

ICNAAM 2012  
Kos, Greece

How individual response to habitat edges affects  
population persistence and spatial spread

Gabriel Andreguetto Maciel

Frithjof Lutscher (University of Ottawa - Canada)

Institute for Theoretical Physics  
São Paulo State University - Brazil

# Population Dynamics





- Number of individuals as a function of time

# Population Dynamics



- Number of individuals as a function of time





- Number of individuals as a function of time

- Explicit consideration of space is particularly important when we consider
  - Invasion processes
  - Heterogeneous environments



# Reaction Diffusion Equations

- Reaction diffusion equations have been successfully employed to assess important questions in spatial ecology



- **Reaction diffusion equations** have been successfully employed to assess important questions in spatial ecology

One single species in homogeneous space

$$\frac{\partial}{\partial t} u(x, t) = f(u(x, t)) + D \frac{\partial^2}{\partial x^2} u(x, t)$$

- **Reaction diffusion equations** have been successfully employed to assess important questions in spatial ecology

## One single species in homogeneous space

$$\frac{\partial}{\partial t} u(x, t) = f(u(x, t)) + D \frac{\partial^2}{\partial x^2} u(x, t)$$

- **Spatial heterogeneity** can be incorporated by replacing the reaction and diffusion terms with the spatially dependent terms  $f(u(x, t), x)$  and  $\partial^2 / \partial x^2 (D(x)u(x, t))$

- **Reaction diffusion equations** have been successfully employed to assess important questions in spatial ecology

## One single species in homogeneous space

$$\frac{\partial}{\partial t} u(x, t) = f(u(x, t)) + D \frac{\partial^2}{\partial x^2} u(x, t)$$

- **Spatial heterogeneity** can be incorporated by replacing the reaction and diffusion terms with the spatially dependent terms  $f(u(x, t), x)$  and  $\partial^2 / \partial x^2 (D(x)u(x, t))$
- Adopting a landscape ecology perspective,  $f$  and  $D$  are constant within habitats

- **Reaction diffusion equations** have been successfully employed to assess important questions in spatial ecology

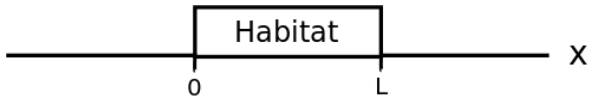
## One single species in homogeneous space

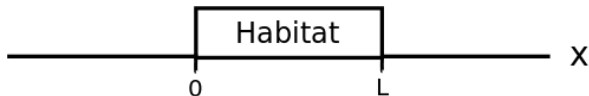
$$\frac{\partial}{\partial t} u(x, t) = f(u(x, t)) + D \frac{\partial^2}{\partial x^2} u(x, t)$$

- **Spatial heterogeneity** can be incorporated by replacing the reaction and diffusion terms with the spatially dependent terms  $f(u(x, t), x)$  and  $\partial^2 / \partial x^2 (D(x)u(x, t))$
- Adopting a landscape ecology perspective,  $f$  and  $D$  are constant within habitats

One then needs to impose interface conditions that relate the population densities and fluxes between two adjacent habitats.

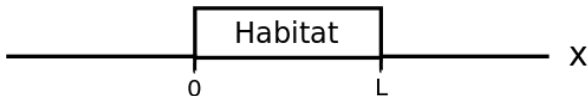
# Boundary Conditions





Dirichlet

$$u(0) = 0, \quad u(L) = 0 \quad \text{lethal boundaries}$$



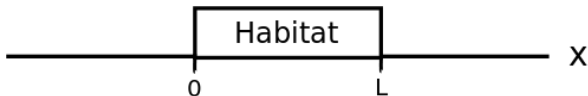
## Dirichlet

$$u(0) = 0, \quad u(L) = 0 \quad \text{lethal boundaries}$$

## Neumann

$$\frac{\partial u}{\partial x}(0) = 0, \quad \frac{\partial u}{\partial x}(L) = 0 \quad \text{no flux at boundaries}$$





## Dirichlet

$$u(0) = 0, \quad u(L) = 0 \quad \text{lethal boundaries}$$

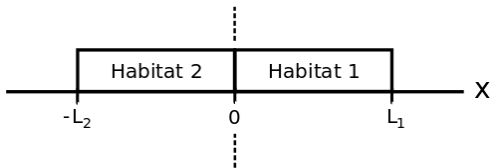
## Neumann

$$\frac{\partial u}{\partial x}(0) = 0, \quad \frac{\partial u}{\partial x}(L) = 0 \quad \text{no flux at boundaries}$$

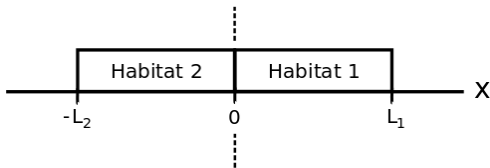
## Robin

$$\frac{\partial u}{\partial x}(0) = \xi u(0), \quad \frac{\partial u}{\partial x}(L) = \eta u(L)$$

- What conditions should be considered at interfaces?

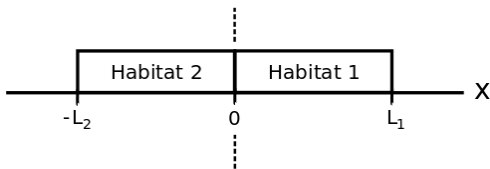


- What conditions should be considered at interfaces?



- Continuous density and flux have long been taken as “natural assumptions”

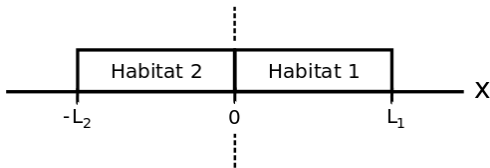
- What conditions should be considered at interfaces?



- Continuous density and flux have long been taken as “natural assumptions”

$$u_1(0^+) = u_2(0^-), \quad D_1 \frac{\partial u_1}{\partial x}(0^+) = D_2 \frac{\partial u_2}{\partial x}(0^-)$$

- What conditions should be considered at interfaces?

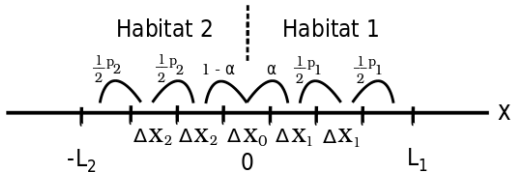


- Continuous density and flux have long been taken as “natural assumptions”

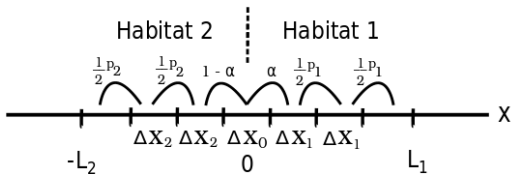
$$u_1(0^+) = u_2(0^-), \quad D_1 \frac{\partial u_1}{\partial x}(0^+) = D_2 \frac{\partial u_2}{\partial x}(0^-)$$

Are these natural assumptions?

- Ovaskainen and Cornell (2003) derived a **discontinuous interface condition** between two habitats

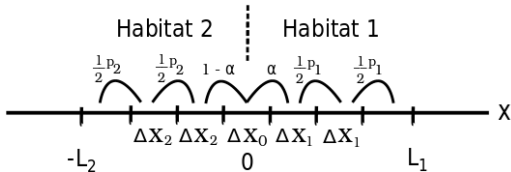


- Ovaskainen and Cornell (2003) derived a **discontinuous interface condition** between two habitats



- **Edge behaviour** is incorporated through a biased movement at the interface (measured by  $\alpha$ )

- Ovaskainen and Cornell (2003) derived a **discontinuous interface condition** between two habitats



- Edge behaviour** is incorporated through a biased movement at the interface (**measured by  $\alpha$** )

### Discontinuous interface condition

$$\alpha p_2 \Delta x_2 u_2(0^-, t) = (1 - \alpha) p_1 \Delta x_1 u_1(0^+, t)$$

$$D_2 \frac{\partial u_2}{\partial x}(0^-, t) = D_1 \frac{\partial u_1}{\partial x}(0^+, t)$$



$$\alpha p_2 \Delta x_2 u_2(0^-, t) = (1 - \alpha) p_1 \Delta x_1 u_1(0^+, t)$$

- By making some assumptions this equation can be written in terms of diffusivities

$$D_2 = \lim_{\Delta x_2, \Delta t \rightarrow 0} p_2 \frac{\Delta x_2^2}{\Delta t}, \quad D_1 = \lim_{\Delta x_1, \Delta t \rightarrow 0} p_1 \frac{\Delta x_1^2}{\Delta t}$$

$$\alpha p_2 \Delta x_2 u_2(0^-, t) = (1 - \alpha) p_1 \Delta x_1 u_1(0^+, t)$$

- By making some assumptions this equation can be written in terms of diffusivities

$$D_2 = \lim_{\Delta x_2, \Delta t \rightarrow 0} p_2 \frac{\Delta x_2^2}{\Delta t}, \quad D_1 = \lim_{\Delta x_1, \Delta t \rightarrow 0} p_1 \frac{\Delta x_1^2}{\Delta t}$$

$$p_2 = p_1$$

$$\alpha \sqrt{D_2} u_2(0^-, t) = (1 - \alpha) \sqrt{D_1} u_1(0^+, t)$$

$$\alpha p_2 \Delta x_2 u_2(0^-, t) = (1 - \alpha) p_1 \Delta x_1 u_1(0^+, t)$$

- By making some assumptions this equation can be written in terms of diffusivities

$$D_2 = \lim_{\Delta x_2, \Delta t \rightarrow 0} p_2 \frac{\Delta x_2^2}{\Delta t}, \quad D_1 = \lim_{\Delta x_1, \Delta t \rightarrow 0} p_1 \frac{\Delta x_1^2}{\Delta t}$$

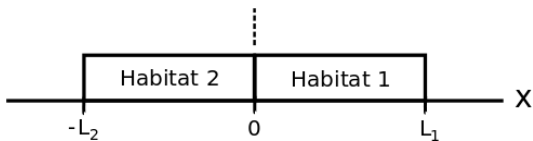
$$p_2 = p_1$$

$$\alpha \sqrt{D_2} u_2(0^-, t) = (1 - \alpha) \sqrt{D_1} u_1(0^+, t)$$

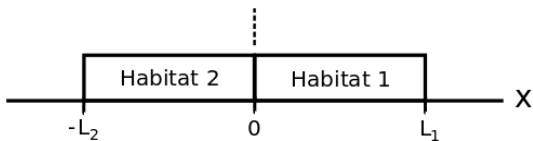
$$\Delta x_2 = \Delta x_1$$

$$\alpha D_2 u_2(0^-, t) = (1 - \alpha) D_1 u_1(0^+, t)$$

- 3 different interface conditions



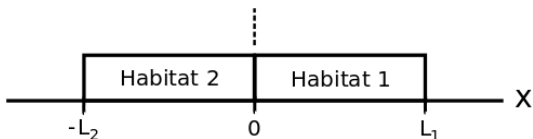
- 3 different interface conditions



Continuous

$$u_2(0^-, t) = u_1(0^+, t)$$

- 3 different interface conditions



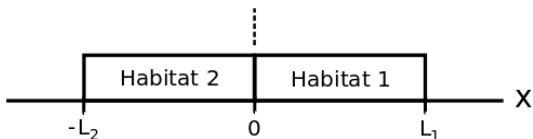
Continuous

$$u_2(0^-, t) = u_1(0^+, t)$$

Discontinuous I

$$\alpha \sqrt{D_2} u_2(0^-, t) = (1 - \alpha) \sqrt{D_1} u_1(0^+, t)$$

- 3 different interface conditions



Continuous

$$u_2(0^-, t) = u_1(0^+, t)$$

Discontinuous I

$$\alpha \sqrt{D_2} u_2(0^-, t) = (1 - \alpha) \sqrt{D_1} u_1(0^+, t)$$

Discontinuous II

$$\alpha D_2 u_2(0^-, t) = (1 - \alpha) D_1 u_1(0^+, t)$$

Plus flux continuity in all cases!

# Invasion in a periodically varying environment



# Invasion in a periodically varying environment

- Shigesada *et al* (1986) studied the **invasion process** of a single species in an 1-D **periodic varying environment**

# Invasion in a periodically varying environment

- Shigesada *et al* (1986) studied the **invasion process** of a single species in an 1-D **periodic varying environment**

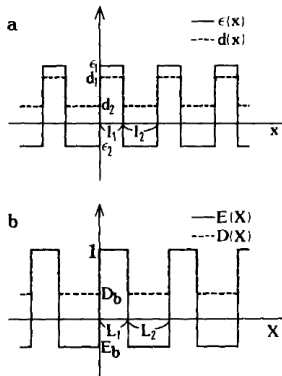
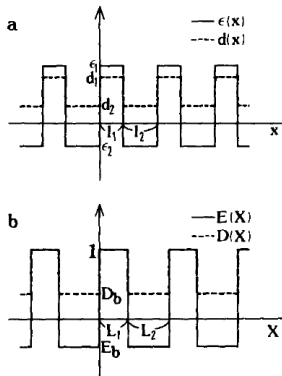


Figure: Shigesada *et al* (1986).

# Invasion in a periodically varying environment

- Shigesada *et al* (1986) studied the **invasion process** of a single species in an 1-D **periodic varying environment**

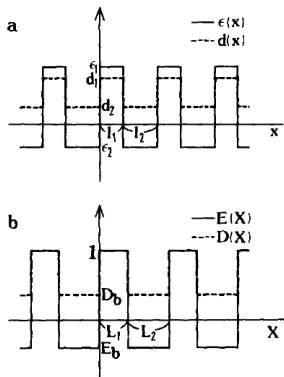


- Different habitats, of sizes  $L_1$  and  $L_2$ , are periodically arranged through the environment

Figure: Shigesada *et al* (1986).

# Invasion in a periodically varying environment

- Shigesada *et al* (1986) studied the **invasion process** of a single species in an 1-D **periodic varying environment**



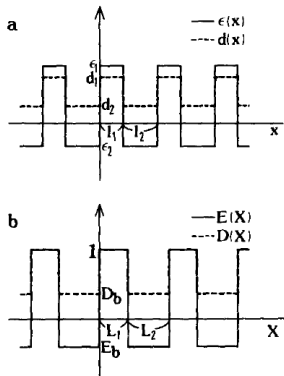
- Different habitats, of sizes  $L_1$  and  $L_2$ , are periodically arranged through the environment
- Habitat 1 is considered more favourable than 2, represented by the relation between **intrinsic growth rates**

$$\epsilon_1 > \epsilon_2$$

Figure: Shigesada *et al* (1986).

# Invasion in a periodically varying environment

- Shigesada *et al* (1986) studied the **invasion process** of a single species in an 1-D **periodic varying environment**



- Different habitats, of sizes  $L_1$  and  $L_2$ , are periodically arranged through the environment
- Habitat 1 is considered more favourable than 2, represented by the relation between **intrinsic growth rates**

$$\epsilon_1 > \epsilon_2$$

- Diffusivities in habitats 1 and 2 are  $d_1$  and  $d_2$

Figure: Shigesada *et al* (1986).

# Invasion in a periodically varying environment

- Population dynamics is described by the reaction diffusion equations

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + (1 - U_1)U_1 \quad \text{in favorable habitats}$$

$$\frac{\partial U_2}{\partial T} = D_b \frac{\partial^2 U_2}{\partial X^2} + (E_b - U_2)U_2 \quad \text{in unfavorable habitats}$$

where:  $D_b = \frac{d_2}{d_1}$  and  $E_b = \frac{\epsilon_2}{\epsilon_1}$ .

# Invasion in a periodically varying environment

- Population dynamics is described by the reaction diffusion equations

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + (1 - U_1)U_1 \quad \text{in favorable habitats}$$

$$\frac{\partial U_2}{\partial T} = D_b \frac{\partial^2 U_2}{\partial X^2} + (E_b - U_2)U_2 \quad \text{in unfavorable habitats}$$

where:  $D_b = \frac{d_2}{d_1}$  and  $E_b = \frac{\epsilon_2}{\epsilon_1}$ .

- Persistence of the population** is guaranteed if the zero solution of this equation is unstable

# Invasion in a periodically varying environment

- Population dynamics is described by the reaction diffusion equations

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + (1 - U_1)U_1 \quad \text{in favorable habitats}$$

$$\frac{\partial U_2}{\partial T} = D_b \frac{\partial^2 U_2}{\partial X^2} + (E_b - U_2)U_2 \quad \text{in unfavorable habitats}$$

where:  $D_b = \frac{d_2}{d_1}$  and  $E_b = \frac{e_2}{e_1}$ .

- Persistence of the population** is guaranteed if the zero solution of this equation is unstable
- We study then the solution of the linearized system

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + U_1 \quad (\text{favorable})$$

$$\frac{\partial U_2}{\partial T} = D_b \frac{\partial^2 U_2}{\partial X^2} + E_b U_2 \quad (\text{unfavorable})$$



# Invasion in a periodically varying environment

**Given**  $U(X, T) = V(X) \exp(\lambda T)$ , **characteristic equations are**

Continuous boundary conditions

$$\sqrt{1 - \lambda} \tan \left( \sqrt{1 - \lambda} \frac{L_1}{2} \right) = \sqrt{(-E_b + \lambda) D_b} \tanh \left( \sqrt{\frac{-E_b + \lambda}{D_b}} \frac{L_2}{2} \right)$$

Discontinuous boundaries I

$$\sqrt{1 - \lambda} \tan \left( \sqrt{1 - \lambda} \frac{L_1}{2} \right) = \frac{1 - \alpha}{\alpha} \sqrt{(-E_b + \lambda)} \tanh \left( \sqrt{\frac{-E_b + \lambda}{D_b}} \frac{L_2}{2} \right)$$

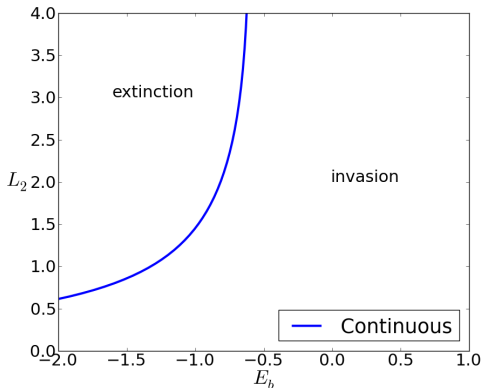
Discontinuous boundaries II

$$\sqrt{1 - \lambda} \tan \left( \sqrt{1 - \lambda} \frac{L_1}{2} \right) = \frac{1 - \alpha}{\alpha} \sqrt{\frac{(-E_b + \lambda)}{D_b}} \tanh \left( \sqrt{\frac{-E_b + \lambda}{D_b}} \frac{L_2}{2} \right)$$

# Invasion in a periodically varying environment

## Persistence conditions

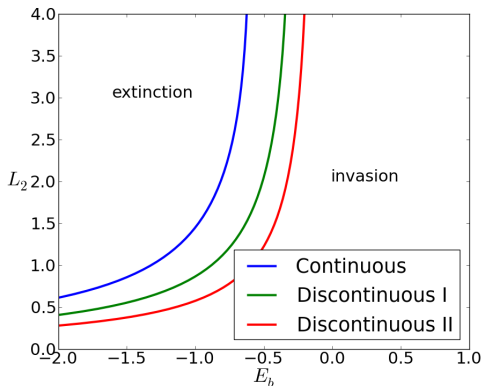
- Unfavorable habitat size ( $L_2$ )  $\times$  intrinsic growth rate in the unfavorable habitat ( $E_b$ )



# Invasion in a periodically varying environment

## Persistence conditions

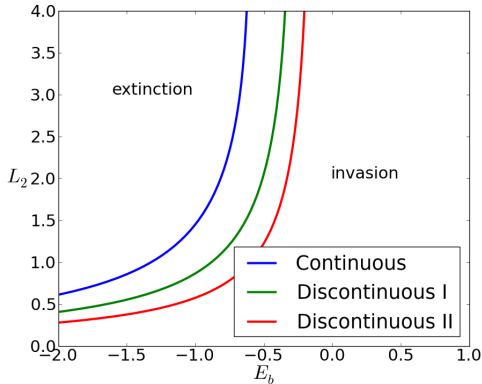
- Unfavorable habitat size ( $L_2$ )  $\times$  intrinsic growth rate in the unfavorable habitat ( $E_b$ )



# Invasion in a periodically varying environment

## Persistence conditions

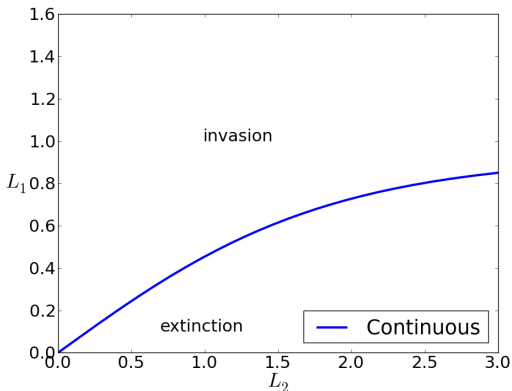
- Unfavorable habitat size ( $L_2$ )  $\times$  intrinsic growth rate in the unfavorable habitat ( $E_b$ )



- No great qualitative changes are found

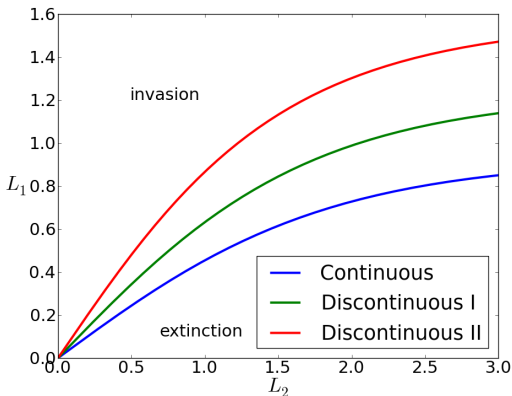
# Invasion in a periodically varying environment

- Favorable habitat size ( $L_1$ ) × unfavorable habitat size ( $L_2$ )



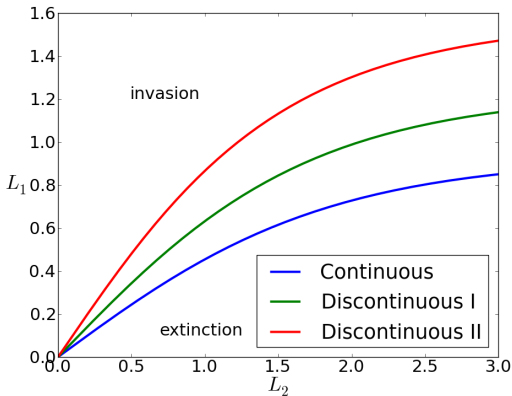
# Invasion in a periodically varying environment

- Favorable habitat size ( $L_1$ )  $\times$  unfavorable habitat size ( $L_2$ )



# Invasion in a periodically varying environment

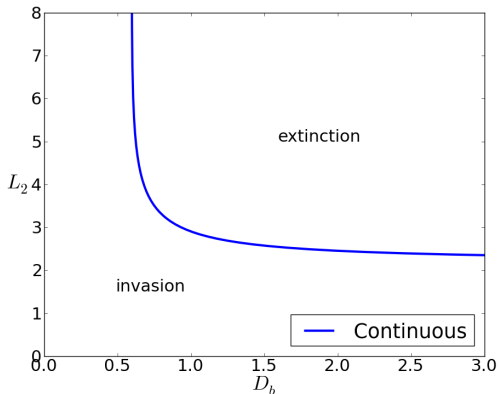
- Favorable habitat size ( $L_1$ )  $\times$  unfavorable habitat size ( $L_2$ )



- Again curves have similar shape

# Invasion in a periodically varying environment

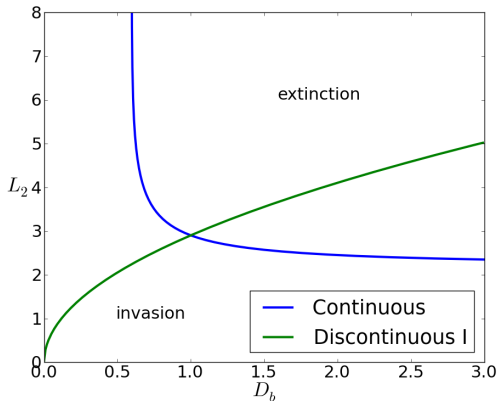
- Unfavorable habitat size ( $L_2$ )  $\times$  diffusion coefficient in the unfavorable habitat ( $D_b$ )





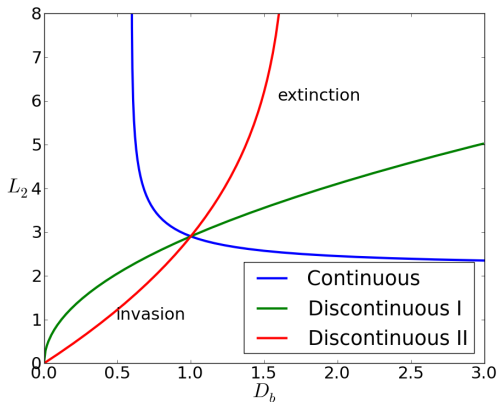
# Invasion in a periodically varying environment

- Unfavorable habitat size ( $L_2$ )  $\times$  diffusion coefficient in the unfavorable habitat ( $D_b$ )



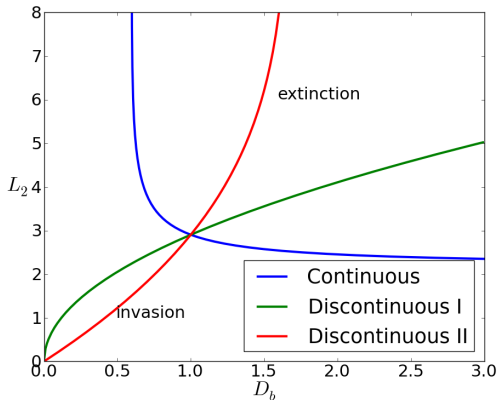
# Invasion in a periodically varying environment

- Unfavorable habitat size ( $L_2$ )  $\times$  diffusion coefficient in the unfavorable habitat ( $D_b$ )



# Invasion in a periodically varying environment

- Unfavorable habitat size ( $L_2$ )  $\times$  diffusion coefficient in the unfavorable habitat ( $D_b$ )



- **Results are strongly affected by the different interface conditions!**

# Traveling periodic waves

- This system also presents **traveling periodic waves**

- This system also presents **traveling periodic waves**
- The **speed of invasion** can be calculated from the linearized problem

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + U_1 \quad \text{in favorable habitats}$$

$$\frac{\partial U_2}{\partial T} = D_b \frac{\partial^2 U_2}{\partial X^2} + E_b U_2 \quad \text{in unfavorable habitats}$$

- This system also presents **traveling periodic waves**
- The **speed of invasion** can be calculated from the linearized problem

$$\frac{\partial U_1}{\partial T} = \frac{\partial^2 U_1}{\partial X^2} + U_1 \quad \text{in favorable habitats}$$

$$\frac{\partial U_2}{\partial T} = D_b \frac{\partial^2 U_2}{\partial X^2} + E_b U_2 \quad \text{in unfavorable habitats}$$

- We look then for traveling wave solutions

$$U(X, T) = f(Z)g(X), \quad Z = X - CT$$

where

$$g(X) = g(X + L), \quad L = L_1 + L_2$$

- Wave speeds  $\times$  intrinsic growth rate in the unfavorable habitats ( $E_b$ ) for different values of  $L_2$

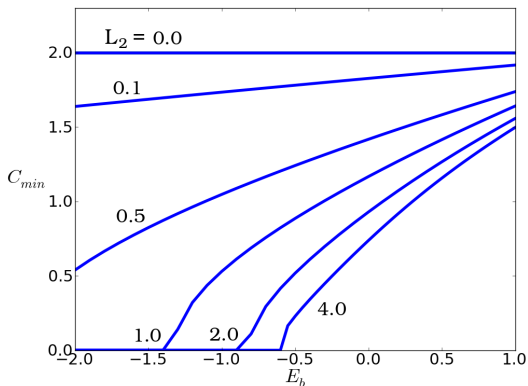


Figure: Continuous interfaces.



- Wave speeds  $\times$  intrinsic growth rate in the unfavorable habitats ( $E_b$ ) for different values of  $L_2$

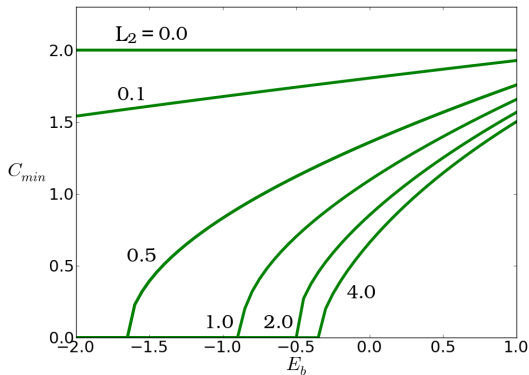


Figure: Discontinuous interfaces I.

- Wave speeds  $\times$  intrinsic growth rate in the unfavorable habitats ( $E_b$ ) for different values of  $L_2$

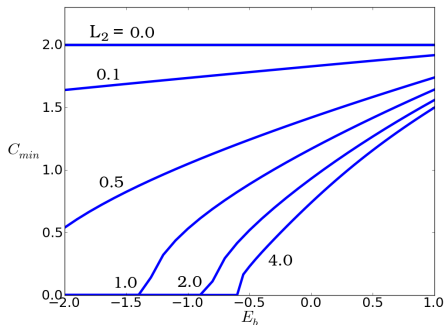


Figure: Continuous interfaces.

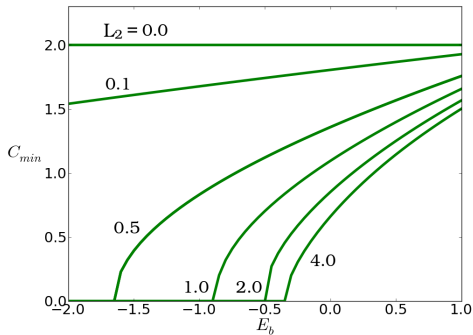


Figure: Discontinuous interfaces I.

- Wave speeds  $\times$  unfavorable habitat sizes ( $L_2$ ) for different values of ( $L_1$ )

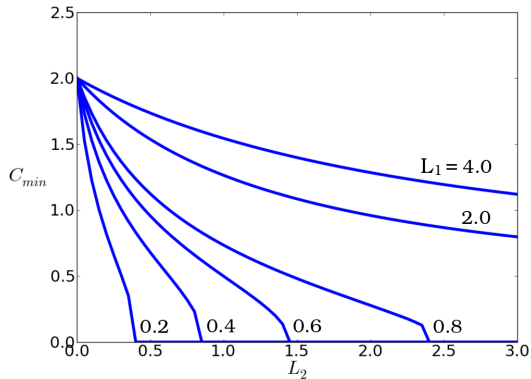


Figure: Continuous interfaces.

- Wave speeds  $\times$  unfavorable habitat sizes ( $L_2$ ) for different values of ( $L_1$ )

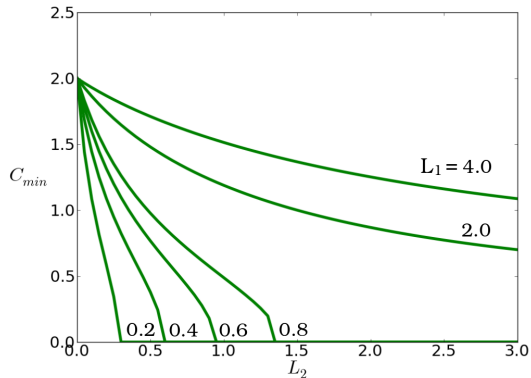


Figure: Discontinuous interfaces I.

# Traveling periodic waves

- Wave speeds  $\times$  unfavorable habitat sizes ( $L_2$ ) for different values of ( $L_1$ )

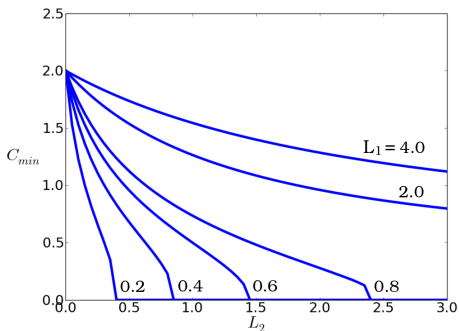


Figure: Continuous interfaces.

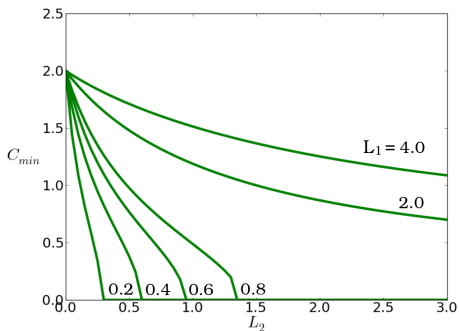


Figure: Discontinuous interfaces I.

- Wave speeds  $\times$  diffusivity in the unfavorable ( $D_b$ ) for different values of  $L_2$

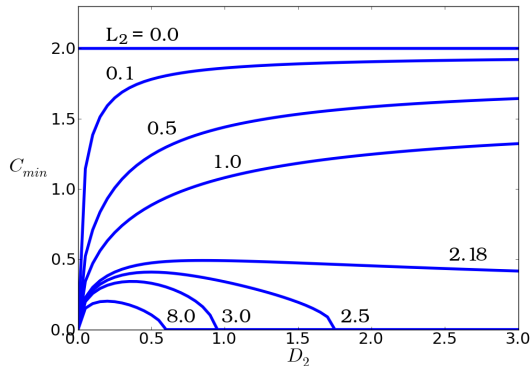


Figure: Continuous interfaces.

- Wave speeds  $\times$  diffusivity in the unfavorable ( $D_b$ ) for different values of  $L_2$

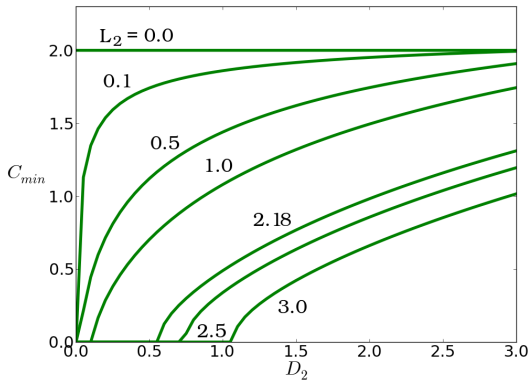


Figure: Discontinuous interfaces I.

# Traveling periodic waves

- Wave speeds  $\times$  diffusivity in the unfavorable ( $D_b$ ) for different values of  $L_2$

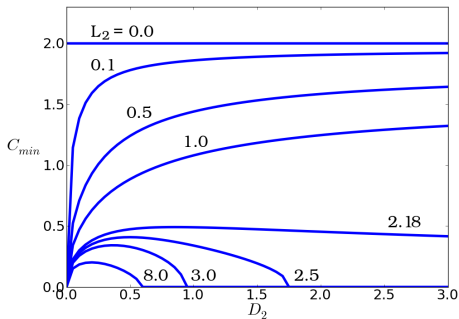


Figure: Continuous interfaces.

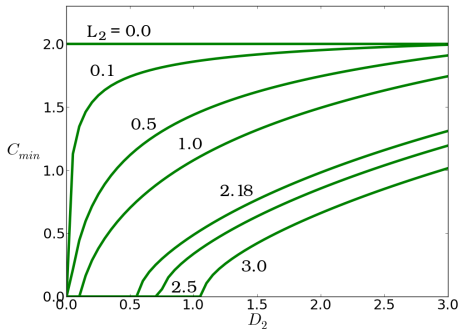


Figure: Discontinuous interfaces I.



# Summary

- Interface conditions must reflect individual movement behaviour across an interface
- Edge behaviour and differential movement between habitats can lead to discontinuous interface conditions
- Results regarding species persistence and spread in heterogeneous environments are strongly affected by interface conditions

## Acknowledgments



Thanks for your attention!