

Locating Transitions from Cycles to Chaos Behind Invasions in Reaction-Diffusion Equations

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University of Edinburgh, 27 October 2011

This talk can be downloaded from www.ma.hw.ac.uk/~jas

This work is in collaboration with:

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(Microsoft Research
Ltd., Cambridge)



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(CWI, Amsterdam)



Outline

- 1 Ecological Motivation and Statement of the Problem
- 2 The Complex Ginzburg-Landau Equation
- 3 Band Width Calculation I: Wavetrain Selection
- 4 Band Width Calculation II: Absolute Stability
- 5 Band Width Calculation III: Formula and Ecological Implications

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Cyclic Predator-Prey Systems

The interaction between a predator population and its prey can cause population cycles.

Example: vole – weasel interaction in Fennoscandia



vole



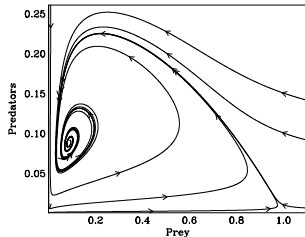
weasel



Cyclic Predator-Prey Systems

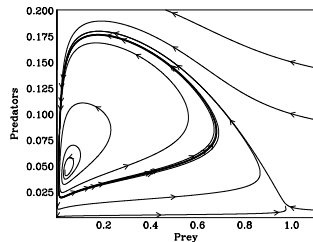
The interaction between a predator population and its prey can cause population cycles.

This has been modelled extensively using systems of two coupled ODEs



constant coexistence

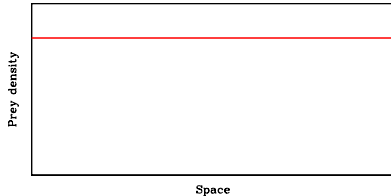
change
→
parameters



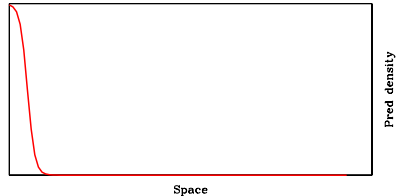
cycles

Predator-Prey Invasion

To model the invasion of a prey population by predators, one can add diffusion terms to represent dispersal.



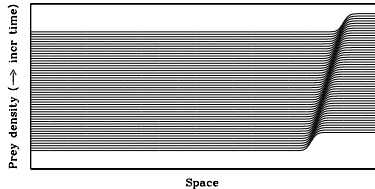
Initially we set the prey to the prey-only equilibrium throughout the domain.



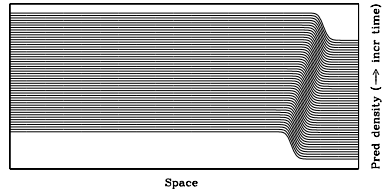
Initially we set the predators to zero except near the left hand boundary.

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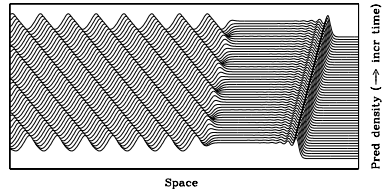
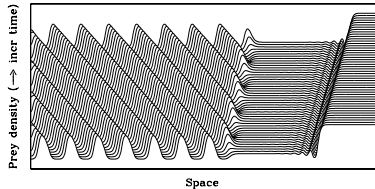
Simple invasion front



(local bhr: constant)

Predator-Prey Invasion

To model the invasion of a prey population by predators, one can add diffusion terms to represent dispersal.



Wavetrain behind an invasion front (local bhr: cycles)

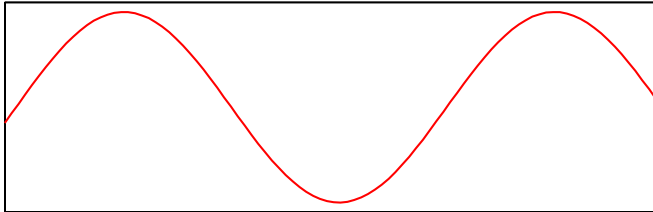
What is a Wavetrain?

A **wavetrain** is a soln of form $f(x \pm st)$, with $f(\cdot)$ periodic.

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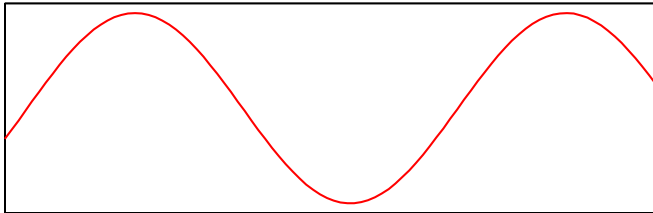


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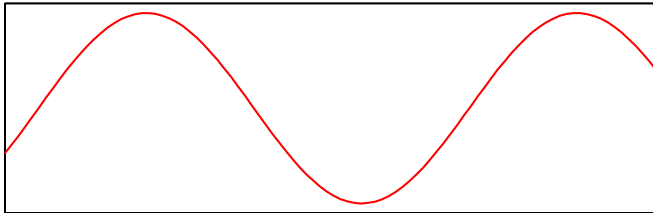


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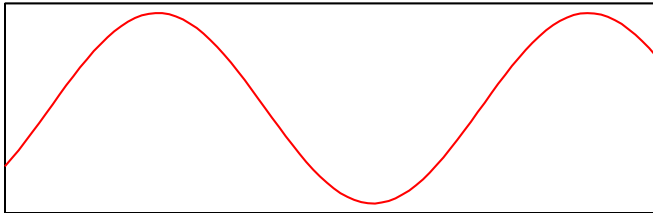


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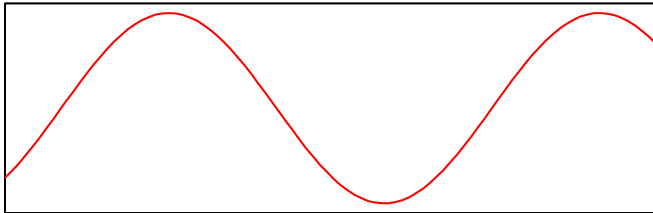


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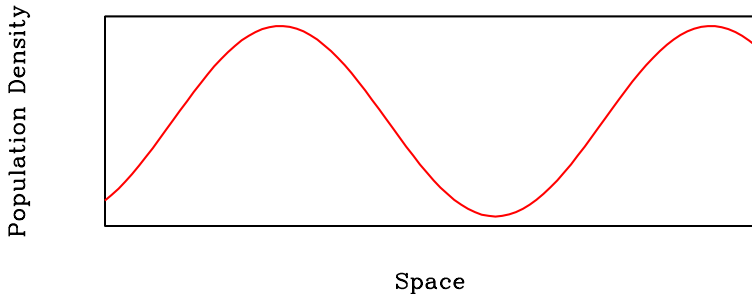
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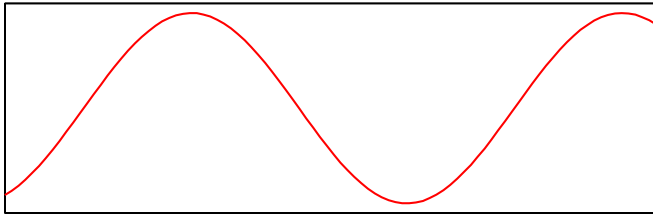
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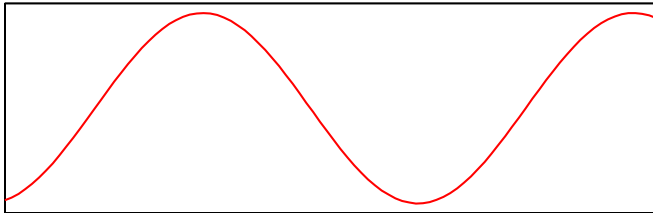


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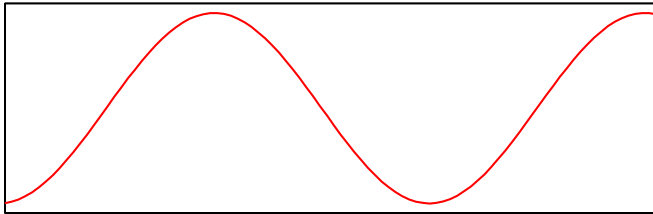


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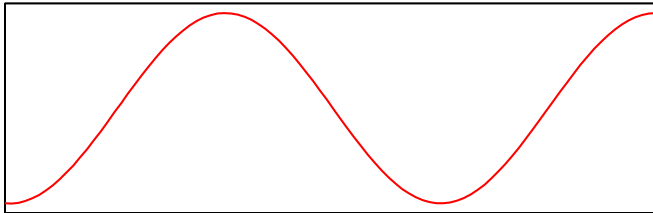


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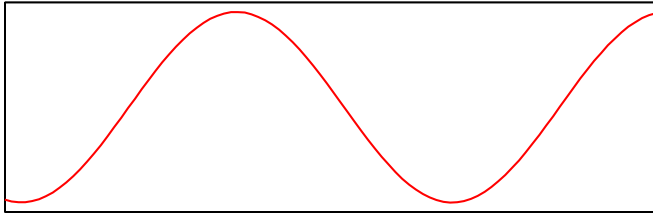


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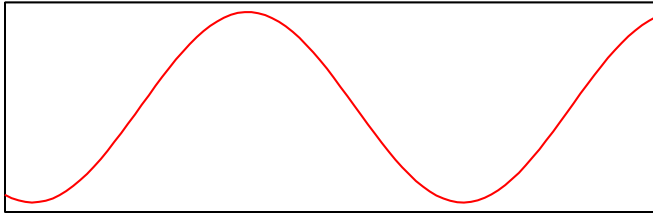


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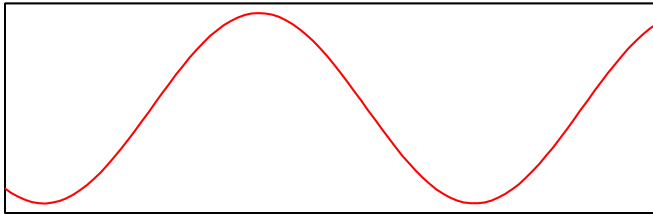


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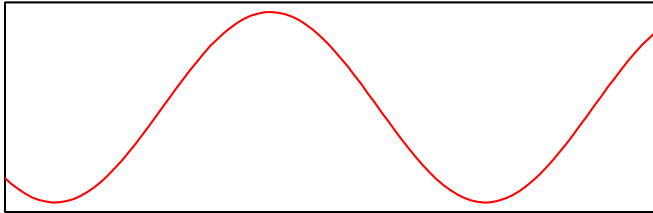


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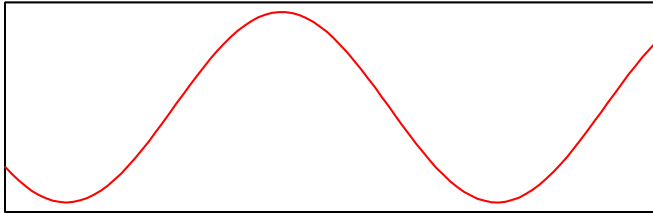


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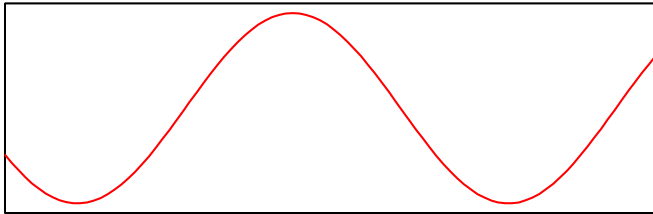


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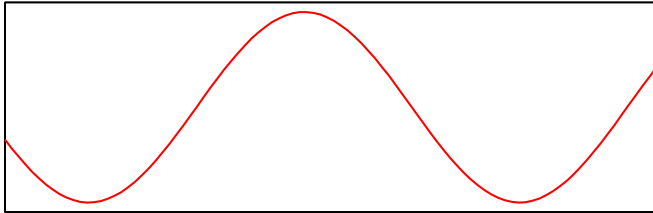


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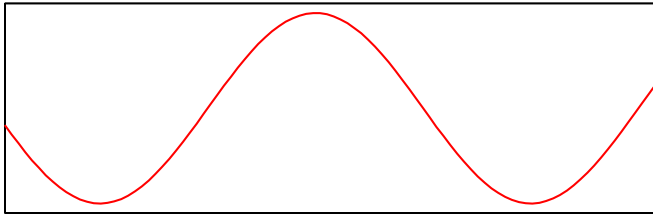


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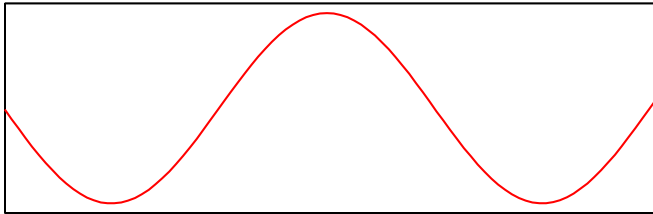


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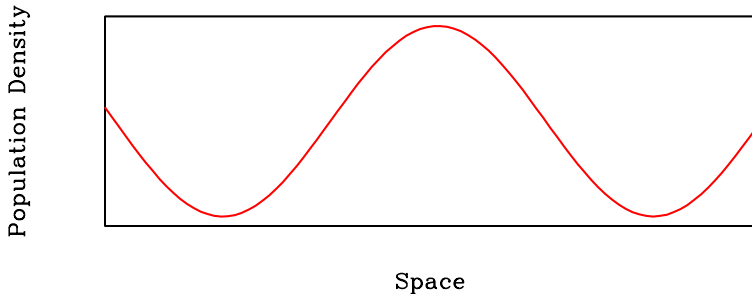
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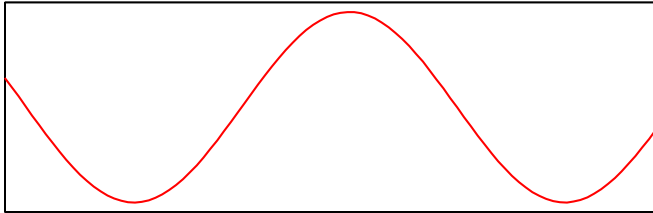
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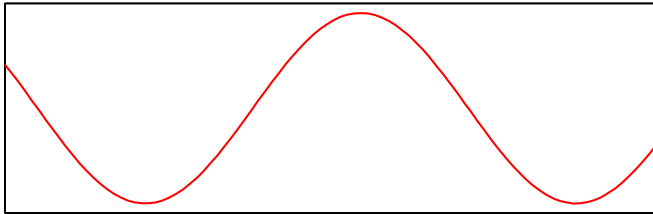


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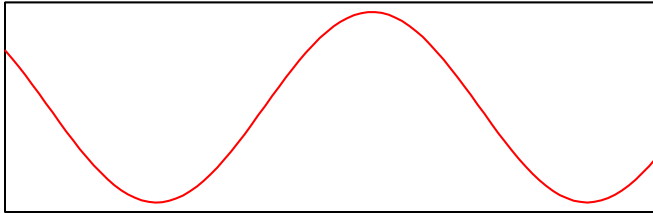


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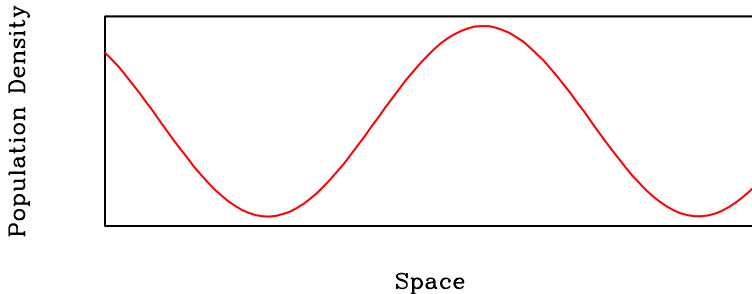
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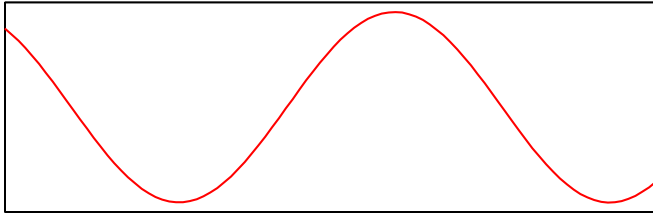
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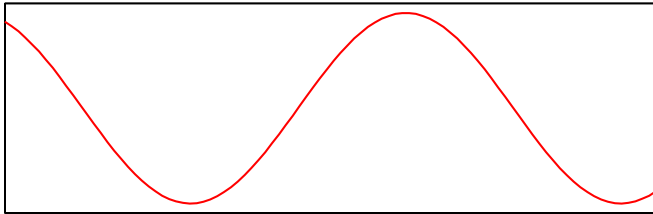


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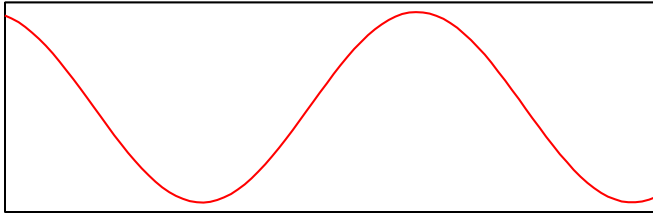


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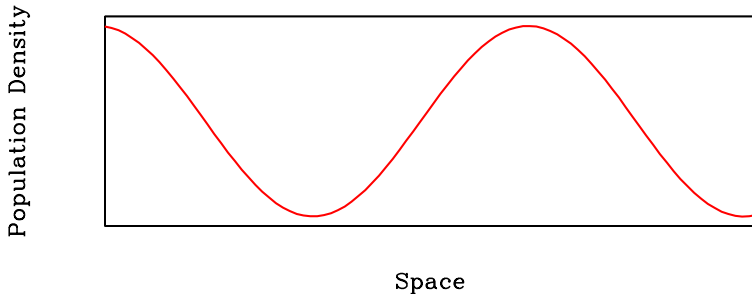
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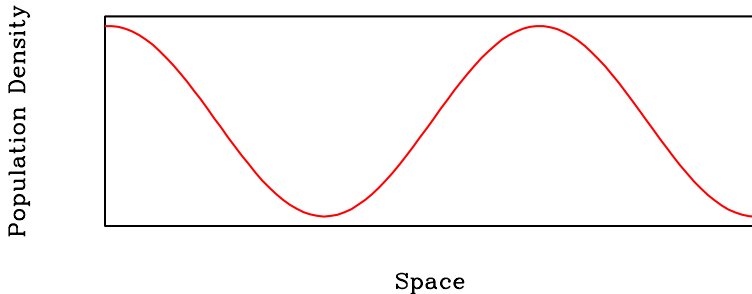
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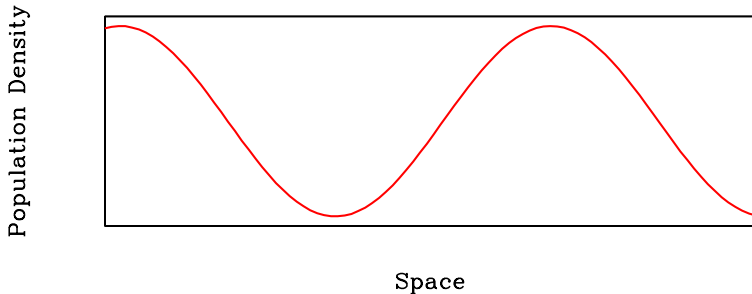
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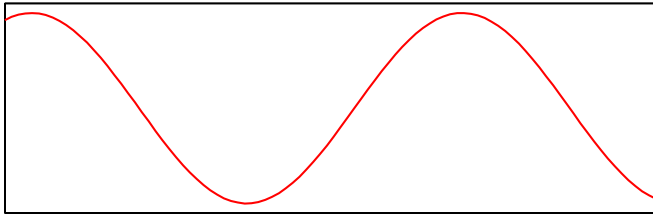
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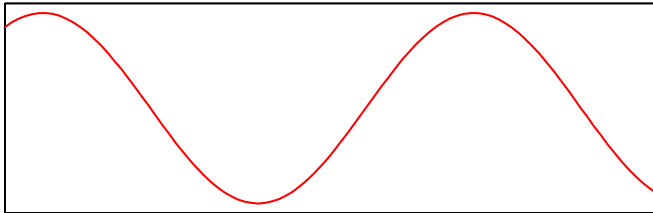


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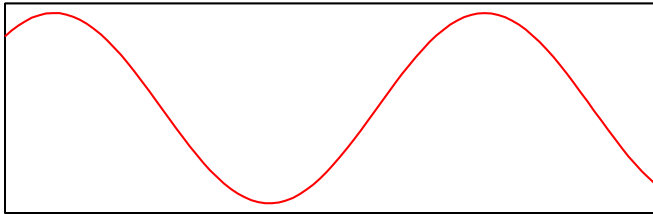


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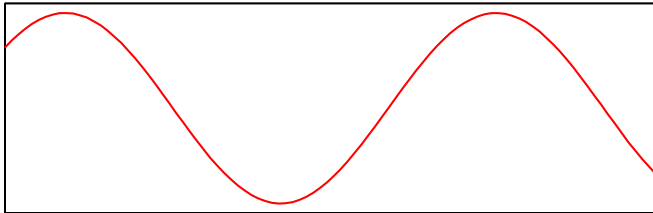


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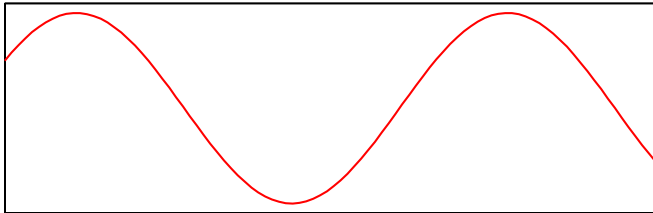


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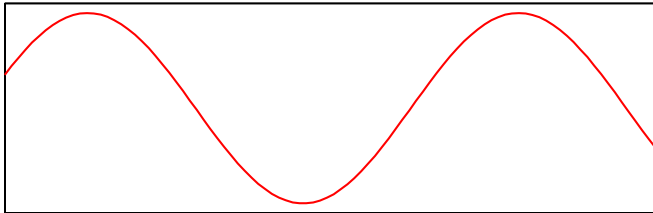


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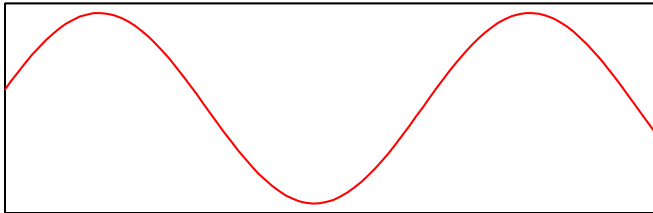


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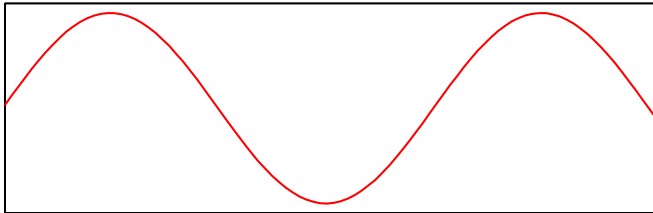


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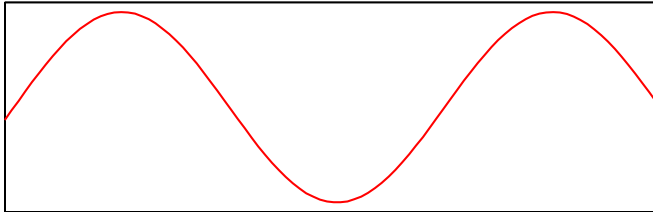


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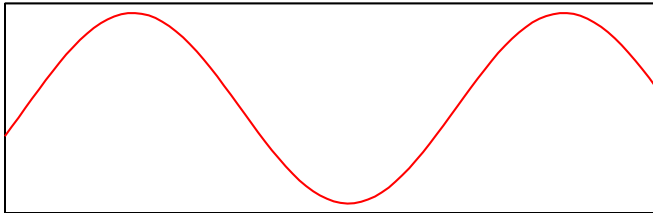


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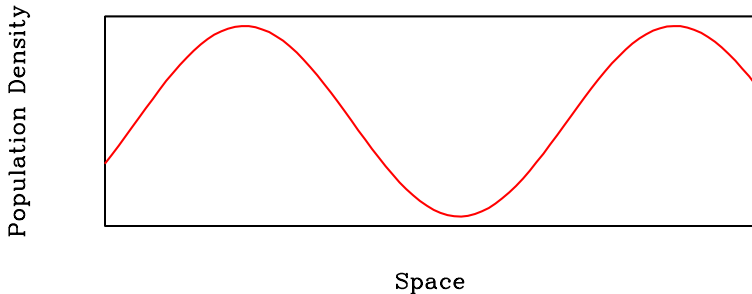
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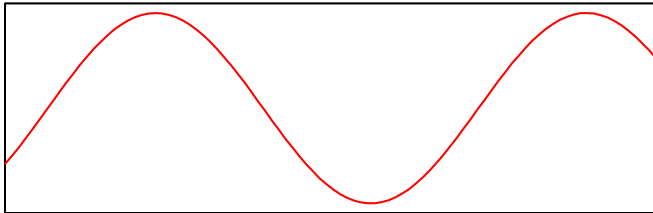
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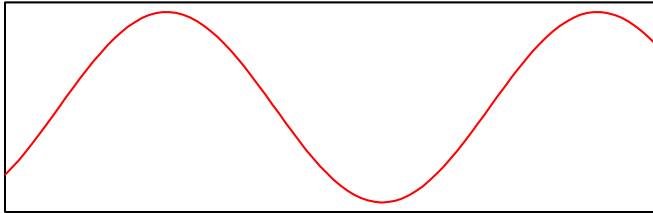


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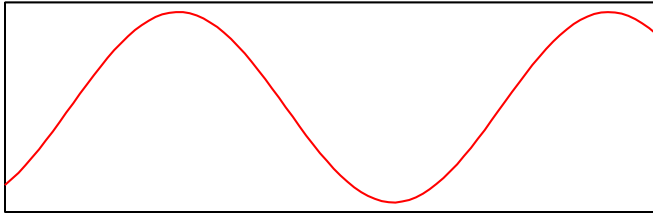


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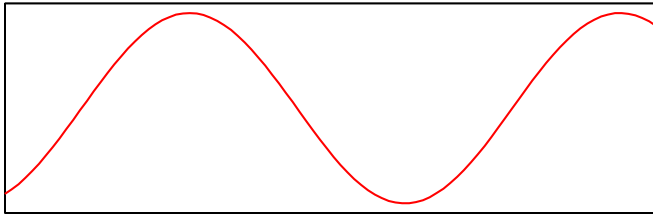


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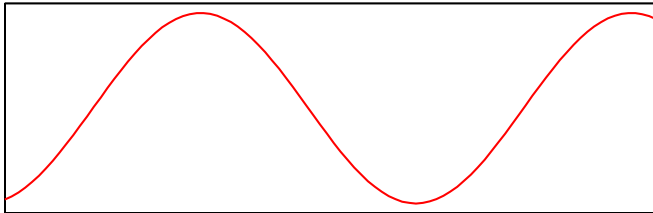


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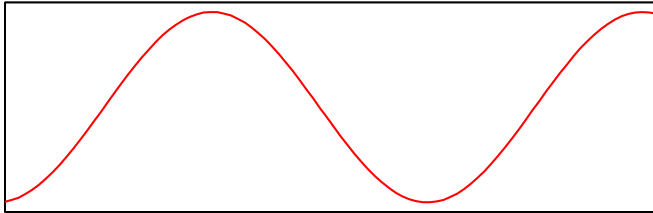


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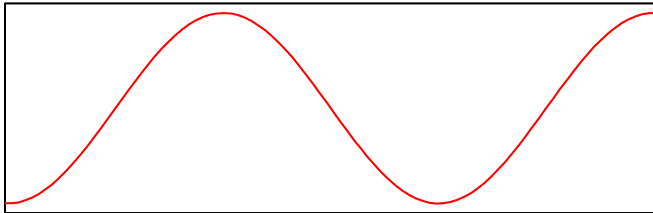


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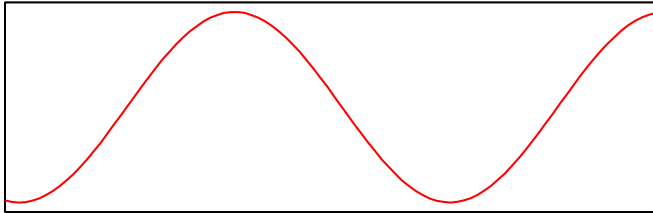


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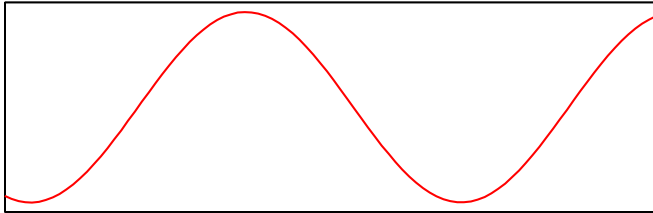


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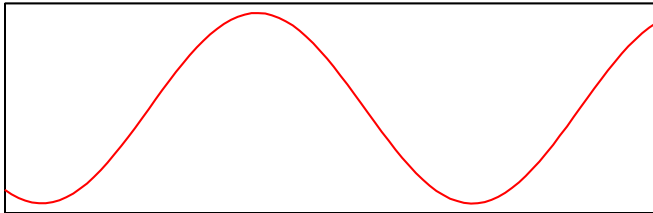


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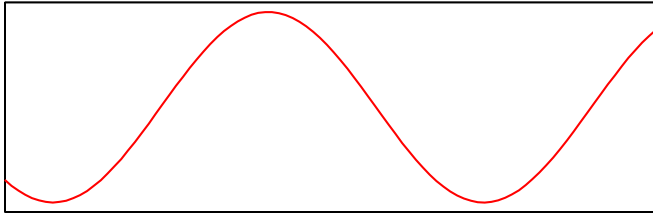


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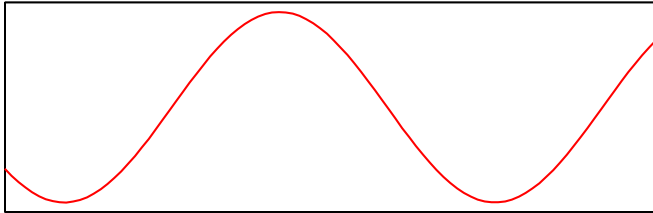


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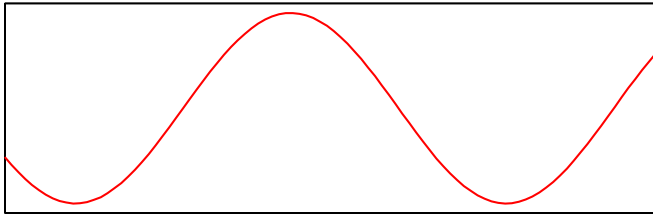


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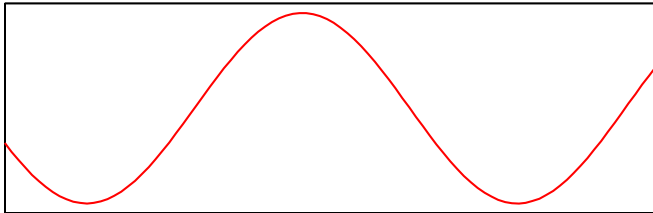


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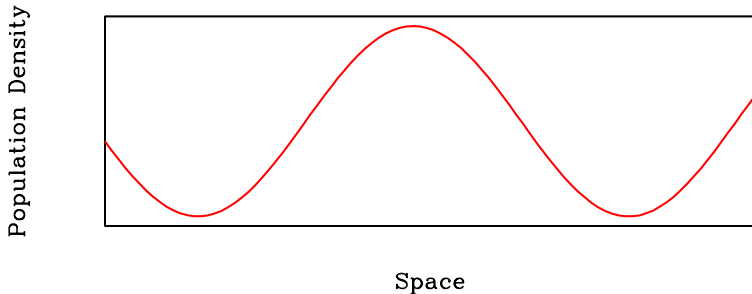
Population Density



Space

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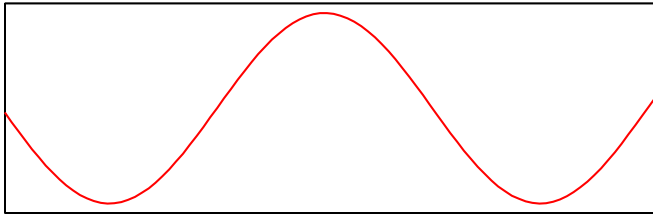
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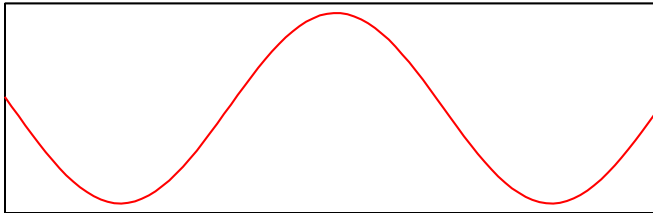


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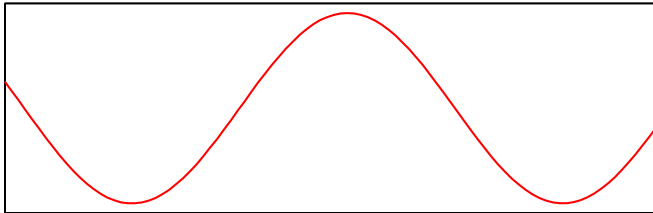


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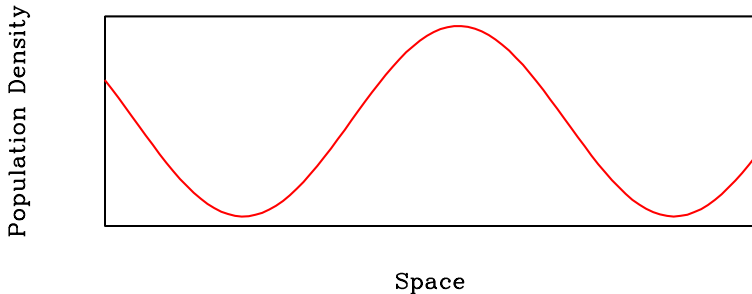
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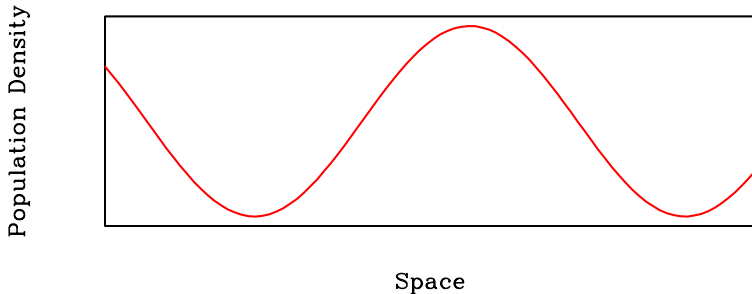
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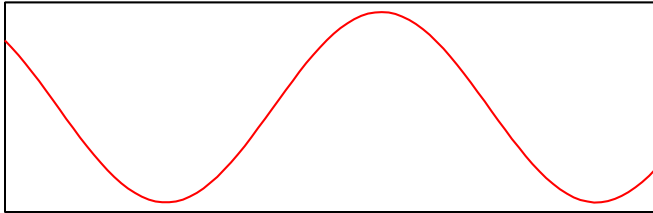
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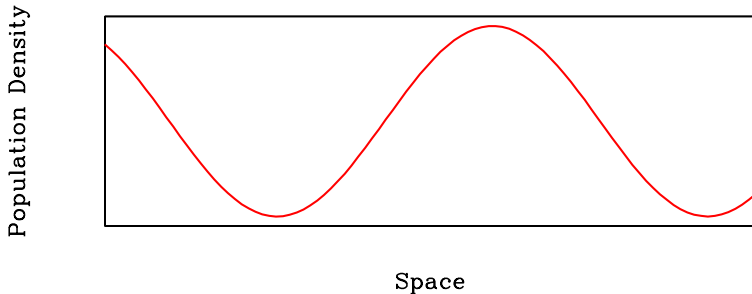
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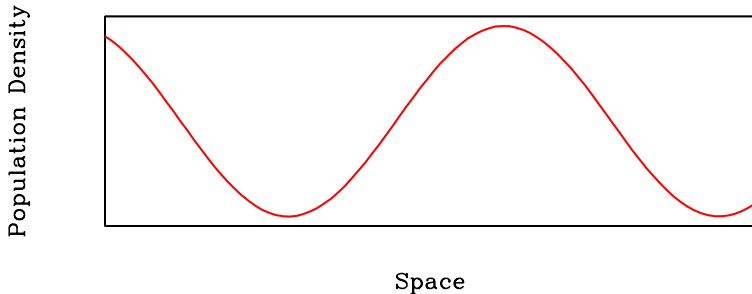
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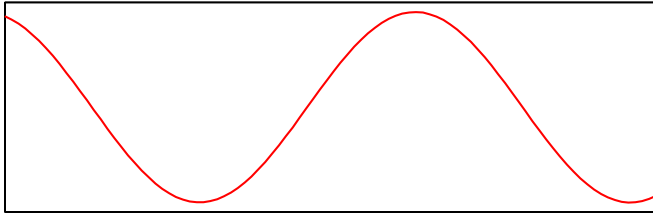
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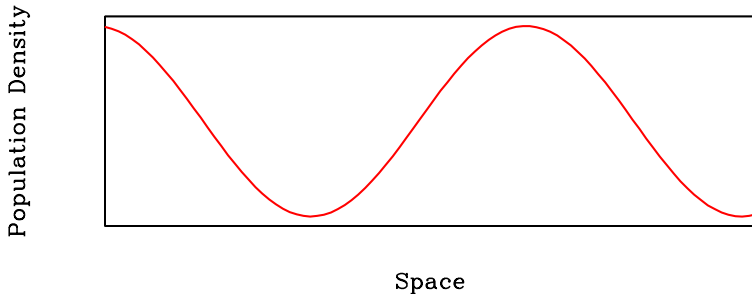
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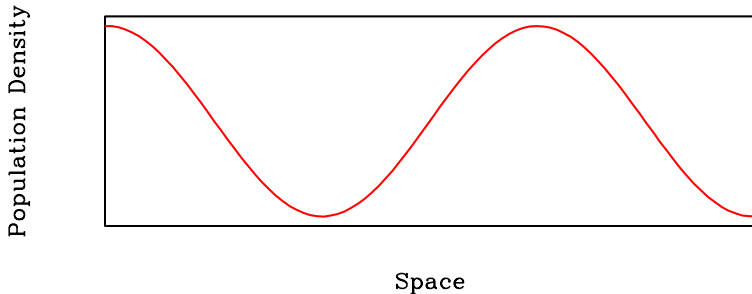
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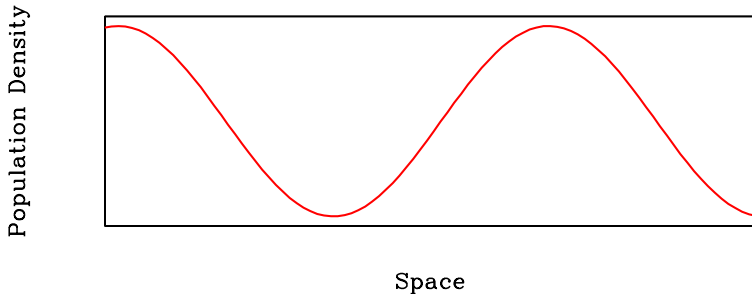
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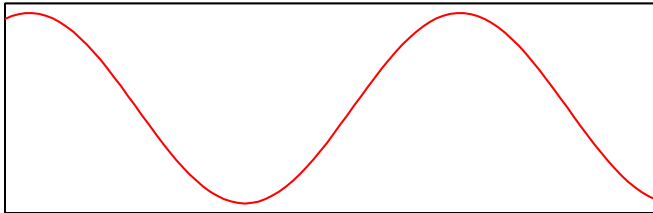
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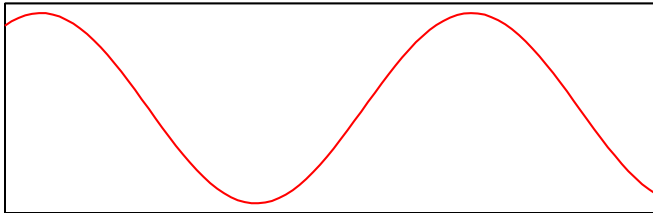


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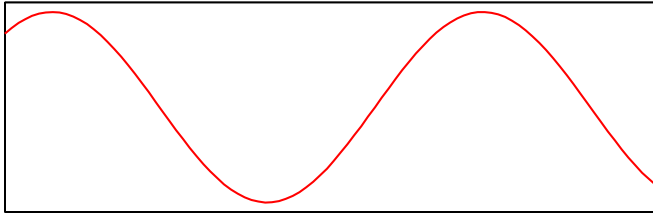


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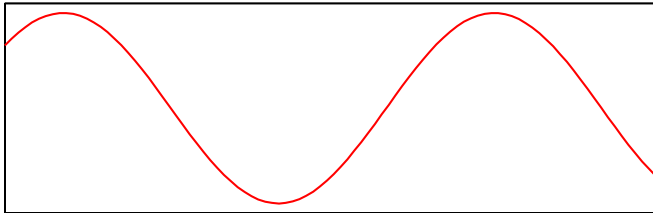


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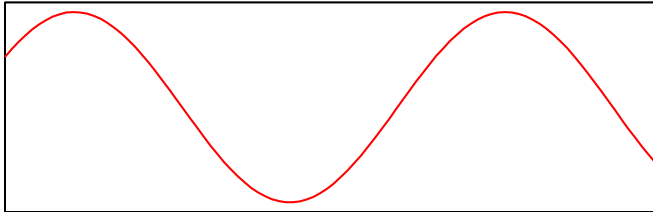


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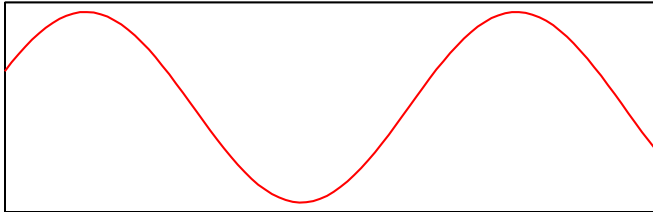


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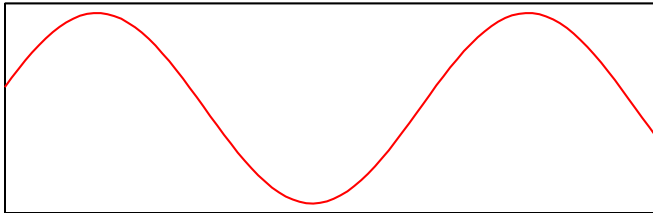


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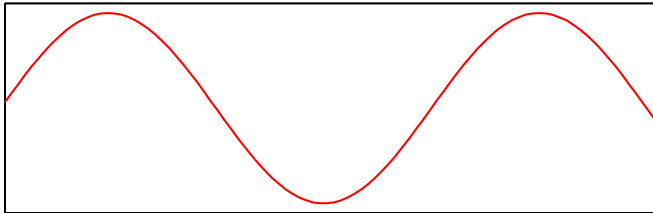


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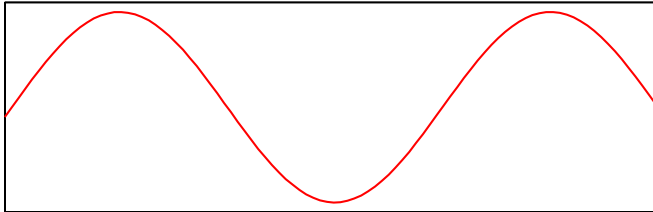


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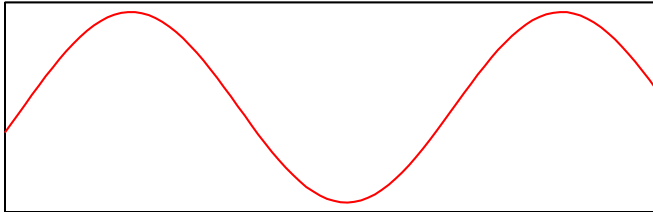


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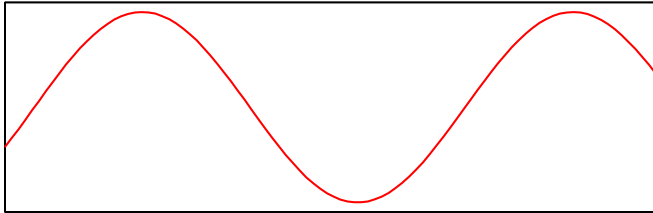


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Population Density



Space

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A wavetrain is a soln of form $f(x \pm st)$, with $f(\cdot)$ periodic.

There is an extensive literature on wavetrains
 in oscillatory reaction-diffusion equations

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

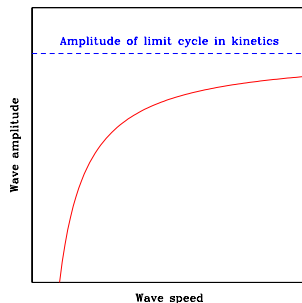
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An oscillatory reaction-diffusion system has a one-parameter family of wavetrain solutions

(if the diffusion coefficients are sufficiently close to one another)

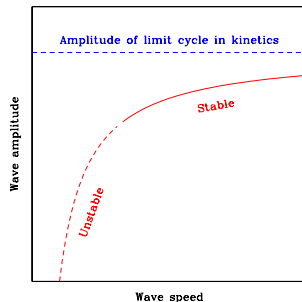
(Kopell, Howard (1973) *Stud Appl Math* 52:291)



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



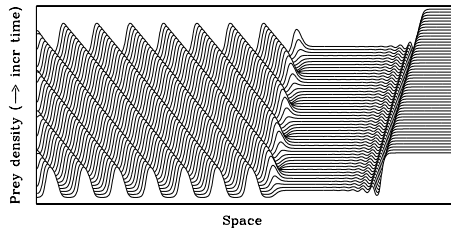
The Wavetrain Band

The invasion process selects a particular member of the wavetrain family (Sherratt (1998) *Physica D* 117:145).

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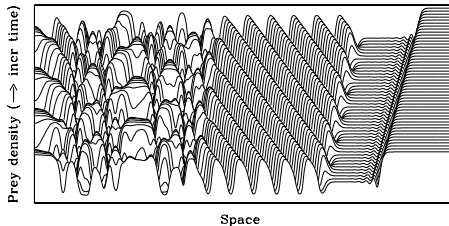
For these parameters,
the selected wavetrain
is stable.



The Wavetrain Band

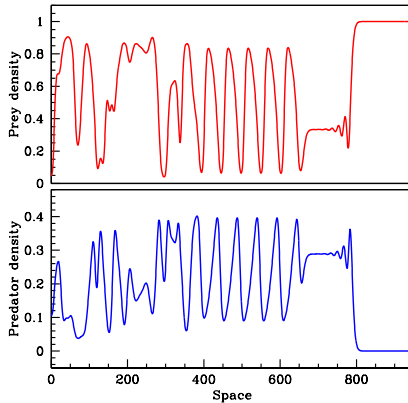
The invasion process selects a particular member of the wavetrain family (Sherratt (1998) *Physica D* 117:145).

A “wavetrain band” occurs when the selected wavetrain is unstable.

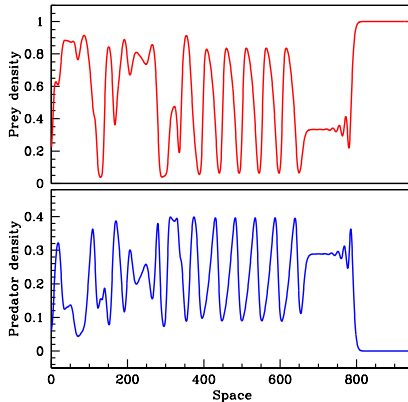


Question: what is the wavetrain band width?

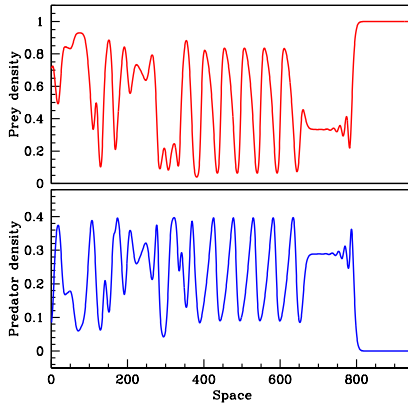
The Wavetrain Band: Animation



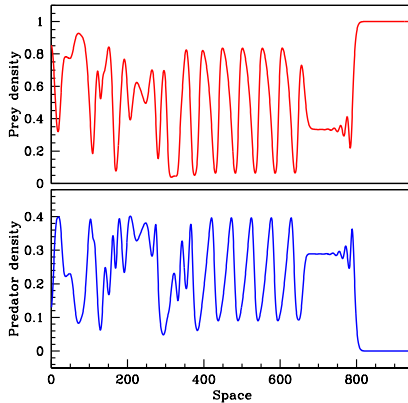
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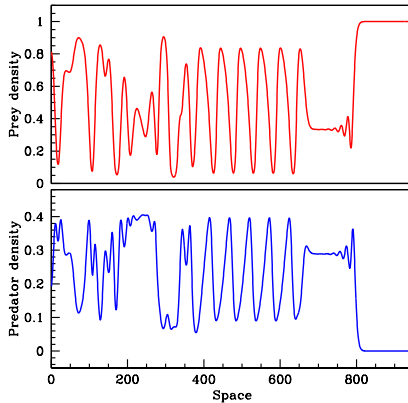
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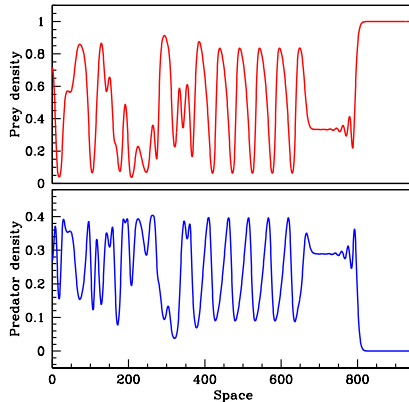
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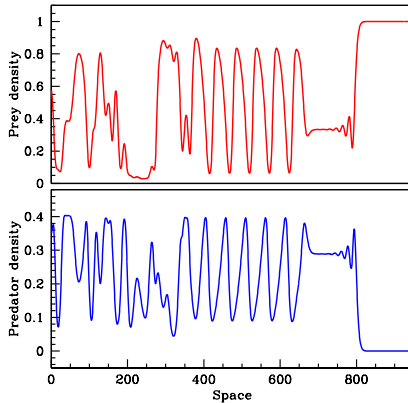
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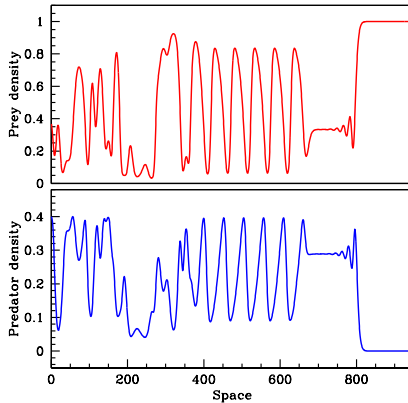
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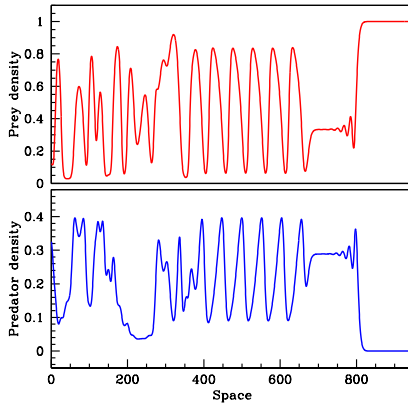
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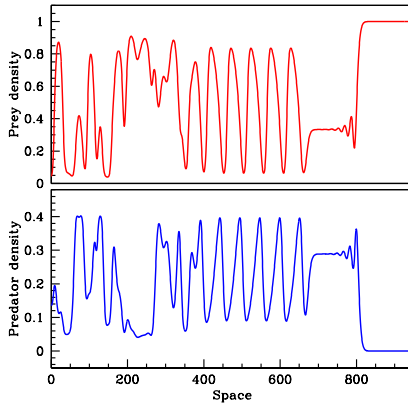
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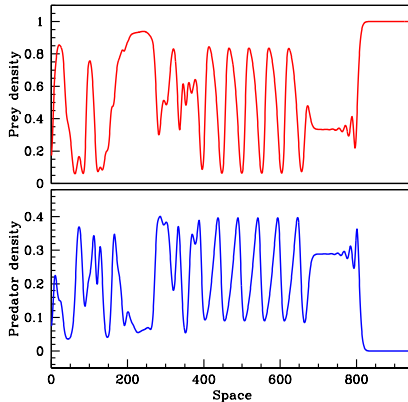
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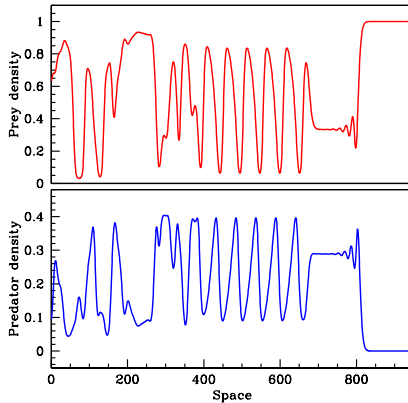
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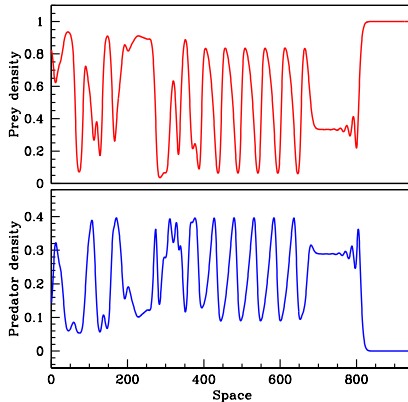
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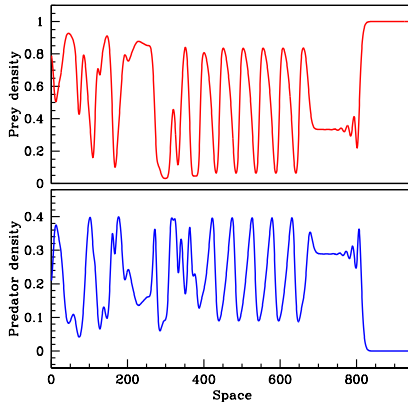
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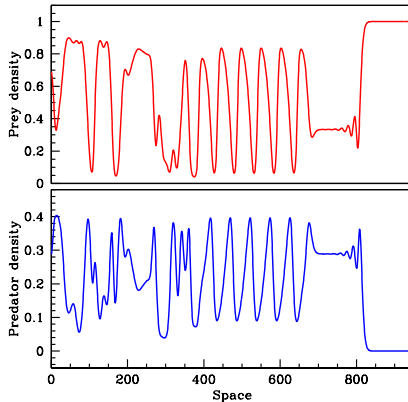
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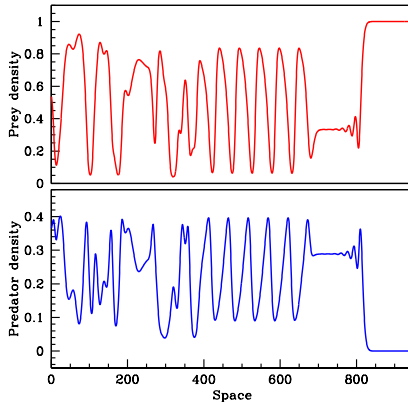
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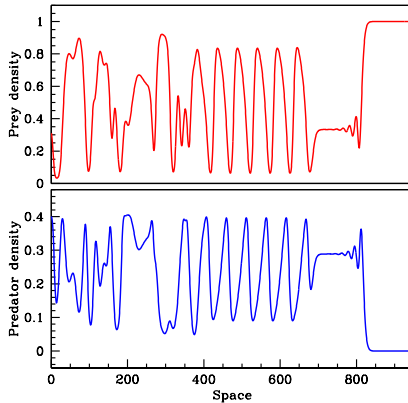
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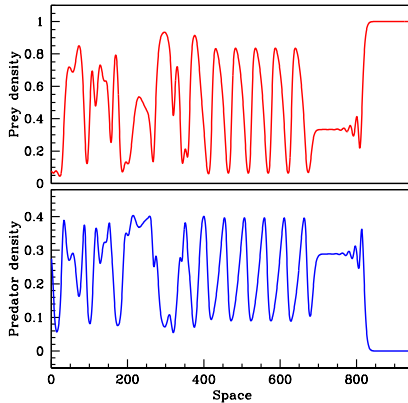
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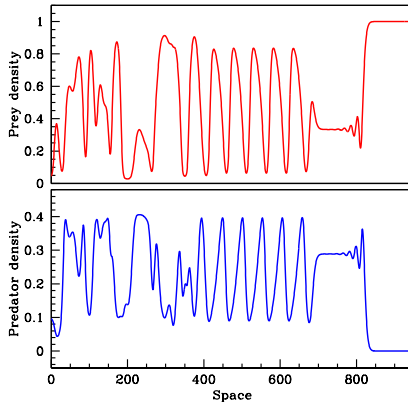
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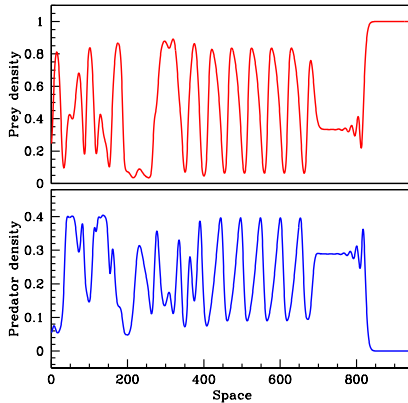
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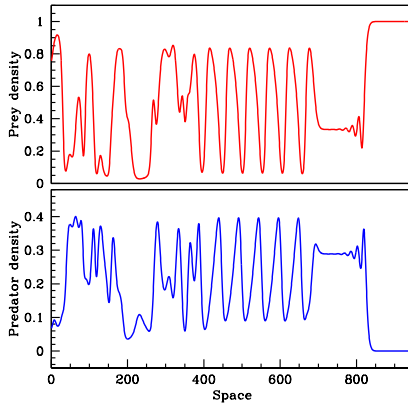
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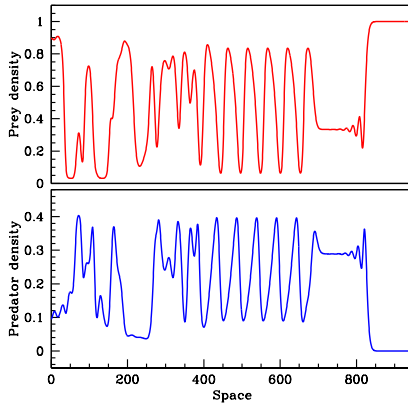
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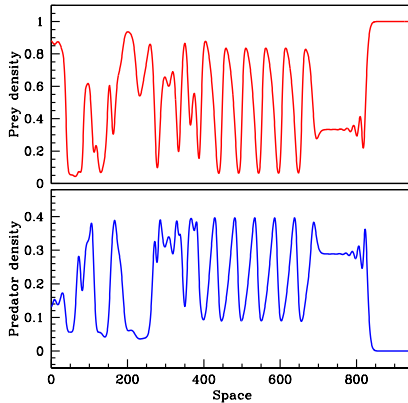
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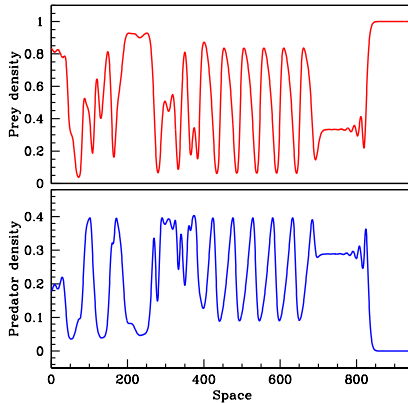
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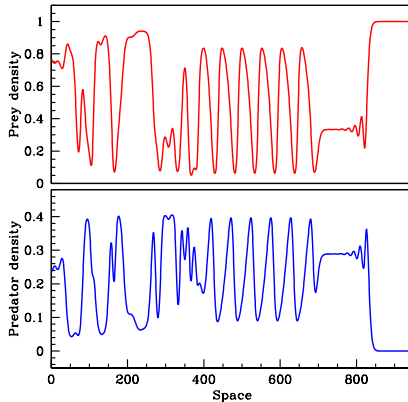
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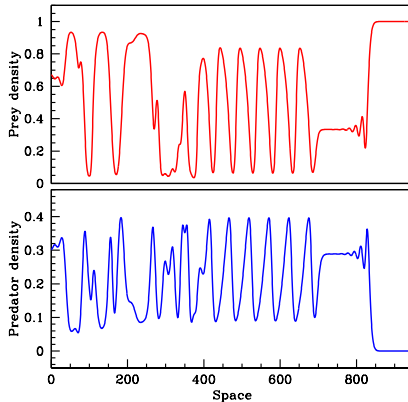
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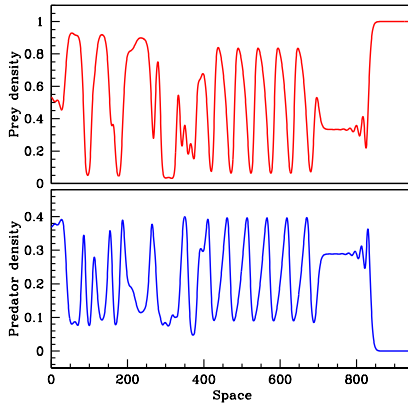
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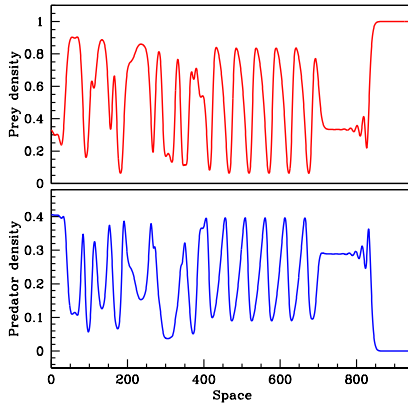
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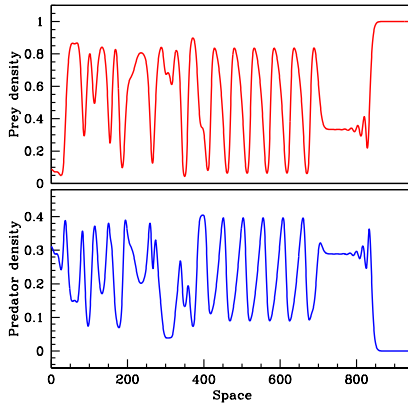
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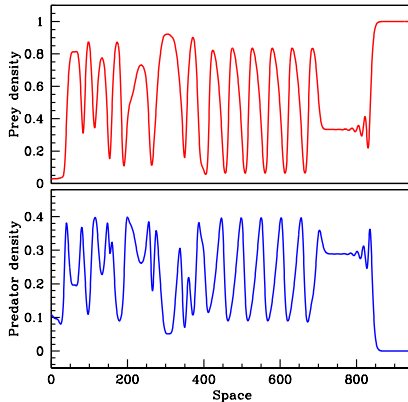
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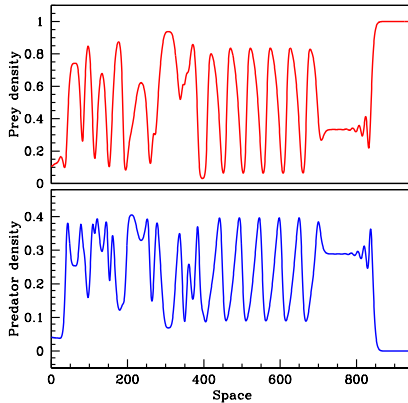
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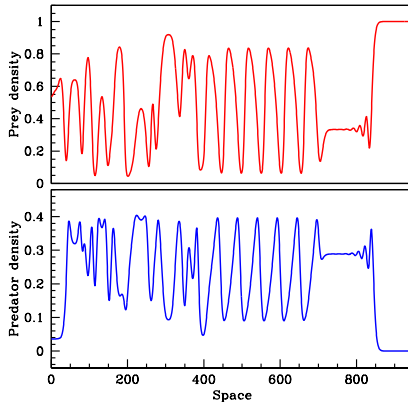
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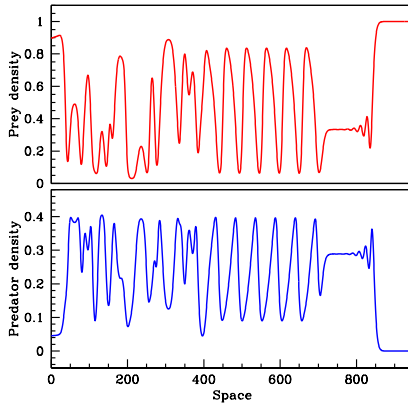
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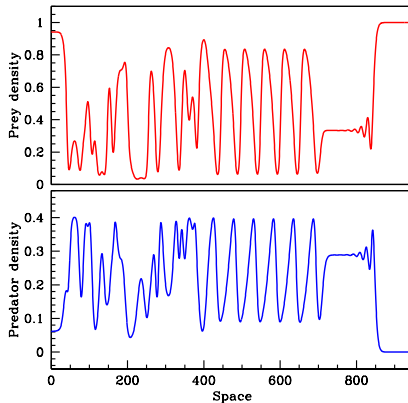
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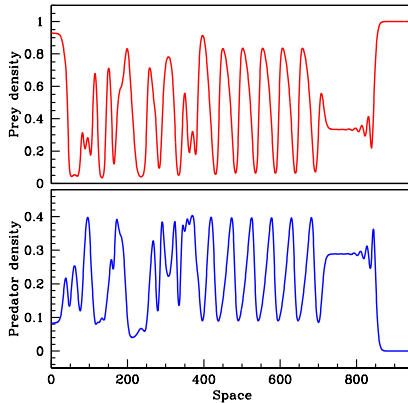
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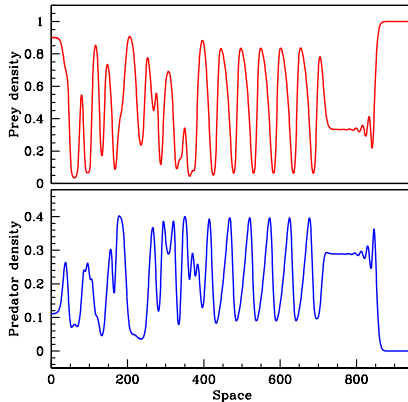
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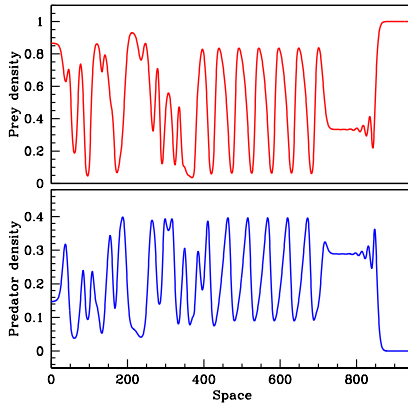
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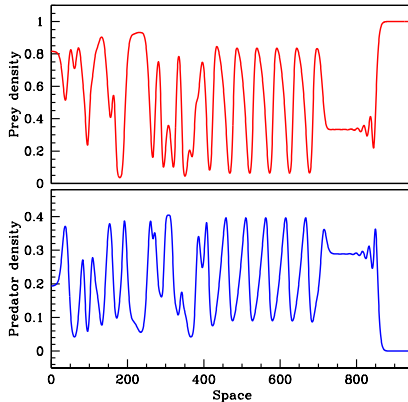
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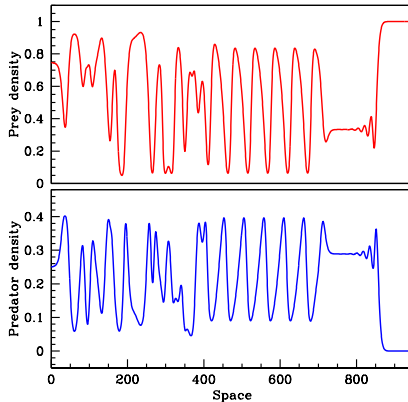
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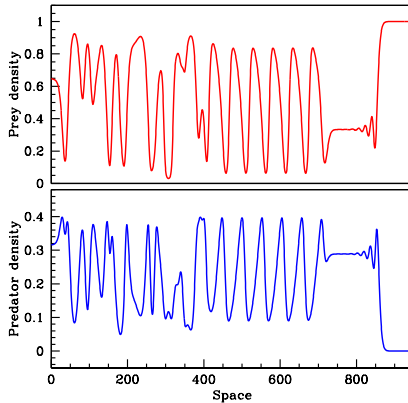
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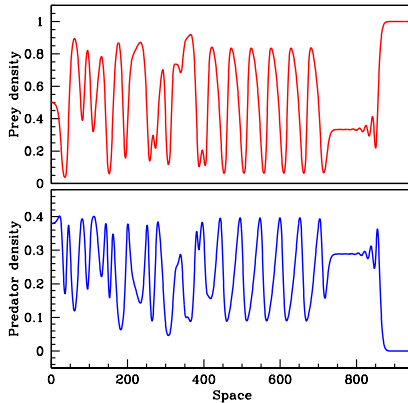
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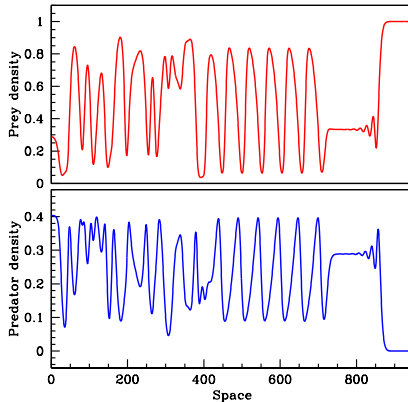
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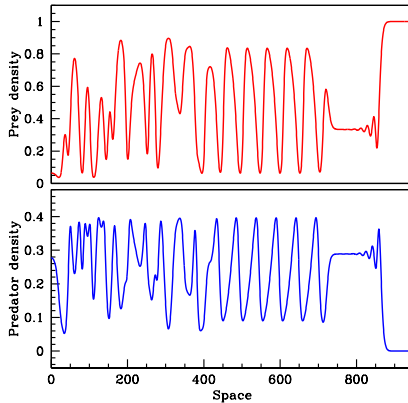
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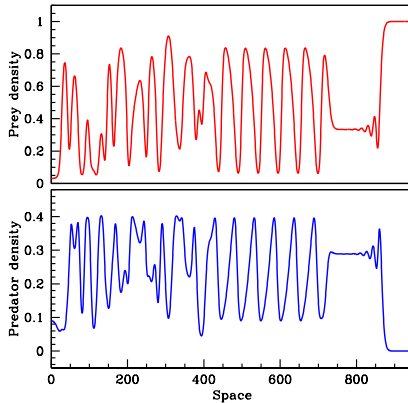
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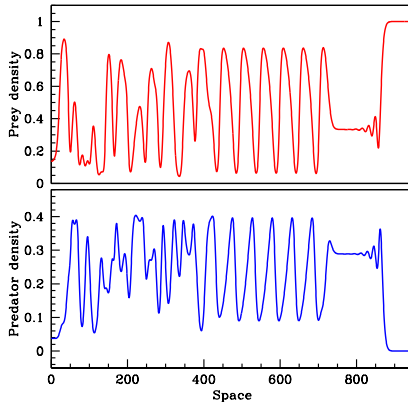
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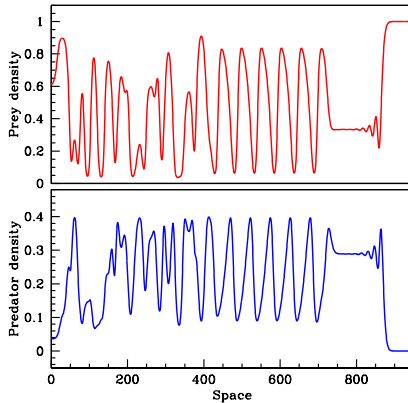
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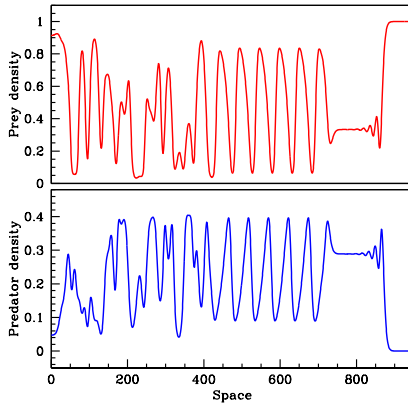
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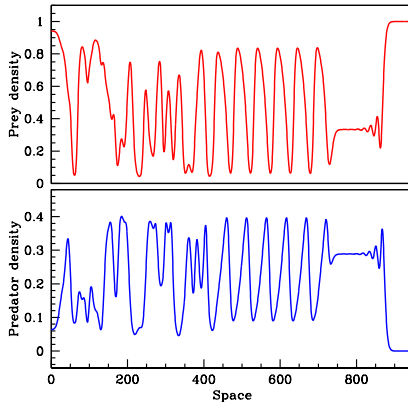
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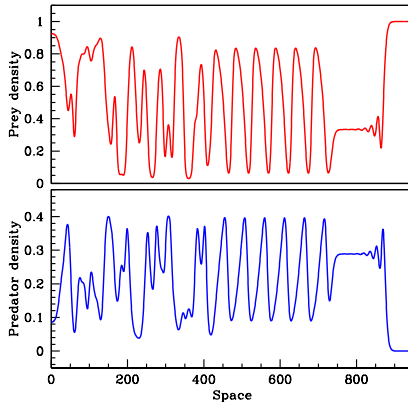
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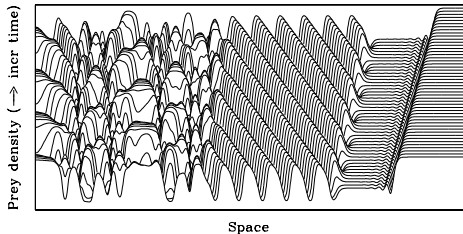


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- 1 Ecological Motivation and Statement of the Problem
- 2 The Complex Ginzburg-Landau Equation**
- 3 Band Width Calculation I: Wavetrain Selection
- 4 Band Width Calculation II: Absolute Stability
- 5 Band Width Calculation III: Formula and Ecological Implications

Using a Normal Form Equation

I consider parameter sets close to the Hopf bifurcation in the coexistence steady state.



Then one can use the normal form (amplitude equation).

The Complex Ginzburg-Landau Equation

The appropriate normal form (amplitude equation) is the CGLE

$$A_t = (1 + ib)A_{xx} + A - (1 + ic)|A|^2 A.$$

$$\text{i.e. } u_t = u_{xx} - bv_{xx} + (1 - r^2)u + cr^2v$$

$$v_t = bu_{xx} + v_{xx} - cr^2u + (1 - r^2)v$$

Here $A = u + iv$, $r = \sqrt{u^2 + v^2} = |A|$,

and b and c are functions of the ecological parameters.

The Complex Ginzburg-Landau Equation

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Here $A = u + iv$, $r = \sqrt{u^2 + v^2} = |A|$.

The wavetrain family is

$$A = \sqrt{1 - Q^2} \exp \left[i \left\{ Qx + (c - bQ^2 - cQ^2)t \right\} \right] \quad (-1 < Q < 1)$$

Invasion in the CGLE

Domain: $0 < x < x_{\max}$

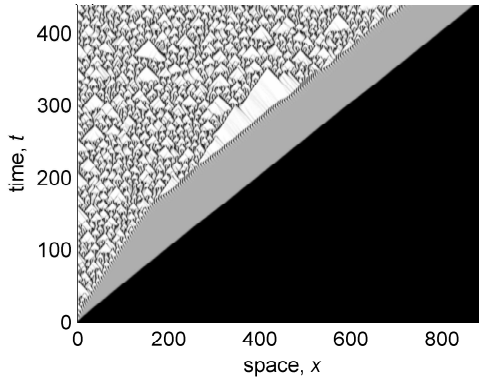
Initial conditions: $u = 0$

$v = 0$

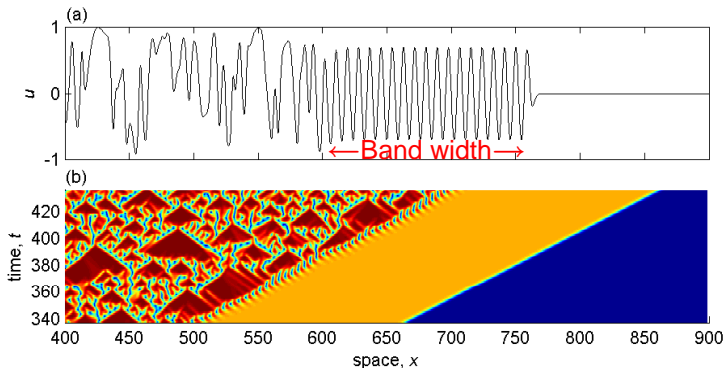
with a small perturbation near $x=0$

Boundary conditions: zero flux (i.e. zero Neumann)

Invasion in the CGLE



Invasion in the CGLE

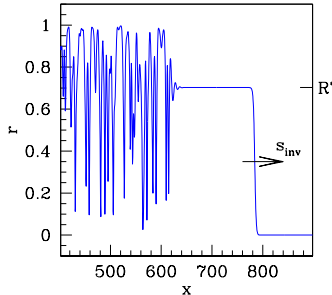


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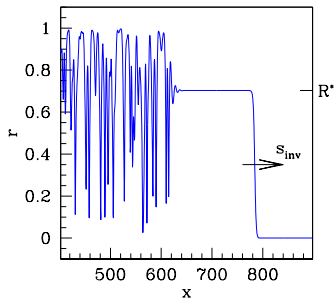
The Selected Wavetrain Amplitude

The form of the invasion solution is



The Selected Wavetrain Amplitude

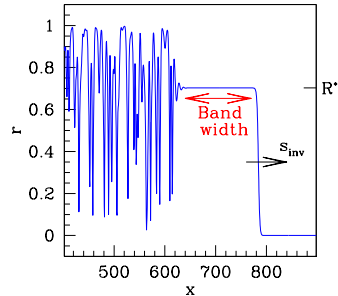
The form of the invasion solution is



The value of R^* can be calculated exactly, as a function of b and c .

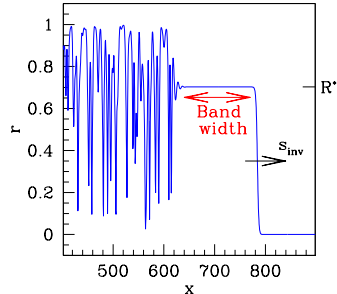
The Band Width Question

- Our question is: how wide is the region in which $r \approx R^*$?



The Band Width Question

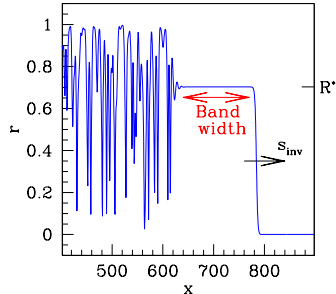
- Our question is: how wide is the region in which $r \approx R^*$?
- We define its left-hand edge as where unstable linear modes generated by the invasion front are amplified by a factor \mathcal{F}
- The band width has the form



$$\underbrace{\log(\mathcal{F})}_{\text{arbitrary}} \cdot \underbrace{\mathcal{W}(b, c)}_{\text{"band width coefficient"}}$$

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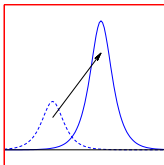
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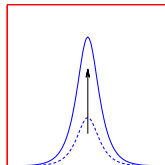
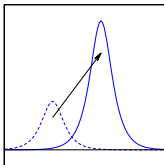
Convective and Absolute Stability

- In spatially extended systems, a solution can be unstable, but with any perturbation that grows also moving. This is “convective instability”.



Convective and Absolute Stability

- In spatially extended systems, a solution can be unstable, but with any perturbation that grows also moving. This is “convective instability”.
- Alternatively, a solution can be unstable with perturbations growing without moving. This is “absolute instability”.



Absolute Stability in a Moving Frame of Reference

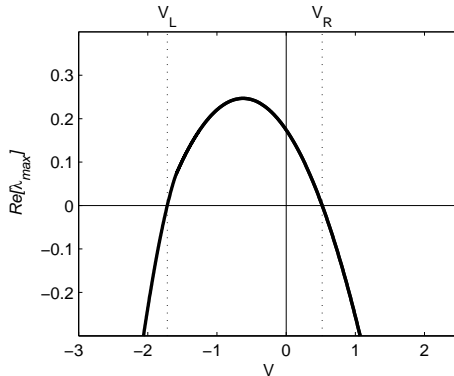
Absolute stability refers to the growth/decay of **stationary** perturbations.

We must consider the growth/decay of perturbations **moving** with a specified velocity V , i.e. absolute stability in a frame of reference moving with velocity V .

Define $\lambda_{max}(V)$ = temporal eigenvalue of the most unstable linear mode

$\nu_{max}(V)$ = the corresponding spatial eigenvalue

Absolute Stability in a Moving Frame of Reference



Calculation of $\lambda_{max}(V)$

Replace x by $x - Vt$ and calculate the “absolute spectrum”

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- 2 \mathcal{D} is a quartic polynomial in ν , roots ν_1, \dots, ν_4 with $\operatorname{Re} \nu_1 \geq \operatorname{Re} \nu_2 \geq \operatorname{Re} \nu_3 \geq \operatorname{Re} \nu_4$
- 3 “Absolute spectrum” $:= \{\lambda \mid \operatorname{Re} \nu_2 = \operatorname{Re} \nu_3\}$
 $\lambda_{\max}(V) = \lambda$ with max Re in the absolute spectrum

The Significance of $\operatorname{Re} \nu_2 = \operatorname{Re} \nu_3$

(Worledge, Knobloch, Tobias, Proctor (1997) *Proc. R. Soc. Lond. A* 453:119)

- Consider the linearised r - θ PDEs on $-\ell < x < +\ell$, ℓ large.
- For given λ , these equations have the solution

$$\underbrace{(\tilde{r}, \tilde{\theta})}_{\text{Linearisation variables}} = e^{\lambda t} \sum_{j=1}^4 \underbrace{(\bar{r}_j, \bar{\theta}_j)}_{\text{eigen-vector}} k_j e^{\nu_j x}$$

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- Suppose that both boundary conditions are $\tilde{r} = 0$, $\tilde{\theta}_x = 0$
- If $\text{Re}(\nu_j)$'s are distinct then since ℓ is large

$$\sum_{j=1}^2 (\bar{r}_j, \nu_j \bar{\theta}_j) k_j e^{+\nu_j \ell} = \sum_{j=3}^4 (\bar{r}_j, \nu_j \bar{\theta}_j) k_j e^{-\nu_j \ell} = (0, 0).$$

Typically this has no non-trivial solutions for the k_j 's

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- Suppose that both boundary conditions are $\tilde{r} = 0$, $\tilde{\theta}_x = 0$
- $\text{Re } (\nu_1) = \text{Re } (\nu_2)$ and/or $\text{Re } (\nu_3) = \text{Re } (\nu_4) \Rightarrow$ no change:

$$\sum_{j=1}^2 (\bar{r}_j, \nu_j \bar{\theta}_j) k_j e^{+\nu_j \ell} = \sum_{j=3}^4 (\bar{r}_j, \nu_j \bar{\theta}_j) k_j e^{-\nu_j \ell} = (0, 0).$$

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- Suppose that both boundary conditions are $\tilde{r} = 0$, $\tilde{\theta}_x = 0$
- But if $\text{Re}(\nu_2) = \text{Re}(\nu_3)$ then

$$\sum_{j=1}^3 (\bar{r}_j, \nu_j \bar{\theta}_j) k_j e^{+\nu_j \ell} = \sum_{j=2}^4 (\bar{r}_j, \nu_j \bar{\theta}_j) k_j e^{-\nu_j \ell} = (0, 0).$$

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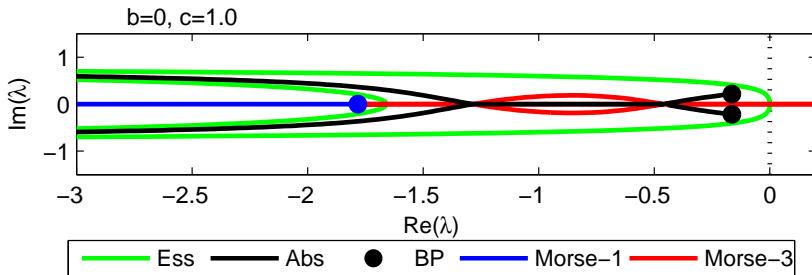
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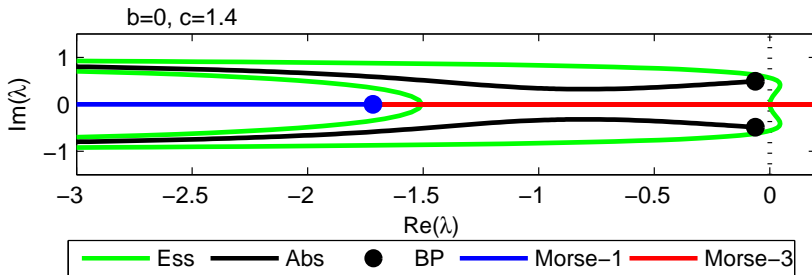


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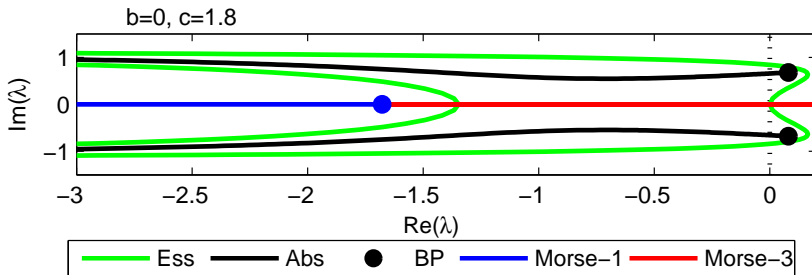


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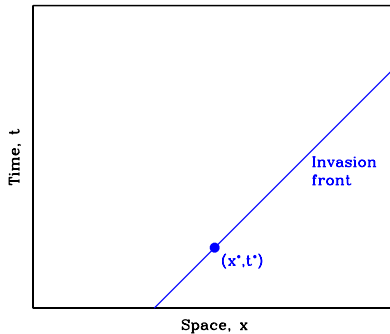
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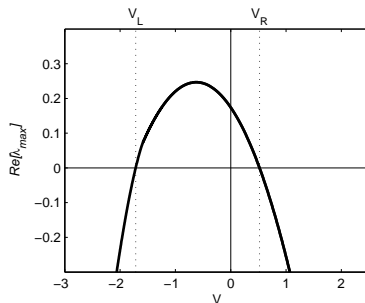
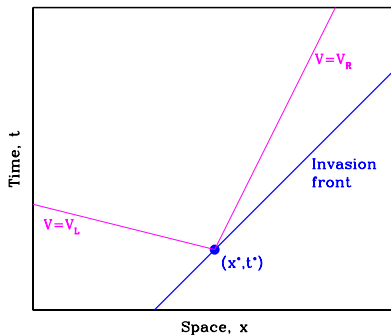
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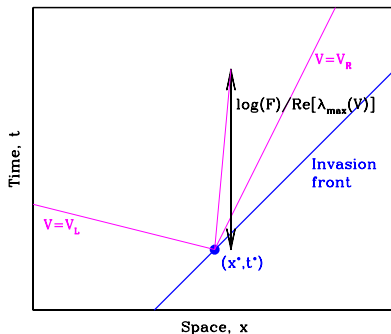
The Band Width Formula



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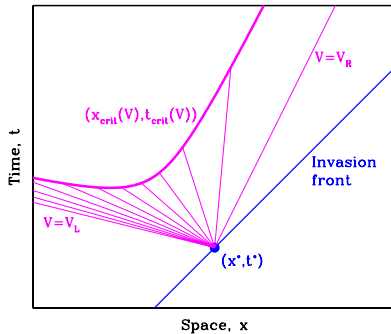
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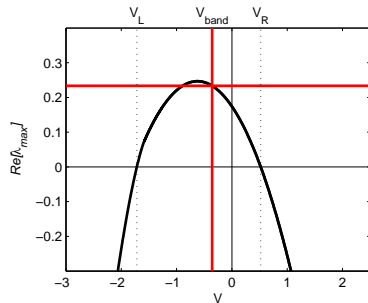
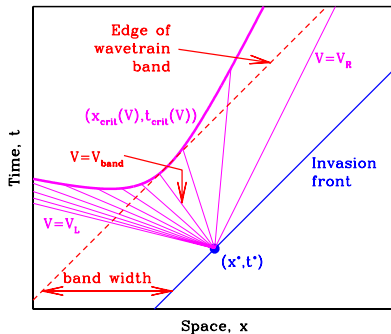
Perturbations moving
 with velocity V grow as
 $\exp[\text{Re}(\lambda_{\max}(V)) \cdot t]$

\Rightarrow amplified by the factor \mathcal{F} after
 time $\log(\mathcal{F}) / \text{Re}(\lambda_{\max}(V))$

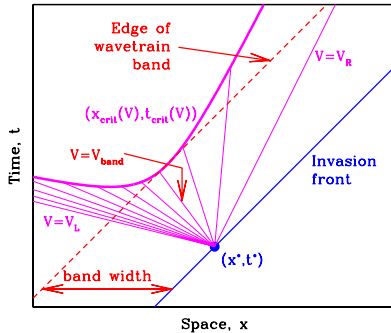
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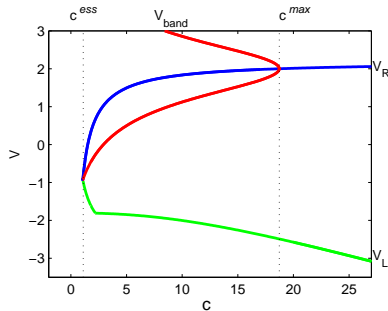
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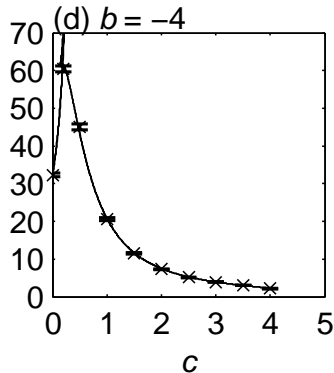
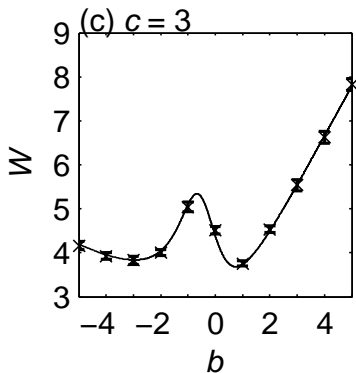
$$\mathcal{W} = 1/\text{Re} [\nu_{\max}(V_{band})]$$

$$\text{where } (V_{band} - s_{inv})\text{Re} [\nu_{\max}(V_{band})] = \text{Re} [\lambda_{\max}(V_{band})]$$

The Form of V_{band} and \mathcal{W}

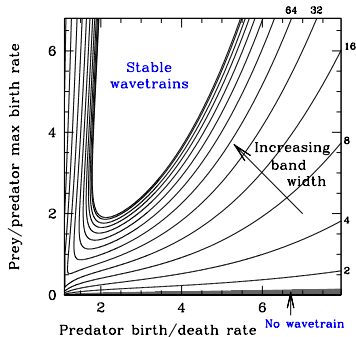


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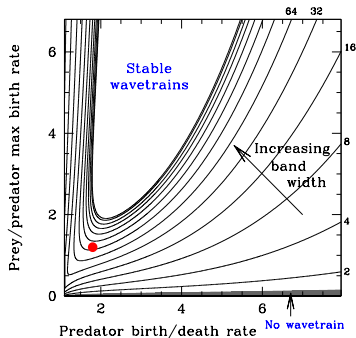
Back to Predator-Prey Invasion

Our formula gives band width vs b and c .
 Normal form calculation gives b and c vs ecological parameters.



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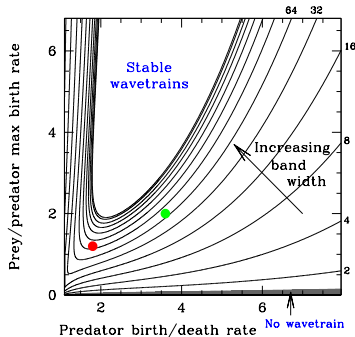


● = weasel-vole demographic parameters, $b = 0$.

5%↑ in vole birth rate
 \Rightarrow 22%↑ in band width.

Back to Predator-Prey Invasion

Our formula gives band width vs b and c .
 Normal form calculation gives b and c vs ecological parameters.



● = plankton demographic parameters, $b = 0$
 (*Daphnia pulex*–*Chlamydomonas reinhardtii*).

5.2%↓ in zooplankton birth rate
 \Rightarrow doubling of band width.

Ecological Implications of Band Width Sensitivity

- Climate change \Rightarrow more frequent invasions.
- It is known that climate change is significantly affecting the parameters of oscillatory ecological systems (e.g. Ims *et al* (2008) *TREE* 23:79).
- We have shown that band width depends sensitively on ecological parameters.
- Our results suggest that the implications of climate change for *spatiotemporal* dynamics may be even more dramatic than for purely temporal behaviour.

References

- **J.A. Sherratt, M.J. Smith, J.D.M. Rademacher:** Locating the transition from periodic oscillations to spatiotemporal chaos in the wake of invasion.
Proc. Natl. Acad. Sci. USA 106, 10890-10895 (2009).
- **M.J. Smith, J.A. Sherratt:** Propagating fronts in the complex Ginzburg-Landau equation generate fixed-width bands of plane waves.
Phys. Rev. E 80, art. no. 046209 (2009).
- **M.J. Smith, J.D.M. Rademacher, J.A. Sherratt:** Absolute stability of wavetrains can explain spatiotemporal dynamics in reaction-diffusion systems of lambda-omega type.
SIAM J. Appl. Dyn. Systems 8, 1136-1159 (2009).

List of Frames

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- Cyclic Predator-Prey Systems
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- The Wavetrain Band
- The Wavetrain Band: Animation

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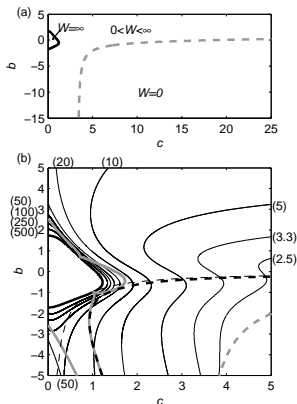
4 Band Width Calculation II: Absolute Stability

- Convective and Absolute Stability
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- The Significance of $\text{Re } \nu_2 = \text{Re } \nu_3$
- Calculation of $\lambda_{max}(V)$ (continued)

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- The Form of V_{band} and \mathcal{W}
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The Form of V_{band} and \mathcal{W}



- band width contour
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- - - abs stab bdy for selected wavetrain in invasion frame of reference
- abs stab bdy for selected wavetrain in stationary frame of reference
- - - Benjamin-Feir-Newell curve
- - - abs stab curve