An Asymptotics Problem from Spatiotemporal Population Cycles

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Applied Asymptotics and Modelling Workshop, June 2006

Work on ecological applications is in collaboration with:

Xavier Lambin

Matthew Smith

Outline

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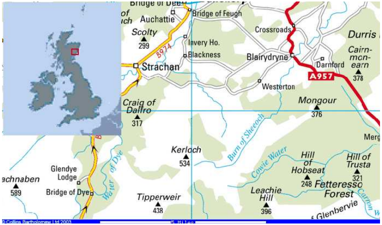
1. Ecological Background
2. Mathematical Modelling
3. Perturbation Theory Problem
4. Conclusions

Habitat Boundaries in Ecology

- Often ecological habitats are surrounded by unfavourable environments
- Examples: a wood surrounded by open terrain
  moorland surrounded by farmland
  marsh surrounded by dry ground

Example: Red Grouse on Kerloch Moor



- Red grouse is a cyclic population (period about 4-6 years)
- The study site is moorland, with farmland at its Northern edge
- Farmland is very hostile for red grouse

Mathematical Representation

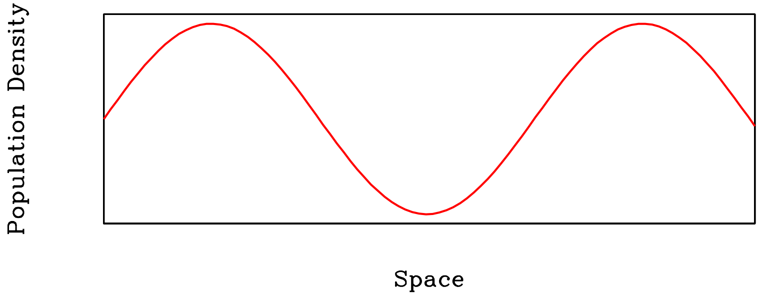
$$\begin{aligned} \text{Habitat} \quad x > 0: \quad \partial w/\partial t &= D\partial^2 w/\partial x^2 + f(w) \\ \text{Surroundings} \quad x < 0: \quad \partial w/\partial t &= D\partial^2 w/\partial x^2 - \gamma w \end{aligned}$$

where $w(x,t)$ denotes population density.

- For $x < 0$, finiteness as $x \to -\infty \Rightarrow w \propto \exp(x\sqrt{\gamma/D})$ at equilibrium
- Equating w and w_x at $x = 0$ implies the Robin boundary condition $\sqrt{D}w_x + \sqrt{\gamma}w = 0$
- Note that γ is large, so that the boundary condition will be close to the Dirichlet limit.

Red Grouse Example (contd)

Spatiotemporal data from Kerloch Moor shows that the red grouse cycles are spatially organised into a periodic travelling wave



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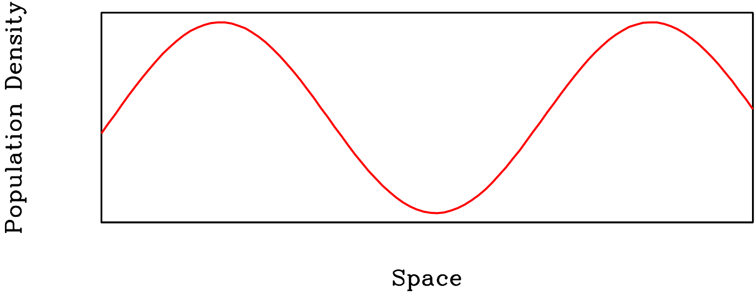

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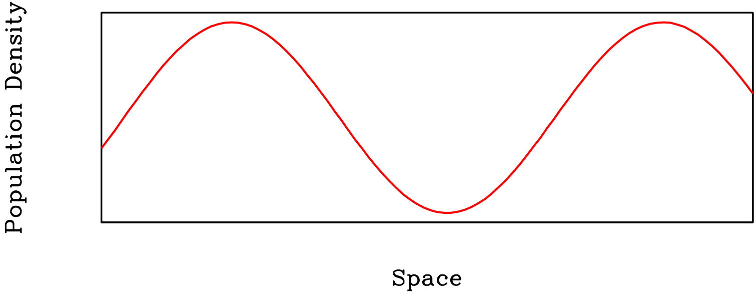

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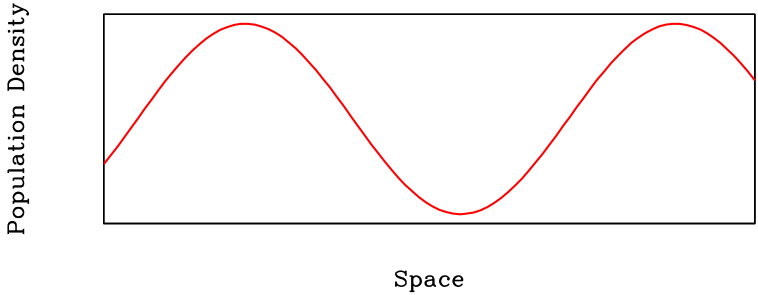

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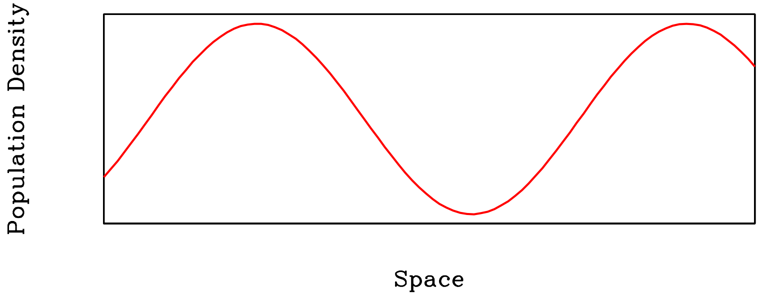

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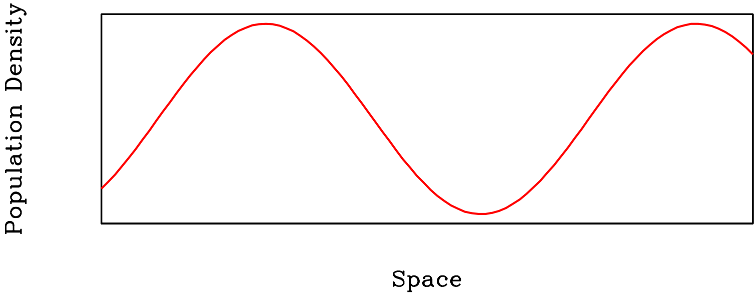

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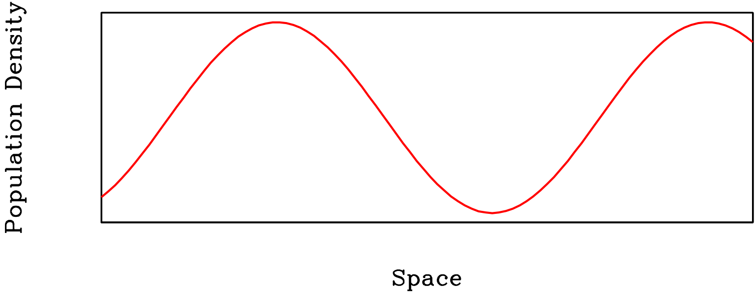

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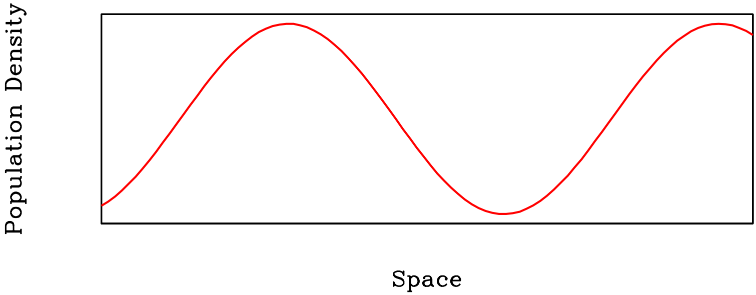

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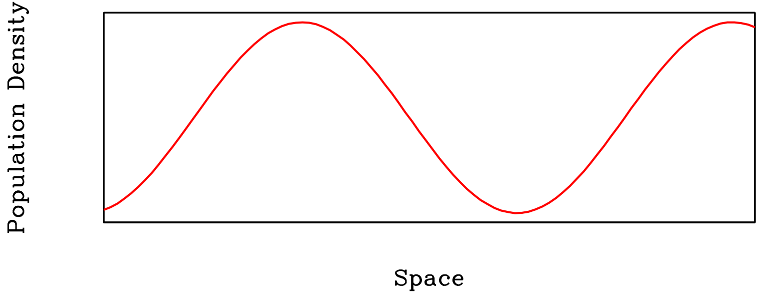

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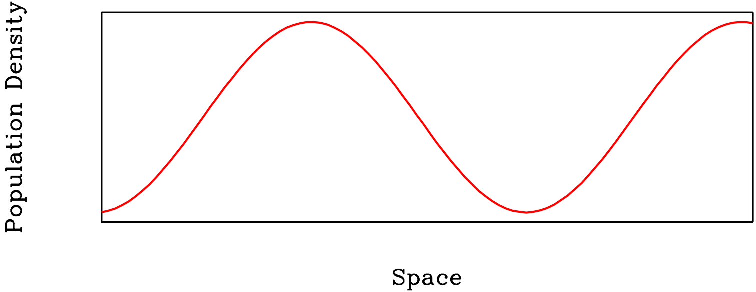

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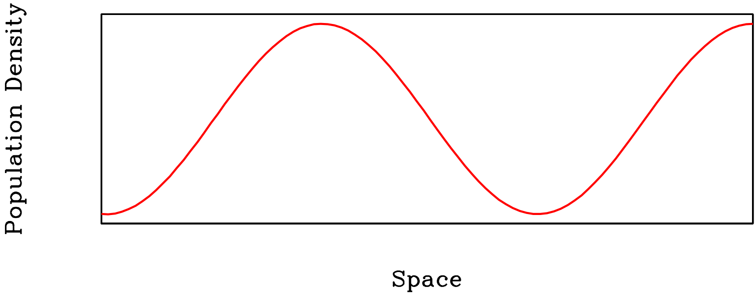

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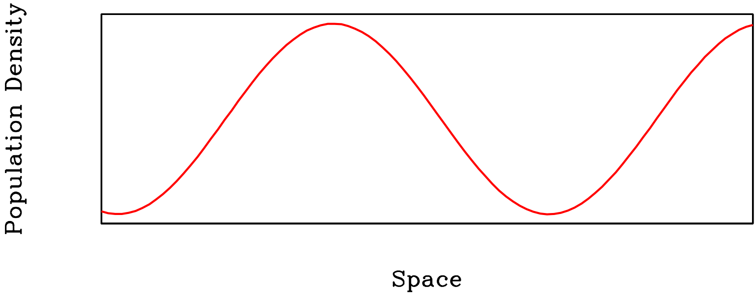

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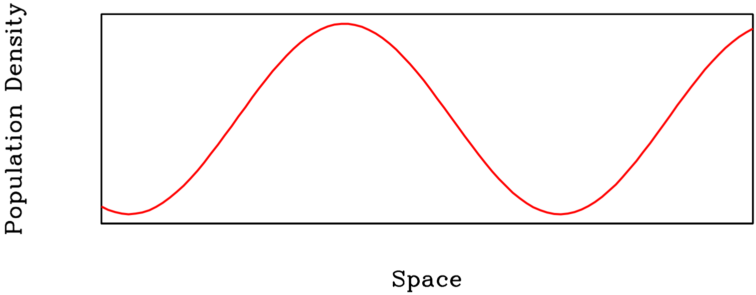

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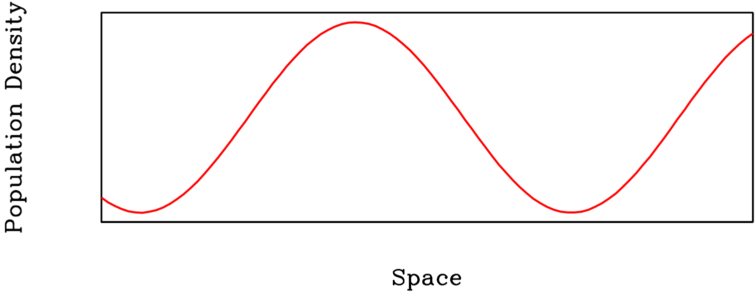

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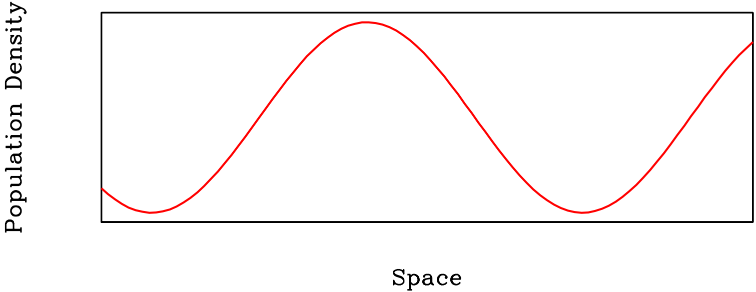

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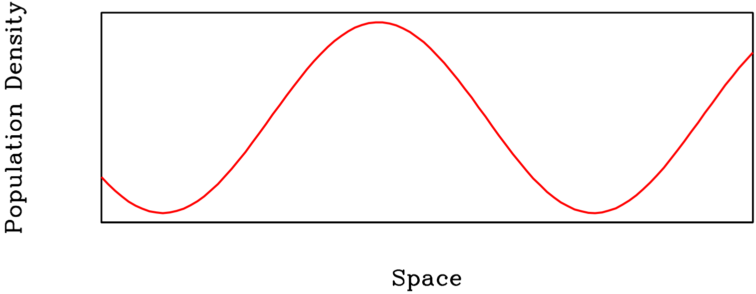

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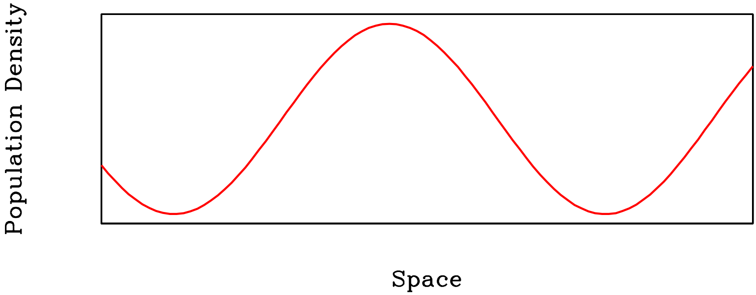

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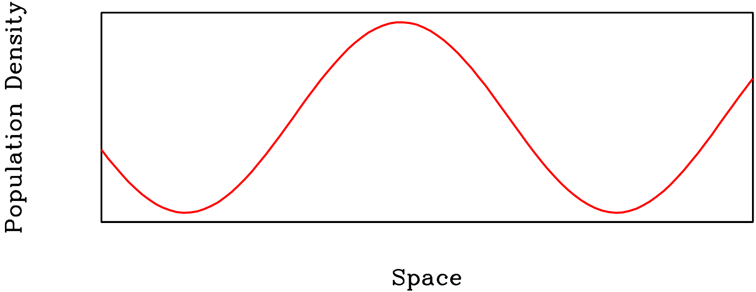

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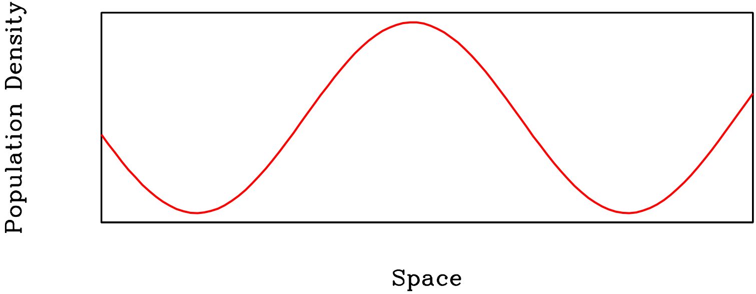

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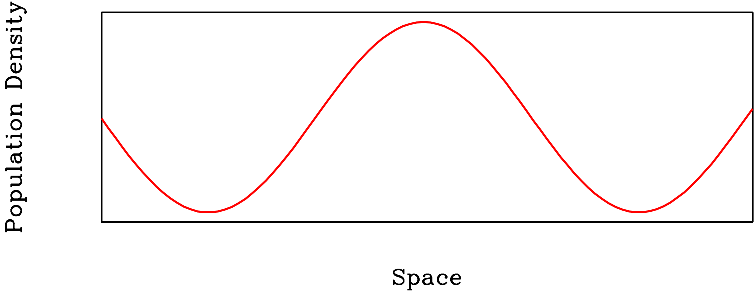

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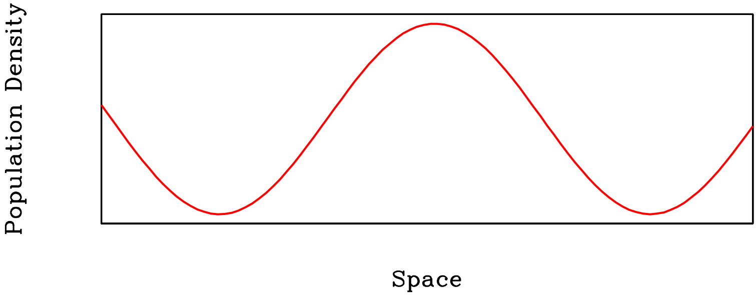

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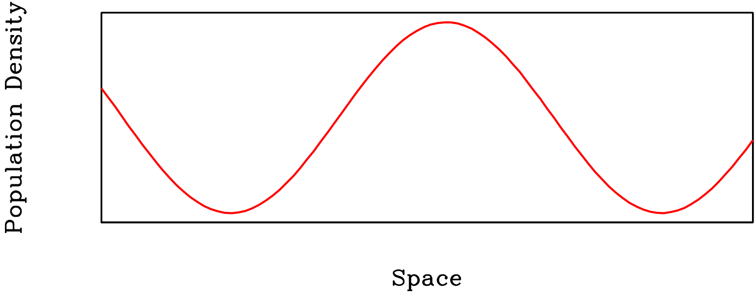

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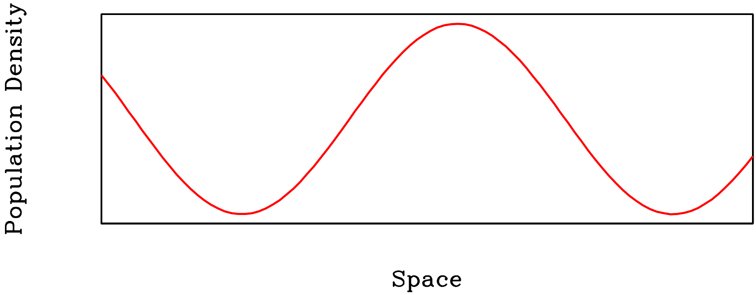

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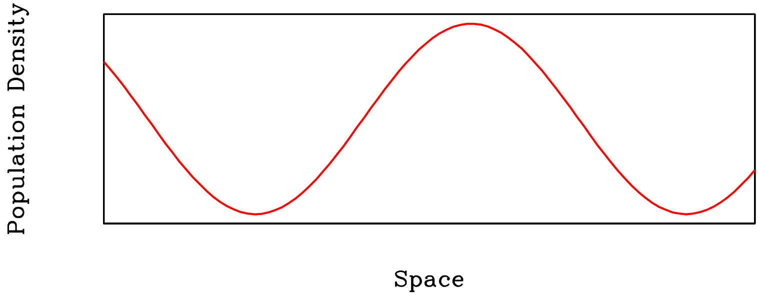

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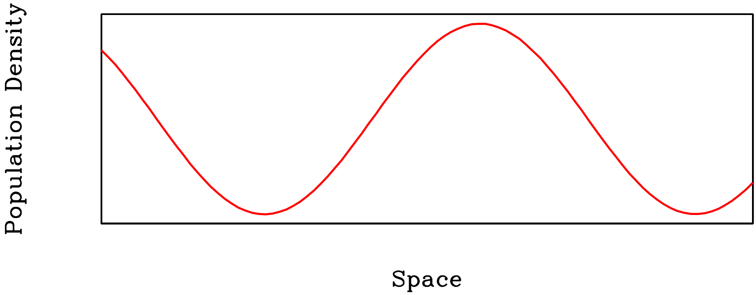

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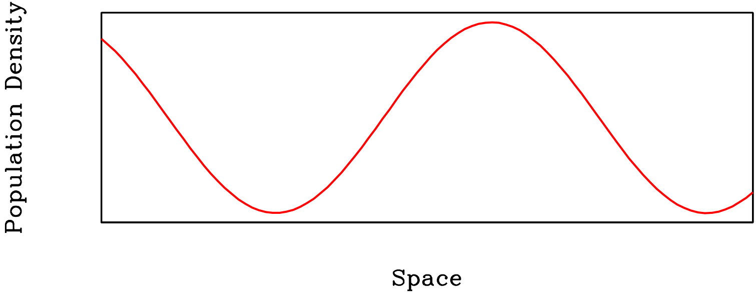

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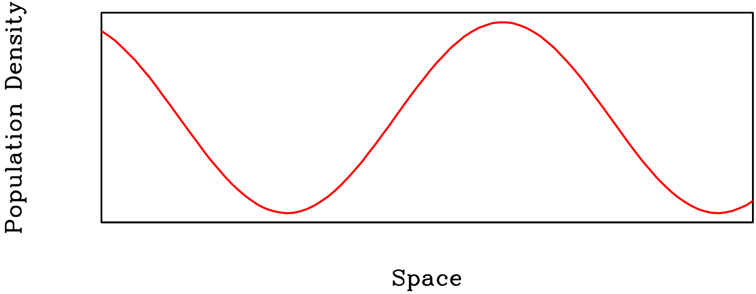

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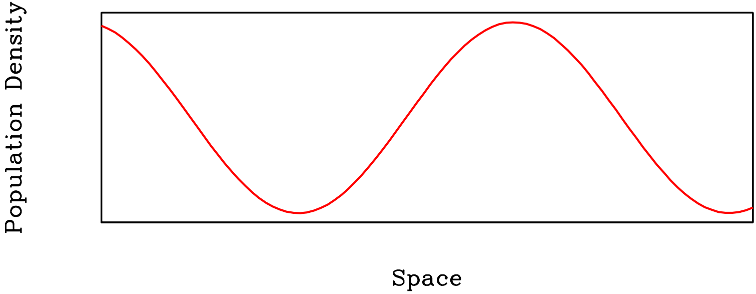

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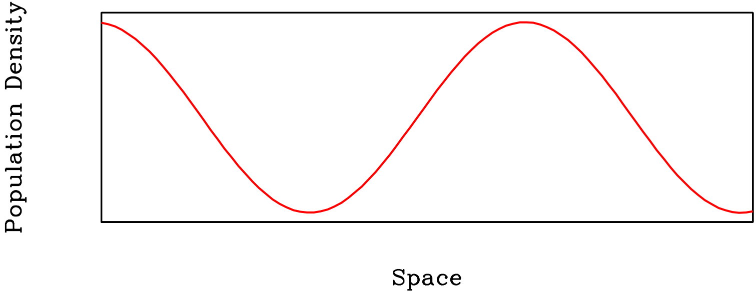

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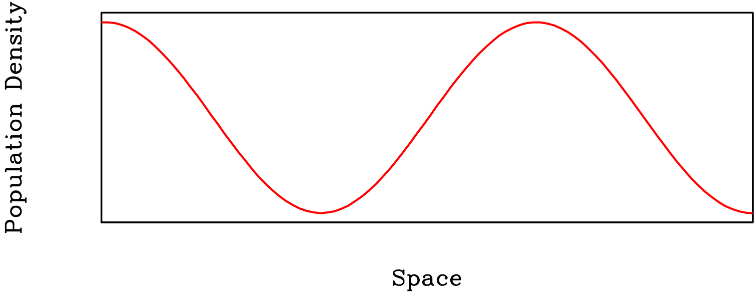

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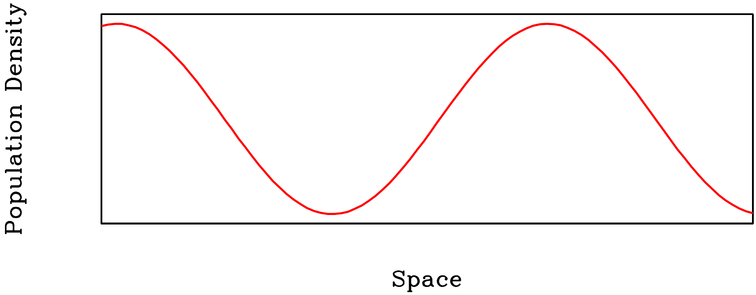

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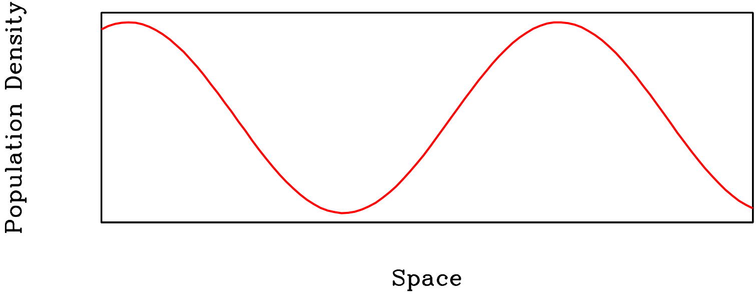

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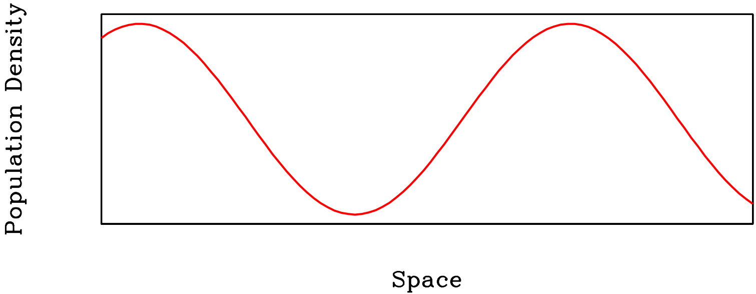

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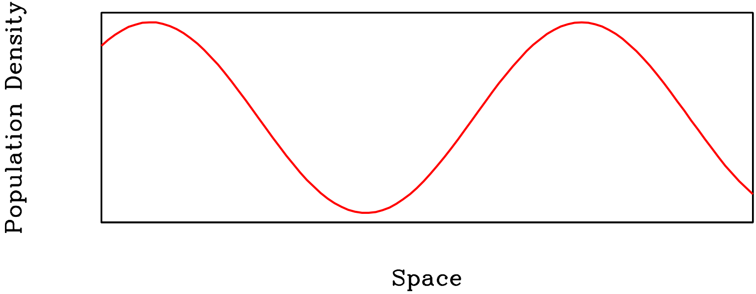

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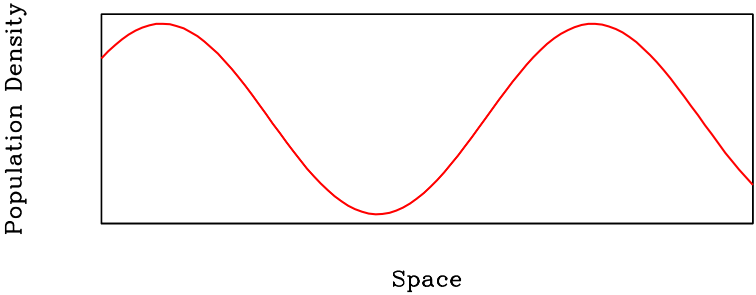

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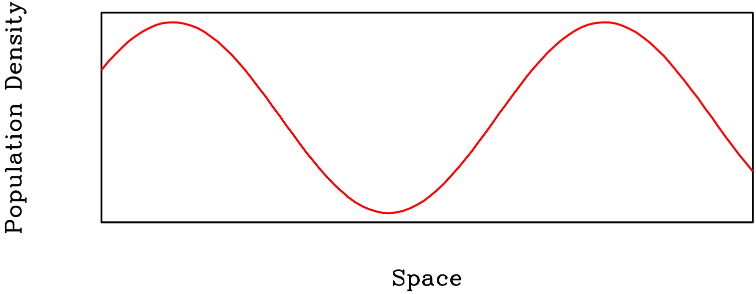

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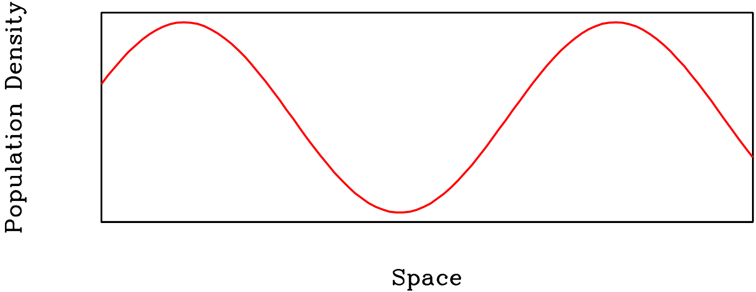

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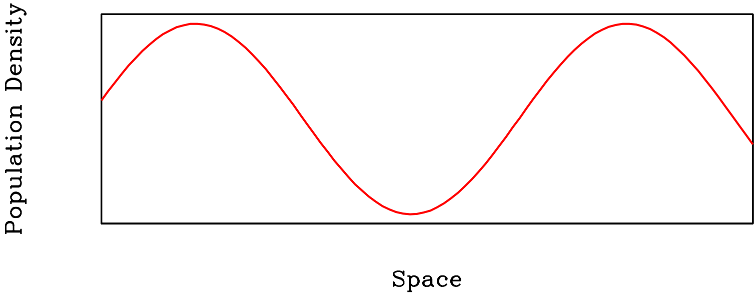

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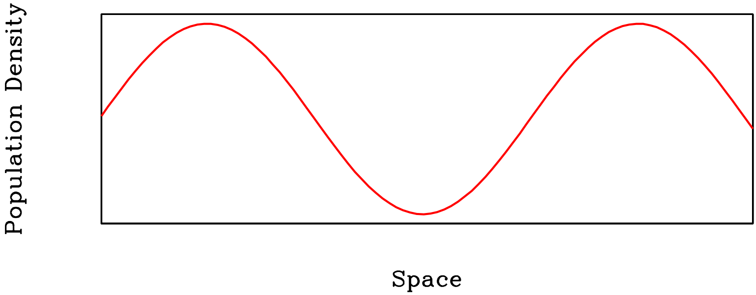

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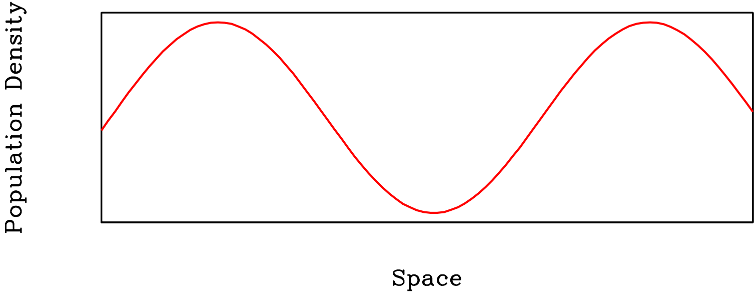

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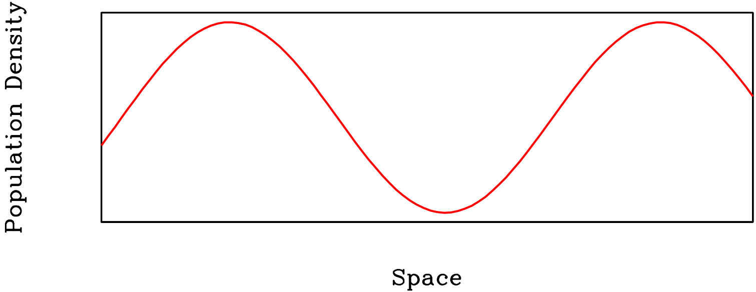

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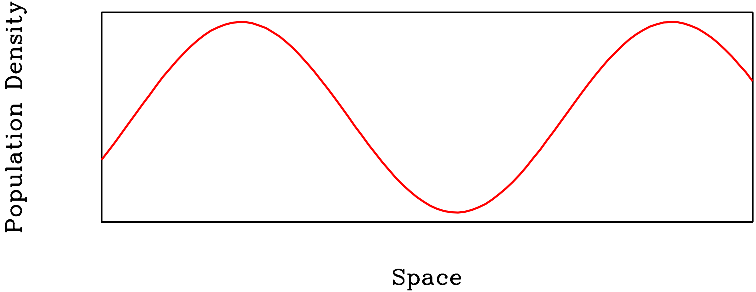

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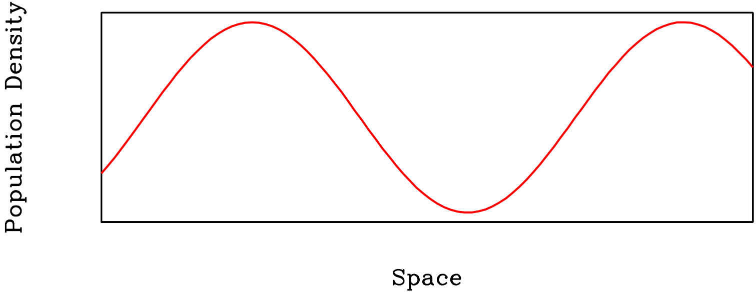

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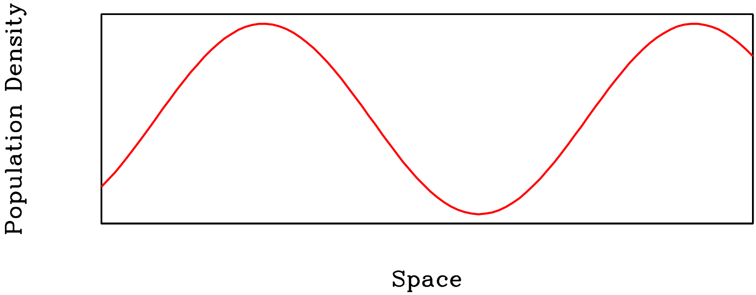

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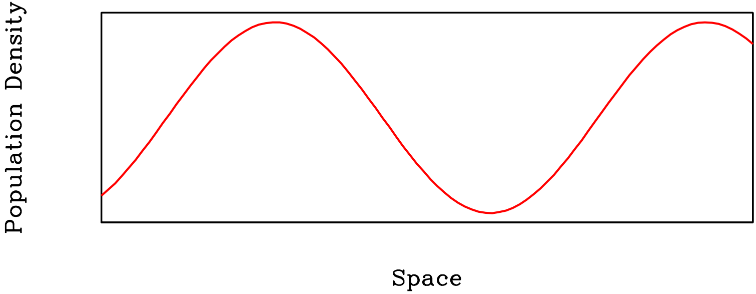

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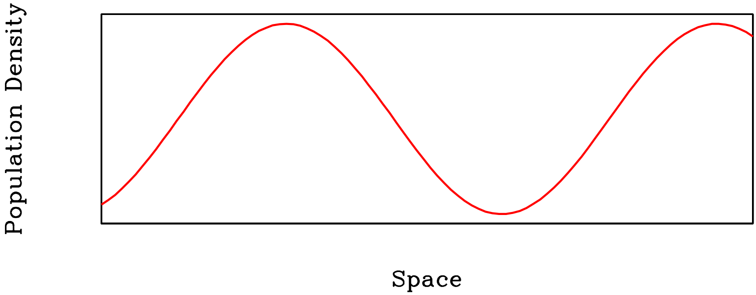

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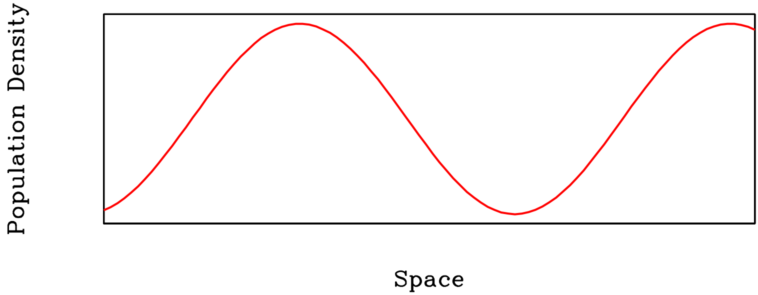

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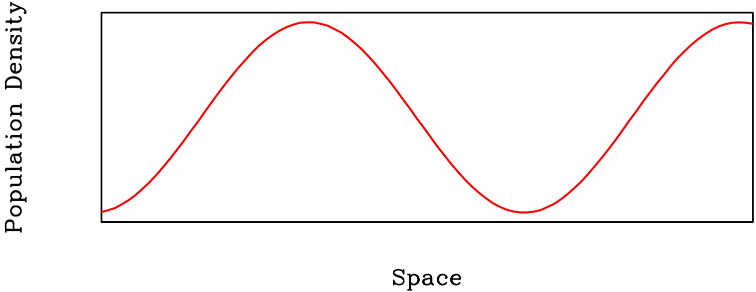

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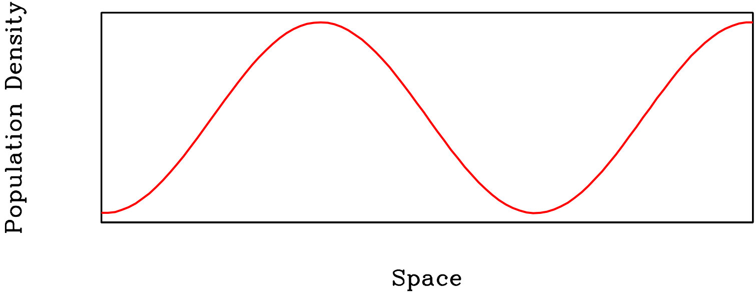

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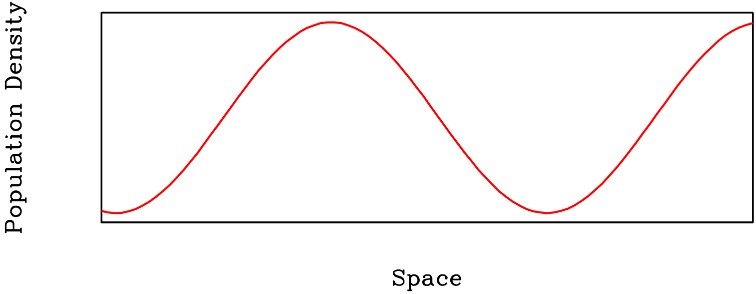

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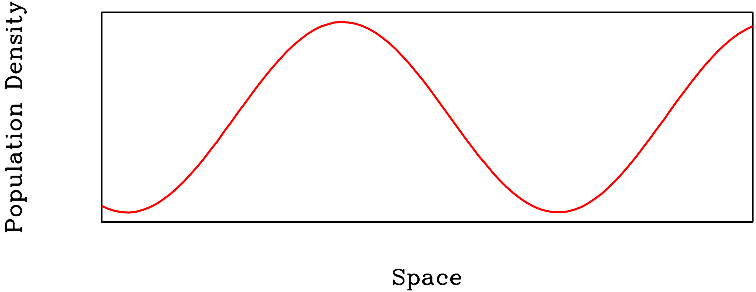

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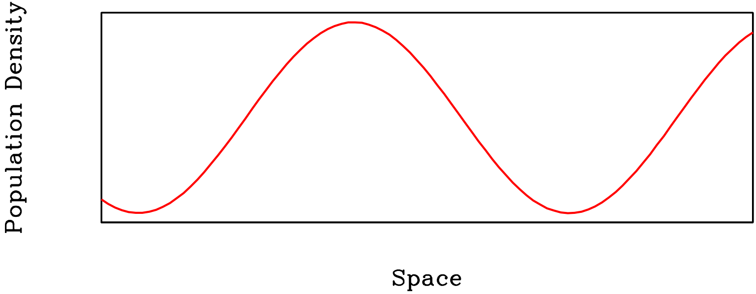

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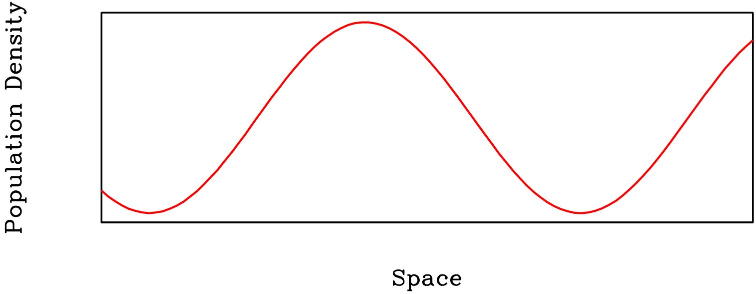

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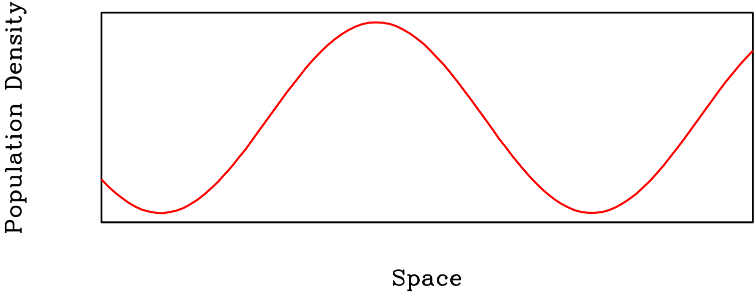

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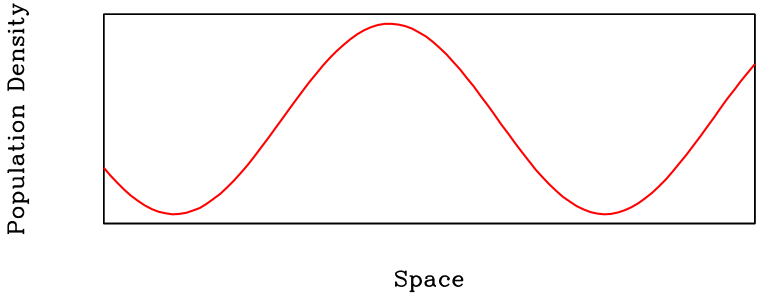

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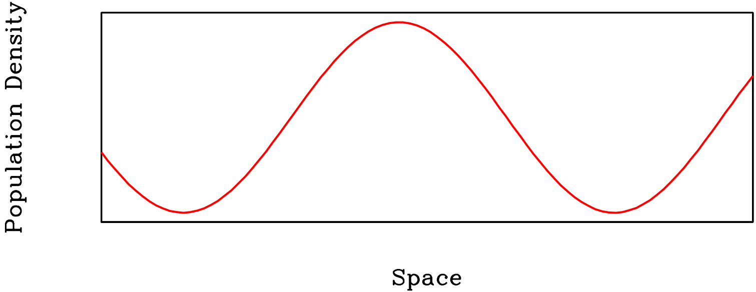

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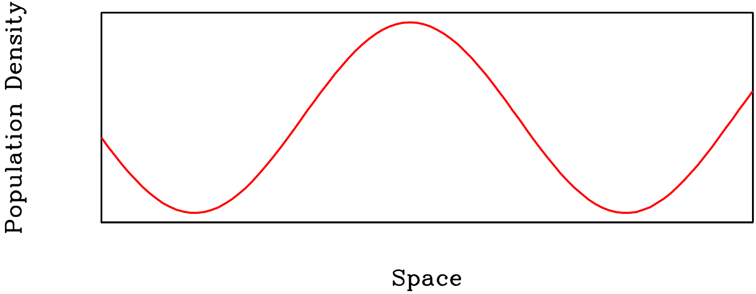

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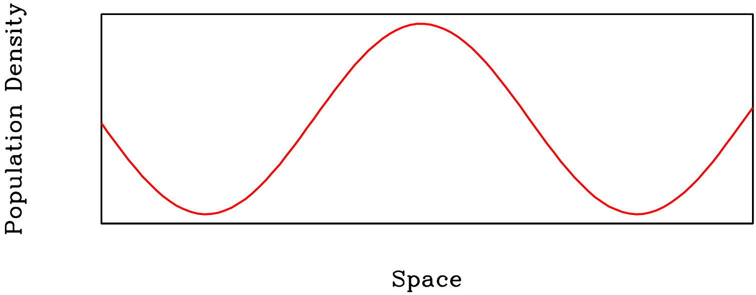

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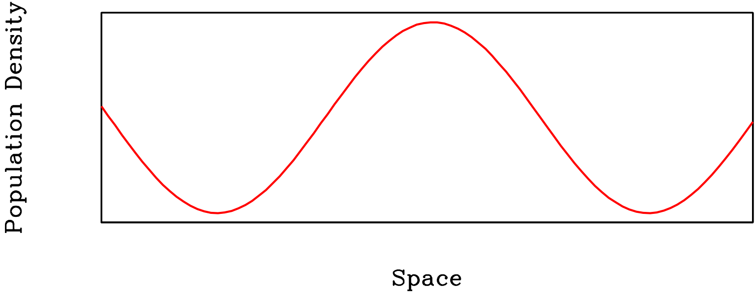

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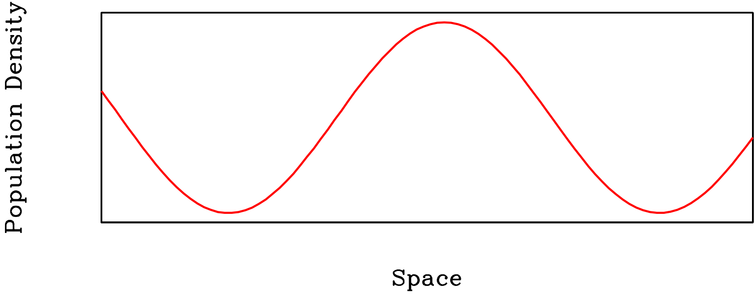

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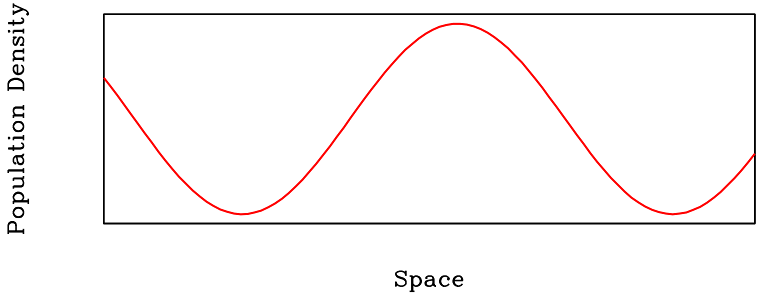

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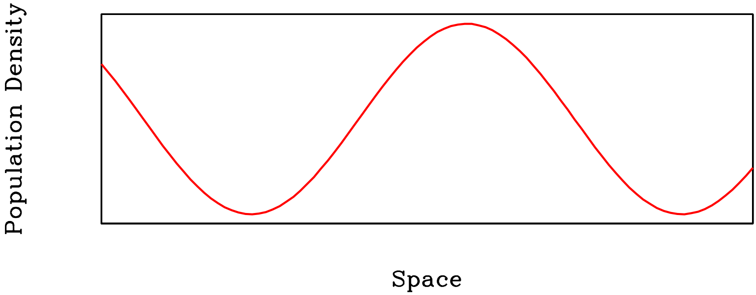

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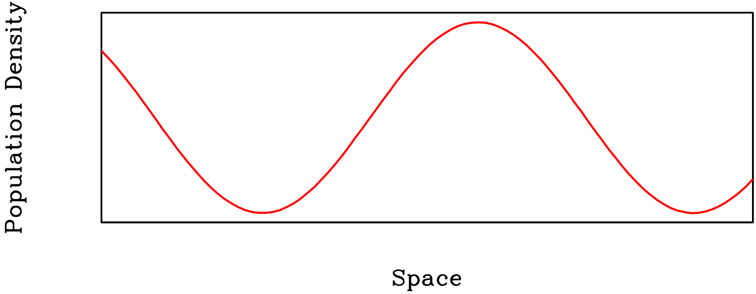

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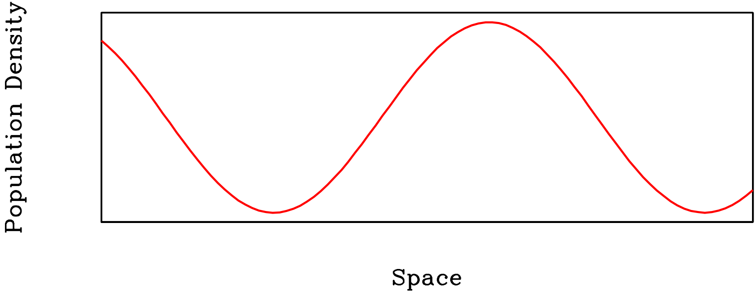

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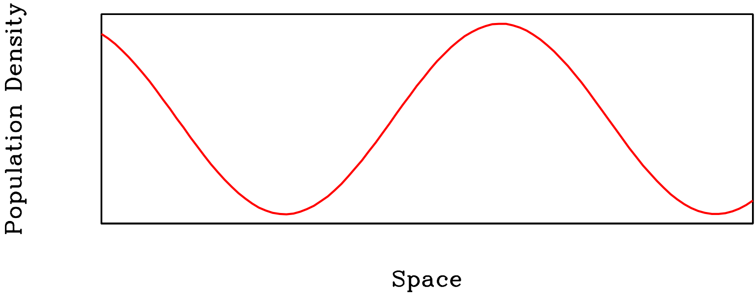

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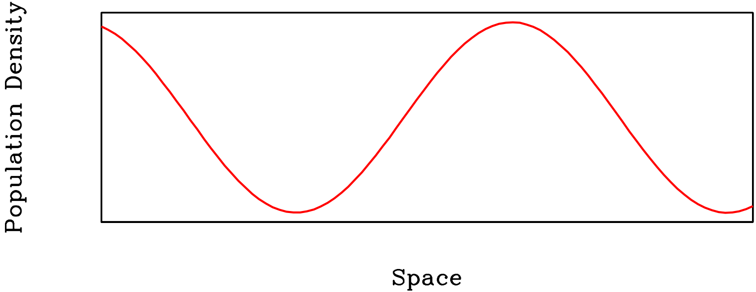

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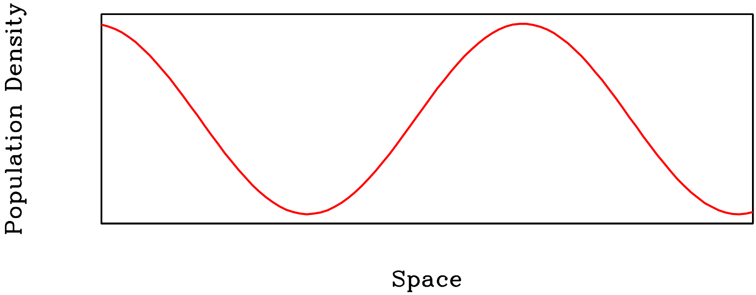

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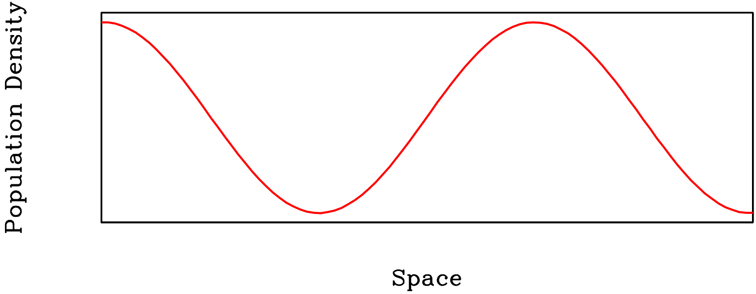

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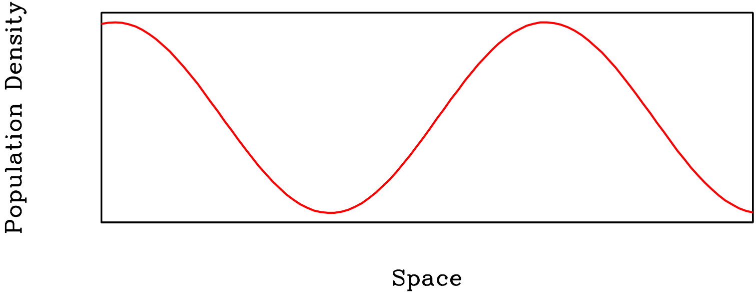

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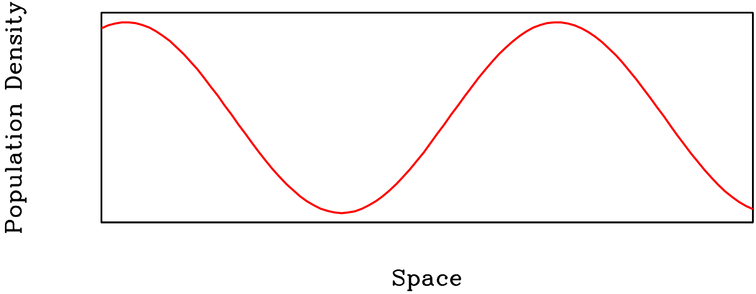

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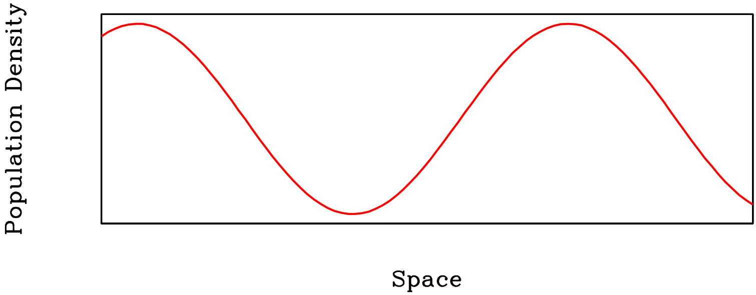

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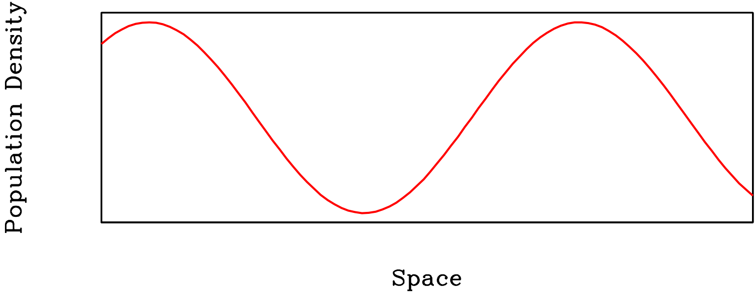

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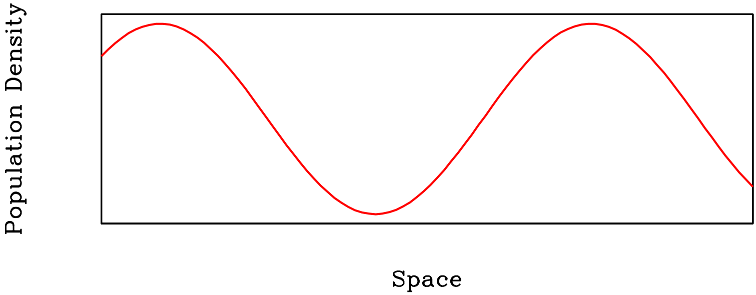

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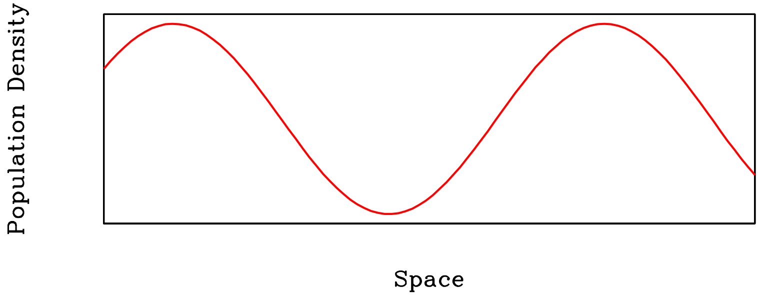

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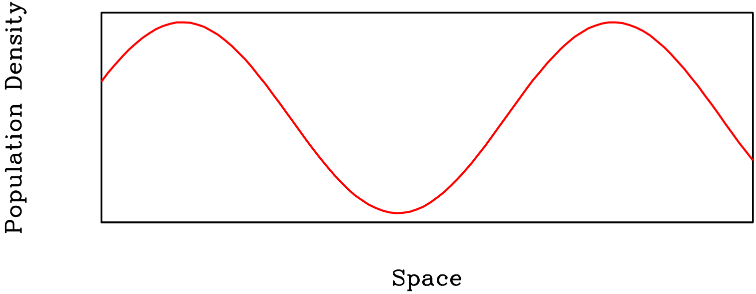

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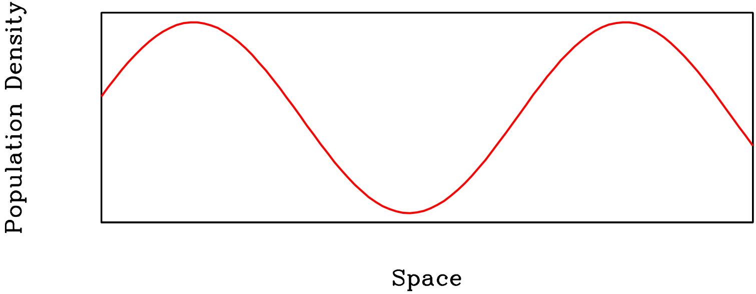

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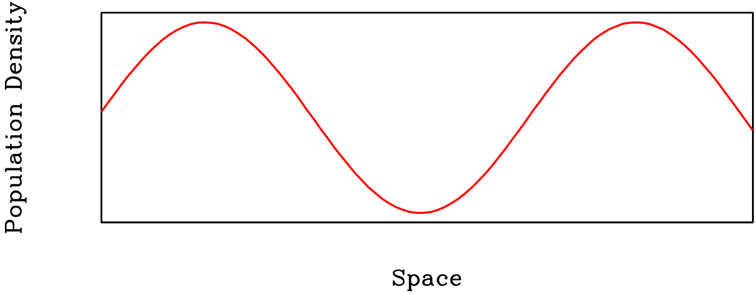

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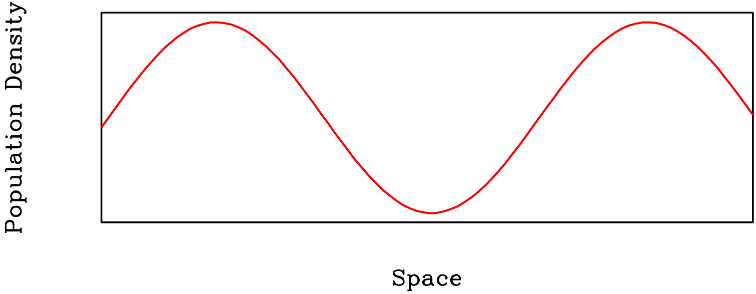

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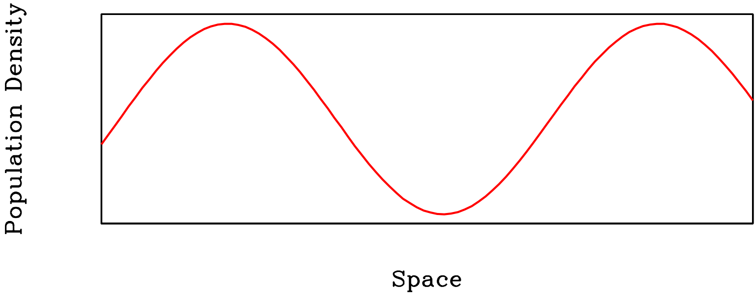

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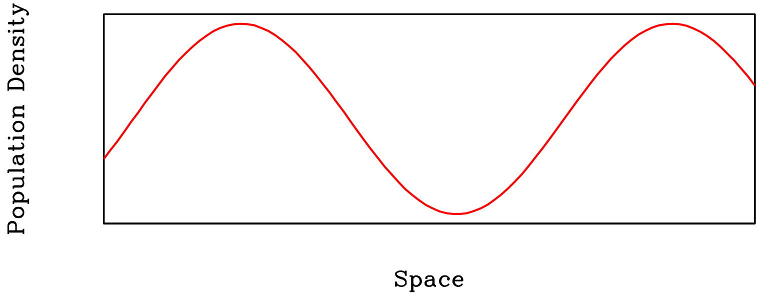
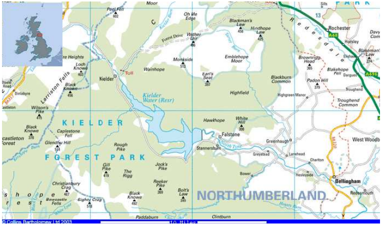


Red Grouse Wave Generation Question

Question

Could the moor/farmland boundary at the Northern edge of the study site play a role in generating the periodic travelling waves?

Second Example: Field Voles in Kielder Forest



Field voles in Kielder Forest are cyclic (period 4 years)
Again, spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave

Boundary Condition at the Reservoir Edge

- Voles are an important prey species for owls and kestrels
- The open expanse of Kielder Water will greatly facilitate hunting at its edge
- Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition

$$\frac{d}{dx}\begin{pmatrix}\text{vole}\\ \text{density}\end{pmatrix} = -\begin{pmatrix}\text{large}\\ \text{constant}\end{pmatrix}\cdot\begin{pmatrix}\text{vole}\\ \text{density}\end{pmatrix}$$

Field Vole Wave Generation Question

Question

Could the boundary condition at the reservoir edge play a role in generating the periodic travelling waves?

Outline

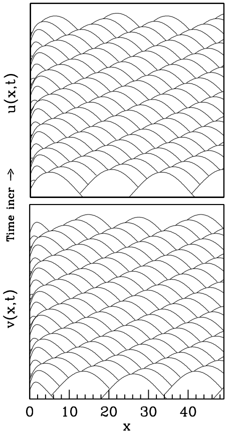
Mathematical Model

I consider a generic oscillator model

$$\begin{aligned}\frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} + \lambda(r)u - \omega(r)v \\ \frac{\partial v}{\partial t} &= \frac{\partial^2 v}{\partial x^2} + \omega(r)u + \lambda(r)v \\ \lambda(r) &= 1 - r^2 \\ \omega(r) &= \omega_0 + \omega_1 r^2.\end{aligned}$$

("λ–ω equations")
This is the normal form of an oscillatory reaction-diffusion system with scalar diffusion close to a supercritical Hopf bifurcation

Typical Model Solutions



Interim Conclusion

Robin boundary conditions do generate periodic travelling waves

Amplitude and Phase Equations

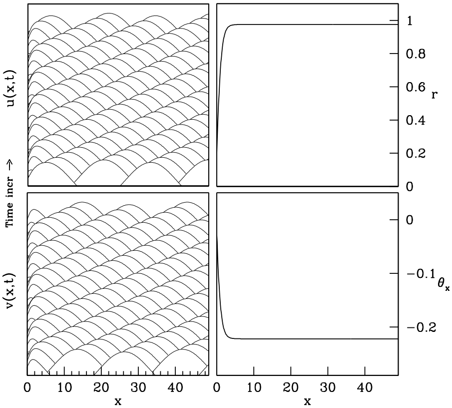
To study the λ–ω equations, it is helpful to replace u and v by $r = \sqrt{u^2 + v^2}$ and $\theta = \tan^{-1}(v/u)$, giving

$$\begin{aligned} r_t &= r_{xx} - r\theta_x^2 + r(1 - r^2) \\ \theta_t &= \theta_{xx} + \frac{2r_x\theta_x}{r} + \omega_0 - \omega_1 r^2 \end{aligned}$$

There is a family of periodic travelling wave equations

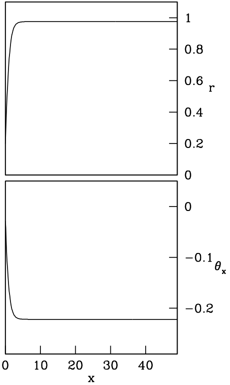
$$\left\{ \begin{array}{l} r = R \\ \theta = \left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \end{array} \right\} \leftrightarrow \left\{ \begin{array}{lcl} u &=& R \cos\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \\ v &=& R \sin\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \end{array} \right\}$$

Typical Solutions Replotted



Replotting the solutions in terms of r and θ_x shows that the long-term solutions for r and θ_x are independent of time

Equilibrium Equations

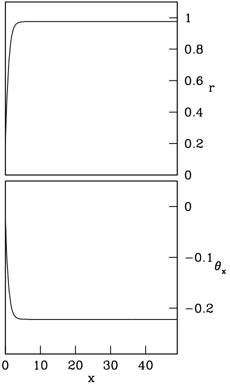


Solns $r = R(x)$, $\theta_x = \Psi(x)$

$$\Rightarrow R_{xx} + R(1 - R^2 - \Psi^2) = 0$$
$$\Psi_x + 2\Psi R_x/R + k - \omega_1 R^2 = 0$$

with $\epsilon R_x - R = \Psi = 0$ at $x = 0$

Equilibrium Equations



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Key question: what is $R(\infty)$, the amplitude of the periodic travelling wave?

Outline

Solution for $\epsilon = 0$

For $\epsilon = 0$ (Dirichlet boundary condition) there is an exact solution

$$R(x) = a \tanh(x/\sqrt{2}) \quad \Psi(x) = -\text{sign}(\omega_1)\sqrt{1-a^2}\tanh(x/\sqrt{2})$$

$$\text{where} \quad a = \left\{ \tfrac{1}{2}\left[1 + \sqrt{1 + \tfrac{8}{9}\omega_1^2}\right] \right\}^{-1/2}$$

It is convenient to write $y = x/\sqrt{2}$, $\phi = -\text{sign}(\omega_1)\Psi$, and to use a rather than ω_1 as a parameter

Perturbation Theory Problem

Equations:

$$d^2R/dy^2 + 2R\left(1 - R^2 - \phi^2\right) = 0$$

$$d\phi/dy + 2(\phi/R)dR/dy + 3\sqrt{1-a^2}(R^2 - A^2)/a^2 = 0$$

Boundary conditions:

$$\epsilon dR/dy = R\sqrt{2} \quad \text{and} \quad \phi = 0 \quad \text{at} \quad y = 0$$

$$R \to A \quad \text{and} \quad \phi \to \sqrt{1-A^2} \quad \text{as} \quad y \to \infty$$

Solution form:

$$R = a\tanh y + \epsilon R_1 + \epsilon^2 R_2 + \ldots$$

$$\phi = \sqrt{1-a^2}\tanh y + \epsilon\phi_1 + \epsilon^2\phi_2 + \ldots$$

$$A = a + \epsilon A_1 + \epsilon^2 A_2 + \ldots$$

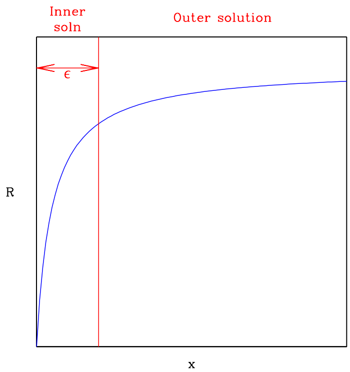
Order ϵ Solution (Outer Equations)

- The $O(\epsilon)$ equations can be solved exactly subject to the boundary conditions at ∞, giving:

$$\begin{aligned}
R_1(y) &= K_w(a)\ \text{sech}^2 y \left[\int_{y_1=0}^{y_1=y} Y^-(y_1) \int_{y_2=y_1}^{y_2=\infty} \frac{Y^+(y_2)g(y_2)}{\cosh^4 y_2}\, dy_2\, dy_1 \right.\\
&\quad \left. - \int_{y_1=0}^{y_1=y} Y^+(y_1) \int_{y_2=y_1}^{y_2=\infty} \frac{Y^-(y_2)g(y_2)}{\cosh^4 y_2}\, dy_2\, dy_1 \right] + C\ \text{sech}^2 y \\
\text{where } Y^{\pm}(y) &= \text{Re}\left[\text{sech}^p y\ F\left(\alpha, \beta, \gamma, (1 \pm \tanh y)/2\right)\right] \\
g(y) &= 24(1-a^2)A_1 \tanh^2 y \\
K_w(a) &= -\text{Re}\ F(\alpha, \beta, \gamma; \tfrac{1}{2}) \cdot \text{Re}\ F'(\alpha, \beta, \gamma; \tfrac{1}{2})
\end{aligned}$$

- There are two undetermined constants, A_1 and C.
- The boundary conditions at $y = 0$ cannot be satisfied for any values of these constants: a boundary layer is needed

Solution Structure

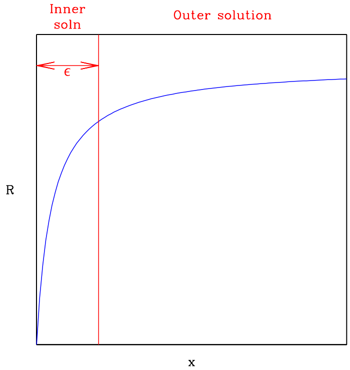


Inner layer rescalings:

$$\tilde{R} = R/\epsilon \quad \tilde{\Psi} = \Psi/\epsilon \quad \tilde{y} = y/\epsilon$$

The inner equations have a simple exact solution, and matching determines all constants.

Solution Structure



Inner layer rescalings:

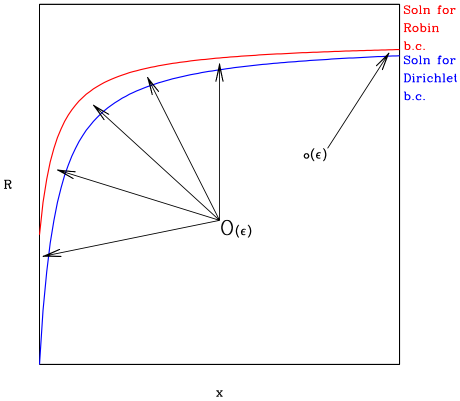
$$\tilde{R} = R/\epsilon \quad \tilde{\Psi} = \Psi/\epsilon \quad \tilde{y} = y/\epsilon$$

The inner equations have a simple exact solution, and matching determines all constants.

Crucially, $\Psi_{\text{OUTER},1}(y) \sim \text{constant}/y^2$ as $y \to 0$, and there is no corresponding term in the inner solution.
Therefore constant $= 0 \Rightarrow A_1 = 0$.

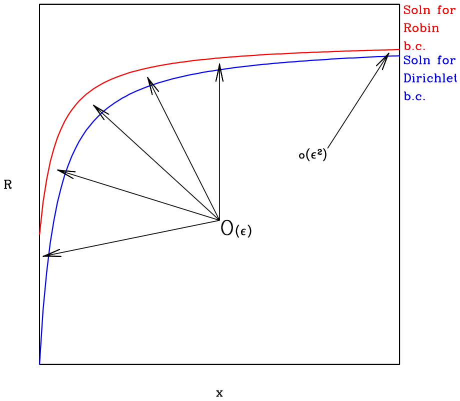
Key Result

The solutions for R and Ψ have a non-zero correction at $O(\epsilon)$, but the periodic travelling wave has no correction at this order



Higher Order Corrections

The next order corrections to the inner and outer solutions can be calculated explicitly. Matching determines all constants, with
$A_2 = 0$
(recall that periodic wave amplitude $A = a + \epsilon A_1 + \epsilon^2 A_2 + \ldots$)



Outline

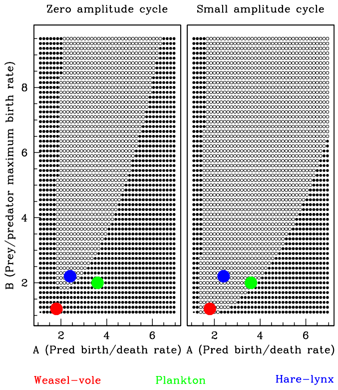
1. Ecological Background
2. Mathematical Modelling
3. Perturbation Theory Problem
4. Conclusions

Conclusions

- A Robin boundary condition does generate periodic travelling waves
- The periodic wave given by the Robin boundary condition is very well approximated by that given by the Dirichlet boundary condition
- This is important because a Dirichlet boundary condition is much simpler both analytically and numerically
- Most ecological models use Dirichlet rather than Robin conditions, without any justification. My results provide justification in the context of periodic travelling wave generation

An Application of the Dirichlet Bdy Cond^n Formula

Using the formula for the periodic wave amplitude generated by the Dirichlet boundary condition, we can predict the stability of the waves as a function of ecological parameters (close to Hopf bifurcation)



Hypothesis

Hypothesis

The periodic wave amplitudes implied by the two boundary conditions differ by an amount that is beyond all all orders in ϵ