Spatiotemporal Dynamics Behind Invasions In Cyclic Populations

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Ecology and Control of Invasive Species, Including Insects Mathematical Biosciences Institute, February 2011

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

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(CWI, Amsterdam)



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(University of Aberdeen)





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Predator-Prey Invasion and Wavetrains

- Periodic Cycles and Chaos after Invaison
- Calculating the Wavetrain Band Width
- Band Width Sensitivity and Ecological Implications



Predator-Prey Invasion and Wavetrains

Periodic Cycles and Chaos after Invaison Calculating the Wavetrain Band Width Band Width Sensitivity and Ecological Implications



Dimate Change and Invasions Cyclic Predator-Prey Systems Predator-Prey Invasion What is a Wavetrain? Vavetrains in Ecology

Predator-Prey Invasion and Wavetrains

- 2 Periodic Cycles and Chaos after Invaison
- 3 Calculating the Wavetrain Band Width
- Band Width Sensitivity and Ecological Implications



Climate Change and Invasions Cyclic Predator-Prey Systems Predator-Prey Invasion What is a Wavetrain? Wavetrains in Ecology

Climate Change and Invasions

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





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

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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.

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Climate Change and Invasions

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



Predatory biocontrol agents can survive outside greenhouses due to warmer temperatures.

Predator-Prey Invasion and Wavetrains

Periodic Cycles and Chaos after Invaison Calculating the Wavetrain Band Width Band Width Sensitivity and Ecological Implications Climate Change and Invasions Cyclic Predator-Prey Systems Predator-Prey Invasion What is a Wavetrain? Wavetrains in Ecology

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.

Climate Change and Invasions Cyclic Predator-Prey Systems Predator-Prey Invasion What is a Wavetrain? Wavetrains in Ecology

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, such as:



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Example: Voles and Weasels in Fennoscandia



Fennoscandian voles



Fennoscandia

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Predator-Prey Invasion

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



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Predator-Prey Invasion

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



Space



Space

Simple invasion front (local bhr: constant)



²red density (→ incr time)

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Predator-Prey Invasion

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



Space



Space

Wavetrain behind an invasion front (local bhr: cycles)

time

²red density (→ incr

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What is a Wavetrain?

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



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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

$$\frac{\partial u}{\partial t} = D_u \frac{\partial^2 u}{\partial x^2} + f(u, v) \frac{\partial v}{\partial t} = D_v \frac{\partial^2 v}{\partial x^2} + g(u, v)$$

kinetics have a stable limit cycle

What is a Wavetrain?

Climate Change and Invasion: Cyclic Predator-Prey Systems Predator-Prey Invasion What is a Wavetrain? Wavetrains in Ecology

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).



Wave speed

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What is a Wavetrain?

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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.



Wave speed

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Periodic Cycles and Chaos after Invaison Calculating the Wavetrain Band Width Band Width Sensitivity and Ecological Implications Climate Change and Invasions Cyclic Predator-Prey Systems Predator-Prey Invasion What is a Wavetrain? Wavetrains in Ecology

Wavetrains in Ecology



Fennoscandian voles Clethrionomys glareolus



Fennoscandia

Ranta & Kaitala: Travelling waves in vole population dynamics. *Nature* 390:456 (1997).

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Kielder forest

Field vole Microtus agrestis

Lambin et al: Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. *Proc. R. Soc. Lond.* B 265:1491 (1998).

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Kerloch moor

Red grouse Lagopus lagopus scoticus

Mougeot et al: Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus*. J. Anim. Ecol. 74:488 (2005).

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FRANCE SWITTERLAND TITALY

Central European Alps

Larch budmoth

Zeiraphera diniana

Bjørnstad et al: Waves of larch budmoth outbreaks in the European Alps. *Science* 298:1020 (2002).

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Autumnal moth Epirrita autumnata



Northern Norway

Tenow et al: Waves and synchrony in *Epirrita autumnata/Operophtera brumata* outbreaks I. *J. Anim. Ecol.* 76:258 (2007).

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The Wavetrain Band The Wavetrain Band: Animation When is the Selected Wavetrain Stable? What is the Wavetrain Bandwidth?





Periodic Cycles and Chaos after Invaison

- 3 Calculating the Wavetrain Band Width
- 4 Band Width Sensitivity and Ecological Implications



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The Wavetrain Band The Wavetrain Band: Animation When is the Selected Wavetrain Stable? What is the Wavetrain Bandwidth?

The Wavetrain Band

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



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The Wavetrain Band

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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.



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The Wavetrain Band

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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.



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The Wavetrain Band The Wavetrain Band: Animation When is the Selected Wavetrain Stable? What is the Wavetrain Bandwidth?

When is the Selected Wavetrain Stable?

 Question: When does the invasion process select a <u>stable</u> wavetrain?



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When is the Selected Wavetrain Stable?

- Question: When does the invasion process select a <u>stable</u> wavetrain?
- Posed in 1995 (Sherratt, Lewis, Fowler (1995) PNAS 92:2524). Answered in 2007 (Sherratt, Smith (2007) Physica D 236:90), using new mathematical theory (Rademacher, Sandstede, Scheel (2007) Physica D 229:166).

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When is the Selected Wavetrain Stable?

- Question: When does the invasion process select a <u>stable</u> wavetrain?
- Posed in 1995 (Sherratt, Lewis, Fowler (1995) PNAS 92:2524). Answered in 2007 (Sherratt, Smith (2007) Physica D 236:90), using new mathematical theory (Rademacher, Sandstede, Scheel (2007) Physica D 229:166).
- But: Parameterising the model for field voles and weasels
 ⇒ the wavetrain is unstable, but the wavetrain band is about 1000km wide.
- More Important Question: When is the wavetrain band width smaller than the typical habitat size?

What is the Wavetrain Bandwidth?

What is the Wavetrain Bandwidth?

Question: what is the wavetrain band width?





Space

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Spatiotemporal Dynamics Behind Invasions



Convective and Absolute Stability Absolute Stability in a Moving Frame of Reference Defining the Band Width The Band Width Formula The Form of W

Predator-Prey Invasion and Wavetrains

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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".





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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".
- Alternatively, a solution can be unstable with perturbations growing without moving. This is "absolute instability".





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Absolute Stability in a Moving Frame of Reference

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

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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

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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 *F*.

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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 *F*.
- Our calculations \Rightarrow band width = $\log(\mathcal{F}) \cdot \mathcal{N}$

"band width coefficient"

- 2

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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 *F*.
- Our calculations \Rightarrow band width = $\log(\mathcal{F}) \cdot \mathcal{V}$

"band width coefficient"

3

• The dependence on ecological parameters is via \mathcal{W} .

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The Band Width Formula





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The Band Width Formula





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The Band Width Formula





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

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

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The Band Width Formula







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The Band Width Formula



Convective and Absolute Stability Absolute Stability in a Moving Frame of Reference Defining the Band Width **The Band Width Formula** The Form of W

The Band Width Formula





$W = 1/\text{Re} \left[\nu_{max}(V_{band})\right]$ where $(V_{band} - c_{inv})\text{Re} \left[\nu_{max}(V_{band})\right] = \text{Re} \left[\lambda_{max}(V_{band})\right]$

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Band Width Sensitivity Ecological Implications References



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Band Width Sensitivity Ecological Implications References

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





Band Width Sensitivity

weasel



vole

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Band Width Sensitivity Ecological Implications References

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




Band Width Sensitivity Ecological Implications References

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.

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Band Width Sensitivity Ecological Implications References

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).
- We have shown that band width depends sensitively on ecological parameters.

Band Width Sensitivity Ecological Implications References

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).
- 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.

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Band Width Sensitivity Ecological Implications References

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Band Width Sensitivity Ecological Implications References

List of Frames



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Band Width Sensitivity Ecological Implications References

The Form of V_{band}



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