue λ_1. (Brown, Cosner, Fleckinger 1990)

The relation here is that having the observed value of $\lambda = 1/d$ exceed λ_1 corresponds to $\sigma > 0$ (and thus persistence), while having λ less than λ_1 corresponds to $\sigma < 0$ (and extinction).

(6) $$\boxed{\sigma = 0 \iff \lambda = \lambda_1}$$

Note: $\lambda > \lambda_1 \iff d < 1/\lambda_1$

Tracking $\sigma = 0$ in (4) corresponds to tracking $\lambda = \lambda_1$ in (5). The advantage to tracking λ_1 is that it is more transparent in terms of the critical parameters in the model; i.e., in terms of r, L, D, and ℓ.

This transparency is based on the fact that the eigenfunction in (5) is a continuously differentiable function on $\mathbb{R}$ (though, of course, not twice continuously differentiable at the points of discontinuity of $m(x)$). On any interval on which m is constant, the form of the eigenfunction is determined. We can use these two facts to obtain a transcendental equation for $\alpha = \sqrt{\lambda_1}$.

(7) $u(x)$ in (5) can be taken as:

$$u(x) = \begin{cases} e^{\alpha x}, & x < 0 \\ c_1 \cos(\alpha r x) + c_2 \sin(\alpha r x), & 0 < x < L \\ c_3 \cosh(\alpha(x-L)) + c_4 \sinh(\alpha(x-L)), & L < x < L+D \\ c_5 \cos(\alpha r(x-L-D)) + c_6 \sin(\alpha r(x-L-D)), & L+D < x < L+D+\ell \\ c_7 e^{-\alpha(x-L-D-\ell)}, & x > L+D+\ell \end{cases}$$

Here we have normalized u by requiring

$$u(0) = 1.$$

We must have u continuously differentiable.

So we must match both u and its derivative

at each of the 4 interfaces at 0, L, $L+D$, and

$L+D+\ell$. We find that $\alpha = \sqrt{\lambda}$, satisfies:

(8)

$$\coth(\alpha D) = \frac{\cosh(\alpha D)}{\sinh(\alpha D)} = \frac{\left(r+\frac{1}{r}\right)^2 \sin(\alpha r \ell)\sin(\alpha r L) - \left(r - \frac{1}{r}\right)\sin(\alpha r(L+\ell)) + 2\cos(\alpha r(L+\ell))}{\left[\left(r-\frac{1}{r}\right)\sin(\alpha r(L+\ell)) - 2\cos(\alpha r(L+\ell))\right]}$$

Equation (8) requires some work to analyze

It can be put into a more amenable form

by letting

$$A = A(r) = \sqrt{\left(r-\frac{1}{r}\right)^2 + (2)^2} = r + \frac{1}{r}$$

There is a unique $\Theta = \Theta(r) \in \left(-\frac{\pi}{2}, \frac{\pi}{2}\right)$

so that

$$(9) \quad \cos\theta = \frac{2}{r+1/r} = \frac{2r}{r^2+1}$$

$$\sin\theta = \frac{r-1/r}{r+1/r} = \frac{r^2-1}{r^2+1}$$

$$\Rightarrow \theta = \sin^{-1}\left(\frac{r^2-1}{r^2+1}\right)$$

$$\theta(r) \begin{cases} \in (-\pi/2, 0) & , r \in (0,1) \\ = 0 & , r = 1 \\ \in (0, \pi/2) & , r > 1 \end{cases}$$

Moreover, $\lim_{r \to 0^+} \theta(r) = -\pi/2$ and $\lim_{r\to\infty} \theta(r) = \pi/2$

Calculations using $\theta(r)$ allow us to re-write (8) as

$$(10) \quad \coth(\alpha D) = \frac{1}{2}\left[\frac{(r+\frac{1}{r})\cos(\alpha r(L-\ell)) - (r-\frac{1}{r})\sin(\alpha r(L+\ell)+\theta(r))}{-\cos(\alpha r(L+\ell)+\theta(r))}\right]$$

The left hand side of (10) is a

monotonically decreasing function in α

with

$$\lim_{\alpha \to 0^+} \coth(\alpha D) = +\infty$$

$$\lim_{\alpha \to +\infty} \coth(\alpha D) = 1 .$$

Further manipulations of the r.h.s. of (10) allow us to write it in the form

$$(11) \qquad \frac{(r + 1/r)\sin(\alpha r L)\sin(\alpha r \ell)}{-\cos(\alpha r(L+\ell) + \theta(r))} - 1$$

The numerator in the first term is positive on $(0, \pi/rL)$, as $\ell \le L$ by assumption

As noted, $\theta(r) \in (-\pi/2, \pi/2)$

Consequently, the denominator is negative until its first zero at

(12) $$\alpha = \frac{\pi/2 - \theta(r)}{r(L+\ell)} < \frac{\pi}{r(L+\ell)} < \frac{\pi}{rL}$$

So the value of the r.h.s. of (10) is negative until α reaches

$$\frac{\pi/2 - \theta(r)}{r(L+\ell)}$$

where the r.h.s. has a vertical asymptote

Let

(13) $$g(\alpha, r, L, \ell) = \frac{(r + \frac{1}{r}) \sin(\alpha r L) \sin(\alpha r \ell)}{-\cos(\alpha r(L+\ell) - \theta(r))} - 1$$

$$\lim_{\alpha \to \left[\frac{\pi/2 - \theta(r)}{r(L+\ell)}\right]^+} g(\alpha, r, L, \ell) = +\infty.$$

Note that $\frac{\ell}{L}\left(\pi/2 - \theta(r)\right) < \pi$

$$\Rightarrow \frac{\pi}{2} - \theta(r) + \frac{\ell}{L}\left(\frac{\pi}{2} - \theta(r)\right) < \frac{3\pi}{2} - \theta(r)$$

$$\Rightarrow \frac{L+\ell}{L}\left(\frac{\pi}{2} - \theta(r)\right) < \frac{3\pi}{2} - \theta(r)$$

$$\Rightarrow \frac{\pi/2 - \theta(r)}{rL} < \frac{3\pi/2 - \theta(r)}{r(L+\ell)}$$

So $g(\alpha, r, L, \ell)$ is well-defined for $\alpha \in \left(\frac{\frac{\pi}{2} - \theta(r)}{r(L+\ell)}, \frac{\frac{\pi}{2} - \theta(r)}{rL} \right]$

Observe that

$$g(\alpha, r, L, \ell) = 1$$

$$\Longleftrightarrow \quad \frac{(r + \frac{1}{r}) \sin(\alpha r L) \sin(\alpha r \ell)}{-\cos(\alpha r (L+\ell) + \theta(r))} - 1 = 1$$

$$\Longleftrightarrow \quad \frac{(r + \frac{1}{r}) \sin(\alpha r L) \sin(\alpha r \ell)}{-\cos(\alpha r (L+\ell) + \theta(r))} = 2$$

$$\Longleftrightarrow \quad -\frac{2}{r + \frac{1}{r}} \cos(\alpha r (L+\ell) + \theta(r)) = \sin(\alpha r L) \sin(\alpha r \ell)$$

So

(14) $$-\cos\theta(r) \cos(\alpha r (L+\ell) + \theta(r)) = \sin(\alpha r L) \sin(\alpha r \ell)$$

$$\Updownarrow$$

$$g(\alpha, r, L, \ell) = 1$$

But now

$$\sin(\alpha r L) = \sin(\alpha r L + \theta - \theta)$$

$$= \sin(\alpha r L + \theta)\cos\theta - \cos(\alpha r L + \theta)\sin\theta$$

and

$$\cos(\alpha r(L+\ell)+\theta) = \cos(\alpha r L+\theta)\cos(\alpha r \ell) - \sin(\alpha r L+\theta)\sin(\alpha r \ell)$$

Incorporating these facts into (14) we get

(15) $$g(\alpha, r, L, \ell) = 1$$
$$\Updownarrow$$
$$-\cos\theta\left[\cos(\alpha r L+\theta)\cos\alpha r\ell - \sin(\alpha r L+\theta)\sin(\alpha r\ell)\right]$$
$$= \left[\sin(\alpha r L+\theta)\cos\theta - \cos(\alpha r L+\theta)\sin\theta\right]\sin\alpha r\ell$$

$$\Longleftrightarrow \cos(\alpha r L+\theta)(-\cos\theta\cos\alpha r\ell) + \sin(\alpha r L+\theta)(\cos\theta\sin\alpha r\ell)$$
$$= \cos(\alpha r L+\theta)(-\sin\theta\sin(\alpha r\ell)) + \sin(\alpha r L+\theta)(\cos\theta\sin\alpha r\ell)$$

$$\Longleftrightarrow \cos(\alpha r L+\theta)\left(\cos(\alpha r\ell)\cos\theta - \sin(\alpha r\ell)\sin\theta\right) = 0$$

$$\Longleftrightarrow \cos(\alpha r L+\theta)\cos(\alpha r\ell+\theta) = 0$$

The smallest value of α for which

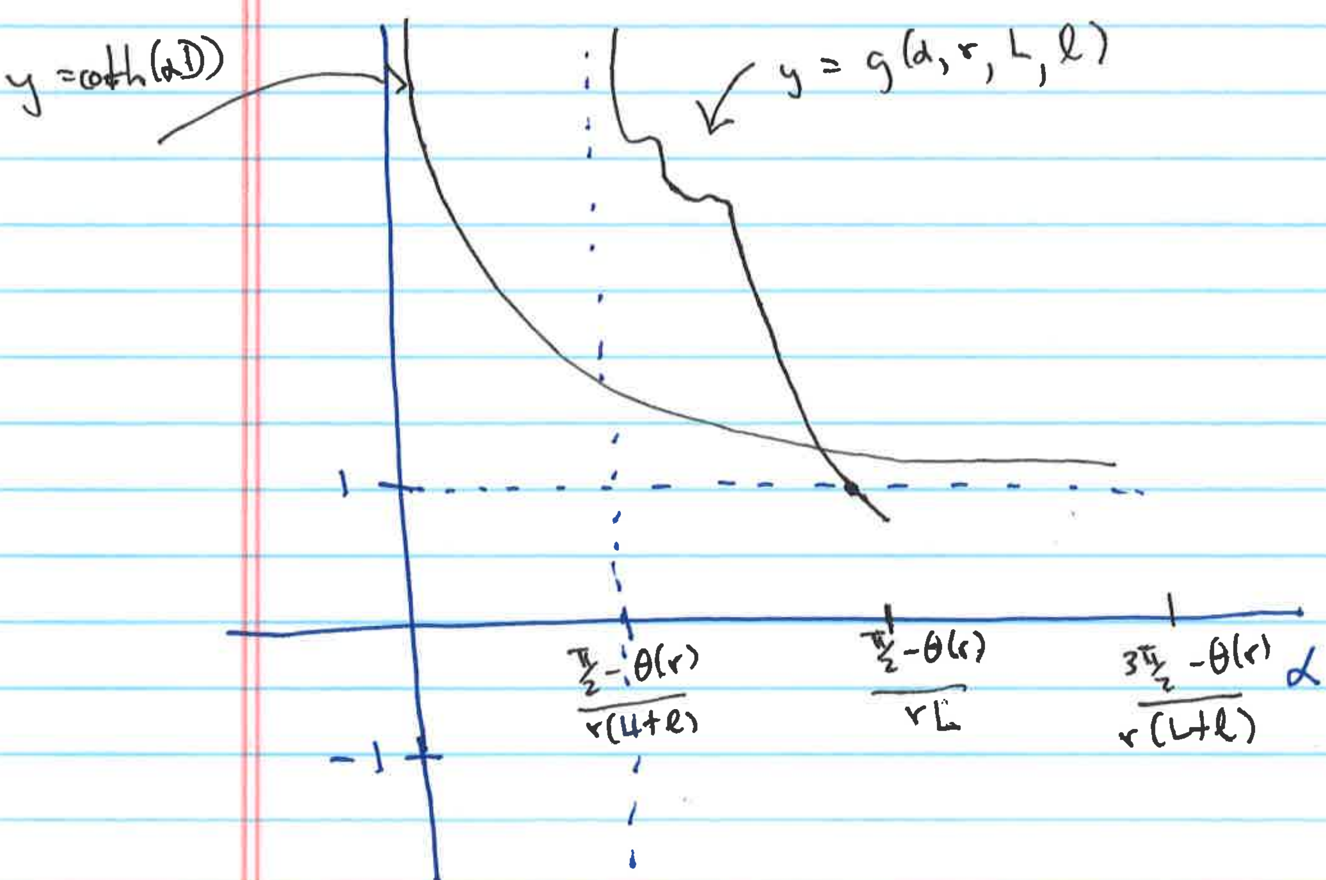
$$\cos(\alpha r L + \theta)\cos(\alpha r \ell + \theta) = 0$$

is $\qquad \alpha = \dfrac{\pi/2 - \theta}{rL}$

So the smallest positive value of α, say α_1, satisfying (10) lies in the interval

$$\left(\frac{\pi/2 - \theta(r)}{r(L+\ell)}, \frac{\pi/2 - \theta(r)}{rL} \right)$$

The basic picture is as follows:



I have not sketched $y = g(\alpha, r, L, \ell)$ as strictly monotonically decreasing in α on $\left(\frac{\pi/2 - \theta(r)}{r(L+\ell)}, \frac{\pi/2 - \theta(r)}{rL}\right]$. It is not immediately evident from the form of g that such is the case. We may argue this point, however, on the basis of the continuity of α_1 in terms of D. The principal eigenvalue is given in Brown, Cosner, and Flectinger (1991) in terms of a variational inequality. So it is the case that α_1 is a continuous function of D, which does not appear in the right hand side of (10). $y = \coth(\alpha D)$ is monotonic in D with $\lim_{D \to 0} \coth(\alpha D) = +\infty$ and $\lim_{D \to \infty} \coth(\alpha D) = 1$ for any fixed $\alpha > 0$.

If $y = g(\alpha, r, L, \ell)$ is increasing on some subinterval of $\left(\frac{\pi/2 - \theta(r)}{r(L+\ell)}, \frac{\pi/2 - \theta(r)}{rL}\right]$, there will be some $D_1^* > 0$ such that $\lim_{D \to D_1^{*+}} \alpha_1(D) \neq \alpha_1(D_1^*)$.

So $y = g(\alpha, r, L, \ell)$ is monotonically decreasing on

$$\left(\frac{\pi/2 - \theta(r)}{r(L+\ell)}, \frac{\pi/2 - \theta(r)}{rL} \right].$$

What are the ramifications of this analysis?

(i) One may make a completely analogous analysis of the asymptotics of (1) when m is replaced by $\tilde{m}$ where

$$\tilde{m}(x) = \begin{cases} -1 & , \quad x < 0 \\ r^2 > 0 & , \quad 0 < x < L+\ell \\ -1 & , \quad x > L+\ell \end{cases}$$

by considering the corresponding eigenvalue problem to (5) in this case. In this event, constructing the equation for α_1 is somewhat simpler. One obtains

$$\alpha_1 = \frac{\pi/2 - \theta(r)}{r(L+\ell)}$$

(ii) The preceding analysis shows that $\alpha_1 = \alpha_1(D, r, L, \ell)$ satisfies

$$\lim_{D \to 0^+} \alpha_1(D, r, L, \ell) = \frac{\pi/2 - \theta(r)}{r(L+\ell)}$$

(iii) The preceding analysis shows that $\alpha_1 =$

$\alpha_1(D, r, L, \ell)$ satisfies

$$\lim_{D \to \infty} \alpha_1(D, r, L, \ell) = \frac{\pi/2 - \theta(r)}{rL}$$

(iv) Suppose now that in (1) d is such that

$$\left(\frac{\pi/2 - \theta(r)}{r(L+\ell)}\right)^2 < \frac{1}{d} < \left(\frac{\pi/2 - \theta(r)}{rL}\right)^2$$

There is a $D_{cr}(r) > 0$ so that

$$\alpha_1^2(D, r, L, \ell) = \frac{1}{d}$$

So for $0 < D < D_{cr}(r)$, we have that

$$\frac{1}{d} > \left(\alpha_1(D, r, L, \ell)\right)^2 \Rightarrow \sigma > 0 \text{ in (1)}$$

$\Rightarrow$ the model predicts persistence of the population in question. However, if $D > D_{cr}(r)$, then

$$\frac{1}{d} < \left(\alpha_1(D, r, L, \ell)\right)^2 \Rightarrow \sigma < 0 \text{ in (1)}$$

$\Rightarrow$ the model predicts extinction of the population in question

Note: $\frac{1}{d} < \left(\frac{\pi/2 - \theta(r)}{rL} \right)^2$ means that the model

predicts extinction of the population in question

in (1) for $\tilde{m}$.

(v) In the situation described in (iv), a patch

of length L is not large enough to sustain

a population of the organism in question

but a patch of length L+l is. The analysis

shows that the two disjoint patches act in concert

to support a population of the organism in question

until the distance increases beyond a critical size,

which depends on the dispersal and reproductive

capabilities of the species and the lengths of the

two patches in question.

(vi) Should $1/d > \left(\frac{\pi/2 - \theta(r)}{rL} \right)^2$, a single large

patch would be sufficient to sustain a population independent of the location of other patches of habitat.

B. Discrete diffusion formulation (Full models)

Initial Goal: Obtain a discrete-diffusion system that approximates the linear diffusion model

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} + r\left[R\,\chi_{\Omega}(x) - \chi_{\mathbb{R}-\Omega}(x)\right]u$$

where Ω = patch 1 (length L) $\cup$ patch 2 (length ℓ)

$\mathbb{R}-\Omega$ = matrix surrounding focal habitat

First we consider the case when $\ell = 0$ and we think of only one focal patch of length L

We want to compartmentalize into three equations: one representing the density of the species in question in the focal habitat and two representing the density of the species in question at the edge of the surrounding matrix (which we think of as having infinite extent).

$$\boxed{u_1} \rightleftarrows \boxed{u_2} \rightleftarrows \boxed{u_3}$$

Since the two pieces of matrix environment surrounding the focal piece of habitat have infinite extent, we can not simply think of the total population in the regions as arising from multiplying a constant density times the length of the region. Rather we employ the diffusion equation on the regions:

$$\frac{\partial u}{\partial t} = d\frac{\partial^2 u}{\partial x^2} - ru$$

and consider the bounded steady-state density, which is a decaying exponential.

For convenience we will view the focal patch of species habitat as occupying the interval $[0, L]$. In that case, the steady-state density on $(-\infty, 0]$ would be

$$u_1 e^{\sqrt{\frac{r}{d}}x},$$

where u_1 is the density at $x = 0$.

The population U_1 in $(-\infty, 0)$ is given by

$$U_1 = \int_{-\infty}^{0} u_1 e^{\sqrt{\frac{r}{d}}x} dx = u_1 \sqrt{\frac{d}{r}}.$$

We get a similar result on (L, ∞)

On the focal piece of habitat $([0, L])$ it is reasonable to view the total population as the product of the average density u_2 and habitat size L.

So we have

$$U_1 = u_1 \sqrt{d/r}$$

$$U_2 = u_2 L$$

$$U_3 = u_3 \sqrt{d/r}$$

The evolution of these quantities are governed by:

$$\frac{dU_1}{dt} = -r_1 U_1 + d_1 u_2 - d_1 u_1$$

$$\frac{dU_2}{dt} = r_1 R U_2 + d_1(u_1 - 2u_2 + u_3)$$

$$\frac{dU_3}{dt} = -r_1 U_3 + d_1(u_2 - u_3)$$

leading to

$$\frac{du_1}{dt} = -ru_1 + \sqrt{rd}\,(u_2 - u_1) \tag{16}$$

$$\frac{du_2}{dt} = Rru_2 + \frac{d}{L}(u_1 - 2u_2 + u_3)$$

$$\frac{du_3}{dt} = -ru_3 + \sqrt{rd}\,(u_2 - u_3)$$

where we take $r_1 = r$ and $d_1 = d$.

For two patches, the same logic leads to:

$$\frac{du_1}{dt} = -ru_1 + \sqrt{rd}\,(u_2 - u_1) \tag{17}$$

$$\frac{du_2}{dt} = rRu_2 + \frac{d}{L}(u_1 - 2u_2 + u_3)$$

$$\frac{du_3}{dt} = -ru_3 + \frac{d}{D}(u_2 - 2u_3 + u_4)$$

$$\frac{du_4}{dt} = rRu_4 + \frac{d}{l}(u_3 - 2u_4 + u_5)$$

$$\frac{du_5}{dt} = -ru_5 + \sqrt{rd}\,(u_4 - u_5)$$

Note: We have the species population in the matrix environment between the two focal patches as the product of average density and pathlength D.

An alternate would be to think of the total population as that which would arise from averaging the populations associated with decaying exponential densities from each of the focal species habitats.

In this event, the third equation in (17) becomes

$$\frac{du_3}{dt} = -ru_3 + \frac{\sqrt{rd}}{1 - e^{-\sqrt{\frac{r}{d}}D}} (u_2 - 2u_3 + u_4)$$

As $D \to 0$, $1 - e^{-\sqrt{\frac{r}{d}}D} \to 0$. It turns out that the predictions of the two models are the same in this case. However, as $D \to \infty$, the initial version seems to capture a more pronounced diminishment in the co-operation between the two focal patches better than the second version, reflecting the p.d.e. model predictions.[8] (16) and (17) can be written as

$$(18)\quad \begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix}' = \begin{pmatrix} -r-\sqrt{rd} & \sqrt{rd} & 0 \\ d/L & Rr-2d/L & d/L \\ 0 & \sqrt{rd} & -r-\sqrt{rd} \end{pmatrix} \begin{pmatrix} u_1 \\ u_2 \\ u_3 \end{pmatrix}$$

and

$$(19)\quad \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \end{pmatrix}' = \begin{pmatrix} -r-\sqrt{rd} & \sqrt{rd} & 0 & 0 & 0 \\ d/L & Rr-2d/L & d/L & 0 & 0 \\ 0 & d/D & -r-2d/D & d/D & 0 \\ 0 & 0 & d/\ell & Rr-2d/\ell & d/\ell \\ 0 & 0 & 0 & \sqrt{rd} & -r-\sqrt{rd} \end{pmatrix} \cdot \begin{pmatrix} u_1 \\ u_2 \\ u_3 \\ u_4 \\ u_5 \end{pmatrix}$$

The off-diagonal elements in the matrices in (18) and (19) are non-negative. Moreover, in each case, when a sufficiently large multiple of the identity matrix is added, a nonnegative irreducible matrix results. Under these circumstances, the matrices have eigenvectors which are componentwise of one sign corresponding to the largest real eigenvalue (i.e. they admit principal eigenvalues σ). When $\sigma > 0$, the zero equilibrium is unstable and a solution to (18) or

(19) corresponding to componentwise positive initial data grows. If $\sigma < 0$, the zero equilibrium is stable and solutions to (18) or (19) corresponding to componentwise positive initial data decay to 0. To analyze (18) or (19), we need only determine the eigenvalues of each. Our interest is in translating conditions for $\sigma > 0$ or $\sigma < 0$ into conditions on the parameters in the problem, particularly L, ℓ and D, for both (18) and (19), comparing as $D \to 0$ or $D \to \infty$.

For (18) the eigenvalues are determined by the values of σ for which

(20)
$$\begin{vmatrix} -r-\sqrt{rd}-\sigma & \sqrt{rd} & 0 \\ d/L & R_r - 2d/L - \sigma & d/L \\ 0 & \sqrt{rd} & -r-\sqrt{rd}-\sigma \end{vmatrix} = 0$$

which can be determined to be:

(21)
$$-r-\sqrt{rd} < 0$$

(22)
$$\frac{R_r - 2d/L - r - \sqrt{rd} \pm \sqrt{(R_r - 2d/L - r - \sqrt{rd})^2 + 4\left(R_r^2 + R_r\sqrt{rd} - \frac{2rd}{L}\right)}}{2}$$

If $R_r^2 + R_r\sqrt{rd} - \frac{2rd}{L} > 0$, the matrix has a positive eigenvalue (i.e. $\sigma > 0$)

(23) $$R_r^2 + R_r\sqrt{rd} - \frac{2rd}{L} > 0$$

$$\Leftrightarrow \quad L > \frac{2rd}{R_r^2 + R_r\sqrt{rd}} = \frac{2}{R\left(\frac{r}{d} + \sqrt{\frac{r}{d}}\right)}$$

If $L \leq \dfrac{2}{R\left(\frac{r}{d} + \sqrt{\frac{r}{d}}\right)}$, $R_r^2 + R_r\sqrt{rd} - \dfrac{2rd}{L} \leq 0$

But then $L < \dfrac{2}{R\left(\frac{r}{d}\right)} = \dfrac{Rr}{d} < \dfrac{2}{L} \Rightarrow R_r - \dfrac{2d}{L} < 0$

$\Rightarrow R_r - \dfrac{2d}{L} - r - \sqrt{rd} < 0$ and $R_r^3 + R_r\sqrt{rd} - \dfrac{2rd}{L} \leq 0$

$\Rightarrow$ the matrix does not have a positive eigenvalue if $L \leq \dfrac{2}{R\left(\frac{r}{d} + \sqrt{\frac{r}{d}}\right)}$

So

(24) $$\sigma > 0 \quad \Leftrightarrow \quad L > \frac{2}{R\left(\frac{r}{d} + \sqrt{\frac{r}{d}}\right)}$$

The eigenvalues for the matrix in (19) are given by solutions to the equation

$$(25)\quad 0 = \begin{vmatrix} -r-\sqrt{rd}-\sigma & \sqrt{rd} & 0 & 0 & 0 \\ d/L & R_r-2d/L-\sigma & d/L & 0 & 0 \\ 0 & d/D & -r-2d/D-\sigma & d/D & 0 \\ 0 & 0 & d/\ell & R_r-\frac{2d}{\ell}-\sigma & \frac{d}{\ell} \\ 0 & 0 & 0 & \sqrt{rd} & -r-\sqrt{rd} \end{vmatrix}$$

Since system (19) is 5×5 versus 3×3 in system (18), (25) is more complicated to analyze in terms of the system parameters than is (20). We can, however, understand what happens as $D\to 0$ and $D\to\infty$ well-enough to compare with the single patch case.

For any $D>0$, (25) $\Longleftrightarrow$

$$0 = \frac{d}{D}\begin{vmatrix} -r-\sqrt{rd}-\sigma & \sqrt{rd} & 0 & 0 & 0 \\ d/L & R_r-\frac{2d}{L}-\sigma & d/L & 0 & 0 \\ 0 & 1 & \frac{D}{d}(-r-\sigma)-2 & 1 & 0 \\ 0 & 0 & d/\ell & R_r-\frac{2d}{\ell}-\sigma & \frac{d}{\ell} \\ 0 & 0 & 0 & \sqrt{rd} & -r-\sqrt{rd}-\sigma \end{vmatrix}$$

$\Longleftrightarrow$

$$0 = \frac{d^5}{\sqrt{rd}} \begin{vmatrix} -\frac{r}{d} - \sqrt{\frac{r}{d}} - \frac{\sigma}{d} & \sqrt{\frac{r}{d}} & 0 & 0 & 0 \\ \frac{1}{L} & R\frac{r}{d} - \frac{2}{L} - \frac{\sigma}{d} & \frac{1}{L} & 0 & 0 \\ 0 & \sqrt{\frac{r}{d}} & \sqrt{\frac{r}{d}}\frac{D}{d}(-r-\sigma) - 2\sqrt{\frac{r}{d}} & \sqrt{\frac{r}{d}} & 0 \\ 0 & 0 & \frac{1}{\ell} & R\frac{r}{d} - \frac{2}{\ell} - \frac{\sigma}{d} & \frac{1}{\ell} \\ 0 & 0 & 0 & \sqrt{\frac{r}{d}} & -\frac{r}{d} - \sqrt{\frac{r}{d}} - \frac{\sigma}{d} \end{vmatrix}$$

Letting $D \to 0$, one has

$$0 = \begin{vmatrix} -\frac{r}{d} - \sqrt{\frac{r}{d}} - \frac{\sigma}{d} & \sqrt{\frac{r}{d}} & 0 & 0 & 0 \\ \frac{1}{L} & R\frac{r}{d} - \frac{2}{L} - \frac{\sigma}{d} & \frac{1}{L} & 0 & 0 \\ 0 & \sqrt{\frac{r}{d}} & -2\sqrt{\frac{r}{d}} & \sqrt{\frac{r}{d}} & 0 \\ 0 & 0 & \frac{1}{\ell} & R\frac{r}{d} - \frac{2}{\ell} - \frac{\sigma}{d} & \frac{1}{\ell} \\ 0 & 0 & 0 & \sqrt{\frac{r}{d}} & -\frac{r}{d} - \sqrt{\frac{r}{d}} - \frac{\sigma}{d} \end{vmatrix}$$

Set $\rho = \frac{r}{d}$.

The equation for σ when $D = 0$ becomes

(26) $$0 = \frac{\sqrt{\rho}}{L}\left(\rho+\sqrt{\rho}+\frac{\sigma}{d}\right)\left\{\left(R\rho-\frac{2}{\ell}-\frac{\sigma}{d}\right)\left(-\rho-\sqrt{\rho}-\frac{\sigma}{d}\right)-\frac{\sqrt{\rho}}{\ell}\right\}$$

$$-2\sqrt{\rho}\left\{\left(-\rho-\sqrt{\rho}-\frac{\sigma}{d}\right)\left(R_\rho-\frac{2}{L}-\frac{\sigma}{d}\right)-\frac{\sqrt{\rho}}{L}\right\}$$

$$\times\left\{\left(R_\rho-\frac{2}{\ell}-\frac{\sigma}{d}\right)\left(-\rho-\sqrt{\rho}-\frac{\sigma}{d}\right)-\frac{\sqrt{\rho}}{\ell}\right\}$$

$$+\frac{\sqrt{\rho}}{\ell}\left(\rho+\sqrt{\rho}+\frac{\sigma}{d}\right)\left\{\left(R_\rho-\frac{2}{L}-\frac{\sigma}{d}\right)\left(-\rho-\sqrt{\rho}-\frac{\sigma}{d}\right)-\frac{\sqrt{\rho}}{L}\right\}$$

Admittedly, (26) is something of a mess. However, one can readily observe that the highest order term in σ is $-\frac{2\sqrt{\rho}}{d^4}\sigma^4$. So if the expression is positive when $\sigma = 0$, it has a positive root!

Setting $\sigma = 0$ in (26), the RHS of (26) simplifies to

(27) $$\rho\sqrt{\rho}\left(\frac{R(\rho+\sqrt{\rho})(3\rho+\sqrt{\rho})}{L}+\frac{R(\rho+\sqrt{\rho})(3\rho+\sqrt{\rho})}{\ell}-\frac{2(2\rho+\sqrt{\rho})}{L\ell}-2R^2\rho(\rho+\sqrt{\rho})^2\right)$$

Set $k = R(\rho+\sqrt{\rho})(L+\ell)$

k is a parameter between 2 and 4

If k is fixed, $L = \dfrac{k}{R(\rho+\sqrt{\rho})} - \ell$

Use this to write (28) in terms of ℓ as

$$f_k(\ell) = (3\rho+\sqrt{\rho})k - 2R^2\rho(\rho+\sqrt{\rho})^2\left[\frac{k}{R(\rho+\sqrt{\rho})} - \ell\right]\ell$$
$$- 2(2\rho+\sqrt{\rho})$$
$$= (3\rho+\sqrt{\rho})k - 2R\rho(\rho+\sqrt{\rho})k\ell$$
$$+ 2R^2\rho(\rho+\sqrt{\rho})^2\ell^2 - 2(2\rho+\sqrt{\rho})$$

$$f_k'(\ell) = -2R\rho(\rho+\sqrt{\rho})k + 4R^2\rho(\rho+\sqrt{\rho})^2\ell$$

$$f_k''(\ell) = 4R^2\rho(\rho+\sqrt{\rho})^2$$

$f_k(\ell)$ has its absolute minimum when $f_k'(\ell) = 0$

$$\Leftrightarrow \quad 4R^2\rho(\rho+\sqrt{\rho})^2\ell = 2R\rho(\rho+\sqrt{\rho})k$$

$$\Leftrightarrow \quad \ell = \frac{2R\rho(\rho+\sqrt{\rho})k}{4R^2\rho(\rho+\sqrt{\rho})^2}$$

$$= \frac{k}{2R(\rho+\sqrt{\rho})} = \frac{L+\ell}{2}$$

So $f_k(\ell) \geq f_k\left(\frac{k}{2R(\rho+\sqrt{\rho})}\right)$

$$= (3\rho+\sqrt{\rho})k - 2R^2\rho(\rho+\sqrt{\rho})^2\left[\frac{k}{R(\rho+\sqrt{\rho})} - \frac{k}{2R(\rho+\sqrt{\rho})}\right]\frac{k}{2R(\rho+\sqrt{\rho})}$$

$$- 2(2\rho+\sqrt{\rho})$$

$$= (3\rho+\sqrt{\rho})k - 2R^2\rho(\rho+\sqrt{\rho})^2\left(\frac{k}{2R(\rho+\sqrt{\rho})}\right)^2$$

$$- 2(2\rho+\sqrt{\rho})$$

$$= (3\rho+\sqrt{\rho})k - \frac{\rho}{2}k^2 - 2(2\rho+\sqrt{\rho})$$

$$= (k-2)\left(-\frac{\rho}{2}k + 2\rho + \sqrt{\rho}\right)$$

Set $g(k) = (k-2)\left(-\frac{\rho}{2}k + 2\rho + \sqrt{\rho}\right)$

$g(k) = 0 \iff k = 2$ or $-\frac{\rho}{2}k + 2\rho + \sqrt{\rho} = 0$

For the latter,

$$\frac{\rho}{2}k = 2\rho + \sqrt{\rho}$$

$$\Rightarrow k = \frac{2}{\rho}\left[2\rho + \sqrt{\rho}\right] = 2\left[2 + \frac{1}{\sqrt{\rho}}\right] > 4$$

$g(3) = -\frac{\rho}{2}\cdot 3 + 2\rho + \sqrt{\rho} = \frac{\rho}{2} + \sqrt{\rho} > 0$

So $g(k) > 0$ for $k \in (2, 4)$

It follows from (27) that the sign of the RHS of (26) when $\sigma = 0$ is determined by

(28) $$R(\rho+\sqrt{\rho})(3\rho+\sqrt{\rho})(L+\ell) - 2R^2\rho(\rho+\sqrt{\rho})^2 L\ell - 2(2\rho+\sqrt{\rho})$$

In the single patch case, $\sigma > 0 \iff L > \dfrac{2}{R(\rho+\sqrt{\rho})}$

In the two patch case, if $\ell \leq L < \dfrac{2}{R(\rho+\sqrt{\rho})}$,

but $L+\ell > \dfrac{2}{R(\rho+\sqrt{\rho})}$, we have

(29) $$\frac{2}{R(\rho+\sqrt{\rho})} < L+\ell < \frac{4}{R(\rho+\sqrt{\rho})}$$

We can show that the quantity in (28) is positive for all $\ell \leq L$ which are such that (29) holds. This means that the quantity corresponding to (28) when $D > 0$ but small is positive when (15) holds. When $D > 0$, the highest order term in the equation for the eigenvalues of the two patch model is

$$-\sqrt{\frac{r}{d}}\,\frac{D}{d^3}\,\sigma^5$$

So we may conclude that $\sigma > 0$ if $\ell \leq L < \dfrac{2}{R(\rho+\sqrt{\rho})}$

and $D > 0$ but small. Roughly

$L + \ell > \frac{2}{R(\rho + \sqrt{\rho})}$

this captures the qualitative features of the reaction-diffusion model. However, the quantity in (28) remains positive

when $\ell \leq L < \frac{2}{R(\rho+\sqrt{\rho})}$ but $L + \ell = \frac{2}{R(\rho+\sqrt{\rho})}$

unless $L = \ell = \frac{1}{R(\rho+\sqrt{\rho})}$

So the two patch model yields $\sigma > 0$ when

$$\ell \leq L < \frac{2}{R(\rho+\sqrt{\rho})}, \quad L+\ell = \frac{2}{R(\rho+\sqrt{\rho})} \quad \text{and } D > 0$$

but small unless $\ell = L = \frac{1}{R(\rho+\sqrt{\rho})}$. In that case, $\sigma = 0$ is a root of (26).

Next, re-examine (25) and let $D \to \infty$. The eigenvalue equation simplifies in this case to

$$0 = (-r-\sigma)\begin{vmatrix} -r-\sqrt{rd}-\sigma & \sqrt{rd} \\ d/L & Rr - \frac{2d}{L} - \sigma \end{vmatrix}\begin{vmatrix} Rr - \frac{2d}{\ell} - \sigma & d/\ell \\ \sqrt{rd} & -r-\sqrt{rd}-\sigma \end{vmatrix}$$

It turns out here that we get a positive root $\sigma \iff$

$$L > \frac{2}{R(\rho+\sqrt{\rho})}, \text{ the same condition as for a single patch.}$$

So we get $\sigma > 0$ when D is large only if the larger patch is sufficient to sustain the population in the single patch model.

C. Discrete-Diffusion Formulation (Abbreviated Model)

If we do not consider loss to $-\infty$ and $+\infty$ from favorable habitat patches but only consider the matrix environment between favorable habitat patches, we get the following reduced model:

(30)
$$\frac{du_1}{dt} = rRu_1 - \frac{du_1}{L} + \frac{du_2}{L}$$
$$\frac{du_2}{dt} = -ru_2 + \frac{du_1}{D} - \frac{2d}{D}u_2 + \frac{du_3}{D}$$
$$\frac{du_3}{dt} = rRu_3 + \frac{du_2}{\ell} - \frac{du_3}{\ell}$$

The eigenvalue equation becomes

(31)
$$\begin{vmatrix} rR - \frac{d}{L} - \sigma & d/L & 0 \\ d/D & -r - \frac{2d}{D} - \sigma & d/D \\ 0 & d/\ell & rR - \frac{d}{\ell} - \sigma \end{vmatrix} = 0$$

By factoring out d from each row and letting

$\rho = \frac{r}{d}$, (31) becomes

$$\begin{vmatrix} R\rho - \frac{1}{L} - \frac{\sigma}{D} & \frac{1}{L} & 0 \\ \frac{1}{D} & -\rho - \frac{2}{D} - \frac{\sigma}{d} & \frac{1}{D} \\ 0 & \frac{1}{\ell} & R\rho - \frac{1}{\ell} - \frac{\sigma}{d} \end{vmatrix} = 0$$

Here if $D \to 0$, one gets that $\sigma = Rr$ or $\sigma = Rr - \frac{d}{2}\left(\frac{1}{L} + \frac{1}{\ell}\right)$, so there is always a prediction of persistence for small D (since there is no loss outside the system.)

When $D \to \infty$, one gets $\sigma = -r,\ Rr - \frac{d}{L},\ Rr - \frac{d}{\ell}$, meaning persistence occurs when D is large provided $L > \frac{1}{R\rho}$. (Here the limiting system is no longer closed.)

Lecture 11 (cont.)

D. Integro-difference formulation.

Starting Point: R.W. Van Kirk and M.A. Lewis, Bulletin of Mathematical Biology 59 (1997), 107-137. (particularly equation (26), p. 118)

Note: In Van Kirk and Lewis, the existence of eigenvalues for (26) can be based on operator theoretic results for so-called Hilbert-Schmidt operators (interval is bounded). In our case, we pose our problem on the real line, where the exponential kernel does not yield a Hilbert-Schmidt integral operator. However, we can base our results on Brown, Cosner and Fleckinger (1991), as in the reaction-diffusion formulation.

The equation corresponding to eq. (26), p. 118 in Van Kirk and Lewis is

$$\lambda \phi(x) = \int_{-\infty}^{\infty} k(x-y)\, m(y)\, \phi(y)\, dy \tag{32}$$

where $k(x-y) = a/_2 \exp(-a|x-y|)$

$$m(y) = \begin{cases} e^{-s} & -\infty < y < 0 \\ e^{r} & 0 < y < L \\ e^{-s} & L < y < L+D \\ e^{r} & L+D < y < L+D+\ell \\ e^{-s} & y > L+D+\ell \end{cases}$$

As in VanKirk and Lewis, one may calculate that

$$(33) \quad \phi'' = \begin{cases} \left(1 - \frac{e^{-s}}{\lambda}\right) a^2 \phi & -\infty < x < 0,\ L < x < L+D,\ x > L+D+\ell \\ \left(1 - \frac{e^{r}}{\lambda}\right) a^2 \phi & 0 < x < L,\ L+D < x < L+D+\ell \end{cases}$$

Here (i) ϕ, ϕ' should be continuous, $\phi > 0$

(ii) $\lambda > e^{-s}$ (want ϕ bounded at $\pm\infty$, $\lambda > e^{-s}$ gives decaying exponentials at $\pm\infty$),

(iii) $\lambda < e^{r}$ (gives sine/cosine terms that allow one to match across interfaces).

We will take $a = 1$ for simplicity, though this is not strictly speaking necessary.

So we have

$$(34) \quad \phi'' + m(x, \lambda)\phi = 0$$

on $\mathbb{R}$. The results of Brown, Cosner and Fleckinger (1991) guarantee the existence of a principal eigenvalue

$$\mu(\lambda)$$

for the problem with corresponding positive eigenfunction.

If $\mu(\lambda) = 1$, then λ is an eigenvalue for (32).

If $\lambda > 1$, (32) predicts growth whereas (32) predicts decline and extinction if $0 < \lambda < 1$.

Our candidate for ϕ (using the definition of m and smoothness of ϕ) is

$$(35) \qquad \phi(x) = \begin{cases} \exp\left(\sqrt{1-\frac{e^{-s}}{\lambda}}\, x\right), & -\infty < x < 0 \\ c_1 \cos\left(\sqrt{\frac{e^{r}}{\lambda}-1}\, x\right) + c_2 \sin\left(\sqrt{\frac{e^{r}}{\lambda}-1}\, x\right), & 0 < x < L \\ c_3 \cosh\left(\sqrt{1-\frac{e^{-s}}{\lambda}}\,(x-L)\right) + c_4 \sinh\left(\sqrt{1-\frac{e^{-s}}{\lambda}}\,(x-L)\right), & L < x < L+D \\ c_5 \cos\left(\sqrt{\frac{e^{r}}{\lambda}-1}\,(x-L-D)\right) + c_6 \sin\left(\sqrt{\frac{e^{r}}{\lambda}-1}\,(x-L-D)\right), & L+D < x < L+D+\ell \\ c_7 \exp\left(-\sqrt{1-\frac{e^{-s}}{\lambda}}\,(x-L-D-\ell)\right), & x > L+D+\ell \end{cases}$$

Matching across the interfaces leads to (similarly to the R-D case)

$$(36) \qquad \coth\left(\sqrt{1-\frac{e^{-s}}{\lambda}}\, D\right) = \frac{\dfrac{e^{r}-e^{-s}}{\sqrt{(\lambda-e^{-s})(e^{r}-\lambda)}} \sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\, L\right) \sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\, \ell\right)}{-\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell) + \sin^{-1}\left(\frac{e^{r}-2\lambda+e^{-s}}{e^{r}-e^{-s}}\right)\right)} - 1$$

which can be re-written as

(37) $$\sqrt{\lambda - e^{-s}}\,\coth\left(\sqrt{\frac{\lambda - e^{-s}}{\lambda}}\,D\right) + \sqrt{\lambda - e^{-s}}$$

$$= \frac{\dfrac{e^{r} - e^{-s}}{\sqrt{e^{r} - \lambda}}\,\sin\left(\sqrt{\dfrac{e^{r}-\lambda}{\lambda}}\,L\right)\sin\left(\sqrt{\dfrac{e^{r}-\lambda}{\lambda}}\,\ell\right)}{-\cos\left(\sqrt{\dfrac{e^{r}-\lambda}{\lambda}}\,(L+\ell) + \sin^{-1}\left(\dfrac{e^{r} - 2\lambda + e^{-s}}{e^{r} - e^{-s}}\right)\right)}$$

To delineate (36) or (37), we will require an analysis of the special case of a single patch of favorable habitat. In this case,

(38) $$m(y) = \begin{cases} e^{-s} & -\infty < y < 0 \\ e^{r} & 0 < y < L+\ell \\ e^{-s} & y > L+\ell \end{cases}$$

Here we can exploit the fact that we have spatial symmetry about the center of the favorable habitat of length $L+\ell$.

So doing we need only consider $[0,\infty)$ and we have as the form for ϕ

(39) $$\phi(x) = \begin{cases} \cos\left(\sqrt{\frac{e^{r}}{\lambda} - 1}\,x\right), & x \in \left[0, \frac{L+\ell}{2}\right] \\ c_1 \exp\left(-\sqrt{1 - \frac{e^{-s}}{\lambda}}\left(x - \left(\frac{L+\ell}{2}\right)\right)\right), & x \geq \frac{L+\ell}{2} \end{cases}$$

So $$\phi\left(\frac{L+\ell}{2}-\right) = \cos\left(\sqrt{\frac{e^r}{\lambda}-1}\left(\frac{L+\ell}{2}\right)\right)$$

$$\phi\left(\frac{L+\ell}{2}+\right) = c_1$$

$$\phi'\left(\frac{L+\ell}{2}-\right) = -\sqrt{\frac{e^r}{\lambda}-1}\,\sin\left(\sqrt{\frac{e^r}{\lambda}-1}\left(\frac{L+\ell}{2}\right)\right)$$

$$\phi'\left(\frac{L+\ell}{2}+\right) = -c_1\sqrt{1-\frac{e^{-s}}{\lambda}}$$

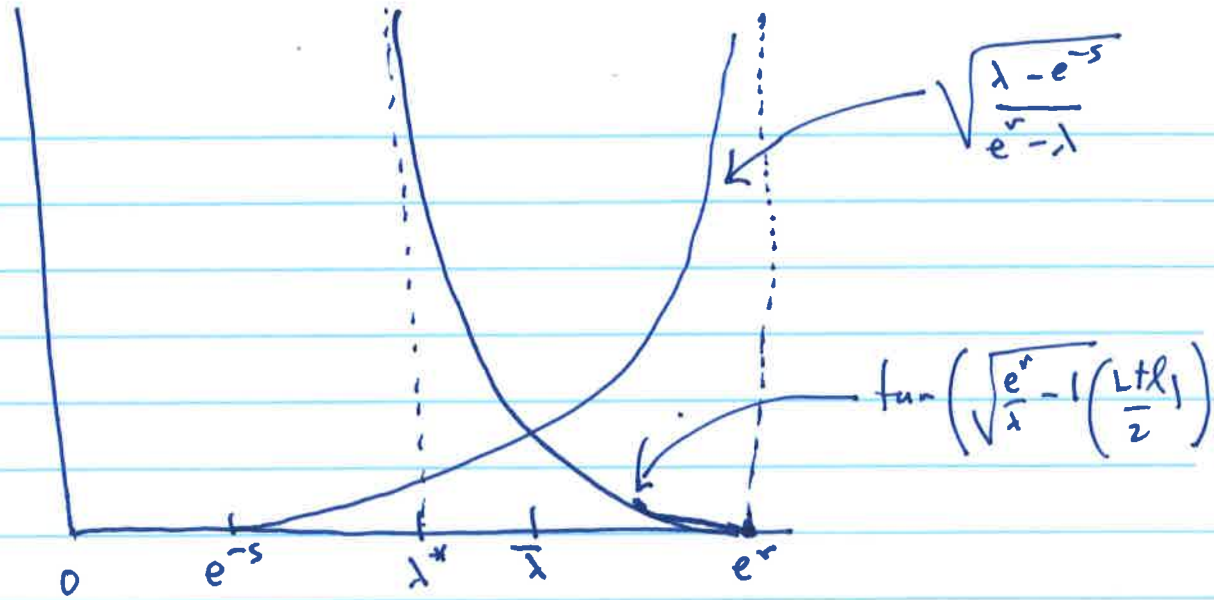
So we get

(40) $$\cos\left(\sqrt{\frac{e^r}{\lambda}-1}\left(\frac{L+\ell}{2}\right)\right) = c_1 = \frac{\sqrt{\frac{e^r}{\lambda}-1}\,\sin\left(\sqrt{\frac{e^r}{\lambda}-1}\left(\frac{L+\ell}{2}\right)\right)}{\sqrt{1-\frac{e^{-s}}{\lambda}}}$$

yielding

(41) $$\tan\left(\sqrt{\frac{e^r}{\lambda}-1}\left(\frac{L+\ell}{2}\right)\right) = \frac{\sqrt{1-\frac{e^{-s}}{\lambda}}}{\sqrt{\frac{e^r}{\lambda}-1}} = \sqrt{\frac{\lambda-e^{-s}}{e^r-\lambda}}$$

One can readily examine (41) graphically.



Here λ^* is the unique positive value of λ so that

$$\sqrt{\frac{e^{r}}{\lambda^*} - 1}\left(\frac{L+\ell}{2}\right) = \pi/2$$

The picture is drawn as if $e^{-s} < \lambda^*$. Such need not be the case. Nevertheless, the curves have a unique intersection at a point

$$\bar{\lambda} > \max\{\lambda^*, e^{-s}\}$$

which is such that

(42) $$\sqrt{\frac{e^{r}}{\bar{\lambda}} - 1}\left(\frac{L+\ell}{2}\right) < \frac{\pi}{2}$$

So ϕ as constructed is positive. So (32) admits a positive solution, which means that $\mu(m(x,\lambda)) = 1$ in this case and that ϕ is a positive eigenfunction for the integral operator corresponding to $\bar{\lambda}$. Note that

$\bar{\lambda} > 1$ and the integrodifference model predicts growth provided

$$\frac{(L+\ell)^2}{(L+\ell)^2 + \pi^2} e^r > 1$$

as

$$\bar{\lambda} > \left(\frac{(L+\ell)^2}{(L+\ell)^2 + \pi^2} \right) e^r$$

Note: Since $e^r > 1$, this gives $\bar{\lambda} > 1$ if $L+\ell$

is large enough.

For (37), we can check that the value $\bar{\lambda}$ in condition (41) which determines solvability when $D = 0$ corresponds to the largest value of λ for which the RHS of (37) has a singularity. Moreover, if we let

$$g^*(\lambda) = \frac{\dfrac{e^r - e^{-s}}{\sqrt{e^r - \lambda}} \sin\left(\sqrt{\frac{e^r}{\lambda} - 1}\, L\right) \sin\left(\sqrt{\frac{e^r}{\lambda} - 1}\, \ell\right)}{-\cos\left(\sqrt{\frac{e^r}{\lambda} - 1}\,(L+\ell) + \sin^{-1}\left(\frac{e^r - 2\lambda + e^{-s}}{e^r - e^{-s}}\right)\right)}$$

$$\lim_{\lambda \to \bar{\lambda}^-} g^*(\lambda) = +\infty, \quad \lim_{\lambda \to \bar{\lambda}^+} g^*(\lambda) = -\infty$$

and $g^*(\lambda) < 0$ on $(\bar{\lambda}, e^r]$

Since the LHS of (37) is positive on (e^{-s}, e^{r}), $\bar{\lambda}$ is an upper bound for λ satisfying (37) for $D > 0$.

Now consider (35). Since $\phi(x) = c_1 \cos\sqrt{\frac{e^r}{\lambda} - 1}\, x + c_2 \sin\sqrt{\frac{e^r}{\lambda} - 1}\, x$

$= \hat{c} \sin\left(\sqrt{\frac{e^r}{\lambda} - 1}\, x + \tilde{\varphi}\right)$ on $(0, L)$ for some $\tilde{c}, \tilde{\varphi}$,

having a positive ϕ requires

(43) $$\sqrt{\frac{e^r}{\lambda} - 1} \cdot L < \pi \iff \lambda > e^r\left(\frac{L^2}{L^2 + \pi^2}\right)$$

$\boxed{\text{Singularity Argument}}$

Now assume $\tan\left(\sqrt{\frac{e^r - \lambda}{\lambda}}\left(\frac{L+\ell}{2}\right)\right) = \sqrt{\frac{\lambda - e^{-s}}{e^r - \lambda}}$

Then $\tan\left(\sqrt{\frac{e^r - \lambda}{\lambda}}\,(L+\ell)\right) = \tan\left(2\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\left(\frac{L+\ell}{2}\right)\right)\right)$

$$= \frac{2\tan\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\left(\frac{L+\ell}{2}\right)\right)}{1 - \tan^2\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\left(\frac{L+\ell}{2}\right)\right)}$$

$$= \frac{2\sqrt{\frac{\lambda - e^{-s}}{e^r - \lambda}}}{1 - \left(\frac{\lambda - e^{-s}}{e^r - \lambda}\right)} = \frac{2\sqrt{(\lambda - e^{-s})(e^r - \lambda)}}{e^r - 2\lambda + e^{-s}} = \frac{2}{\gamma - \frac{1}{\gamma}}$$

where $\gamma = \sqrt{\frac{e^r - \lambda}{\lambda - e^{-s}}}$

$$\therefore \quad \frac{\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)}{\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)} = \frac{2}{\gamma - \frac{1}{\gamma}}$$

$$\Rightarrow \; 2\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right) - \left(\gamma - \tfrac{1}{\gamma}\right)\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right) = 0$$

$$\Rightarrow \; \frac{2}{\gamma + \frac{1}{\gamma}}\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right) - \left(\frac{\gamma - \frac{1}{\gamma}}{\gamma + \frac{1}{\gamma}}\right)\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right) = 0$$

$$\Rightarrow \; \cos\left(\sin^{-1}\left(\frac{\gamma - \frac{1}{\gamma}}{\gamma + \frac{1}{\gamma}}\right)\right)\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right) - \sin\left(\sin^{-1}\left(\frac{\gamma - \frac{1}{\gamma}}{\gamma + \frac{1}{\gamma}}\right)\right)\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)$$

$$= 0$$

$$\Rightarrow \; \cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell) + \sin^{-1}\left(\frac{\gamma - \frac{1}{\gamma}}{\gamma + \gamma}\right)\right) = 0$$

$\Rightarrow$ RHS of (37) is singular.

Suppose now that the RHS of (37) is singular.

Then
$$\frac{\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)}{\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)} = \frac{\frac{2}{\gamma + \frac{1}{\gamma}}}{\frac{\gamma - \frac{1}{\gamma}}{\gamma + \frac{1}{\gamma}}}$$

So we can take $\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right) = \frac{2}{\gamma + \frac{1}{\gamma}}$

and $\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\,(L+\ell)\right) = \dfrac{\gamma - 1/\gamma}{\gamma + 1/\gamma}$

Then $\tan\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\left(\frac{L+\ell}{2}\right)\right)$

$$= \frac{1 - \cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\,(L+\ell)\right)}{\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\,(L+\ell)\right)}$$

$$= \frac{1 - \left(\frac{\gamma - 1/\gamma}{\gamma + 1/\gamma}\right)}{\frac{2}{\gamma + 1/\gamma}} = \frac{\frac{\gamma + 1/\gamma - (\gamma - 1/\gamma)}{\gamma + 1/\gamma}}{\frac{2}{\gamma + 1/\gamma}}$$

$$= \frac{2/\gamma}{2} = \frac{1}{\gamma} = \sqrt{\frac{\lambda - e^{-s}}{e^r - \lambda}}$$

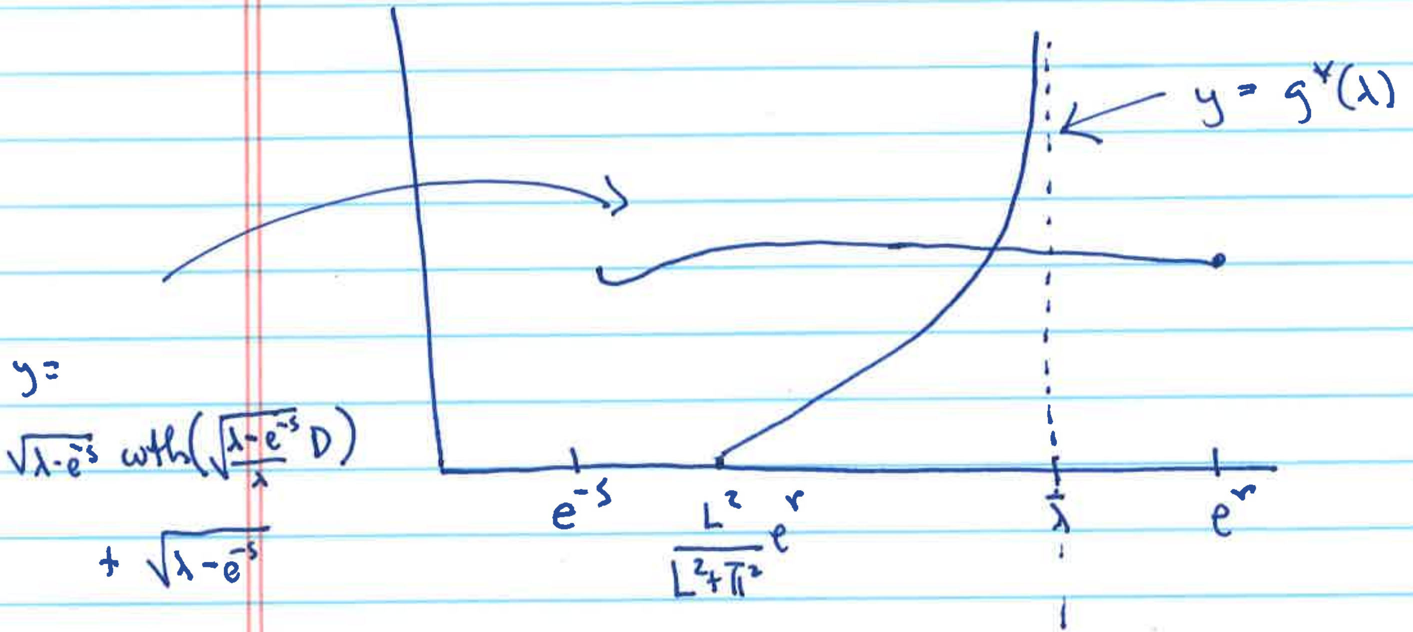
End of singularity Argument

So all values λ for $D > 0$ must be in the interval $\left[\frac{L^2}{L^2+\pi^2}e^r, \bar{\lambda}\right]$

If we let $\lambda = \frac{L^2}{L^2+\pi^2}e^r$,

$$\sin\left(\sqrt{\frac{e^r}{\lambda}-1}\;L\right) = \sin\left(\sqrt{\frac{L^2+\pi^2}{L^2}-1}\cdot L\right) = \sin\left(\frac{\pi}{L}\cdot L\right) = \sin\pi = 0$$

So graphing the LHS and RHS of (37) simultaneously gives



Note: We have drawn the picture as if $e^{-s} < \frac{L^2}{L^2+\pi^2}e^{r}$.

It does not matter whether such is the case or not. We still get an intersection at a point

$$\lambda > \max\left\{ e^{-s}, \frac{L^2}{L^2+\pi^2}e^{r} \right\}$$

* check

We can argue that there is exactly one intersection.

If we let $D \to +\infty$, (37) reduces to

(44)
$$2 = \frac{\dfrac{e^{r} - e^{-s}}{\sqrt{(\lambda - e^{-s})(e^{r}-\lambda)}}\, \sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\, L\right)\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\, \ell\right)}{-\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell) + \sin^{-1}\left(\frac{e^{r}-2\lambda+e^{-s}}{e^{r}-e^{-s}}\right)\right)}$$

Let $\theta = \sin^{-1}\left(\dfrac{e^{r}-2\lambda+e^{-s}}{e^{r}-e^{-s}}\right)$.

Then $$\sin\theta = \frac{e^{r}-2\lambda+e^{-s}}{e^{r}-e^{-s}}$$

$$\cos\theta = \frac{2\sqrt{(\lambda-e^{-s})(e^{r}-\lambda)}}{e^{r}-e^{-s}}$$

so that

$$\cos\theta = \frac{\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\, L\right)\sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\, \ell\right)}{-\cos\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)\cos\theta + \sin\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,(L+\ell)\right)\sin\theta}$$

So
$$-\cos\theta\left[\cos\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, L\right)\cos\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, \ell\right) - \sin\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, L\right)\sin\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, \ell\right)\right]\cos\theta$$
$$+\cos\theta\left[\sin\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, L\right)\cos\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, \ell\right) + \cos\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, L\right)\sin\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, \ell\right)\right]\sin\theta$$
$$-\sin\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, L\right)\sin\left(\sqrt{\tfrac{e^{r}-\lambda}{\lambda}}\, \ell\right) = 0$$

$$\Leftrightarrow \left(\cos^2\theta - 1\right)\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)$$

$$+ \cos\theta\sin\theta\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)$$

$$+ \cos\theta\sin\theta\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)$$

$$- \cos^2\theta\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right) = 0$$

$$\Leftrightarrow -\sin^2\theta\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)$$

$$+\cos\theta\sin\theta\left(\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)\right)$$

$$+\cos\theta\sin\theta\left(\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)\right)$$

$$-\cos^2\theta\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right) = 0$$

$$\Leftrightarrow$$

(45) $$\left(-\sin\theta\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right) + \cos\theta\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\right)$$

$$\left(\sin\theta\sin\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right) - \cos\theta\cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}\ell\right)\Bigg) = 0$$

From (45) we get

$$-\sin\theta\sin\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right) + \cos\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right)\cos\theta = 0$$

or $$\tan\left(\sqrt{\frac{e^r-\lambda}{\lambda}}L\right) = \frac{\cos\theta}{\sin\theta} = \frac{2\sqrt{(\lambda-e^{-s})(e^r-\lambda)}}{e^r-2\lambda+e^{s}} = \frac{2\left(\sqrt{\frac{\lambda-e^{s}}{e^r-\lambda}}\right)}{\frac{e^r-2\lambda+e^{-s}}{e^r-\lambda}}$$

$$= \frac{2\left(\sqrt{\frac{\lambda - e^{-s}}{e^{r}-\lambda}}\right)}{1-\left(\sqrt{\frac{\lambda-e^{-s}}{e^{r}-\lambda}}\right)^2}$$ so that

(46) $$\tan\left(\sqrt{\frac{e^{r}-\lambda}{\lambda}}\,\frac{L}{2}\right) = \sqrt{\frac{\lambda-e^{-s}}{e^{r}-\lambda}}$$

(46) is the equation for the eigenvalue λ in (32) for the situation of a single patch of habitat of length L

Let $\bar{\bar{\lambda}} > \max\left\{\frac{L^2}{L^2+\pi^2}e^{r}, e^{-s}\right\}$ denote the value of λ satisfying (46). (37) is equivalent to (36). $\bar{\bar{\lambda}}$ corresponds to the unique value of $\lambda >$ $\max\left\{\frac{L^2}{L^2+\pi^2}e^{r}, e^{-s}\right\}$ for which the RHS of (36) is equal to 1, by (44).

For $\lambda \in (\bar{\bar{\lambda}}, \bar{\lambda})$, the RHS of (36) must always exceed 1. Again, denote the RHS of (36) by $g(\lambda)$. So for $\lambda \in (\bar{\bar{\lambda}}, \bar{\lambda})$, $g(\lambda) > 1$,

g is smooth and $\lim_{\lambda \to \bar{\lambda}^-} g(\lambda) = +\infty$.

Therefore, for $\lambda \in (\bar{\bar{\lambda}}, \bar{\lambda})$, (36) is equivalent to

(47) $$D = \frac{1}{2}\sqrt{\frac{\lambda}{\lambda - e^{-s}}} \ln\left(\frac{g(\lambda)+1}{g(\lambda)-1}\right)$$

We use (47) to define $D(\lambda)$ for $\lambda \in (\bar{\bar{\lambda}}, \bar{\lambda})$

Then $m(x,\lambda)$ with $D = D(\lambda)$ has the property that

$$\lambda \to m(x,\lambda)$$

is continuous as a map from $(\bar{\bar{\lambda}}, \bar{\lambda}]$ into $L^p_{loc}(\mathbb{R})$ for any $p \in [1,\infty)$ (Note that $\lim_{\lambda \to \bar{\lambda}} D(\lambda) = 0$)

For any such λ, $m(x,\lambda)$ satisfies the hypotheses of Theorem 2.1 of Brown, Cosner and Fleckinger (1991).

So the eigenvalue problem

(48) $$\phi'' = \mu m(x,\lambda)\phi \quad \text{on } (-\infty,\infty)$$
$$\phi \to 0 \quad \text{as } x \to \pm\infty$$

admits a unique principal positive eigenvalue $\mu(\lambda)$ given by

(49) $$\mu(\lambda) = \inf \left\{ \int_{\mathbb{R}} (u'')^2 \Big/ \int_{\mathbb{R}} m(x,\lambda) u^2 \;\Big|\; u \in H^1(\mathbb{R}),\ \int_{\mathbb{R}} m(x,\lambda) u^2 > 0 \right\}$$

Since $\lambda \to m(x,\lambda)$ is continuous from $(\bar{\bar{\lambda}}, \bar{\lambda}]$ into $L^p_{loc}(\mathbb{R})$ for any $p \in [1,\infty)$, it follows that $\lambda \to \mu(\lambda)$ is continuous from $(\bar{\bar{\lambda}}, \bar{\lambda}]$ into $\mathbb{R}$.

Now λ is an eigenvalue for (32) $\Leftrightarrow \mu(\lambda) = 1$.
Now $D(\bar{\lambda}) = 0$ and $\phi(\bar{\lambda}) > 0$ on $\mathbb{R}$ by construction It follows that $\mu(\bar{\lambda}) = 1$.

The functions we construct by the matching process with $D = D(\lambda)$ have the property that $\phi(\lambda) \to \phi(\bar{\lambda})$ uniformly on any bounded subset of $\mathbb{R}$ as $\lambda \to \bar{\lambda}$.

In particular, we have convergence on $[a,b]$ where $a < 0$ is arbitrary and $b > L + \ell$.

For λ close enough to $\bar{\lambda}$, $L+\ell+D(\lambda) < b$ and $\phi(\lambda)$ is positive on $[a,b]$. Since $m(x,\lambda)$ is a positive constant on $(-\infty,0) \cup (L+\ell+D(\lambda),\infty)$, it must be the case that $\phi(\lambda)$ is in fact positive on $\mathbb{R}$ for λ close enough to $\bar{\lambda}$. So $\phi(\lambda)$ is a solution of (33) and is positive on $\mathbb{R}$. $\therefore$ $\mu(\lambda) \equiv 1$ for λ close enough to $\bar{\lambda}$.

So we have $\mu(\lambda) = 1$ with eigenfunction $\phi(\lambda) > 0$ on $\mathbb{R}$ for $\lambda \in (\hat{\lambda}, \bar{\lambda})$ for some $\hat{\lambda} < \bar{\lambda}$. Since $\phi(\lambda) > 0$ on $\mathbb{R}$ for $\lambda \in (\hat{\lambda}, \bar{\lambda}]$, it follows that $\phi(\hat{\lambda}) \geq 0$ on $\mathbb{R}$. $\phi(\hat{\lambda}) \not\equiv 0$ from its construction. Since

$$\phi'' - \phi \leq 0$$

on $[a,b]$ with $a < 0$ and $L+\ell+D(\hat{\lambda}) < b$

the maximum principle $\Rightarrow \phi(\tilde{\lambda}) > 0$ on $[a, b]$ and then hence on $\mathbb{R}$.

We may repeat the argument to obtain that $\mu(\lambda) \equiv 1$ on $(\bar{\bar{\lambda}}, \bar{\lambda}]$ with $\phi(\lambda)$ as constructed by the matching procedure.

It is not immediately clear that $g(\lambda)$ is monotonic on all of $[\bar{\bar{\lambda}}, \bar{\lambda})$. However, we can show by p.d.e. arguments that if L, ℓ and D are fixed, along with e^{r} and e^{-s}, then there can be only one

* check.

$\lambda \in (\bar{\bar{\lambda}}, \bar{\lambda})$ so that (33) admits a positive solution.

Were $g(\lambda)$ not monotonically increasing on all of $(\bar{\bar{\lambda}}, \bar{\lambda})$, there would be two values of λ, say λ_1 and λ_2 so that $D(\lambda_1) = D(\lambda_2)$.

Such is not possible, so $g(\lambda)$ is monotonically increasing. So for any $D > 0$, there is a unique $\lambda = \lambda(D) \in (\bar{\bar{\lambda}}, \bar{\lambda})$ so that (33) admits a positive solution.

Moreover, $\lim_{D\to 0^+} \lambda(D) = \bar{\lambda}$ and $\lim_{D\to\infty} \lambda(D) = \bar{\bar{\lambda}}$

So if $\bar{\lambda} > 1 > \bar{\bar{\lambda}}$, we have that the integro-difference model predicts growth for $D < D(1)$ and extinction for $D > D(1)$

E. Average Dispersal Success Formulation.

Original Model would have the form

$$u(x,t+1) = \int_\Omega k(x,y) e^r u(y,t)\, dy$$

Use $\bar{u} = \frac{1}{|\Omega|}\int_\Omega u(y,t)\, dy$ (average density)

$$* \quad \bar{k}(y) = \frac{1}{|\Omega|}\int_\Omega k(x,y)\, dx \quad \text{(average arrival rate) from } y$$

$$u(x,t+1) \approx e^r \int_\Omega \left(\frac{1}{|\Omega|}\int_\Omega k(x,y)\,dx\right)\left(\frac{1}{|\Omega|}\int_\Omega u(z,t)\,dz\right)dy$$

$$\approx e^r \frac{1}{|\Omega|}\left[\int_\Omega\int_\Omega k(x,y)\,dx\,dy\right]\bar{u}(t)$$

$$\bar{u}(t+1) = e^r\left(\frac{1}{|\Omega|}\right)\left(\int_\Omega\int_\Omega k(x,y)\,dx\,dy\right)\bar{u}(t)$$

For the n habitat case,

$$\bar{u}_i(t+1) = \sum_{j=1}^{n} p_{ij} e^{r_j} \bar{u}_j(t)$$

where $p_{ij} = \frac{1}{|\Omega_i|} \int_{\Omega_i} \int_{\Omega_j} k(x,y)\,dy\,dx$

and $\bar{u}_i$ = average density on patch i

(i) Model for two patches as one habitat

Let $\Omega(D) = (0,L) \cup (L+D, L+D+\ell)$

$|\Omega(D)| = L+\ell$

(50) $$\bar{u}(t+1) = \frac{e^r}{L+\ell} \left[\int_{\Omega(D)} \int_{\Omega(D)} k(x,y)\,dx\,dy \right] \bar{u}(t)$$

Note: $\int_{\Omega(D)} \int_{\Omega(D)} k(x,y)\,dx\,dy$

$$= \int_{\Omega} \int_{\Omega} k(x,y)\, \chi_{\Omega(D)}(x)\, \chi_{\Omega(D)}(y)\,dx\,dy$$

when $\Omega(D) \subseteq \Omega$. As $D \to 0$, (50) converges to the case for $D = 0$ by Dominated Convergence provided $\int_{\Omega}\int_{\Omega} k(x,y)\,dx\,dy < \infty$

In general,

$$\int_{\Omega(D)}\int_{\Omega(D)} k(x,y)\,dx\,dy = \int_0^L\int_0^L k(x,y)\,dx\,dy$$

$$+ \int_0^L\int_{L+D}^{L+D+\ell} k(x,y)\,dx\,dy + \int_{L+D}^{L+D+\ell}\int_0^{L} k(x,y)\,dx\,dy$$

$$+ \int_{L+D}^{L+D+\ell}\int_{L+D}^{L+D+\ell} k(x,y)\,dx\,dy$$

$$\to \int_0^L\int_0^L k(|x-y|)\,dx\,dy + \int_0^\ell\int_0^\ell k(|x-y|)\,dx\,dy$$

as $D \to \infty$, provided $k(x,y) = k(|x-y|)$

So (50) becomes

(51) $$\bar{u}(t+1) = \frac{e^r}{L+\ell}\Big[\int_0^L\int_0^L k(|x-y|)\,dx\,dy + \int_0^\ell\int_0^\ell k(|x-y|)\,dx\,dy\Big]$$

$\bar{u}(t)$

as $D \to \infty$.

When $k(x,y) = k(|x-y|)$, in the case of a single patch of length L, one has

(52) $$\bar{u}(t+1) = \frac{e^r}{L}\left[\int_0^L \int_0^L k(|x-y|)\,dx\,dy\right]\bar{u}(t)$$

Let $k(x,y)$ be the exponential kernel

$$k(x,y) = \frac{1}{2}e^{-|x-y|}$$

Then (51) is:

(53) $$\bar{u}(t+1) = \frac{e^r}{L+\ell}\left[L+\ell - (1-e^{-L}) - (1-e^{-\ell})\right]\bar{u}(t)$$

while (52) yields:

(54) $$\bar{u}(t+1) = \frac{e^r}{L}\left[L - (1-e^{-L})\right]\bar{u}(t)$$

It is not hard to show that

$$\frac{1}{L}\left[L-(1-e^{-L})\right] > \frac{1}{L+\ell}\left[L+\ell - (1-e^{-L}) - (1-e^{-\ell})\right]$$

for $0 < \ell < L$ with equality if $L = \ell$.

So having $\frac{e^r}{L}\left[L - (1-e^{-L})\right] > 1$

does not necessarily imply $\frac{e^r}{L+\ell}\left[L+\ell - (1-e^{-L}) - (1-e^{-\ell})\right] > 1$, BUT having $\frac{1}{L+\ell}\left[L+\ell-(1-e^{-L})-(1-e^{-\ell})\right]>1$

does imply $\frac{1}{L}\left[L-(1-e^{-L})\right]>1$

So existence on a single patch does not necessarily imply existence in the case when $D\to\infty$, but existence as $D\to\infty$ requires existence on a single patch of length L (assuming exponential kernels)

(ii) Think of the two patches as two habitats.

$$p_{11}=\frac{1}{L}\int_0^L\int_0^L k\,dy\,dx \equiv \frac{1}{L}I_1$$

$$p_{12}=\frac{1}{L}\int_0^L\int_{L+D}^{L+D+\ell} k\,dy\,dx \equiv \frac{1}{L}I_2$$

$$p_{21}=\frac{1}{\ell}\int_{L+D}^{L+D+\ell}\int_0^L k\,dy\,dx \equiv \frac{1}{\ell}I_4 = \frac{1}{\ell}I_2 \text{ if}$$

$k=k(|x-y|)$

if k is symmetric

$$p_{22}=\frac{1}{\ell}\int_{L+D}^{L+D+\ell}\int_{L+D}^{L+D+\ell} k\,dy\,dx \equiv \frac{1}{\ell}I_3 = \frac{1}{\ell}\int_0^\ell\int_0^\ell k\,dy\,dx$$

In this case the approximate model is:

(55) $$\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_{t+1} = e^r \begin{pmatrix} p_{11} & p_{12} \\ p_{21} & p_{22} \end{pmatrix} \begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_t$$

Assume $k = k(|x-y|)$ with $k(z) \to 0$ as $z \to \infty$

$D \to \infty \Rightarrow \rho_{12}, \rho_{21} \to 0$ since $|x-y| > D$

for those integrals.

So as $D \to \infty$, the system decouples and

(55) has the form

(56) $$\bar{u}_1(t+1) = \frac{e^r}{L} \int_0^L \int_0^L k(|x-y|)\,dy\,dx\; \bar{u}_1(t)$$

$$\bar{u}_2(t+1) = \frac{e^r}{\ell} \int_0^\ell \int_0^\ell k(|x-y|)\,dy\,dx\; \bar{u}_2(t)$$

On the other hand, as $D \to 0$, (55) becomes

(57) $$\begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_{t+1} = e^r \begin{pmatrix} I_1/L & I_2/L \\ I_2/\ell & I_3/\ell \end{pmatrix} \begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}_t$$

with $I_2 = \int_0^L \int_\ell^{L+\ell}$

In this setting, in a single habitat patch of the length $L+\ell$ one would have

(58) $$\bar{u}(t+1) = \frac{e^r}{L+\ell}\left(I_1 + 2I_2 + I_3\right)\bar{u}(t)$$

The characteristic polynomial of the matrix in (57) is

$$\lambda^2 - \left[\left(I_1/L\right) + \left(I_3/\ell\right)\right]\lambda + \frac{I_1 I_3 - I_2^2}{L\ell}$$

so the principal eigenvalue for (57) is:

(59) $$\lambda^* = \frac{e^r}{2}\left(\frac{I_1}{L} + \frac{I_3}{\ell} + \sqrt{\left(\frac{I_1}{L} - \frac{I_3}{\ell}\right)^2 + 4\frac{I_2^2}{L\ell}}\right)$$

If $L = \ell$, $I_1 = I_3$ and so λ^* becomes

(60) $$\lambda^* = \frac{e^r}{2L}\left(I_1 + I_3 + 2I_2\right)$$

which agrees with the case of a single patch of length $L+\ell$ in this case.

If we now let $k(x,y) = \frac{1}{2} e^{-|x-y|}$,

$$I_1 = L + (1 - e^{-L})$$

$$I_2 = \tfrac{1}{2} e^{-D} (1 - e^{-\ell})(1 - e^{-L})$$

$$I_3 = \ell + (1 - e^{-\ell})$$

If $\ell < L$, we get that

$$\lambda^* > \frac{e^r}{L+\ell} (I_1 + 2I_2 + I_3),$$

so λ^* could be > 1 for small D,

even though $\frac{e^r}{L+\ell} (I_1 + 2I_2 + I_3) < 1$

So the models do not entirely agree as $D \to 0$.

(iii) Think of the overall environment as 3 patches

$$(0, L) = \Omega_1$$
$$(L, L+D) = \Omega_2$$
$$(L+D, L+D+\ell) = \Omega_3$$

$$(61) \qquad \bar{u}_i(t+1) = \sum_{j=1}^{3} e^{r_j} p_{ij} \bar{u}_j(t) \qquad r_j = \begin{cases} r, & j = 1, 3 \\ -s, & j = 2 \end{cases}$$

$$e^{r_1} p_{11} = \frac{e^{r}}{L} \int_0^L \int_0^L k\,dy\,dx \qquad e^{r_1} p_{21} = \frac{e^{r}}{D} \int_L^{L+D} \int_0^L k\,dy\,dx$$

$$e^{r_2} p_{12} = \frac{e^{-s}}{L} \int_0^L \int_L^{L+D} k\,dy\,dx \qquad e^{r_2} p_{22} = \frac{e^{-s}}{D} \int_L^{L+D} \int_L^{L+D} k\,dy\,dx$$

$$e^{r_3} p_{13} = \frac{e^{r}}{L} \int_0^L \int_{L+D}^{L+D+\ell} k\,dy\,dx \qquad e^{r_3} p_{23} = \frac{e^{r}}{D} \int_L^{L+D} \int_{L+D}^{L+D+\ell} k\,dy\,dx$$

$$e^{r_1} p_{31} = \frac{e^{r}}{\ell} \int_{L+D}^{L+D+\ell} \int_0^L k\,dy\,dx$$

$$e^{r_2} p_{32} = \frac{e^{-s}}{\ell} \int_{L+D}^{L+D+\ell} \int_L^{L+D} k\,dy\,dx$$

$$e^{r_3} p_{33} = \frac{e^{r}}{\ell} \int_{L+D}^{L+D+\ell} \int_{L+D}^{L+D+\ell} k\,dy\,dx$$

Assume k is bounded and continuous.
Then as $D \to 0$ $e^{r_j} p_{ij}$ terms with $i \neq 2$

converge as before.

Now $\frac{1}{D} \int_L^{L+D} \left[\int_a^b k(x,y)\,dy \right] dx$

$$\to \int_a^b k(L,y)\,dy \qquad \text{as } D \to 0$$

So as $D \to 0$, the terms in (61) become:

$$e^{r_1} p_{11} = \frac{e^r}{L} \int_0^L \int_0^L k \, dy \, dx$$

$$e^{r_2} p_{12} = 0$$

$$e^{r_3} p_{13} = \frac{e^r}{L} \int_0^L \int_L^{L+\ell} k \, dy \, dx$$

$$e^{r_1} p_{21} = e^r \int_0^L k(L, y) \, dy$$

$$e^{r_2} p_{22} = 0 \quad , \text{ since } \frac{e^{-s}}{D} \int_L^{L+D} \int_L^{L+D} k \, dy \, dx$$

$$\leq (\max k) \frac{e^{-s}}{D} (D)^2 \to 0 \quad \text{as } D \to 0$$

$$e^{r_3} p_{23} = e^r \int_L^{L+\ell} k(L, y) \, dy$$

$$e^{r_1} p_{31} = \frac{e^r}{\ell} \int_L^{L+\ell} \int_0^L k \, dy \, dx$$

$$e^{r_2} p_{32} = 0$$

$$e^{r_3} p_{33} = \frac{e^r}{\ell} \int_L^{L+\ell} \int_L^{L+\ell} k \, dy \, dx$$

Thus the limiting matrix has the form

$$\begin{vmatrix} A_{11} & 0 & A_{13} \\ A_{21} & 0 & A_{23} \\ A_{31} & 0 & A_{33} \end{vmatrix}$$

which has eigenvalues $\lambda = 0$ and λ such that

$$\begin{vmatrix} \lambda - A_{11} & -A_{13} \\ -A_{31} & \lambda - A_{33} \end{vmatrix} = 0$$

This is the same as (57). So the conclusions are the same as in the case where we view the two habitats as two patches.

What happens as $D \to \infty$?

Suppose $k = k(|x-y|)$ with $k(z) \to 0$ as $z \to \infty$.

$$\int_0^L \int_{L+D}^{L+D+\ell} k(x,y)\,dy\,dx = \int_0^L \int_L^{L+\ell} k(|z-x+D|)\,dz\,dx \to 0$$

So we get $e^{r_3} p_{13} \to 0$ and $e^{r_1} p_{31} \to 0$ as $D \to \infty$

Now fix $k(x,y)$ as $\frac{1}{2}\exp(-|x-y|)$

$$\int_0^L \int_L^{L+D} k(x,y)\,dy\,dx = \frac{1}{2}\int_0^L \int_L^{L+D} e^{-y+x}\,dy\,dx = \frac{1}{2}\left(e^{-L} - e^{-L-D}\right)\int_0^L e^{x}\,dx$$

$$= \frac{1}{2}\left(1 - e^{-D} - e^{-L} + e^{-L-D}\right) \to \frac{1-e^{-L}}{2} \text{ as } D \to \infty$$

So $e^{v_2} p_{12} \to \frac{e^{-s}}{2L}(1 - e^{-L})$

$e^{v_1} p_{21} \to 0$ (Here we have $\frac{1}{\ell}$ in place of $\frac{1}{L}$)

Now $\int_{L+D}^{L+D+\ell} \int_{L}^{L+D} k \, dy \, dx = \int_{L+D}^{L+D+\ell} \int_{L}^{L+D} \frac{1}{2} e^{-x+y} \, dy \, dx$

$= \frac{1}{2}\left[1 - e^{-D} - e^{-\ell} + e^{-(D+\ell)}\right] \to \frac{1}{2}(1 - e^{-\ell})$

as $D \to \infty$

So $e^{v_3} p_{23} \to 0$

and $e^{v_2} p_{32} \to \frac{e^{-s}}{2\ell}(1 - e^{-\ell})$

$e^{v_3} p_{33} = \frac{e^{v}}{\ell} \int_0^{\ell} \int_0^{\ell} k(x,y) \, dy \, dx = \frac{e^{v}}{\ell}(\ell - (1 - e^{-\ell}))$

$= e^{v}\left(1 - \frac{1 - e^{-\ell}}{\ell}\right)$

Now $\int_{L}^{L+D} \int_{L}^{L+D} k(x,y) \, dy \, dx = \int_0^D \int_0^D k(x,y) \, dy \, dx$

$= D - (1 - e^{-D})$

So $\frac{1}{D}\int_L^{L+D}\int_L^{L+D} k\,dy\,dx = 1 - \frac{1-e^{-D}}{D} \to 1$ as $D \to \infty$

So $e^{r_2} p_{22} \to e^{-s}$

So as $D \to \infty$ the matrix becomes

$$\begin{pmatrix} \frac{e^r}{L}\int_0^L\int_0^L k & \frac{e^{-s}}{2L}(1-e^{-L}) & 0 \\ 0 & e^{-s} & 0 \\ 0 & \frac{e^{-s}}{2\ell}(1-e^{-\ell}) & \frac{e^r}{\ell}\int_0^\ell\int_0^\ell k \end{pmatrix},$$

which decouples into 3 independent patches.

In its most basic form (Levins 1969) metapopulation theory describes a species which inhabits an environment consisting of discrete sites, and which may colonize empty sites or experience local extirpations in occupied sites. Suppose now that p represents the fraction of sites under consideration

The Levins model (62) ignores aspects of the population structure (Ovaskainen and Hanski 2001), in particular the size and geographic arrangement of the patches of habitat in question. These features are incorporated into refinements of the Levins model (1), due to Hanski and his collaborators (see, for example, Hanski 1997, 1999, Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001 for discussion and references); and are of the form

(63) $$\frac{dp_i}{dt} = \Big(\sum_{\substack{j=1 \\ j\neq i}}^{n} C\, e^{-\alpha d_{ij}} A_j\, p_j\Big)(1-p_i) - \Big(\frac{E}{A_i}\Big)p_i .$$

In (63), the archipelago of habitats consists of n patches, with patch i having area A_i and d_{ij} designating the nearest distance between patch i and patch j. The state variable p_i now represents the probability that patch i is occupied by the species in question, while C,

α and E are positive rate constants describing the propensity of the species in question to send out colonists, to die during transit through the matrix between patches, and to experience local extinctions, respectively.

Let us now examine the special case of two patches in a one-dimensional world. In this case, (2) reduces to

(64)

$$\begin{aligned} \frac{dp_1}{dt} &= Ce^{-\alpha D} \ell p_2 (1-p_1) - \frac{E}{L} p_1 \\ \frac{dp_2}{dt} &= Ce^{-\alpha D} L p_1 (1-p_2) - \frac{E}{\ell} p_2, \end{aligned} \tag{3}$$

where $D = d_{12} = d_{21}$ is the distance between the two patches, $A_1 = L$ is the length of patch 1, and $A_2 = \ell$ is the length of patch 2. Without loss of generality, we adopt the convention that $\ell \leq L$. As p_1 and p_2 are interpreted as probabilities, (64) is only meaningful on the set of values

$\{(p_1, p_2) : 0 \le p_i \le 1, \; i = 1, 2\}$. It is evident from the structure of (64) that the system is invariant on this set. Moreover, it follows as in Cantrell and Cosner (2003) that (64) (3) predicts the probability that the species in question is present on both patches is positive long term precisely when the linearization of the right hand side of (64) about $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ has a positive eigenvalue which admits a componentwise positive eigenvector. Otherwise, the species is expected to go extinct on both patches. Now the linearization of the right hand side of (64) about $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ is

(65) $$\begin{pmatrix} -E/L & C e^{-\alpha D} \ell \\ C e^{-\alpha D} L & -E/\ell \end{pmatrix} \qquad (4)$$

Since the off-diagonal terms in (65) are both positive, it follows from the theory of nonnegative matrices (Berman and Plemmons 1979) that both eigenvalues of (65) are real-valued and that the larger of the two eigenvalues admits a componentwise positive eigenvector. It is easy to calculate that the eigenvalues of $\Lambda^{(65)}$ are

$$\frac{-\frac{E(L+\ell)}{L\ell} \pm \sqrt{\left(\frac{E(L+\ell)}{L\ell}\right)^2 + 4C^2 e^{-2\alpha D} L\ell - \frac{4E^2}{L\ell}}}{2}$$

$$= \frac{1}{2}\left\{-\frac{E(L+\ell)}{L\ell} \pm \sqrt{\left(\frac{E(L-\ell)}{L\ell}\right)^2 + 4C^2 e^{-2\alpha D} L\ell}\right\}$$

so that $\Lambda^{(65)}$ has a positive eigenvalue precisely when

(66) $$C^2 e^{-2\alpha D} L\ell > \frac{E^2}{L\ell}$$

Note that (5) requires that

(67) $$L\ell > \frac{E}{C}$$

and that

(68) $$D < \frac{1}{\alpha}\ln\left(\frac{CL\ell}{E}\right)$$

(69) Since

$$L+\ell \geq 2\sqrt{L\ell}$$

(67) imposes the requirement

$$L + \ell > 2\sqrt{\frac{E}{C}} \tag{70}$$

on the minimum combined size of habitat fragments relative to the colonization and extinction rates that is necessary for a prediction of persistence of the species in the two-patch archipelago. In turn (68) may be viewed as a limit on how far apart the fragments may be, given that (67) holds.

Notice that (70) is not equivalent to (67), since equality obtains in (69) only when $L = \ell$. This fact has significant ramifications for the model. To this end, suppose we fix an $M > 2\sqrt{\frac{E}{C}}$, let $\ell \in [0, M/2]$ and set $L = M - \ell$. Then for any $\ell \in [0, \frac{M}{2}]$, (70) holds. If $\ell = M/2$, $L\ell = \frac{M^2}{4} > \frac{1}{4}\left(\frac{4E}{C}\right) = \frac{E}{C}$

and thus (67) holds. However, since $\lim_{\ell \to 0} \ell(M-\ell) = 0$,

$L\ell \leq \frac{E}{C}$ for ℓ small enough relative to L. In such cases, (67) fails and the model predicts extinction for the species in question, no matter how close the two habitat fragments of length L and ℓ are to each other. This feature is a consequence of the assumption in the model that the extinction rate in a habitat patch is inversely proportional to the the size of ~~the~~ patch. Thus if the smaller habitat patch is too small relative to the size of the larger patch, realistic metapopulation theory predicts extinction in the two-patch system even when the combined size of the two patches is large enough to sustain the metapopulation in the case of patches of equal size that are sufficiently close to each other.