Ecological Invasions in Cyclic Populations

Jonathan A. Sherratt

Department of Mathematics
Heriot-Watt University

Multiply Structured Populations in Biology
University of Bath, July 2009

This talk can be downloaded from my web site
`www.ma.hw.ac.uk/~jas`

This work is in collaboration with:

Matthew Smith

(Microsoft Research Cambridge)

Jens Rademacher

(CWI, Amsterdam)

Xavier Lambin

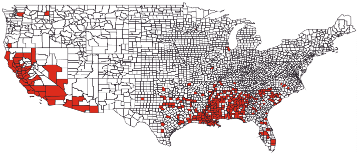
(University of Aberdeen)

Outline

Outline

Climate Change and Invasions

- Climate change ⇒ more frequent ecological invasions.
- Examples:



In California, argentine ants do not decrease foraging time as temperatures rise, in contrast to native ant species.

Climate Change and Invasions

- Climate change $\Rightarrow$ more frequent ecological invasions.
- Examples:

White-cloud mountain minnows (an aquarium fish) are released into the Great Lakes and could invade if water temperatures increase.

Climate Change and Invasions

- Climate change $\Rightarrow$ more frequent ecological invasions.
- Examples:

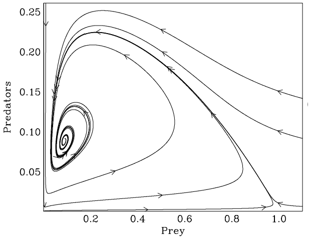
Water hyacinth may overwinter in New England due to climate change.

Climate Change and Invasions

- Climate change $\Rightarrow$ more frequent ecological invasions.
- My focus: invasion of a prey population by predators when the population dynamics are cyclic.

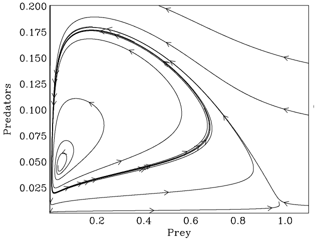
Cyclic Predator-Prey Systems

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 $\longrightarrow$ parameters



cycles

Example: Voles and Weasels in Fennoscandia

Fennoscandian voles

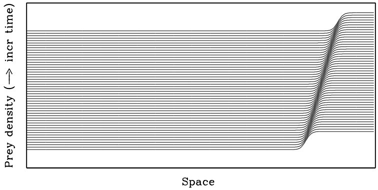
Fennoscandia

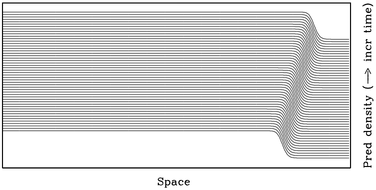
Predator-Prey Invasion

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

Predator-Prey Invasion

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

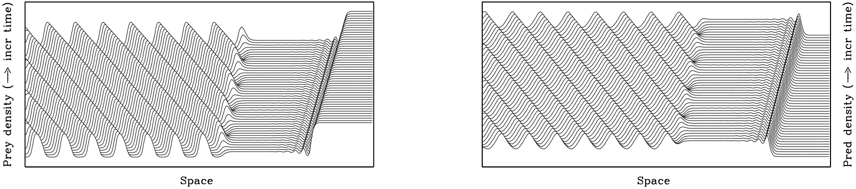




Simple invasion front (local bhr: constant)

Predator-Prey Invasion

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



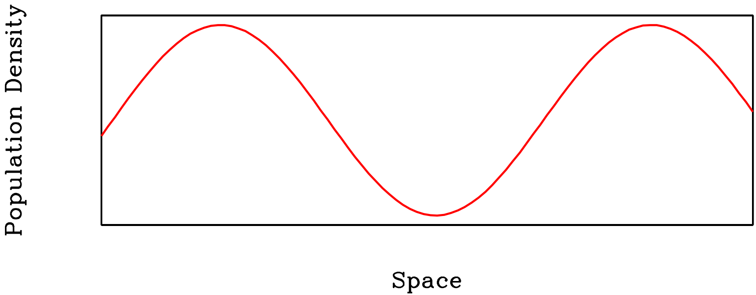
Wavetrain behind an invasion front (local bhr: cycles)

What is a Wavetrain?

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

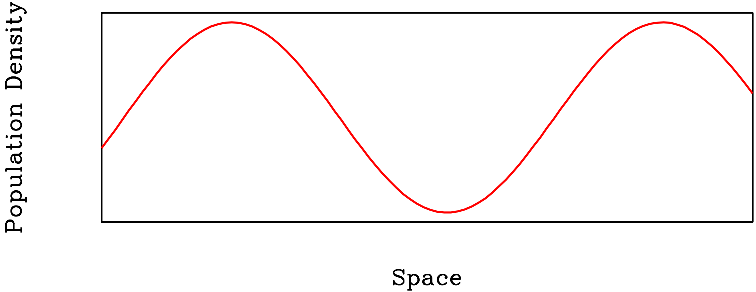
What is a Wavetrain?

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



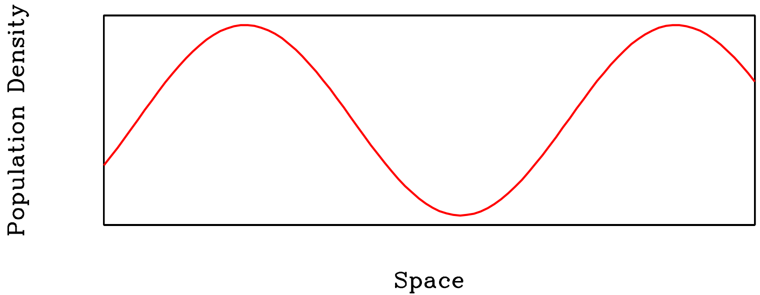
What is a Wavetrain?

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



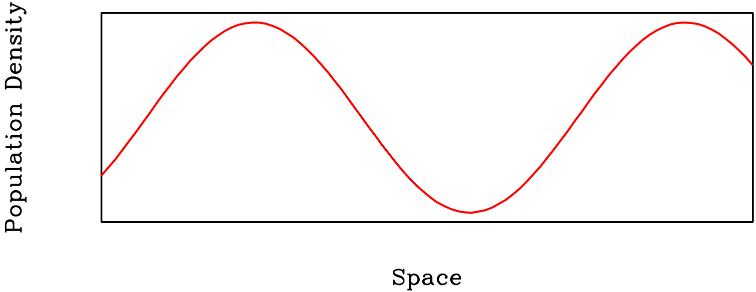
What is a Wavetrain?

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



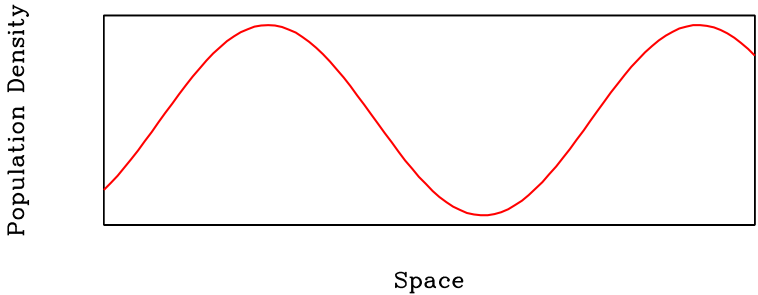
What is a Wavetrain?

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



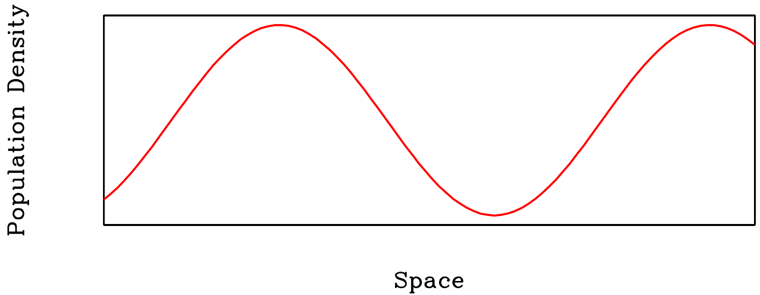
What is a Wavetrain?

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



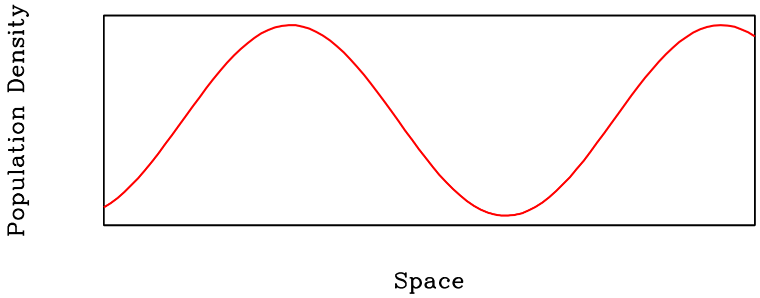
What is a Wavetrain?

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



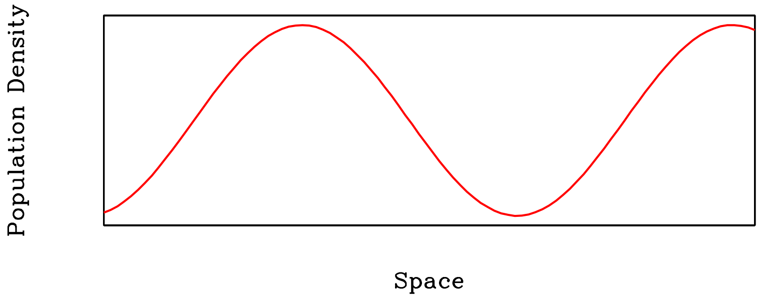
What is a Wavetrain?

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



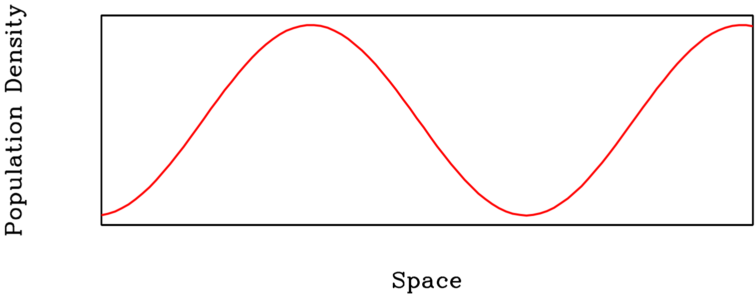
What is a Wavetrain?

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



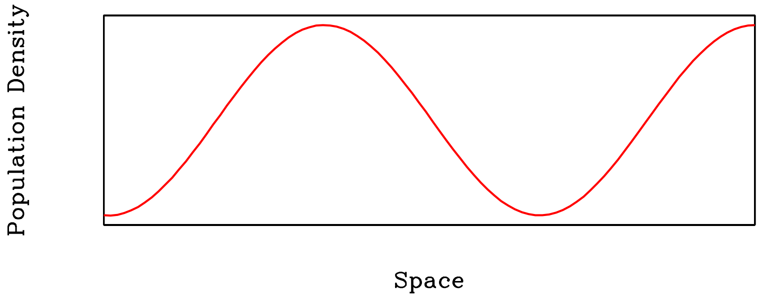
What is a Wavetrain?

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



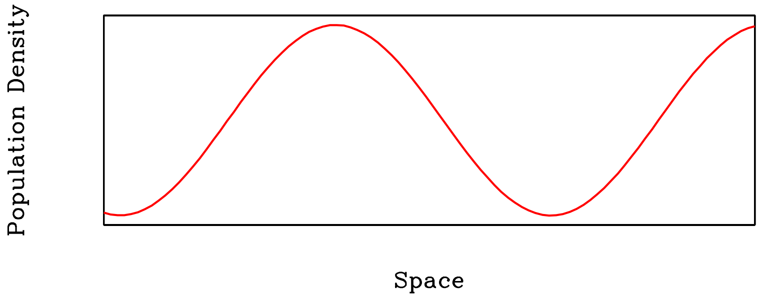
What is a Wavetrain?

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



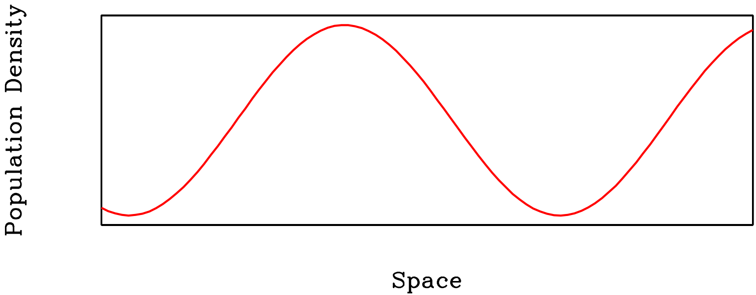
What is a Wavetrain?

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



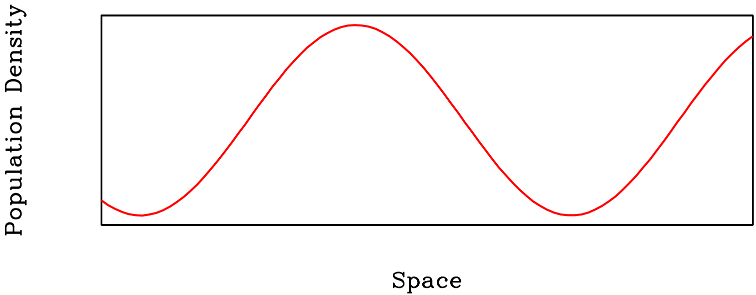
What is a Wavetrain?

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



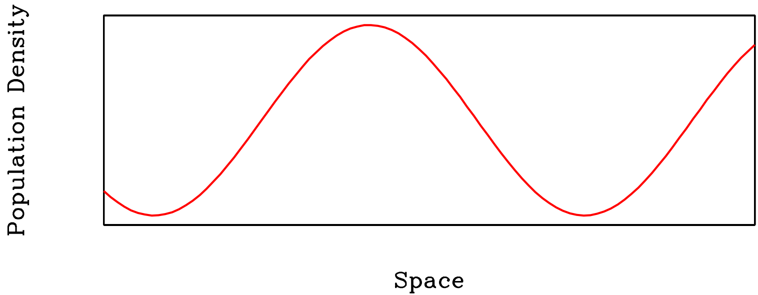
What is a Wavetrain?

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



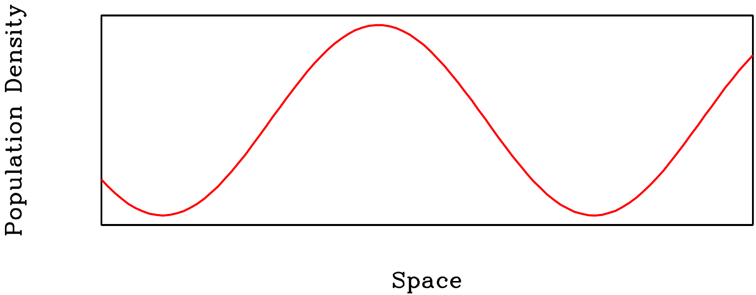
What is a Wavetrain?

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



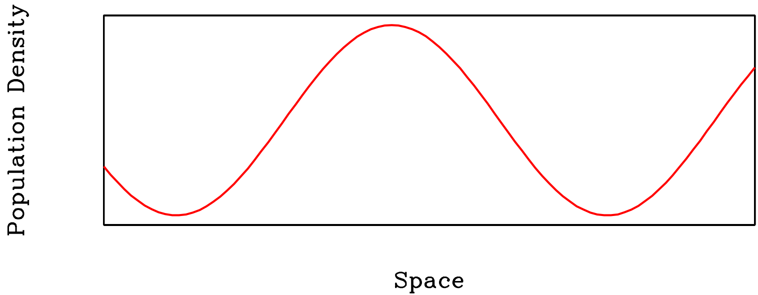
What is a Wavetrain?

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



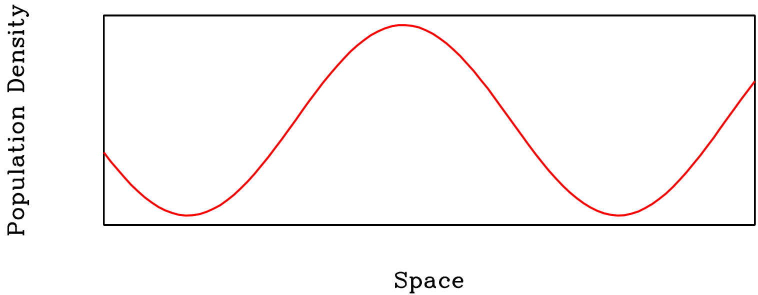
What is a Wavetrain?

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



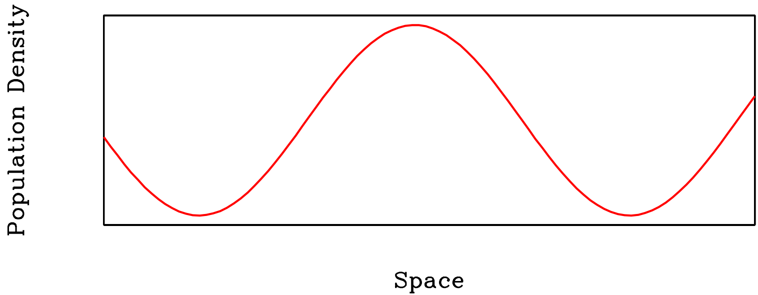
What is a Wavetrain?

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



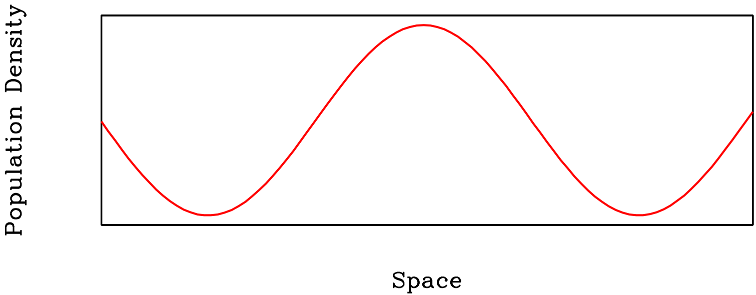
What is a Wavetrain?

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



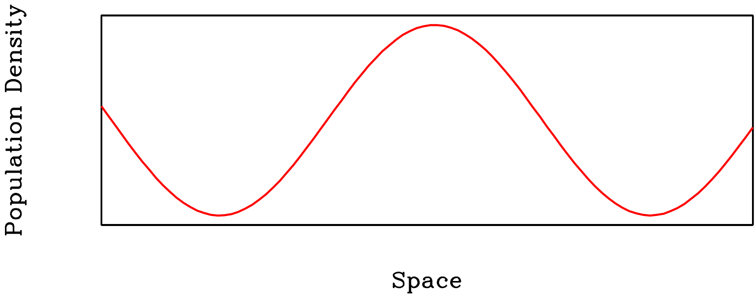
What is a Wavetrain?

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



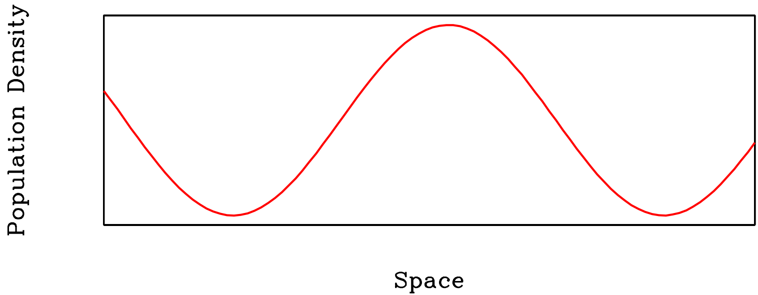
What is a Wavetrain?

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



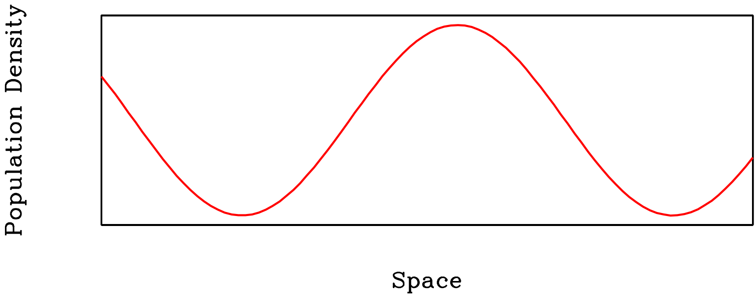
What is a Wavetrain?

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



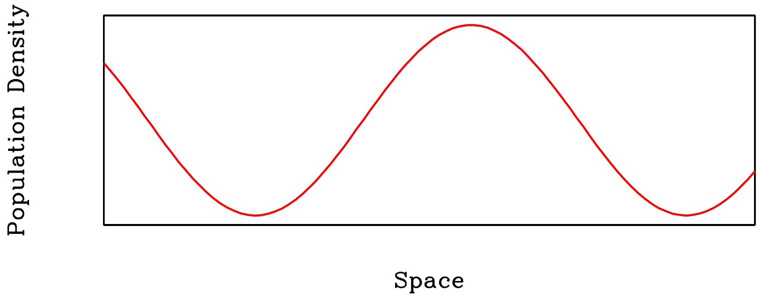
What is a Wavetrain?

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



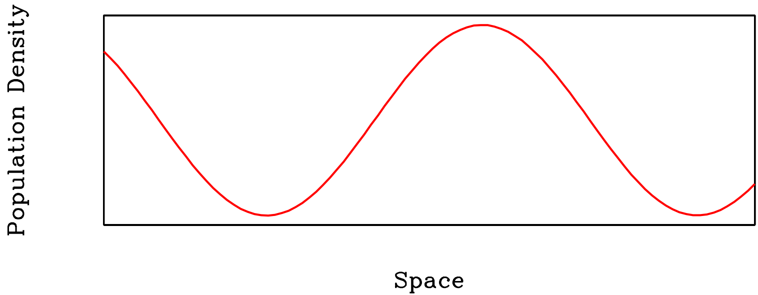
What is a Wavetrain?

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



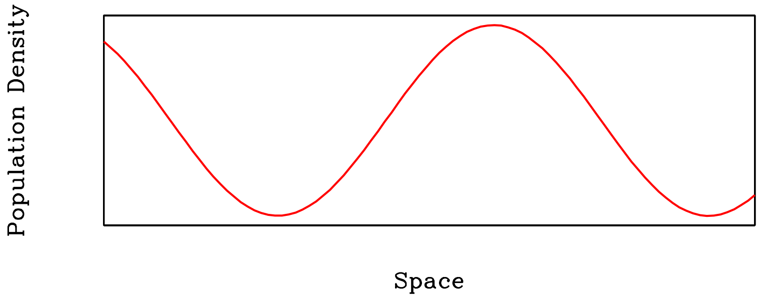
What is a Wavetrain?

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



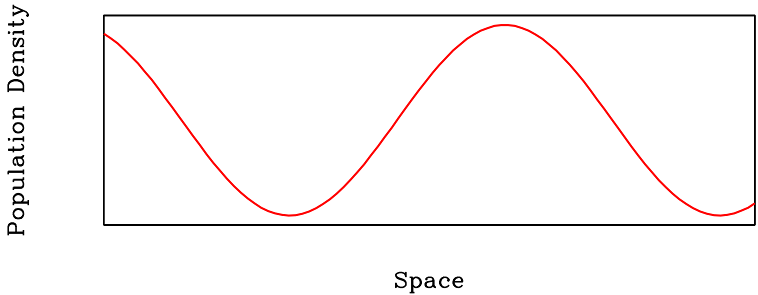
What is a Wavetrain?

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



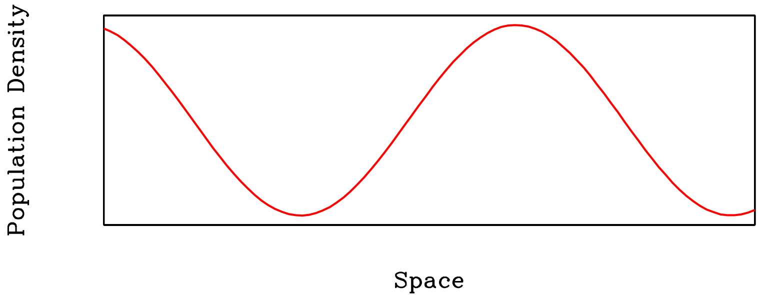
What is a Wavetrain?

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



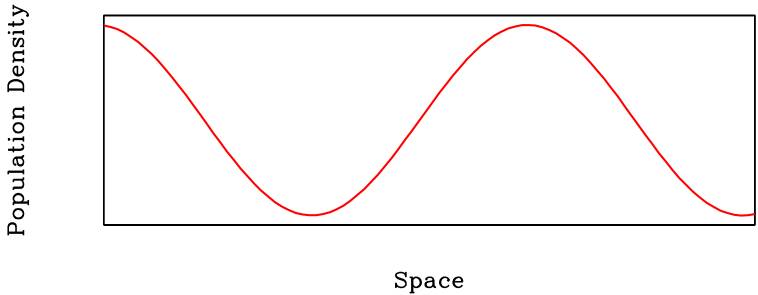
What is a Wavetrain?

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



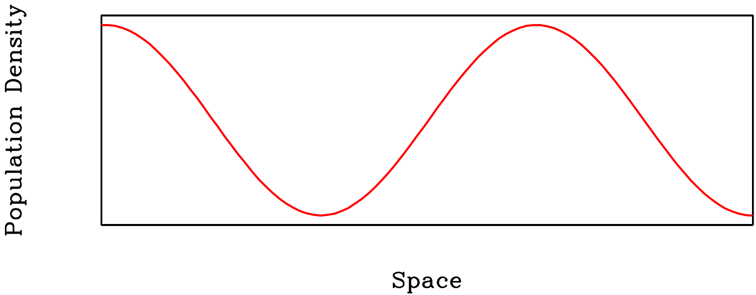
What is a Wavetrain?

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



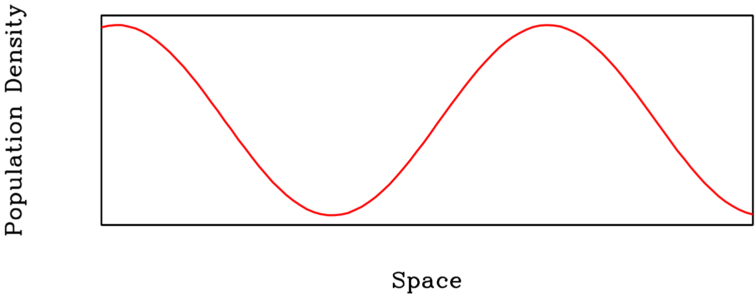
What is a Wavetrain?

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



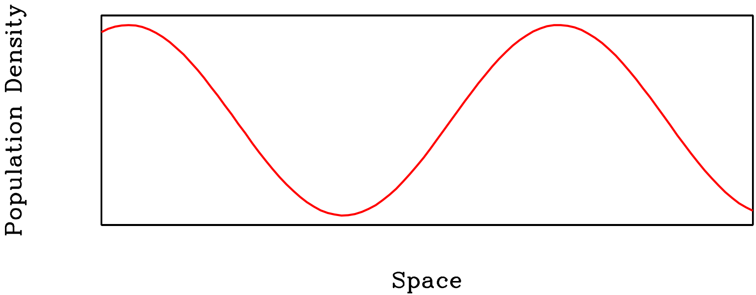
What is a Wavetrain?

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



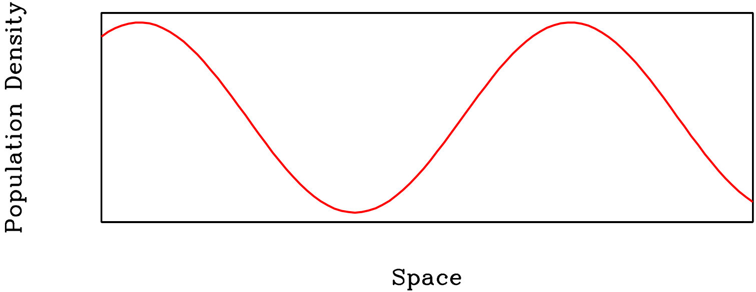
What is a Wavetrain?

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



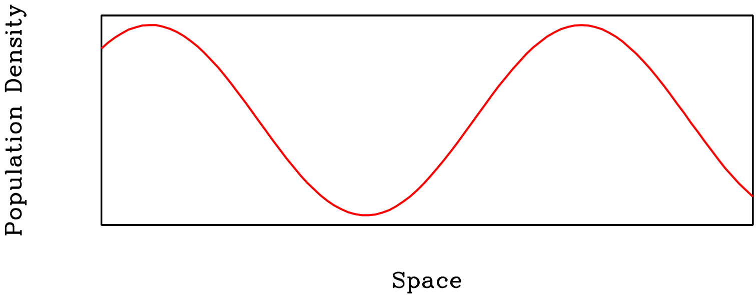
What is a Wavetrain?

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



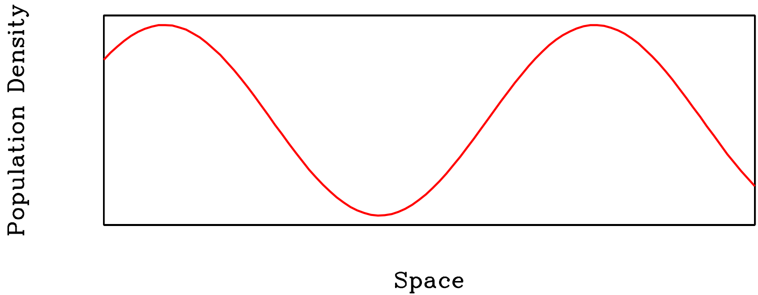
What is a Wavetrain?

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



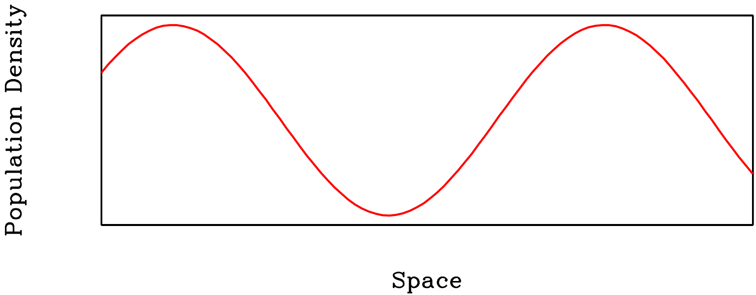
What is a Wavetrain?

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



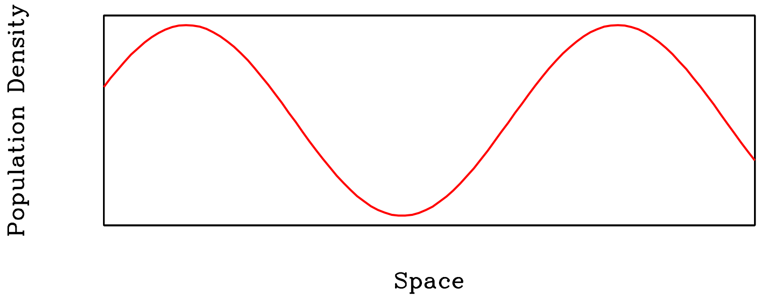
What is a Wavetrain?

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



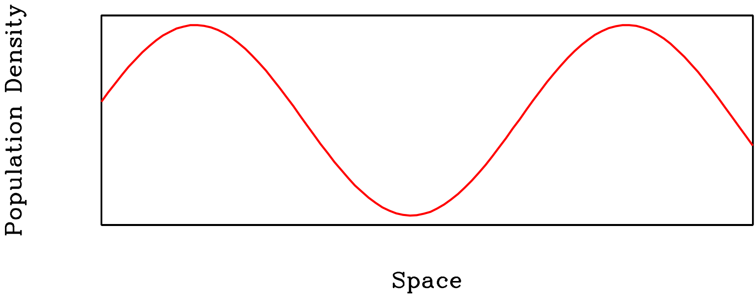
What is a Wavetrain?

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



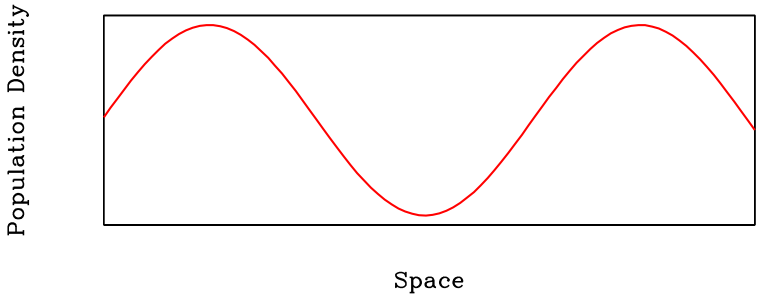
What is a Wavetrain?

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



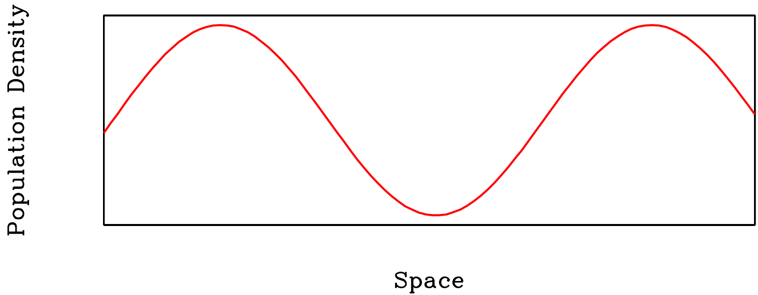
What is a Wavetrain?

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



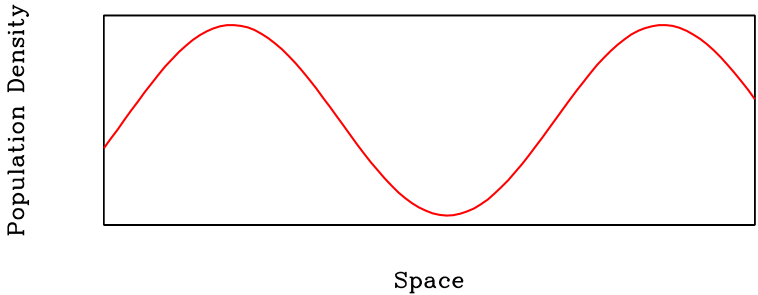
What is a Wavetrain?

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



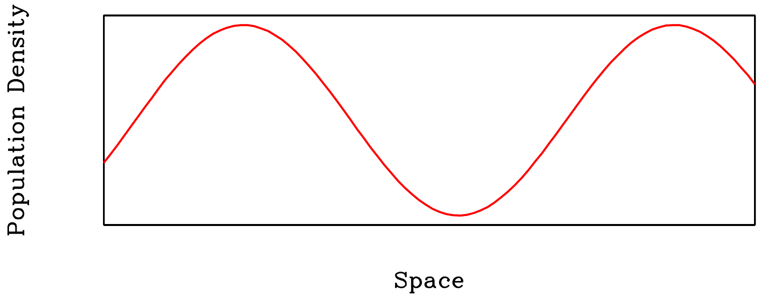
What is a Wavetrain?

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



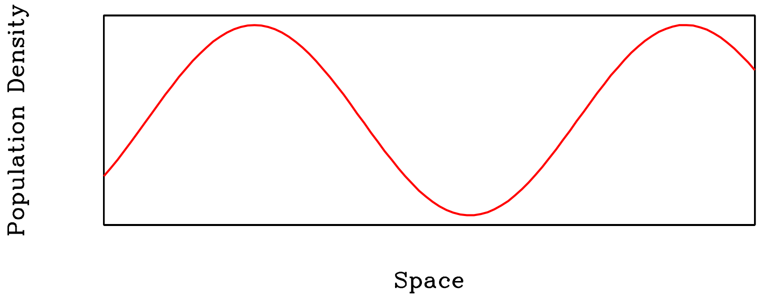
What is a Wavetrain?

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



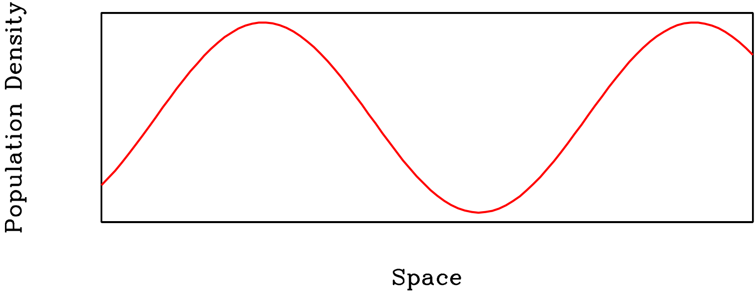
What is a Wavetrain?

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



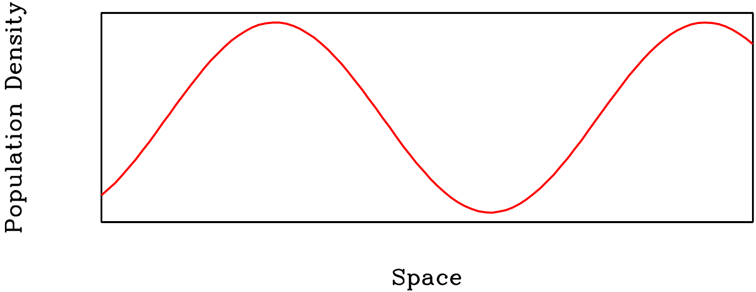
What is a Wavetrain?

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



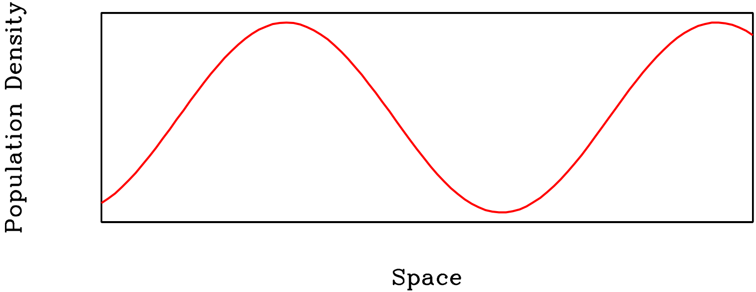
What is a Wavetrain?

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



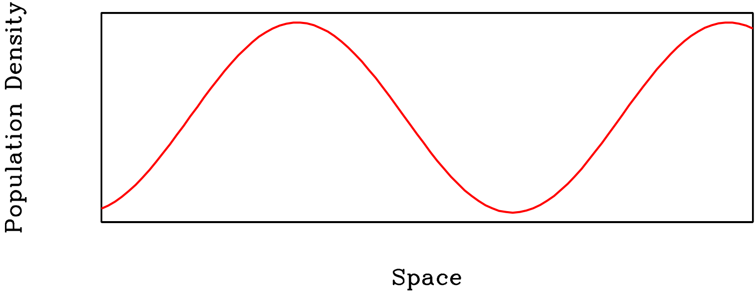
What is a Wavetrain?

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



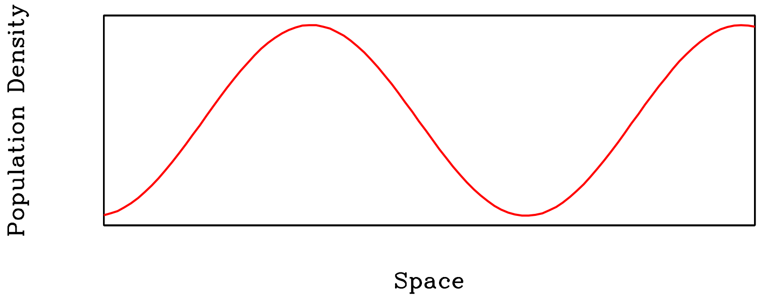
What is a Wavetrain?

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



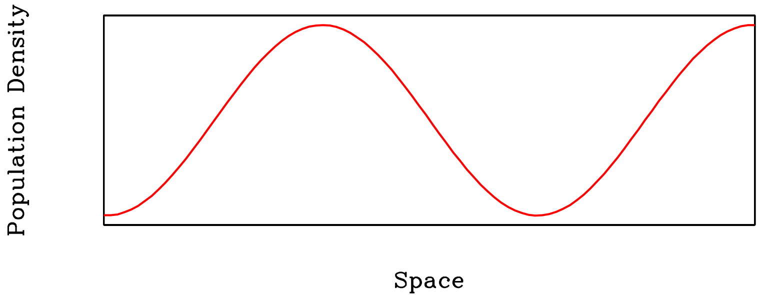
What is a Wavetrain?

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



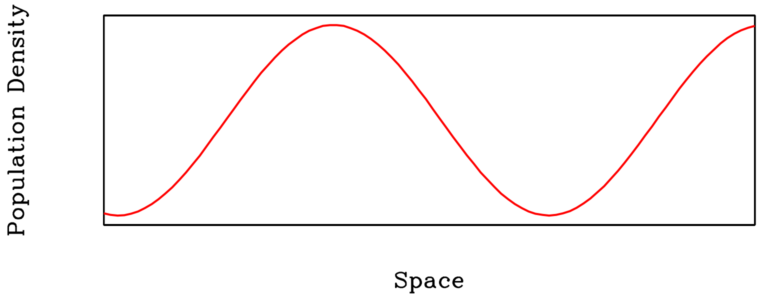
What is a Wavetrain?

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



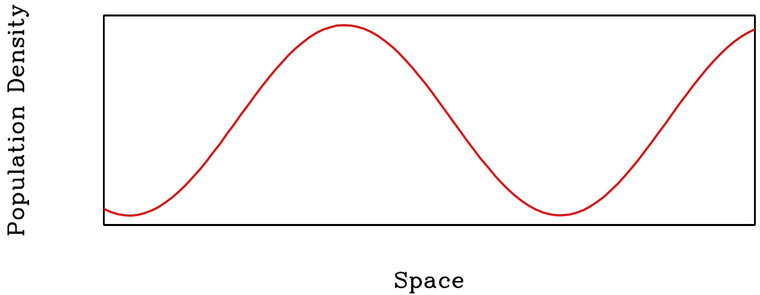
What is a Wavetrain?

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



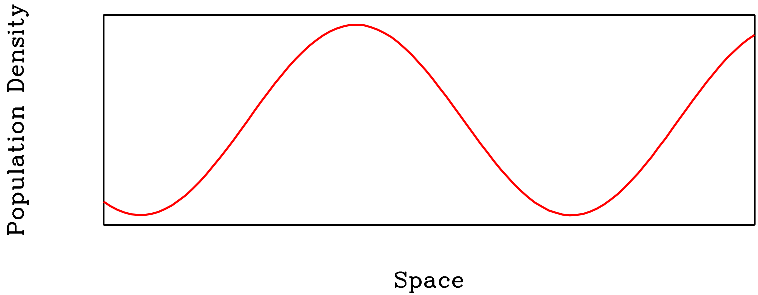
What is a Wavetrain?

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



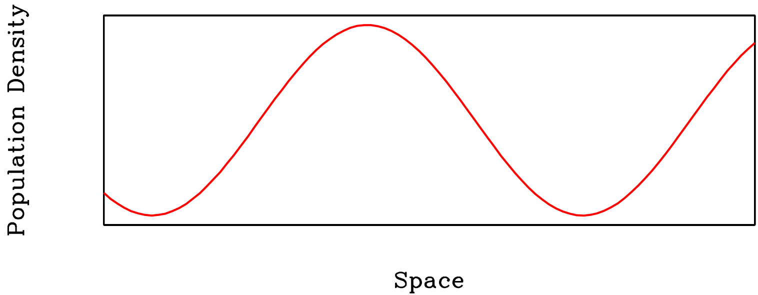
What is a Wavetrain?

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



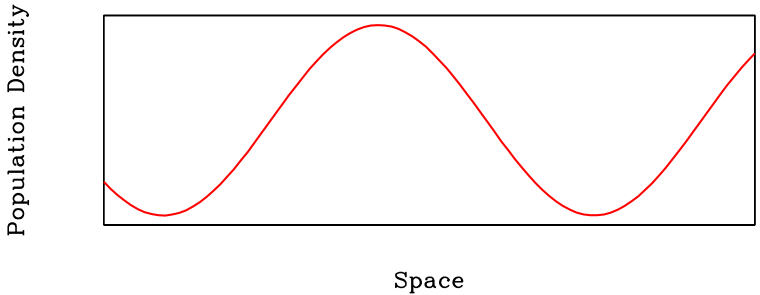
What is a Wavetrain?

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



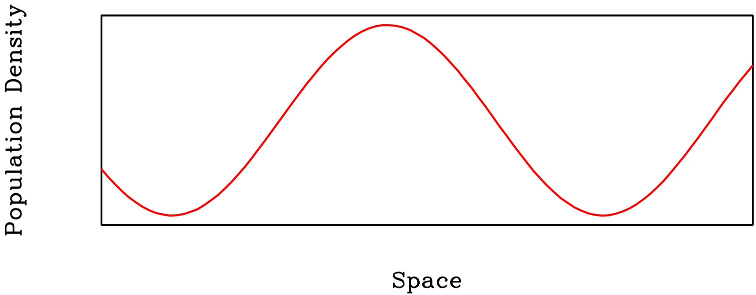
What is a Wavetrain?

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



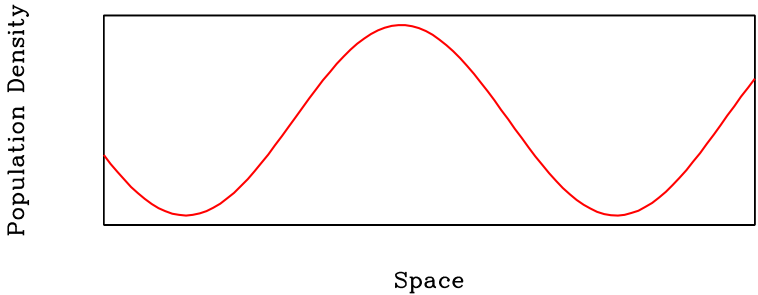
What is a Wavetrain?

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



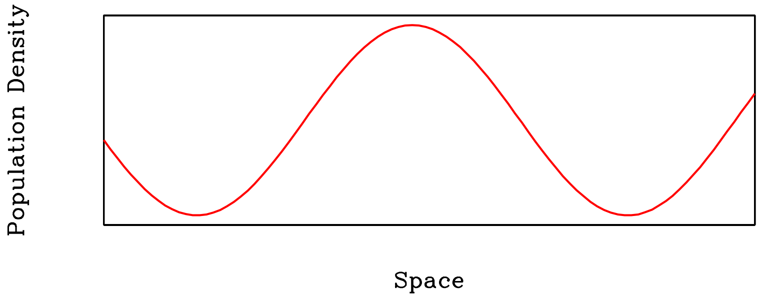
What is a Wavetrain?

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



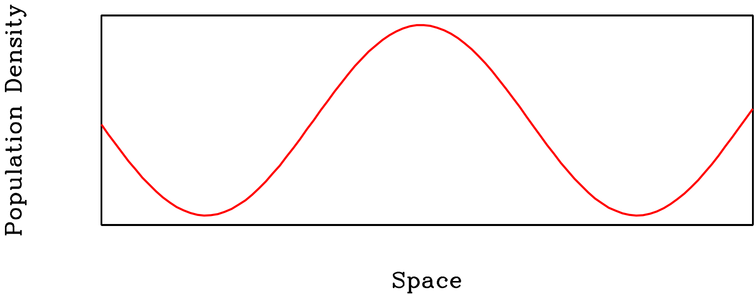
What is a Wavetrain?

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



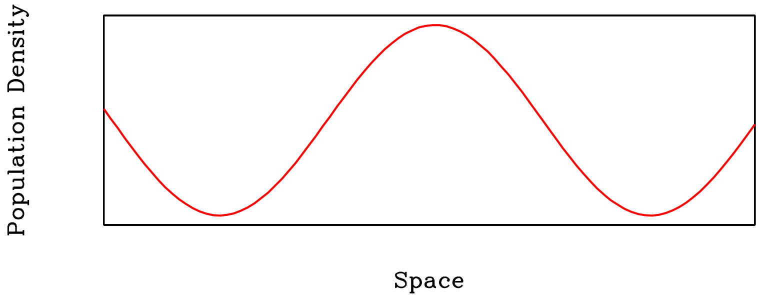
What is a Wavetrain?

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



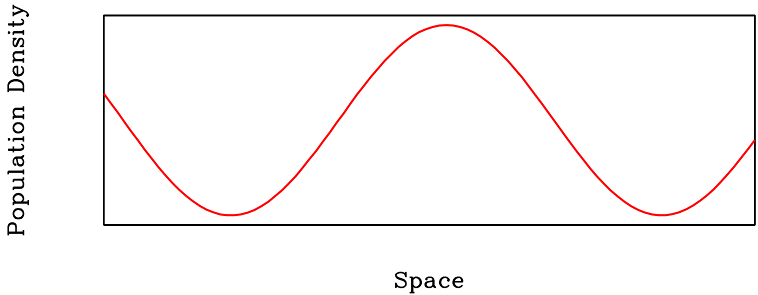
What is a Wavetrain?

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



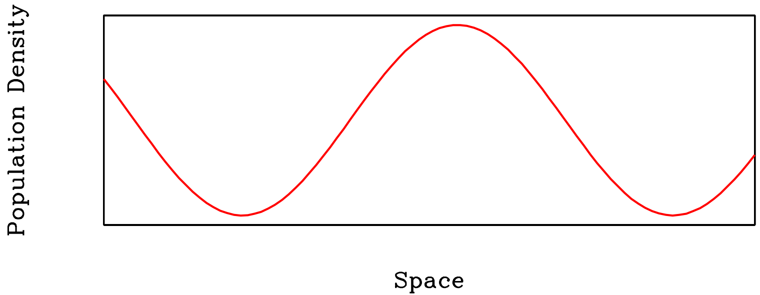
What is a Wavetrain?

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



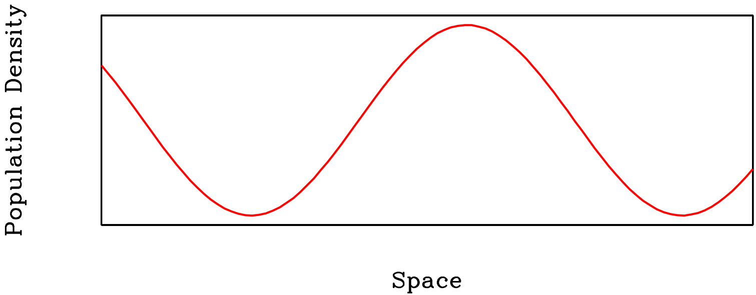
What is a Wavetrain?

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



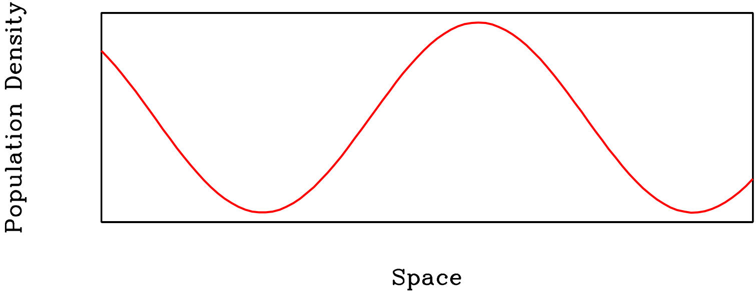
What is a Wavetrain?

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



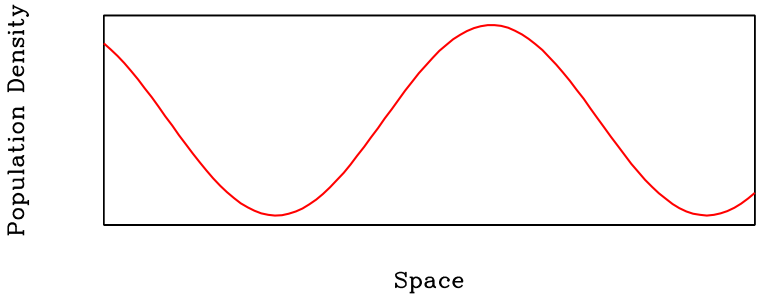
What is a Wavetrain?

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



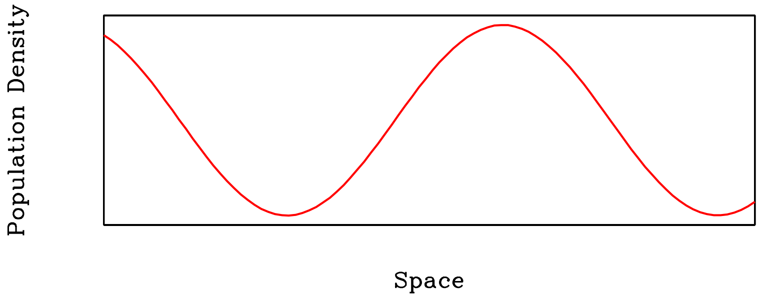
What is a Wavetrain?

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



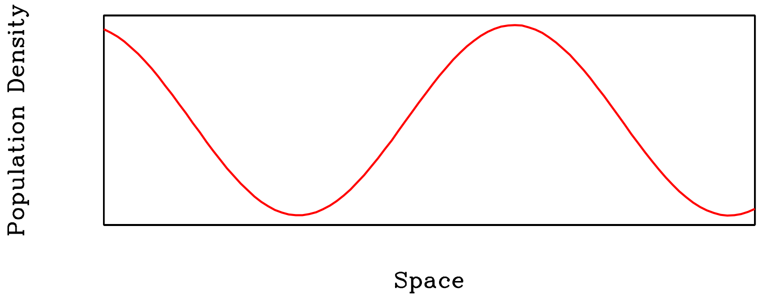
What is a Wavetrain?

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



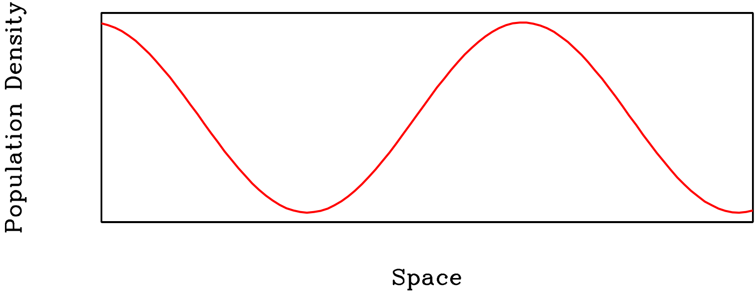
What is a Wavetrain?

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



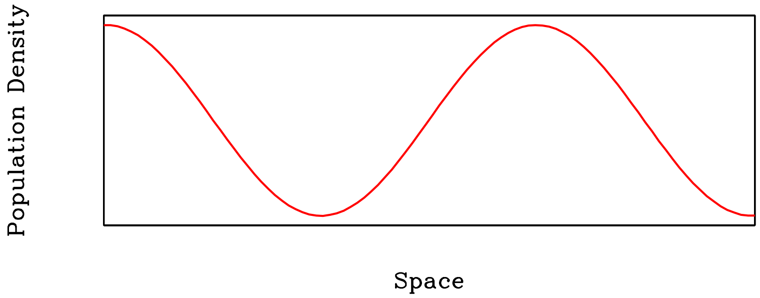
What is a Wavetrain?

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



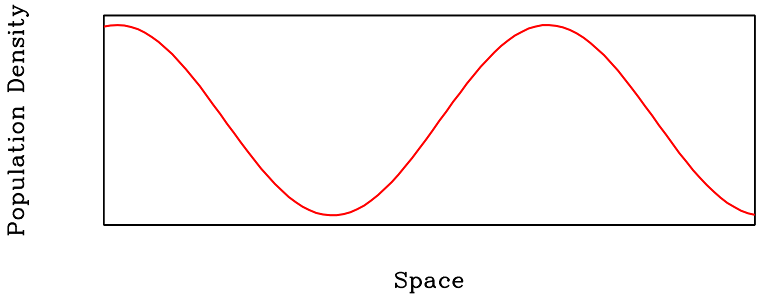
What is a Wavetrain?

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



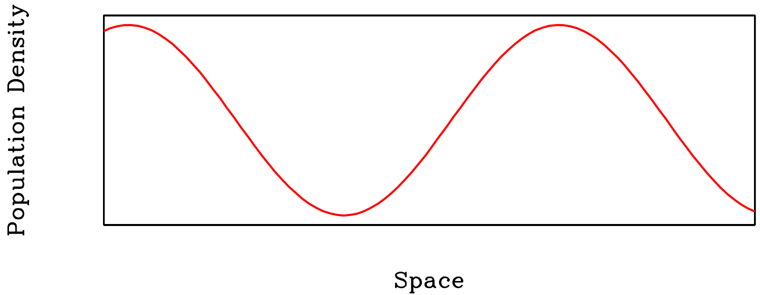
What is a Wavetrain?

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



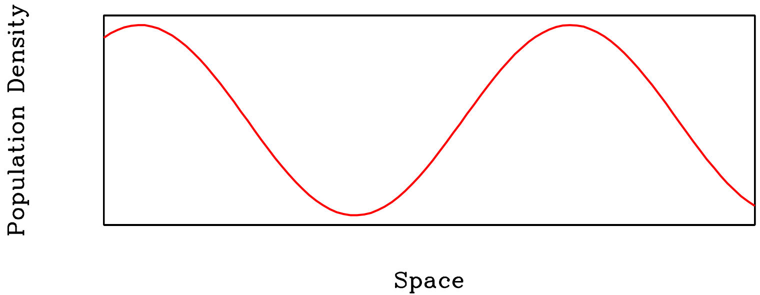
What is a Wavetrain?

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



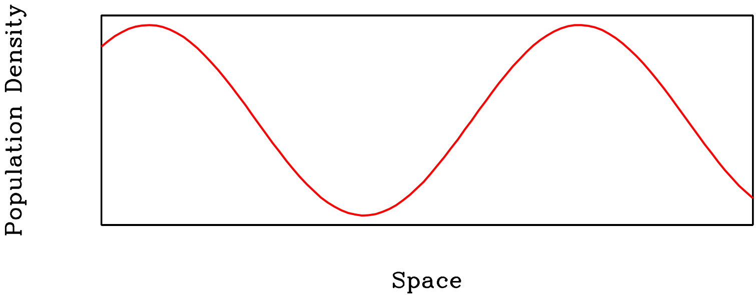
What is a Wavetrain?

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



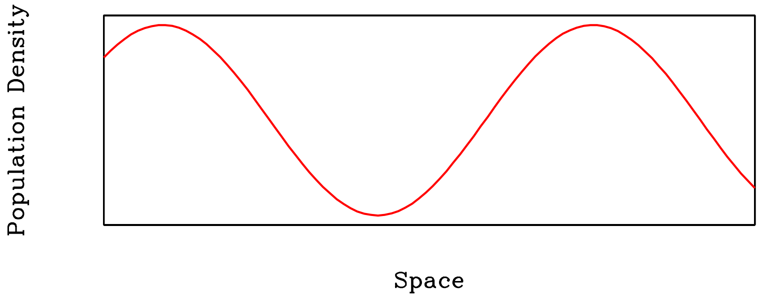
What is a Wavetrain?

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



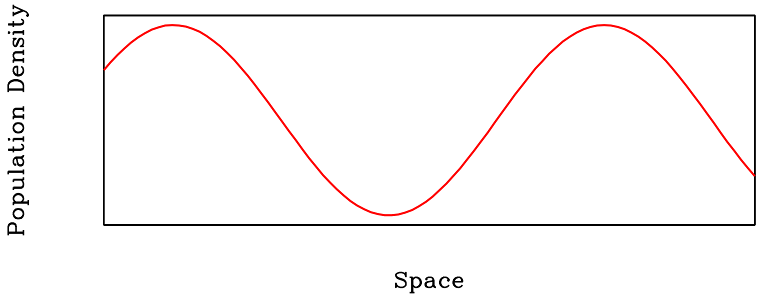
What is a Wavetrain?

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



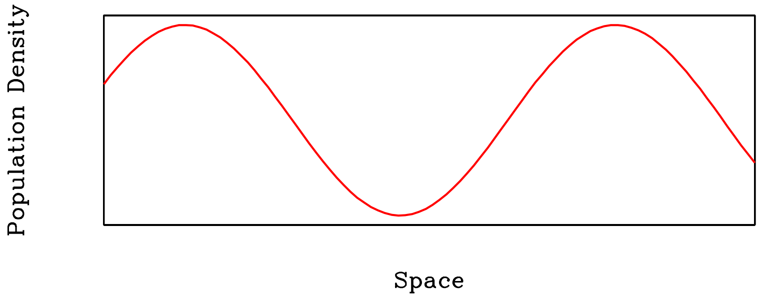
What is a Wavetrain?

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



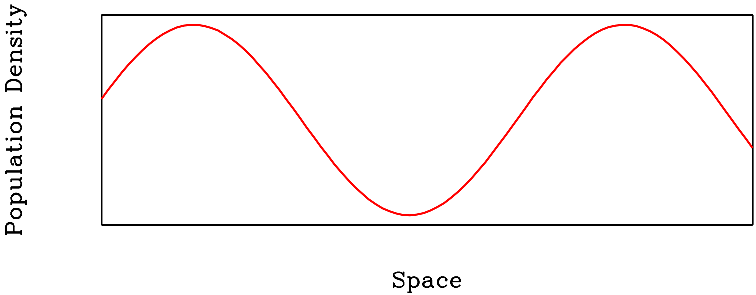
What is a Wavetrain?

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



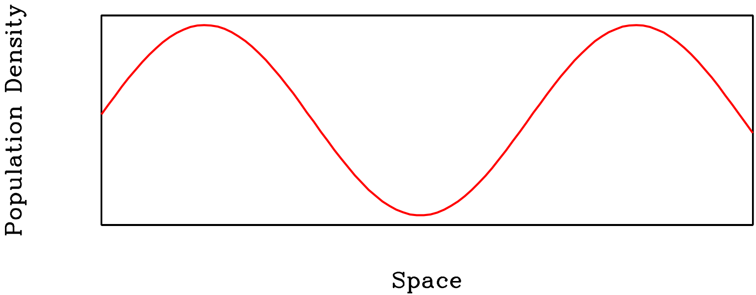
What is a Wavetrain?

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



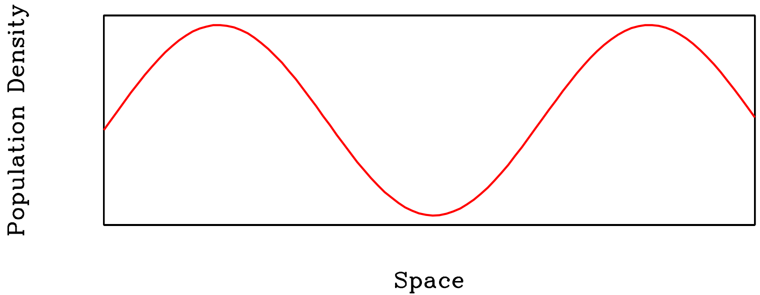
What is a Wavetrain?

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



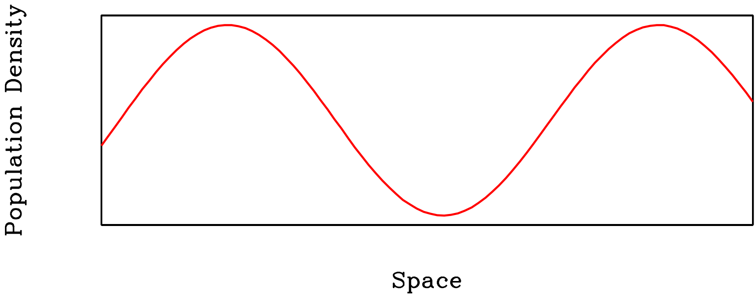
What is a Wavetrain?

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



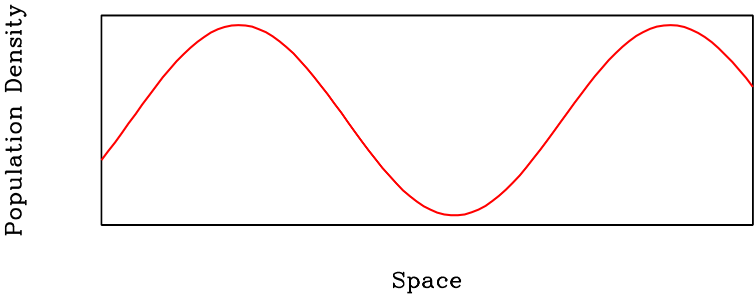
What is a Wavetrain?

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



What is a Wavetrain?

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



What is a Wavetrain?

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

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

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

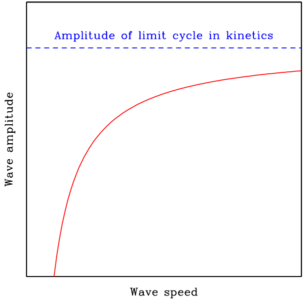
What is a Wavetrain?

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

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

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

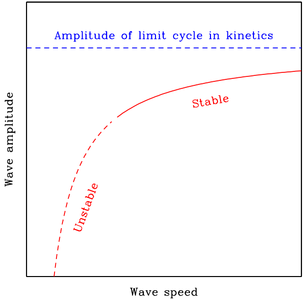
(Kopell & Howard, 1973).



What is a Wavetrain?

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

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



Wavetrains in Ecology

Fennoscandian voles

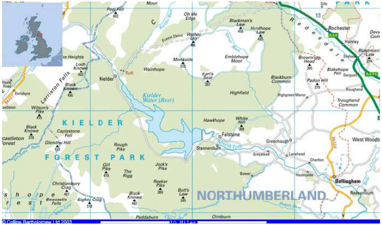
Clethrionomys glareolus

Fennoscandia

Wavetrains in Ecology

Field vole

Microtus agrestis

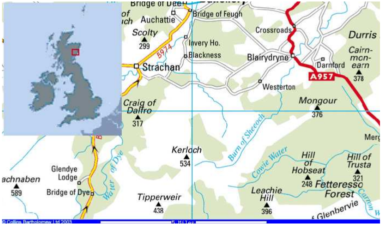


Kielder forest

Wavetrains in Ecology

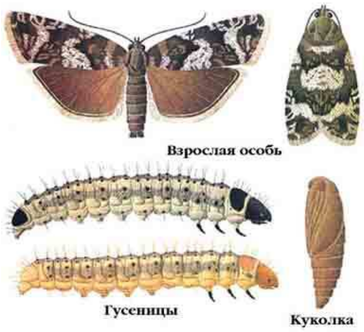
Red grouse

Lagopus lagopus scoticus



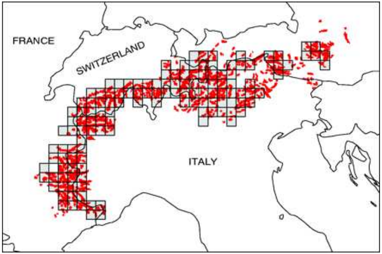
Kerloch moor

Wavetrains in Ecology



Larch budmoth

Zeiraphera diniana



Central European Alps

Wavetrains in Ecology

Canadian lynx

Lynx canadensis

Canada

Wavetrains in Ecology

Autumnal moth

Epirrita autumnata

Northern Norway

Outline

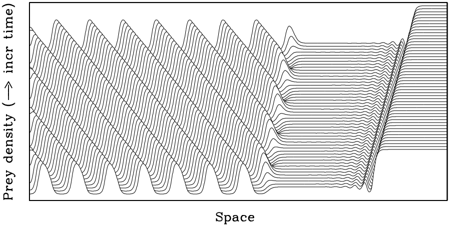
The Wavetrain Band

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

The Wavetrain Band

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

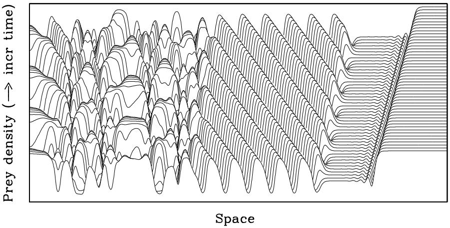
For these parameters, the selected wavetrain is stable.



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.

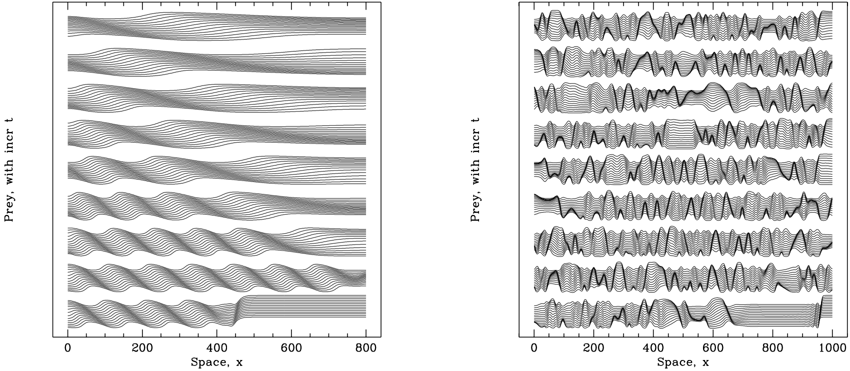


Behaviour after Invasion

A key ecological question is: what is the behaviour after the entire habitat has been invaded?

Behaviour after Invasion

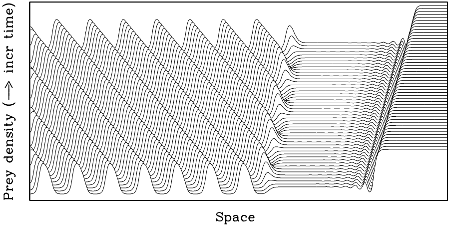
A key ecological question is: what is the behaviour after the entire habitat has been invaded?



Behaviour after Invasion

A key ecological question is: what is the behaviour after the entire habitat has been invaded?

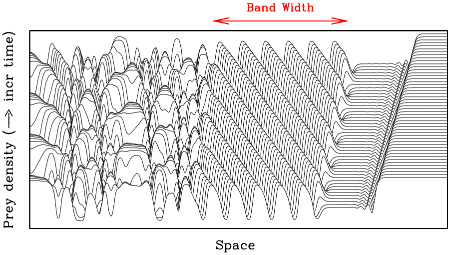
When the selected wavetrain is stable, the behaviour after invasion is homogeneous oscillations.



Behaviour after Invasion

A key ecological question is: what is the behaviour after the entire habitat has been invaded?

When the selected wavetrain is unstable, the behaviour after invasion depends on whether domain length is shorter than “band width”.

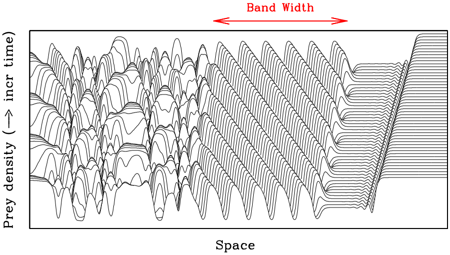


Behaviour after Invasion

A key ecological question is: what is the behaviour after the entire habitat has been invaded?

Band width $<$ domain length
$\Rightarrow$ spatiotemporal chaos

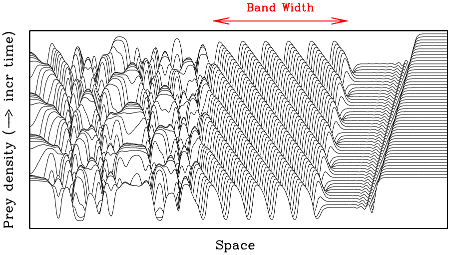
Band width $>$ domain length
$\Rightarrow$ homogeneous oscillations



Behaviour after Invasion

A key ecological question is: what is the behaviour after the entire habitat has been invaded?

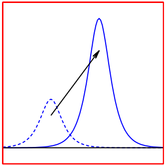
Question: what is the wavetrain band width?



Outline

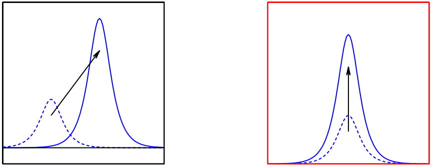
Convective and Absolute Stability

- 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".



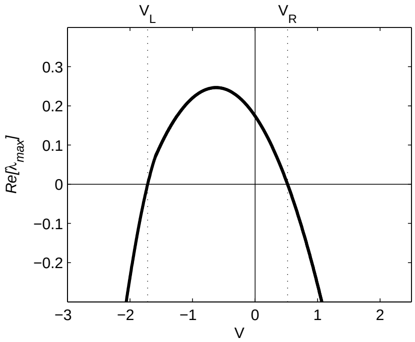
Absolute Stability in a Moving Frame of Reference

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.

$$\begin{aligned}\text{Define } \lambda_{max}(V) &= \text{temporal eigenvalue of the most unstable linear mode} \\ \nu_{max}(V) &= \text{the corresponding spatial eigenvalue}\end{aligned}$$

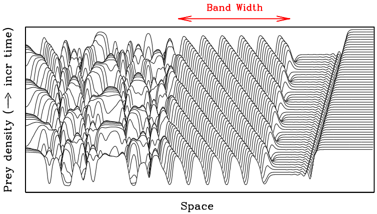
Absolute Stability in a Moving Frame of Reference



A tutorial guide to calculating absolute stability is freely available at

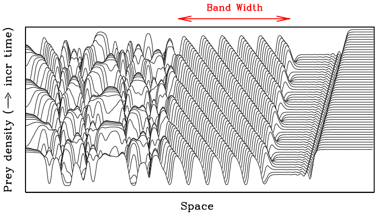
`http://research.microsoft.com/en-us/projects/loptw/tutorial.aspx`

Defining the Band Width



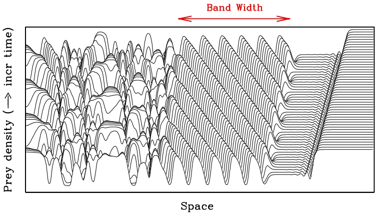
- We define the left-hand edge of the wavetrain band as where unstable linear modes first become amplified by a factor $\mathcal{F}$.

Defining the Band Width



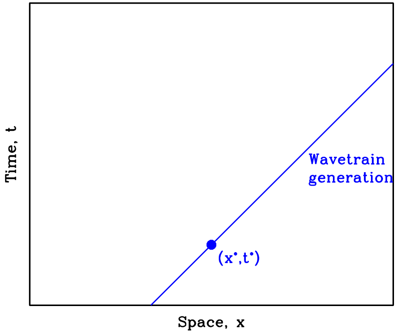
- We define the left-hand edge of the wavetrain band as where unstable linear modes first become amplified by a factor $\mathcal{F}$.
- Our calculations ⇒ band width $= \underbrace{\log(\mathcal{F})}_{\text{arbitrary}} \cdot \underbrace{\mathcal{W}}_{\text{“band width coefficient”}}$

Defining the Band Width

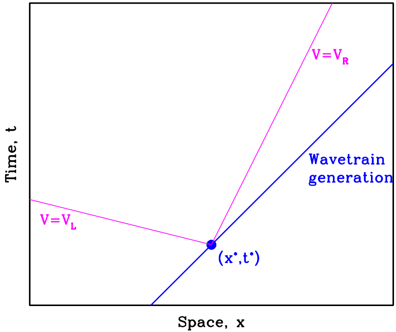


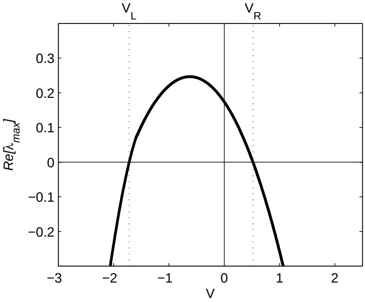
- We define the left-hand edge of the wavetrain band as where unstable linear modes first become amplified by a factor $\mathcal{F}$.
- Our calculations $\Rightarrow$ band width $= \underbrace{\log(\mathcal{F})}_{\text{arbitrary}} \cdot \underbrace{\mathcal{W}}_{\text{“band width coefficient”}}$
- The dependence on ecological parameters is via $\mathcal{W}$.

The Band Width Formula

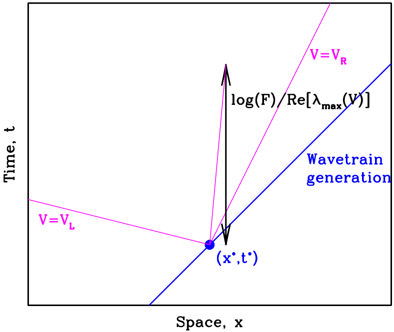


The Band Width Formula





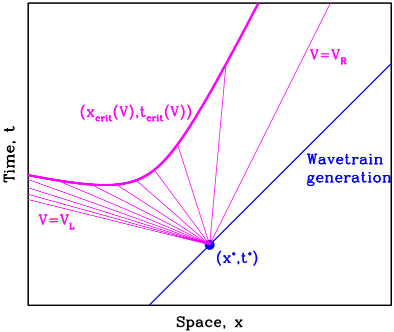
The Band Width Formula



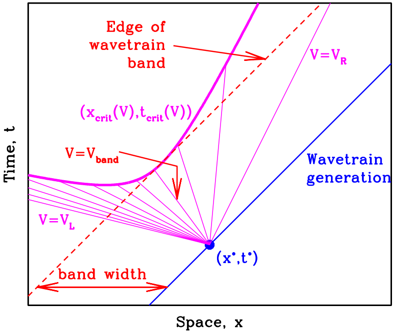
Perturbations moving with velocity V grow as $\exp[\mathrm{Re}\,(\lambda_{max}(V))\cdot t]$

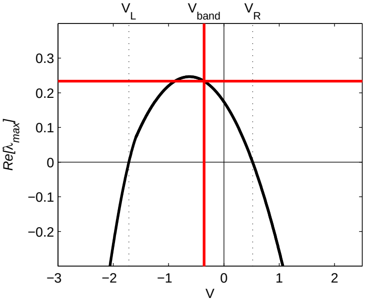
$\Rightarrow$ amplified by the factor $\mathcal{F}$ after time $\log(\mathcal{F})/\mathrm{Re}\,(\lambda_{max}(V))$

The Band Width Formula

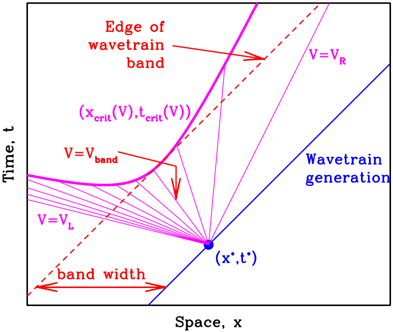


The Band Width Formula





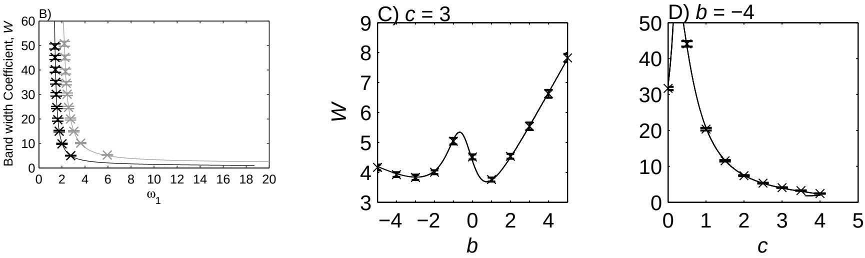
The Band Width Formula



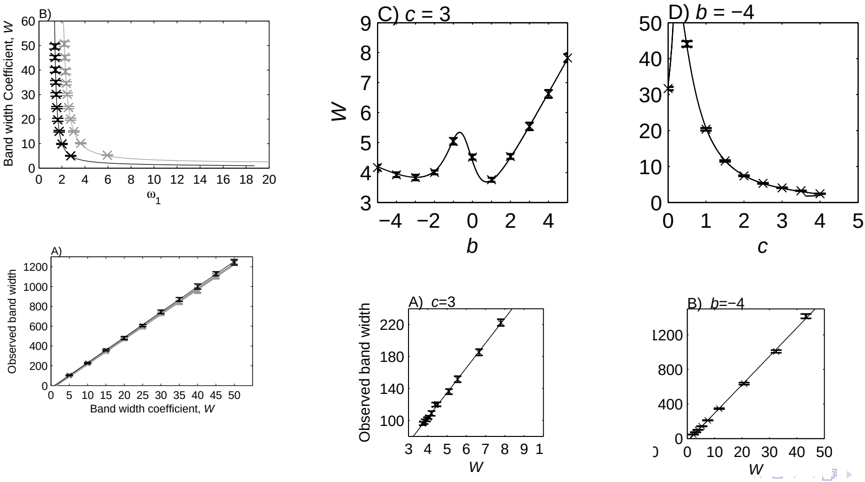
$$\mathcal{W} = 1/\text{Re}\,[\nu_{max}(V_{band})]$$

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

The Form of W


B)
Band width Coefficient, W
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 18 20
ω1
C) c = 3
W
9
8
7
6
5
4
3
−4 −2 0 2 4
b
D) b = −4
50
40
30
20
10
0
0 1 2 3 4 5
c

The Form of W

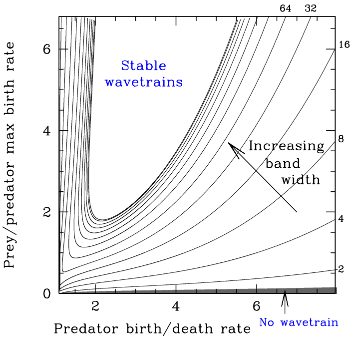

B)
Band width Coefficient, W
ω1
C) c = 3
W
b
D) b = −4
c
A)
Observed band width
Band width coefficient, W
A) c=3
Observed band width
W
B) b=−4
W

Outline

1. Predator-Prey Invasion and Wavetrains
2. Wavetrain Band and Behaviour after Invasion
3. Calculating the Band Width
4. Band Width Sensitivity and Ecological Implications

Band Width Sensitivity

Our formula gives band width vs ecological parameters.



Band Width Sensitivity

Our formula gives band width vs ecological parameters.

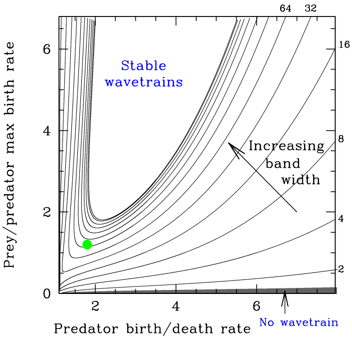
Example: vole – weasel interaction in Fennoscandia

vole

weasel

Band Width Sensitivity

Our formula gives band width vs ecological parameters.



● = weasel–vole parameters.

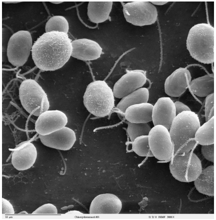
5%↑ in vole birth rate
⇒ 22%↑ in band width.

Band Width Sensitivity

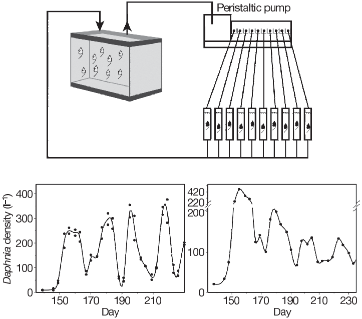
Our formula gives band width vs ecological parameters.

Example: *Daphnia pulex–Chlamydomonas reinhardii* interaction

Daphnia pulex



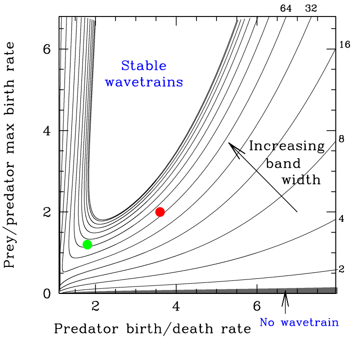
Chlamydomonas reinhardii



(from McCauley *et al* (2008), *Nature* 455:1240, 2008)

Band Width Sensitivity

Our formula gives band width vs ecological parameters.



● = plankton parameters
(*Daphnia pulex–Chlamydomonas reinhardii*).

5.2%↓ in Daphnia birth rate
⇒ doubling of band width.

Ecological Implications

- 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).
- The band width determines whether one sees spatiotemporal chaos or periodic homogeneous oscillations after invasion
- We have shown that band width depends sensitively on ecological parameters.

Ecological Implications

- 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).
- The band width determines whether one sees spatiotemporal chaos or periodic homogeneous oscillations after invasion
- We have shown that band width depends sensitively on ecological parameters.
- This suggests that the implications of climate change for *spatio* temporal dynamics may be even more dramatic than for purely temporal behaviour.

References

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

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, published online (open access).

List of Frames

The Form of V_{band}