Periodic Travelling Waves in Field Vole Populations

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Heriot-Watt University

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This talk can be downloaded from my web site
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In collaboration with:

Matthew Smith

Xavier Lambin

Outline

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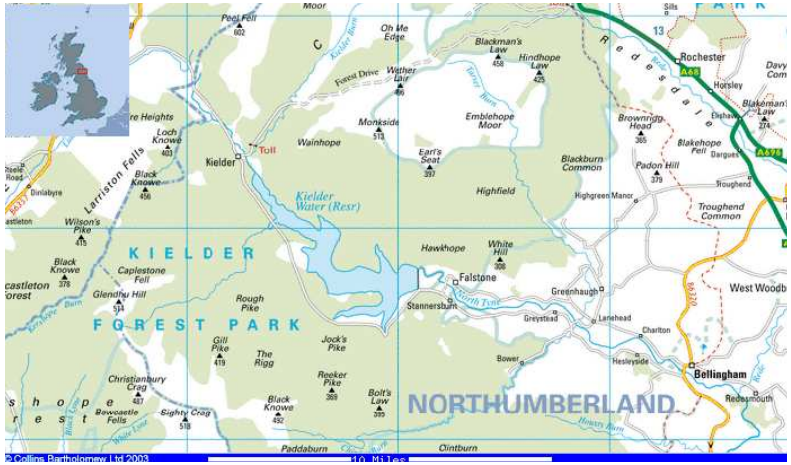
Field Voles in Kielder Forest



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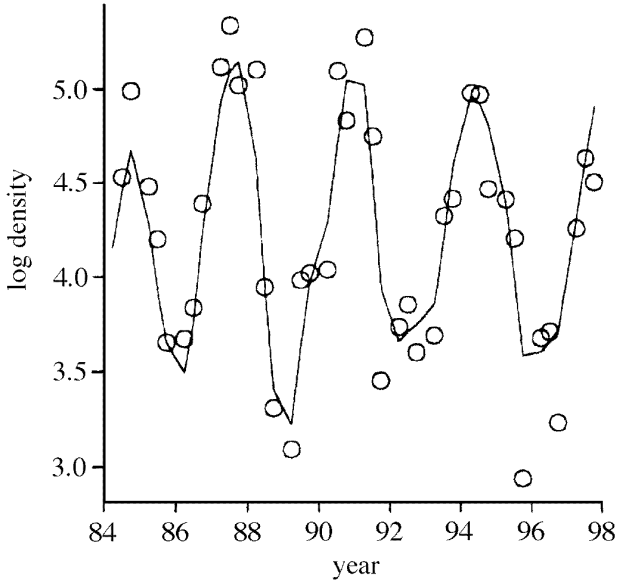

Field voles in Kielder Forest are cyclic (period 4 years).

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We assume that vole cycles are caused by predation by weasels, and study using a predator-prey model.

A Standard Predator-Prey Model

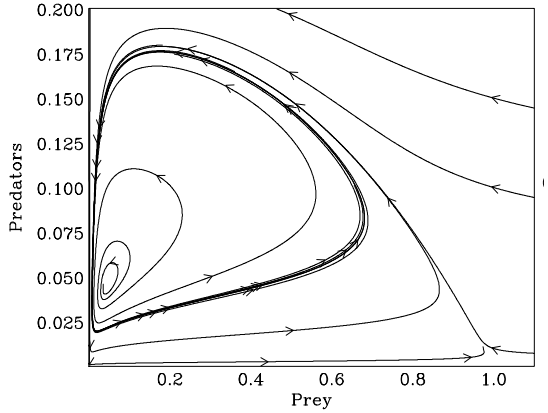
$\boxed{\text{predators}}$

$$\partial p/\partial t = \underbrace{D_p \nabla^2 p}_{\text{dispersal}} + \underbrace{akph/(1+kh)}_{\text{benefit from predation}} - \underbrace{bp}_{\text{death}}$$

$\boxed{\text{prey}}$

$$\partial h/\partial t = \underbrace{D_h \nabla^2 h}_{\text{dispersal}} + \underbrace{rh(1-h/h_0)}_{\text{intrinsic birth \& death}} - \underbrace{ckph/(1+kh)}_{\text{predation}}$$

Phase plane of local dynamics:



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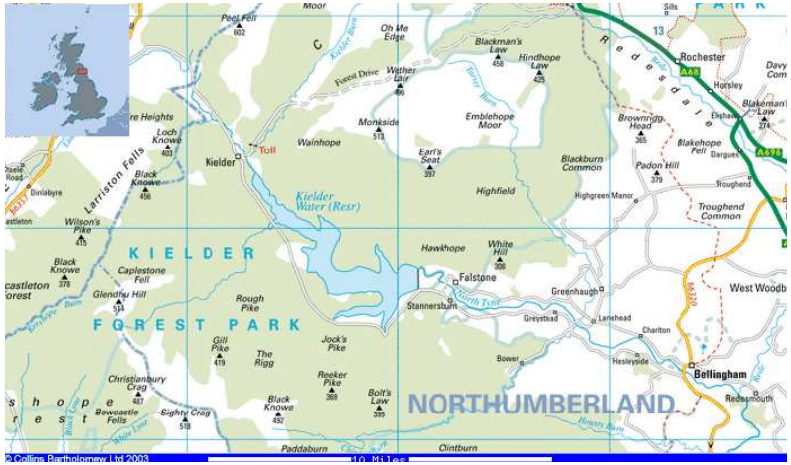

Spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave,
speed 19km/year, direction 72° from N.

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Everyday example: Mexican wave

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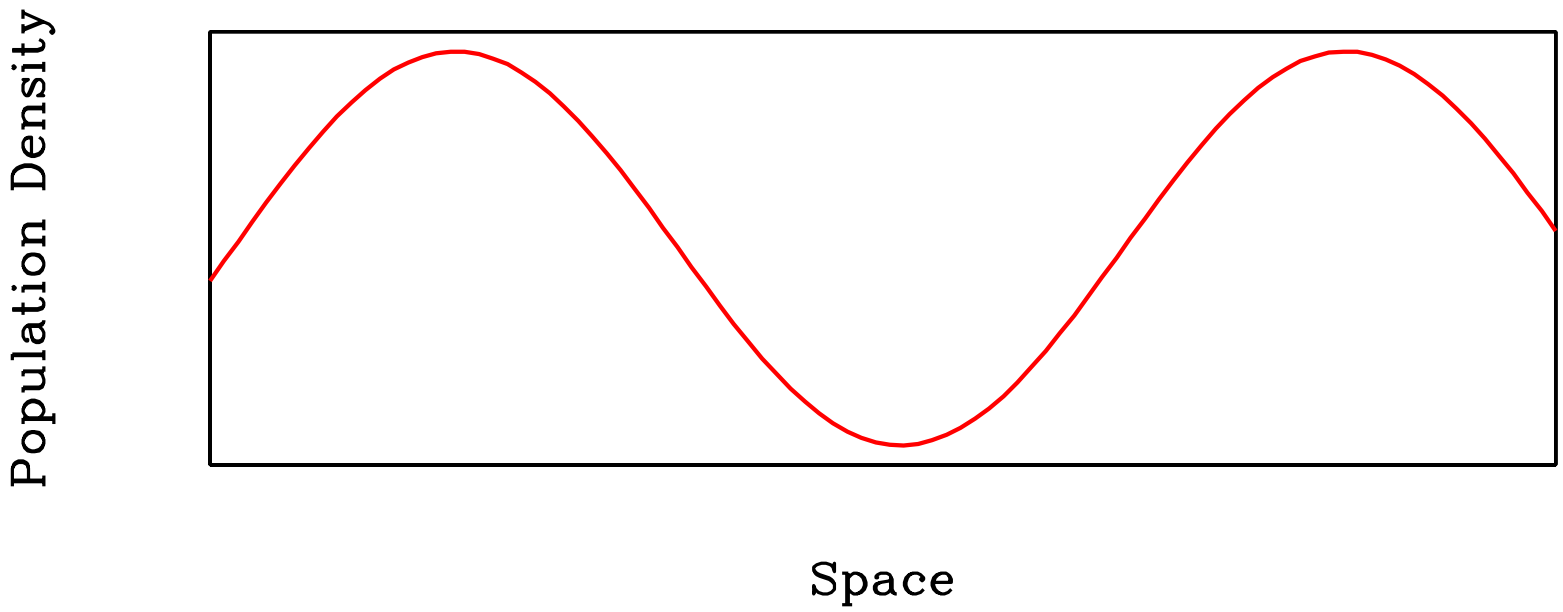

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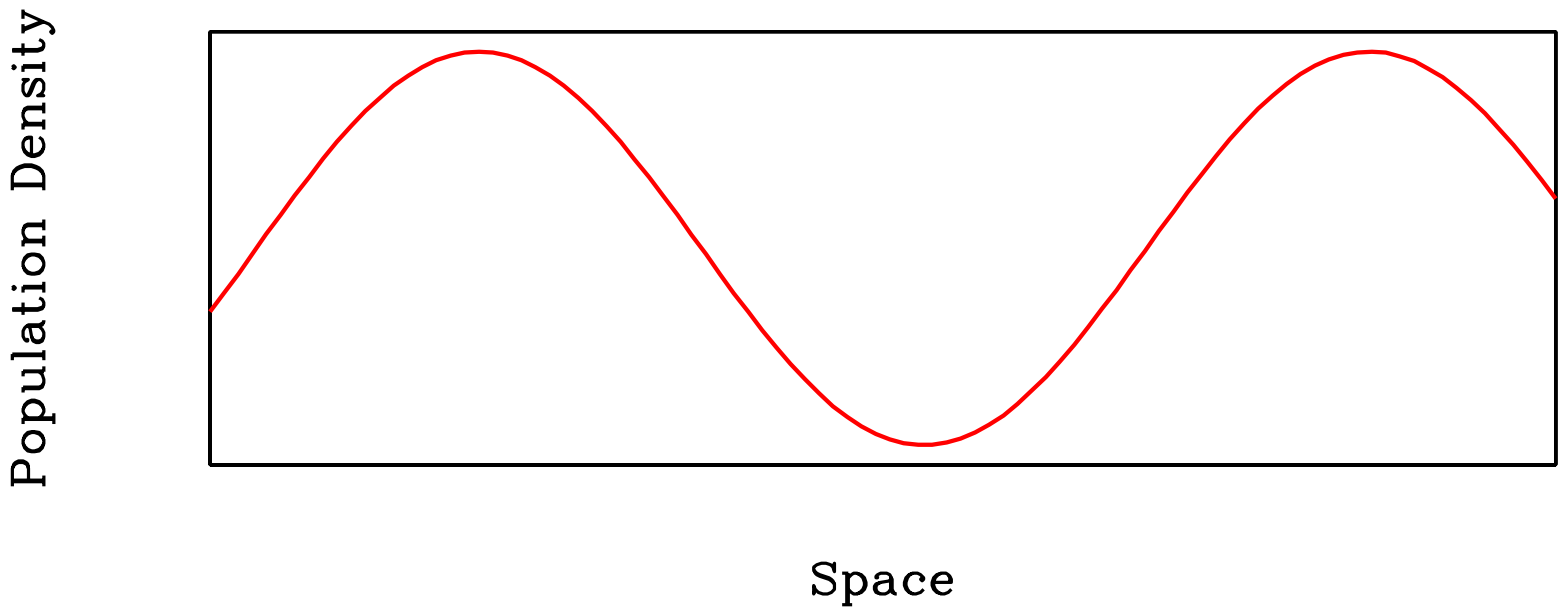

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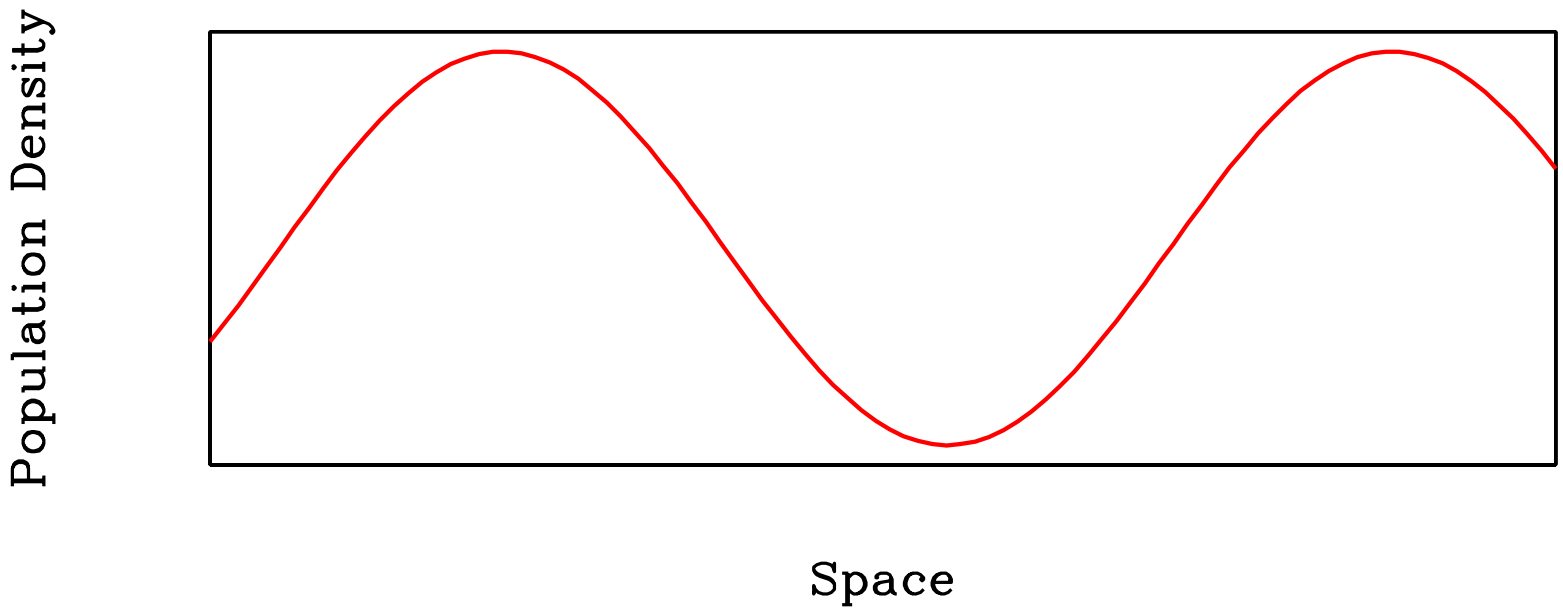

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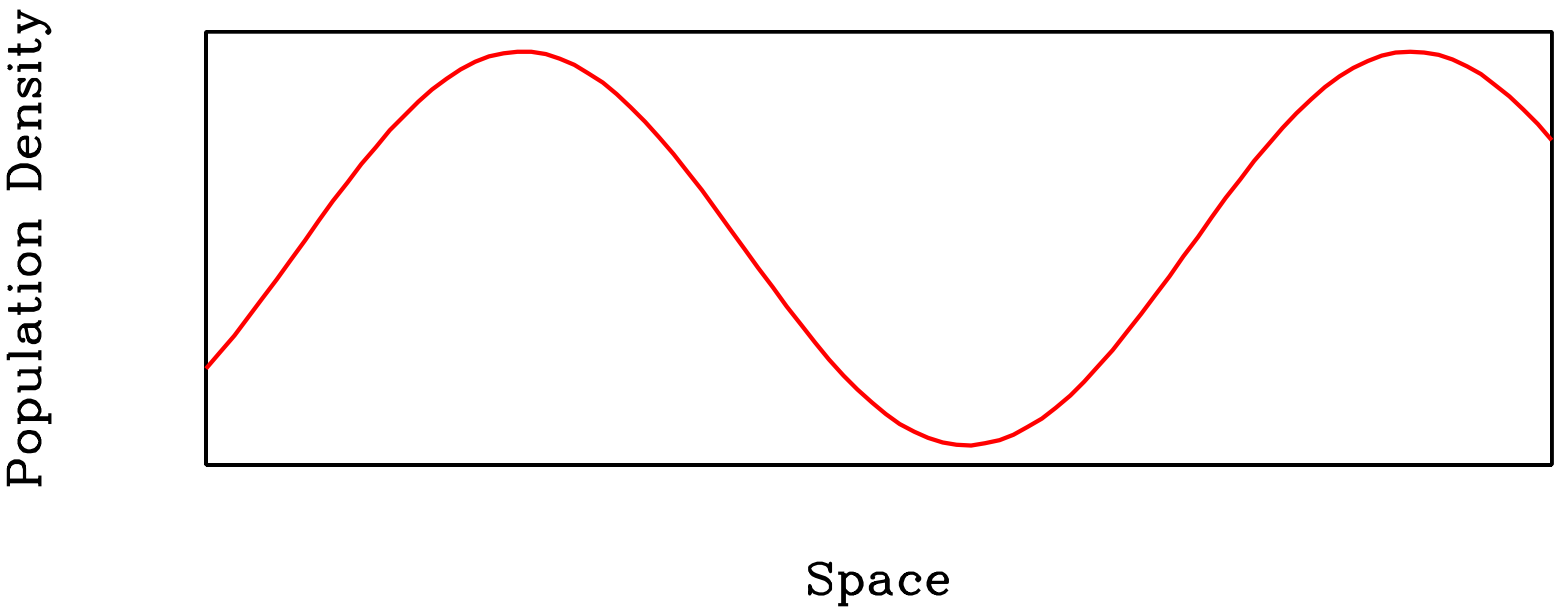

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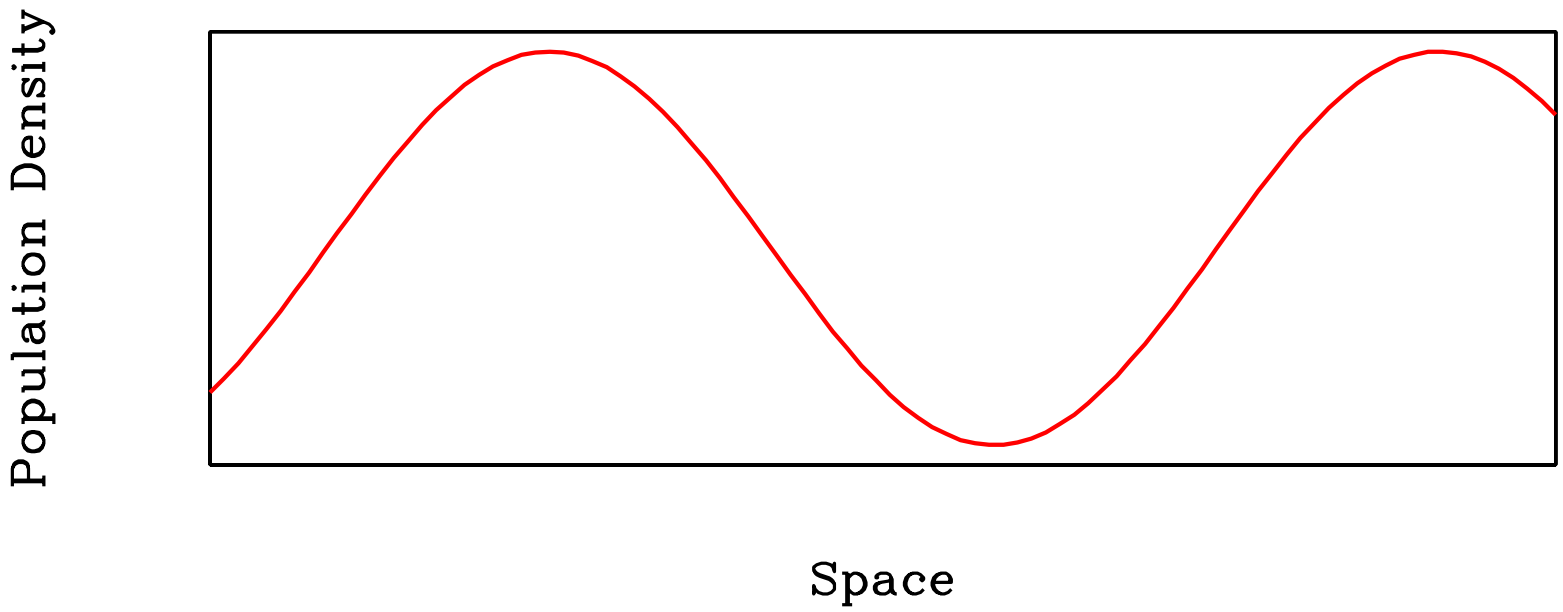

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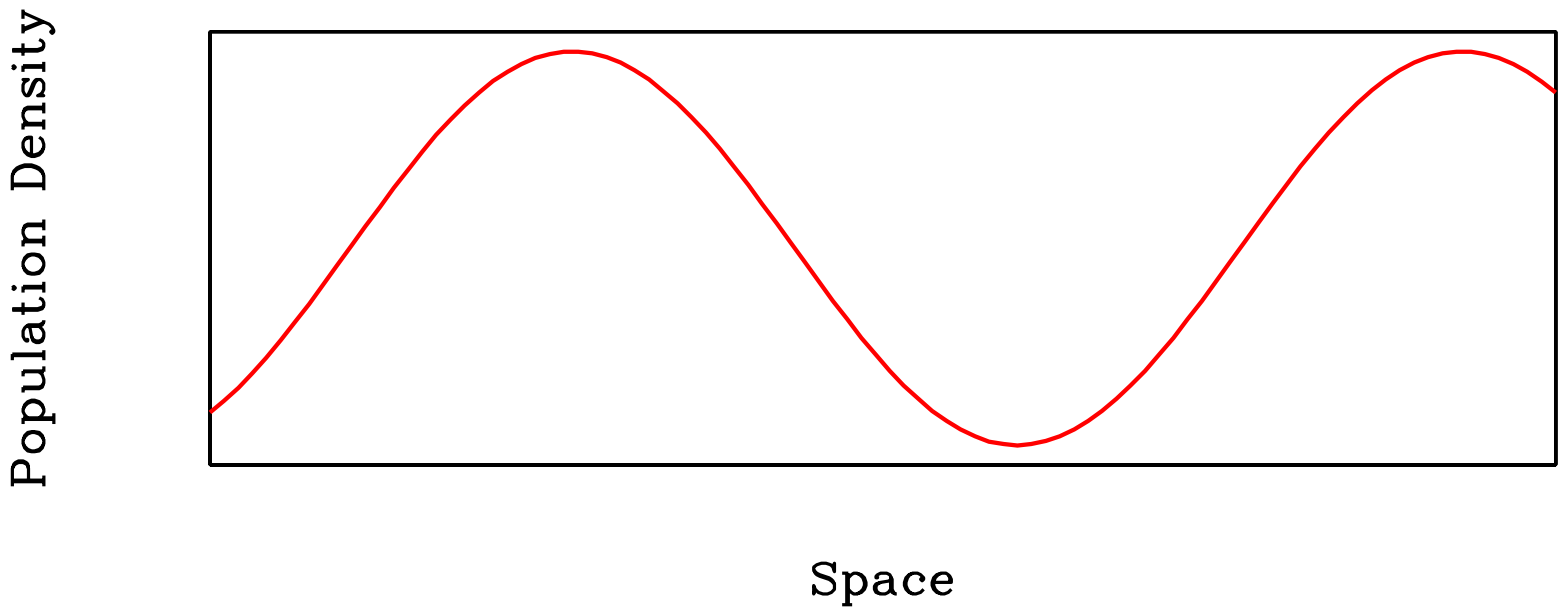

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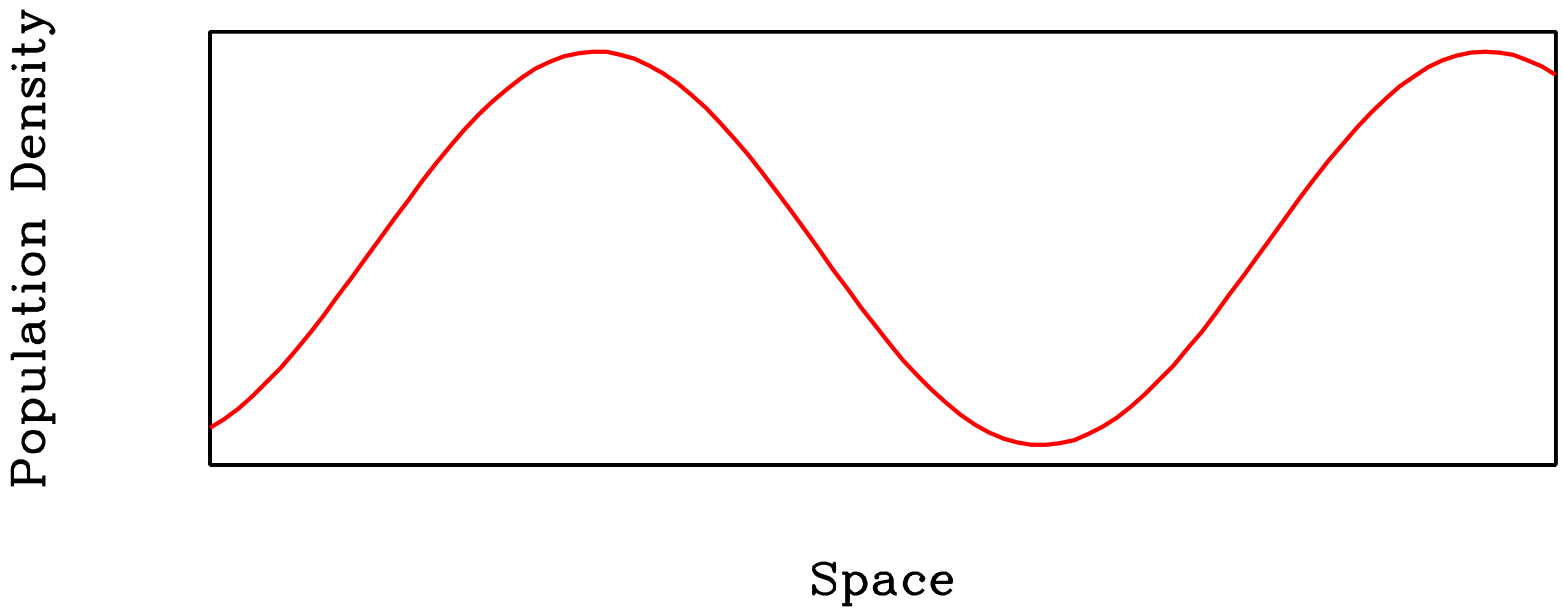

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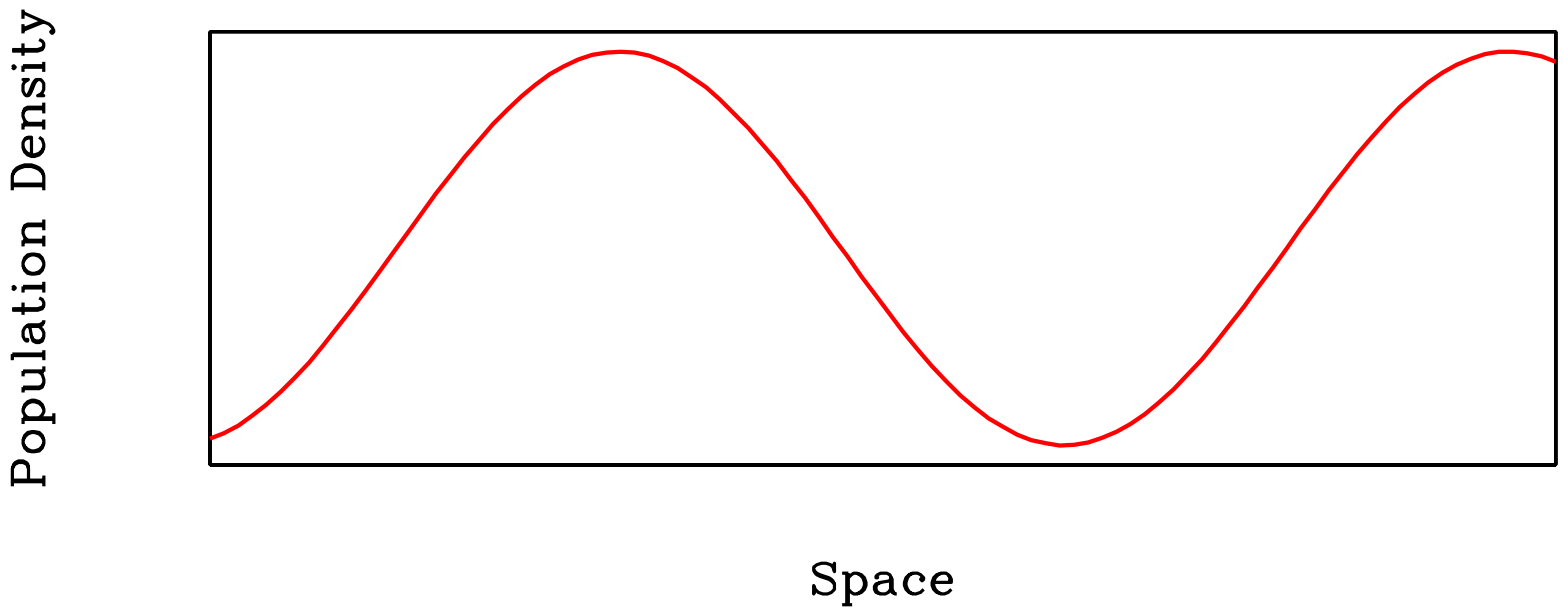

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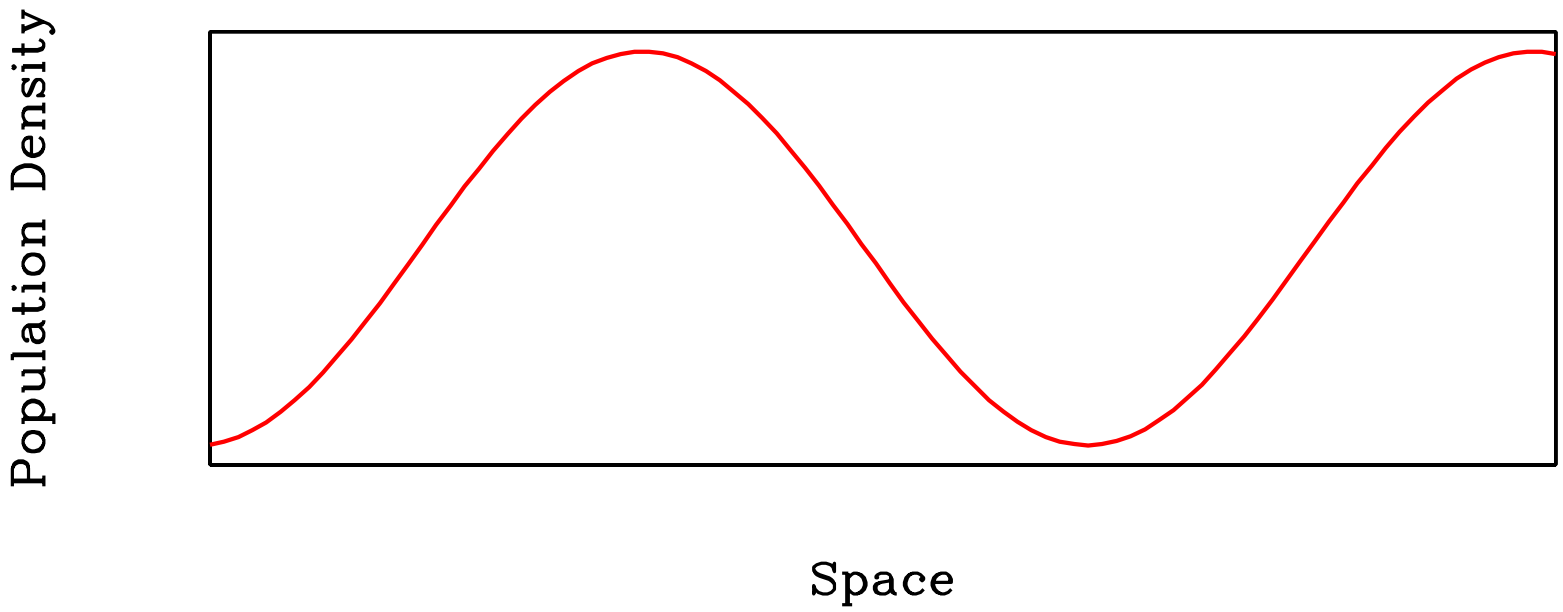

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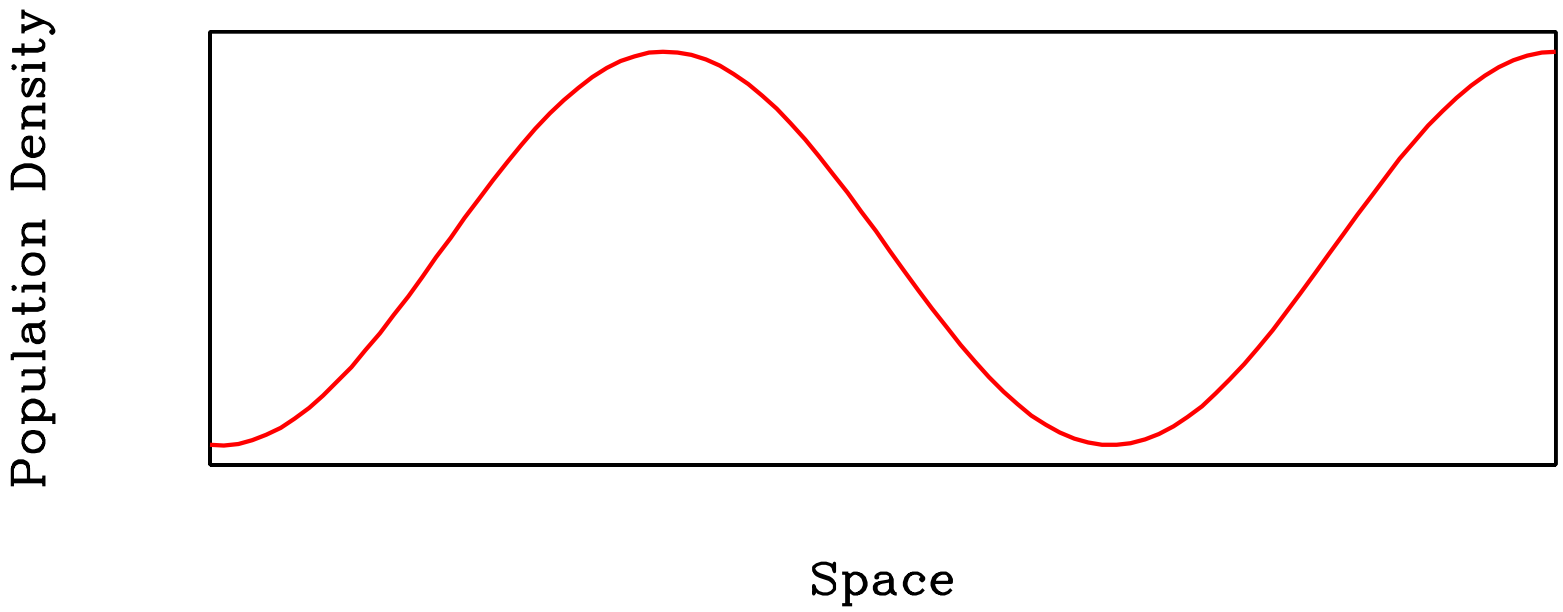

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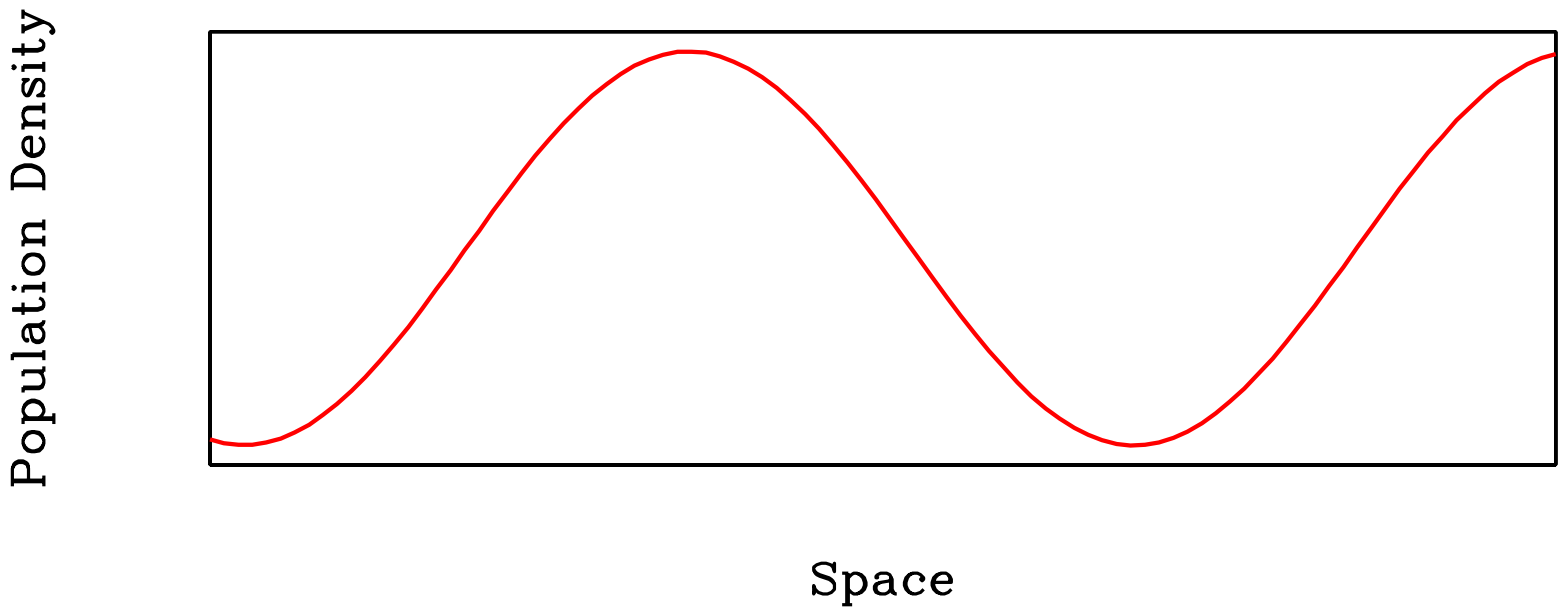

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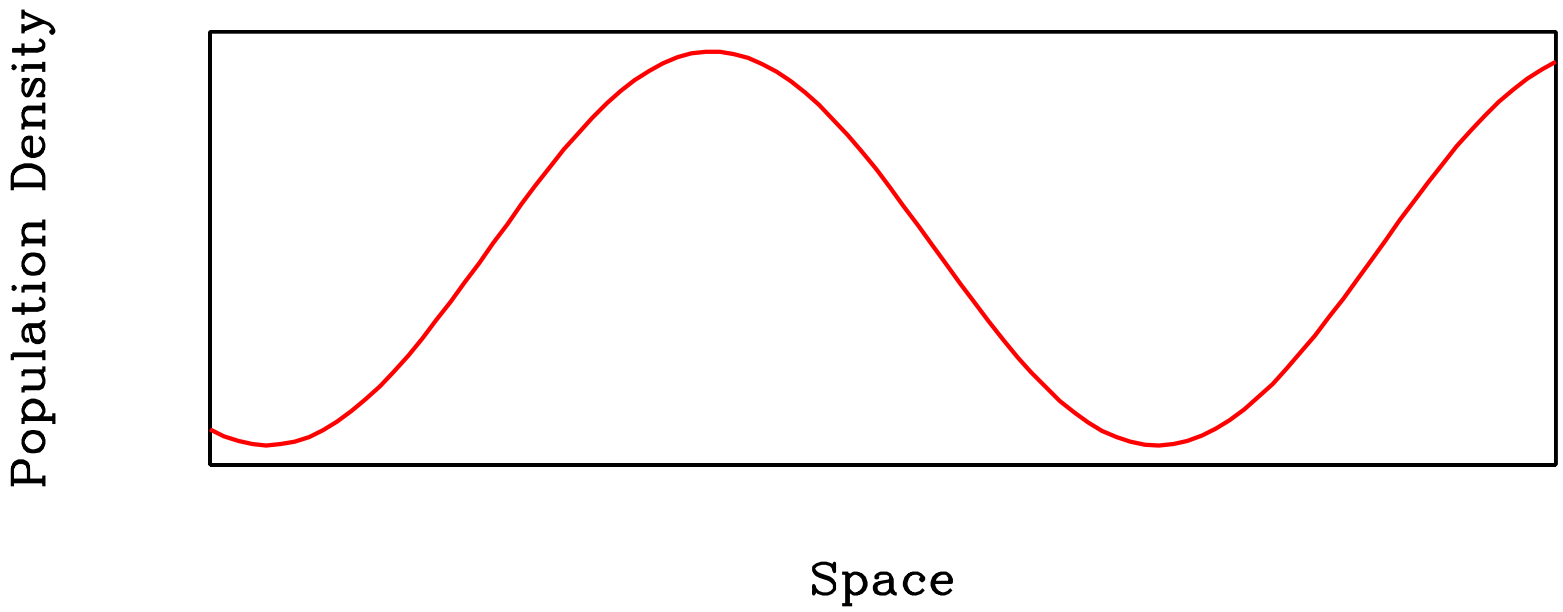

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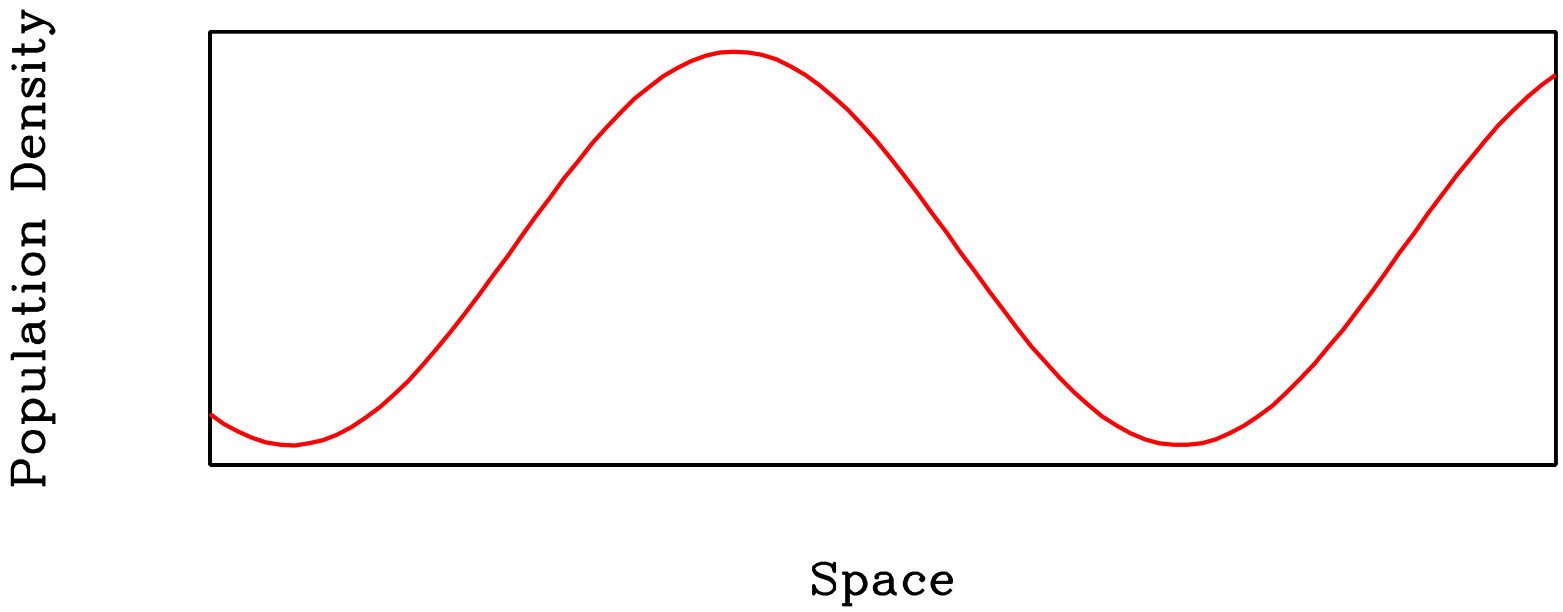

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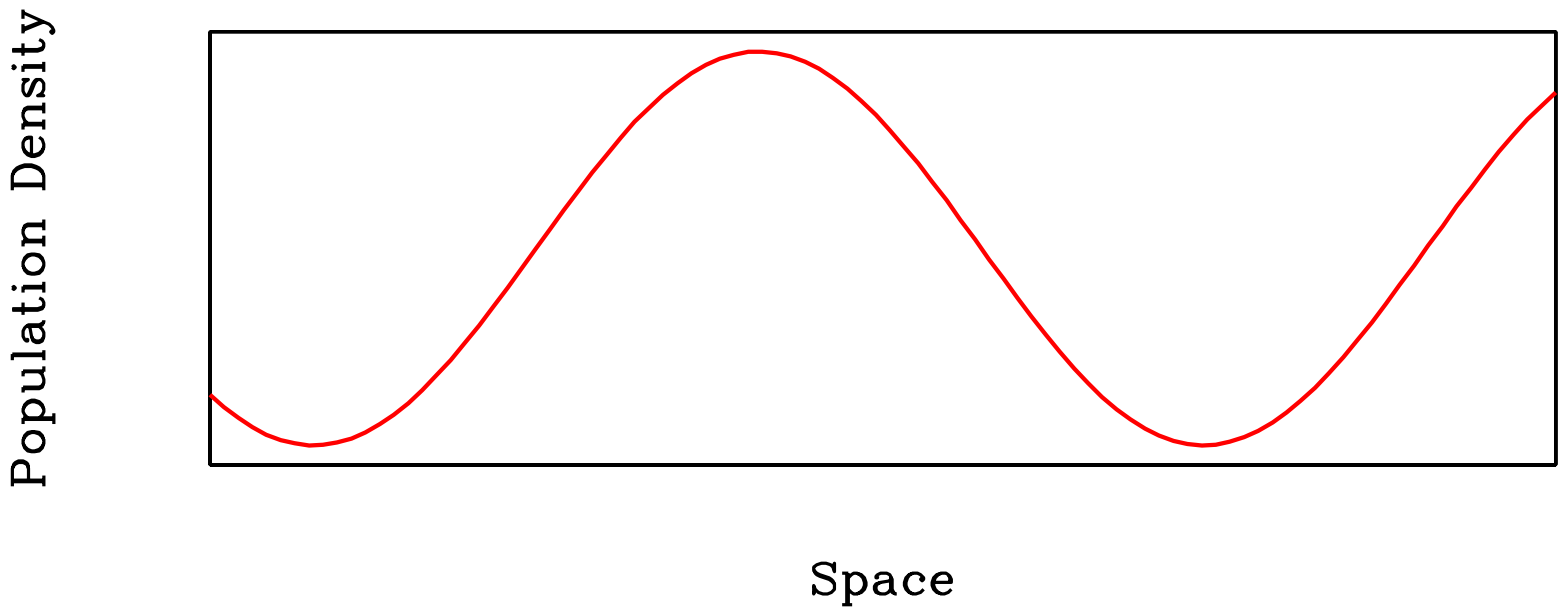

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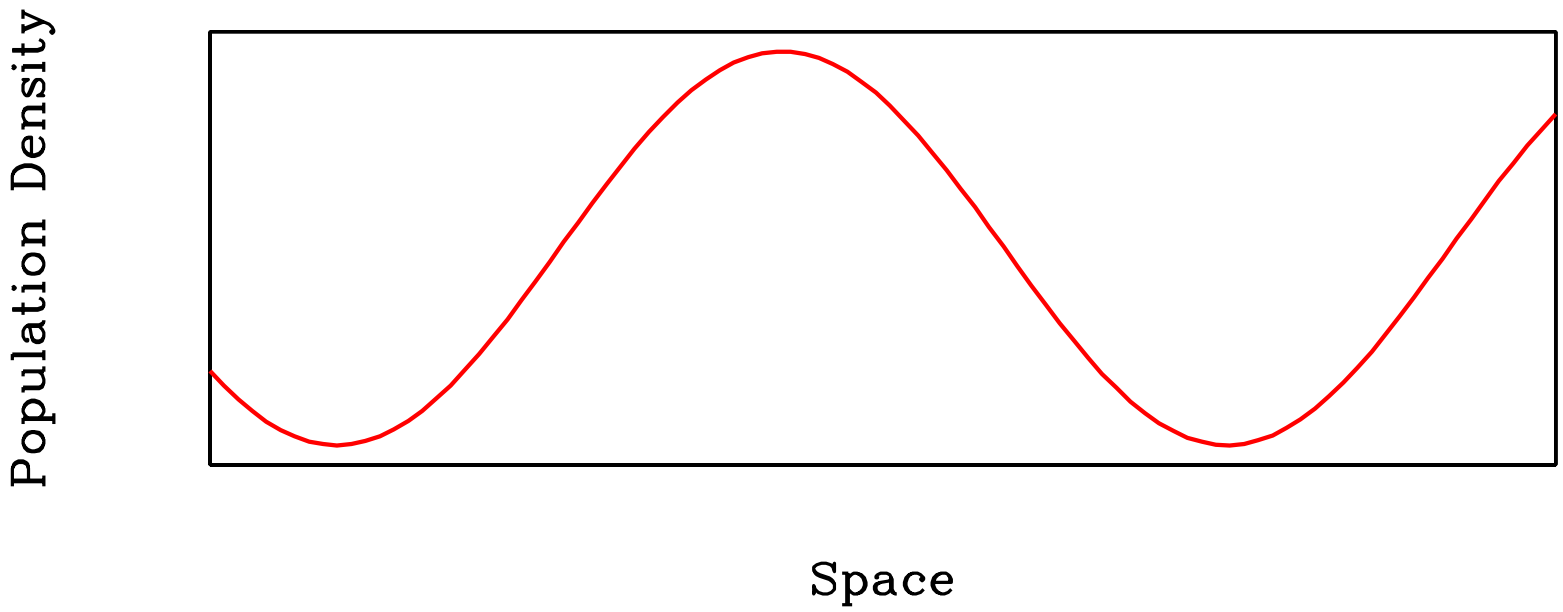

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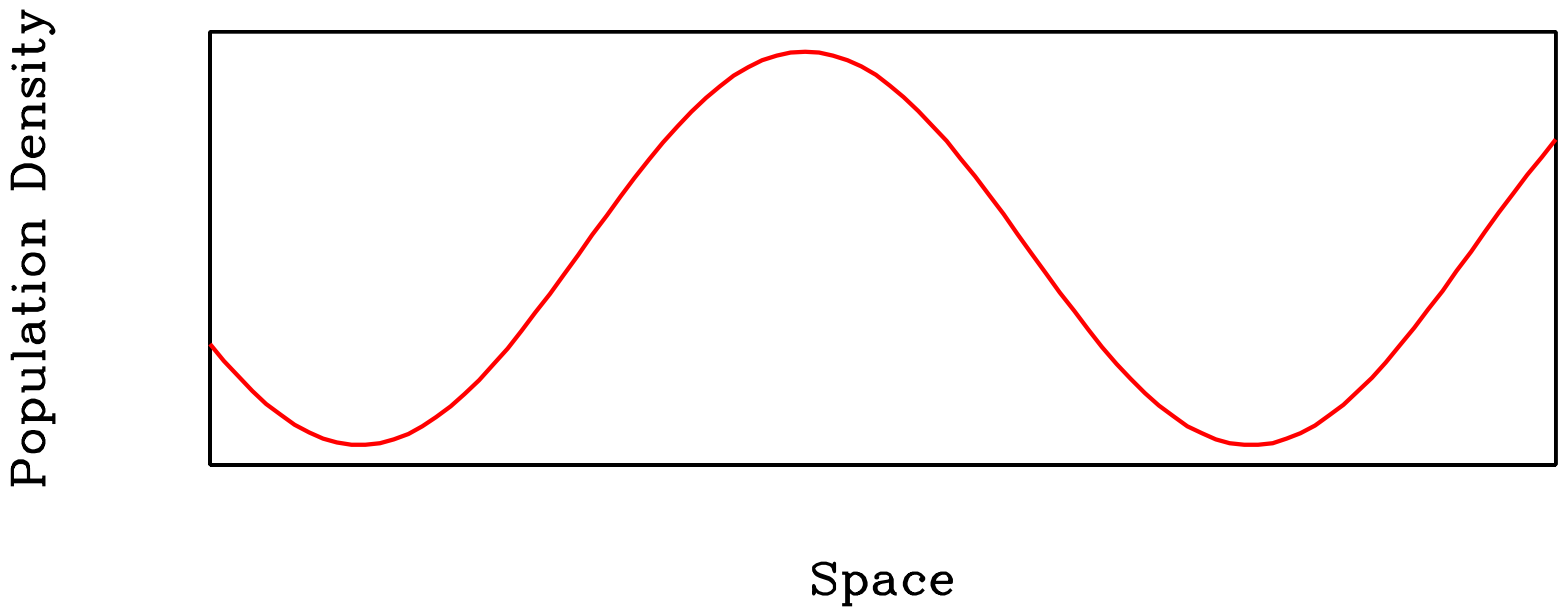

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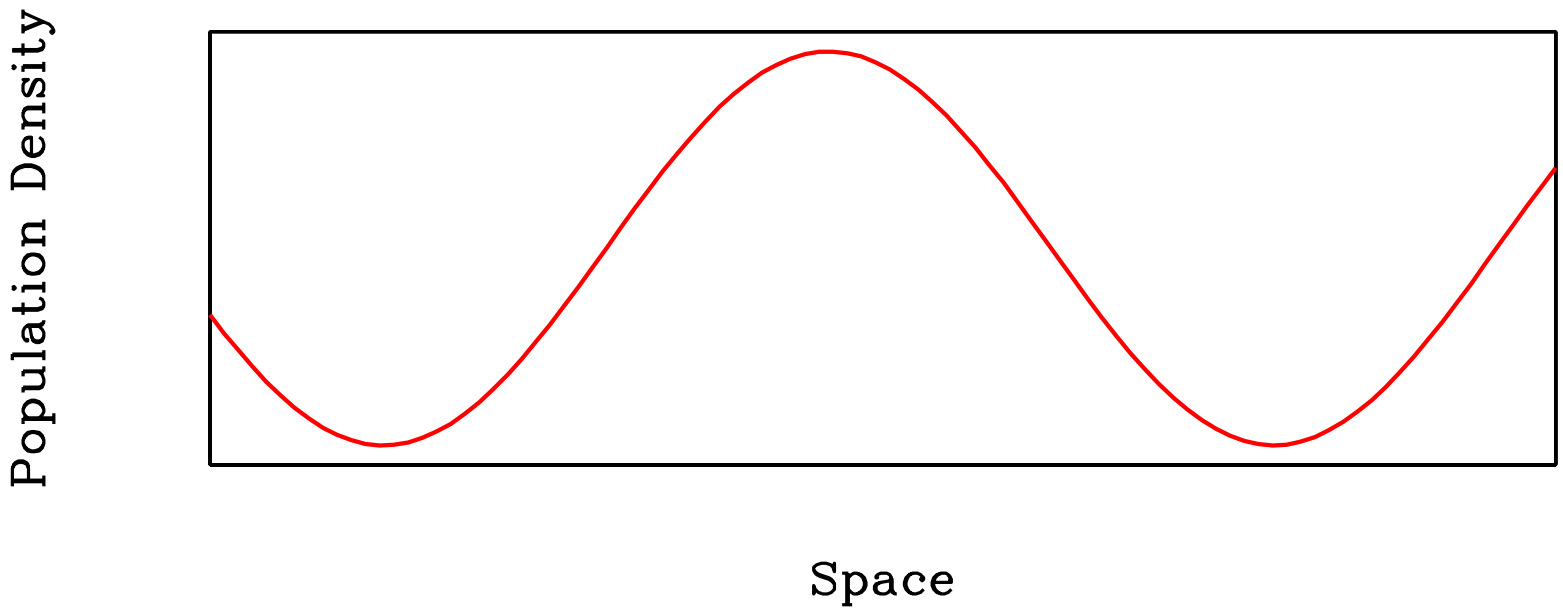

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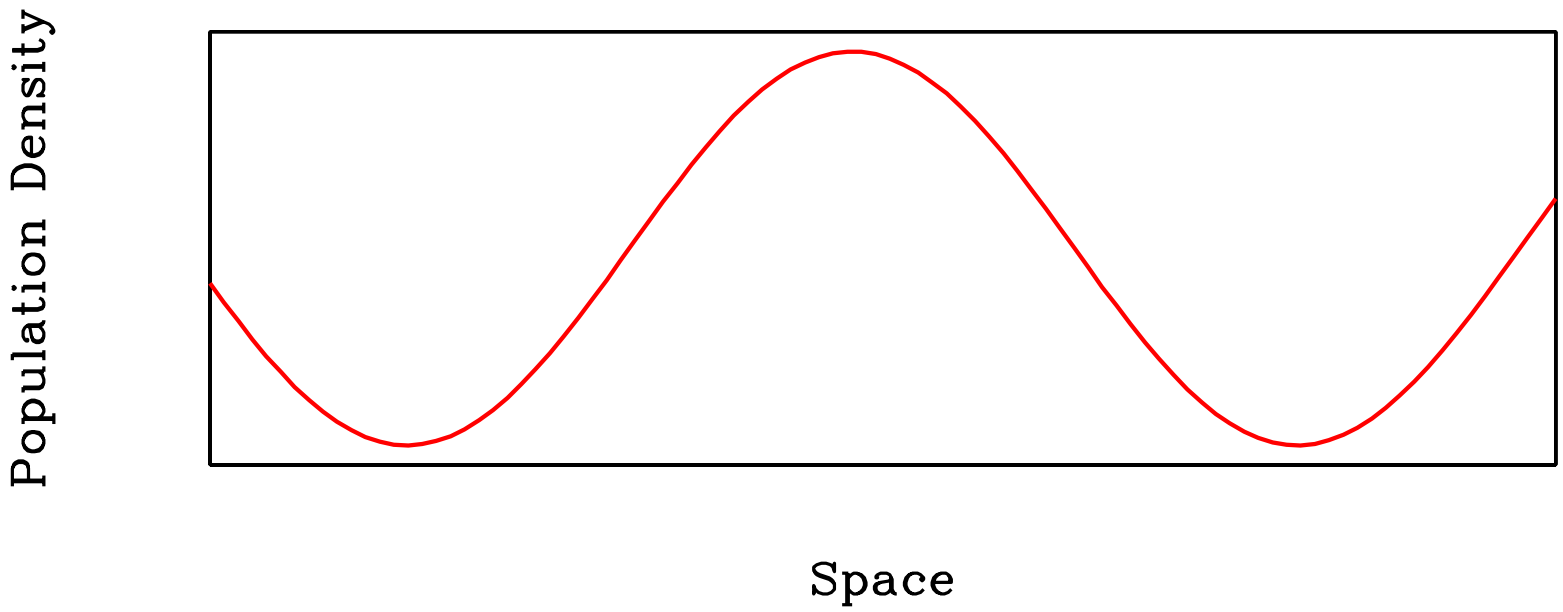

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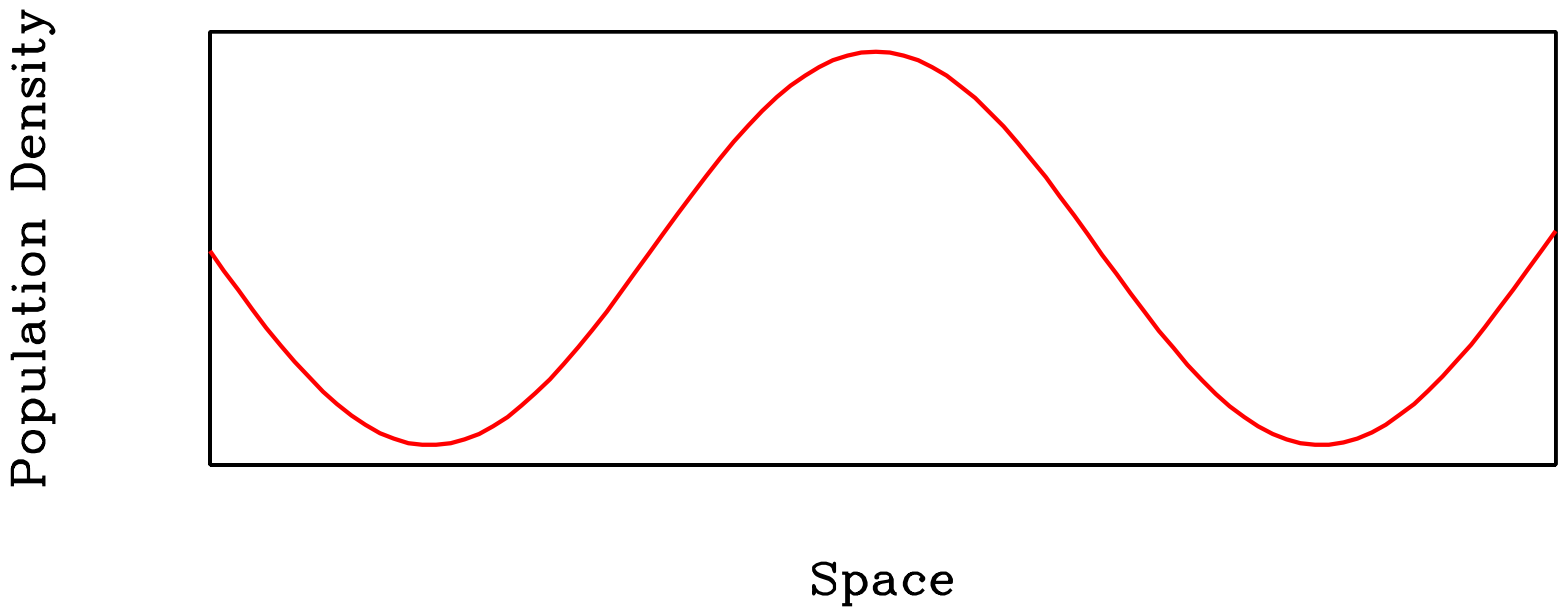

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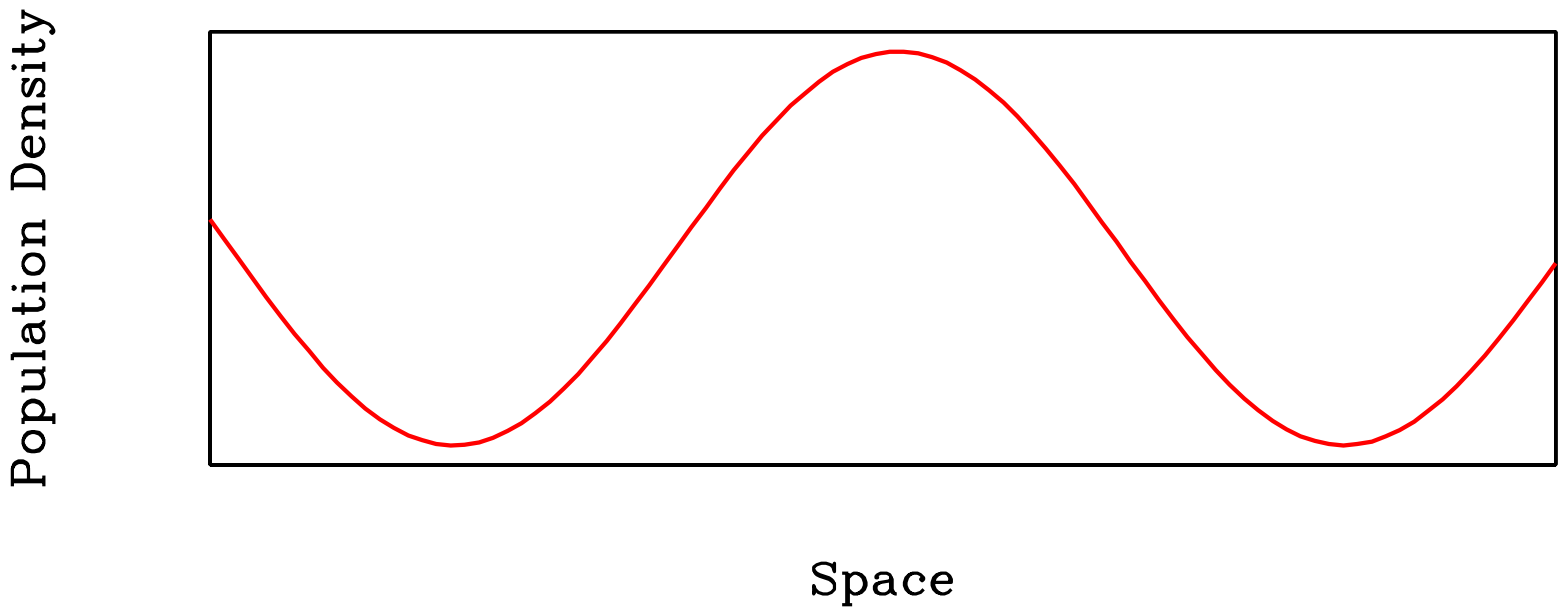

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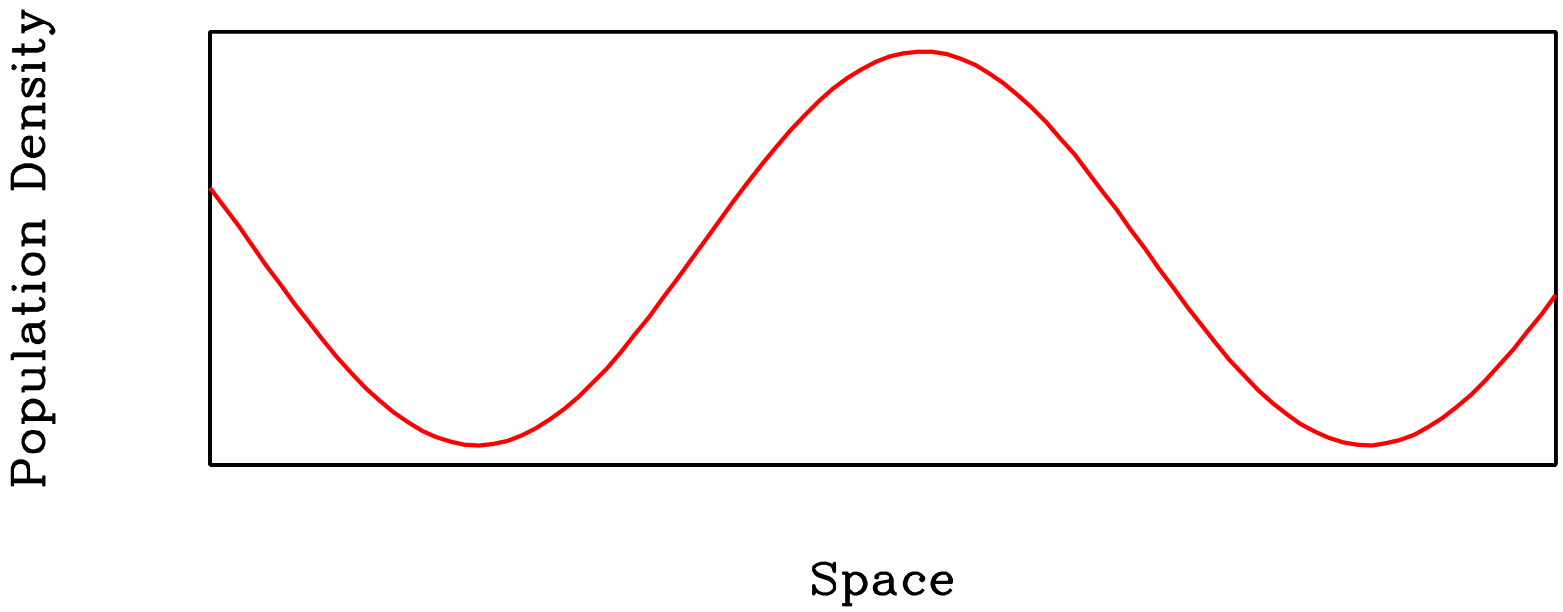

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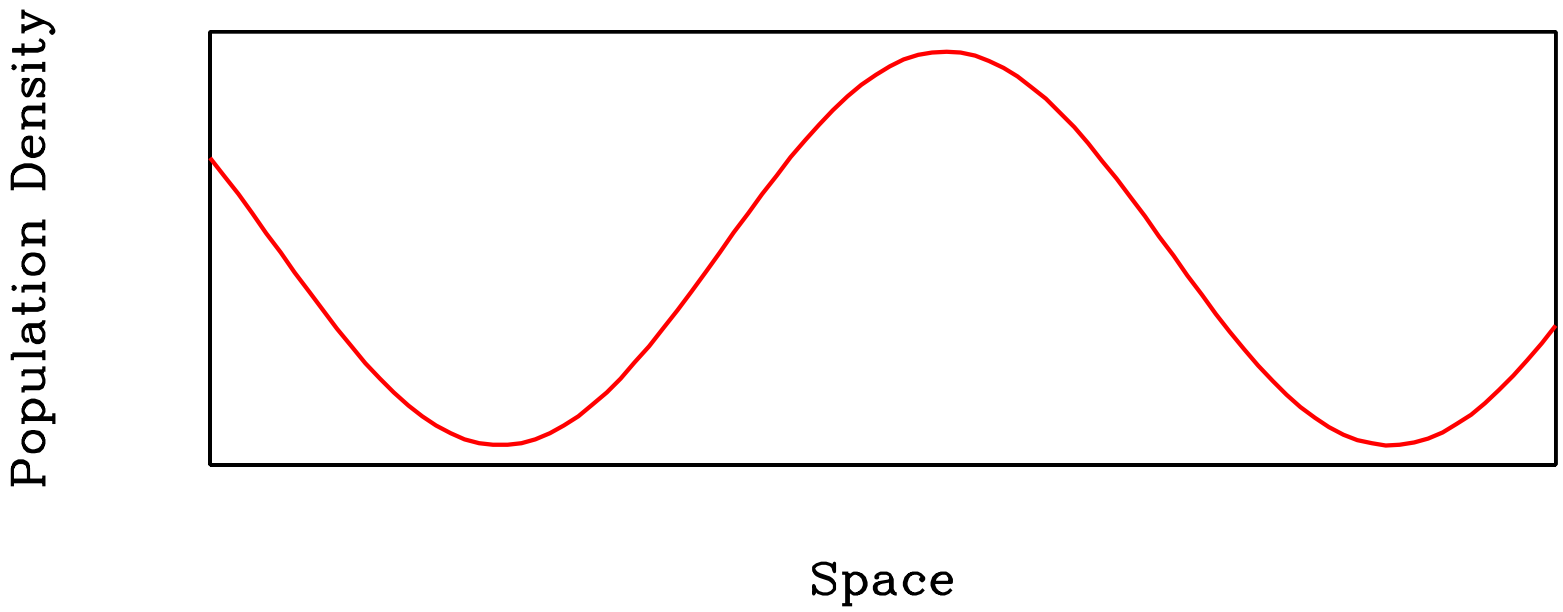

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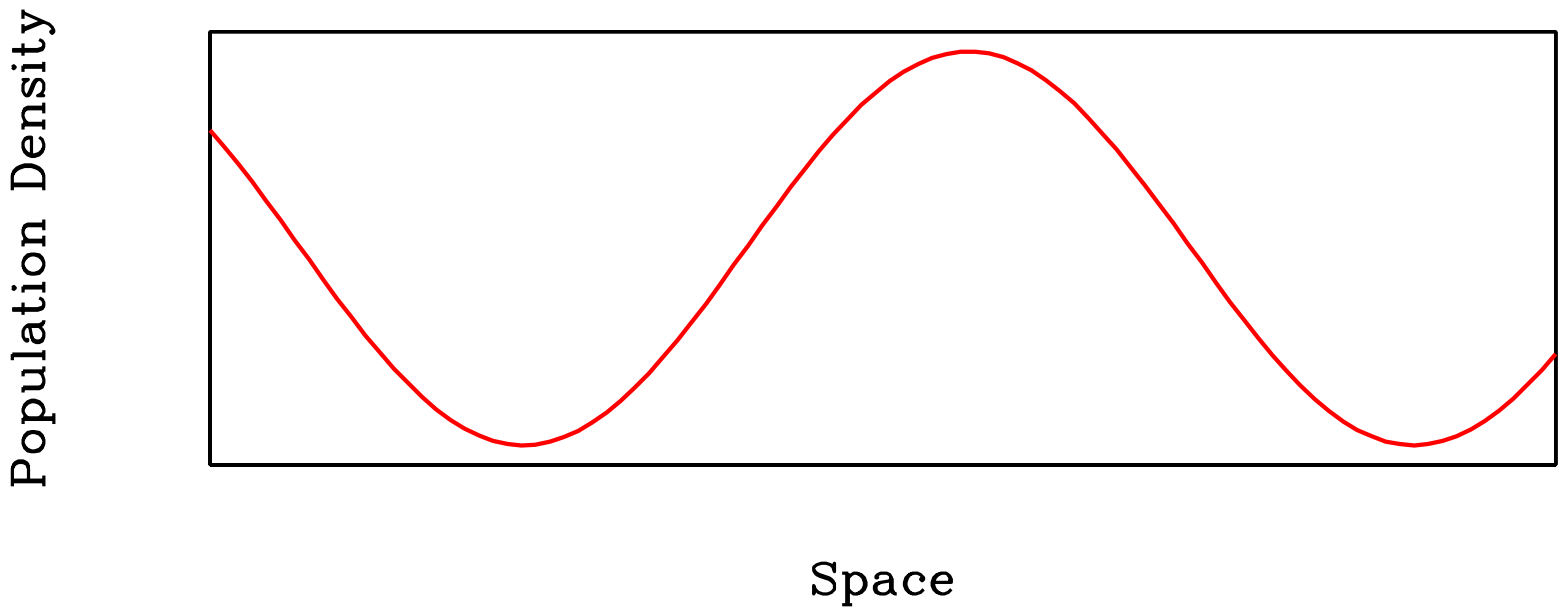

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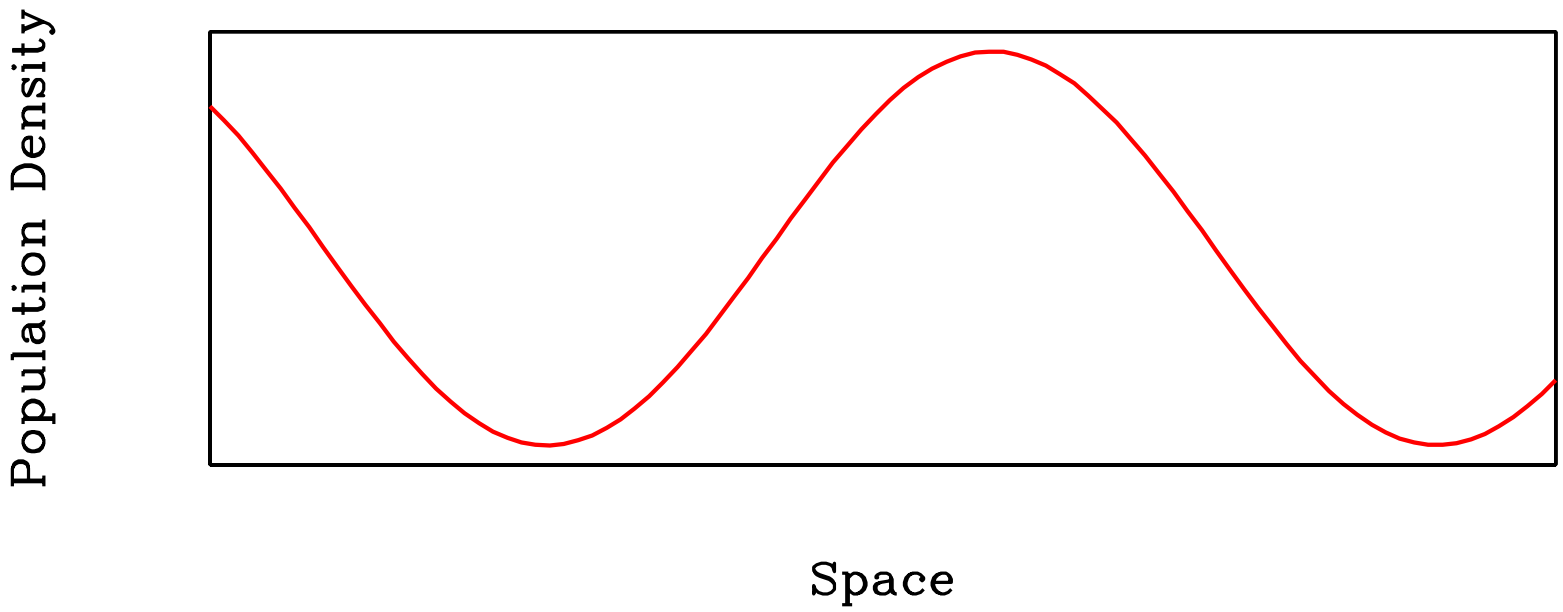

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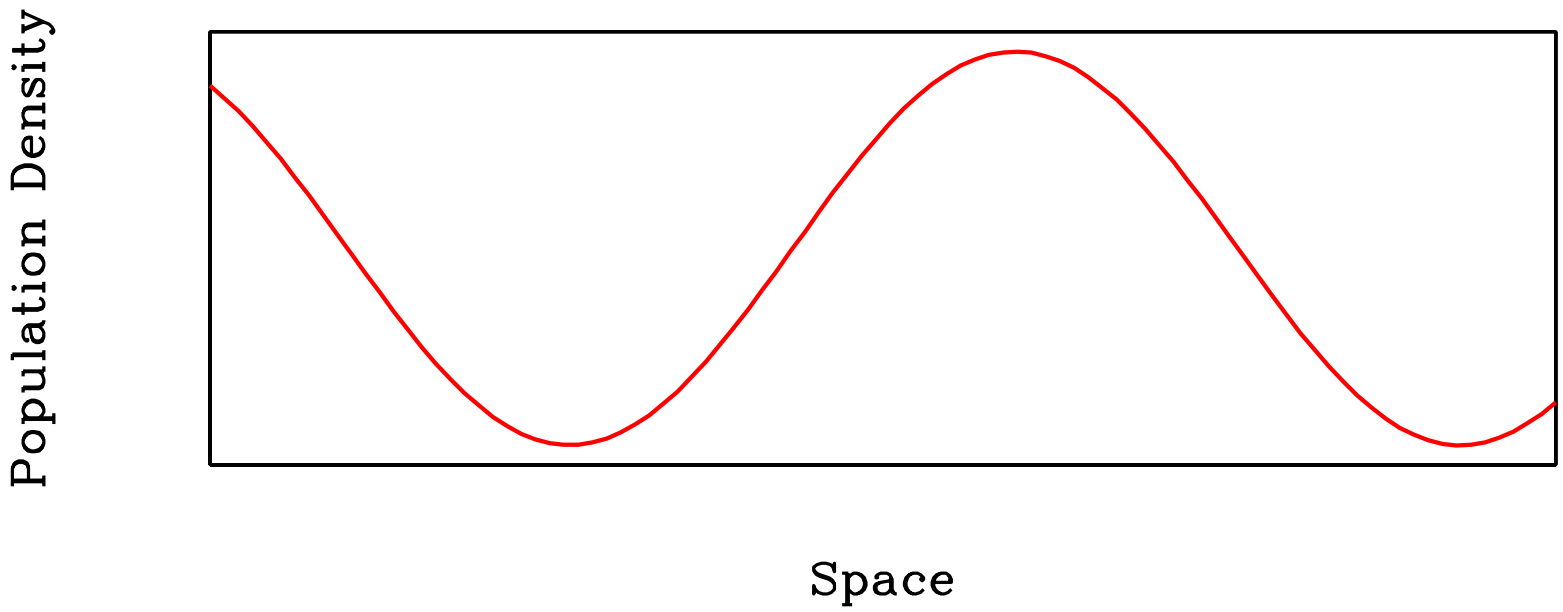

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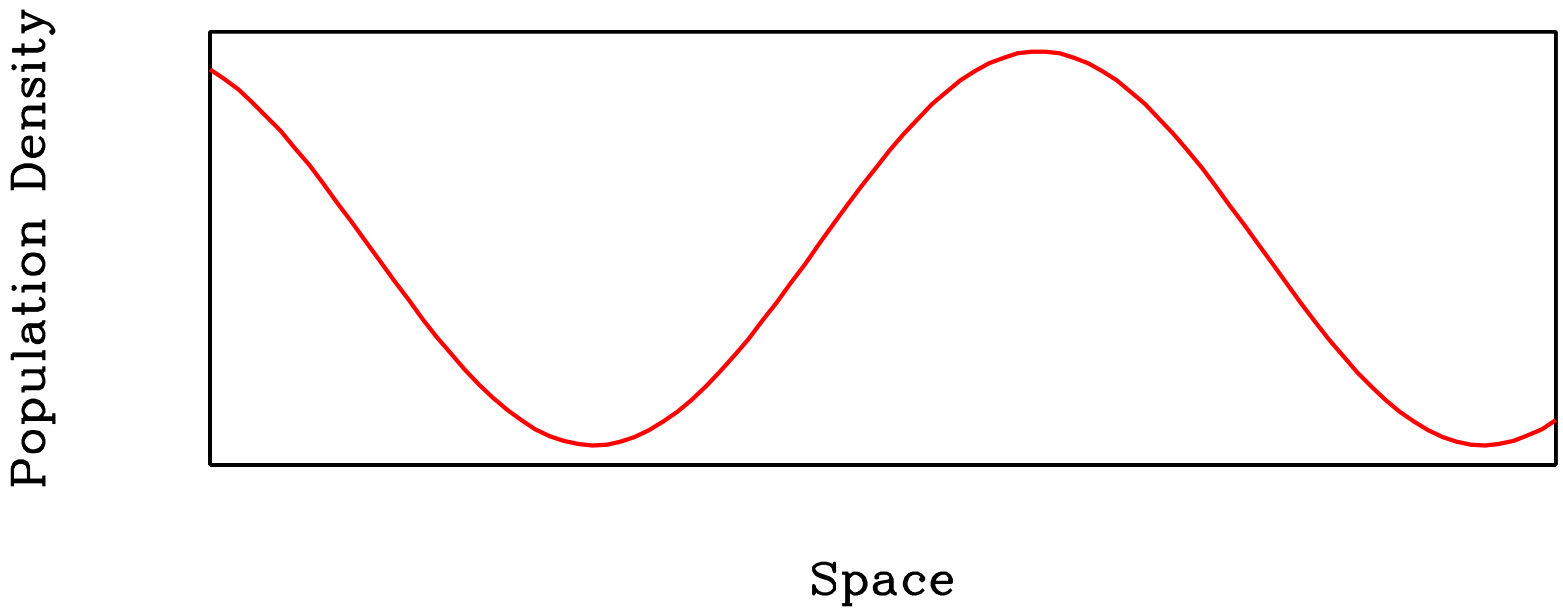

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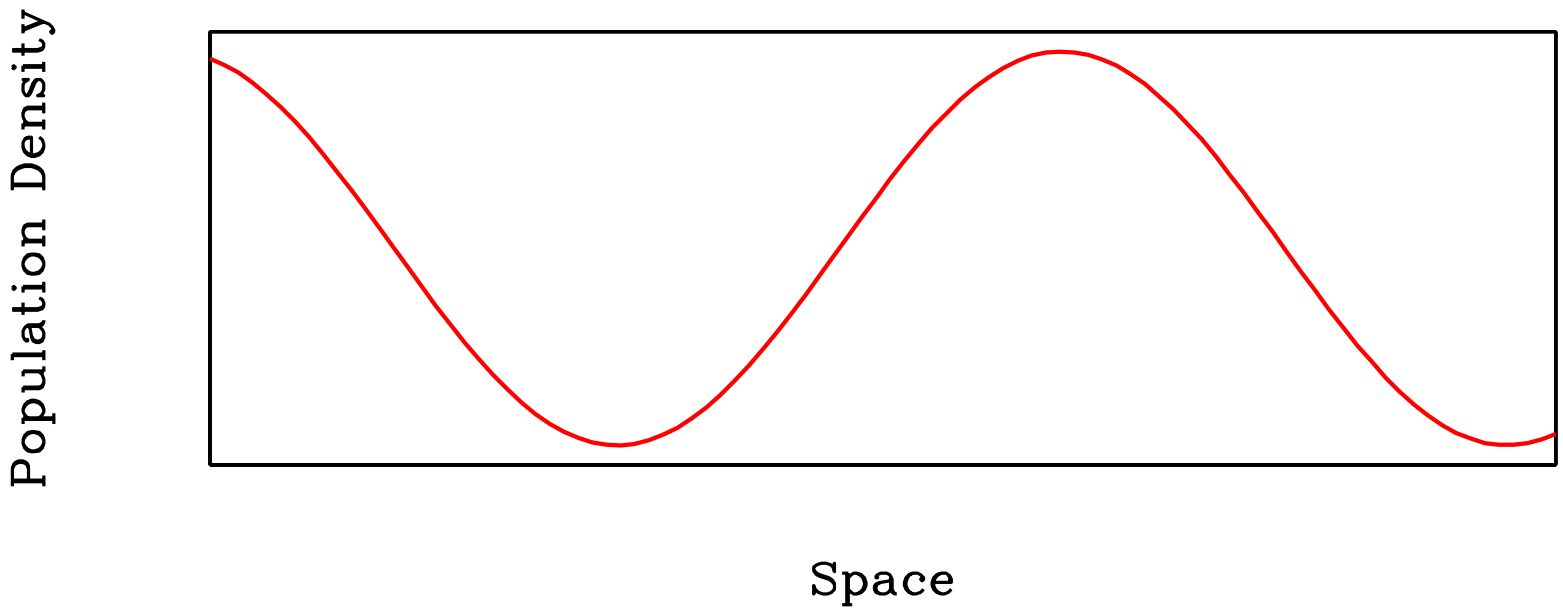

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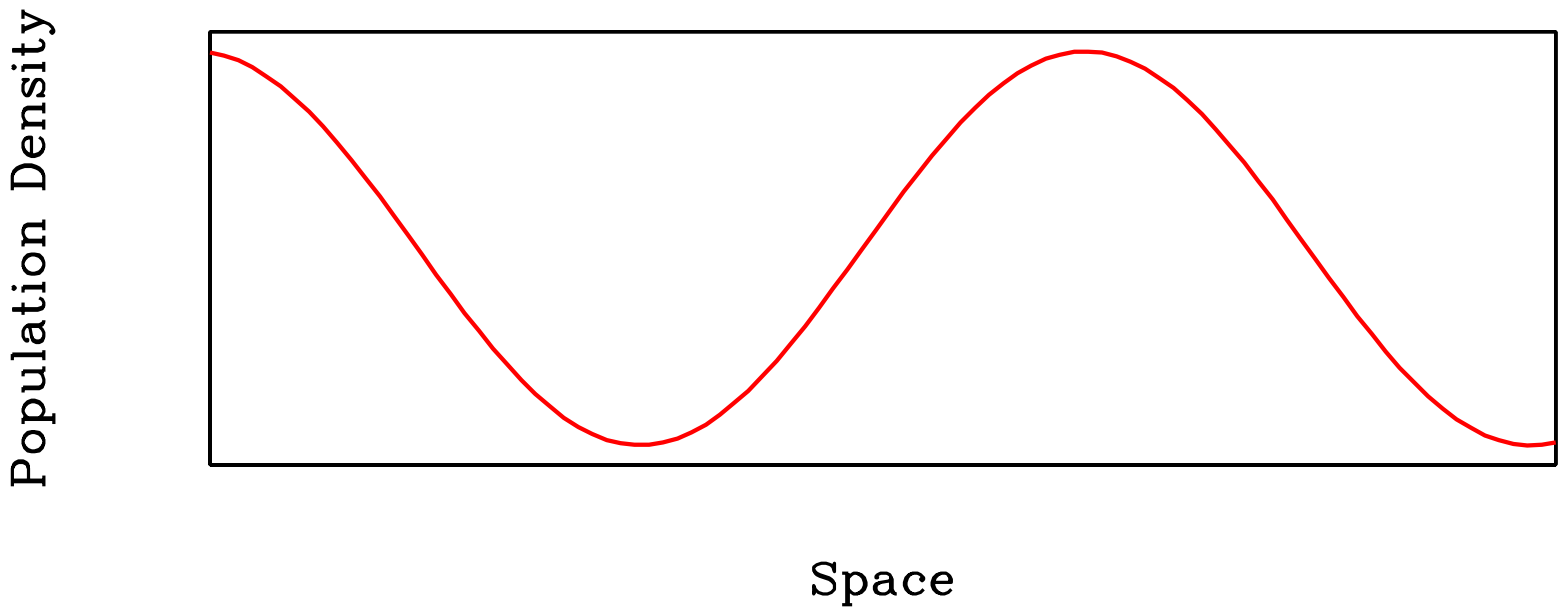

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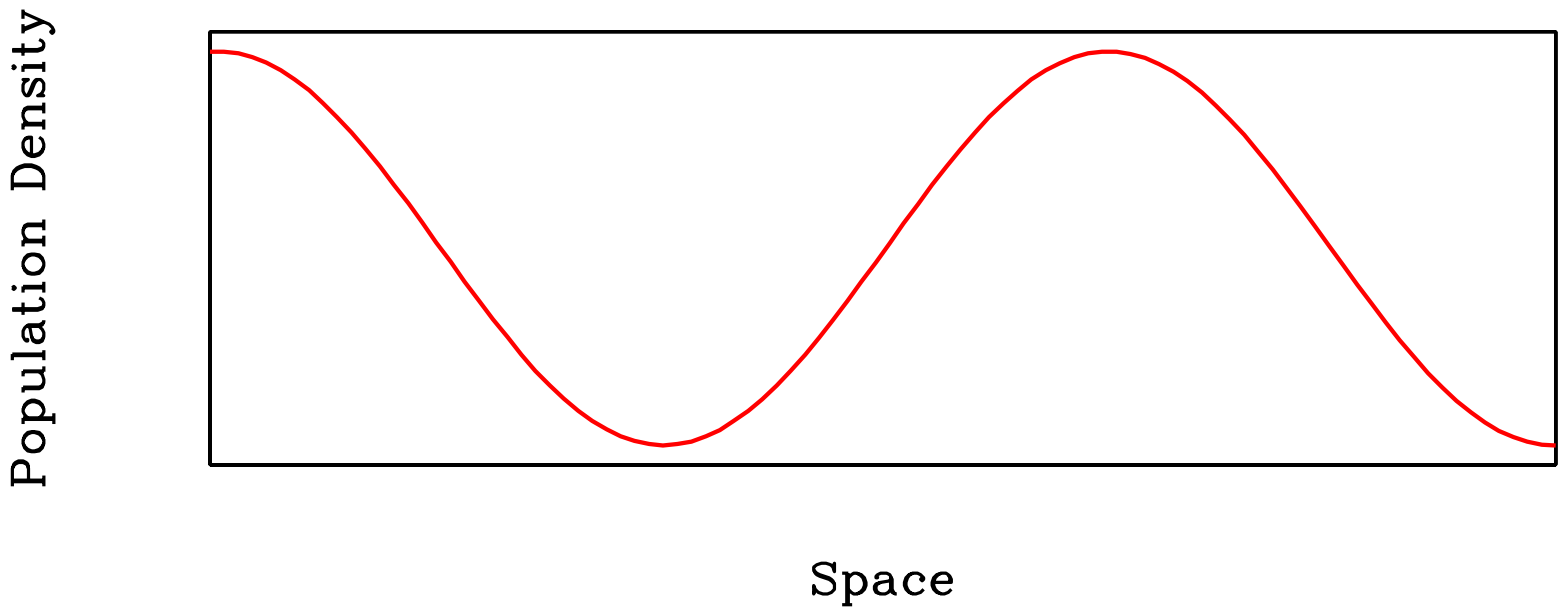

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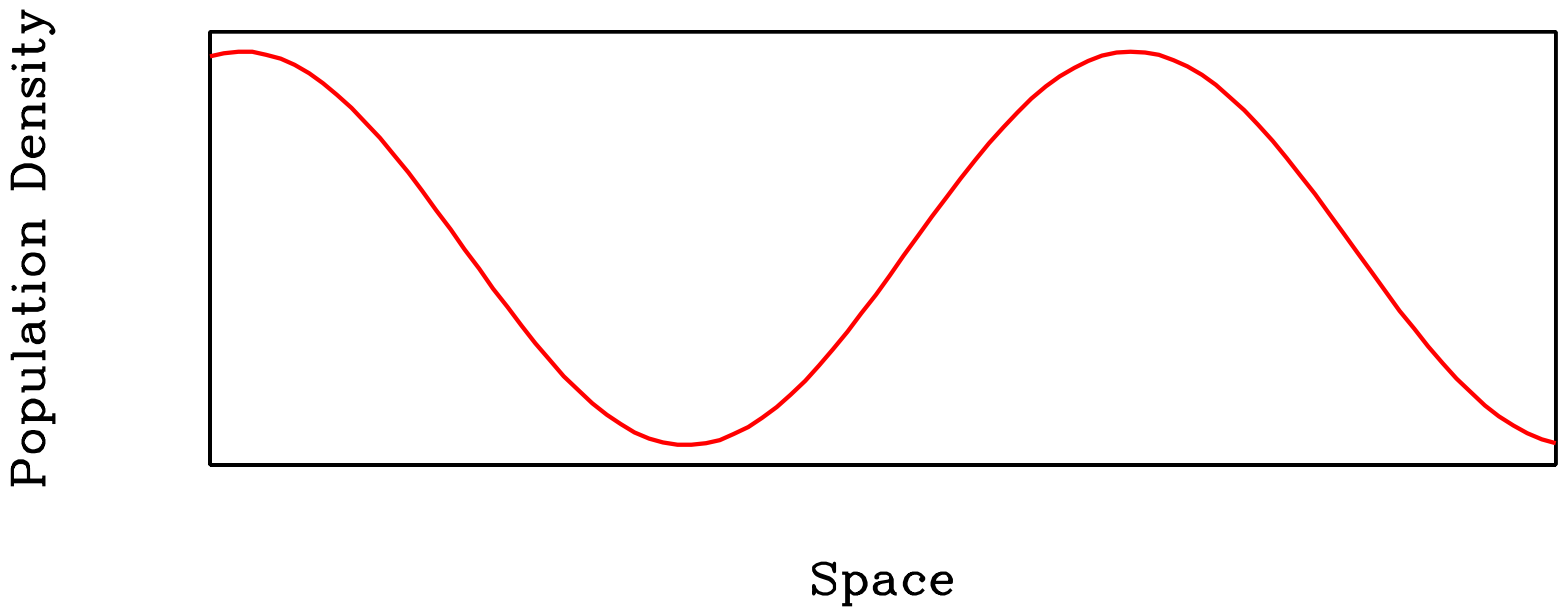

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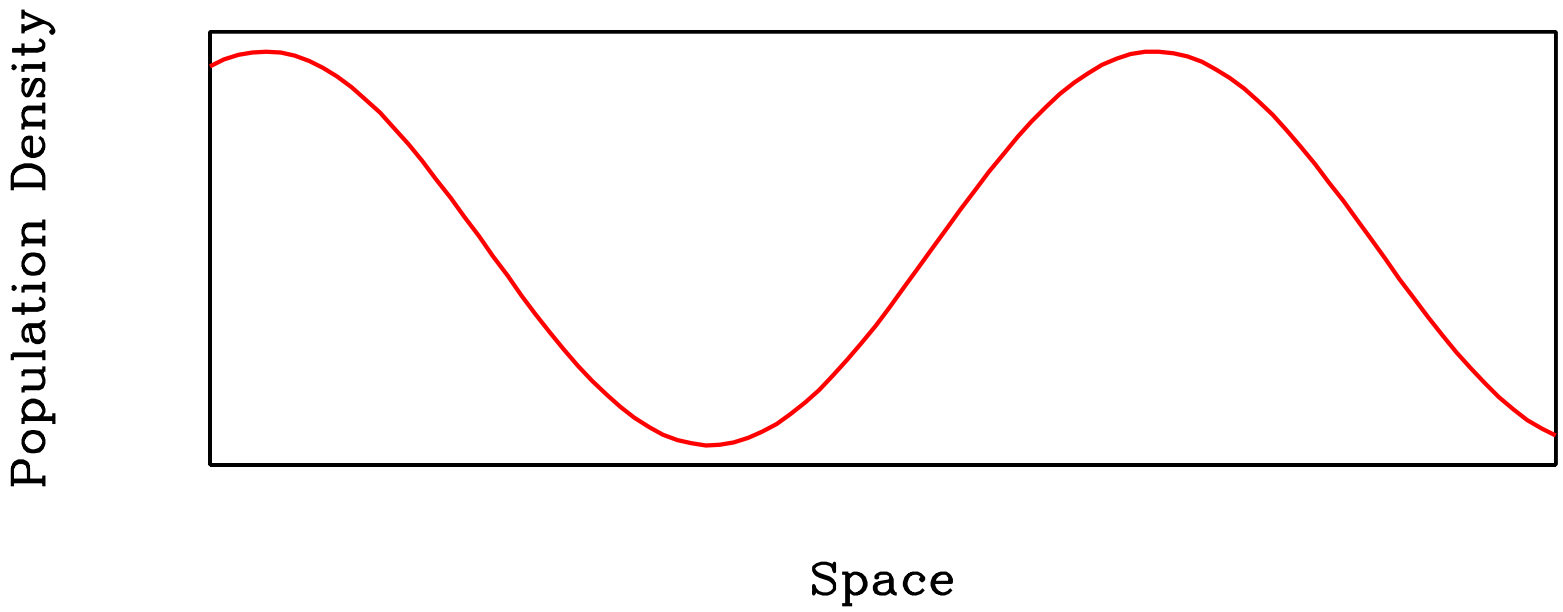

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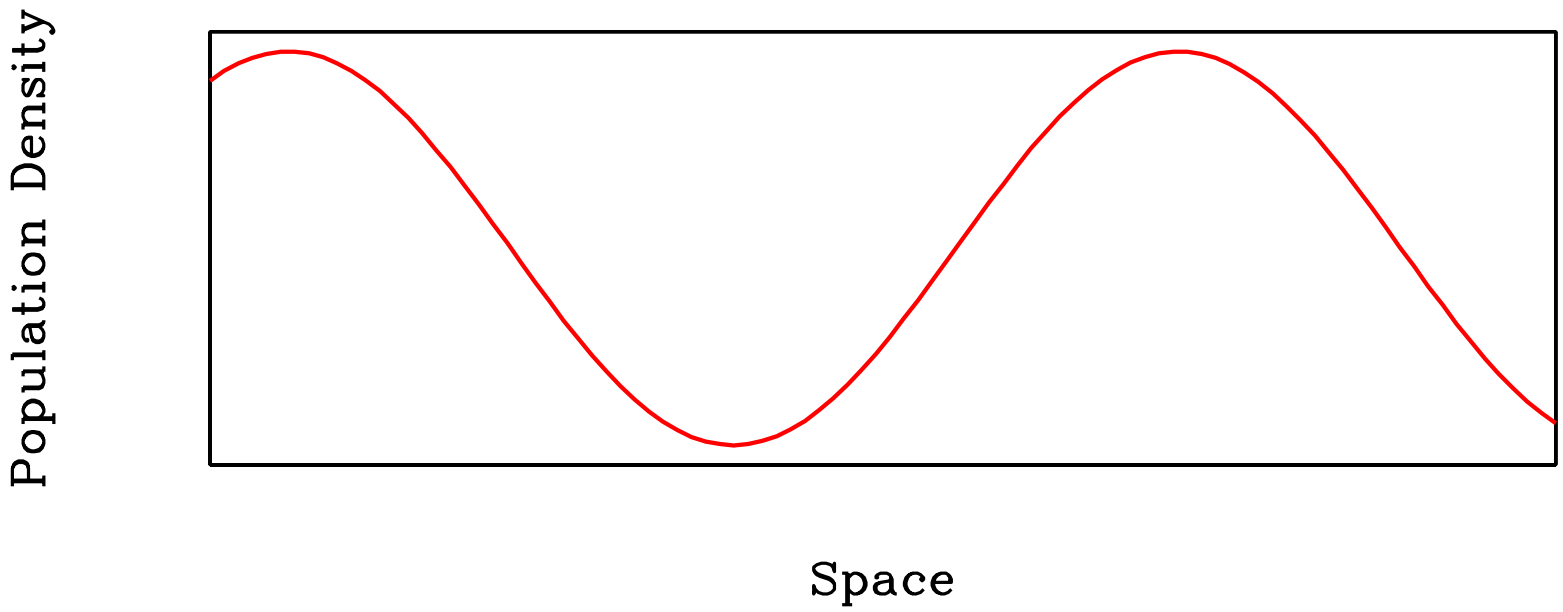

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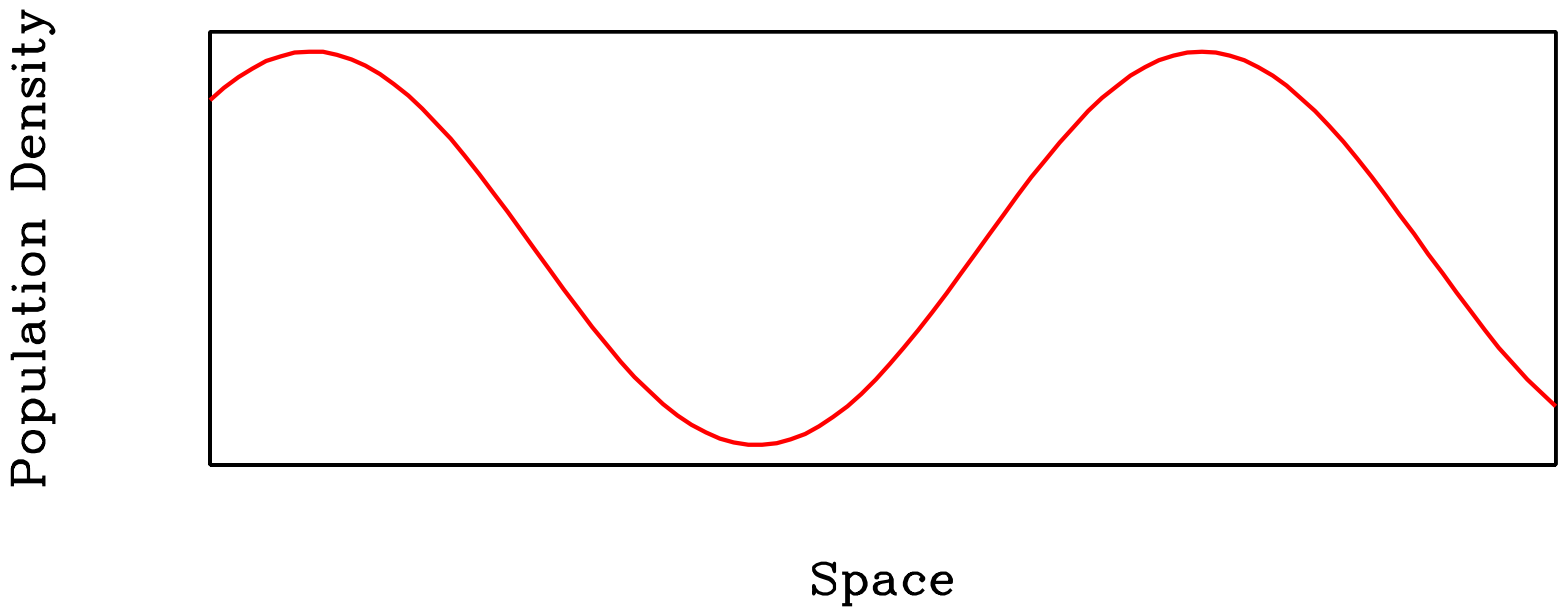

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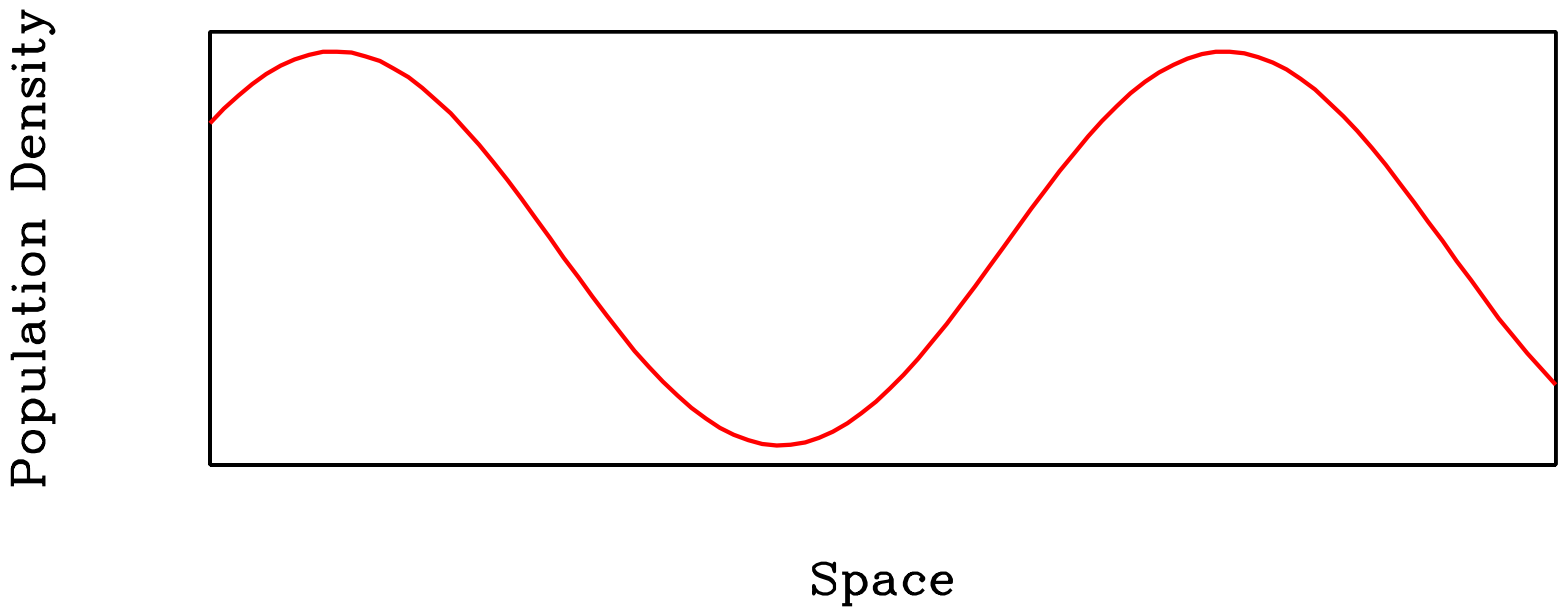

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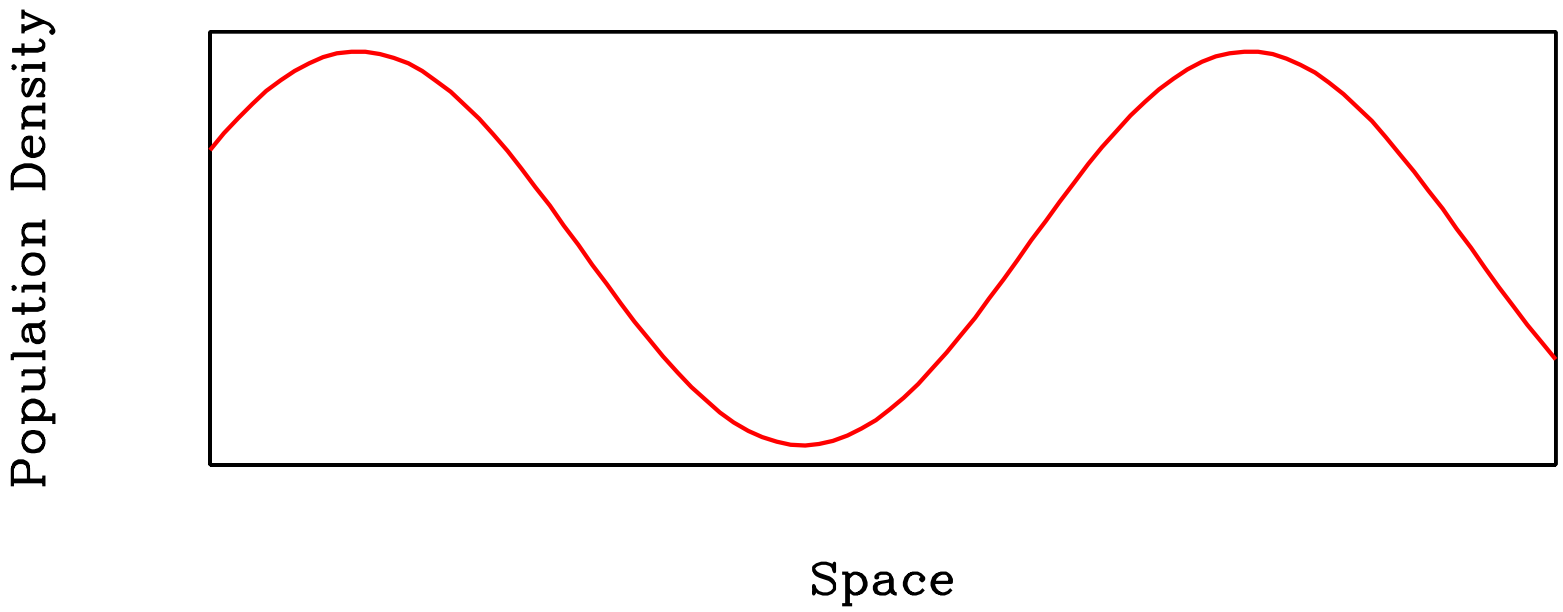

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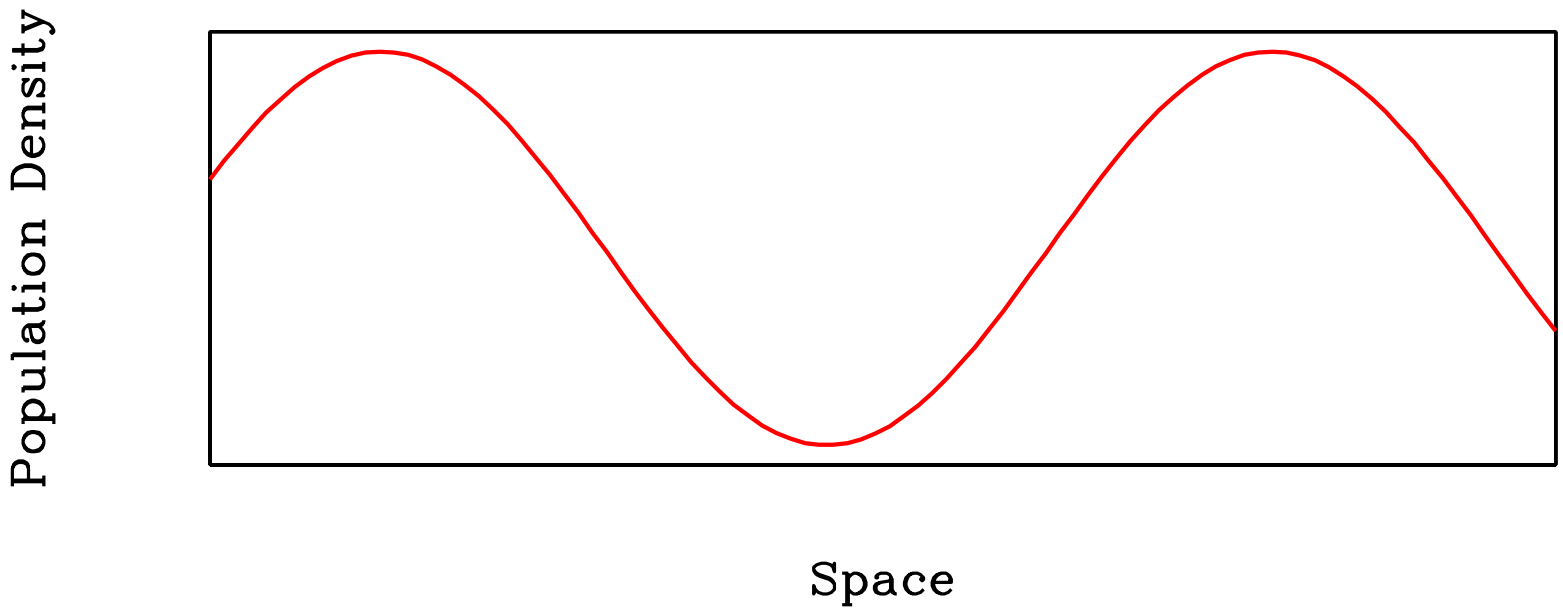

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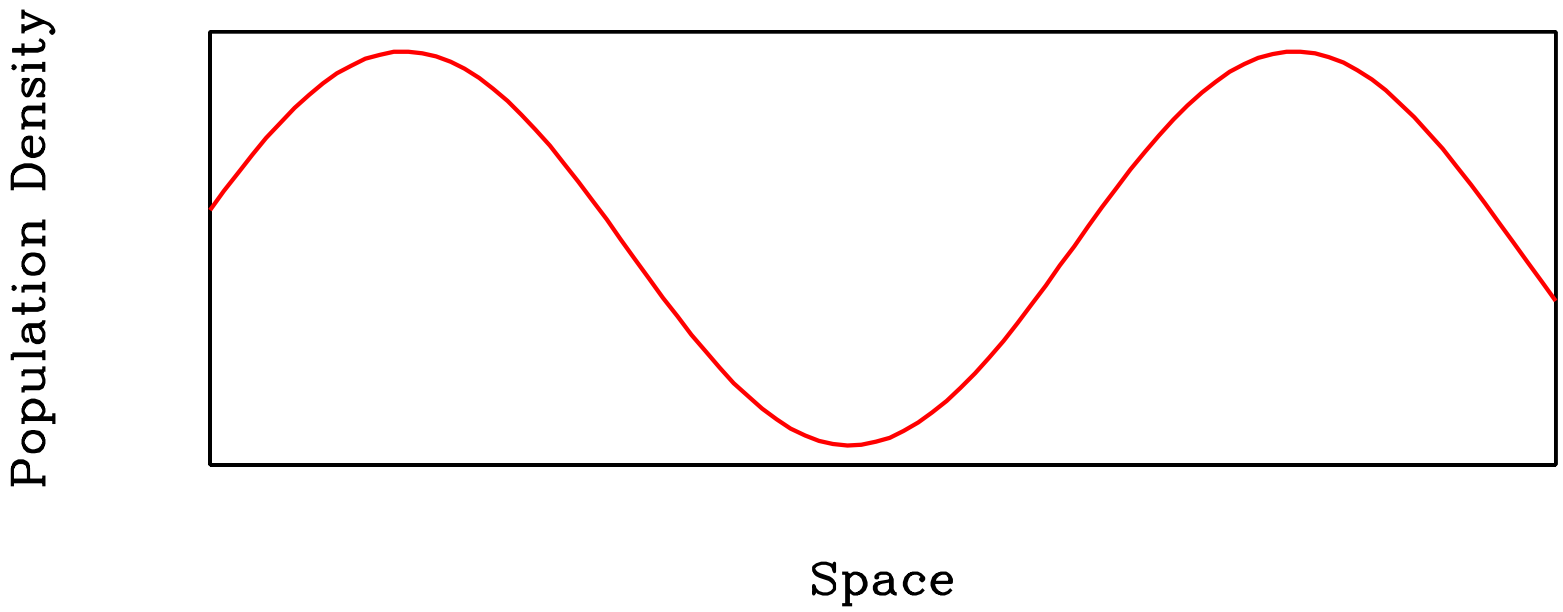

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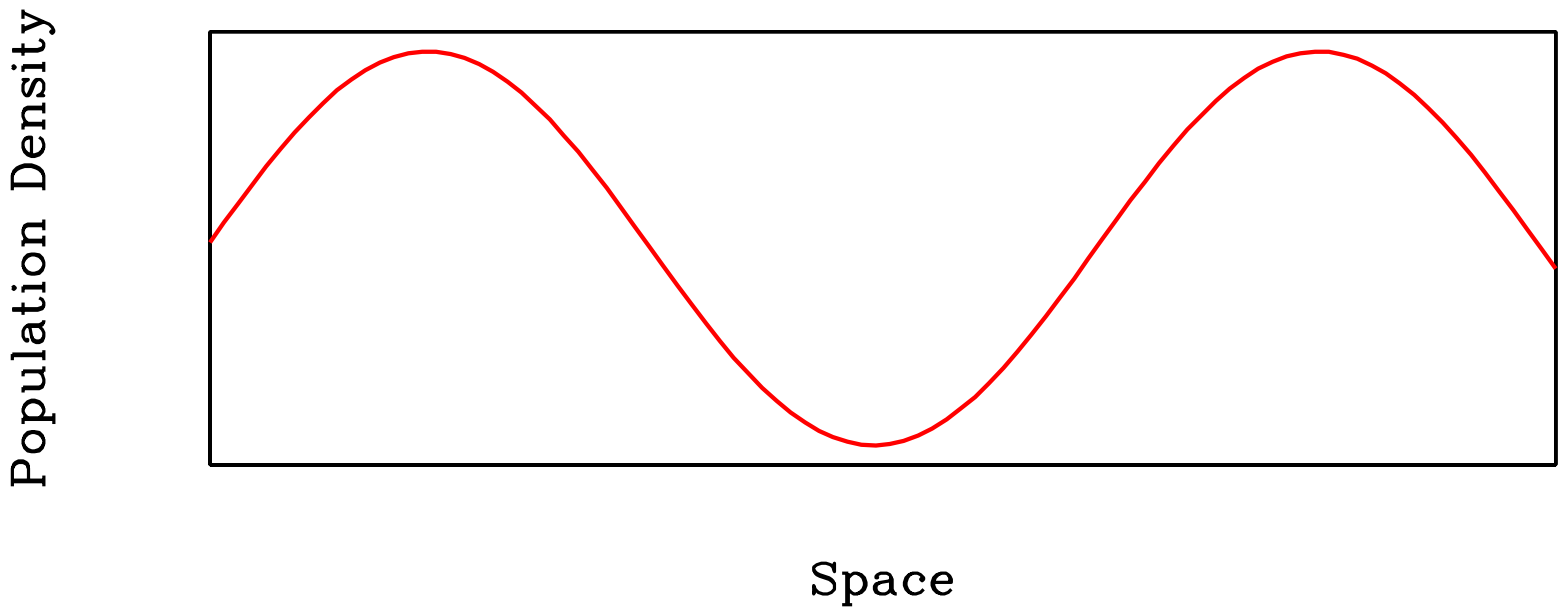

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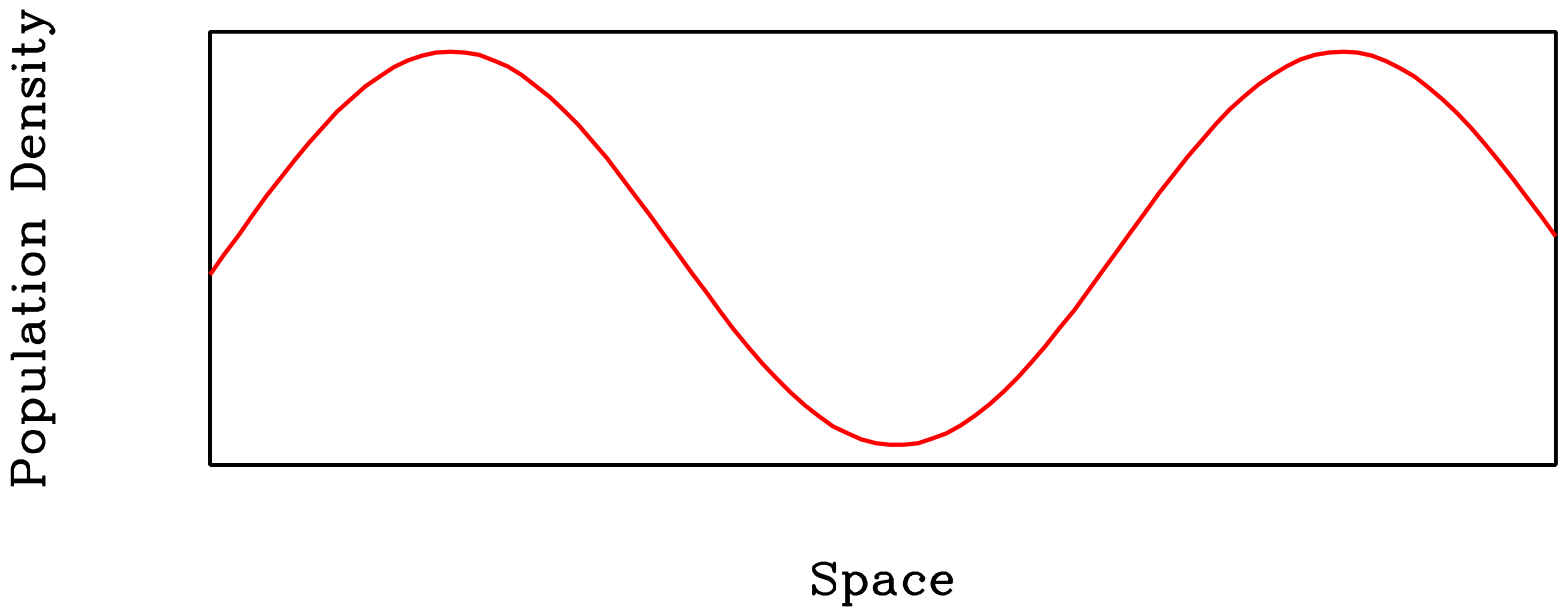

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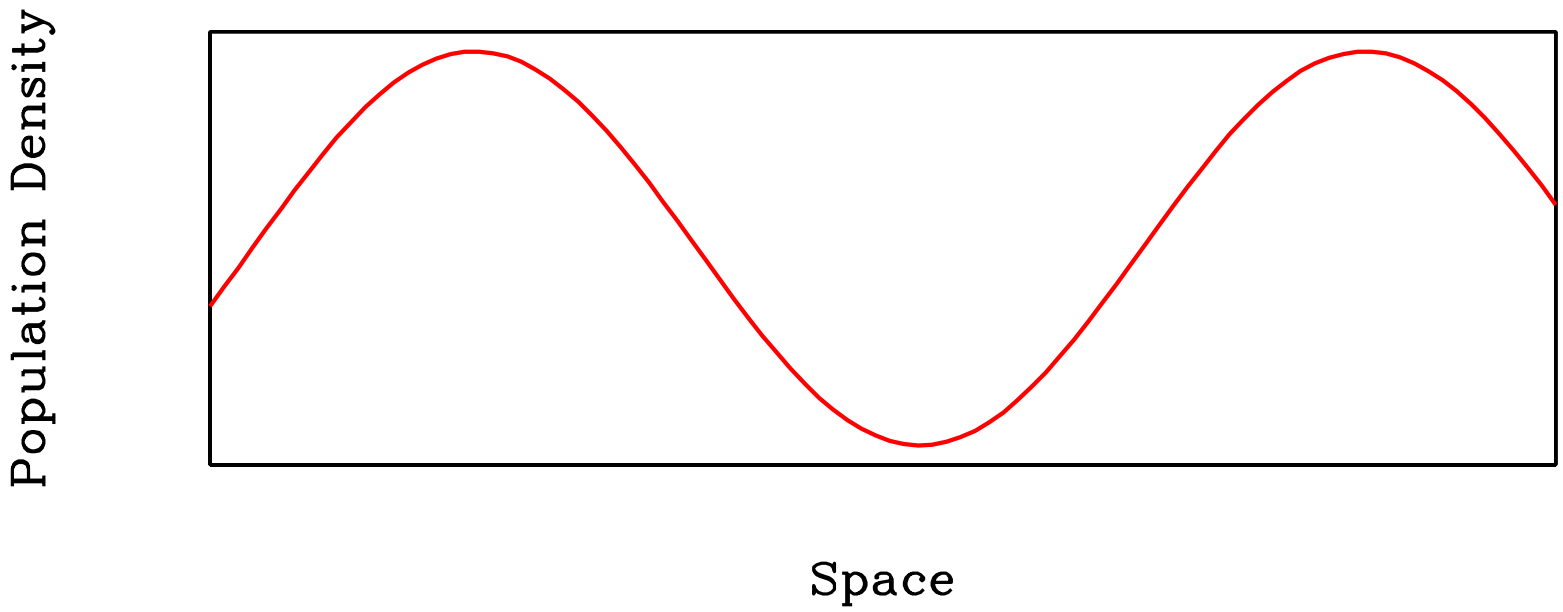

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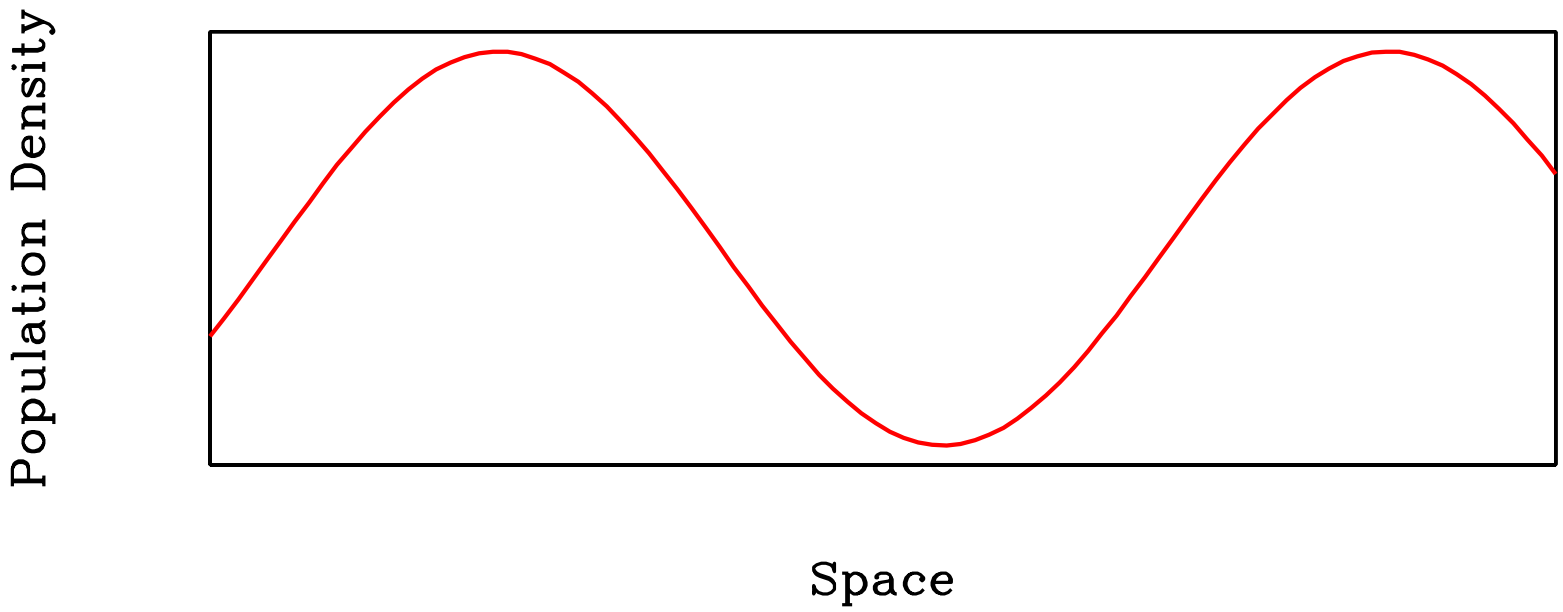

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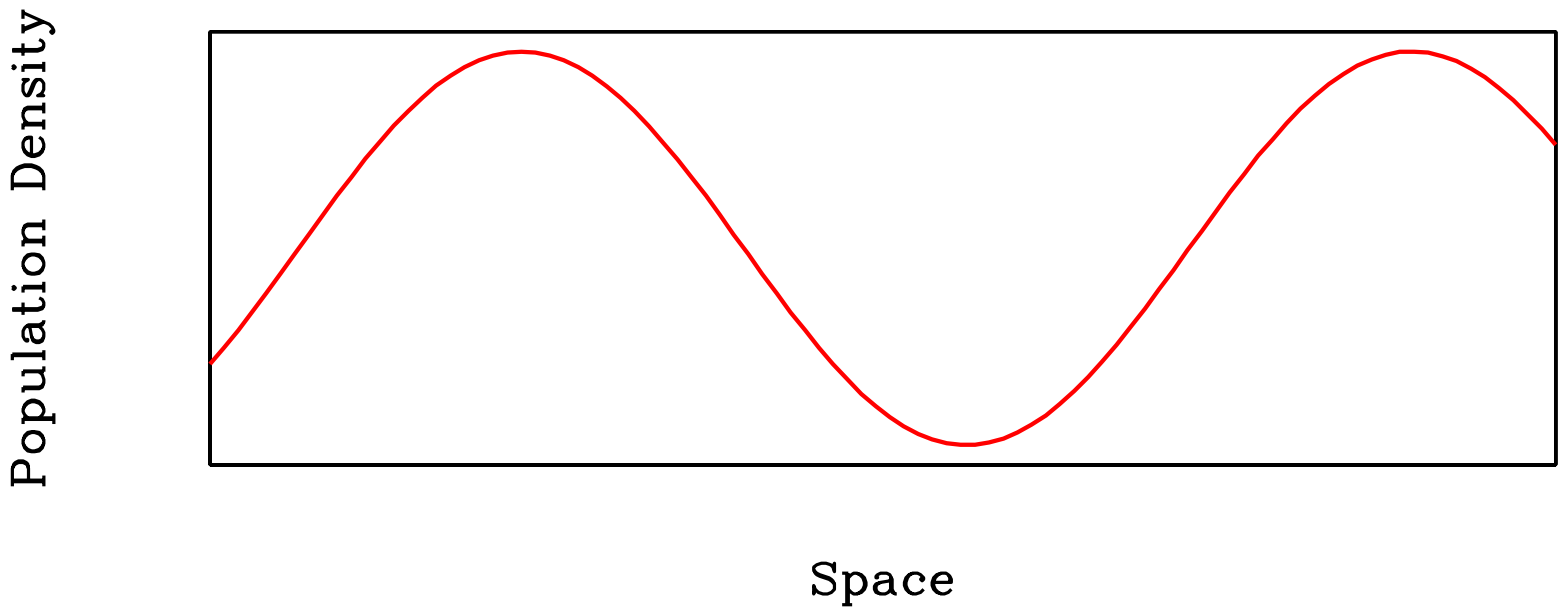

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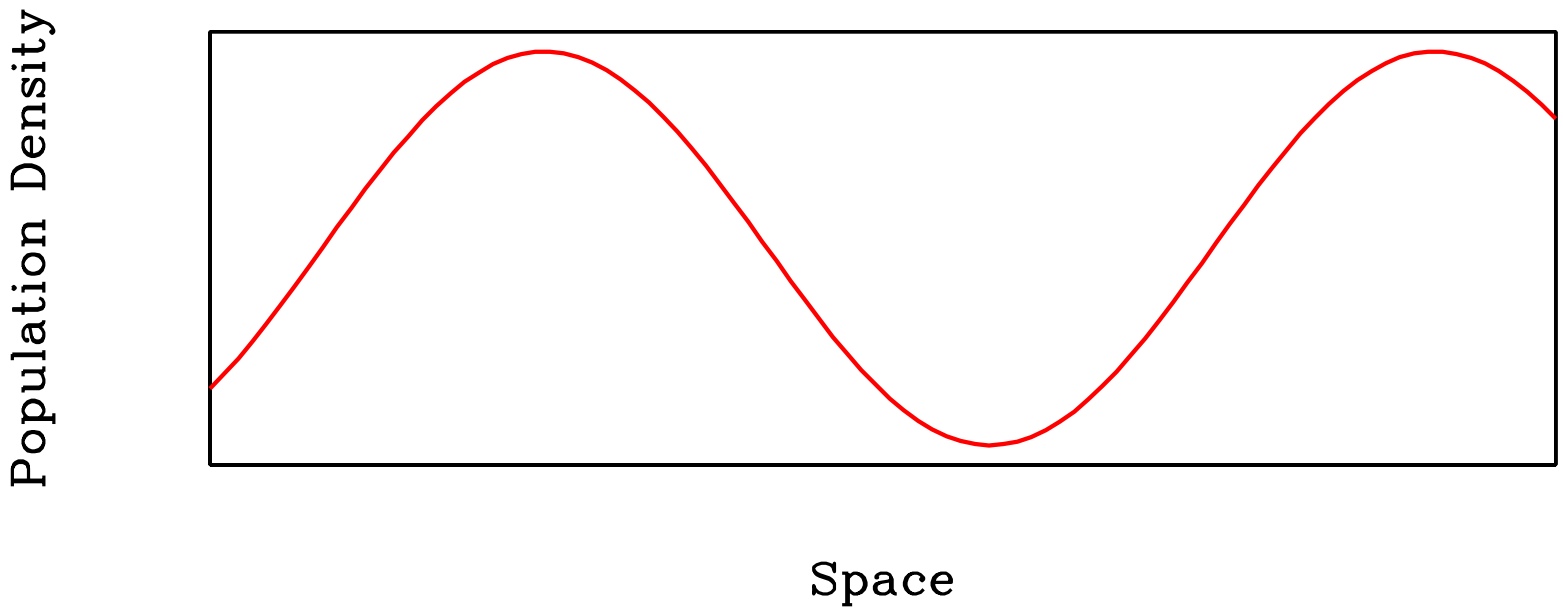

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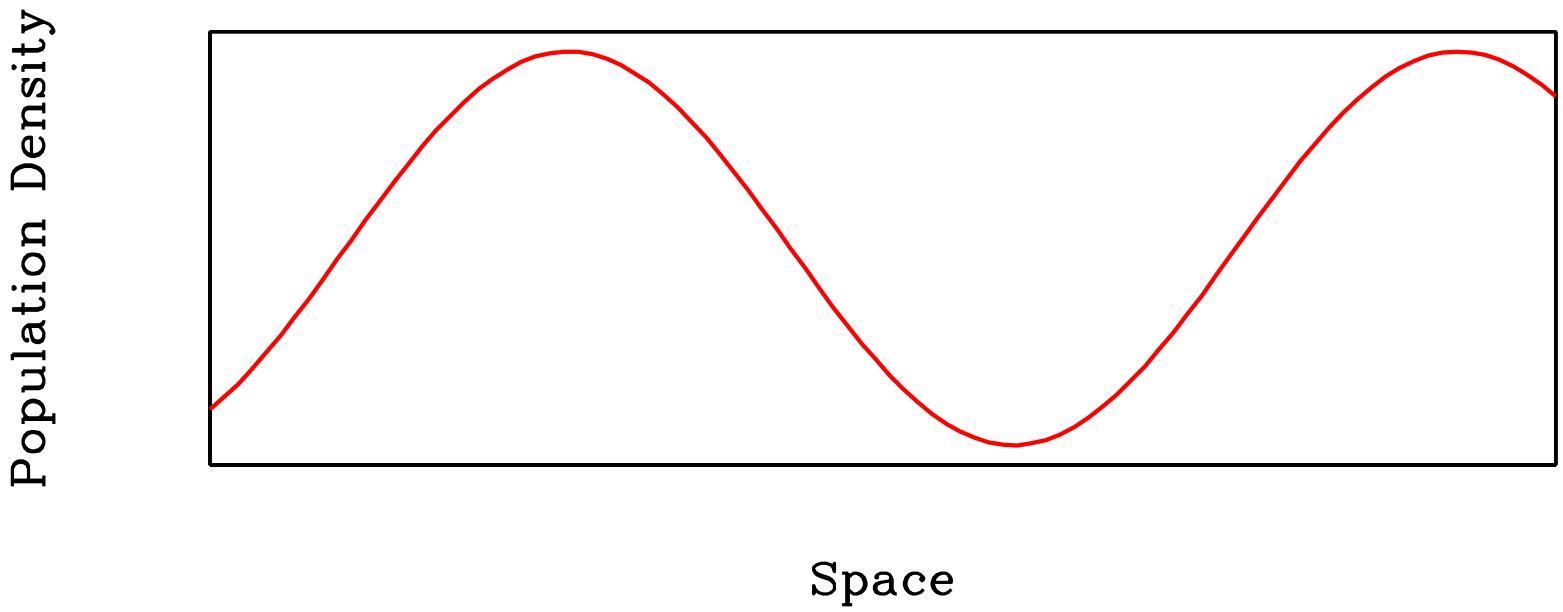

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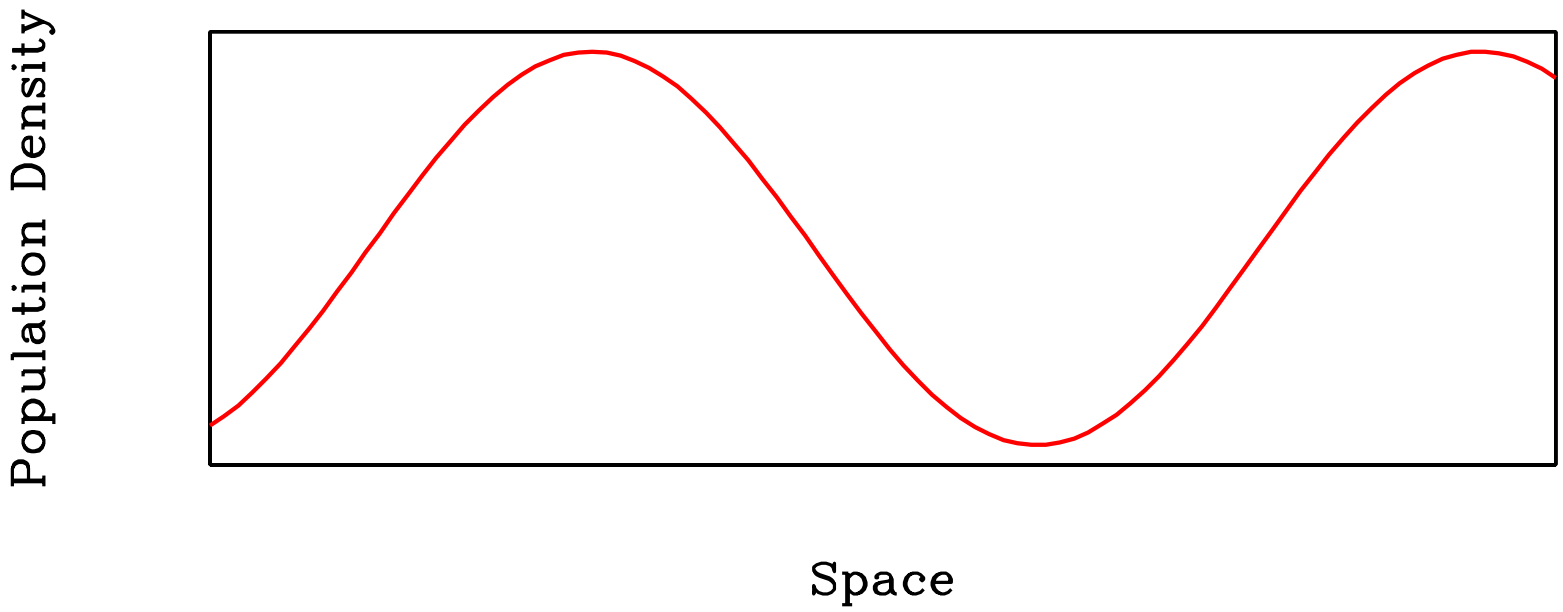

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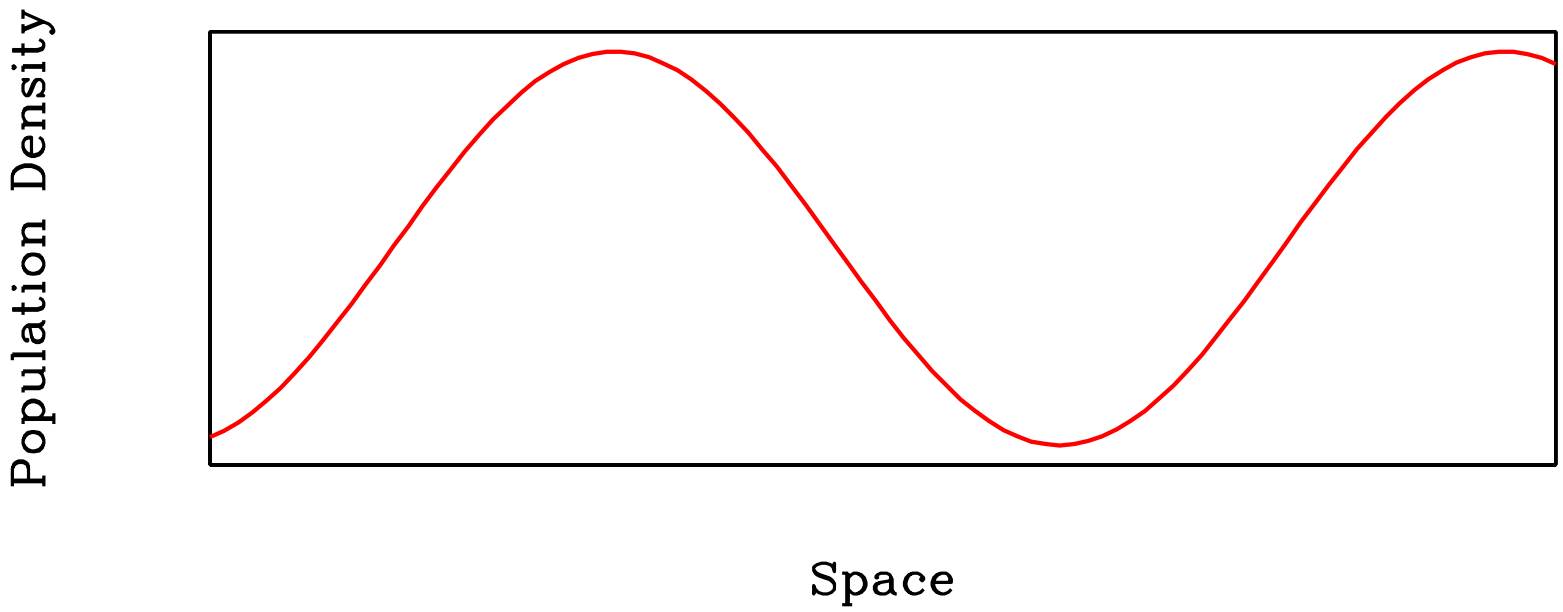

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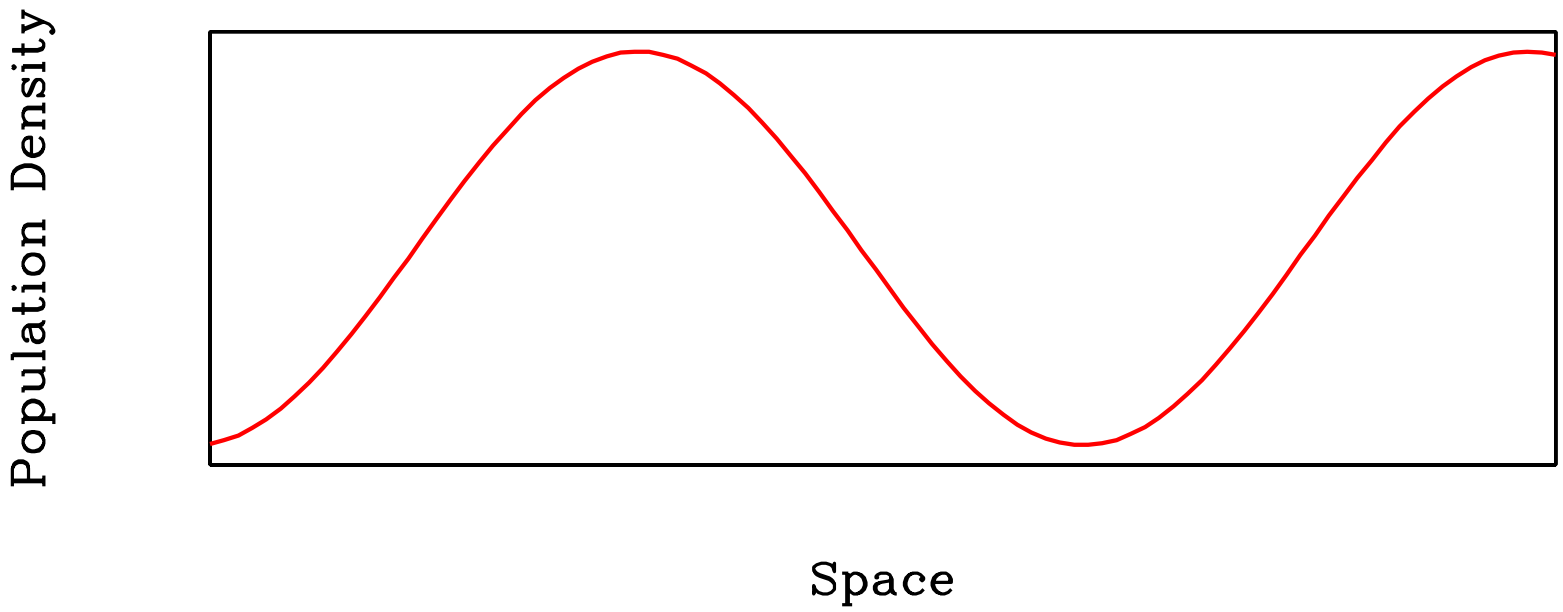

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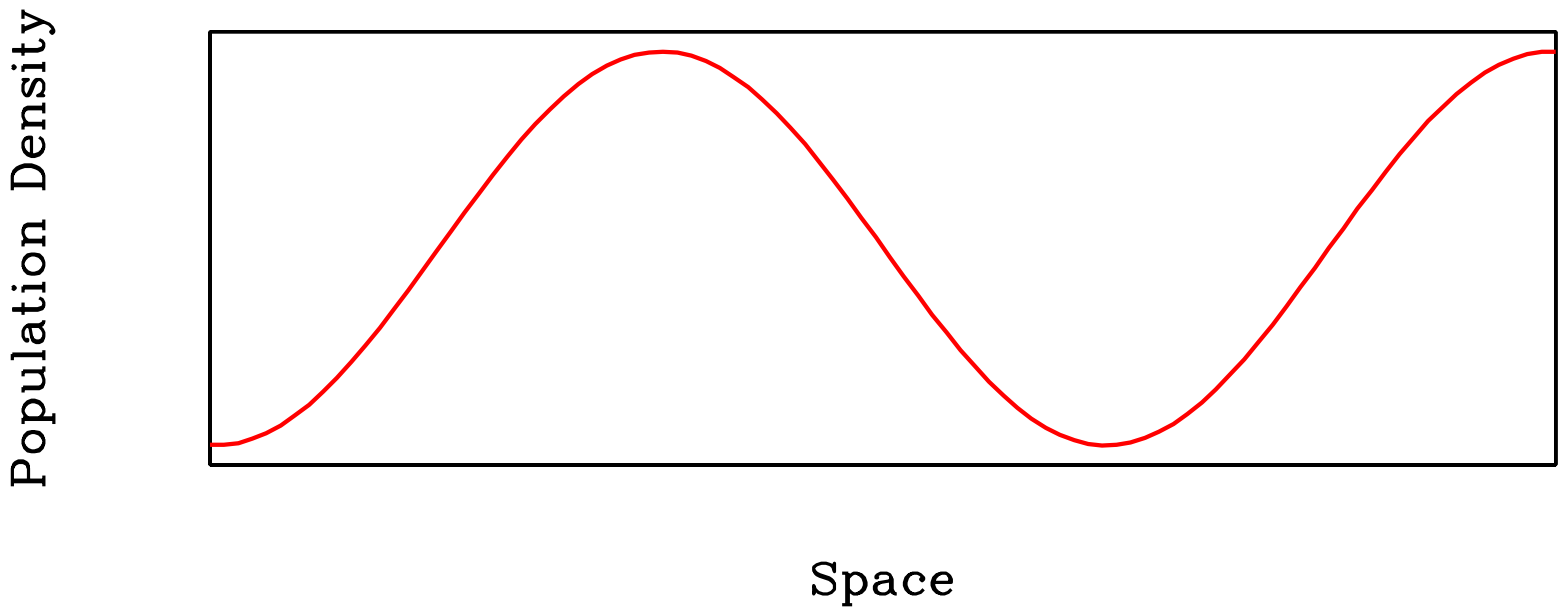

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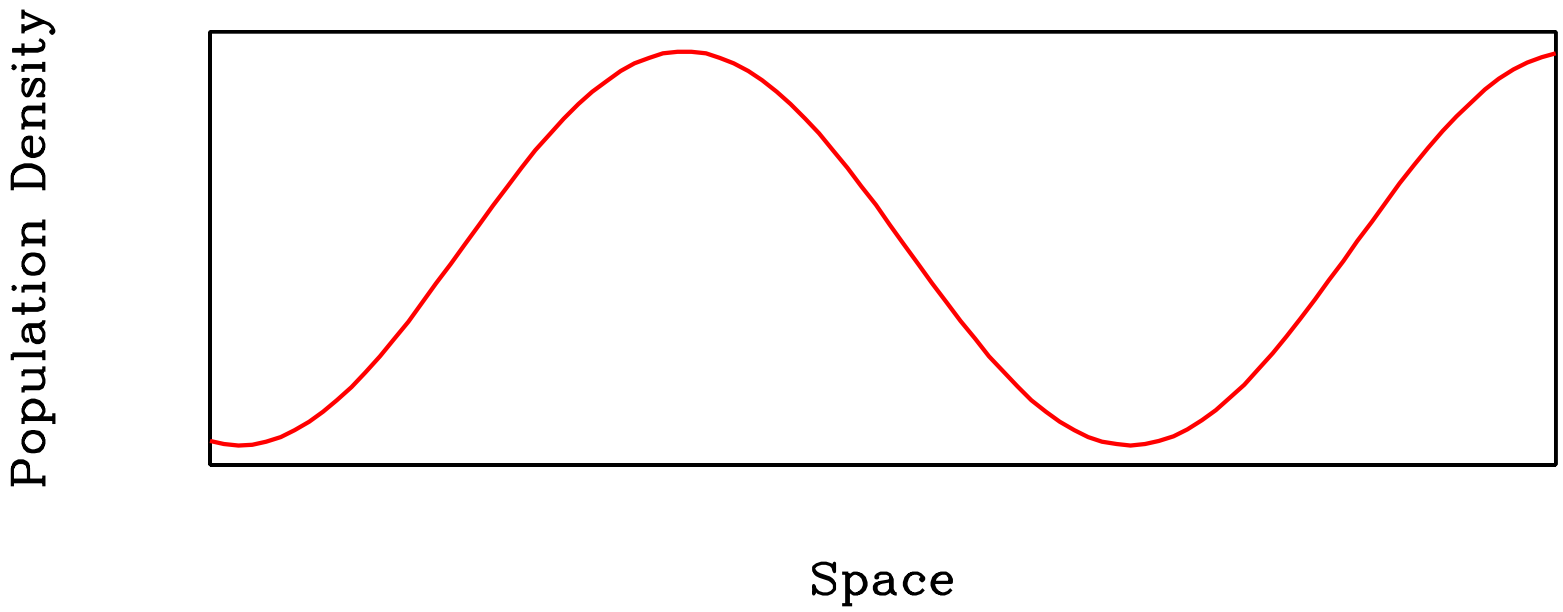

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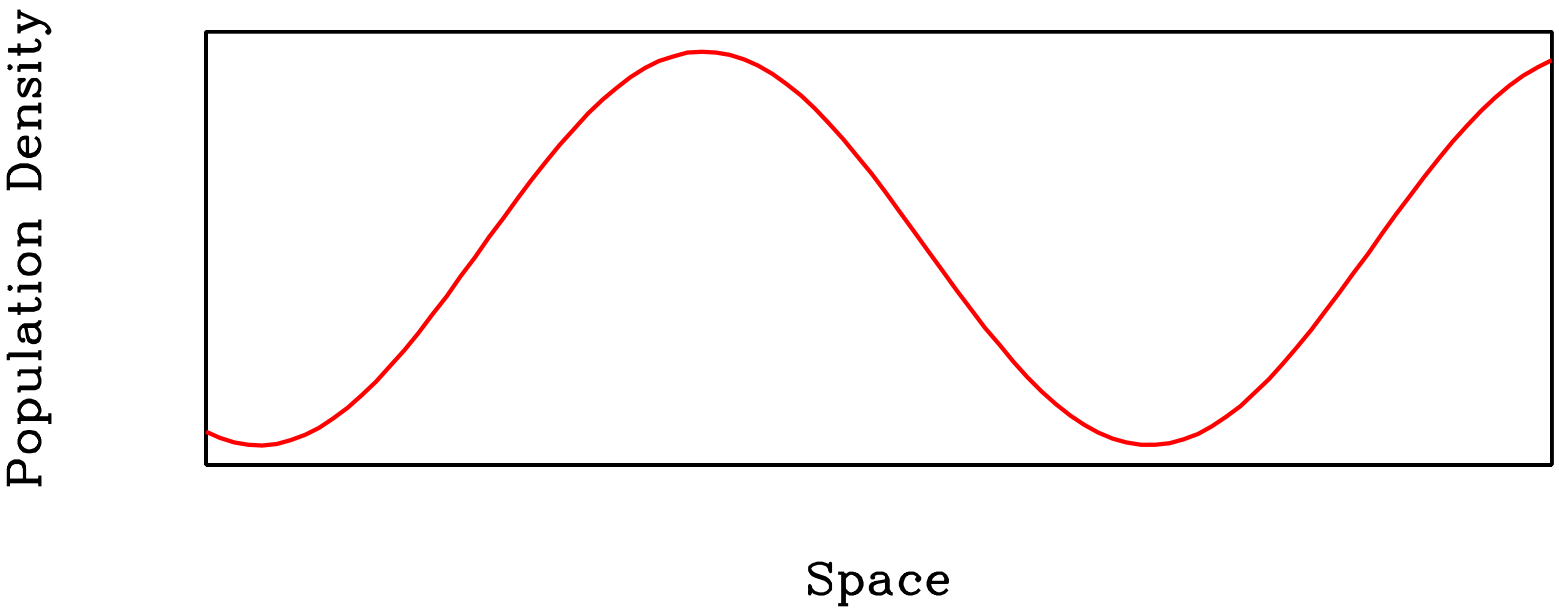

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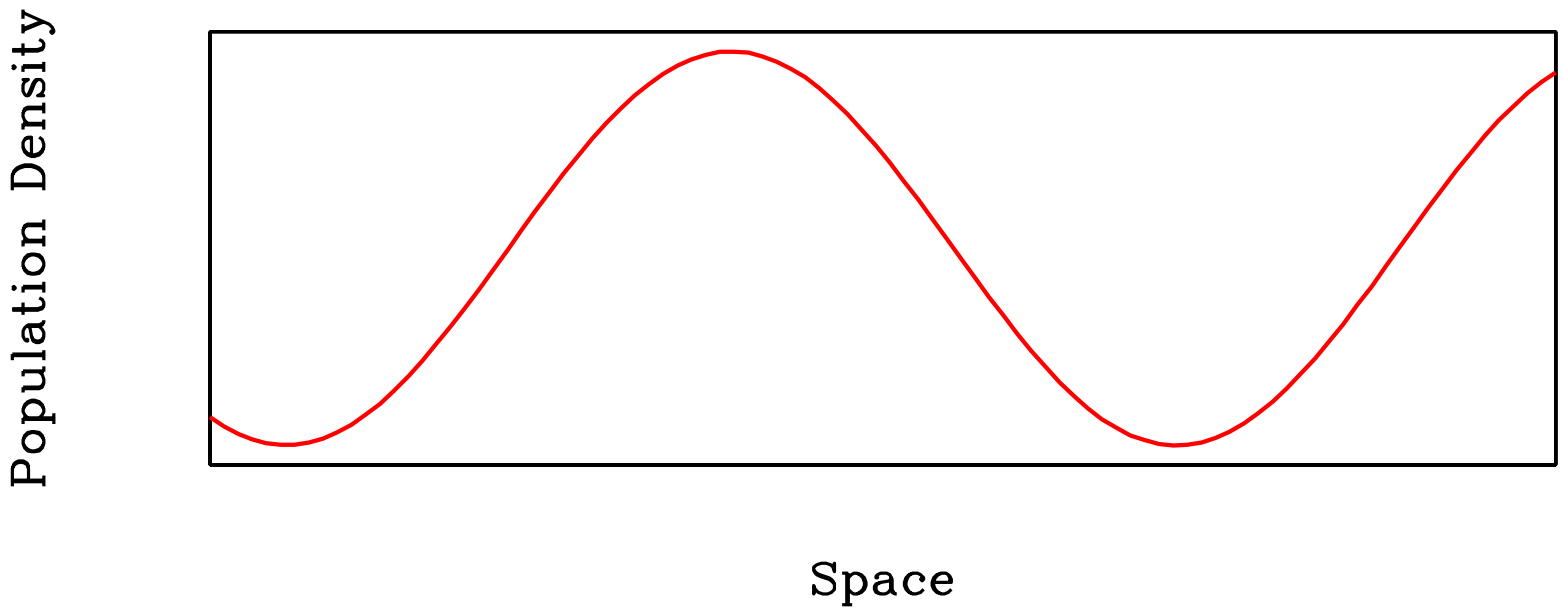

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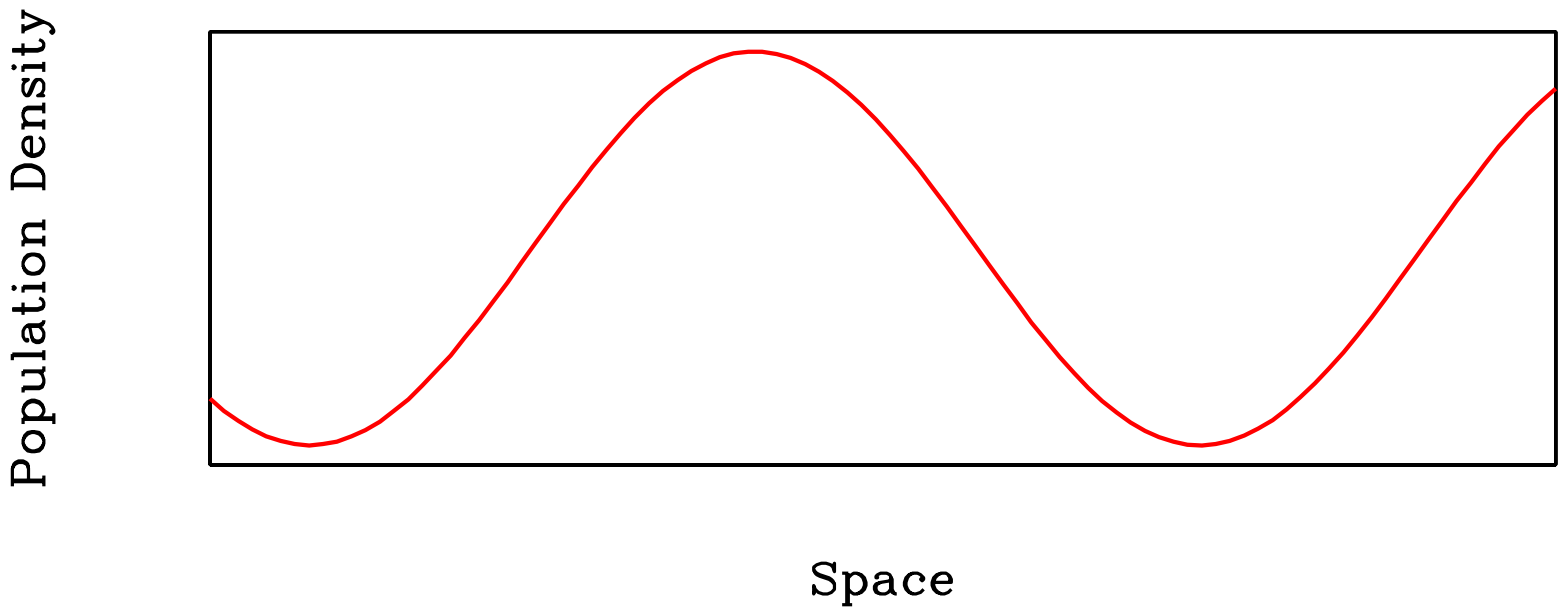

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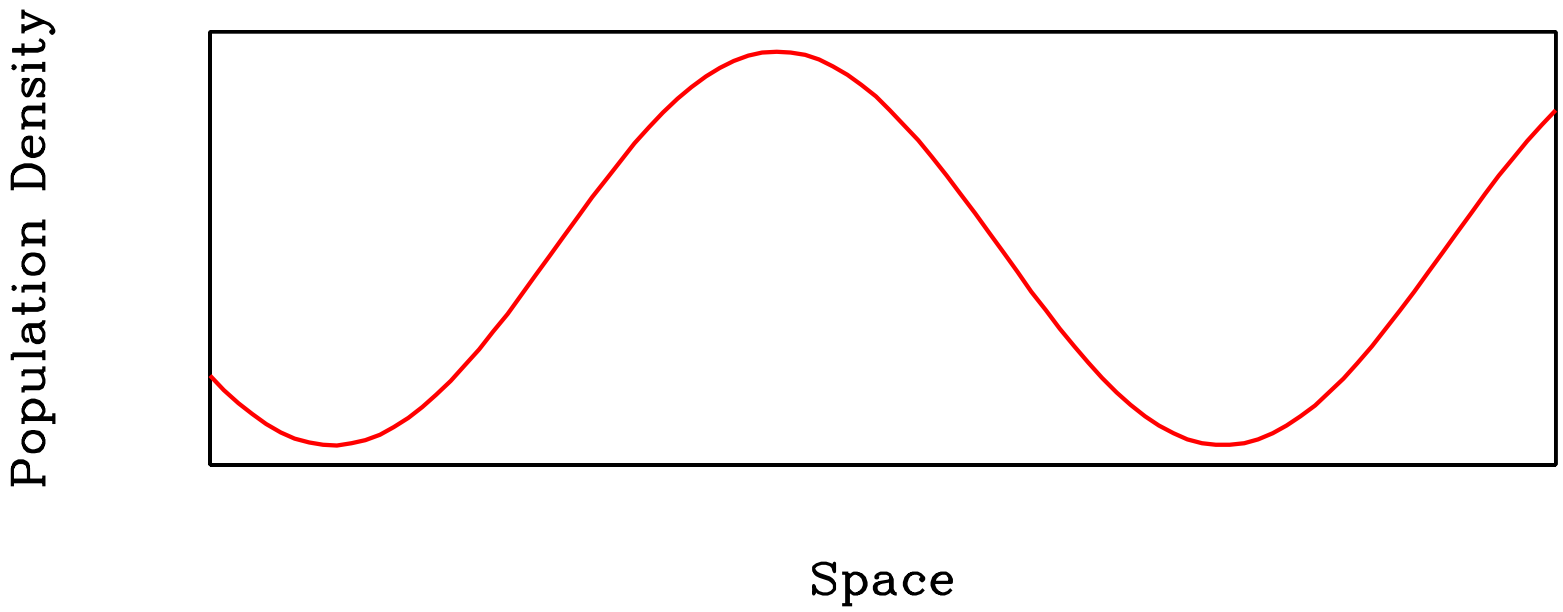

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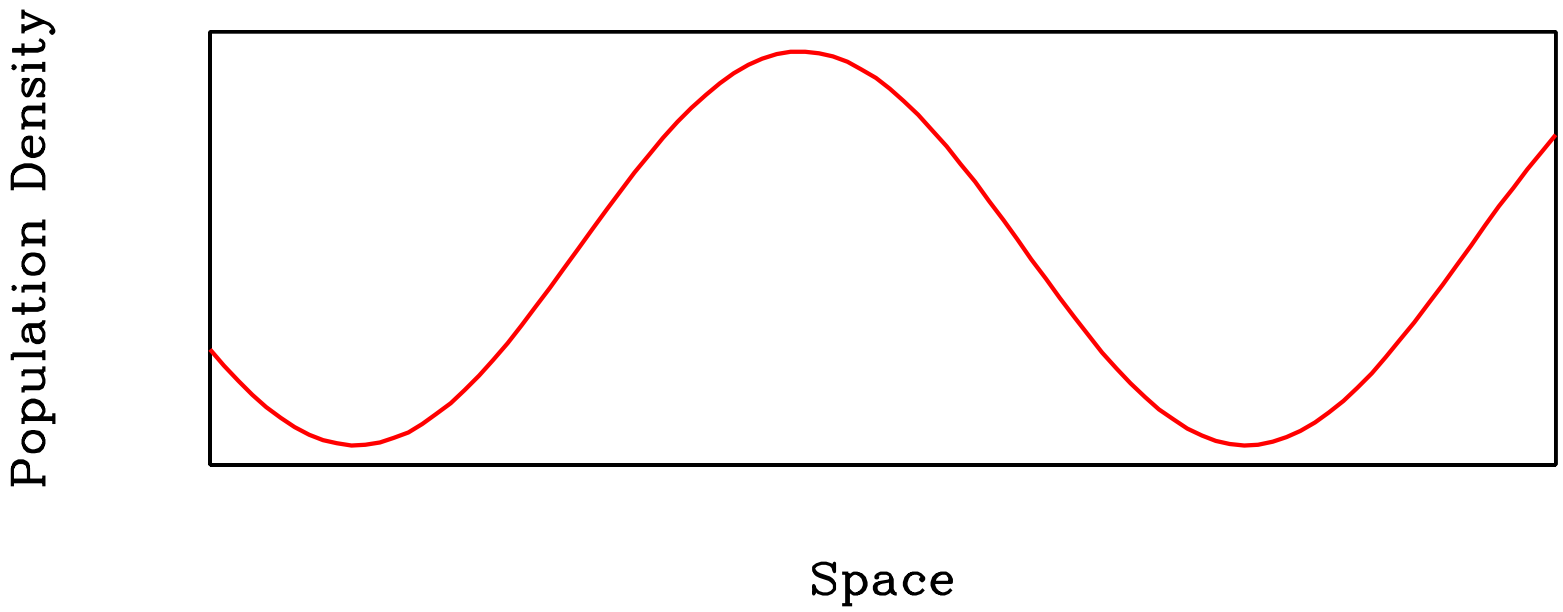

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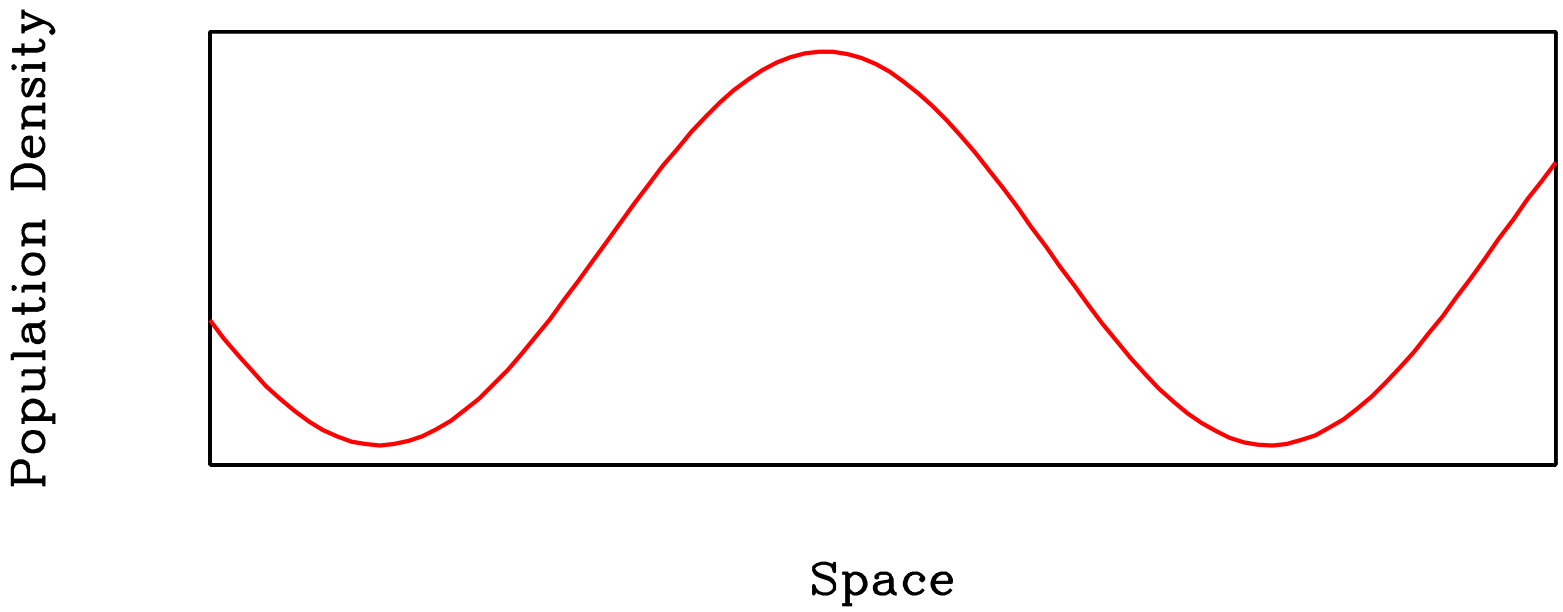

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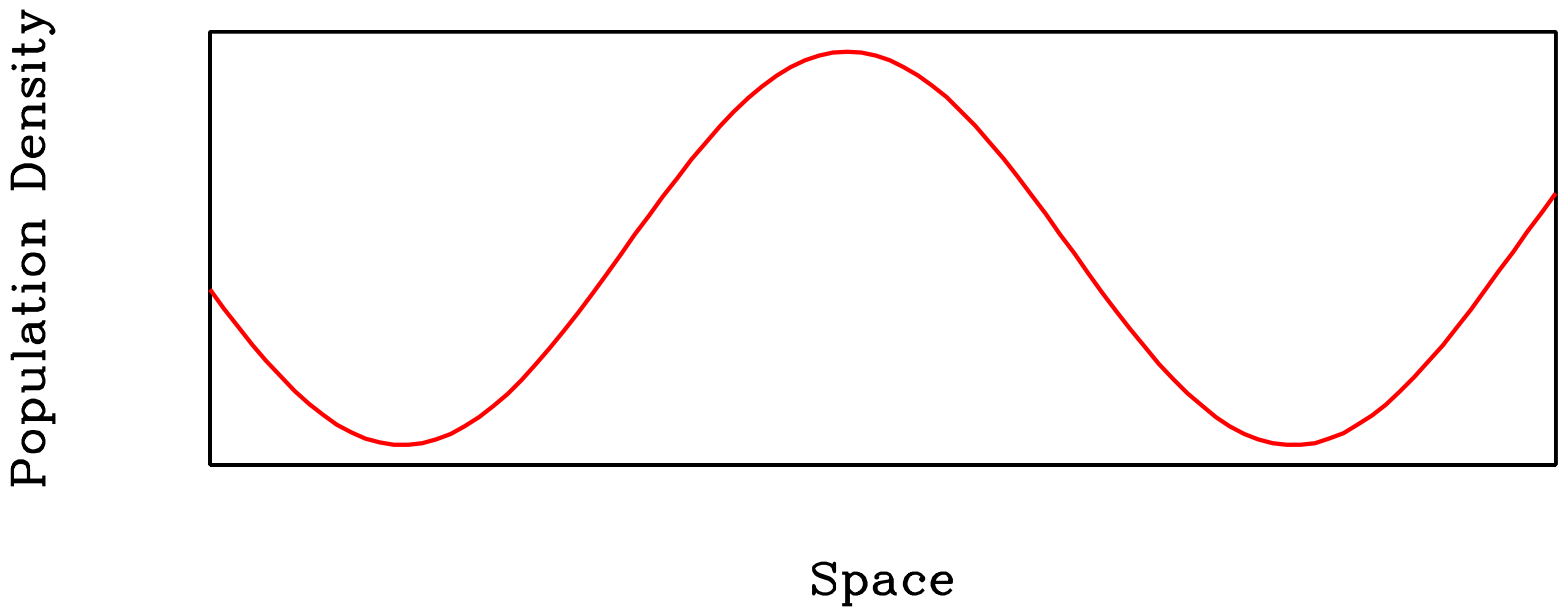

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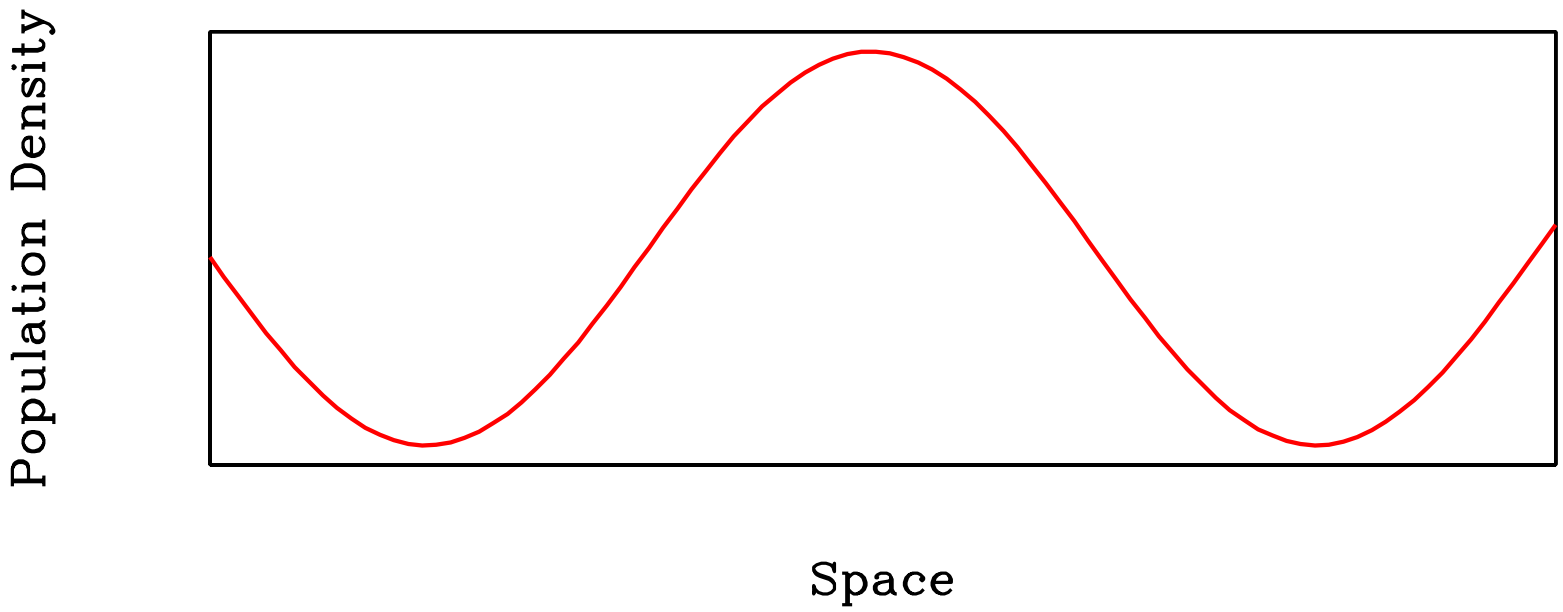

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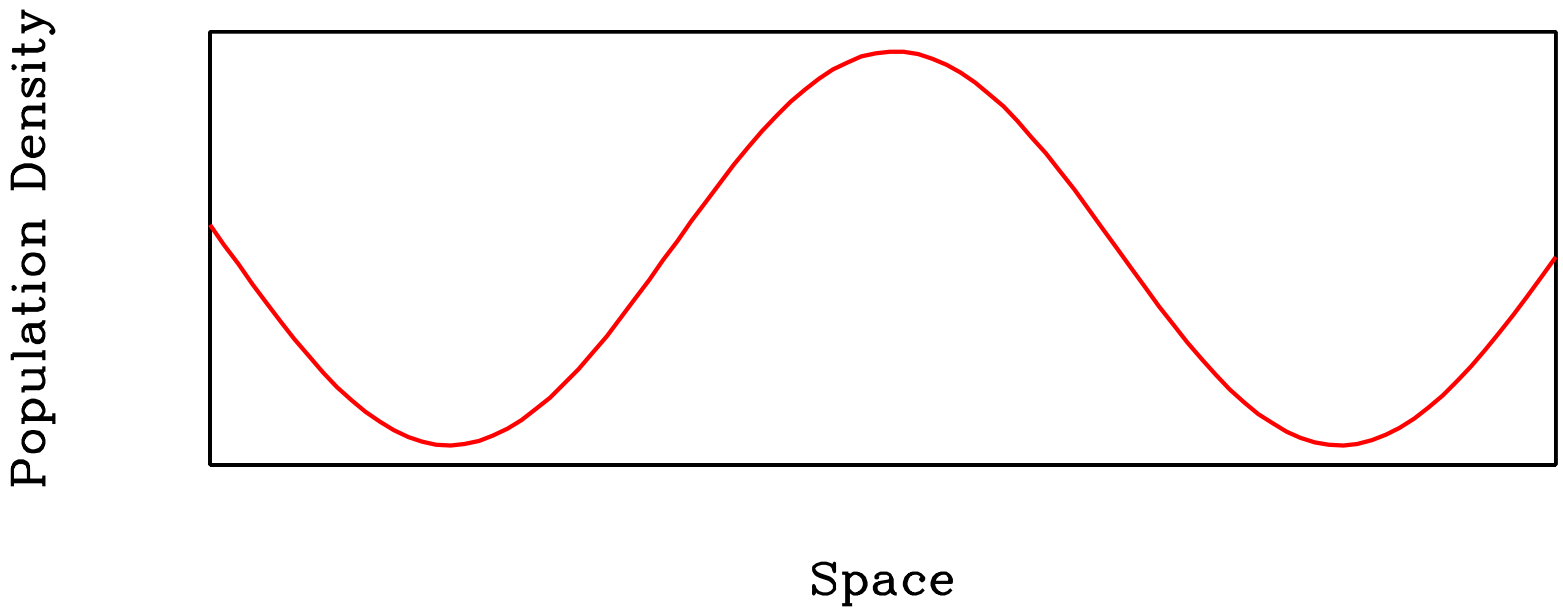

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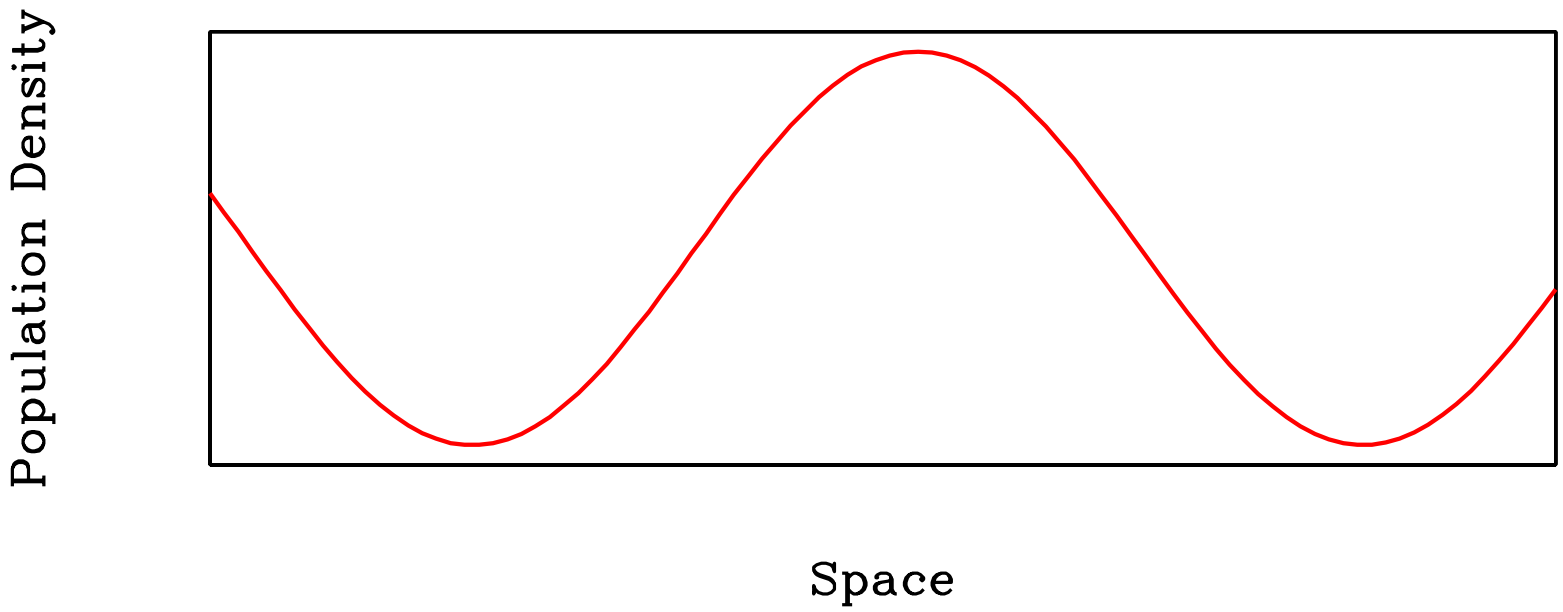

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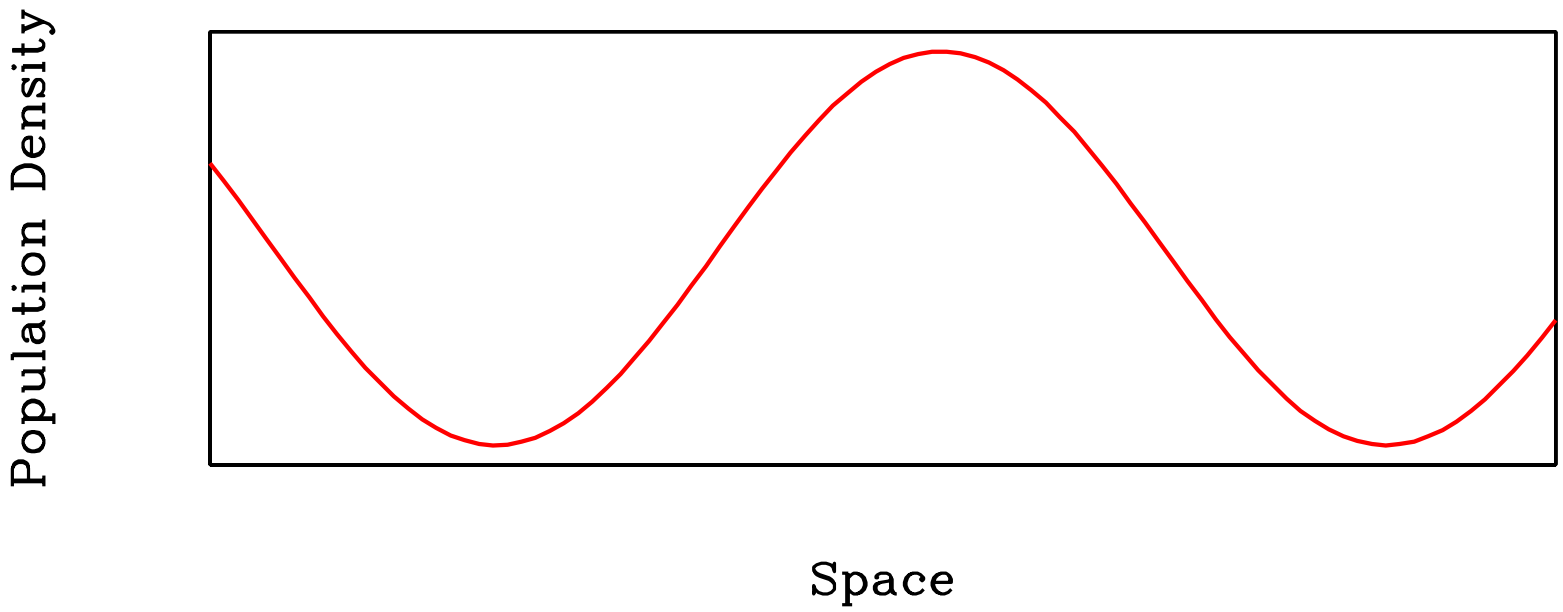

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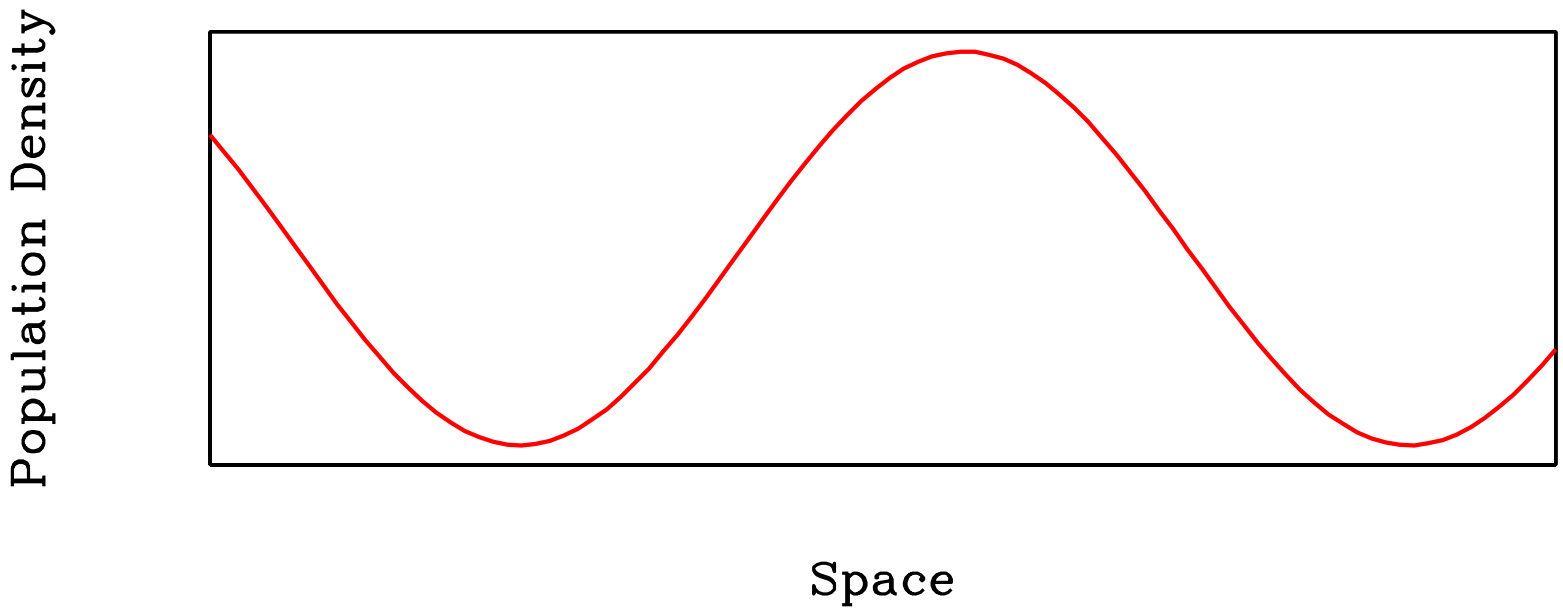

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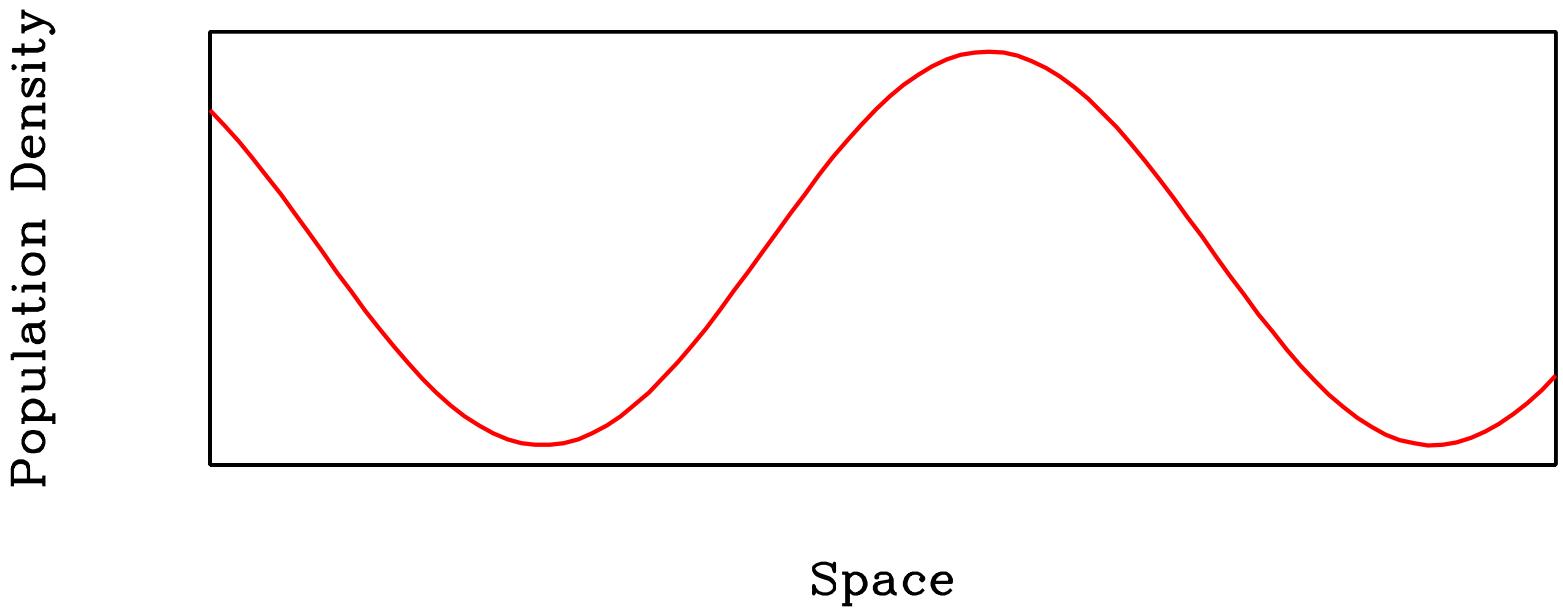

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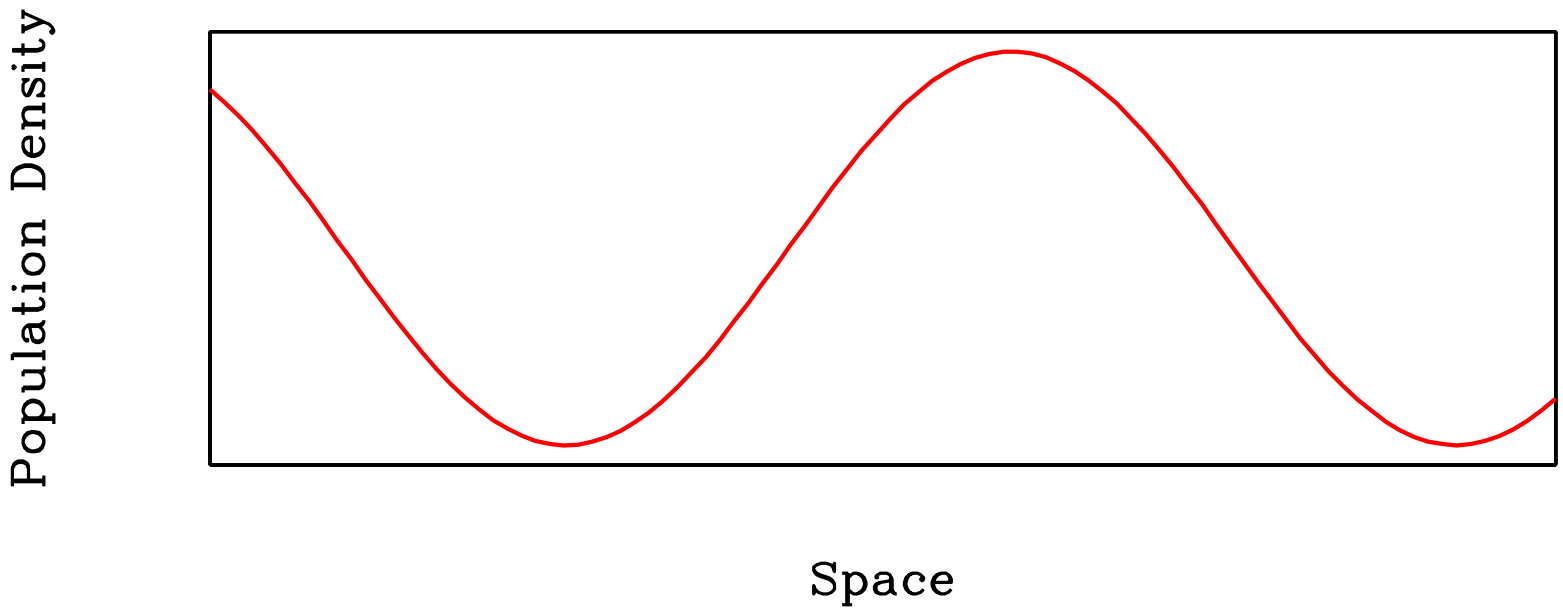

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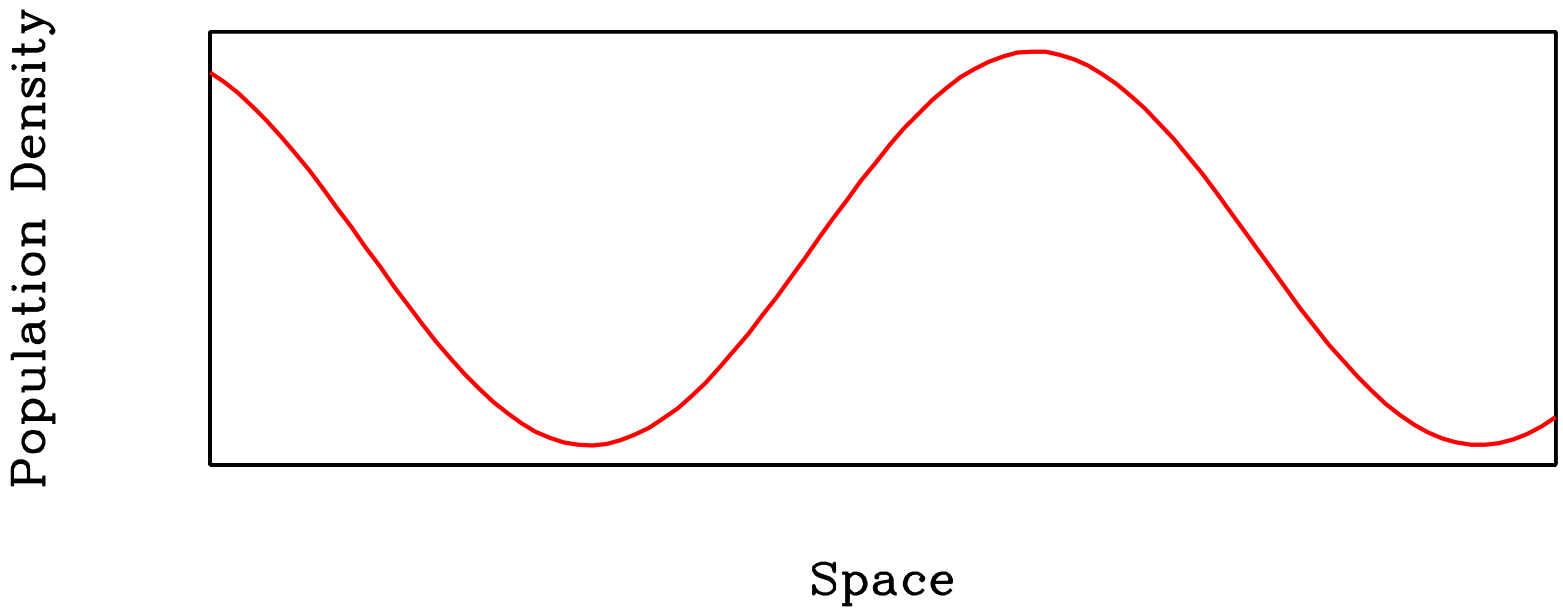

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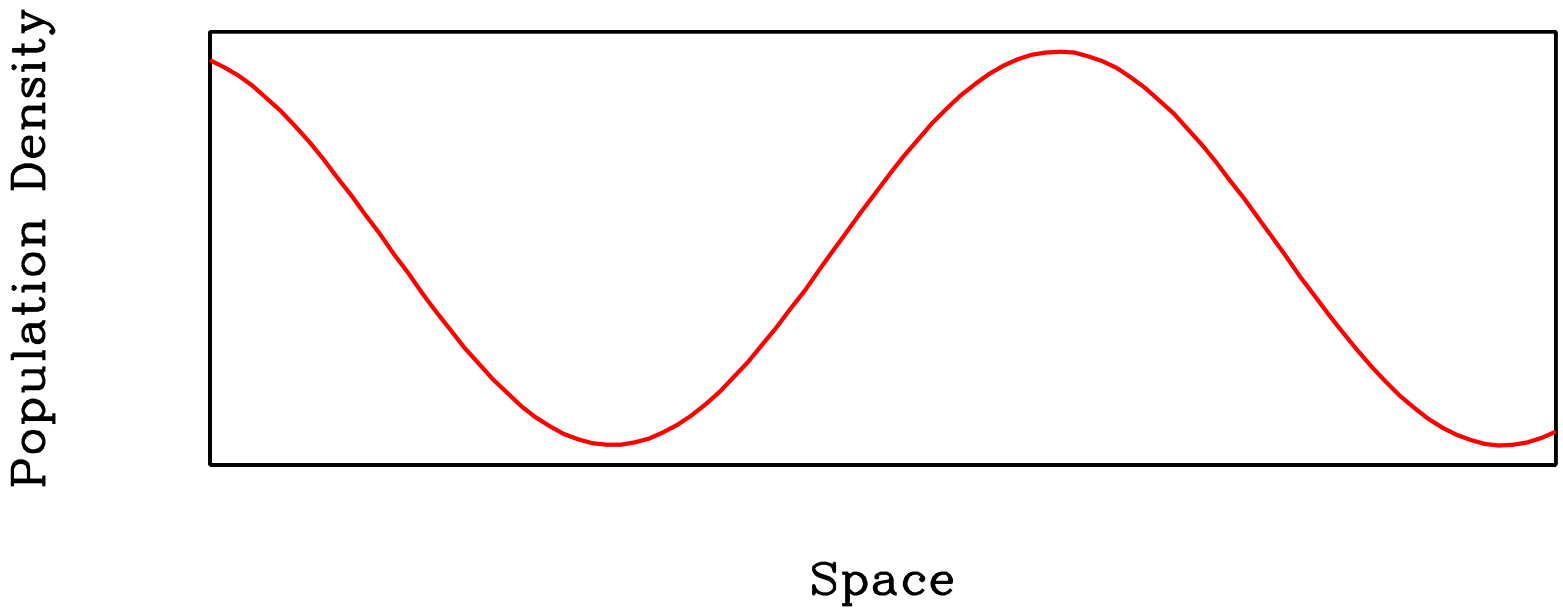

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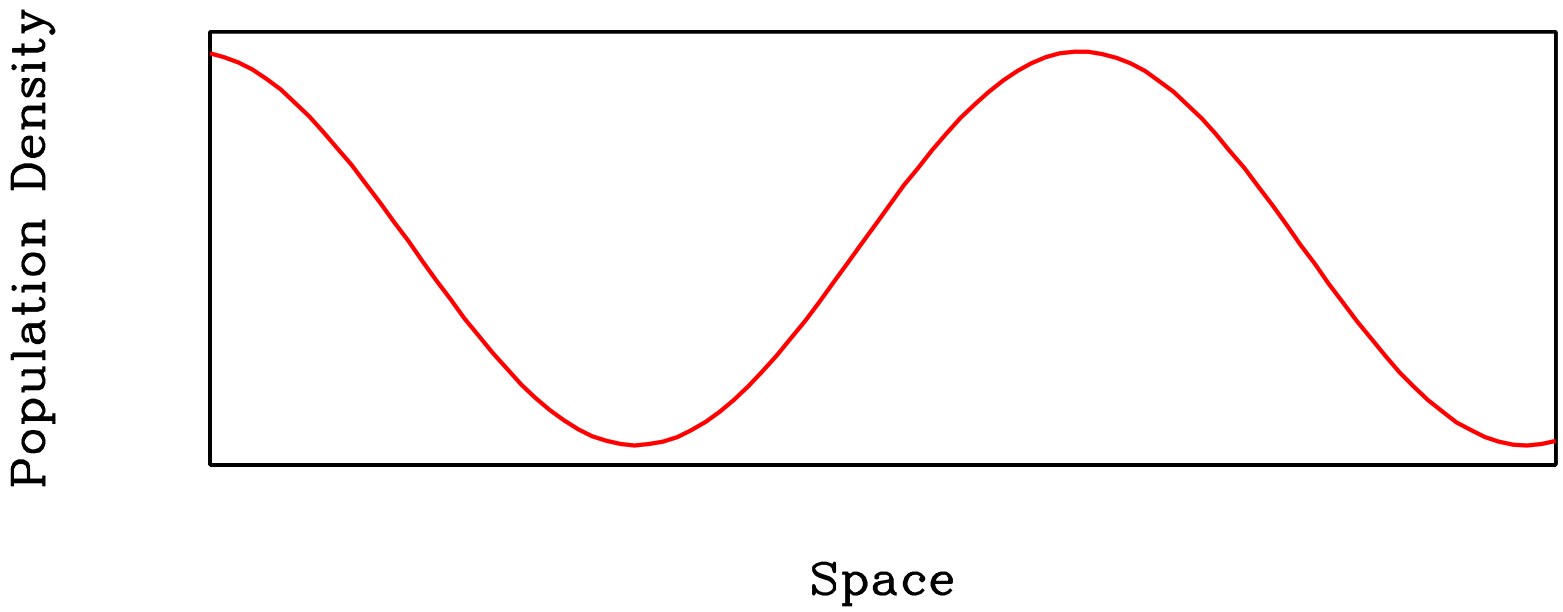

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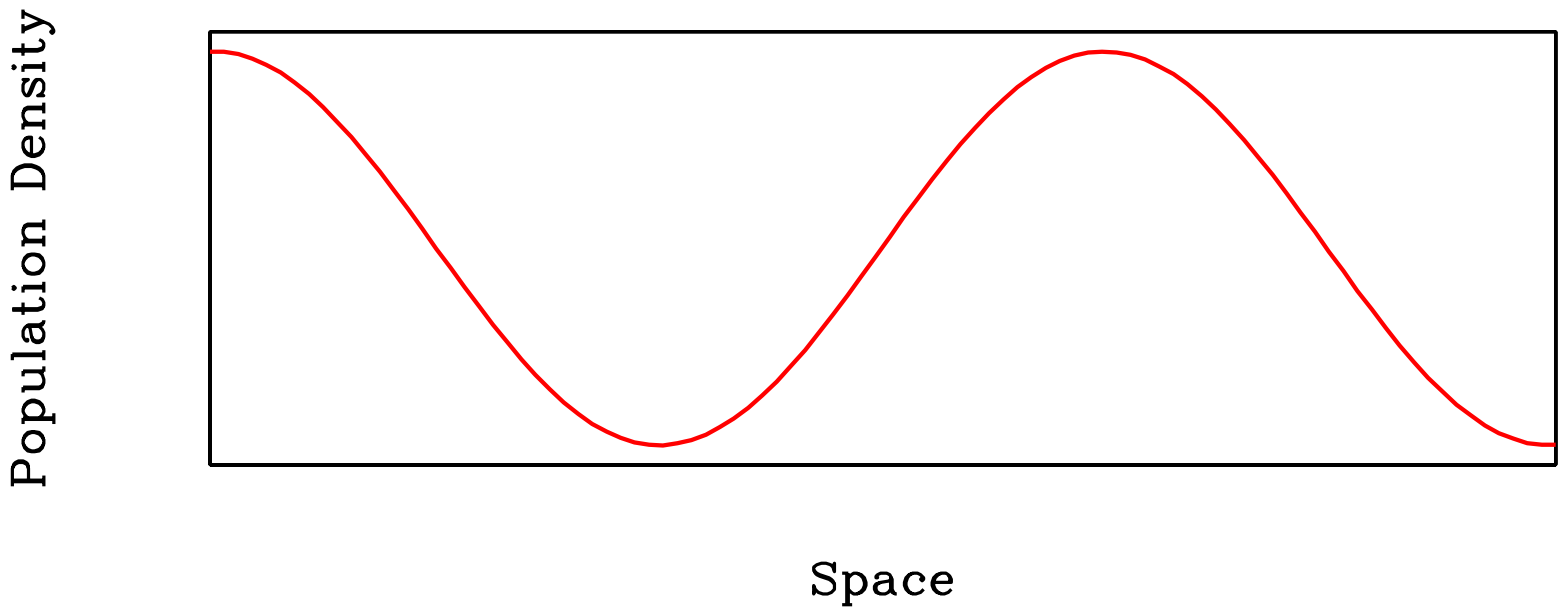

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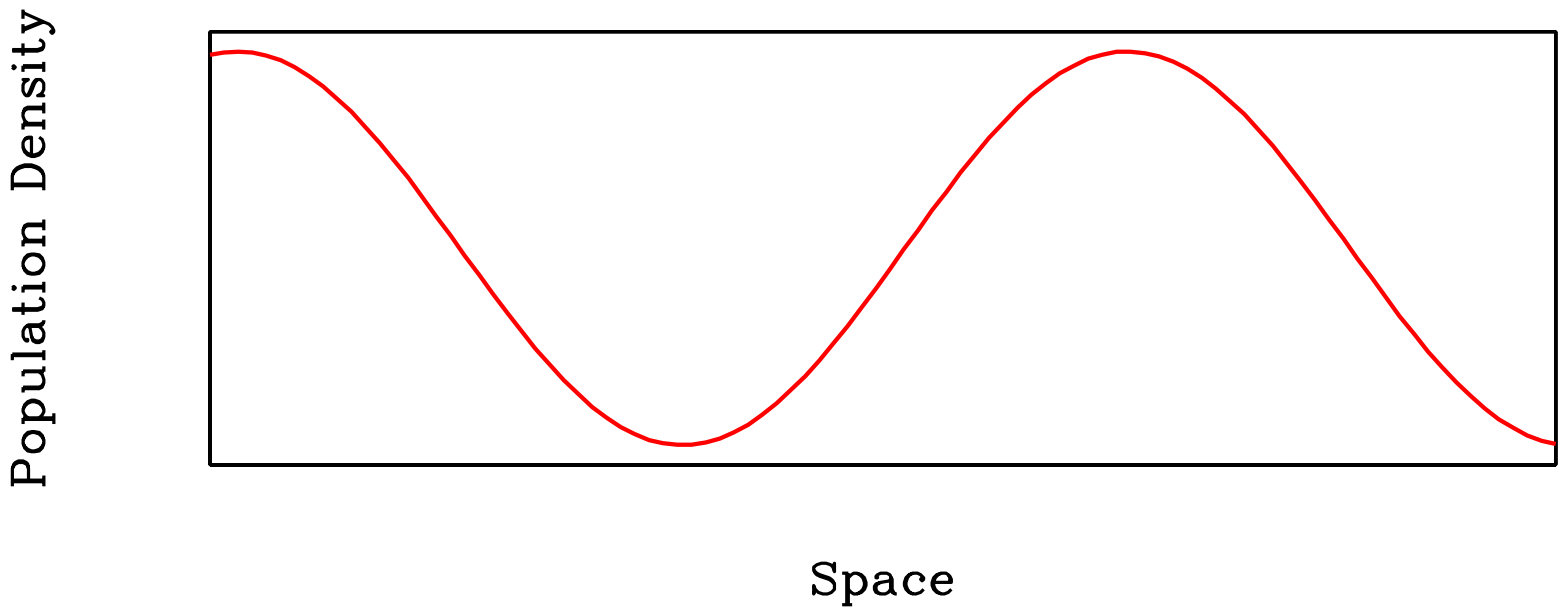

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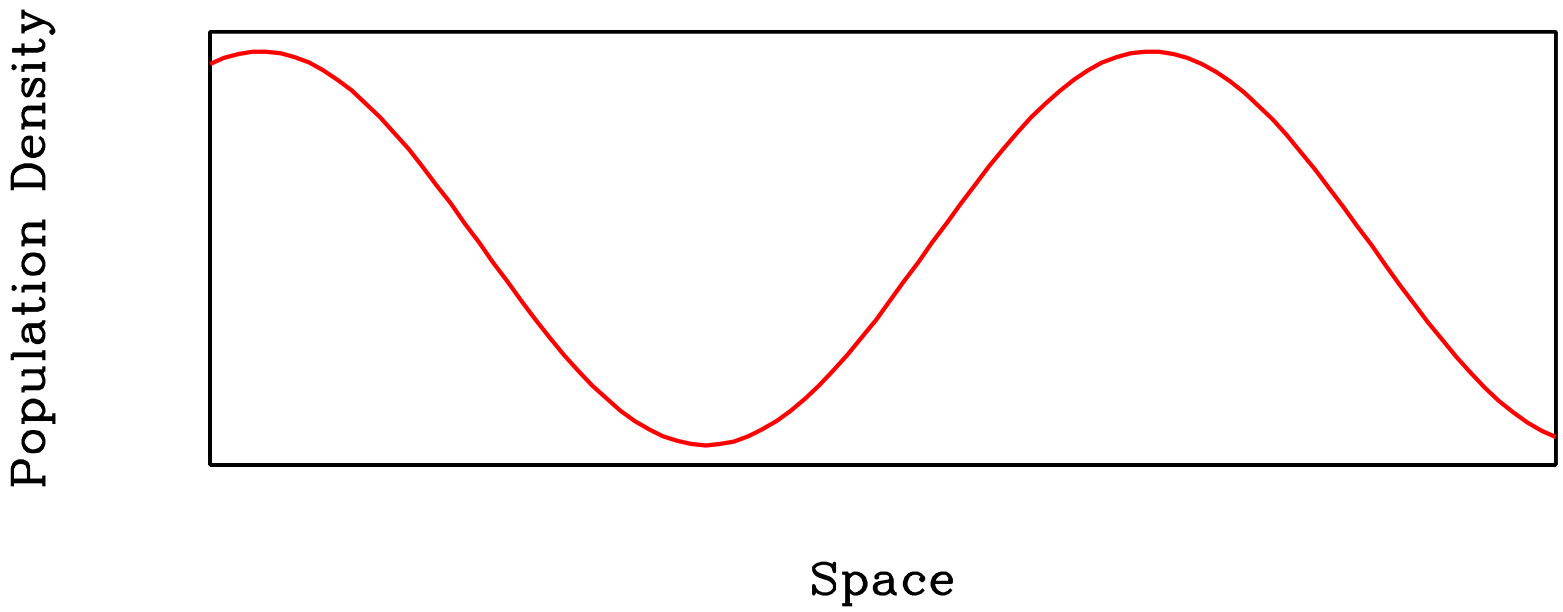

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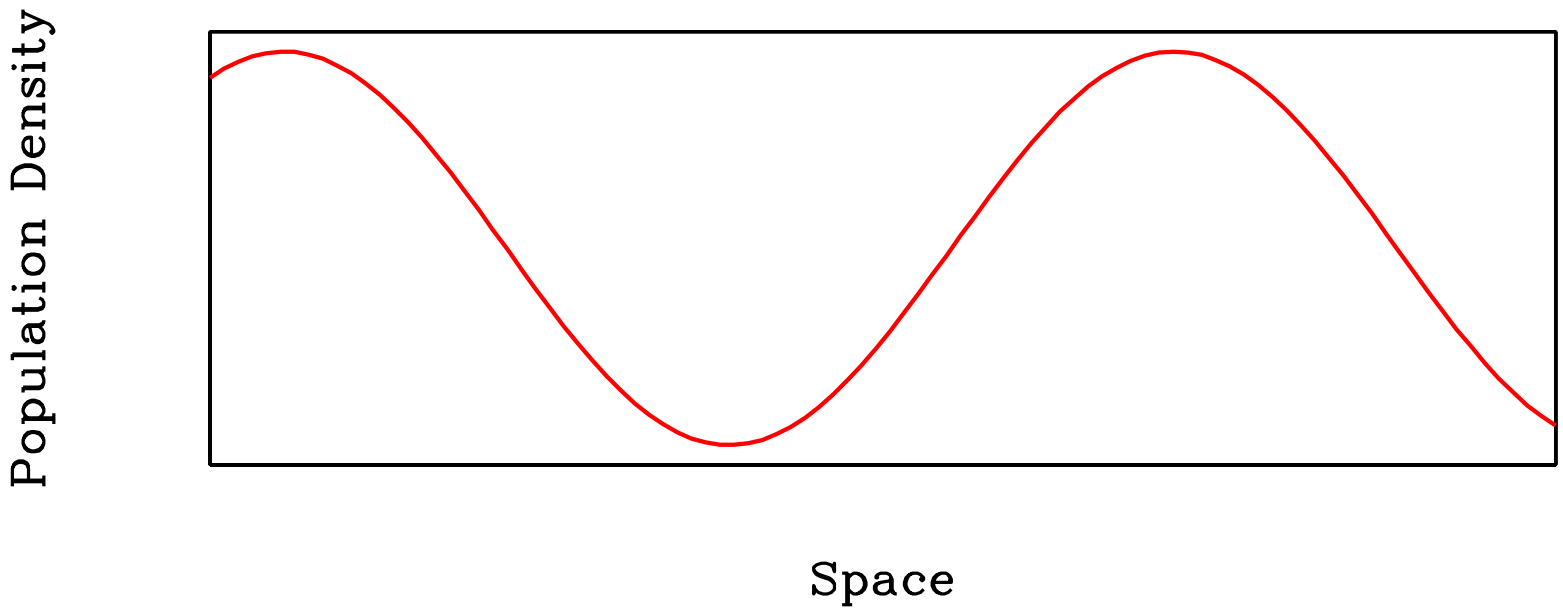

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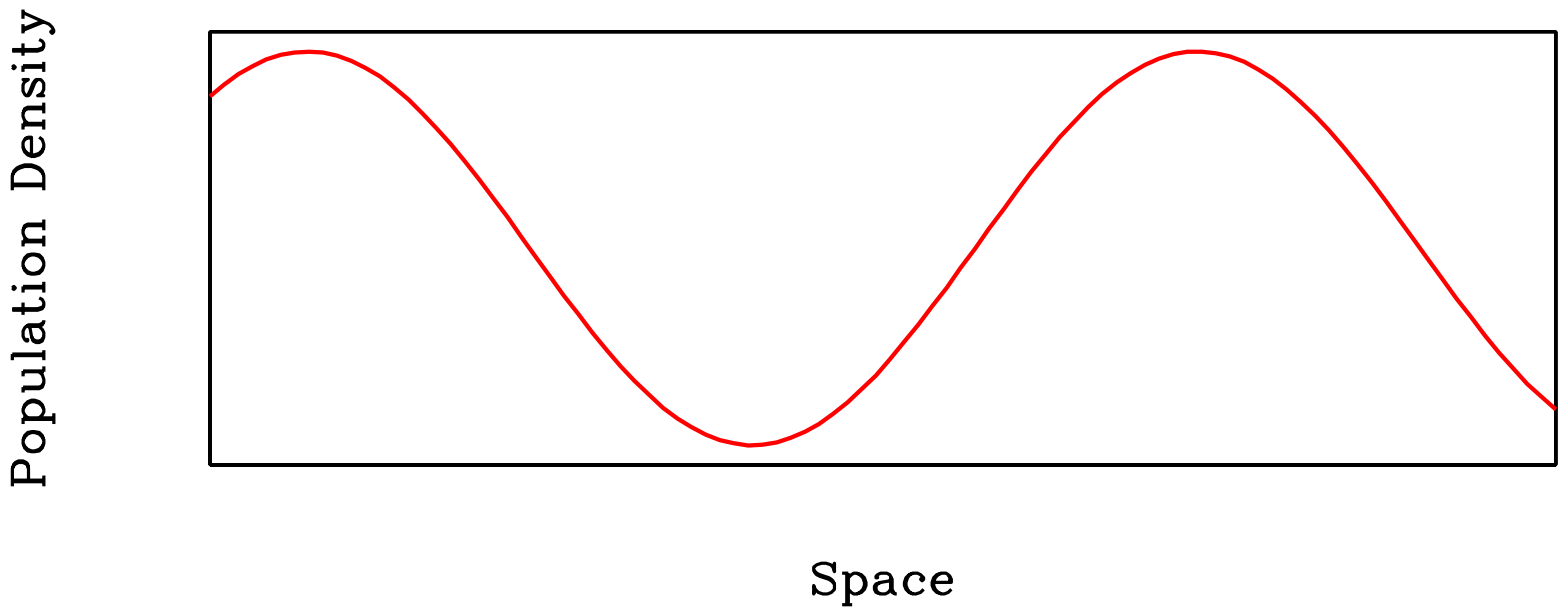

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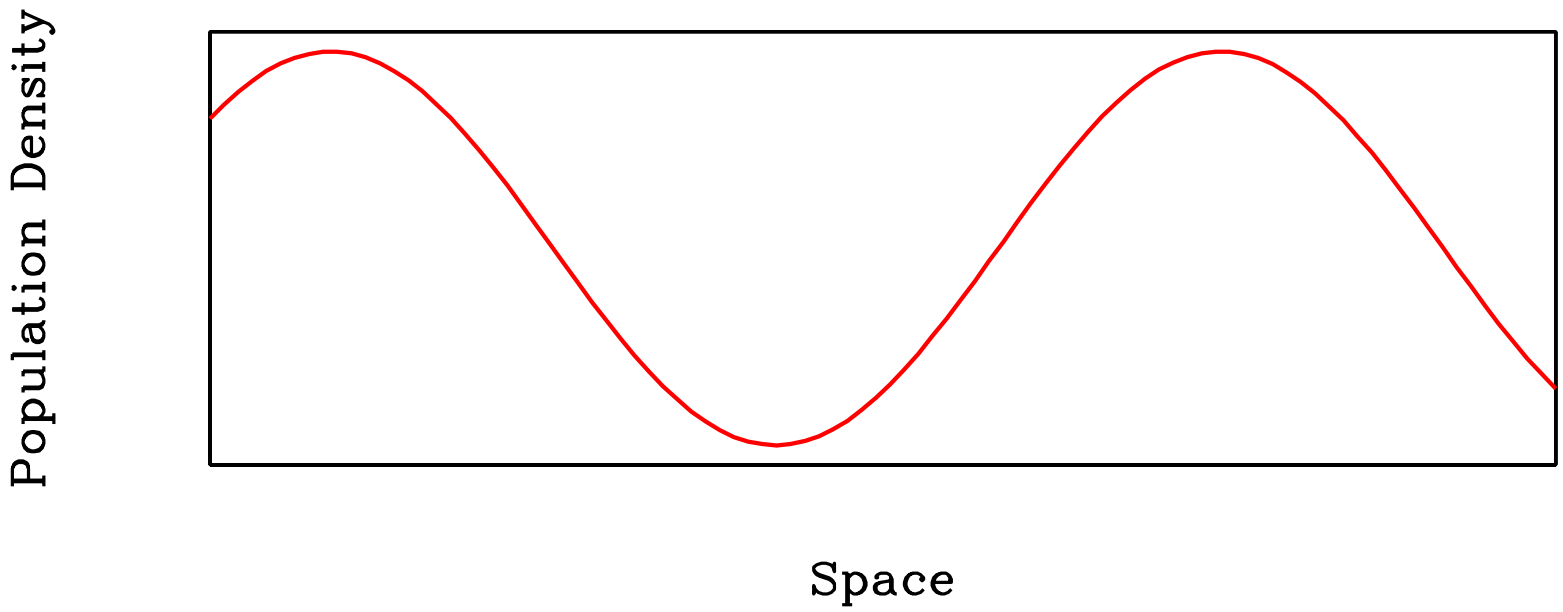

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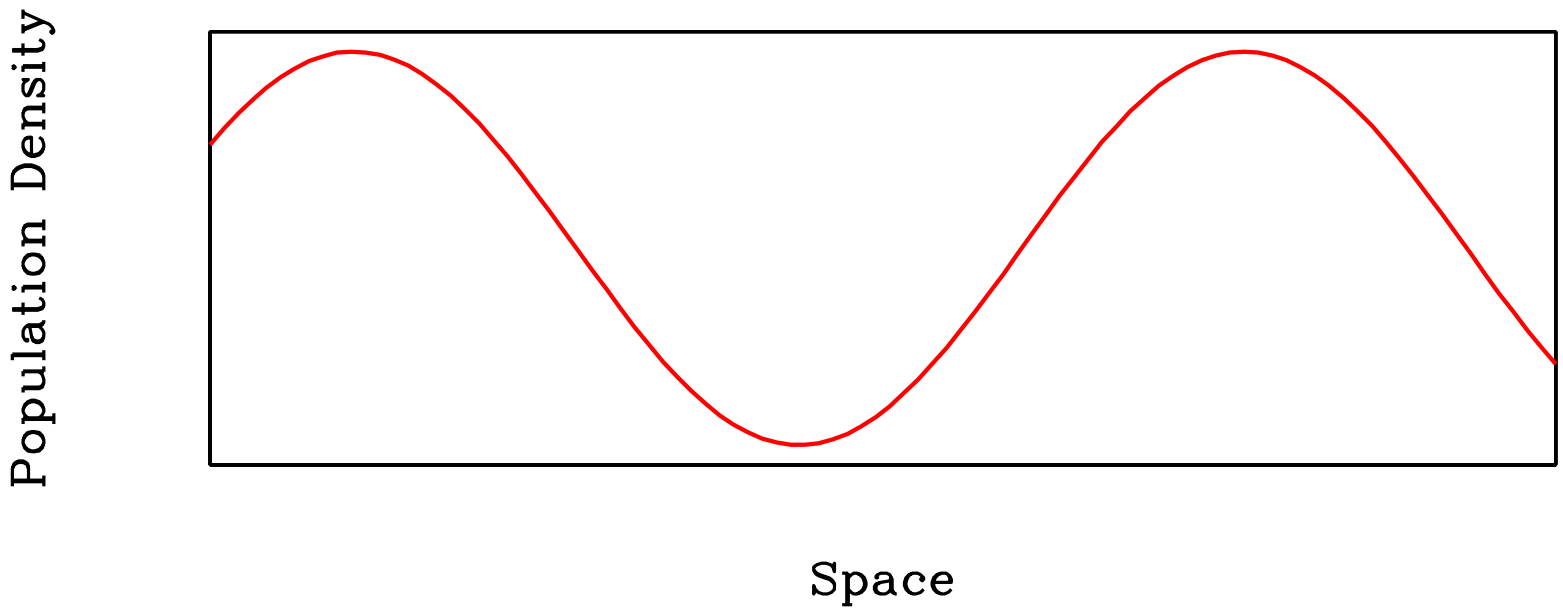

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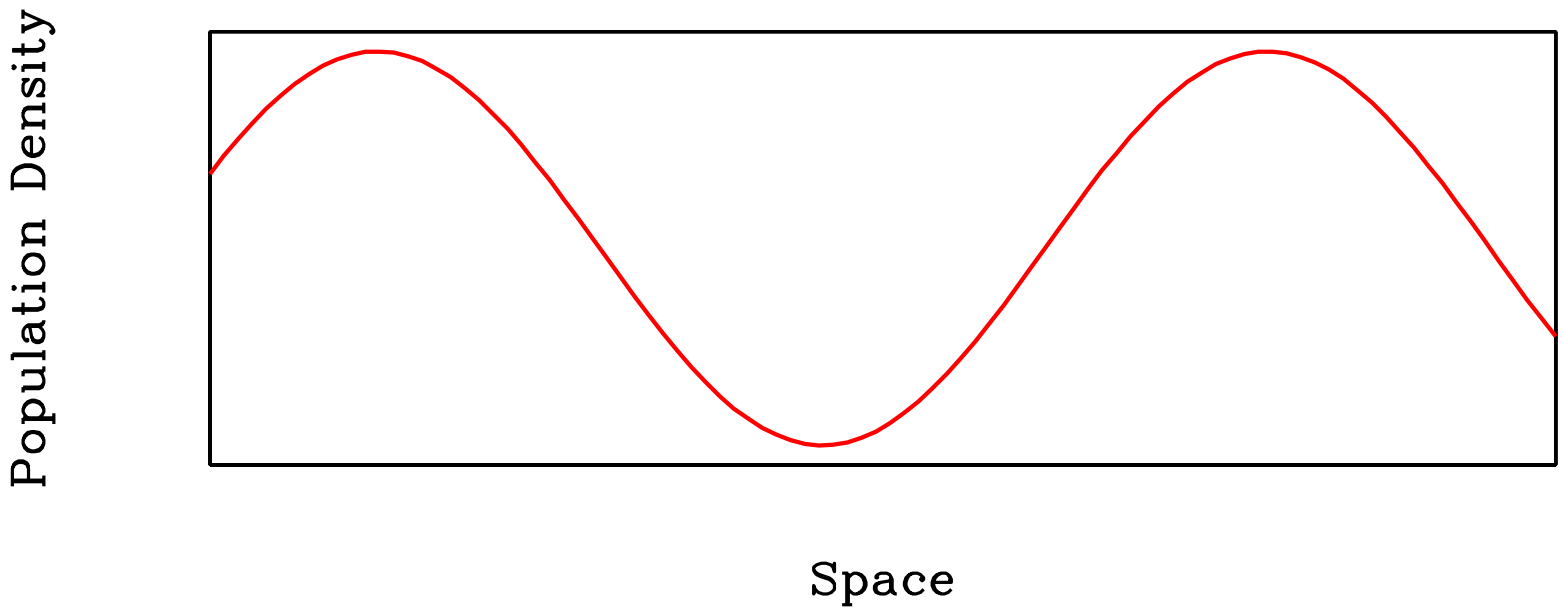

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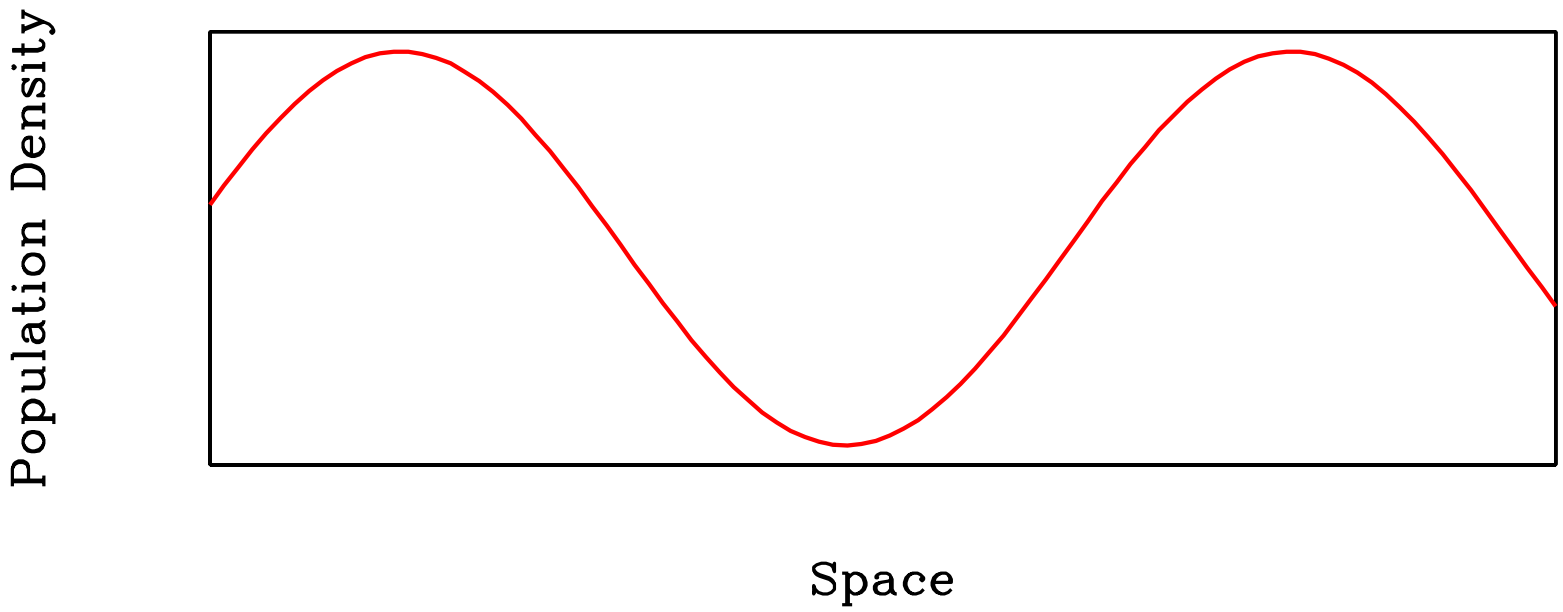

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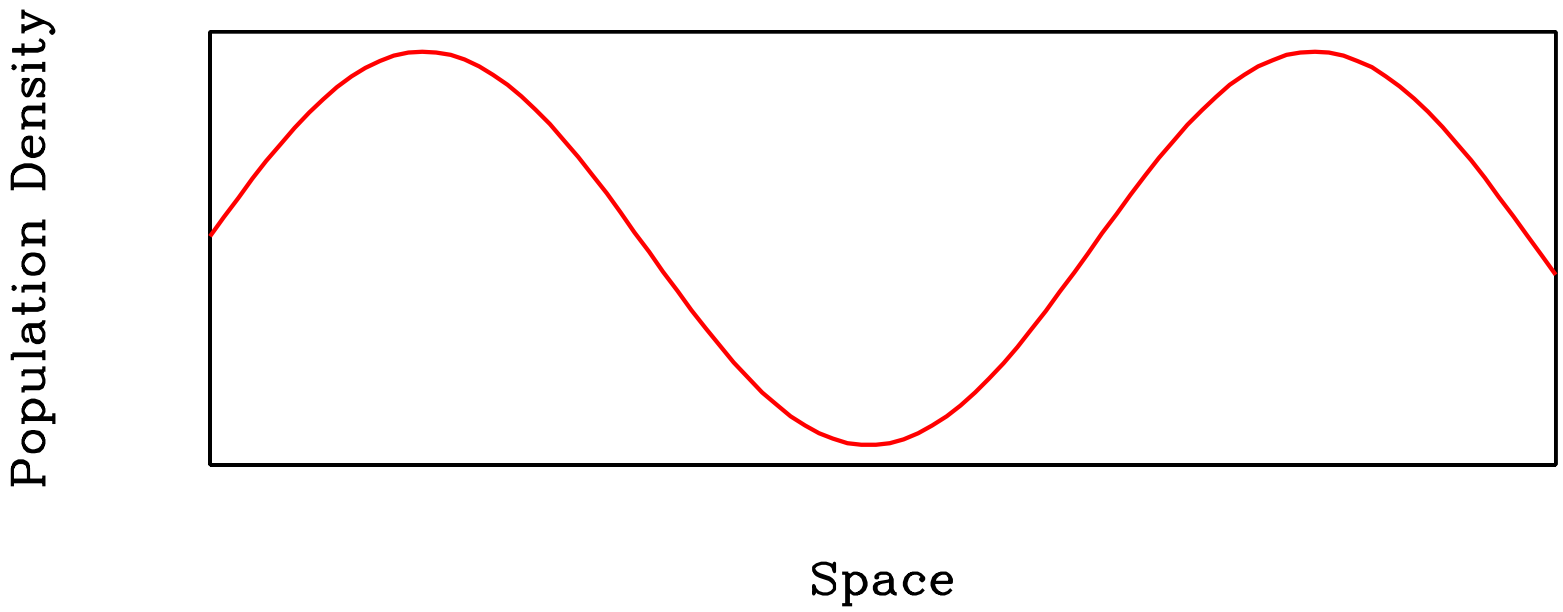

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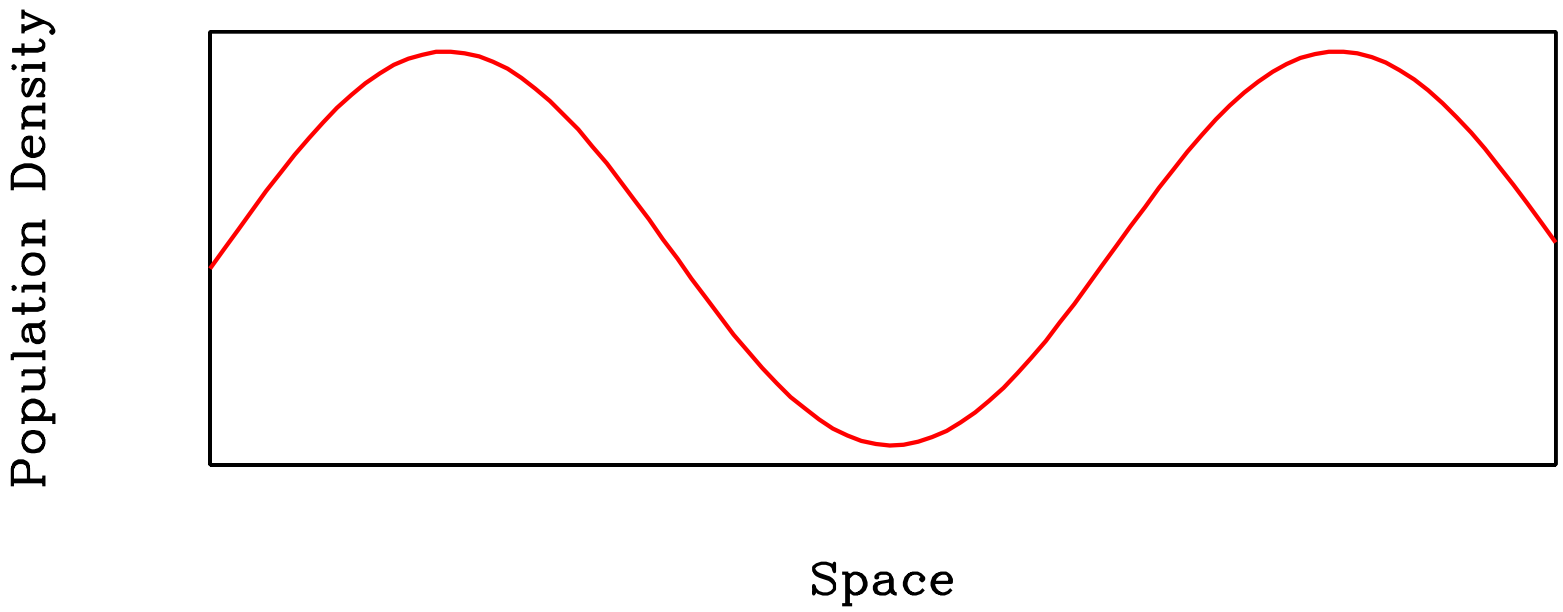

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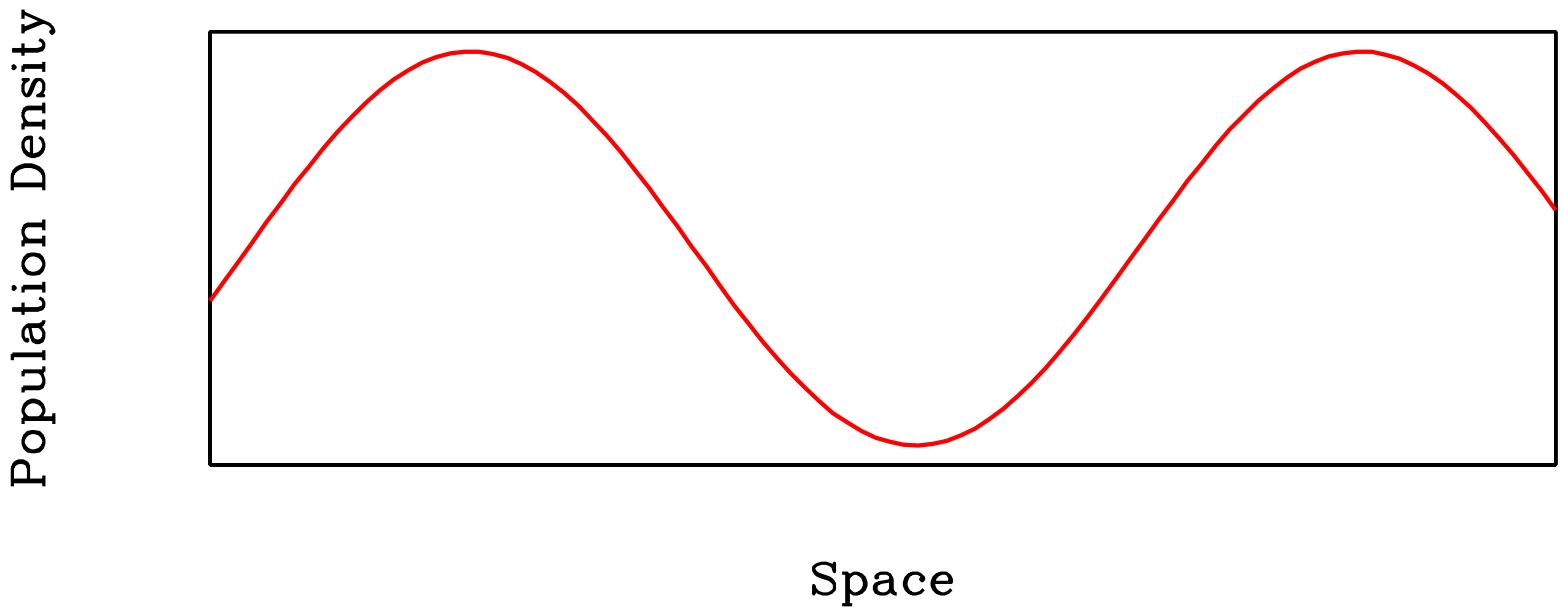

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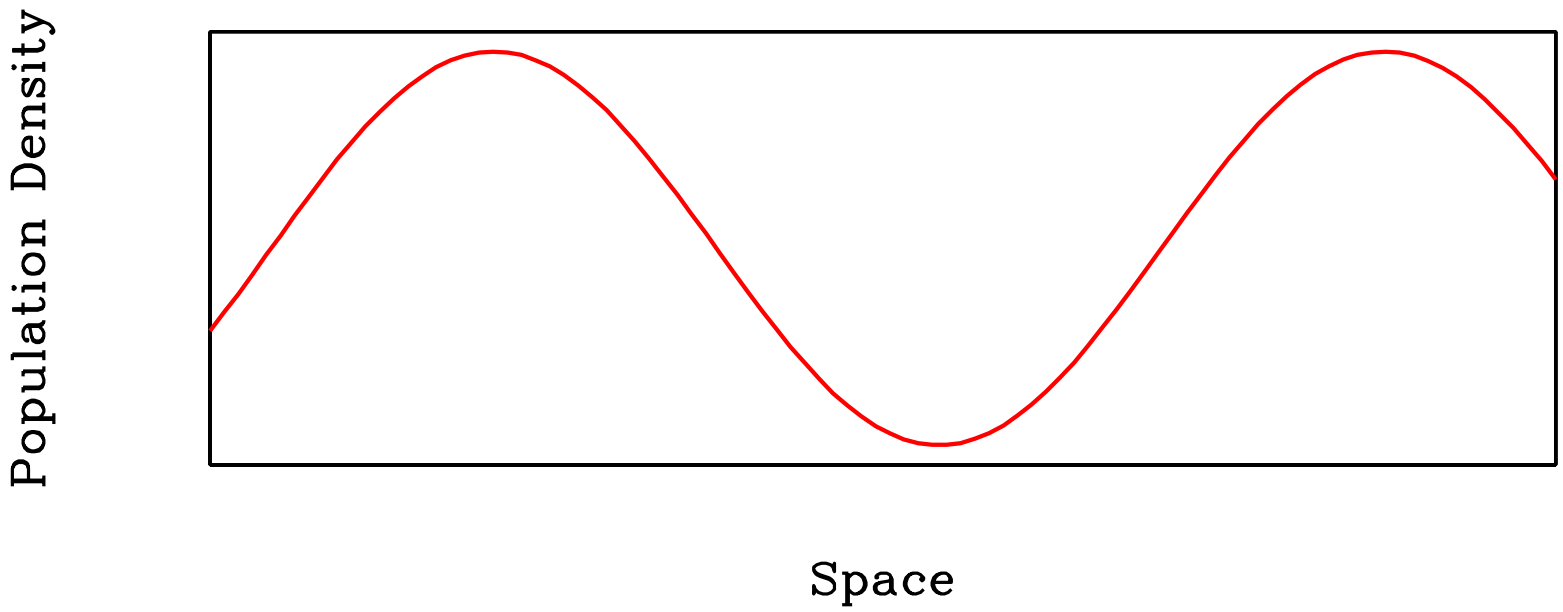


What is a Periodic Travelling Wave?

Everyday example: Mexican wave

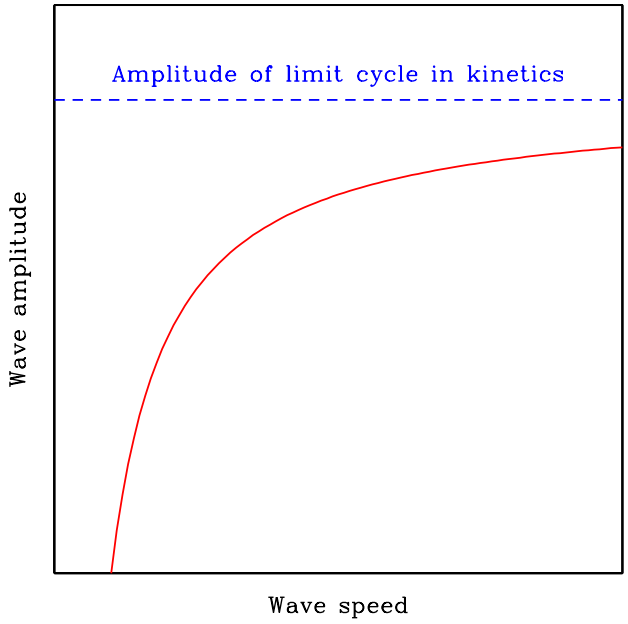
There is an extensive literature on periodic travelling waves in oscillatory reaction-diffusion equations

$$\begin{aligned} \partial u/\partial t &= D_u\, \partial^2 u/\partial x^2 &+ \quad f(u,v) \\ \partial v/\partial t &= D_v\, \partial^2 v/\partial x^2 &+ \quad \underbrace{g(u,v)}_{\substack{\text{kinetics have} \\ \text{a stable} \\ \text{limit cycle}}} \end{aligned}$$

What is a Periodic Travelling Wave?

Everyday example: Mexican wave

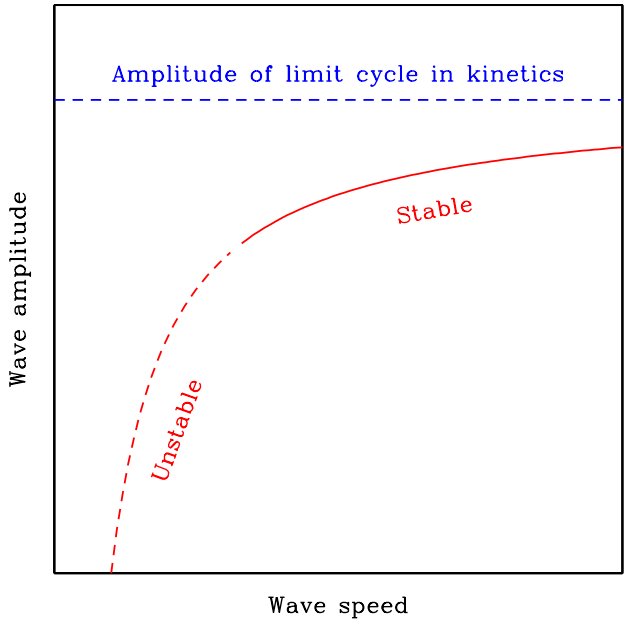
Theorem (Kopell & Howard, 1973):
An oscillatory reaction-diffusion system has a one-parameter family of periodic travelling wave solutions if the diffusion coefficients are sufficiently close to one another.



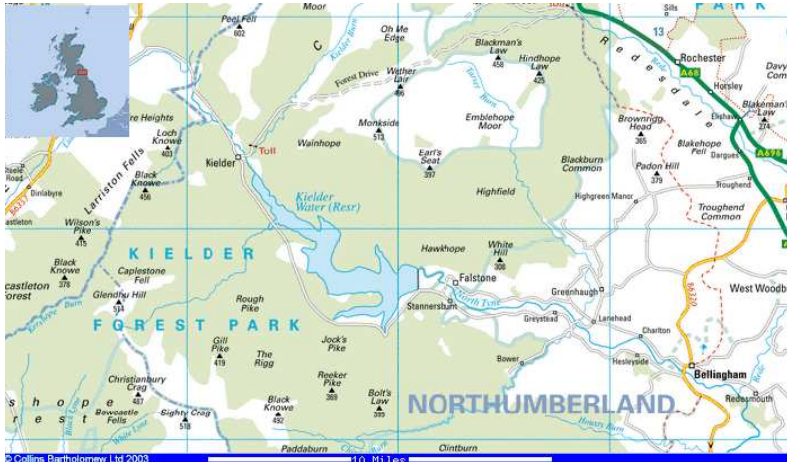
What is a Periodic Travelling Wave?

Everyday example: Mexican wave

Some members of the periodic travelling wave family are stable as solutions of the partial differential equations, while others are unstable.



What Causes the Spatial Component of the Oscillations?



Hypothesis: the periodic travelling waves are caused by the large central reservoir.

Outline

Boundary Conditions in the Field Vole Example

- Voles are an important prey species for owls and kestrels
- The open expanse of Kielder Water will greatly facilitate hunting at its edge

Short eared owl

Common kestrel

Boundary Conditions in the Field Vole Example

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- Therefore we expect very high vole loss at the reservoir edge, implying a Robin boundary condition

$$\frac{\partial}{\partial n}\left(\begin{array}{c}\text{vole}\\ \text{density}\end{array}\right) = -\left(\begin{array}{c}\text{large}\\ \text{constant}\end{array}\right)\cdot\left(\begin{array}{c}\text{vole}\\ \text{density}\end{array}\right)$$

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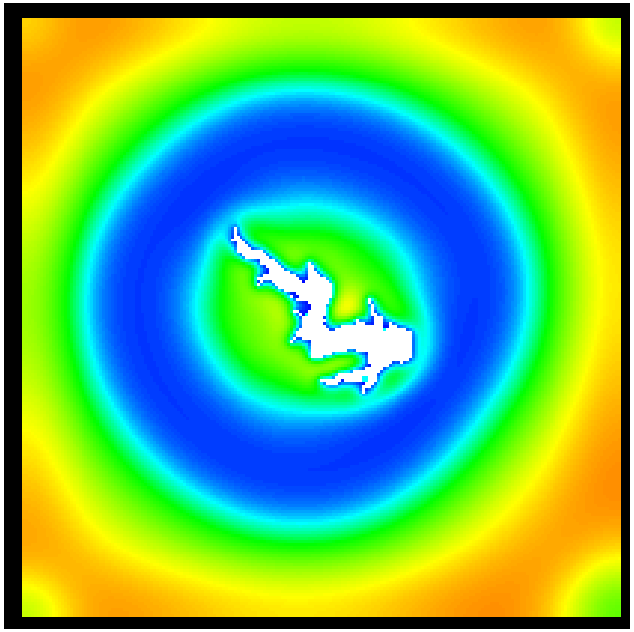
- To a good approx, vole density $= 0$ at the reservoir edge
- At the edge of the forest, a zero flux boundary condition is a natural assumption

Typical Model Solution



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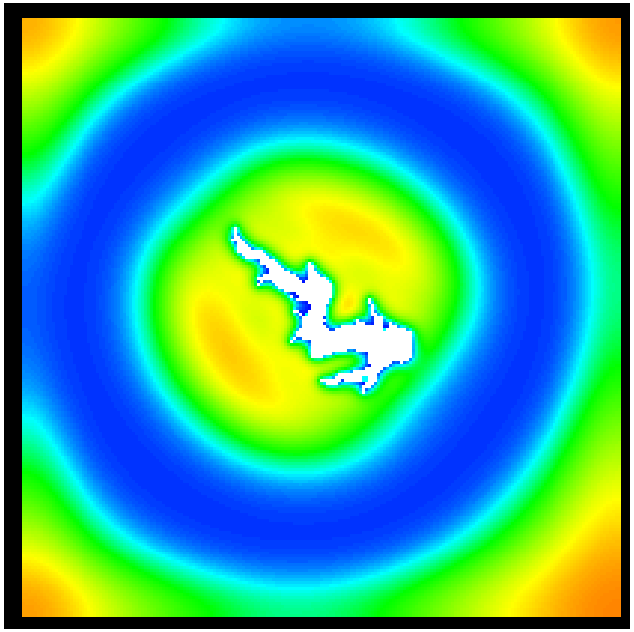

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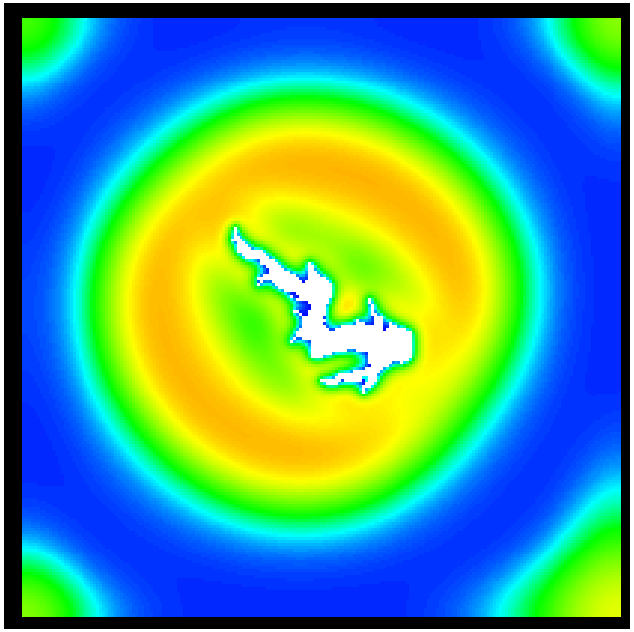

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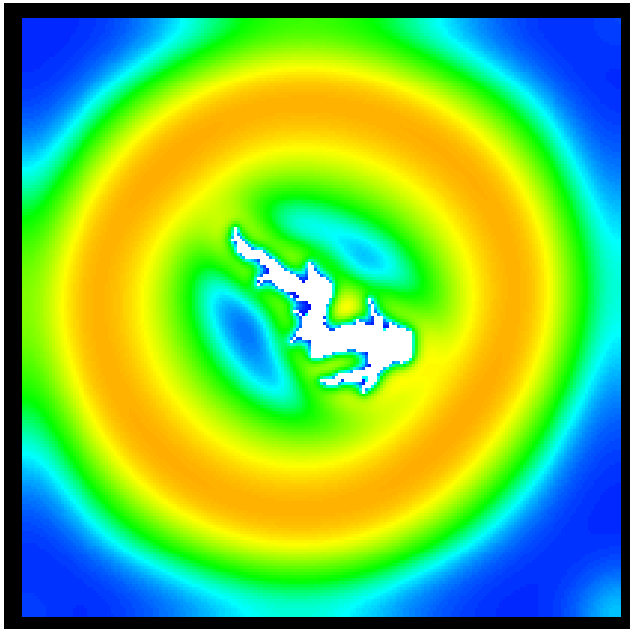

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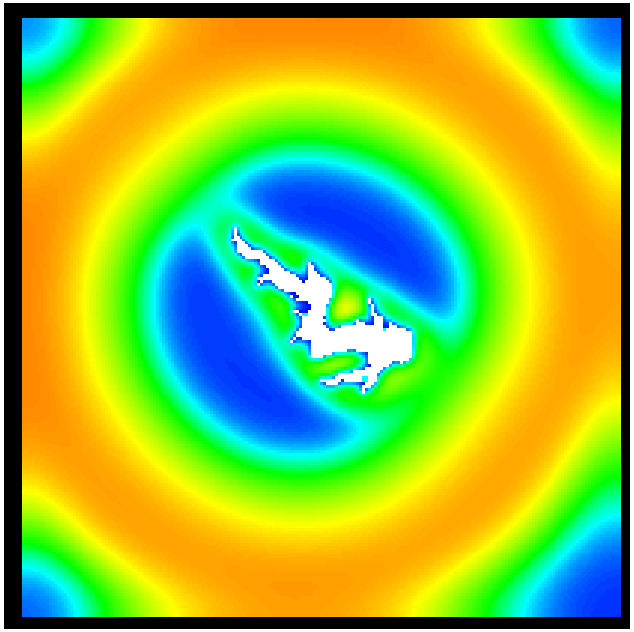

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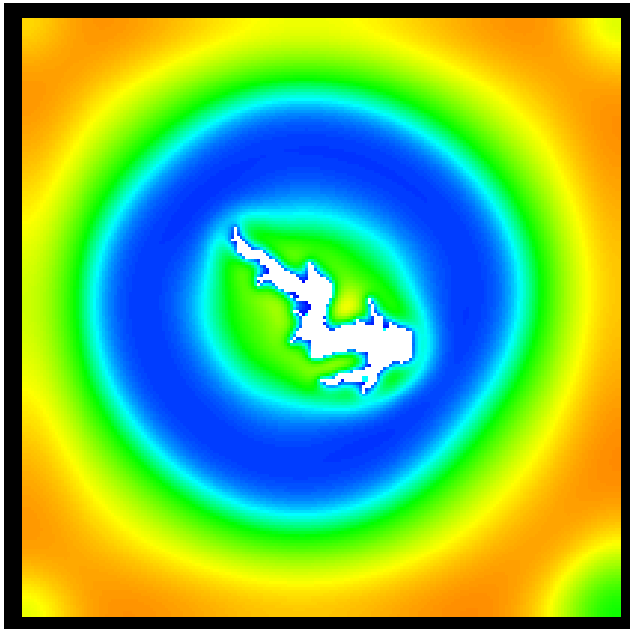
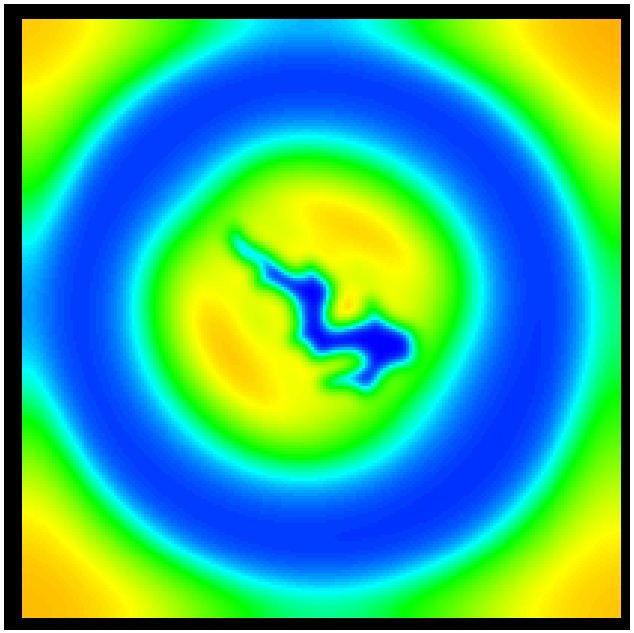


Movie of Typical Model Solution

Click here to
play the movie

Removing the Reservoir

The periodic waves are driven by the reservoir. This is most easily demonstrated by simulating removal of the reservoir.



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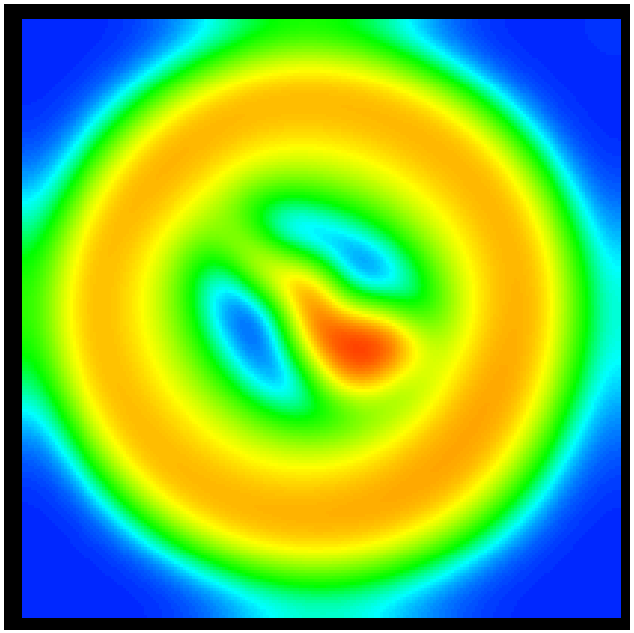

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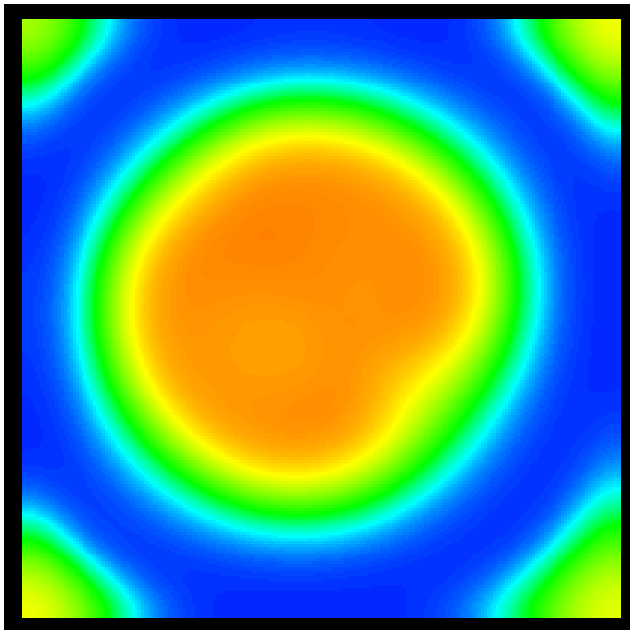

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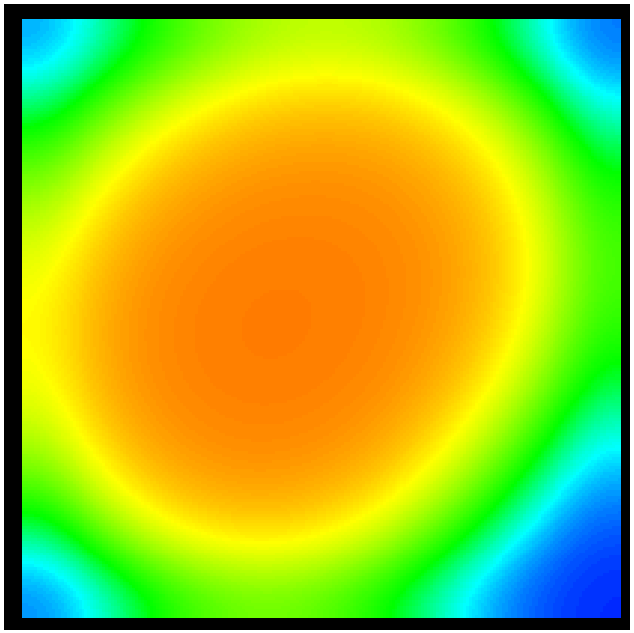

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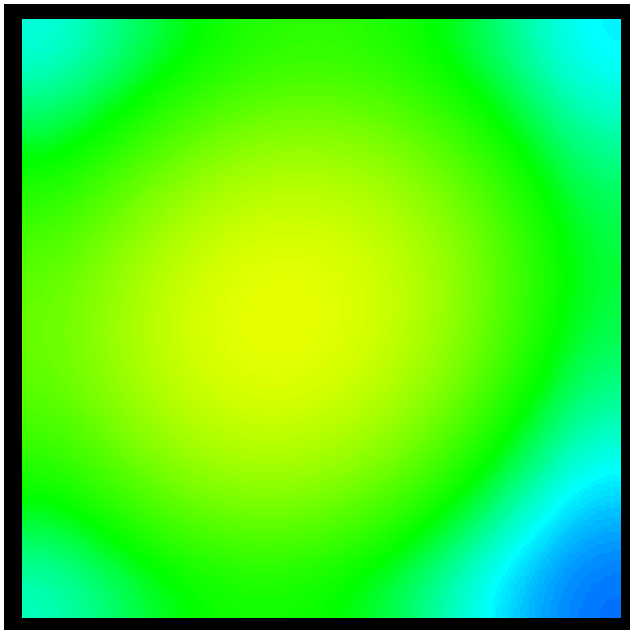
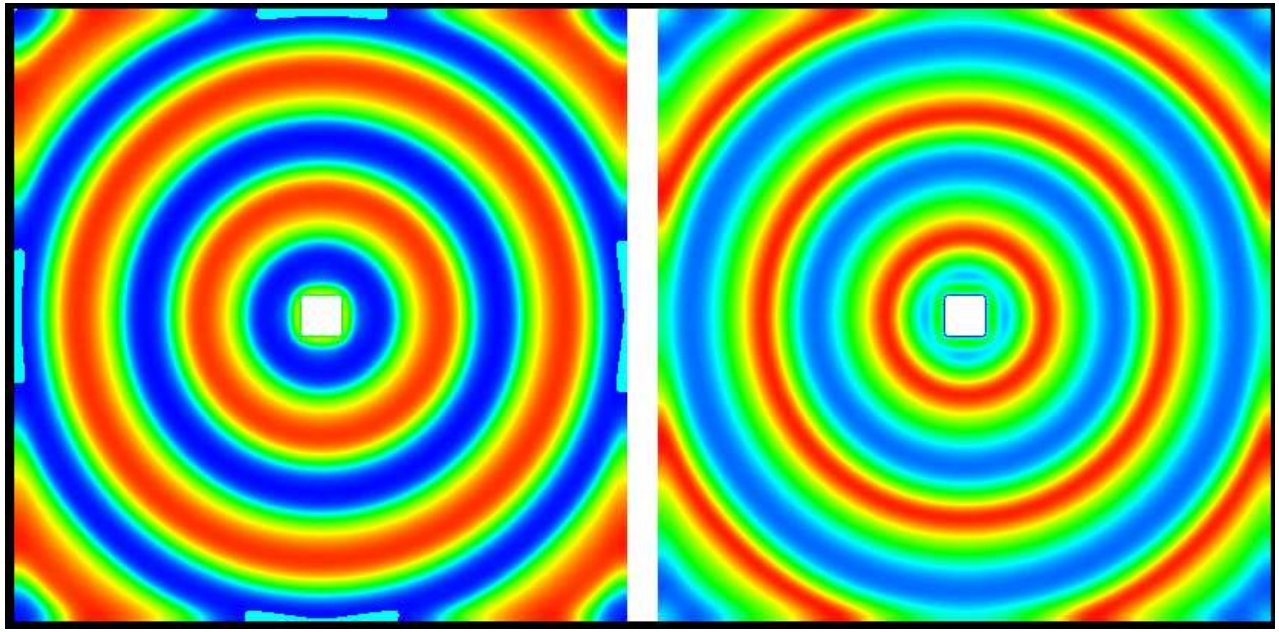


Removing the Reservoir

The periodic waves are driven by the reservoir. This is most easily demonstrated by simulating removal of the reservoir.

Periodic Wave Generation on a Large Domain

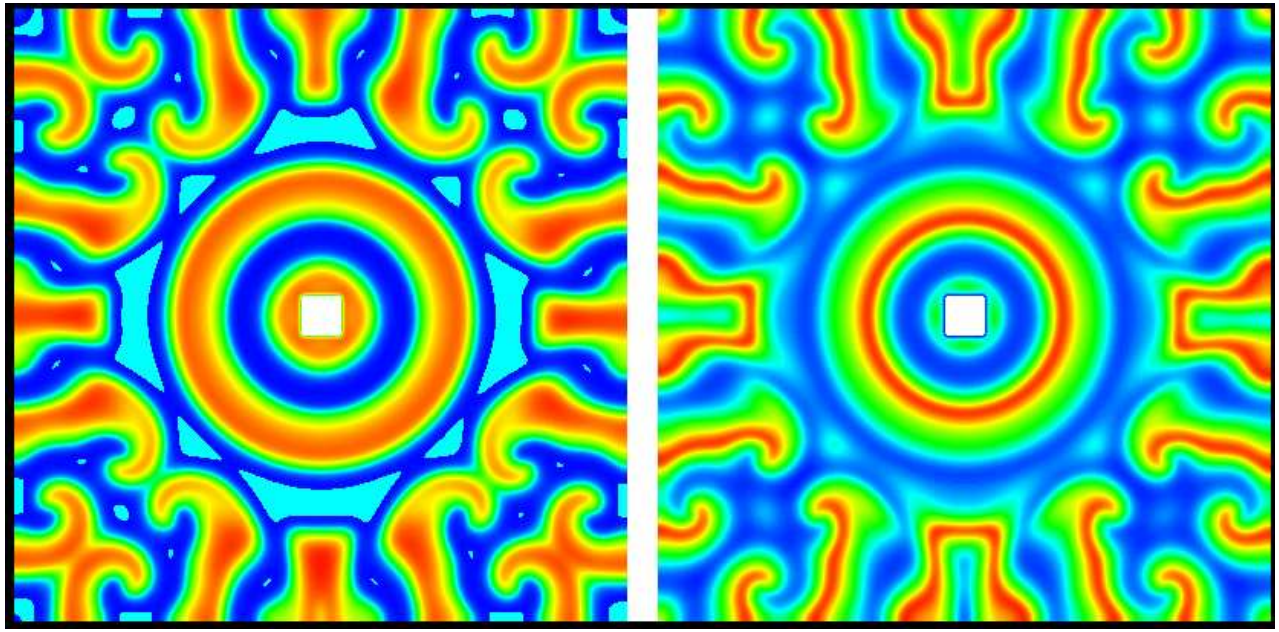


Movie of Wave Generation on a Large Domain

Click here to
play the movie

An Example of Irregular Pattern Generation

For some parameter values, obstacles with Dirichlet boundary conditions generate irregular spatiotemporal patterns.



Movie of Irregular Pattern Generation

Click here to
play the movie

Mathematical Goal

Mathematical goal: predict which parameter sets will give periodic travelling waves, and which will give spatiotemporal irregularity.

Outline

One-Dimensional Problem

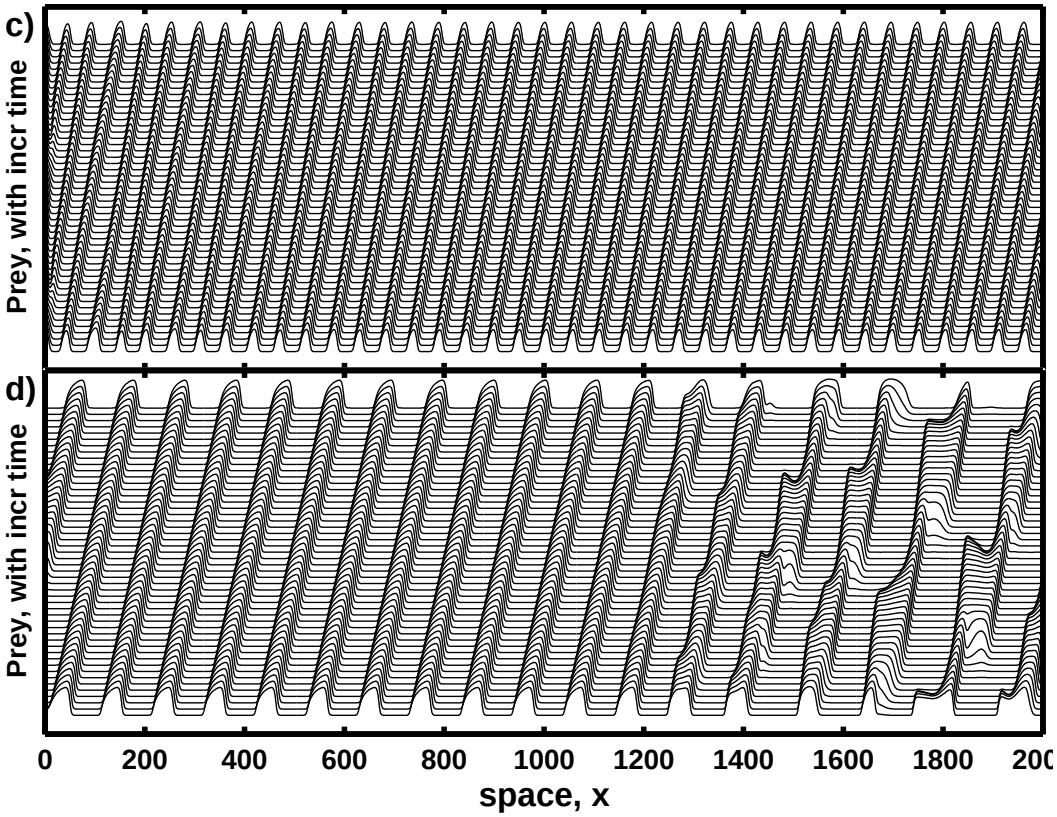
To simplify, solve on $0 < x < x_{max}$ with

$$\begin{aligned} h = p = 0 \quad &\text{at} \quad x = 0 \qquad && \leftrightarrow \text{edge of reservoir} \\ h_x = p_x = 0 \quad &\text{at} \quad x = x_{max} && \leftrightarrow \text{edge of forest.} \end{aligned}$$

In fact the condition at $x = x_{max}$ plays no significant role, and we can consider the equations on $0 < x < \infty$.

Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:



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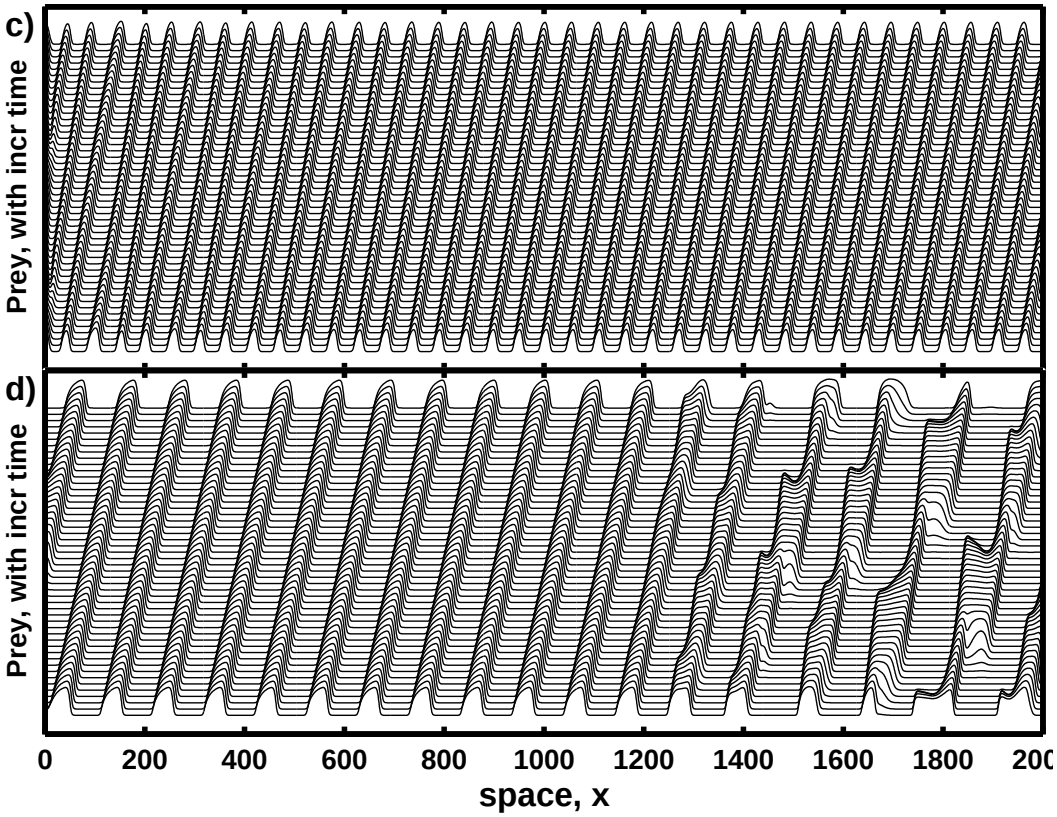
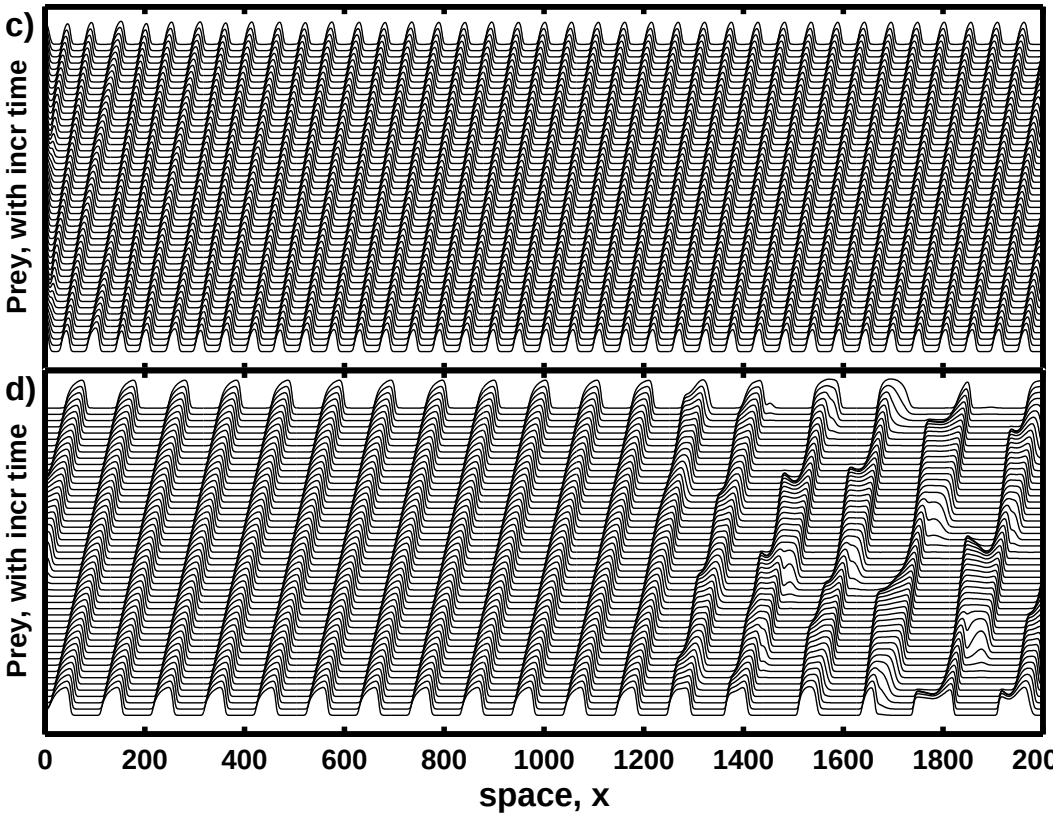


Conclusion: irregular patterns occur when the Dirichlet boundary condition at $x = 0$ generates a periodic travelling wave that is unstable.

Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:



Conclusion: irregular patterns occur when the Dirichlet boundary condition at $x = 0$ generates a periodic travelling wave that is unstable.

Therefore we must investigate wave stability in detail.

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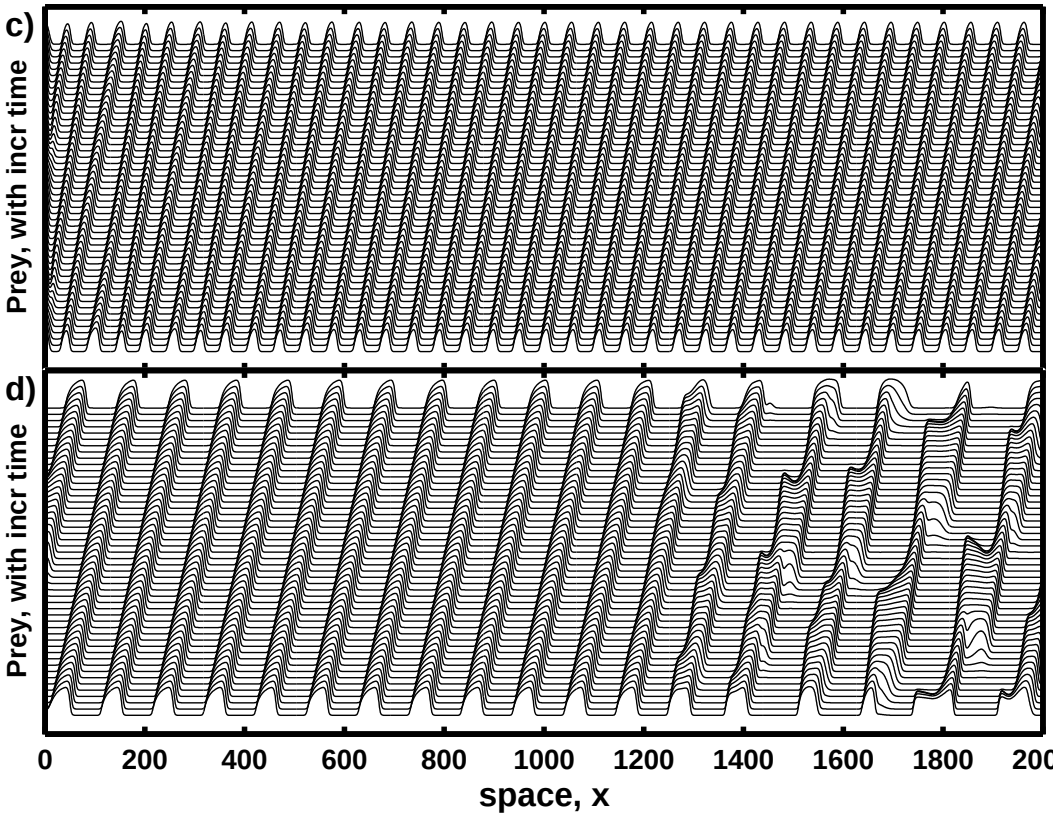

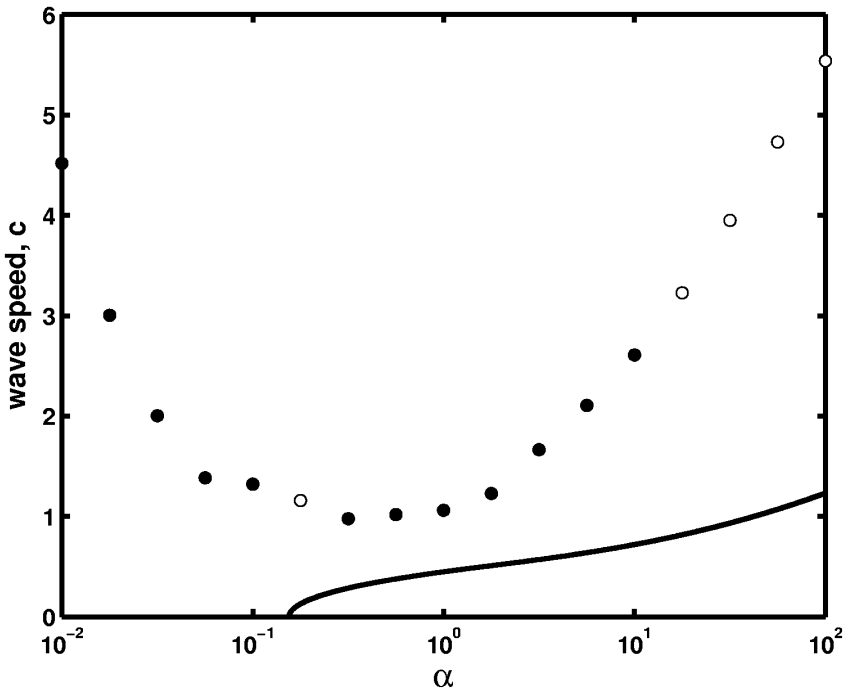

Model Equations in a Moving Frame

Model eqns:
$$\begin{aligned} \partial u/\partial t &= D_u\, \partial^2 u/\partial x^2 + f(u,v) \\ \partial v/\partial t &= D_v\, \partial^2 v/\partial x^2 + g(u,v) \end{aligned}$$

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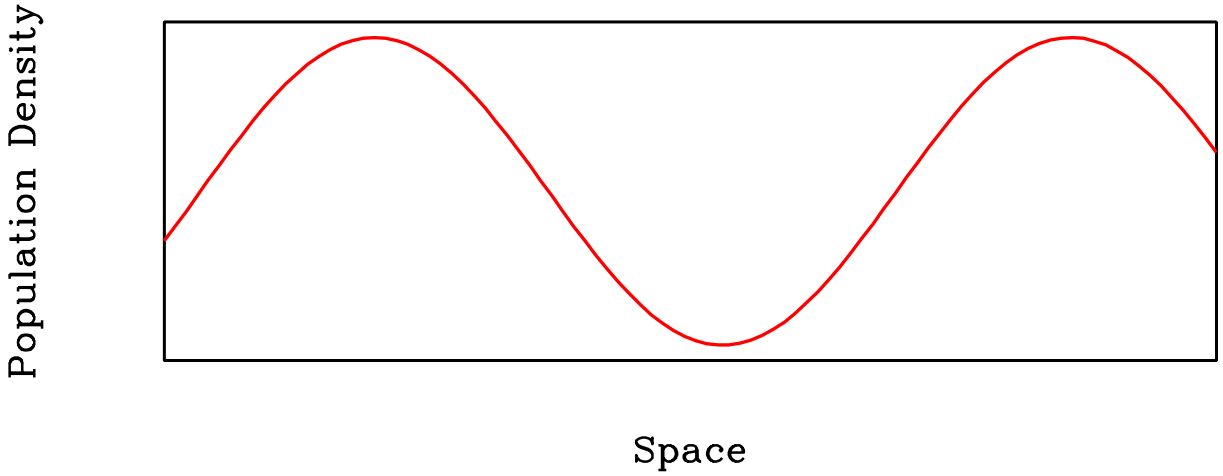

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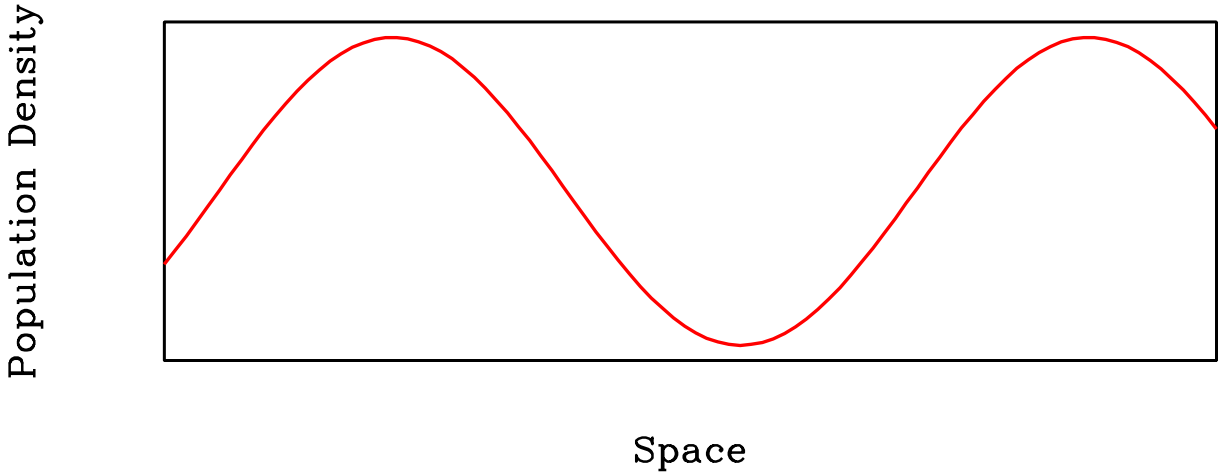

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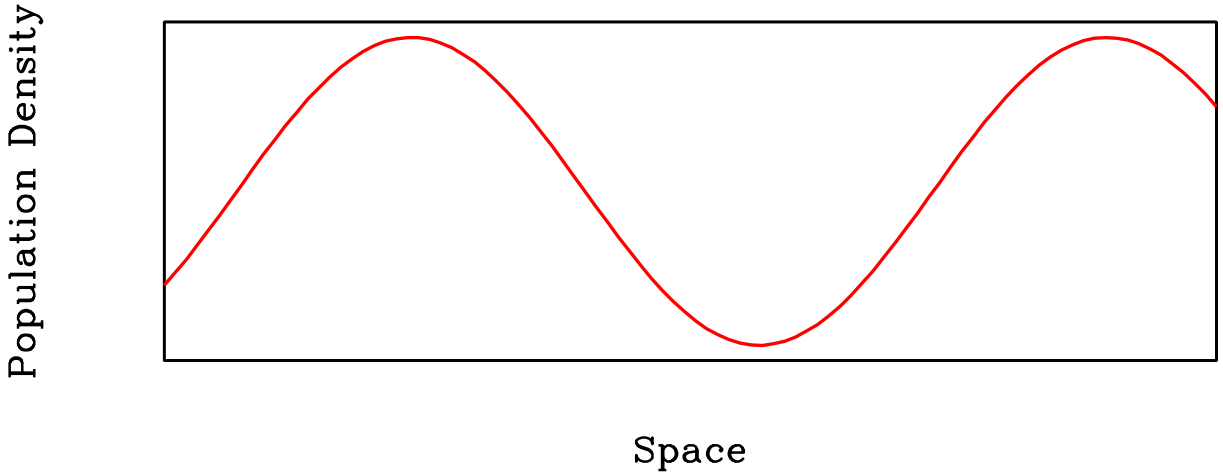

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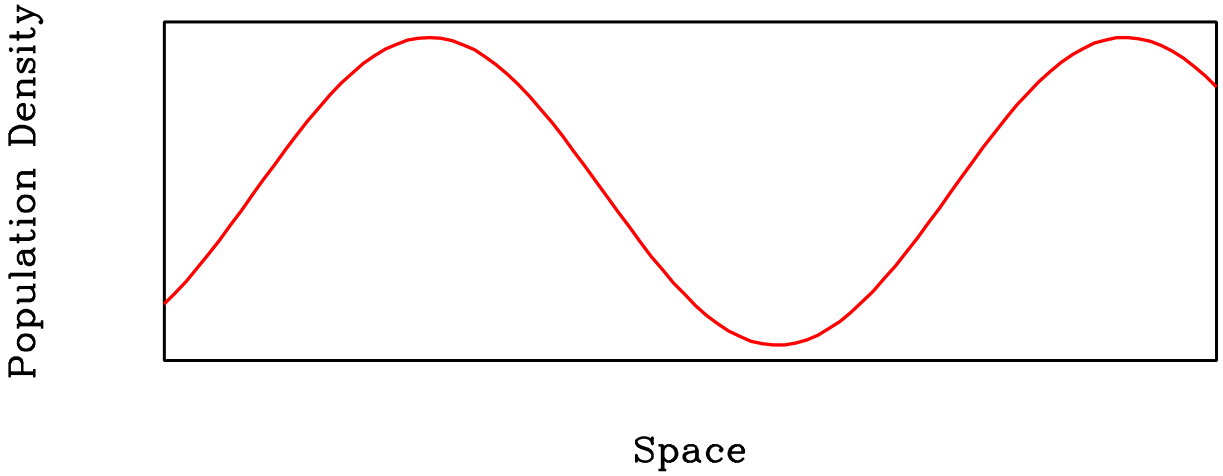

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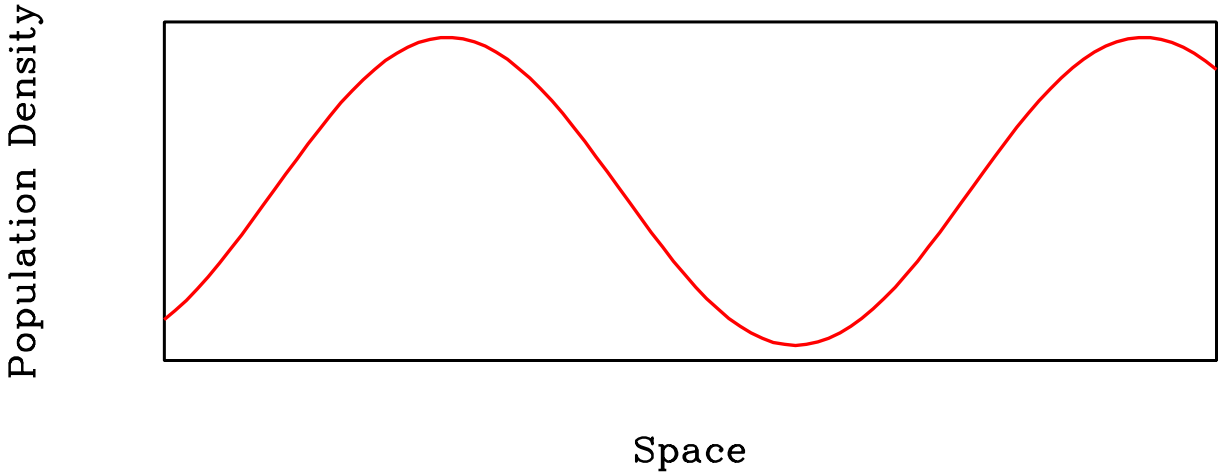

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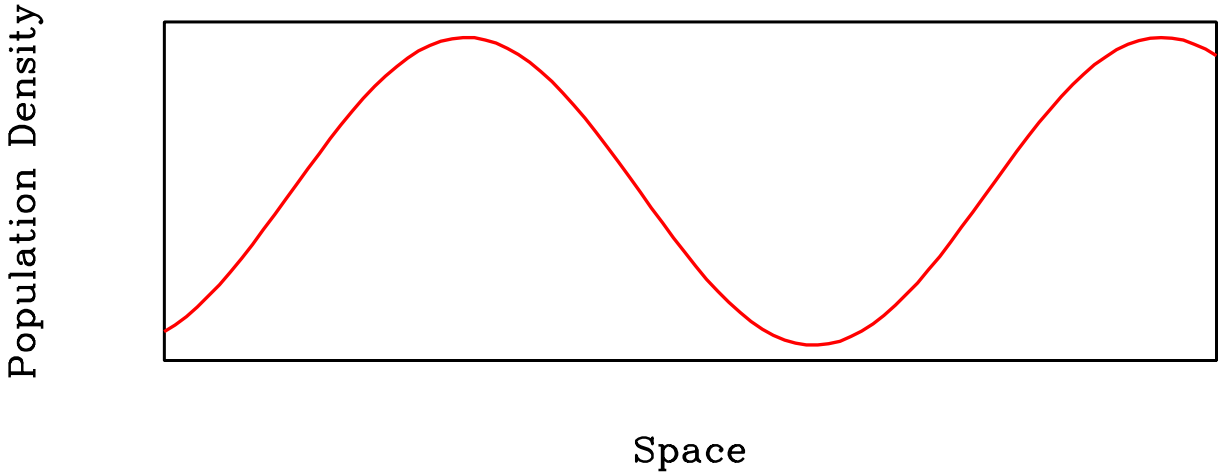

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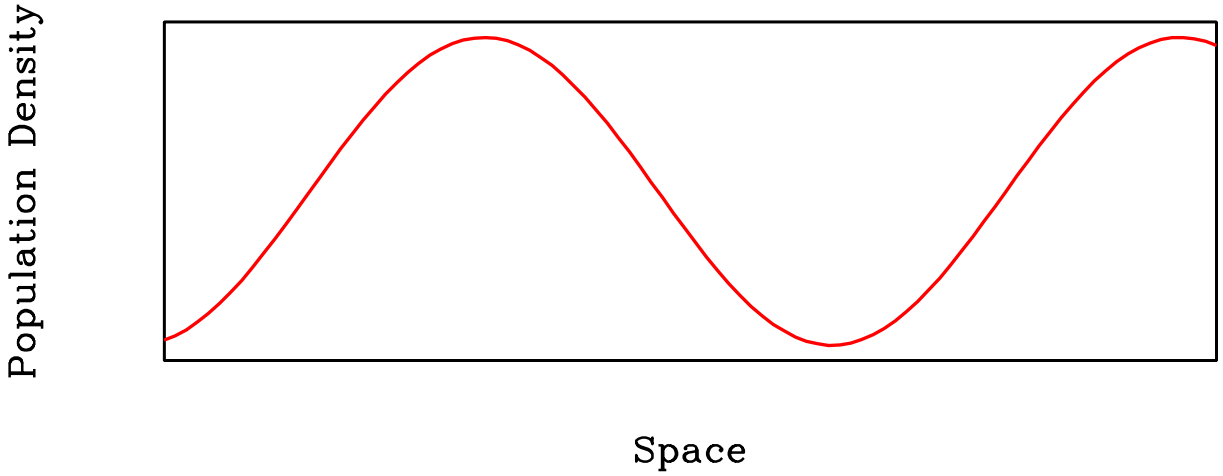

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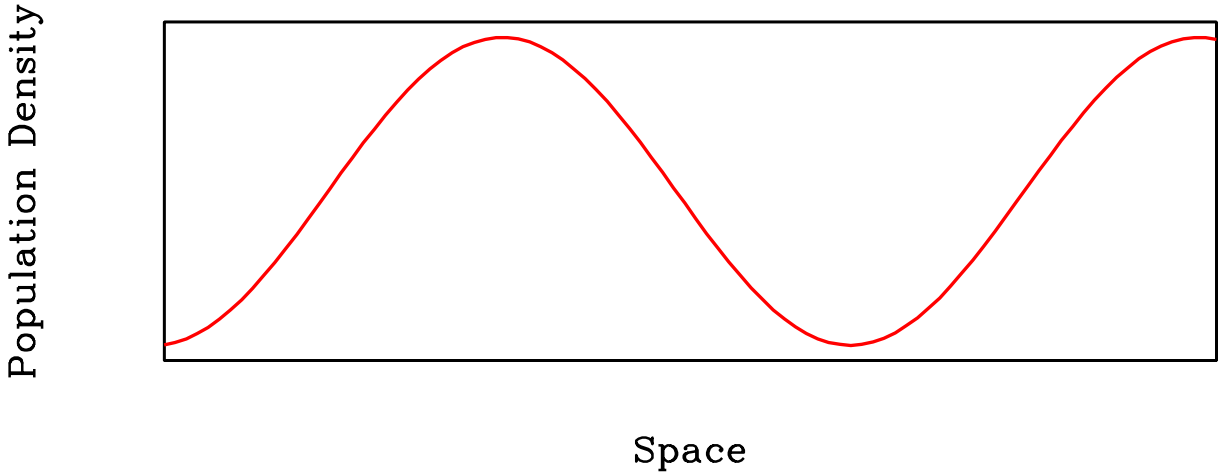

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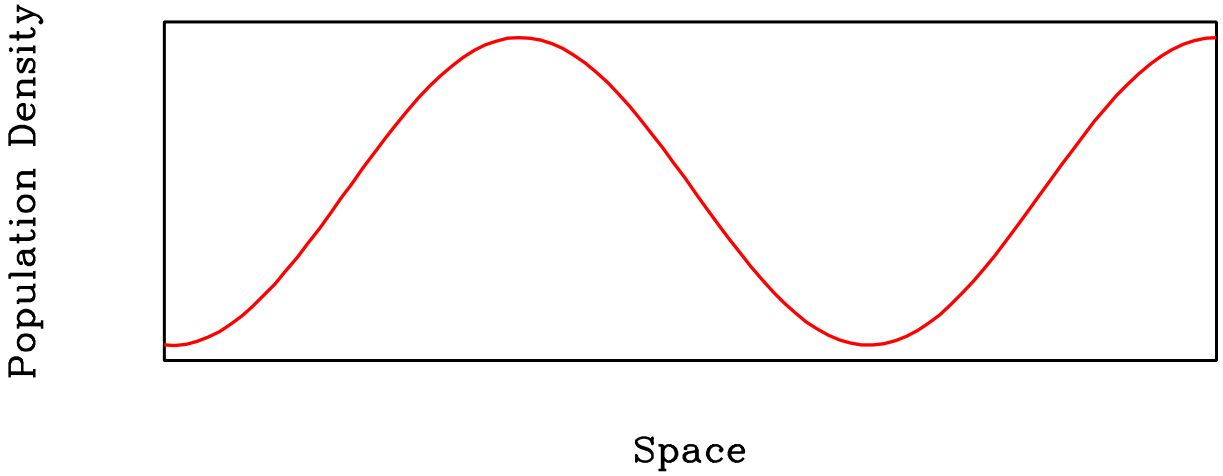

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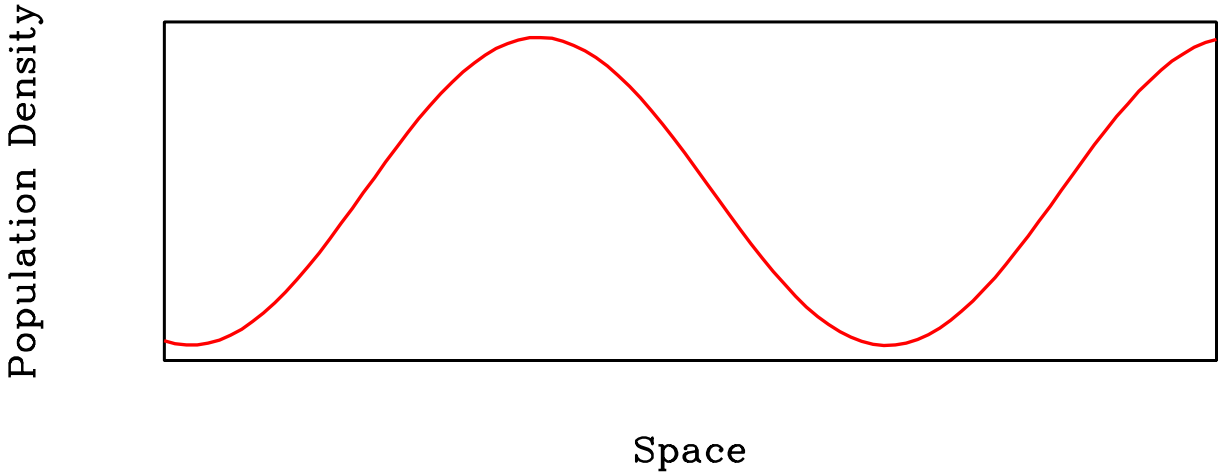

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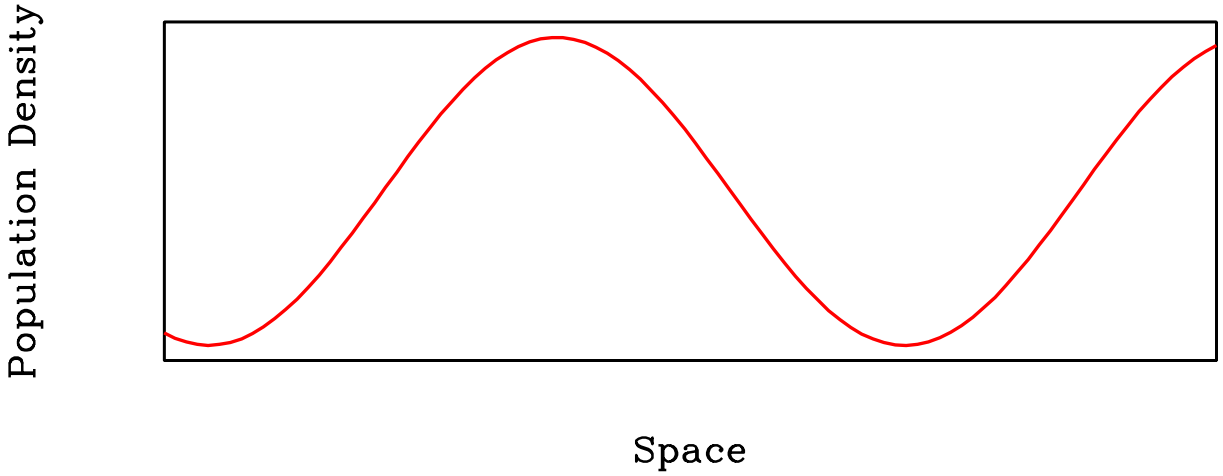

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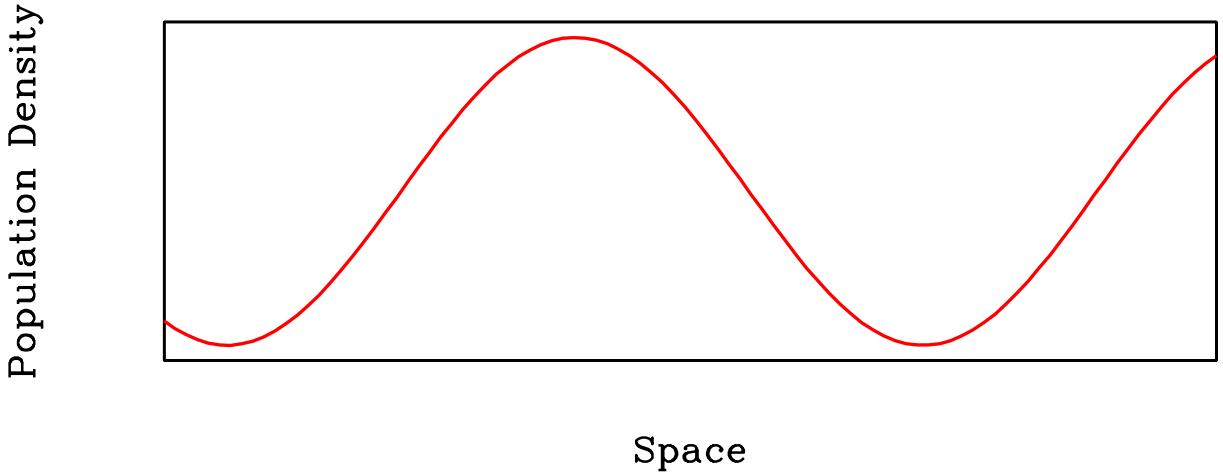

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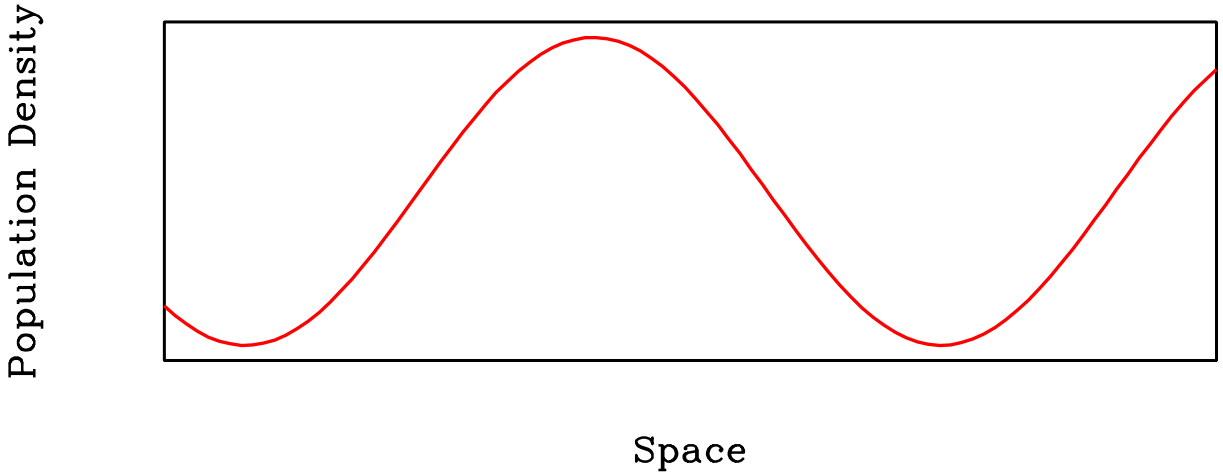

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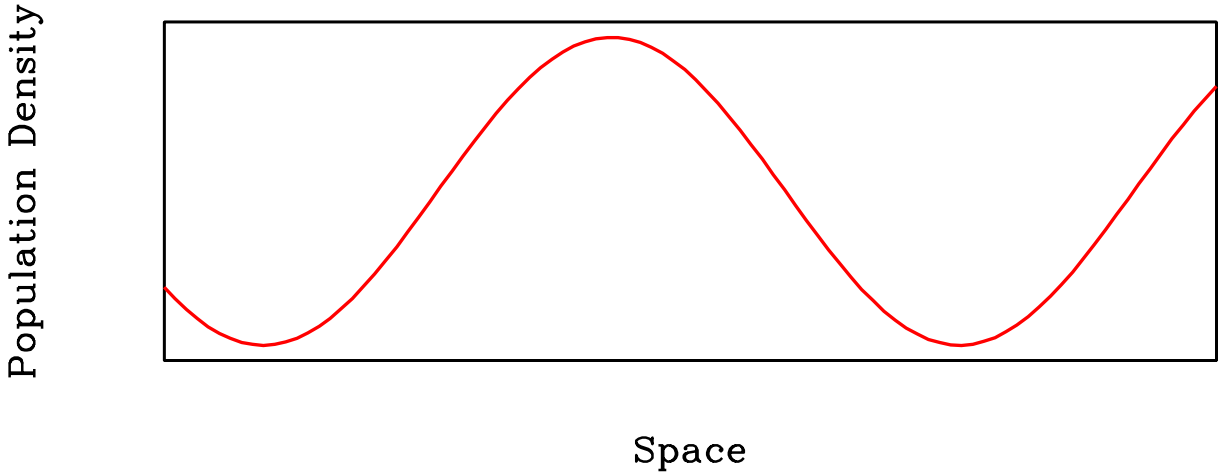

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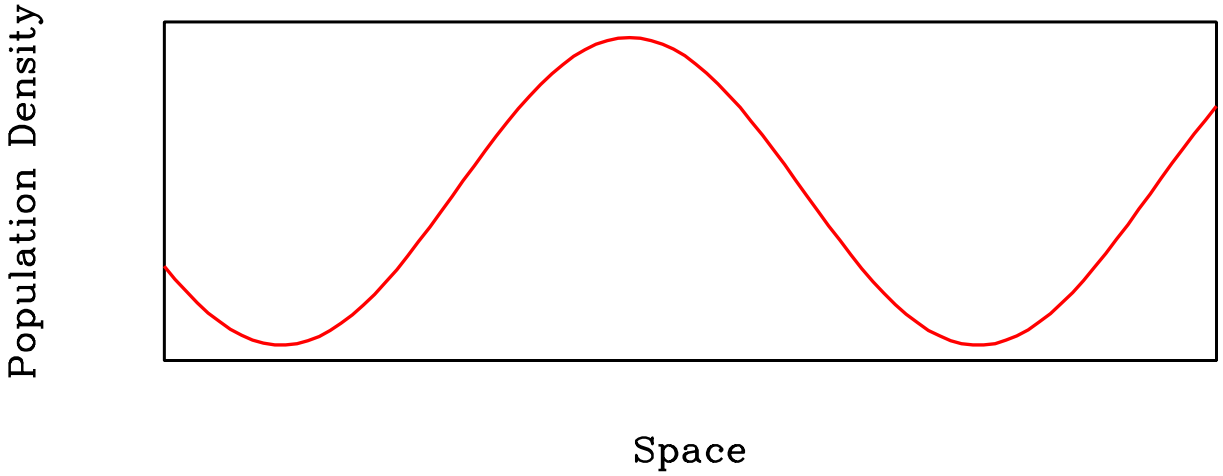

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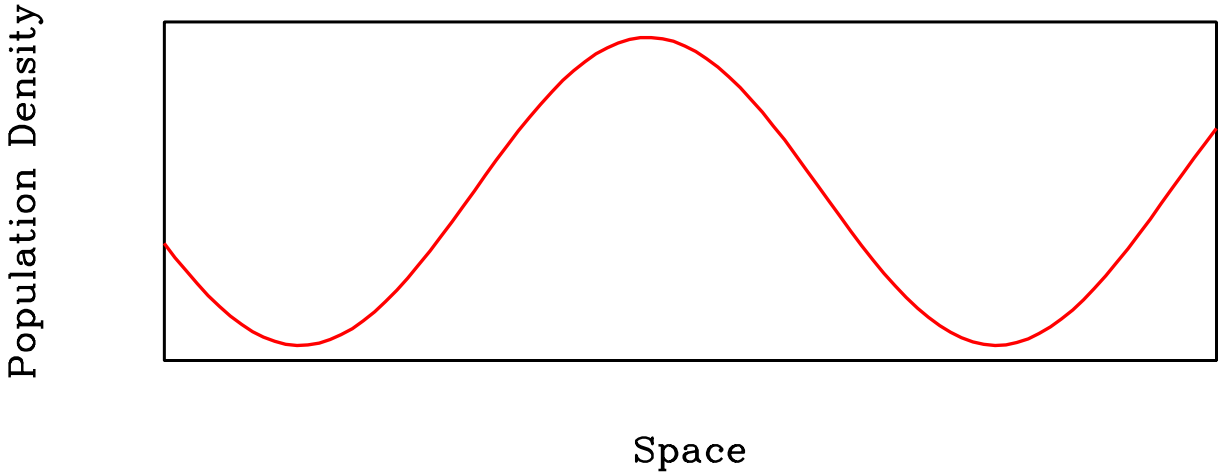

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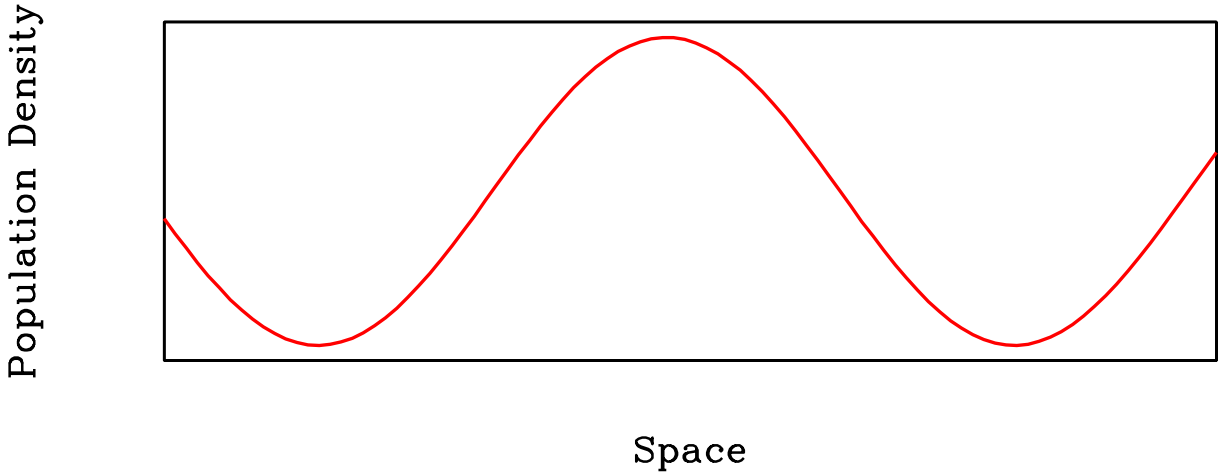

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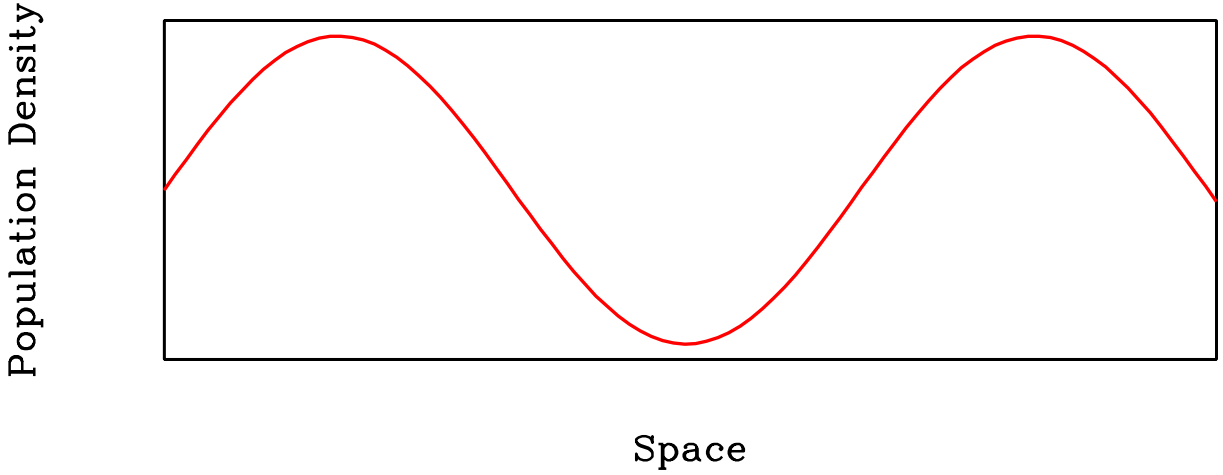

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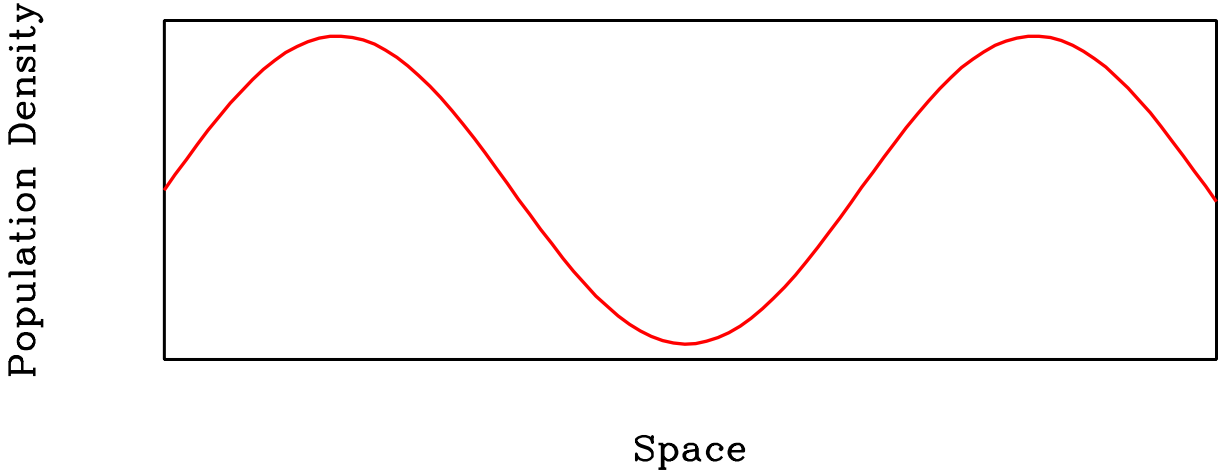

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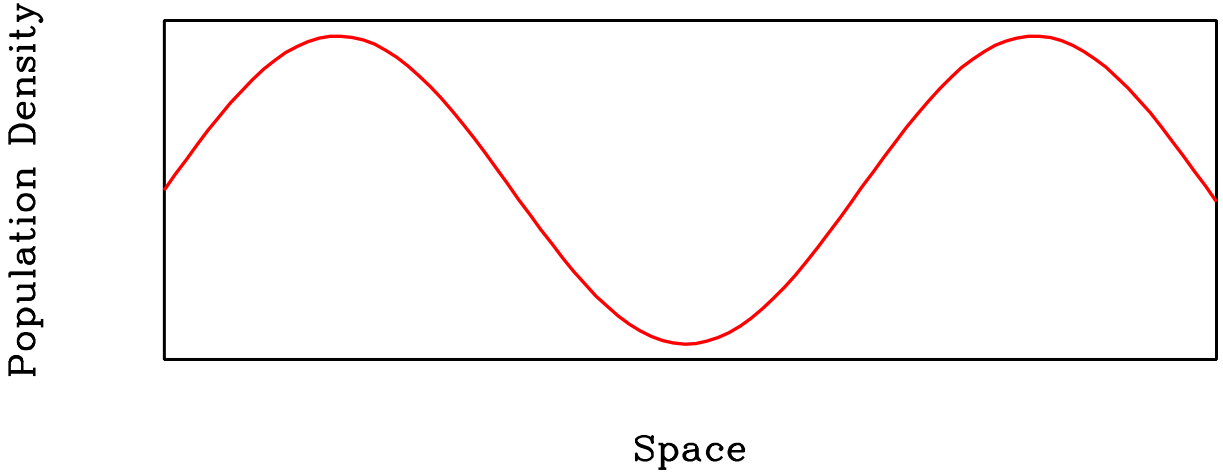

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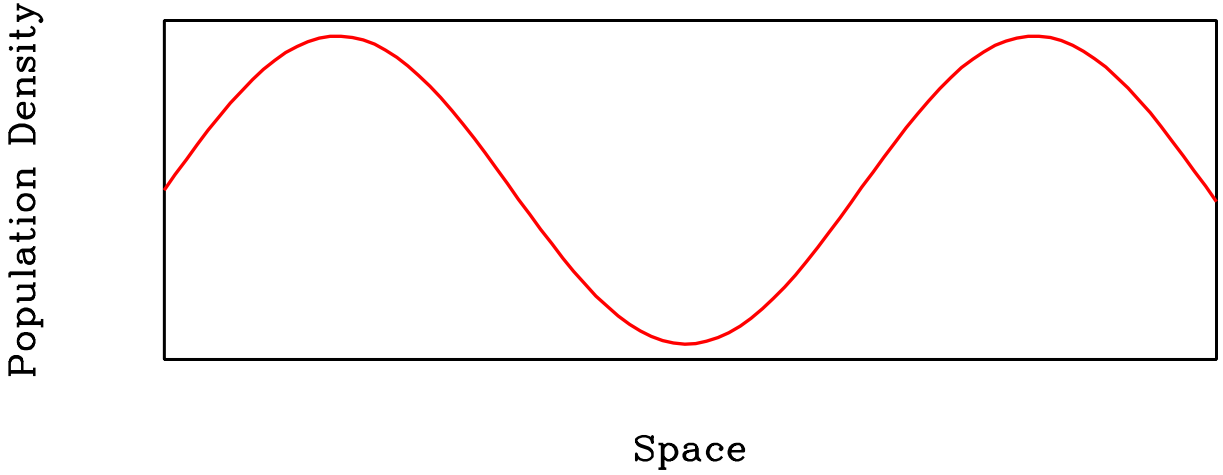

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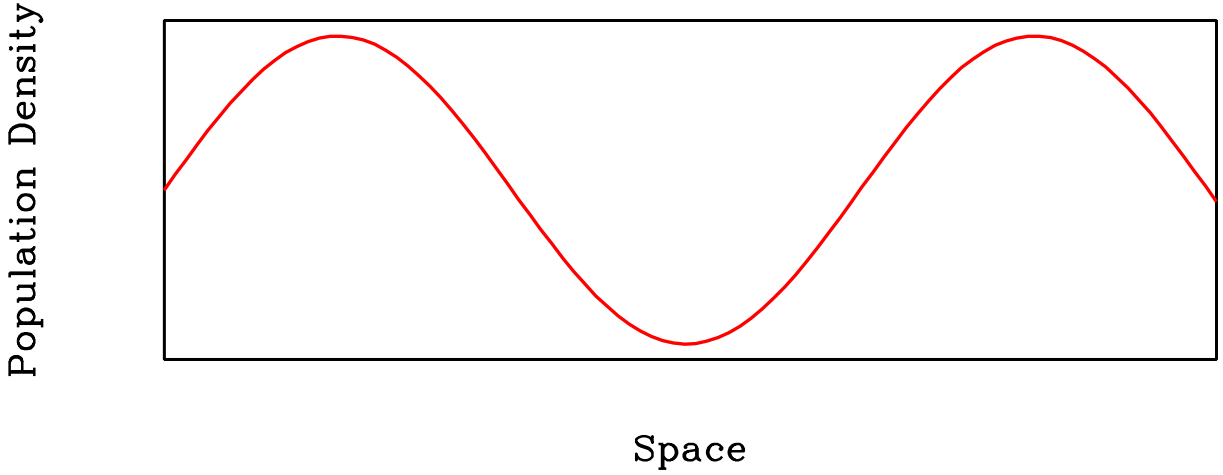

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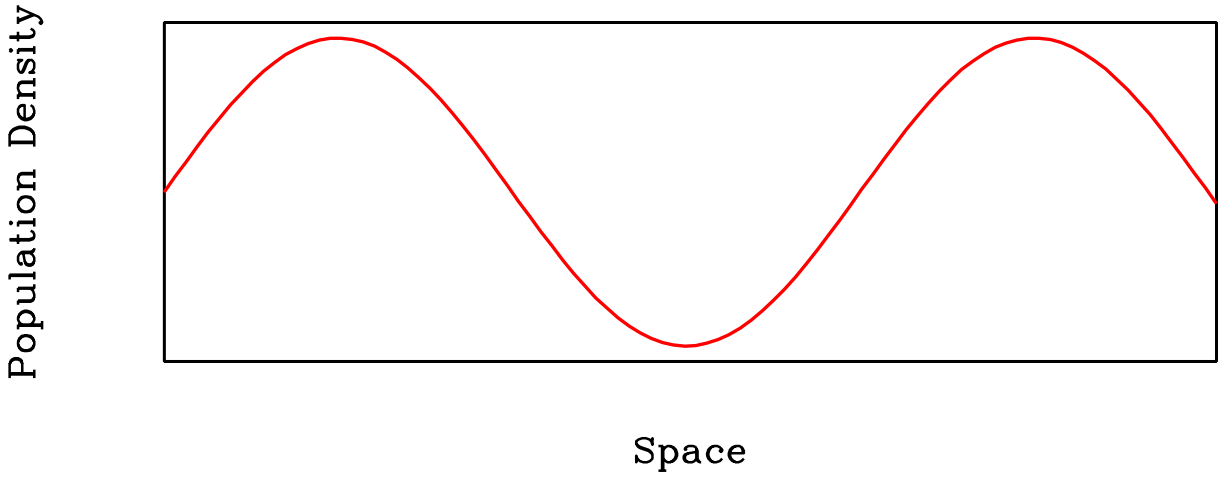

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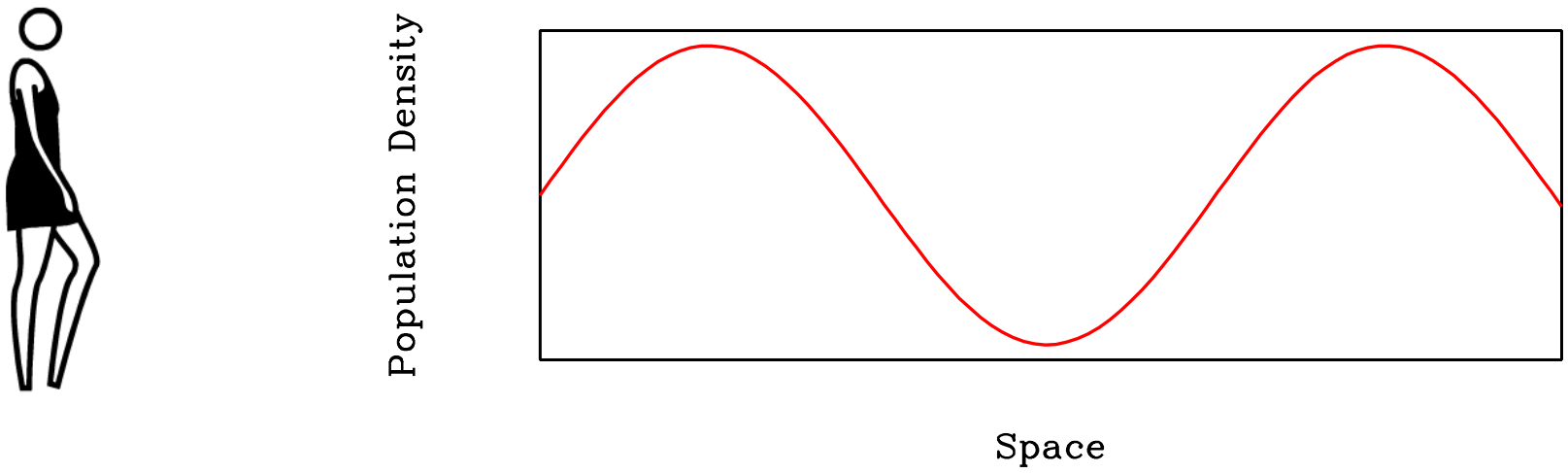

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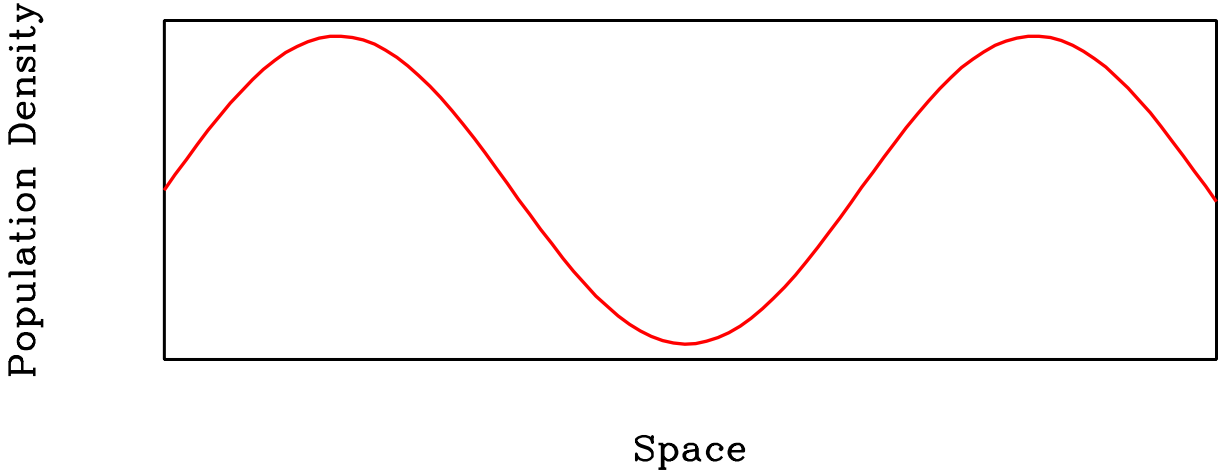

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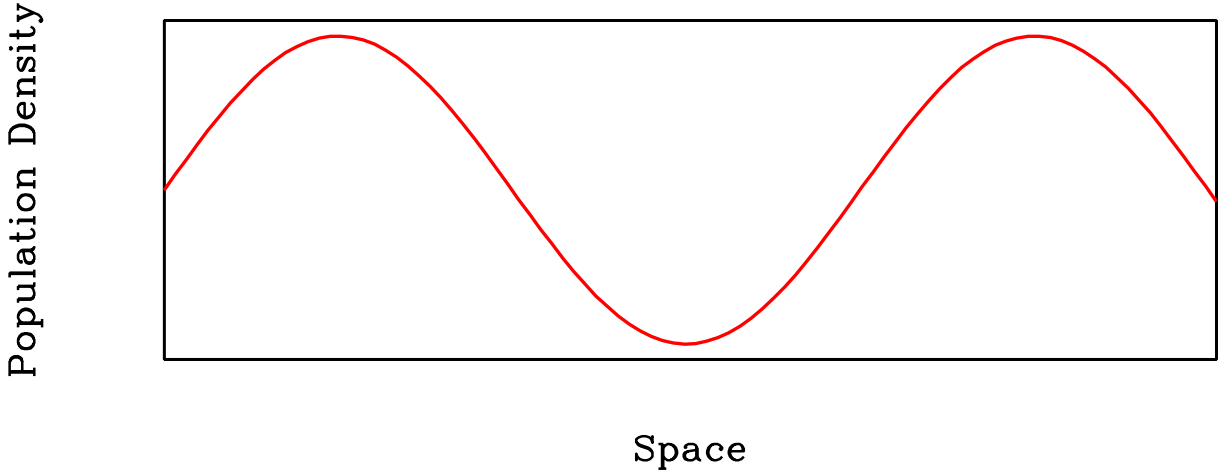

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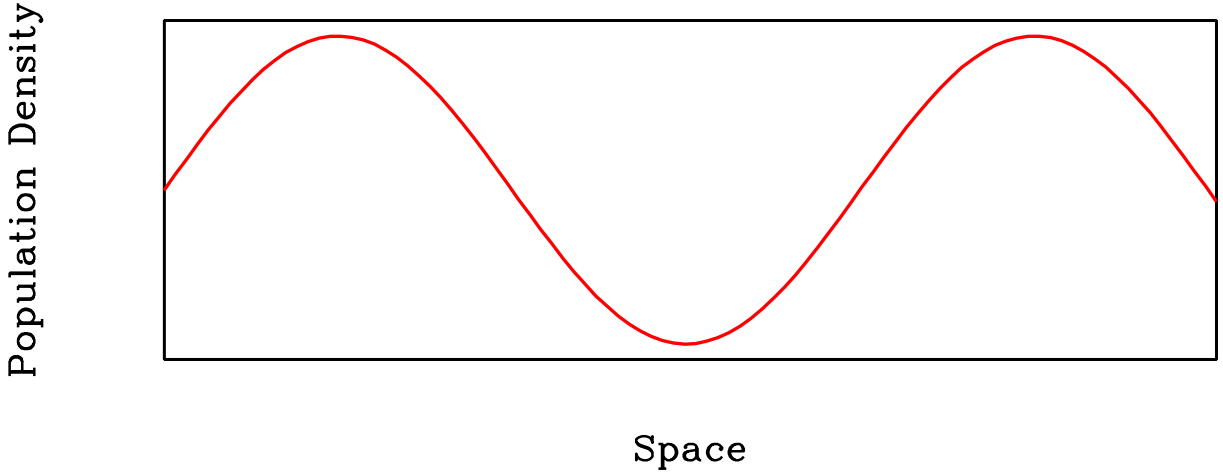

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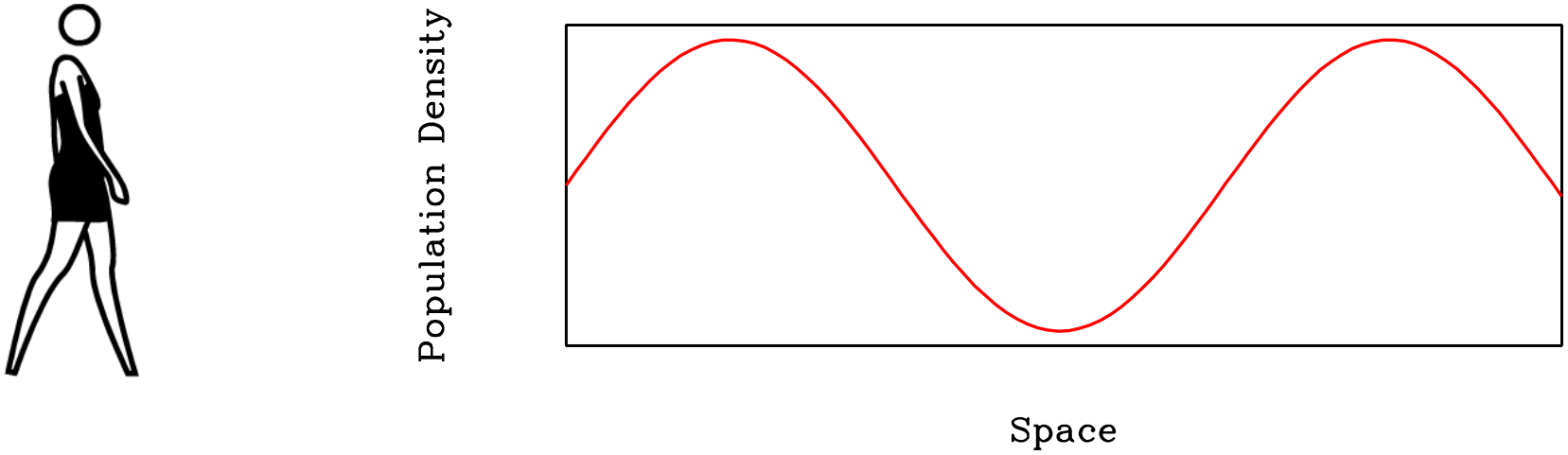

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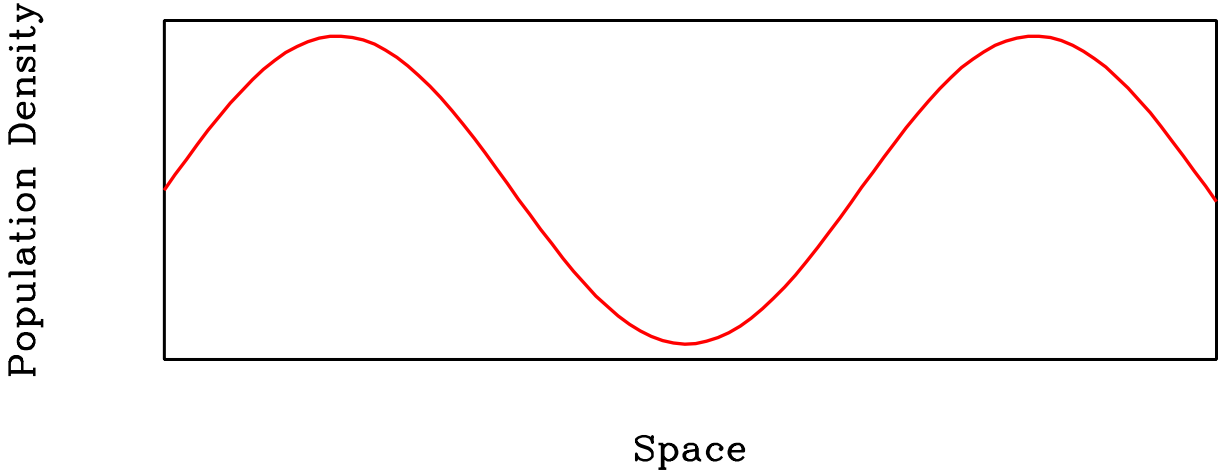

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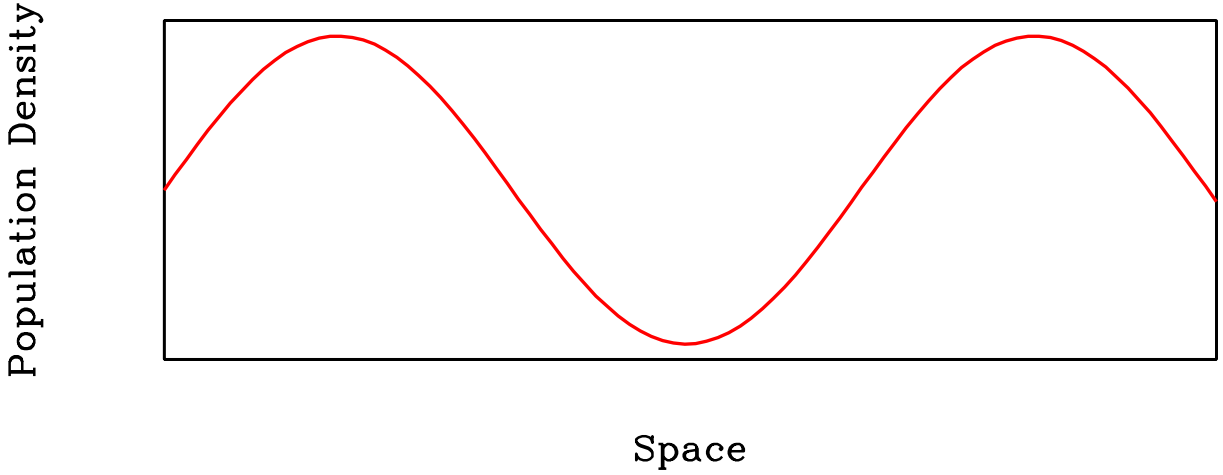

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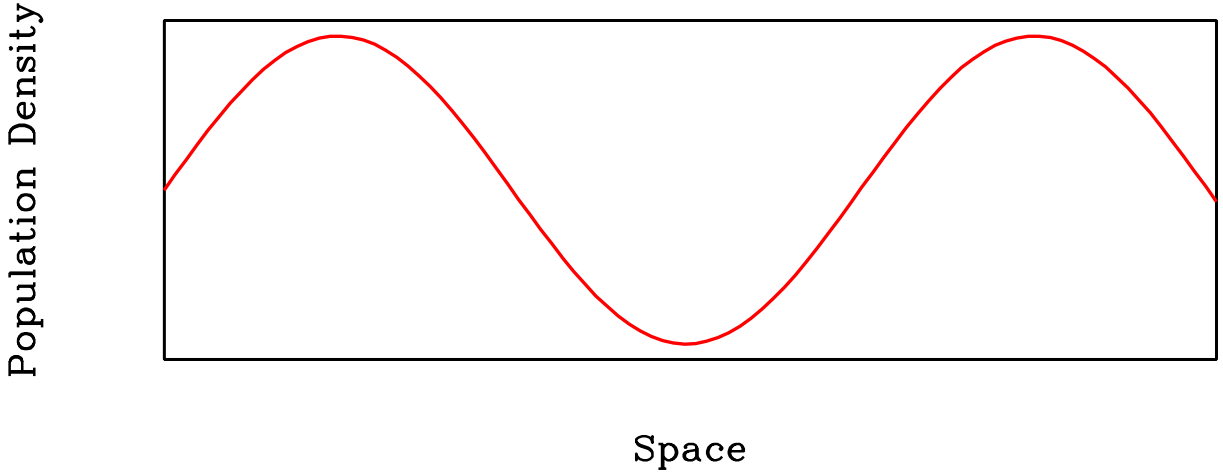

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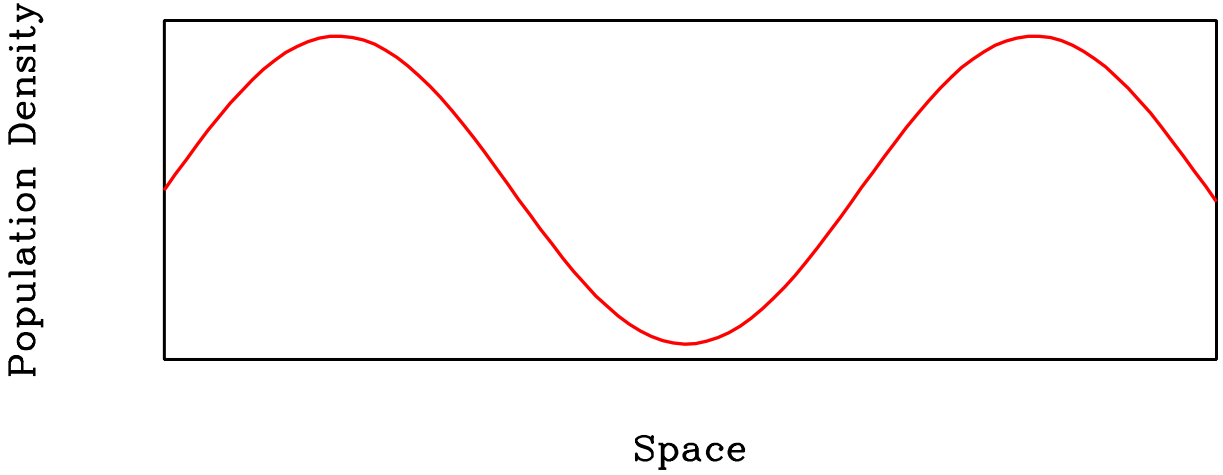

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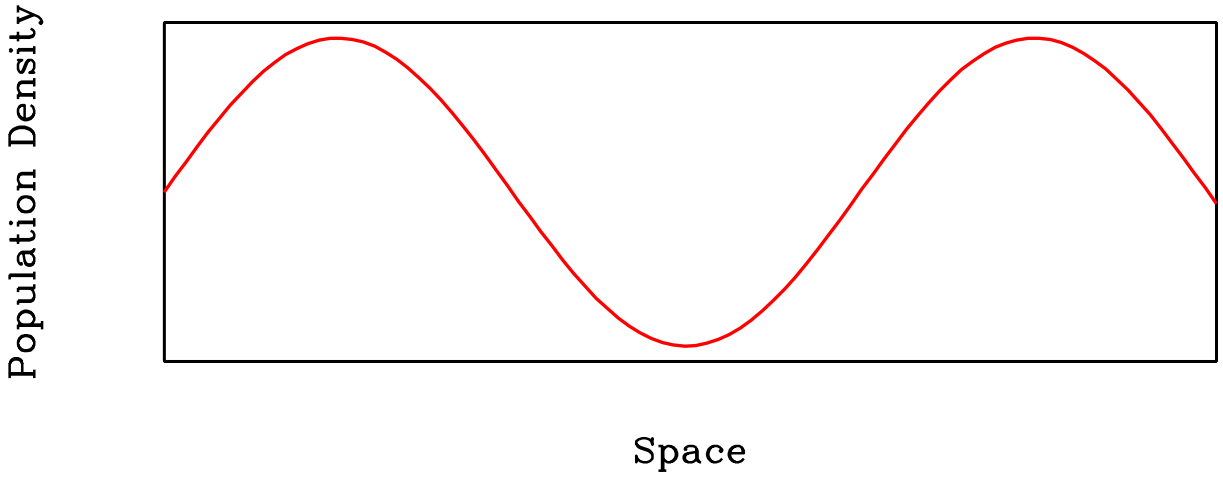

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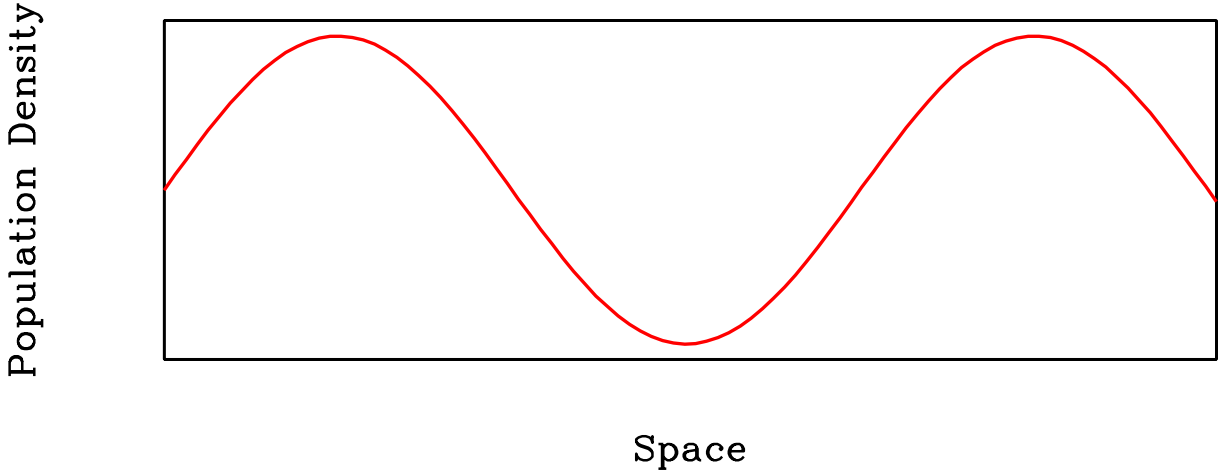

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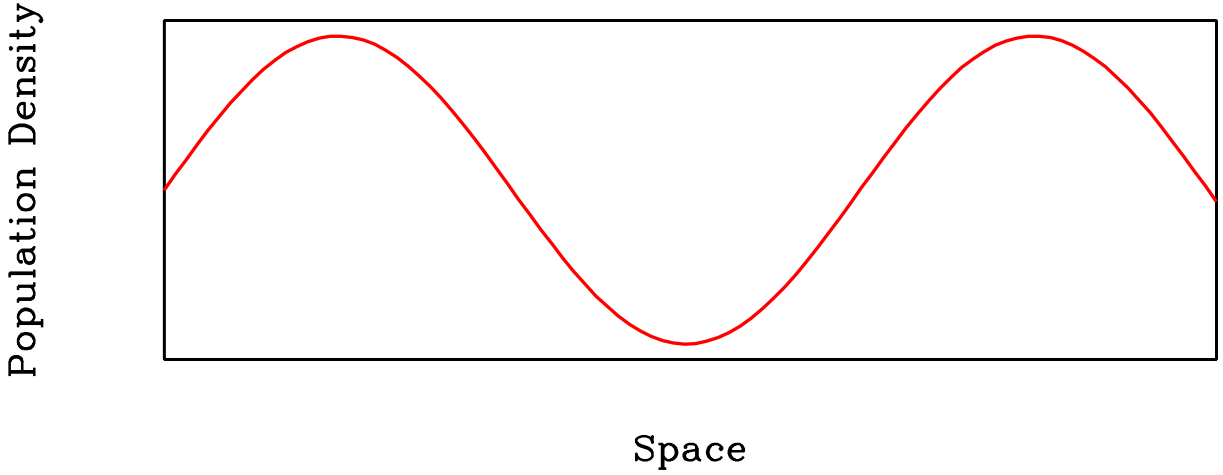

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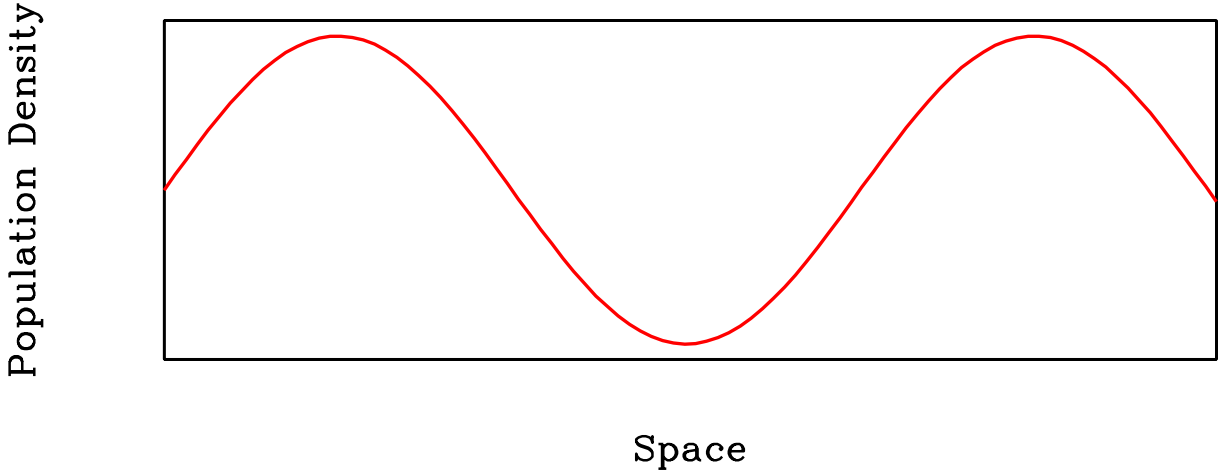

Use "travelling wave" coordinate $z = x - ct$

$$\Rightarrow \partial u/\partial t = D_u\, \partial^2 u/\partial z^2 + c\, \partial u/\partial z + f(u,v)$$
$$\partial v/\partial t = D_v\, \partial^2 v/\partial z^2 + c\, \partial v/\partial z + g(u,v)$$

The Eigenvalue Problem

$$\text{Model eqns: } \begin{aligned} u_t &= D_u u_{zz} + c u_z + f(u,v) \\ v_t &= D_v v_{zz} + c v_z + g(u,v) \quad (z = x - ct) \end{aligned}$$

$$\text{Periodic wave satisfies: } \begin{aligned} 0 &= D_u U_{zz} + c U_z + f(U,V) \\ 0 &= D_v V_{zz} + c V_z + g(U,V) \quad \text{period}=L \end{aligned}$$

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Soln form is:

$$\begin{aligned} \tilde{u}(z,t) &= e^{\lambda t}\,\overline{u}(z) \quad \text{with } |\overline{u}| \ll |U| \\ \tilde{v}(z,t) &= e^{\lambda t}\,\overline{v}(z) \quad \text{with } |\overline{v}| \ll |V| \end{aligned}$$

Note that λ, $\overline{u}$, $\overline{v}$ are complex-valued

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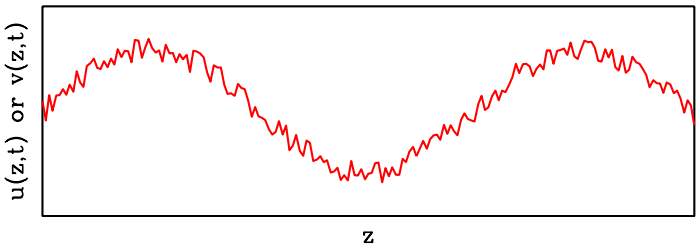
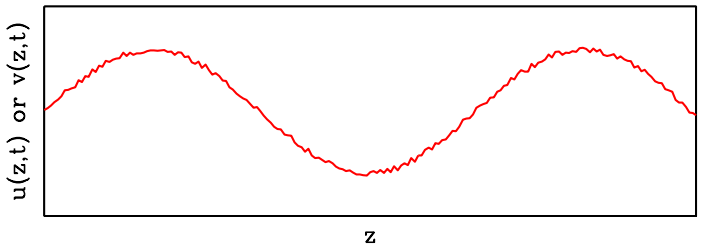


$\mathrm{Re}(\lambda) < 0$

$\longrightarrow$



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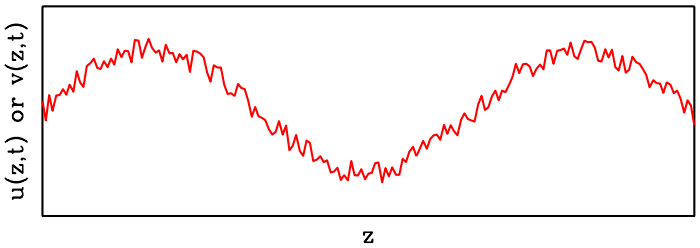

$\mathrm{Re}(\lambda) > 0$

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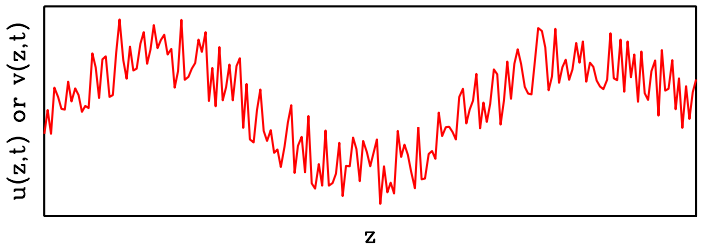

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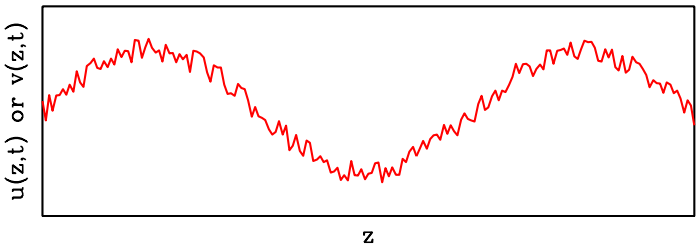

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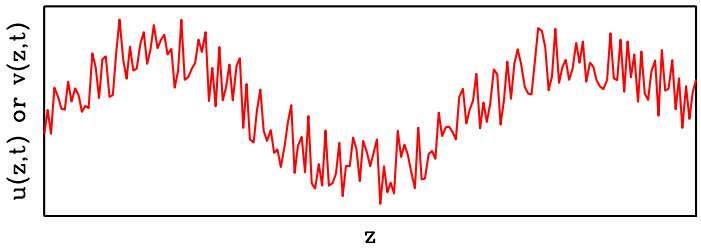

Periodic wave is stable $\Leftrightarrow$ $\mathrm{Re}(\lambda) < 0$ for all possible values of λ.

The Eigenvalue Problem

$\Rightarrow$ Eigenfunction eqn:

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We solve on $0 < z < L$; need to consider boundary conditions.

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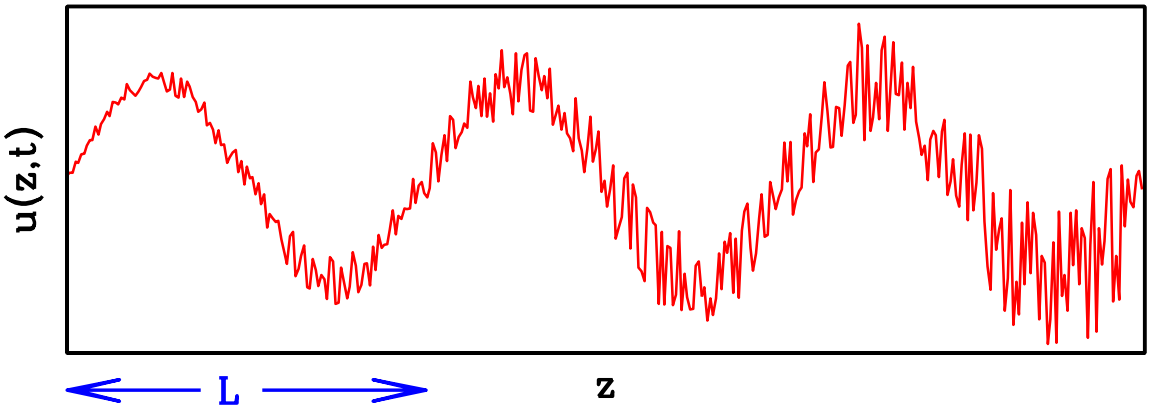

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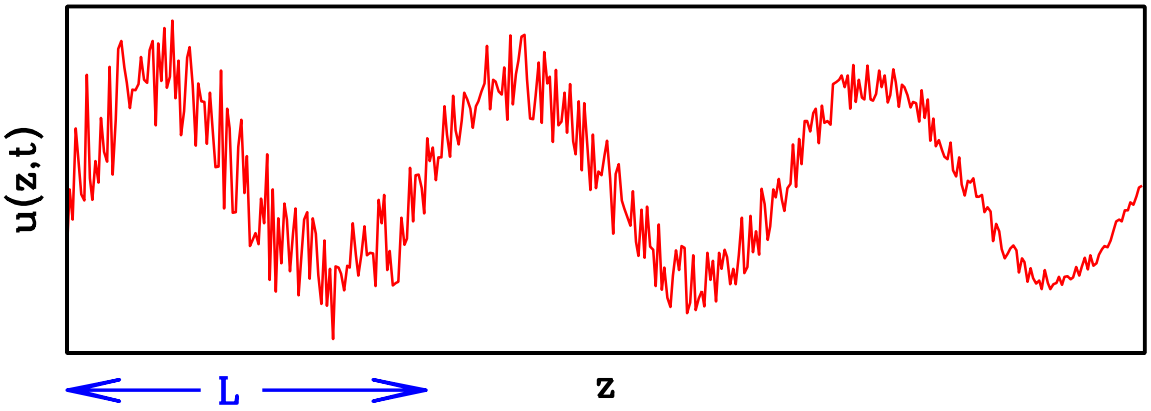

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However there can be a phase difference between $\overline{u}(0)$ and $\overline{u}(L)$ (and similarly for $\overline{v}$).

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$\Rightarrow$ Boundary conditions:
$$\overline{u}(0) = \overline{u}(L)e^{i\gamma} \quad (0 \leq \gamma < 2\pi)$$
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Numerical Calculation of Eigenvalue Spectrum

(based on Jens Rademacher, Bjorn Sandstede, Arnd Scheel Physica D 229 166-183, 2007)

Step 1: solve numerically for the periodic wave by continuation in c from a Hopf bifurcation point in the periodic wave eqns

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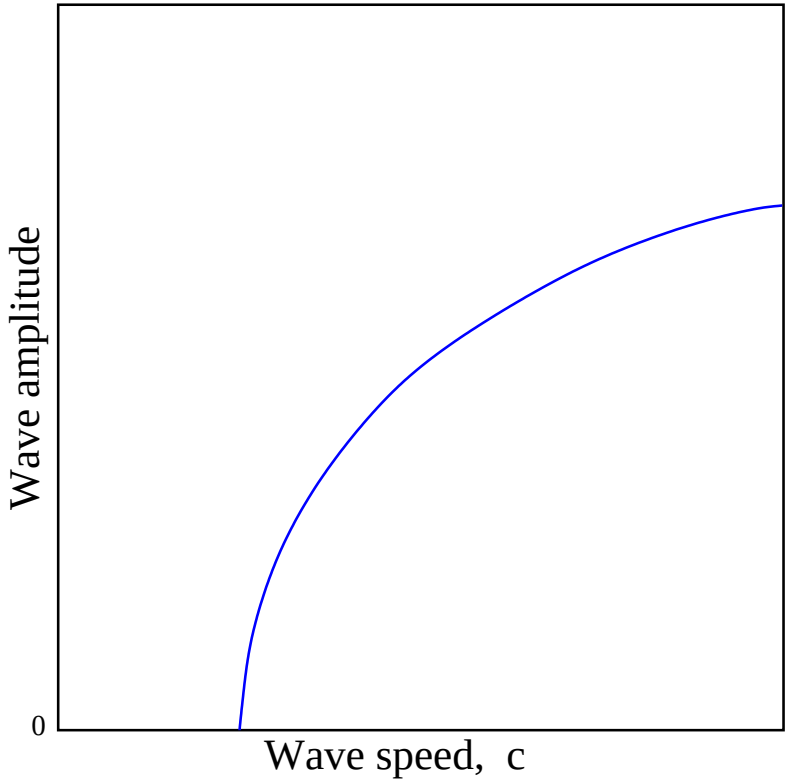

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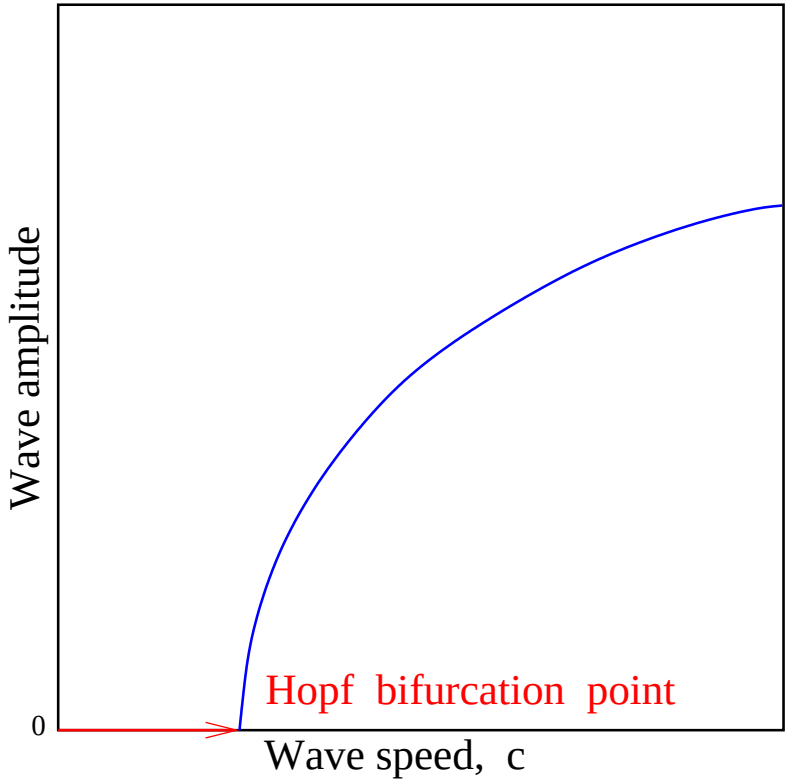

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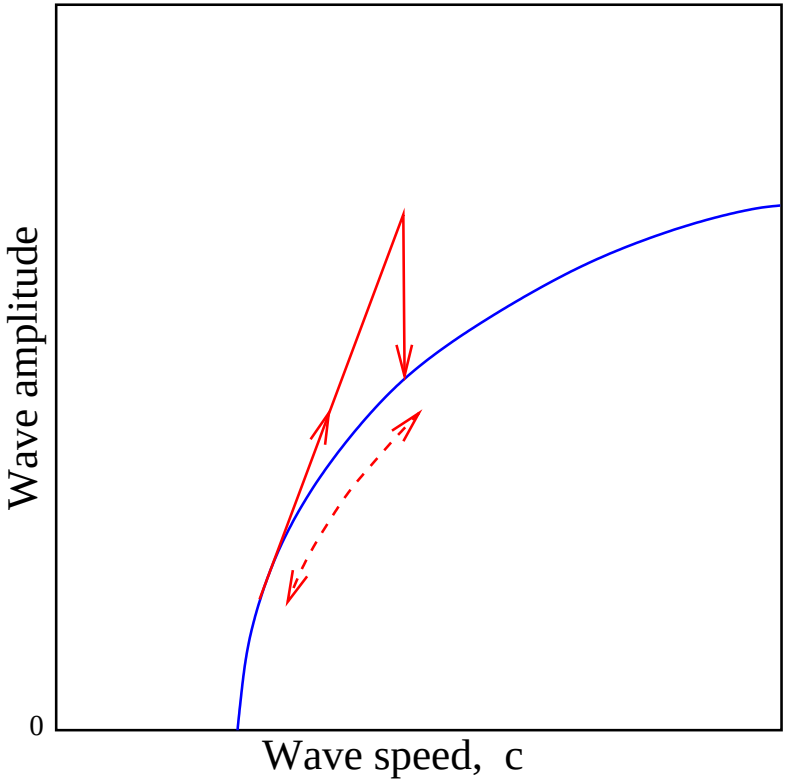

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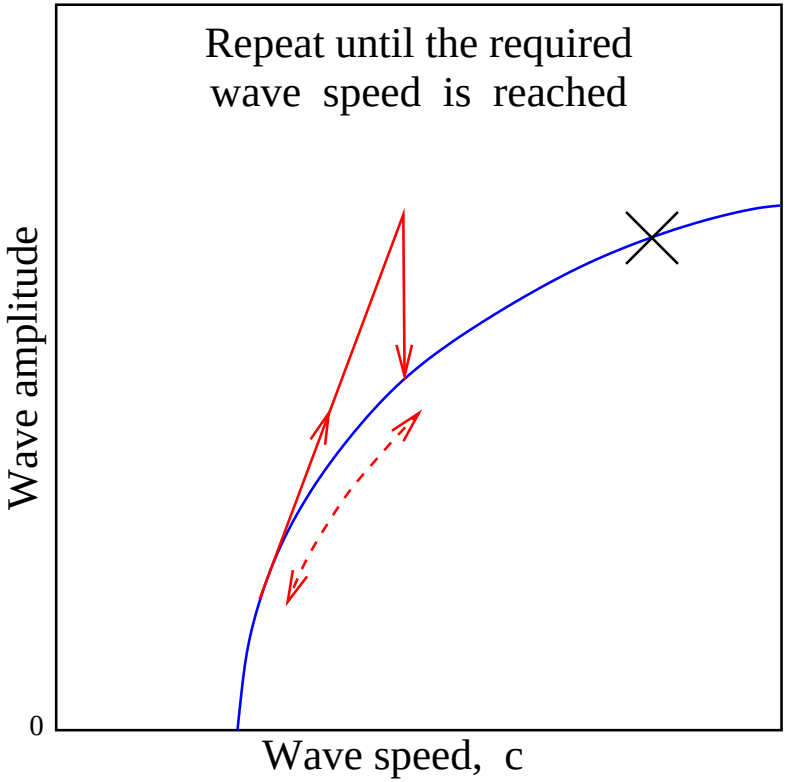

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$$\begin{aligned} z &\mapsto 0 = z_1, z_2, \ldots, z_N = L \\ \overline{u} &\mapsto \overline{u}_1, \overline{u}_2, \ldots, \overline{u}_N \\ d\overline{u}/dz &\mapsto (\overline{u}_{i+1} - \overline{u}_{i-1})/(z_{i+1} - z_{i-1}) \\ \gamma = 0 &\Rightarrow \overline{u}(0) = \overline{u}(L) \mapsto \overline{u}_1 = \overline{u}_N \end{aligned}$$

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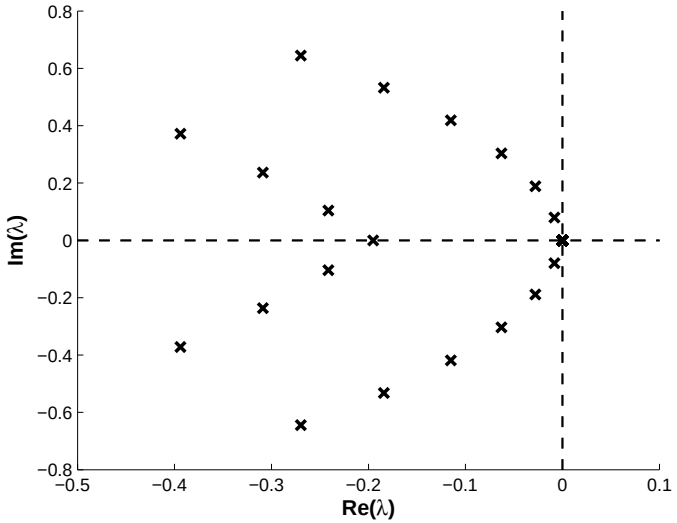

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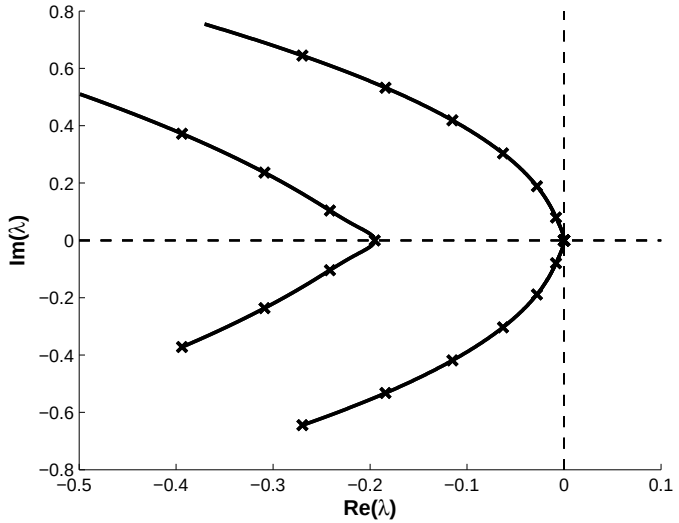

Numerical Calculation of Eigenvalue Spectrum

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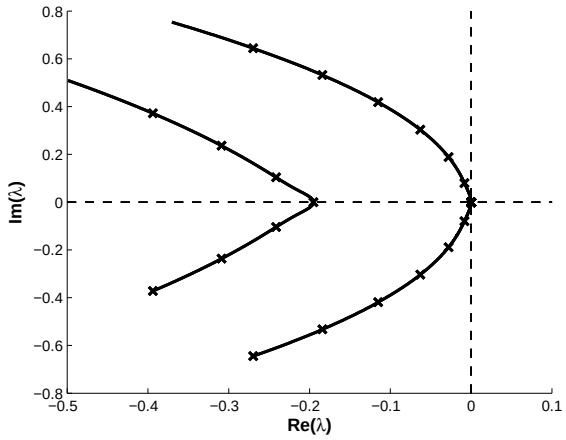
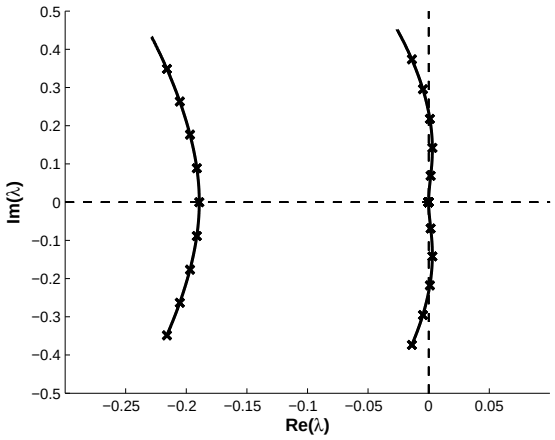
This gives the eigenvalue spectrum, and hence (in)stability



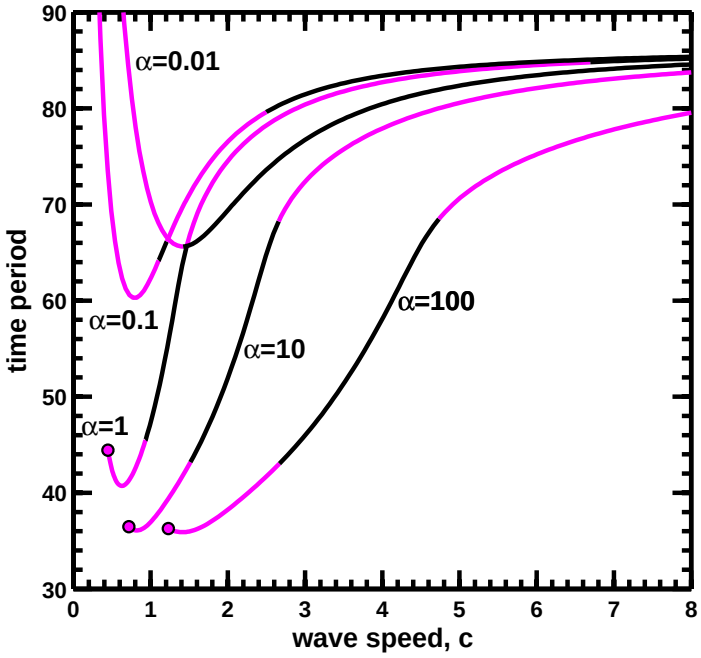
STABLE

Eckhaus instability



UNSTABLE

Periodic Wave Families with Stability



$$\alpha = D_{\text{prey}}/D_{\text{predator}}$$

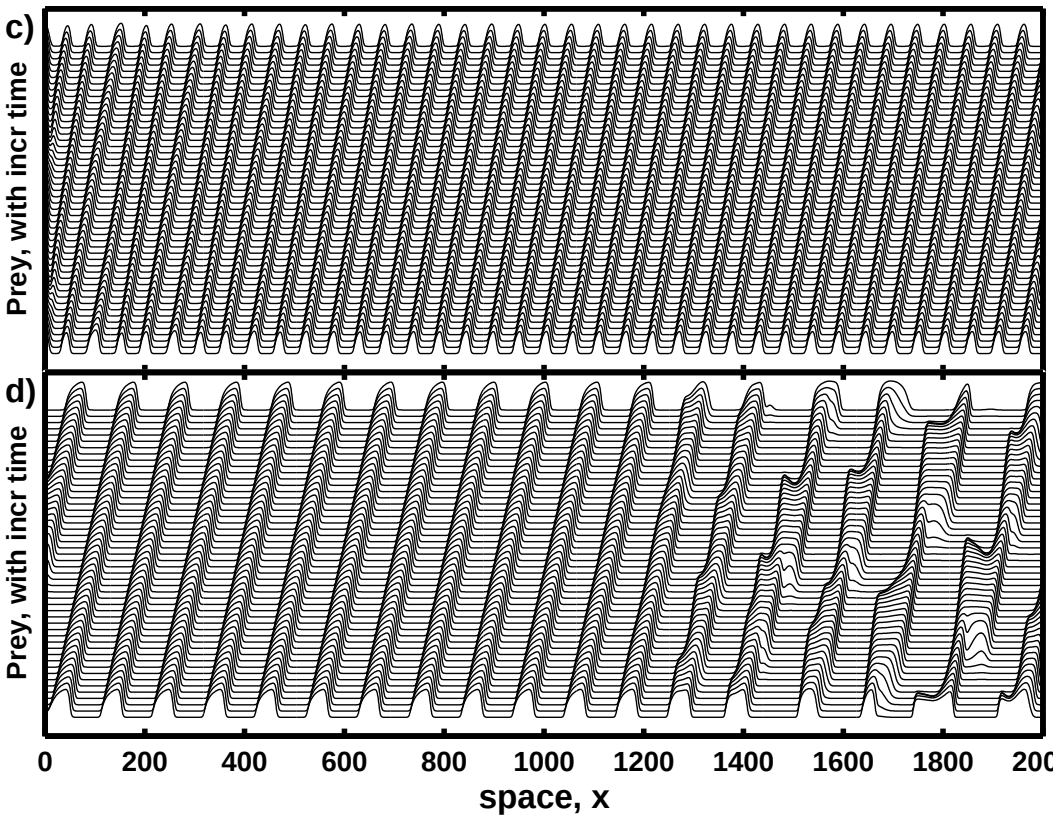
Stability in a Parameter Plane

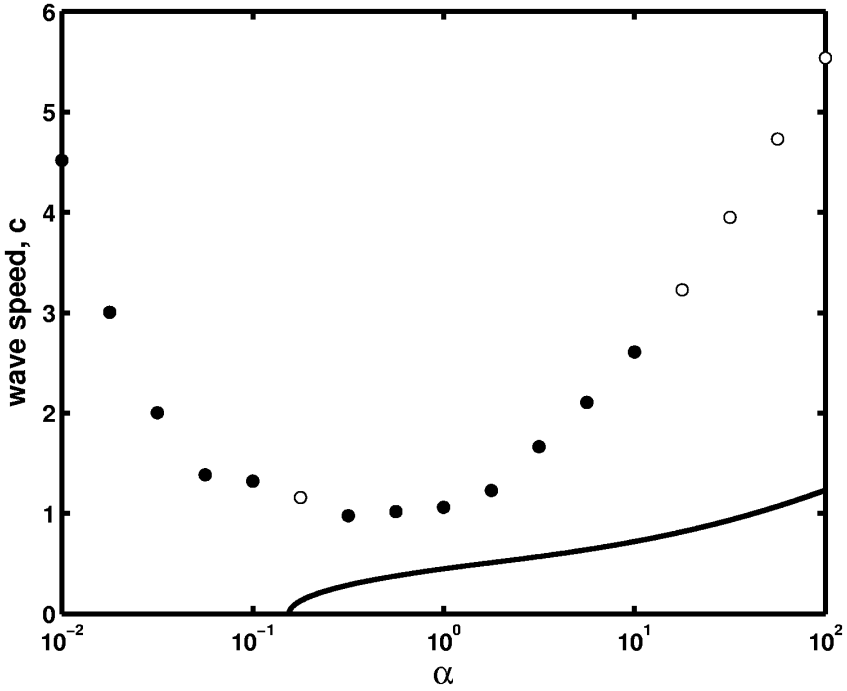
By following this procedure at each point on a grid in parameter space, regions of stability/instability can be determined.

In fact, stable/unstable boundaries can be computed accurately by numerical continuation of Eckhaus instability points.

Periodic Wave Generation in 1-D Simulations

Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:





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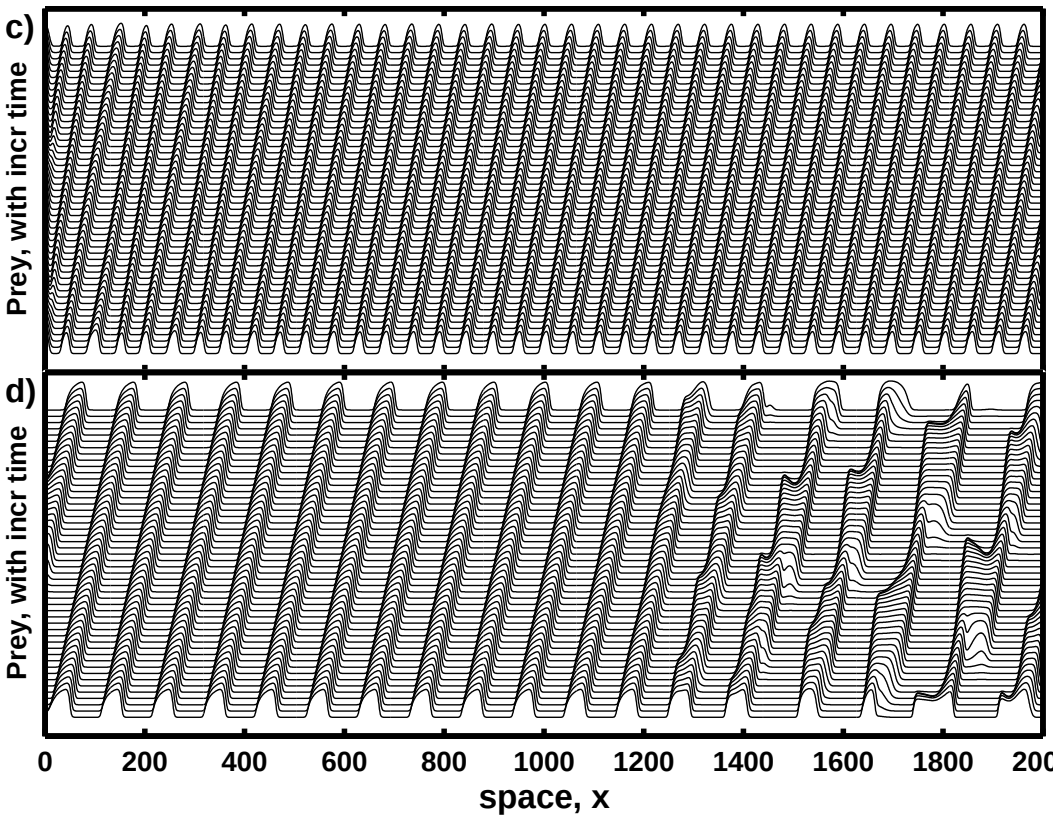
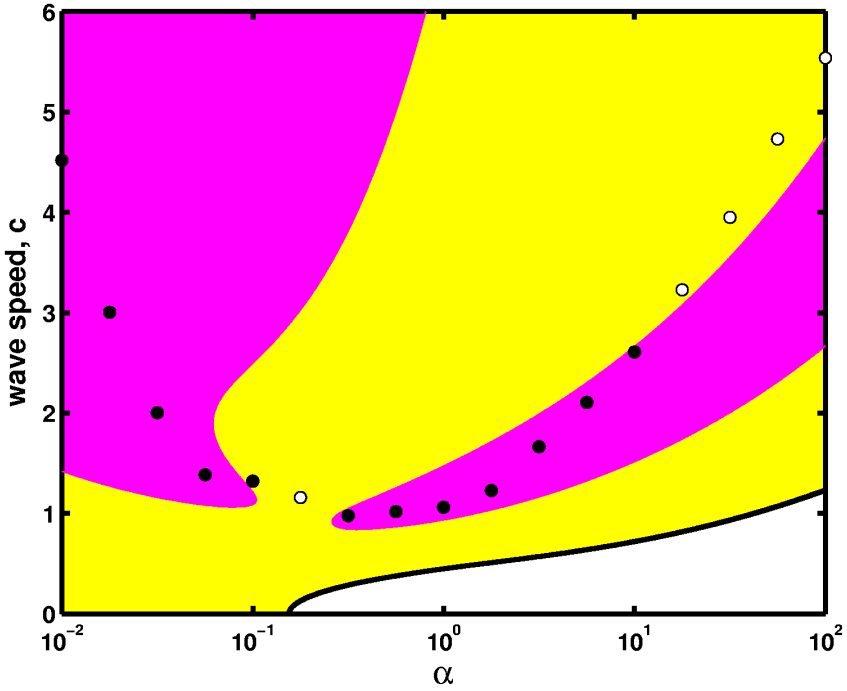
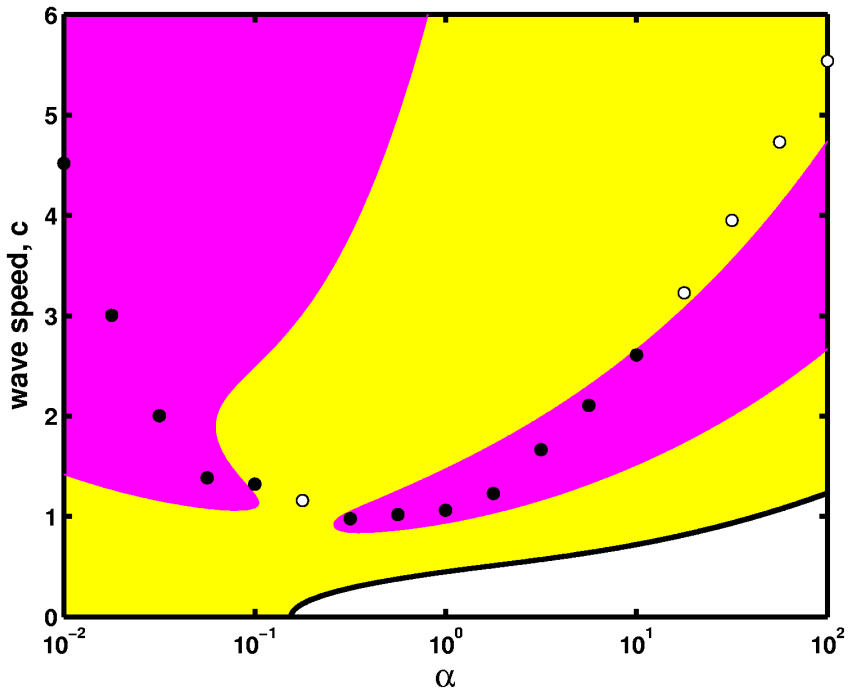




Periodic Wave Generation in 1-D Simulations

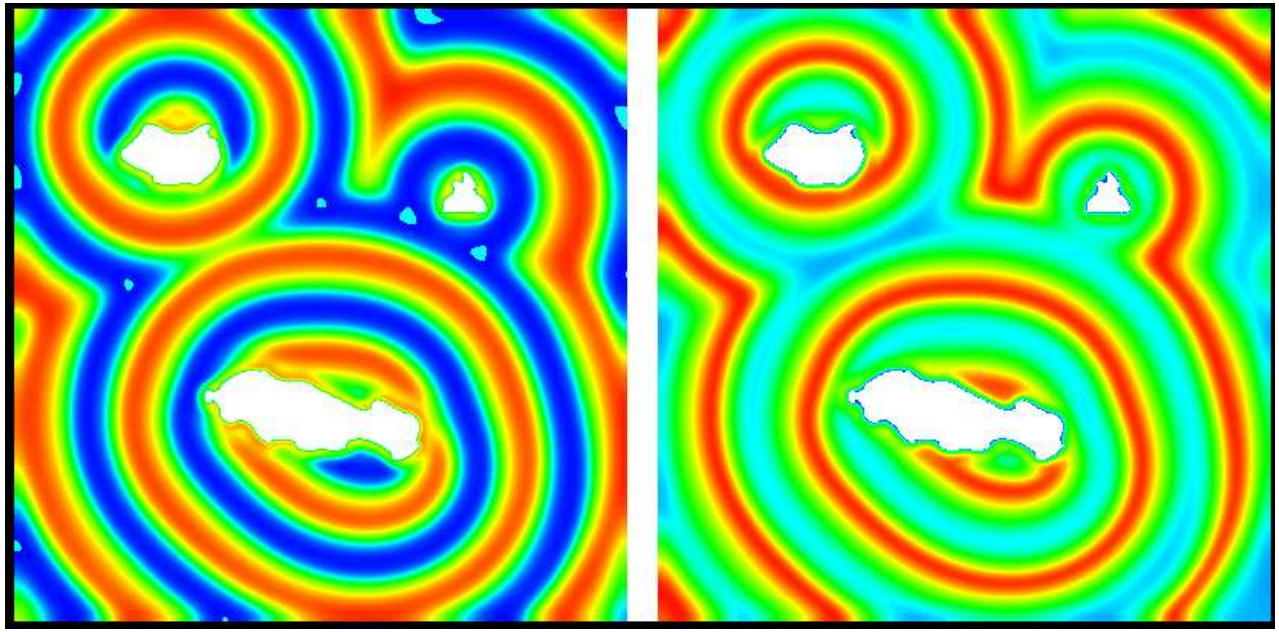
Example of periodic wave generation by Dirichlet boundary conditions in the predator-prey model:

Our stability calculations explain the surprising results from simulations of periodic wave generation.



Outline

Typical Predator-Prey Solution with Multiple Obstacles



Movie of Solution with Multiple Obstacles

Click here to
play the movie

Competition between Obstacles

Question: How do the waves generated by different obstacles interact?

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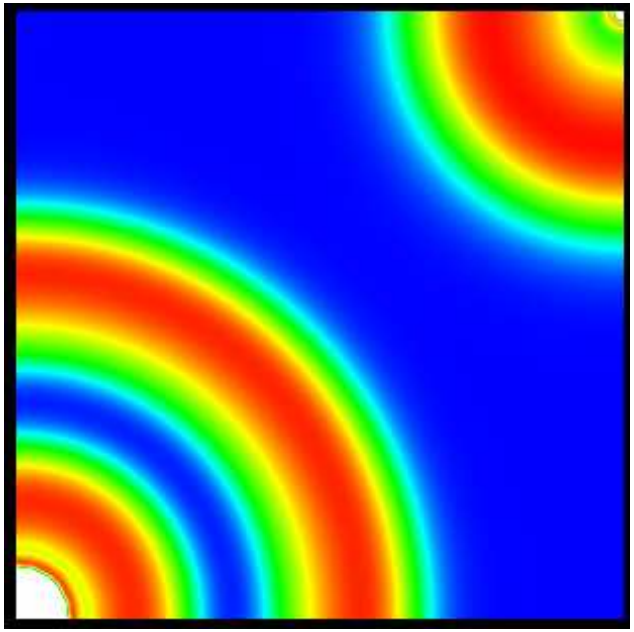

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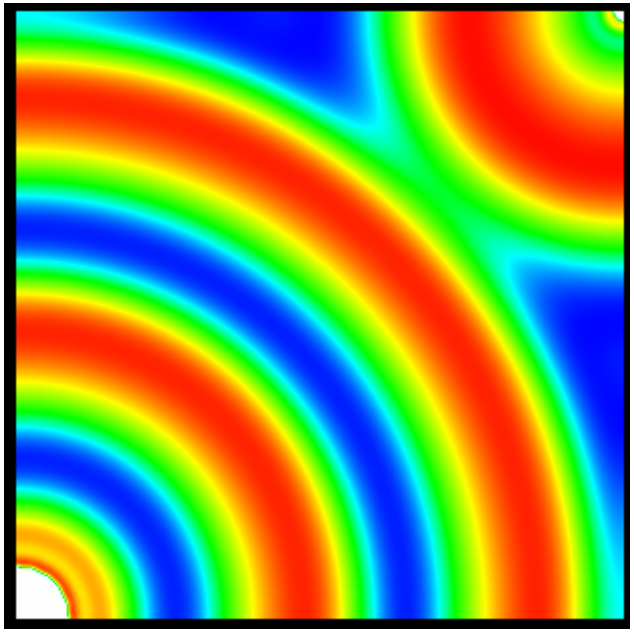

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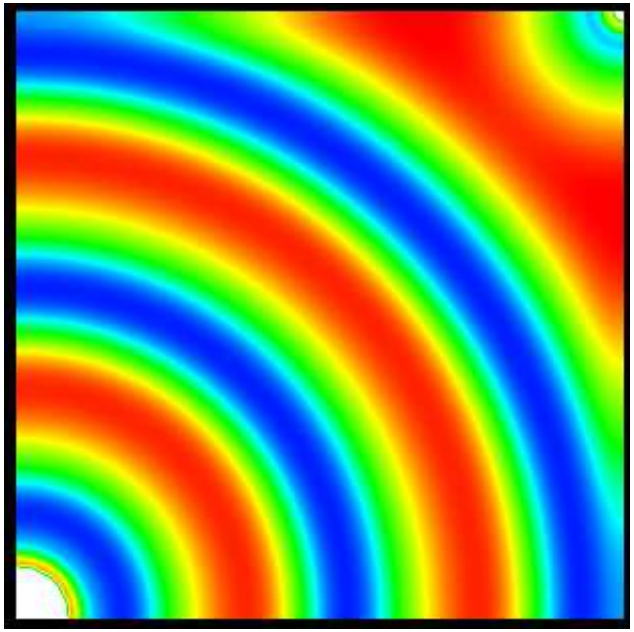

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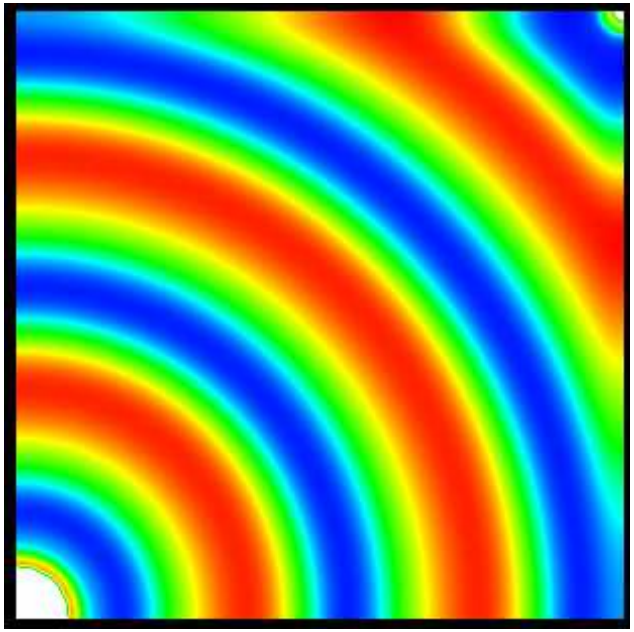


Competition between Obstacles

Question: How do the waves generated by different obstacles interact?

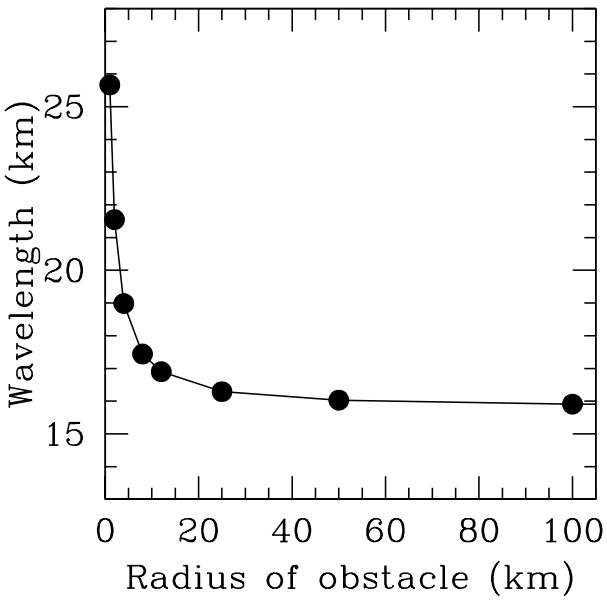
Answer: the wave generated by a larger obstacle dominates that generated by a smaller obstacle

Movie of Competition between Obstacles

Click here to
play the movie

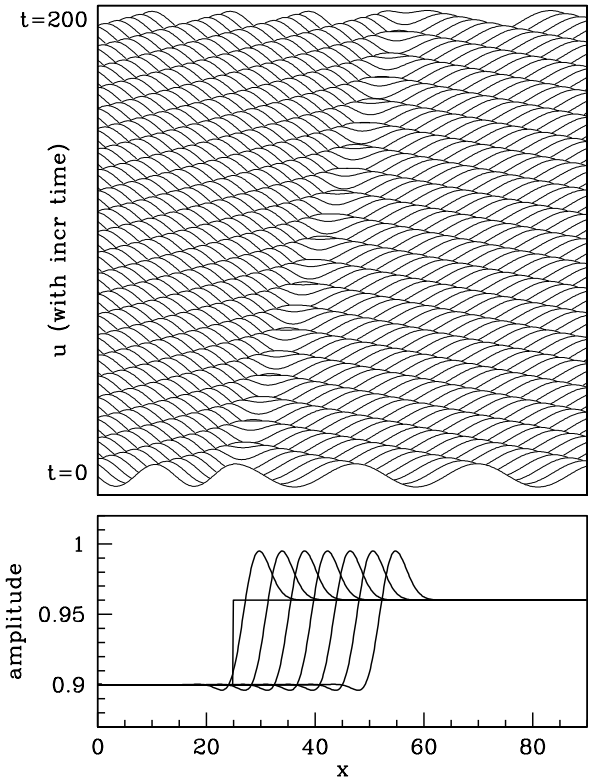
Wavelength vs Obstacle Radius

Numerical solutions for circular obstacles indicate that wavelength far from the obstacle varies with obstacle radius.



Explanation of Competition between Obstacles

Consider an interface between periodic waves in 1-D



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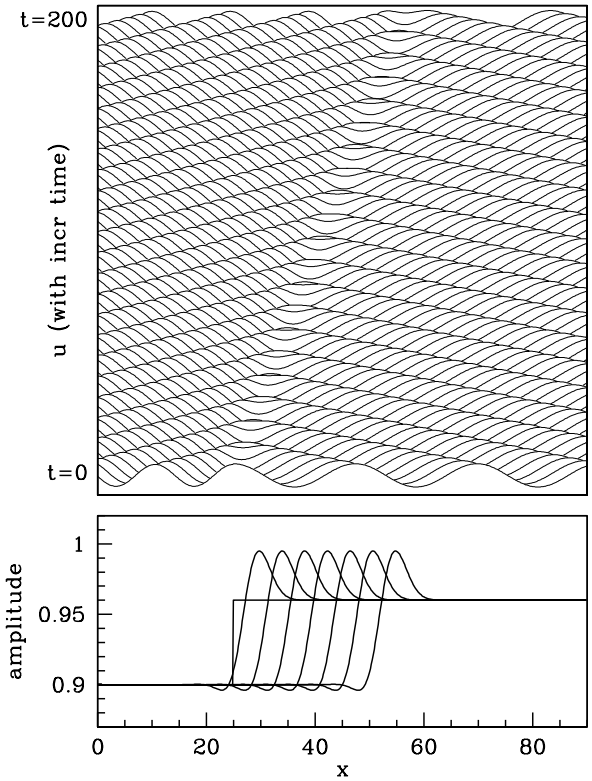

Analytical study of transition fronts in periodic wave amplitude shows that these move from a lower to a higher amplitude wave.

Therefore the wave generated by a larger obstacle will replace that generated by a smaller obstacle.

Outline

Conclusions

- The expected behaviour at the edge of Kielder Water provides a possible explanation for the periodic travelling waves that are observed in field vole density.
- For other parameter sets, the same mechanism generates spatiotemporal irregularity. A detailed explanation of this is possible via numerical calculation of wave stability.
- Results on obstacle size and multiple obstacles are consistent with intuitive expectations, and explain why very large obstacles are required to give detectable periodic waves.

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Future Work

The major outstanding issues are:

- Analytical prediction of wave stability away from Hopf bifurcation.
- Detailed study of how obstacle shape affects periodic travelling wave selection.

Review Paper and Software

J.A. Sherratt, M.J. Smith (2008) Periodic travelling waves in cyclic populations: field studies and reaction-diffusion models. *J. R. Soc. Interface* 5, 483-505.

This paper is a review of periodic travelling waves in ecological field data and in mathematical models of cyclic populations. The associated online material contains a detailed tutorial on numerical calculation of periodic travelling wave stability, including computer code (in Fortran).

The paper and the online material are freely available from my web site: `www.ma.hw.ac.uk/~jas`

List of Frames