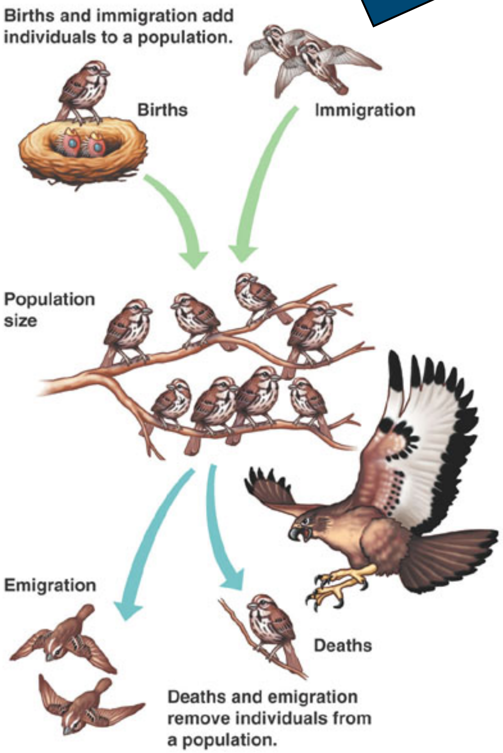
Mean occupancy time: linking mechanistic movement models and landscape ecology to population persistence

Christina Cobbold (Glasgow)

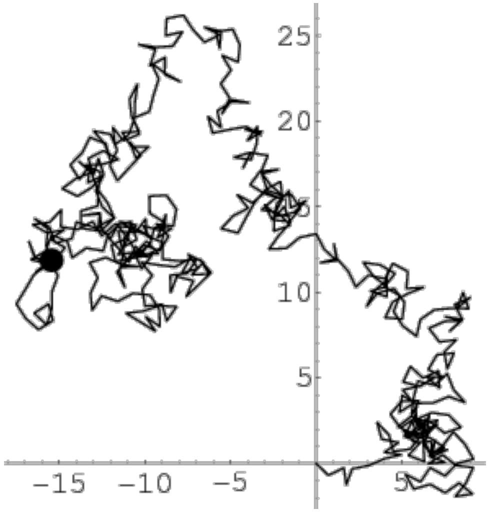
Conservation biology and population persistence

POPULATION PERSISTENCE

Population dynamics



Movement

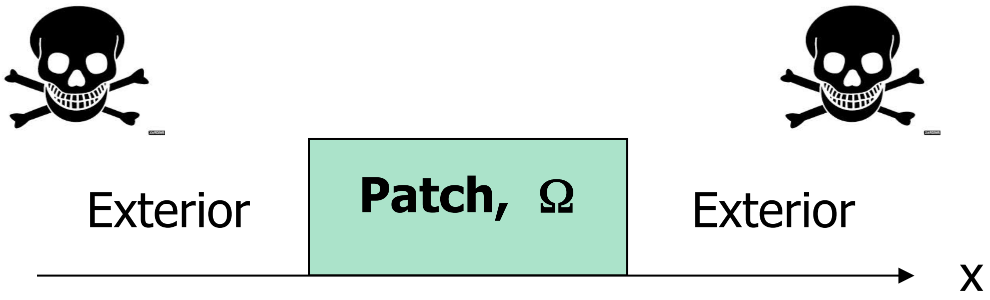


Landscape

Skellam 1951, Kierstead and Slobodkin 1953

Simple example: Critical patch size problem

Given the population dynamics how big should the patch be for persistence?



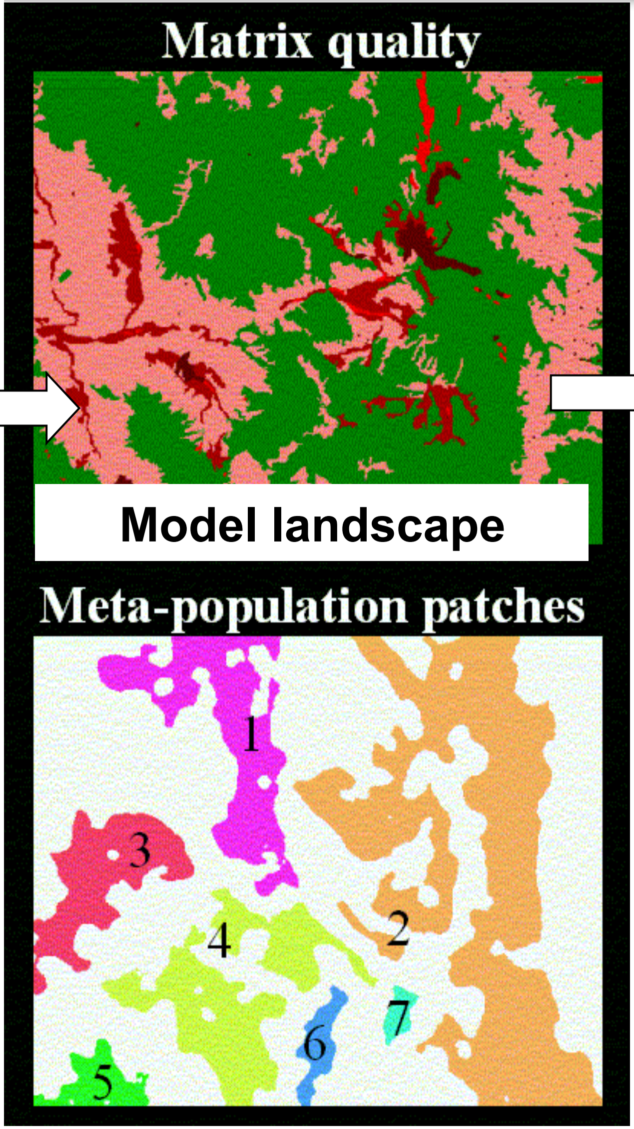
Exterior **Patch, Ω** Exterior

x

Solution: eigenvalue problem of a reaction-diffusion equation

Landscape ecology

Actual landscape

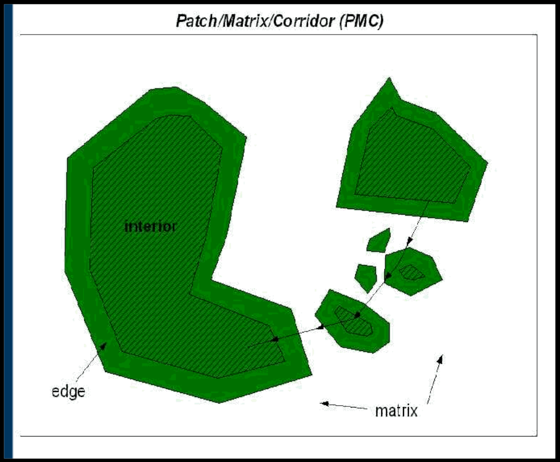


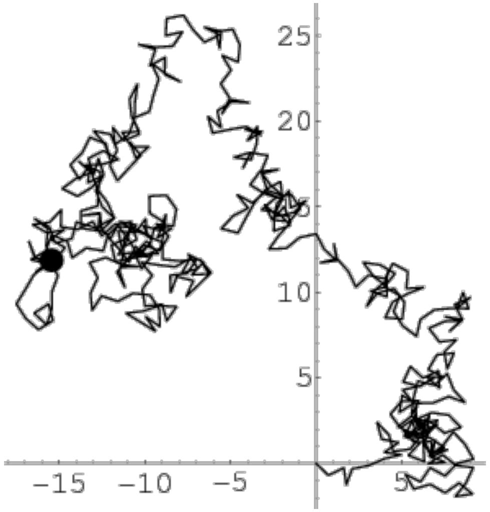
Model landscape

Connectivity
Edges
Size
Isolation
Shape…

Landscape pattern

How does landscape affect populations?





- Landscape ecology
  - Spatial scale of landscape heterogeneity and patterns
  - Ignore details of individual movement (metapopulation models, patch models)
- Reaction-diffusion models
  - Typically spatial scale of landscape homogeneity
  - Include details of individual movement (random walk derivations)

Goal

- Translate reaction-diffusion models into patch models in the ‘best’ possible way.
  - How do we scale up from individual random walks on a patchy landscape to migration rates between patches?
  - How well do the patch models estimate persistence conditions?

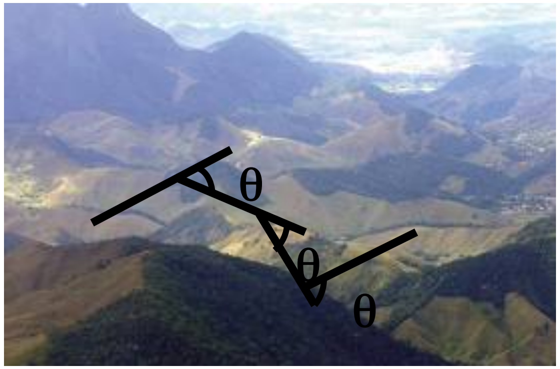
Outline

- Patch models
- Mean first passage time
  - Eigenvalue approximation
  - Steady state approximation
- Improving the approximation
  - Mean occupancy time
- Examples of persistence conditions
  - Single patch, hostile/non-hostile exterior
  - Behaviour at the boundary
  - Finite number of patches

Population models on heterogeneous landscapes

- PDE: Continuous environmental variation

$$\frac{\partial u}{\partial t} = \underbrace{\mathcal{M}(u,x)}_{\text{Movement operator}} + \underbrace{f(u,x)}_{\text{Net growth}}$$



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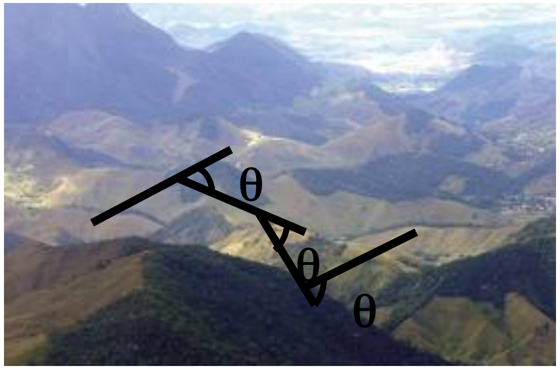
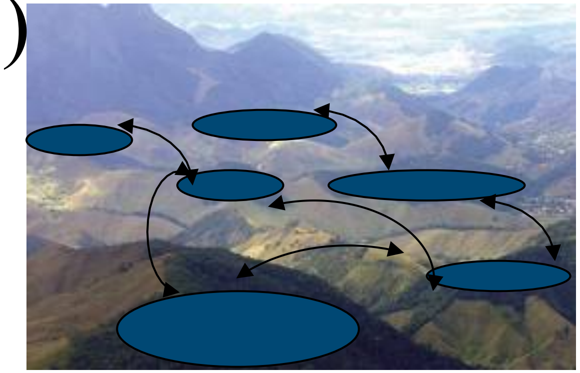


- Patch model: Assemblage of homogeneous patches

$$\frac{d\bar{u}_i}{dt} = -\text{emigration} + \text{imigration} + f(\bar{u}_i)$$



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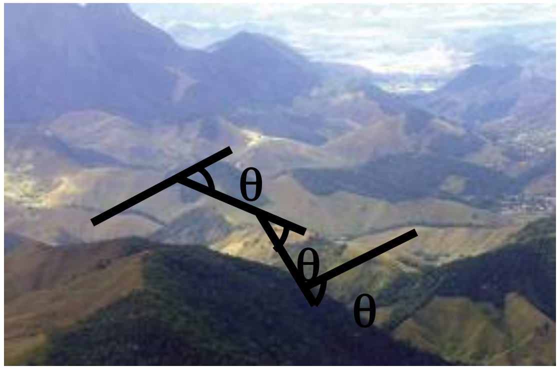
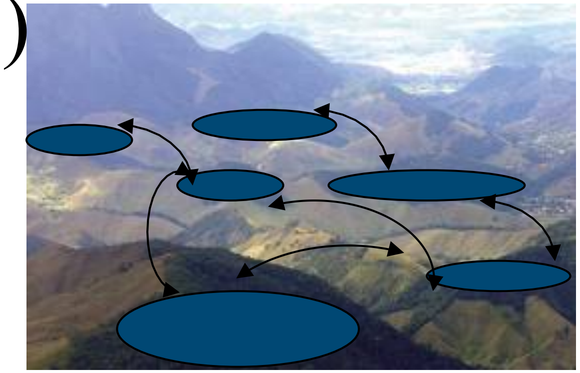


- Patch model: Assemblage of homogeneous patches

$$\frac{d\bar{u}_i}{dt} = -\alpha_i \bar{u}_i + f(\bar{u}_i)$$



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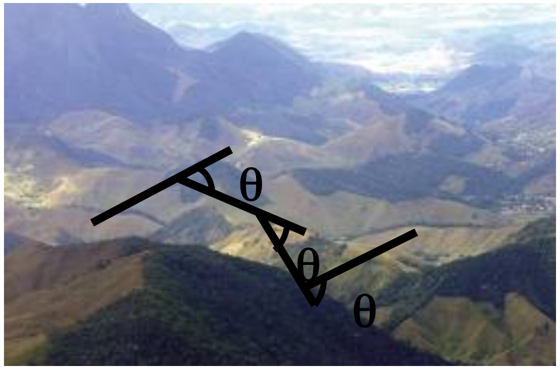
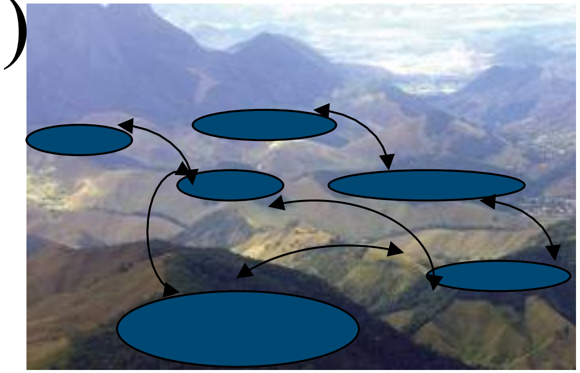


- Patch model: Assemblage of homogeneous patches

$$\frac{d\bar{u}_i}{dt} = -\alpha_i\,\bar{u}_i + f(\bar{u}_i)$$

$1/\alpha_i$ is the mean residency time

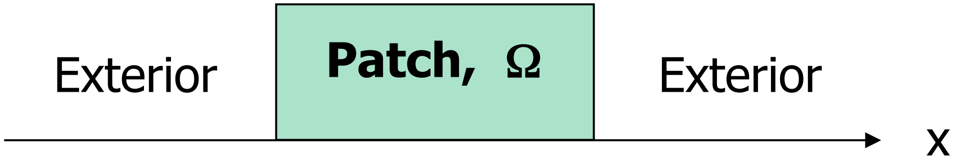


Berg 1993, Redner 2001, Ovaskainen 2003

Mean first passage time (MFPT) and emigration rate

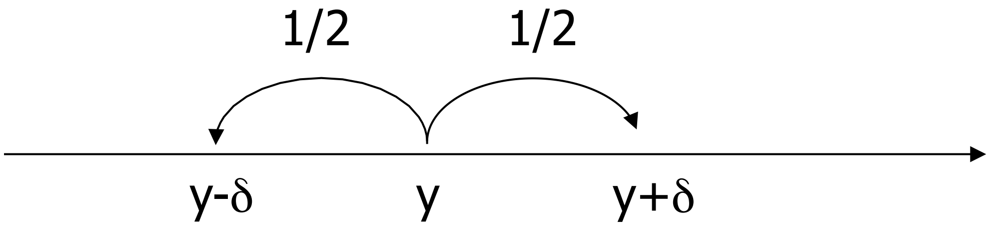
T(y) = MFPT, for an individual starting at y, the mean time spent in some specified region before exiting the region for the first time.

- Alternative to mean squared displacement



- Emigration rate =1/average MFPT

MFPT from a simple random walk



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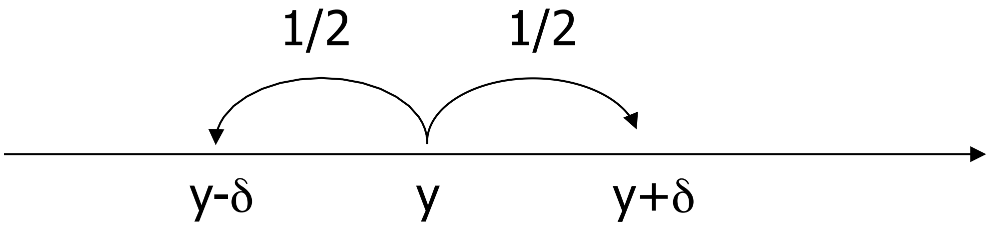
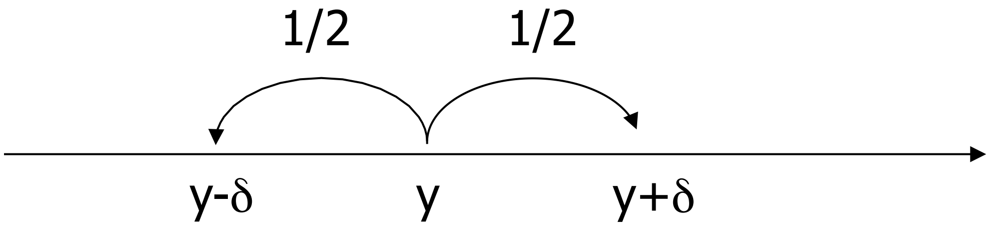


Master equation

$$T(y) = \tau + \underbrace{\frac{1}{2}T(y-\delta)}_{\text{MFPT from left}} + \underbrace{\frac{1}{2}T(y+\delta)}_{\text{MFPT from right}}$$

Time for
One jump

MFPT from a simple random walk



Master equation

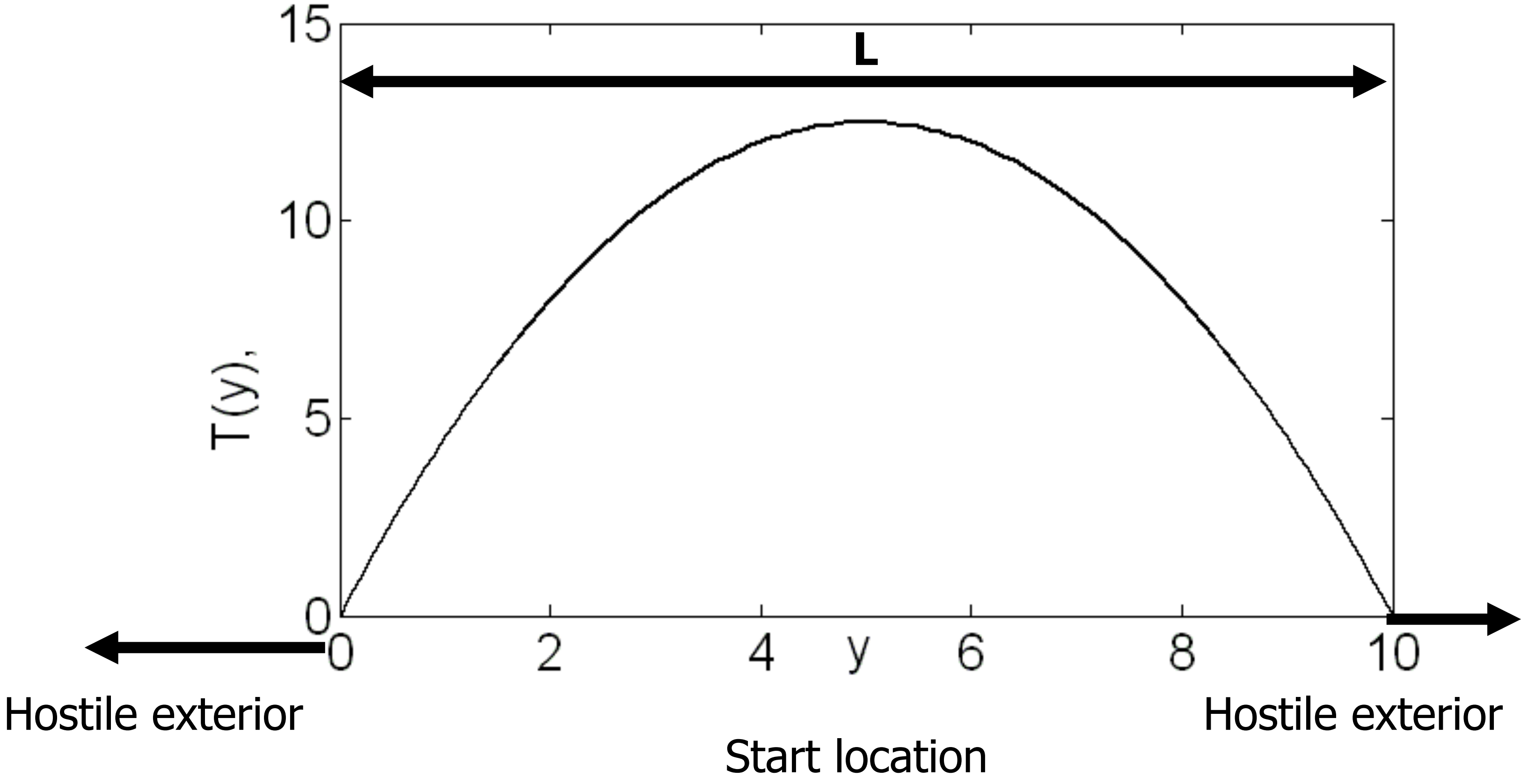
$$T(y) = \underset{\nearrow\ \text{Time for One jump}}{\tau} + \underbrace{\frac{1}{2}T(y-\delta)}_{\text{MFPT from left}} + \underbrace{\frac{1}{2}T(y+\delta)}_{\text{MFPT from right}}$$

Diffusion approximation:

limit as $\delta, \tau \to 0$

$$D\frac{d^2T}{dy^2} = -1$$

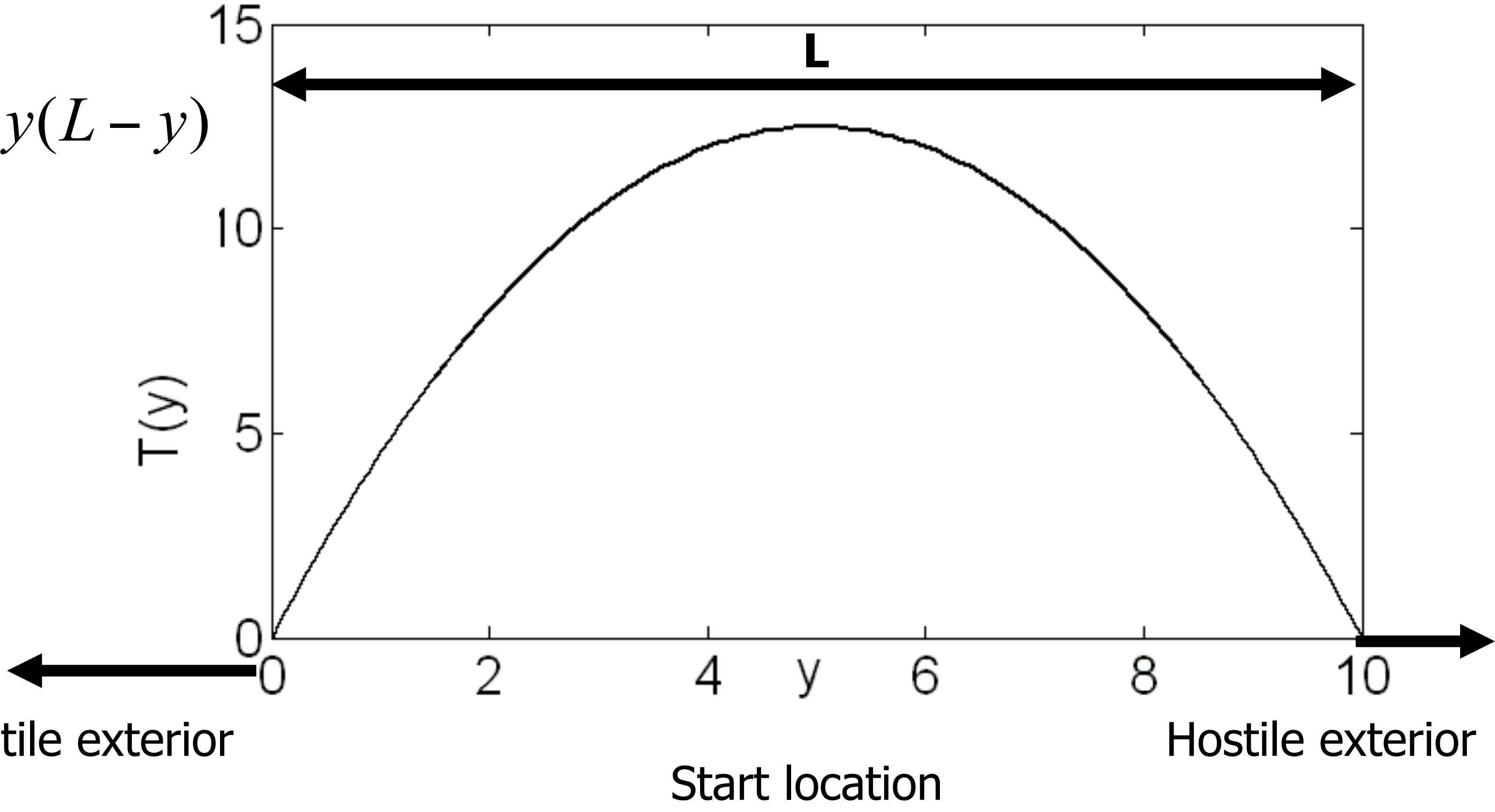
Example: MFPT



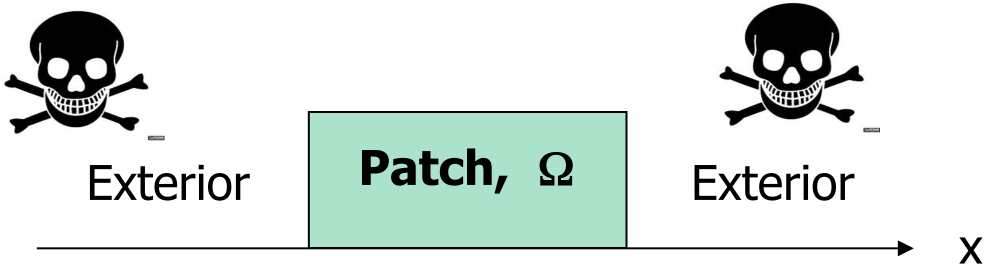
Example: MFPT

$$T(y) = \frac{1}{2D} y(L - y)$$

$$\overline{T} = \frac{L^2}{12D}$$



Simple example: a single patch with hostile exterior



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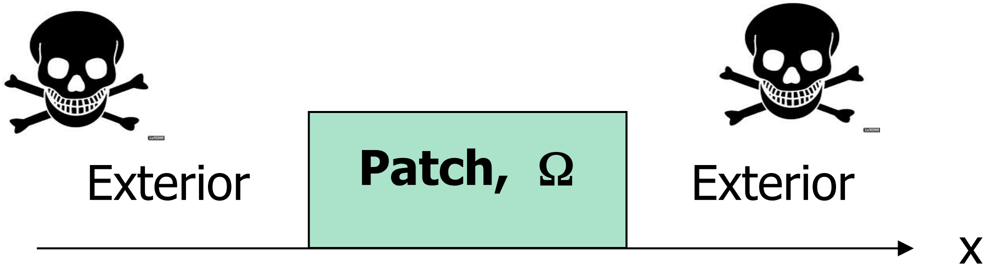

Exterior

Patch, Ω

Exterior

x

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + bu,$$

$$\frac{d\bar{u}}{dt} = -\frac{1}{\overline{T}}\bar{u} + b\bar{u}$$

Skellam 1951

Simple example: single patch hostile exterior

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PDE Persistence condition:

$$L > L_c = \pi\sqrt{\frac{D}{b}}$$

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Simple example: single patch hostile exterior

PDE Persistence condition: $L > L_c = \pi\sqrt{\frac{D}{b}}$

MFPT Persistence condition: $L > \hat{L}_c = \sqrt{12}\sqrt{\frac{D}{b}}$

Simple example: single patch hostile exterior

PDE Persistence condition: $L > L_c = \pi\sqrt{\frac{D}{b}}$

MFPT Persistence condition: $L > \hat{L}_c = \sqrt{12}\sqrt{\frac{D}{b}}$

$\sqrt{12} = 3.464 > \pi$ Only 10% error.

Why does the MFPT work as an emigration rate?

The dominant eigenvalue associated to the zero steady state of the PDE is equal to the dominant eigenvalue of the patch model.

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2}$$

Reaction-diffusion model:

- dominant eigenvalue, -λ

$$\frac{d\bar{u}}{dt} = -\frac{1}{\bar{T}}\bar{u}$$

Patch model:

- dominant eigenvalue, $-1/\bar{T}$

Redner 2001

MFPT and Greens Functions

$$\frac{\partial G}{\partial t} = D\frac{\partial^2 G}{\partial x^2}, \quad x \in \Omega \qquad u(x,0) = \delta(x-y), \quad x \in \Omega$$ + boundary conditions

Redner 2001

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$$\underbrace{S(y,t)}_{\text{Survival probability start at y still in }\Omega\text{ at t}} = \int_\Omega G(x,y,t)dx \qquad \int_0^t \underbrace{F(y,t)}_{\text{First passage probability}} dt = 1 - S(y,t)$$

MFPT and Greens Functions

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MFPT:

$$T(y) = \int_0^\infty tF(y,t)dt = -\int_0^\infty t\frac{\partial S}{\partial t}dt = \int_0^\infty\int_\Omega G(x,y,t)dxdt$$

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$$\lim_{t \to \infty} S(y,t) = 0$$

Finite domain - Individuals will exit eventually (zero flux BCs not allowed unless death is in the movement operator)

Eigenvalue approximations

Eigenvalue problem for the PDE:

$$\phi(x)e^{-\lambda t} = \int_{\Omega} G(x,y,t)\phi(y)dy$$

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Taking spatial averages and letting $\phi(x) = \bar{\phi} + \phi(x) - \bar{\phi}$

$$\bar{\phi}e^{-\lambda t} = \frac{\bar{\phi}}{|\Omega|}\int_{\Omega}\int_{\Omega} G(x,y,t)dydx + \frac{1}{|\Omega|}\int_{\Omega}\int_{\Omega} \left(G(x,y,t)(\phi(y) - \bar{\phi}\right)dydx$$

University of Glasgow

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Assume spatial average is a good approximation to the eigenfunction. Integrate with respect to t:

$$\boxed{\frac{1}{\lambda} \approx \frac{1}{|\Omega|}\int_{0}^{\infty}\int_{\Omega}\int_{\Omega} G(x,y,z)dxdydt = \frac{1}{|\Omega|}\int_{\Omega} T(y)dy = \bar{T}}$$

Steady state approximations

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + f(u), \quad x \in \Omega \qquad u(x,0) = u_0(x), \quad x \in \Omega$$

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Steady state solution to the PDE written using Green’s functions
and
Taylor expand f about spatially averaged steady state

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Steady state solution to the PDE written using Green's functions
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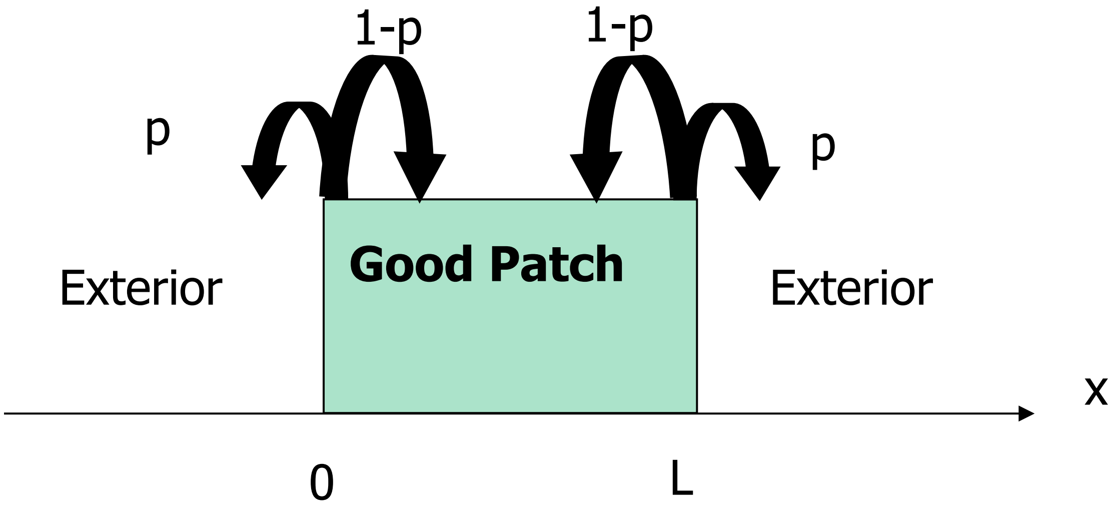
$$\boxed{u^*(x) = f(\overline{u}^*)T(x)}$$

Ludwig 1979

Example: Biased movement at the boundary



p= probability of leaving the patch when the boundary is reached.

PDE: $$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + \frac{bu}{1+\alpha u} - mu,$$

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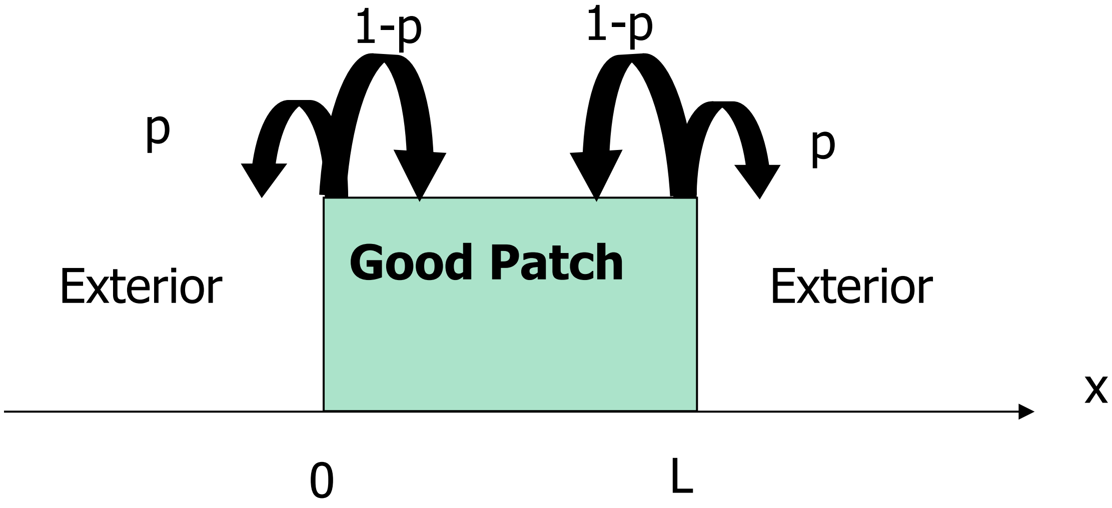

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BCs: $$u_x(0,t) = \chi u(0,t) \quad u_x(L,t) = -\chi u(L,t) \quad \text{where } \chi = \frac{p}{1-p}\sqrt{\frac{b-m}{D}}$$

Patch ODE

$$\frac{d\bar{u}}{dt} = -\frac{1}{\bar{T}}\bar{u} + \frac{b\bar{u}}{1+\alpha\bar{u}} - m\bar{u},$$

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Diffusion in the patch

Patch size

Properties of the exterior /patch boundary

$$T(x) = \frac{1}{2D}\left(-x^2 + xL + \frac{L}{\chi}\right)$$

$$\bar{T} = \frac{L^2}{12D}\left(1 + \frac{6}{L\chi}\right)$$

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Steady state approximation

$$u^*(x) = \left(\frac{b\bar{u}^*}{1 + \alpha\bar{u}^*} - m\bar{u}^*\right)T(x)$$

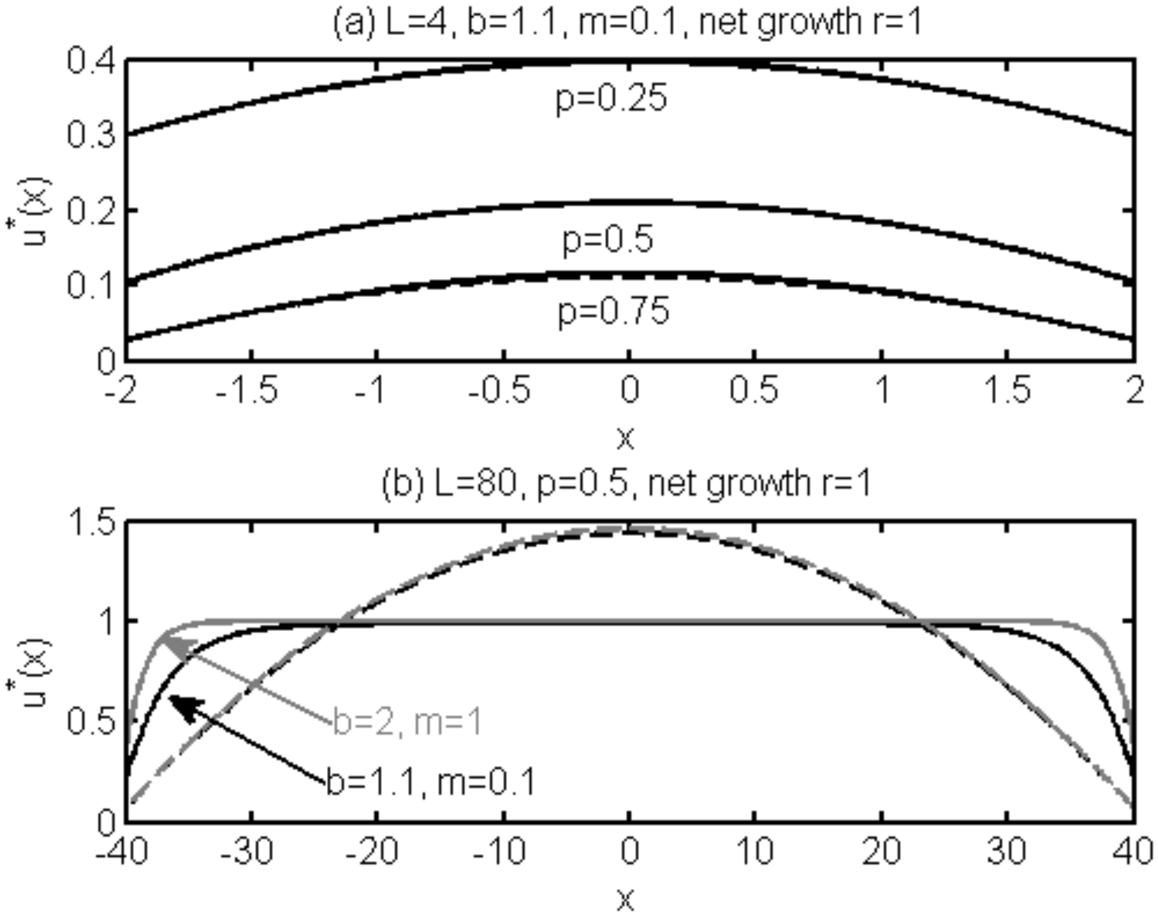
$$\bar{u}^* = \left(\frac{b\bar{u}^*}{1 + \alpha\bar{u}^*} - m\bar{u}^*\right)\bar{T}$$

Steady state approximation: No death in the movement operator

$$D\frac{d^2T}{dy^2} = -1$$

MFPT approximation

Steady state approximation: No death in the movement operator



Small patch

Large patch

——— PDE solution

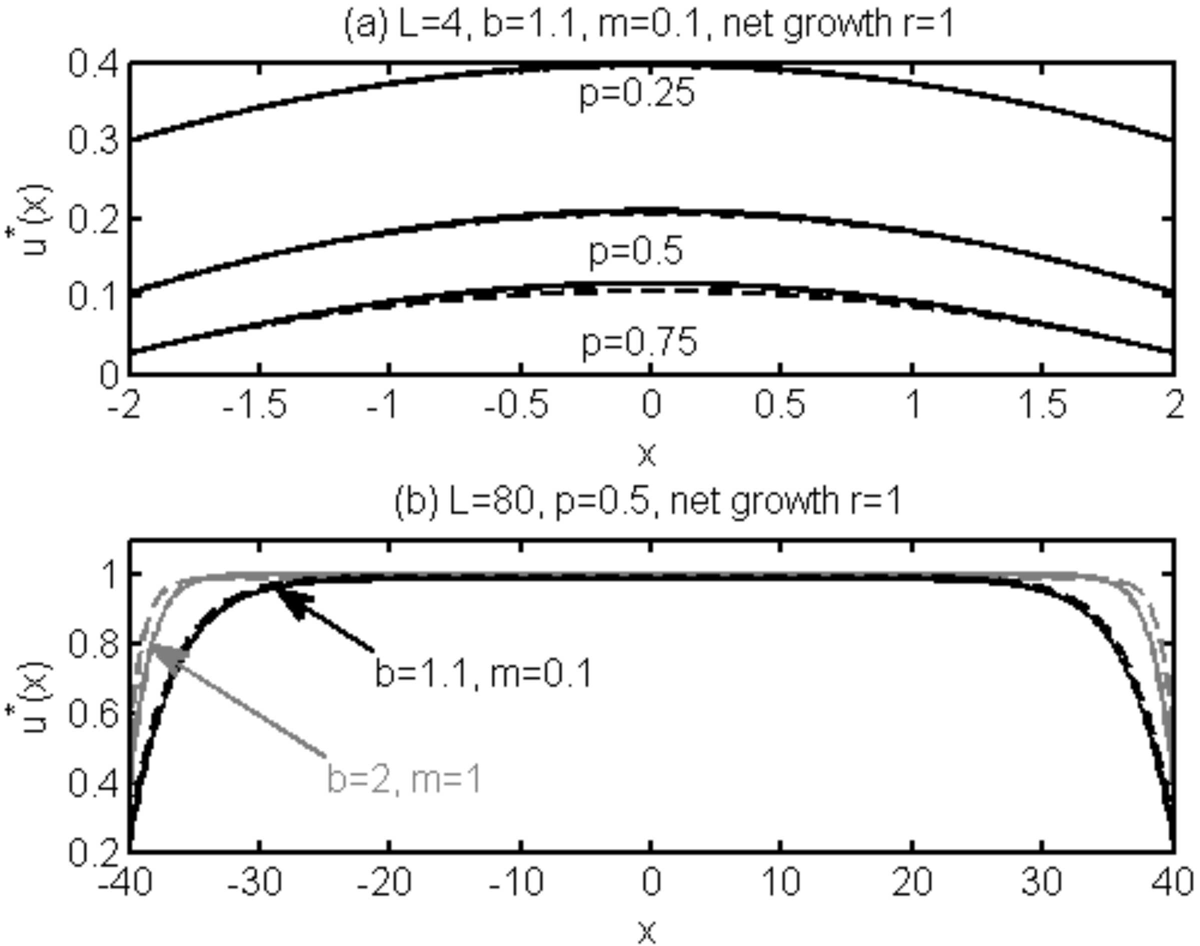
- - - - MFPT approximation

Steady state approximation: Death in the movement operator

$$D\frac{d^2T}{dy^2} - mT = -1$$

MOT (Mean Occupancy time) approximation

Steady state approximation: Death in the movement operator



Small patch

Large patch

PDE solution

MOT approximation

Why put death in the movement operator?

- Approximation to the steady state profile is improved.
- Individuals die in the correct location
- We can deal with no flux boundary conditions
- Death in the movement operator gives Mean Occupancy Time (MOT) instead of MFPT.

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r=b-m net growth
fixed

$$m = \underbrace{m_1}_{\text{Operator}} + \underbrace{(m - m_1)}_{\text{Dynamics}}$$

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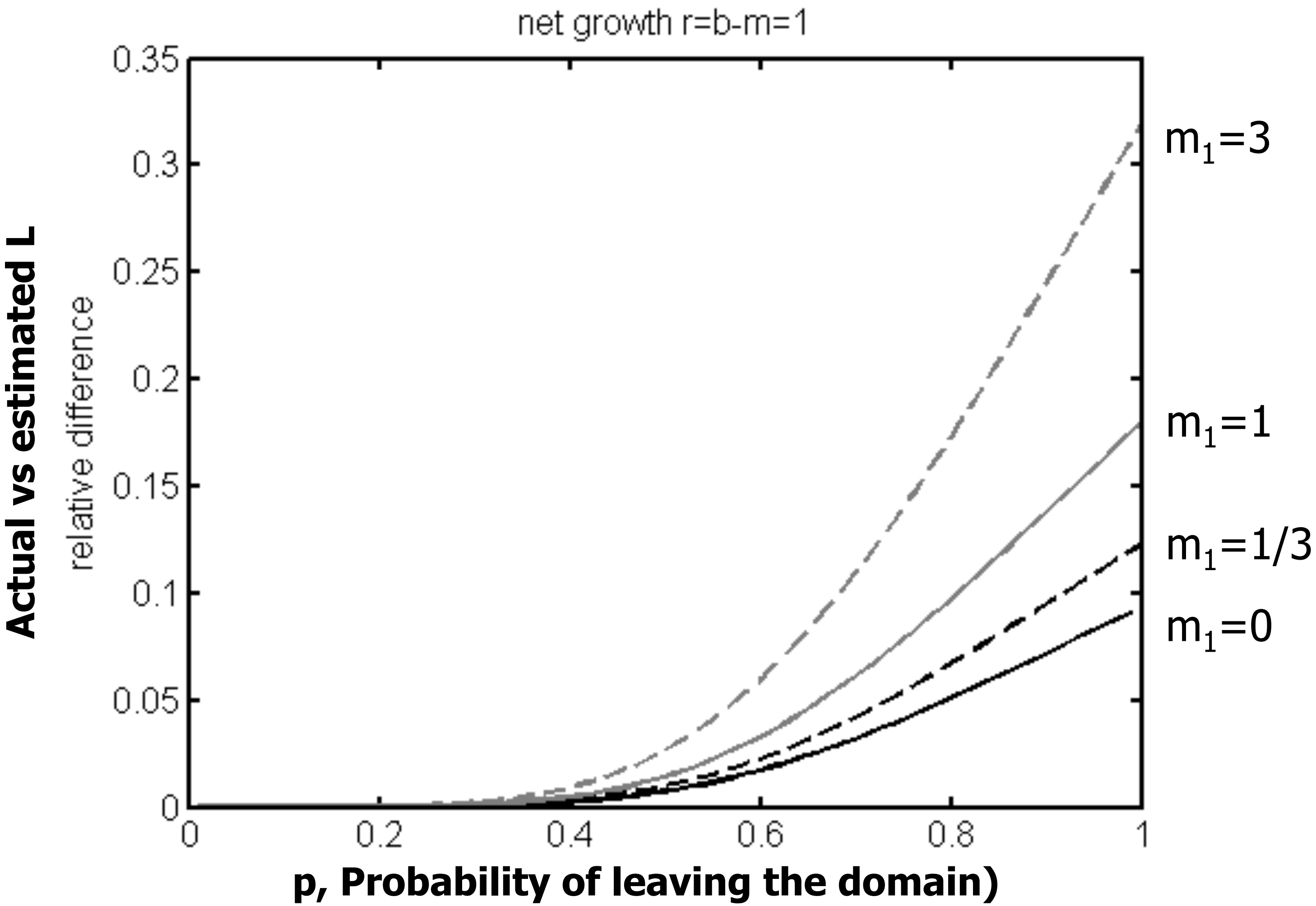
MOT persistence condition $1 = \left(b - (m - m_1)\right)\overline{T}(m_1)$

MFPT vs MOT


net growth r=b-m=1
Actual vs estimated L
relative difference
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.2
0.4
0.6
0.8
1
p, Probability of leaving the domain)
$m_1=3$
$m_1=1$
$m_1=1/3$
$m_1=0$

Why put death in the movement operator?

- Population steady state for persisting populations
  - larger domains
  - loss out of the boundary has small effect on domain interior
  - dying in the right location important, MOT does better.

- Extinction steady state – persistence conditions
  - Smaller domains
  - high probability, p, of leaving the domain before death so MOT exaggerates overestimation of critical patch size

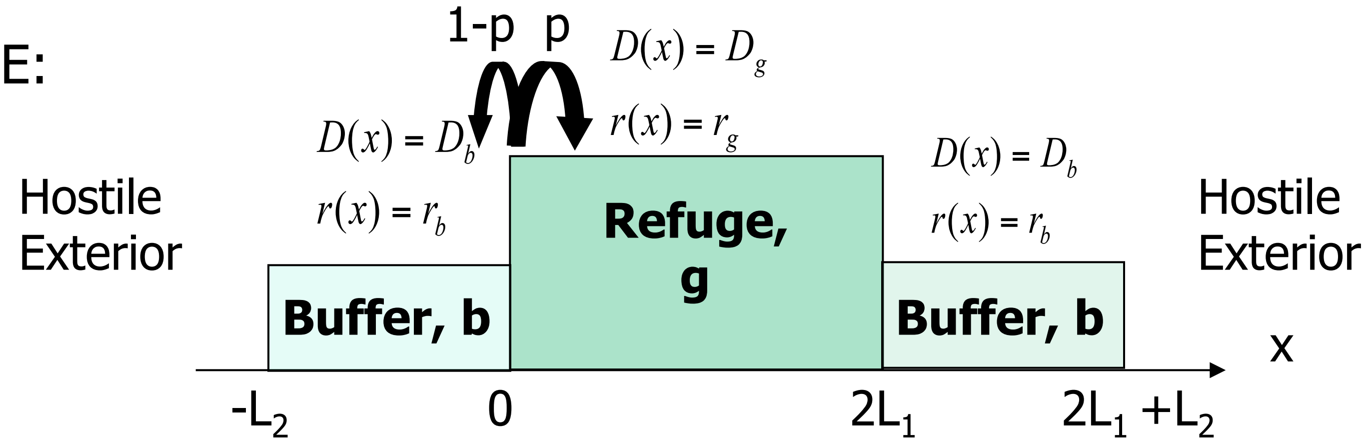
$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + bu - mu,$$

$$m = \underbrace{m_1}_{\text{Operator}} + \underbrace{(m - m_1)}_{\text{Dynamics}}$$

Cantrell & Cosner 2003
Lutscher 2007

Multiple patches

PDE:



Hostile Exterior

$D(x) = D_b$
$r(x) = r_b$

Buffer, b

1-p p

$D(x) = D_g$
$r(x) = r_g$

Refuge, g

$D(x) = D_b$
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Buffer, b

Hostile Exterior

x

$-L_2$ 0 $2L_1$ $2L_1 + L_2$

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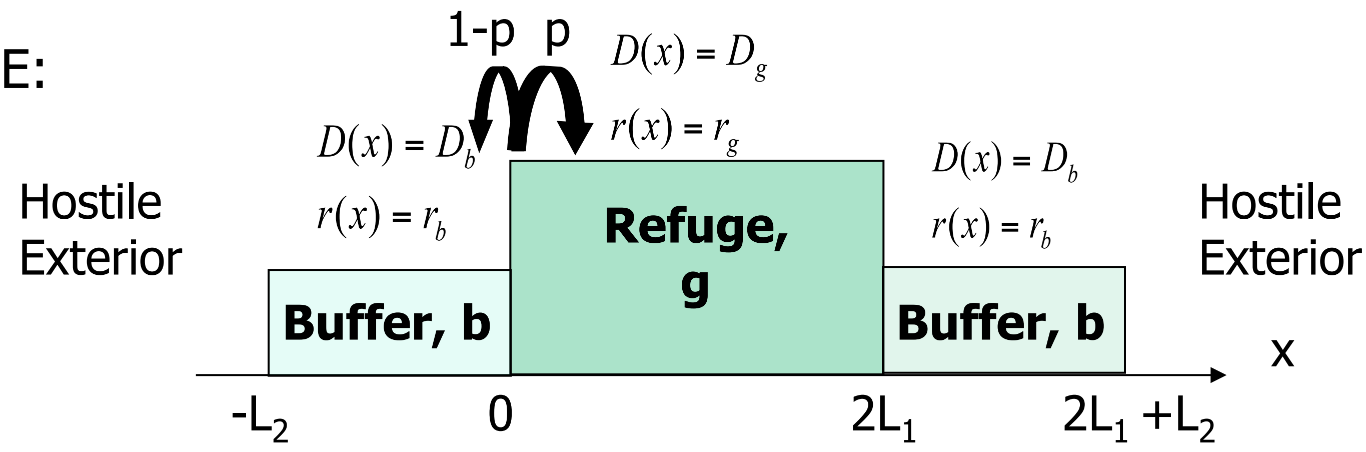

1-p p

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$D(x) = D_b$

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Hostile Exterior

Refuge, g

Buffer, b

Buffer, b

Hostile Exterior

x

$-L_2$ 0 $2L_1$ $2L_1 + L_2$

MFPT ODE:

$$\begin{pmatrix} \dfrac{d\bar{u}_g}{dt} \\ \dfrac{d\bar{u}_b}{dt} \end{pmatrix} = -\bar{T}^{-1}\begin{pmatrix} \bar{u}_g \\ \bar{u}_b \end{pmatrix} + \begin{pmatrix} b_g\bar{u}_g \\ b_b\bar{u}_b \end{pmatrix} \qquad \bar{T} = \begin{pmatrix} \bar{T}_{gg} & \bar{T}_{gb} \\ \bar{T}_{bg} & \bar{T}_{bb} \end{pmatrix}$$

Ways to calculate MOT

- Random walk derivation (McKenzie et al 2009)
  - Useful for connection to IBMs
- First passage probabilities (Redner 2001)
  - Useful for derivation of the theory
- Adjoint of the movement operator (Ovaskainen 2003)
  - Useful for practical calculations
- Data (Point release experiments) (Schultz and Crone 2001)
  - Useful for practical calculations

Multiple patches

$$\underbrace{\mathcal{M}^{*}(T(y))}_{\text{Adjoint of the Movement operator}} = -1, \quad y \in \Omega_i$$

$$\mathcal{M}^{*}(T(y)) = 0, \quad y \notin \Omega_i$$

Multiple patches

$$\underbrace{\mathcal{M}^*(T(y))}_{\text{Adjoint of the Movement operator}} = -1, \quad y \in \Omega_i$$

$$\mathcal{M}^*(T(y)) = 0, \quad y \notin \Omega_i$$

$$\mathcal{M}^*(T(y)) = D(y)\frac{d^2T}{dy^2} - m(y)T, \quad D(y) = \begin{cases} D_g, & y \in [0, \mathrm{L}_1] \\ D_b, & y \in [L_1, L_2] \end{cases} \quad m(y) = \begin{cases} 0 & y \in [0, \mathrm{L}_1] \\ m_b & y \in [L_1, L_2] \end{cases}$$

Multiple patches

$$\underbrace{\mathcal{M}^*(T(y))}_{\text{Adjoint of the Movement operator}} = -1, \quad y \in \Omega_i$$

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$$\bar{T} = \begin{pmatrix} \bar{T}_{gg} & \bar{T}_{gb} \\ \bar{T}_{bg} & \bar{T}_{bb} \end{pmatrix}$$

Multiple patches

$$\underbrace{\mathcal{M}^*(T(y))}_{\text{Adjoint of the Movement operator}} = -1, \quad y \in \Omega_i$$

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$$\bar{T} = \begin{pmatrix} \bar{T}_{gg} & \bar{T}_{gb} \\ \bar{T}_{bg} & \bar{T}_{bb} \end{pmatrix}$$

Ω=[0,L1]=good patch
Time spent in good patch

Multiple patches

$$\underbrace{\mathcal{M}^*(T(y))}_{\text{Adjoint of the Movement operator}} = -1, \quad y \in \Omega_i$$

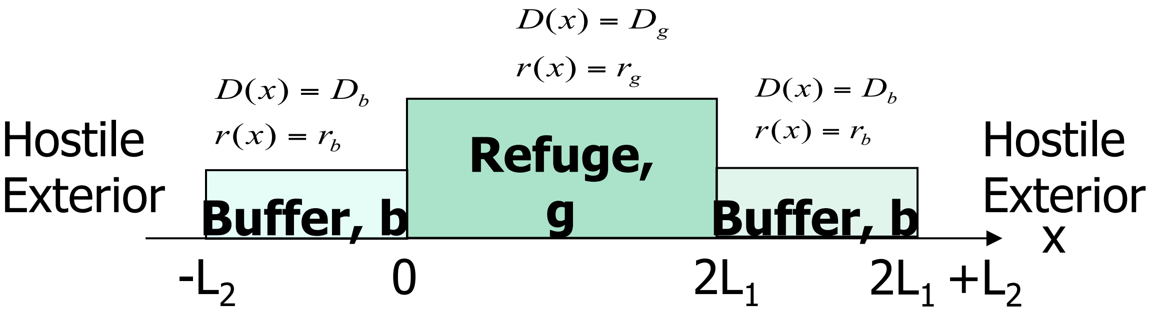
$$\mathcal{M}^*(T(y)) = 0, \quad y \notin \Omega_i$$

$$\mathcal{M}^*(T(y)) = D(y)\frac{d^2T}{dy^2} - m(y)T, \quad D(y) = \begin{cases} D_g, & y \in [0, \mathrm{L}_1] \\ D_b, & y \in [L_1, L_2] \end{cases} \quad m(y) = \begin{cases} 0 & y \in [0, \mathrm{L}_1] \\ m_b & y \in [L_1, L_2] \end{cases}$$

$$\bar{T} = \begin{pmatrix} \bar{T}_{gg} & \bar{T}_{gb} \\ \bar{T}_{bg} & \bar{T}_{bb} \end{pmatrix}$$

Ω=[0,L1]=good patch
Time spent in good patch

Ω=[0,L2]=bad patch
Time spent in bad patch



$D(x) = D_g$

$r(x) = r_g$

Hostile Exterior

$D(x) = D_b$

$r(x) = r_b$

Buffer, b

Refuge, g

$D(x) = D_b$

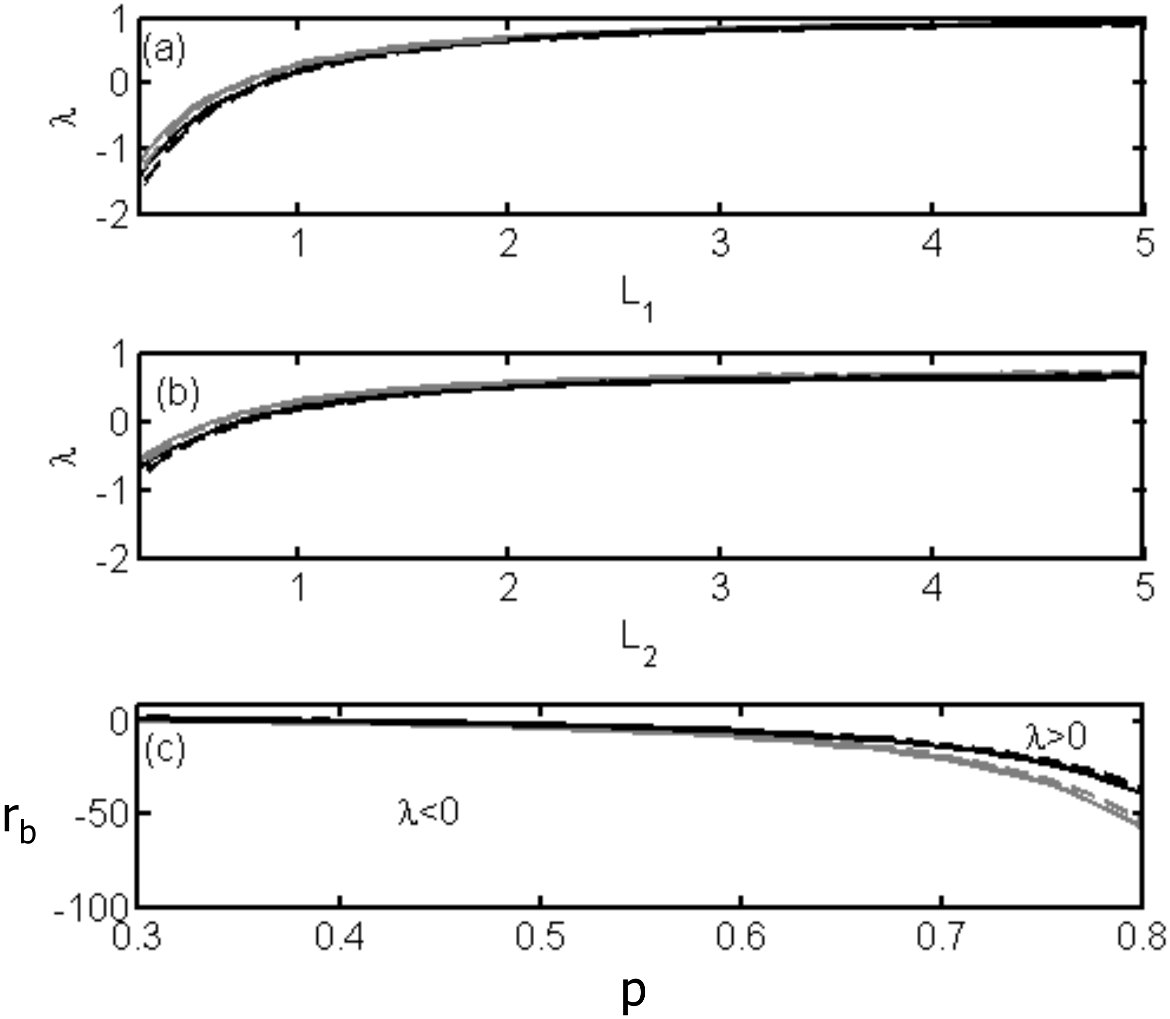
$r(x) = r_b$

Buffer, b

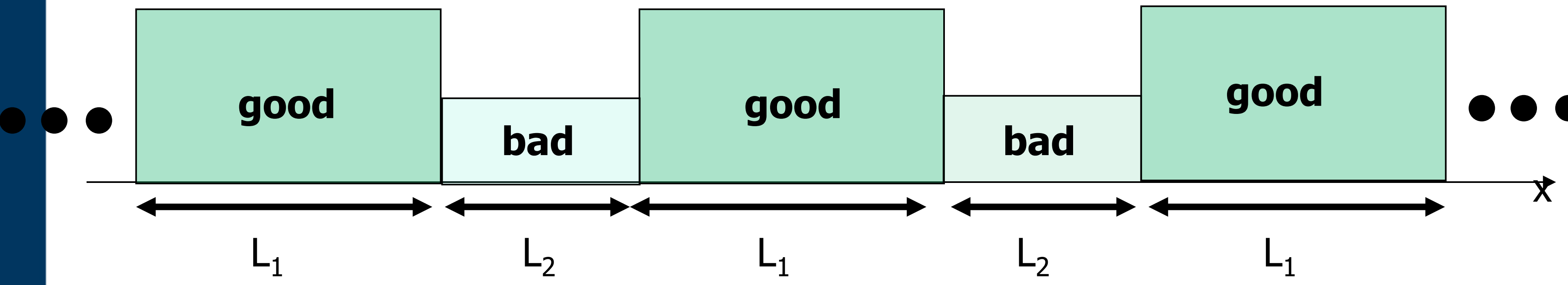
Hostile Exterior

x

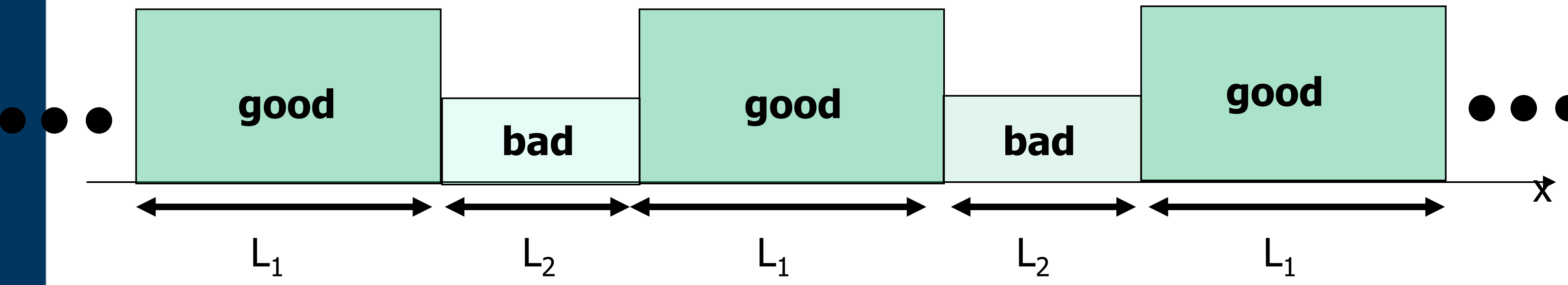
$-L_2$ 0 $2L_1$ $2L_1 + L_2$



Multiple patches:Periodic habitat – no loss out of the domain

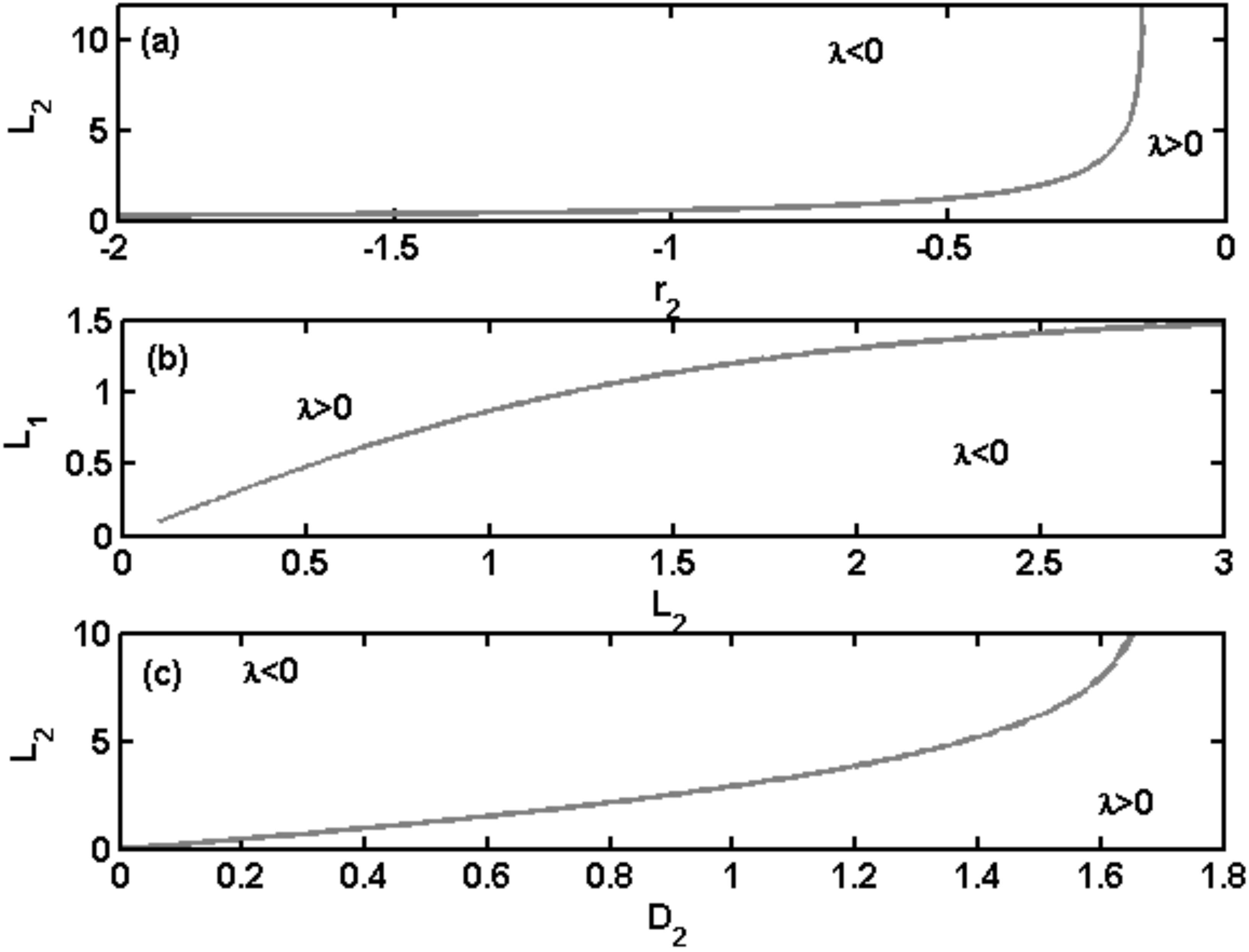


Multiple patches:Periodic habitat – no loss out of the domain



$$\begin{pmatrix} \dfrac{d\bar{u}_g}{dt} \\ \dfrac{d\bar{u}_b}{dt} \end{pmatrix} = -\bar{T}^{-1}\begin{pmatrix} \bar{u}_g \\ \bar{u}_b \end{pmatrix} + \begin{pmatrix} \text{birth of g} \\ \text{birth of b} \end{pmatrix} \qquad \bar{T} = \begin{pmatrix} \bar{T}_{gg} & \bar{T}_{gb} \\ \bar{T}_{bg} & \bar{T}_{bb} \end{pmatrix}$$

Shigesada et al1986



Conclusions

- M0T ODE patch models can be used to approximate persistence conditions and population growth rate
  - M0T can be measured directly
  - Emigration rates summarise movement behaviour and habitat attributes (size, shape, quality)
- Simple steady state approximation
- Theory applies to n-dimensions any reaction diffusion equation (e.g including advection, taxis etc)

Acknowledgements

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Types of data

- Move length and turning angle distributions from GPS data
  - Red fox data (Siniff and Jessen 1969)
  - Prairie butterfly (Schultz and Crone 2001)
- Empirically estimated first passage times
  - search time along a path (Fauchauld & Tveraa 2003)
  - distinguishing movement behaviours at different scales (Frair et al 2005)