

Slides are available on my website.
<http://lukaseigentler.github.io>

Modelling dryland vegetation patterns

University of Glasgow Applied Mathematics seminar

21 November 2024

*Lukas Eigentler (University of Warwick)
joint work with Jonathan A Sherratt (Heriot-Watt Univ.),
Jamie JR Bennett (ex Heriot-Watt Univ.), Mattia Sensi (Politecnico di Torino)*

Vegetation patterns

Vegetation patterns are a classic example of a **self-organisation principle** in ecology.

Stripe pattern in Ethiopia¹.



Gap pattern in Niger².



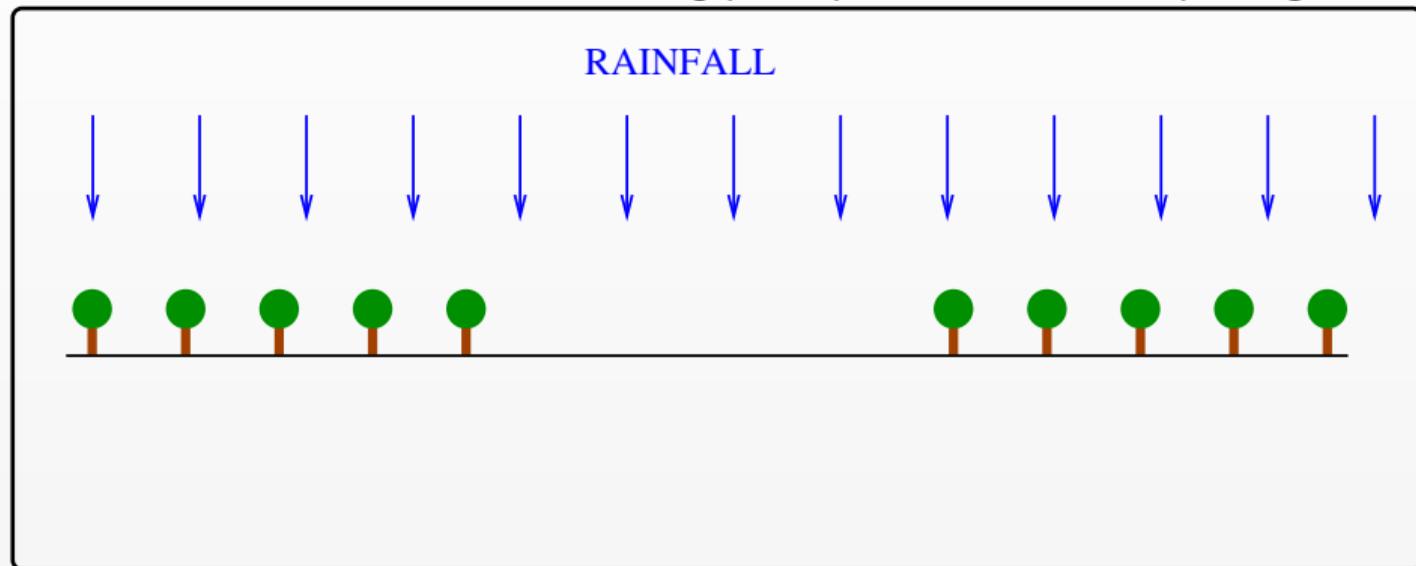
- Plants increase water infiltration into the soil ⇒ **positive feedback loop**.

¹Source: Google Maps

²Source: Wikimedia Commons

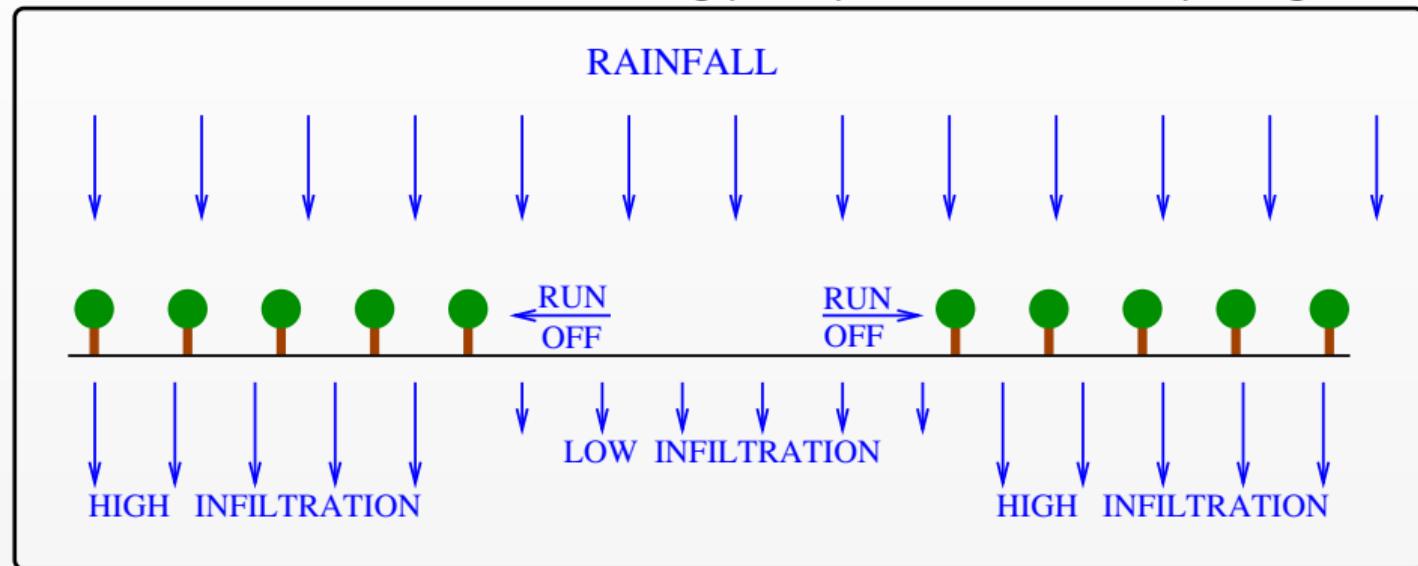
Local facilitation in vegetation patterns

Positive feedback loop: Water infiltration into the soil depends on local plant density ⇒ redistribution of water towards existing plant patches ⇒ further plant growth.



Local facilitation in vegetation patterns

Positive feedback loop: Water infiltration into the soil depends on local plant density ⇒ redistribution of water towards existing plant patches ⇒ further plant growth.



Vegetation patterns

Vegetation patterns are a classic example of a **self-organisation principle** in ecology.

Stripe pattern in Ethiopia³.



Gap pattern in Niger⁴.



- On sloped ground, stripes grow **parallel to the contours**.

³Source: Google Maps

⁴Source: Wikimedia Commons

Klausmeier model

One of the most basic phenomenological models is the **extended Klausmeier reaction-advection-diffusion model**.⁵

$$\begin{aligned}\frac{\partial u}{\partial t} &= \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$

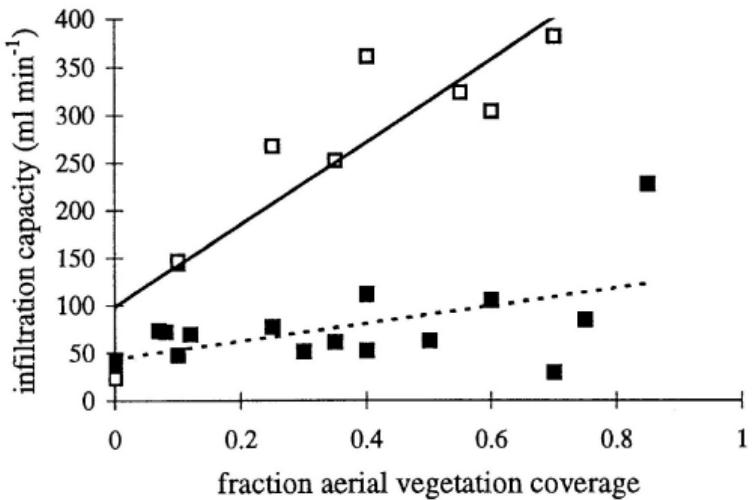
⁵ Klausmeier, C. A.: *Science* 284.5421 (1999).

Klausmeier model

One of the most basic phenomenological models is the **extended Klausmeier reaction-advection-diffusion model**.

$$\begin{aligned}\frac{\partial u}{\partial t} &= \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$

Water uptake



Infiltration capacity increases with plant density⁶

The nonlinearity in the water uptake and plant growth terms arises because plants increase the soil's water infiltration capacity.

⇒ Water uptake = Water density × plant density × infiltration rate.

⁶Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000)

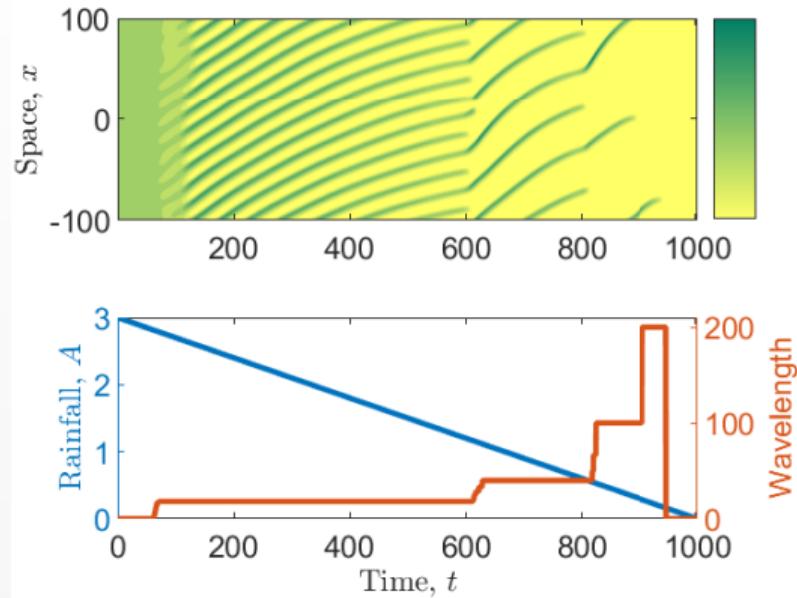
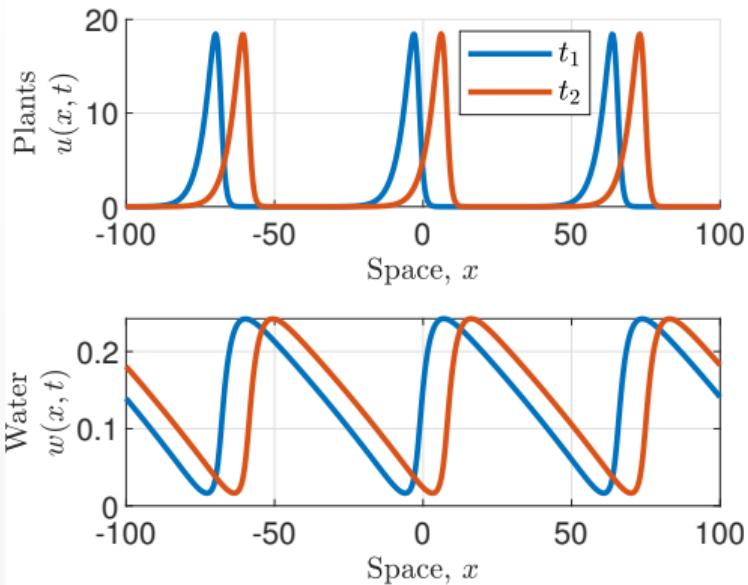
Klausmeier model

One of the most basic phenomenological models is the **extended Klausmeier reaction-advection-diffusion model**.⁷

$$\begin{aligned}\frac{\partial u}{\partial t} &= \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$

⁷ Klausmeier, C. A.: *Science* 284.5421 (1999).

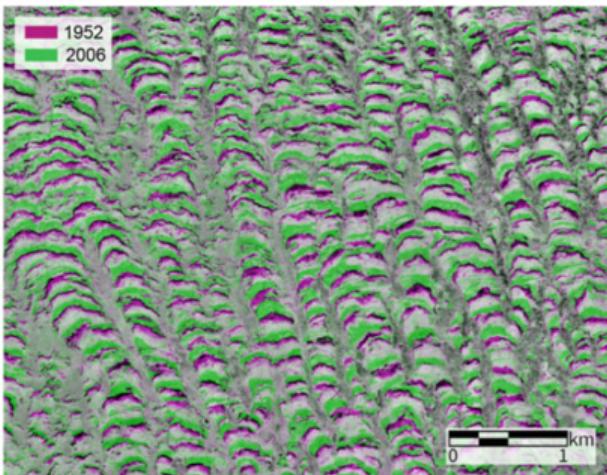
Periodic travelling waves



- Model represents vegetation patterns as **periodic travelling waves**.
- Along rainfall gradient, transition from uniform vegetation to desert occurs via several pattern transitions.

Uphill movement (or not?)

Timeseries data.⁸



Uphill migration due to water gradient.⁹



- Contrasting field data: stripes either **move uphill** (< 1m per year) or are **stationary**¹⁰.
- No reports of downhill movement.

⁸Gandhi, P. et al.: *Dryland ecohydrology*. Springer International Publishing, 2019, pp. 469–509.

⁹Dunkerley, D.: *Desert* 23.2 (2018).

¹⁰Deblauwe, V. et al.: *Ecol. Monogr.* 82.1 (2012).

Research question 1

- How can the contrasting field data on uphill movement be explained?

Research question 1

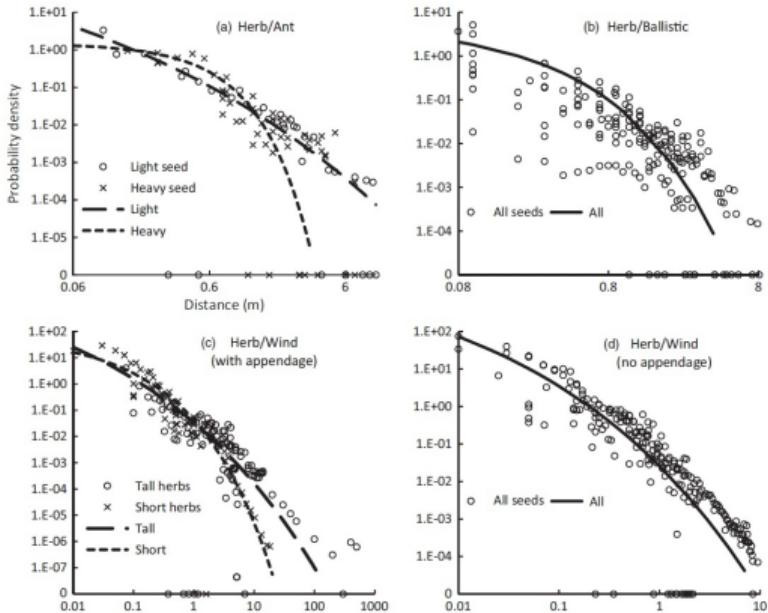
- How does nonlocal seed dispersal affect onset, existence and stability of patterns?
⇒ How can the contrasting field data on uphill movement be explained?

Local Model

The Klausmeier model models plant dispersal by a diffusion term, i.e. a local process.

$$\frac{\partial u}{\partial t} = \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{local plant dispersal}},$$
$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.$$

Nonlocal seed dispersal



Data of long range seed dispersal ¹¹

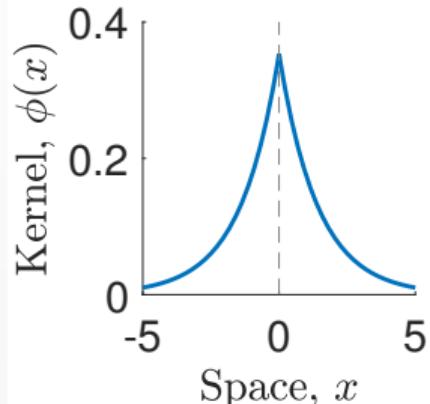
More realistic: **Include effects of nonlocal processes**, such as dispersal by wind or large mammals.

¹¹Bullock, J. M. et al.: *J. Ecol.* 105.1 (2017)

Nonlocal model

Diffusion is replaced by a **convolution of the plant density u with a dispersal kernel ϕ** . The scale parameter a controls the width of the kernel.

$$\begin{aligned}\frac{\partial u}{\partial t} &= \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \overbrace{C(\phi(\cdot; a) * u(\cdot, t) - u)}^{\text{nonlocal plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$



Laplacian kernel

If ϕ decays exponentially as $|x| \rightarrow \infty$, and $C = 2/\sigma(a)^2$, then the nonlocal model tends to the local model as $\sigma(a) \rightarrow 0$.

E.g. Laplace kernel

$$\phi(x) = \frac{a}{2} e^{-a|x|}, \quad a > 0, \quad x \in \mathbb{R}.$$

Useful because

$$\hat{\phi}(k) = \frac{a^2}{a^2 + k^2}, \quad k \in \mathbb{R}.$$

and allows transformation into a local model. If $v(x, t) = \phi(\cdot; a) * u(\cdot; t)$, then

$$\frac{\partial^2 v}{\partial x^2}(x, t) = a^2(v(x, t) - u(x, t))$$

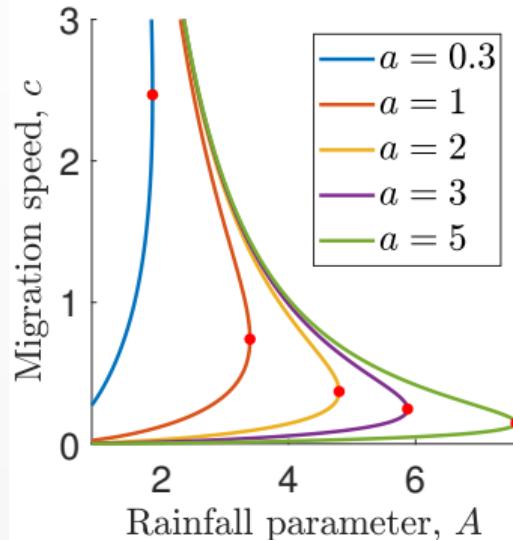
Pattern onset

Using $\nu \gg 1$, we can analytically calculate the locus of a Hopf bifurcation causing pattern onset and the rainfall level at which pattern onset occurs

$$A_{\max} = \left(\frac{3C - B - 2\sqrt{2C}\sqrt{C - B}}{(B + C)^2} \right)^{\frac{1}{4}} a^{\frac{1}{2}} B^{\frac{5}{4}} \nu^{\frac{1}{2}},$$

valid to leading order in ν as $\nu \rightarrow \infty$.

- Decrease in a (i.e. increase in kernel width) causes decrease of A_{\max} .
- Decrease in kernel width causes decrease in migration speed (but c does not approach 0).

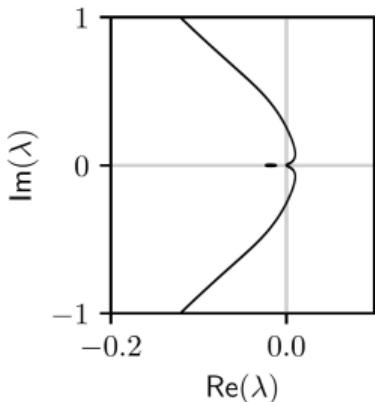


Locus of Hopf bifurcation for fixed C and varying a .¹²

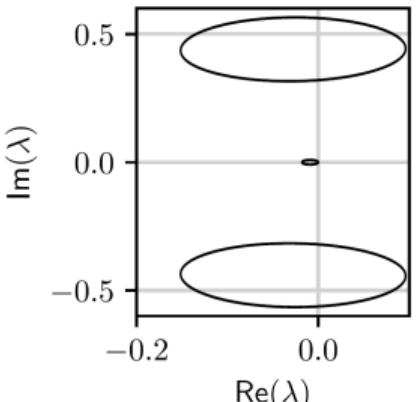
¹²EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018)

Pattern stability

- The **essential spectrum** of a periodic travelling wave determines the behaviour of small perturbations. \Rightarrow Tool to determine pattern stability.
- Two different types stability boundaries: **Eckhaus-type** and **Hopf-type**.
- Essential spectra and stability boundaries are calculated using the numerical continuation method by Rademacher et al.¹³



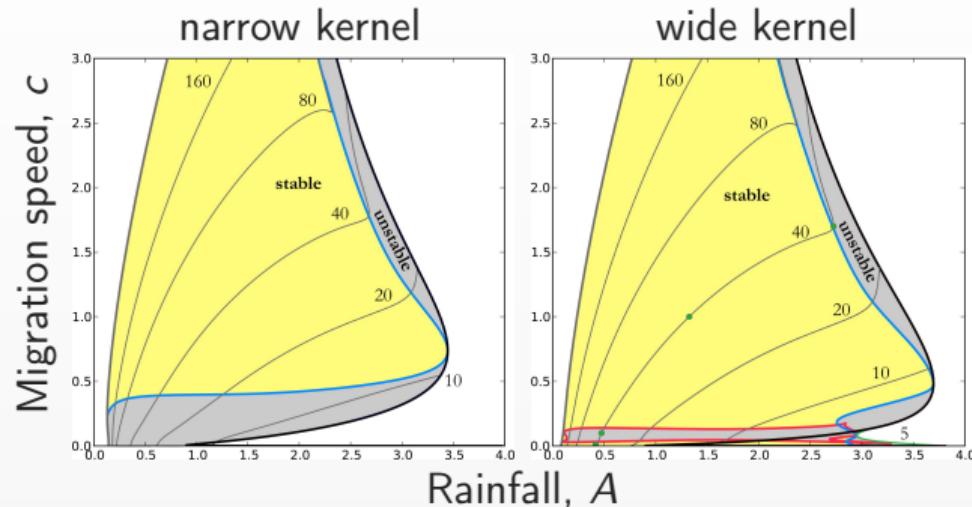
Eckhaus-type



Hopf-type

¹³Rademacher, J. D., Sandstede, B. and Scheel, A.: *Phys. D* 229.2 (2007)

Pattern existence and stability



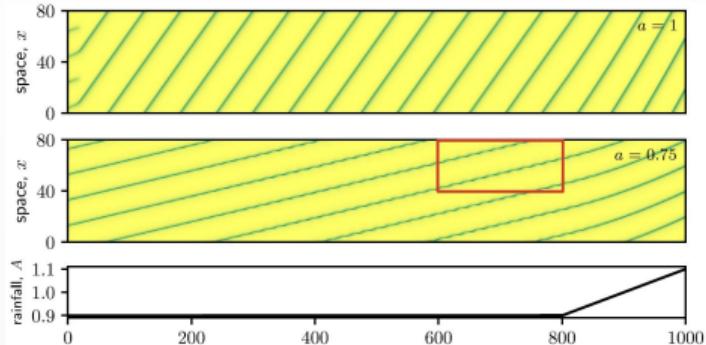
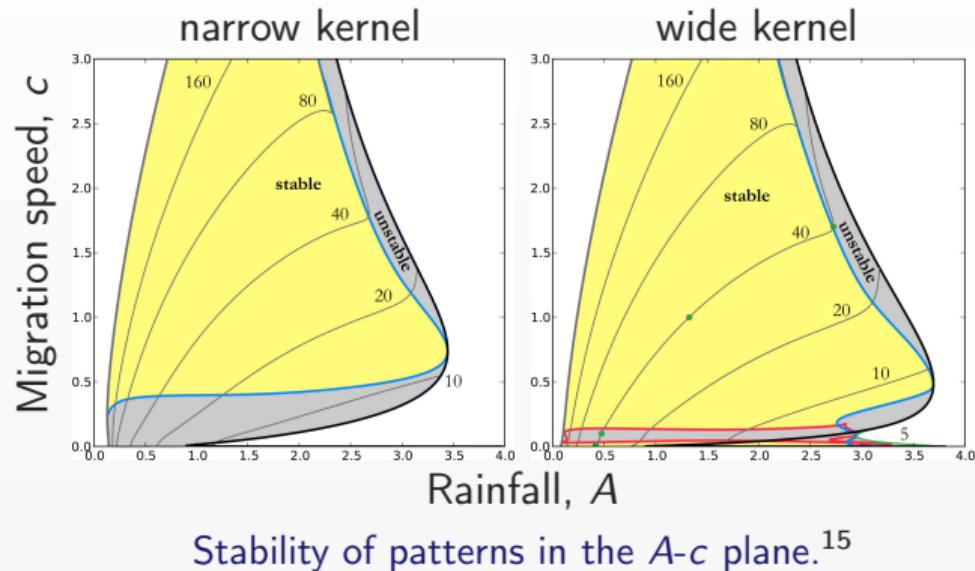
Stability of patterns in the A - c plane.¹⁴

For wide kernels, the stability boundary towards the desert state changes from Eckhaus to Hopf-type. This yields

- increased resilience due to oscillating vegetation densities in peaks,

¹⁴ Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Pattern existence and stability

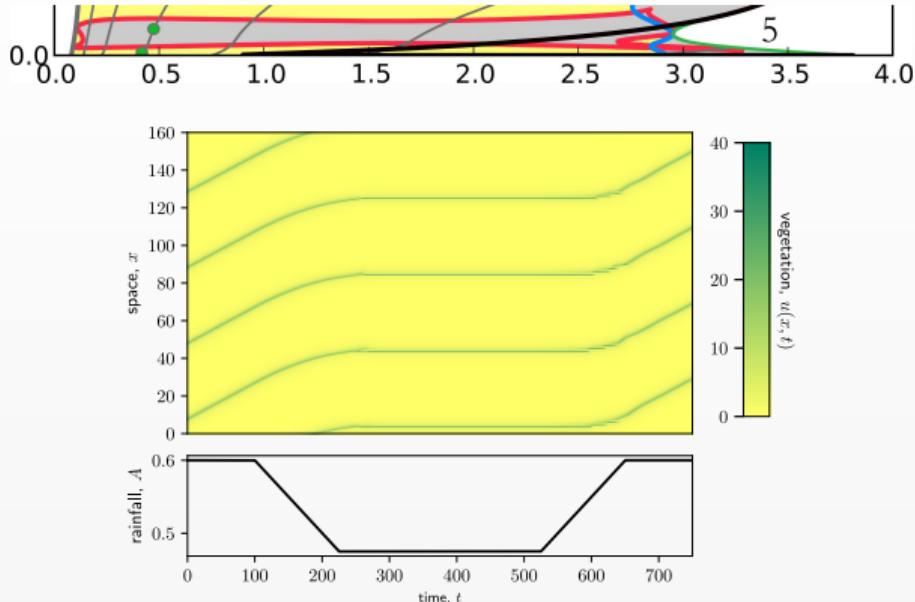


For wide kernels, the stability boundary towards the desert state changes from Eckhaus to Hopf-type. This yields

- increased resilience due to oscillating vegetation densities in peaks,

¹⁵Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Pattern existence and stability



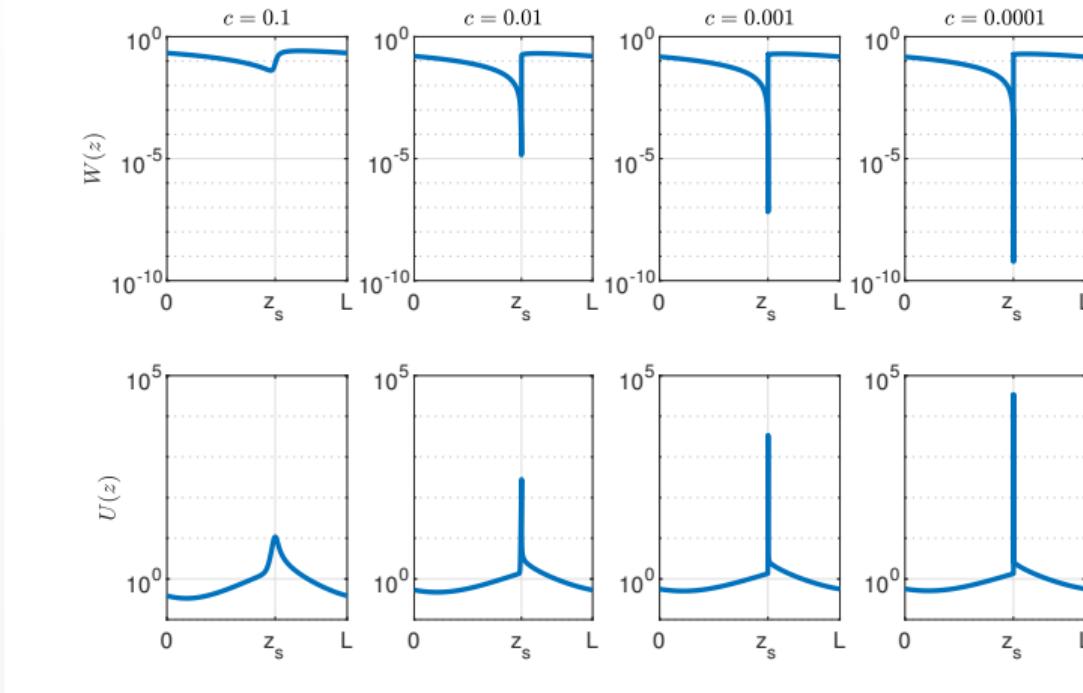
For wide kernels, the stability boundary towards the desert state changes from Eckhaus (sideband) to Hopf-type. This yields

- increased resilience due to oscillating vegetation densities in peaks,
- existence of stable patterns with small migration speed ($c \ll 1$).

Existence of stable (almost) stationary patterns.¹⁶

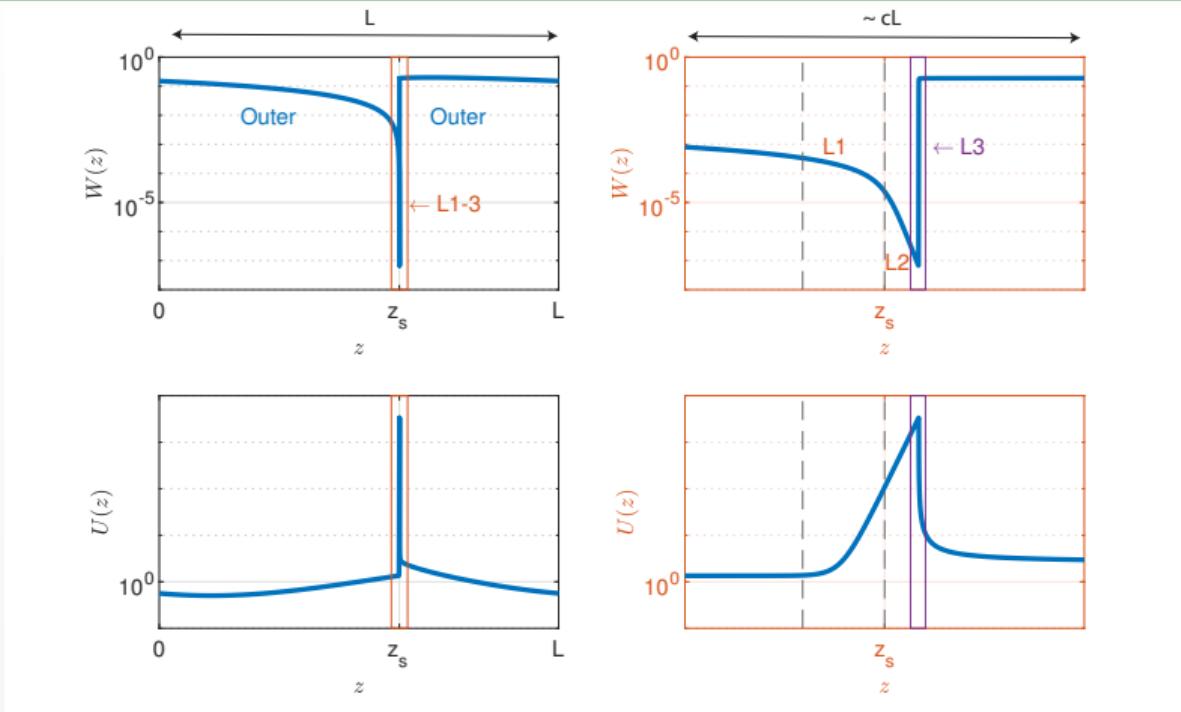
¹⁶ Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Almost stationary spike patterns



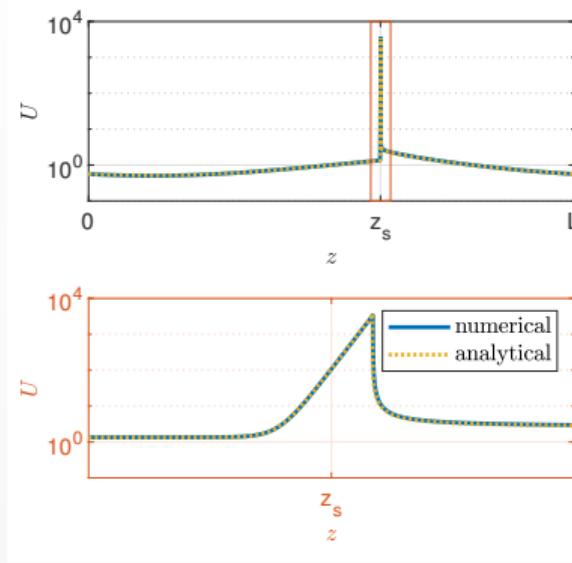
As c decreases, plant density develops a “spike”.

Almost stationary spike patterns



Layered structure of spike solution

Almost stationary spike patterns



Existence of almost stationary patterns is confirmed analytically using a singular perturbation theory approach, exploiting $c \ll 1$.

Analytical calculation of (almost) stationary patterns.¹⁷

¹⁷EL and Sherratt, J. A.: *J Math Biol* 86.15 (2023)

Main conclusion

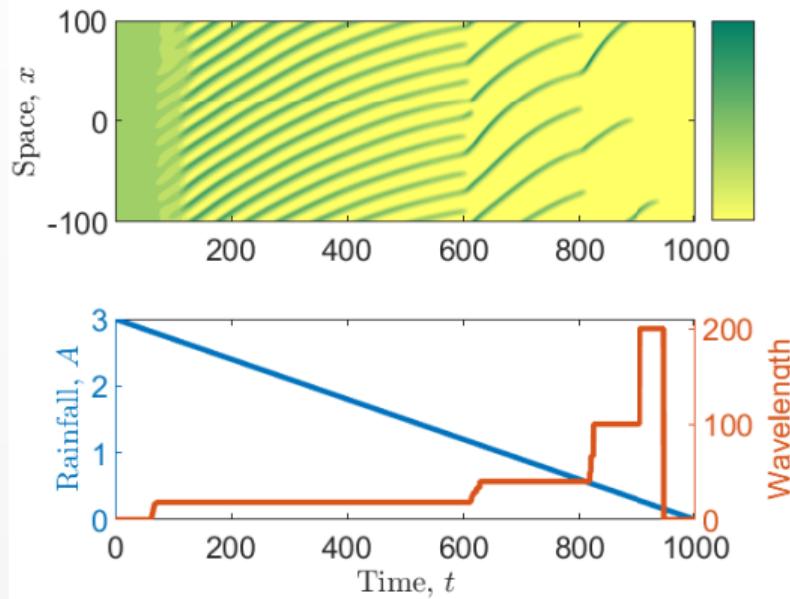
- How can the contrasting field data on uphill movement be explained?

For long seed dispersal distances moving (uphill) and stationary patterns can occur for the same parameter values.

Numerical simulations (pattern onset) and space discretisation to avoid nonlocality (calculation of essential spectra) show no qualitative differences for other kernel functions.

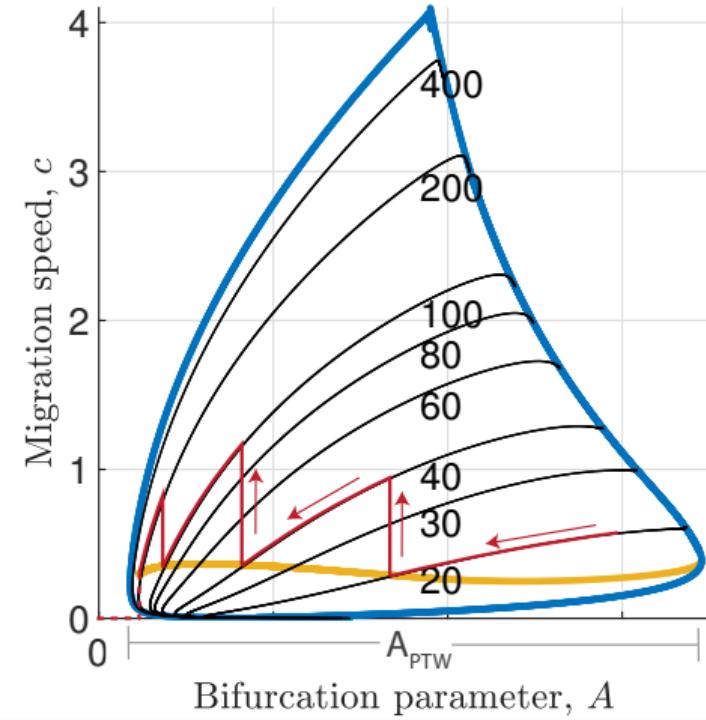
Research question 2

- How do transitions between patterns (= wavelength changes) occur?



Wavelength changes

- Wavelengths are preserved, provided they remain stable.
- Upon destabilisation at an Eckhaus stability boundary, a wavelength change occurs.

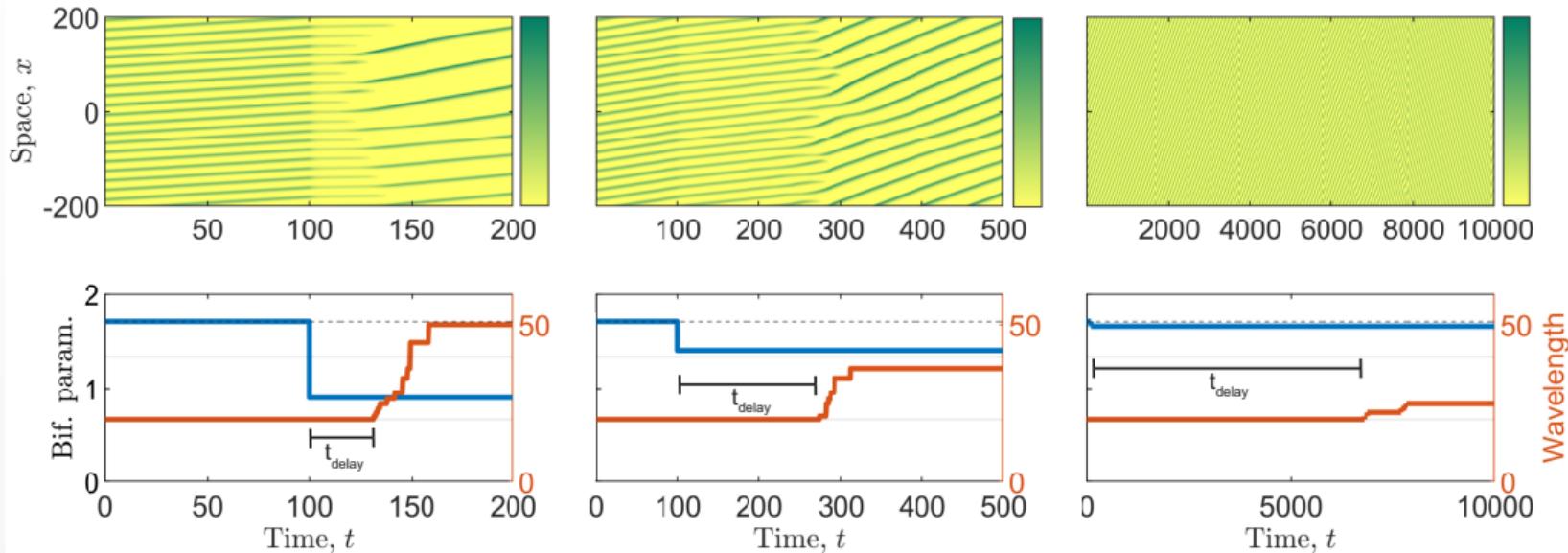


Wavelength changes

alternative video link.

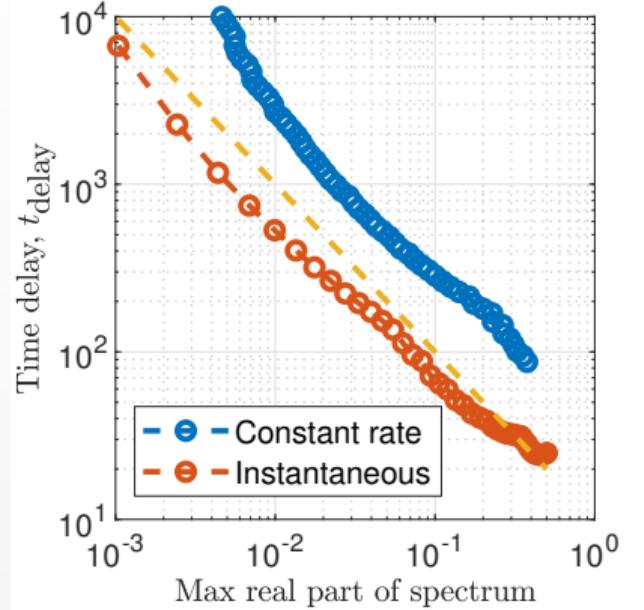
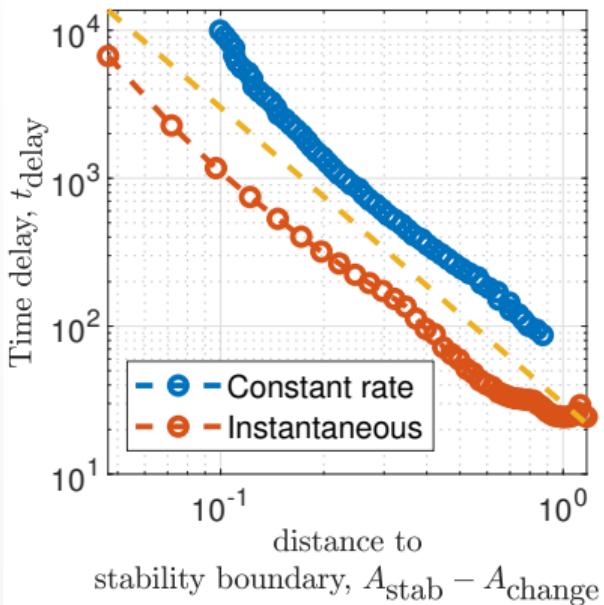
- Significant delays between crossing a stability boundary and observing wavelength changes occur.

Delays to wavelength changes



Significant delays between crossing a stability boundary and observing wavelength changes occur. Order of magnitude differences in delay depending on parameter values.

Predicting delays



There are clear trends between delay and bifurcation parameter and delay and max real part of the spectrum. **no predictive power**

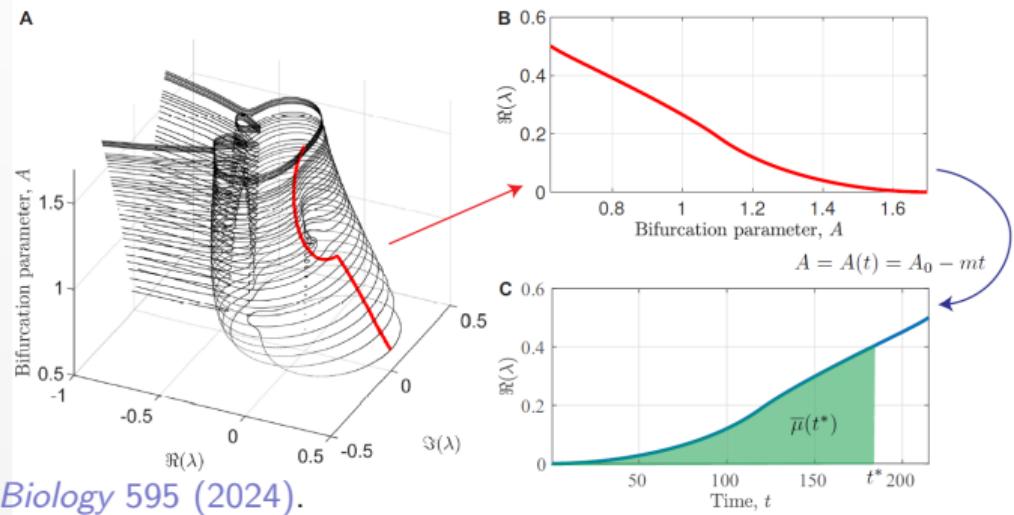
Predicting delays

Can predict the **order of magnitude of the delay** through the **accumulated maximal instability**¹⁸

$$\bar{\mu}(A(t)) = \int_{t_{\text{stab}}}^t \mu(\tau) d\tau, \quad t \geq t_{\text{stab}}.$$

t_{stab} is the time of the last crossing of the stability boundary.

$\mu(t)$ is the max real part of the spectrum at time t .



¹⁸EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

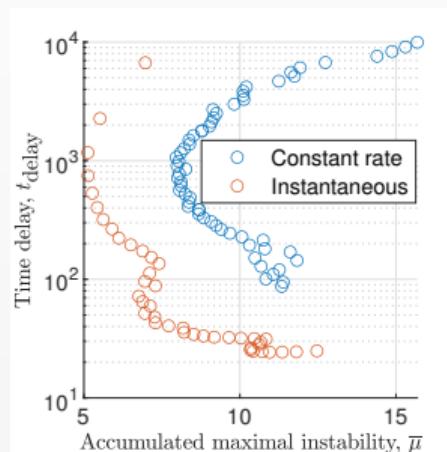
Predicting delays

Can predict the **order of magnitude of the delay** through the **accumulated maximal instability**¹⁸

$$\bar{\mu}(A(t)) = \int_{t_{\text{stab}}}^t \mu(\tau) d\tau, \quad t \geq t_{\text{stab}}.$$

t_{stab} is the time of the last crossing of the stability boundary.

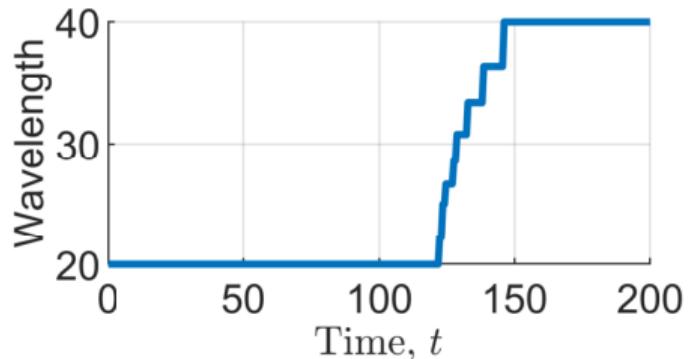
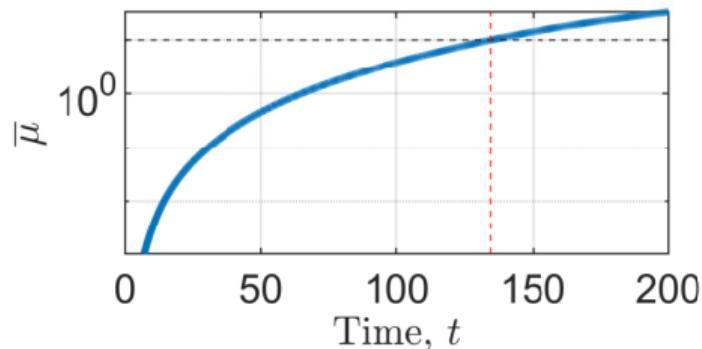
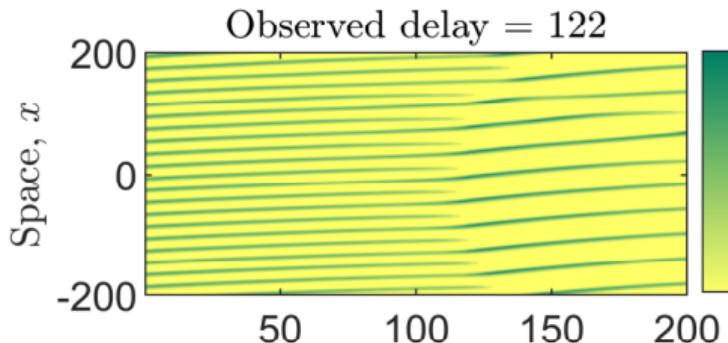
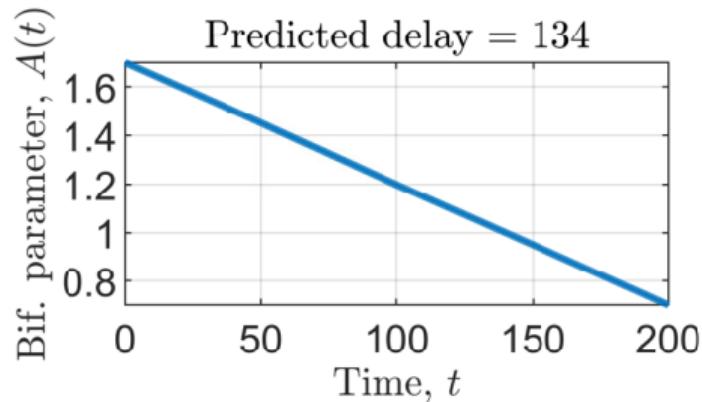
$\mu(t)$ is the max real part of the spectrum at time t .



Wavelength change occurs when $\bar{\mu} \approx 10$

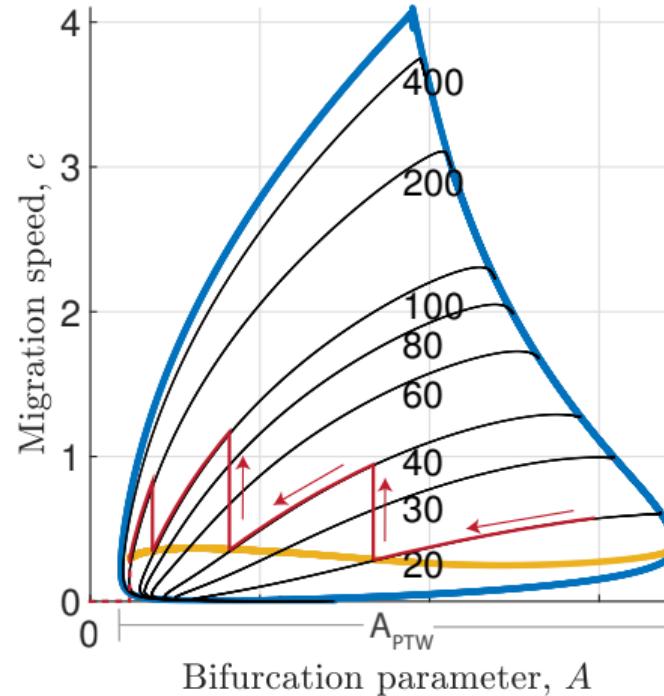
¹⁸EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024).

Delay prediction in practice



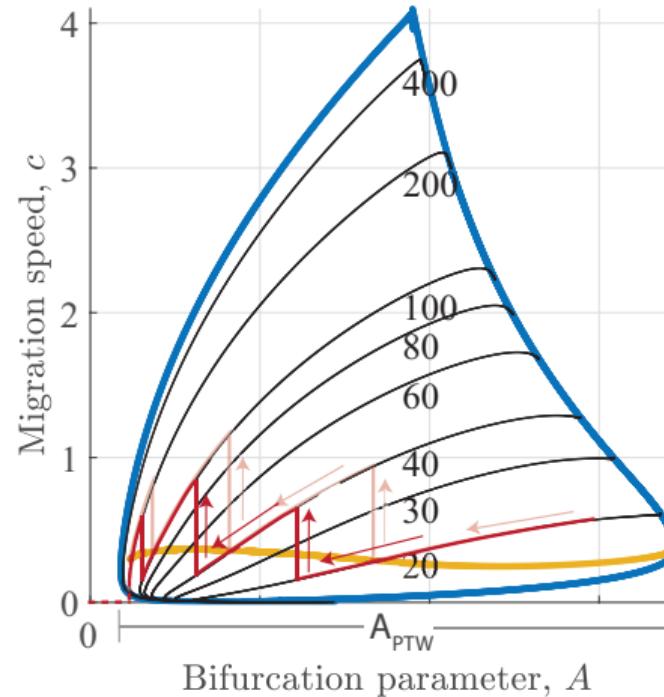
Conclusions 2

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.



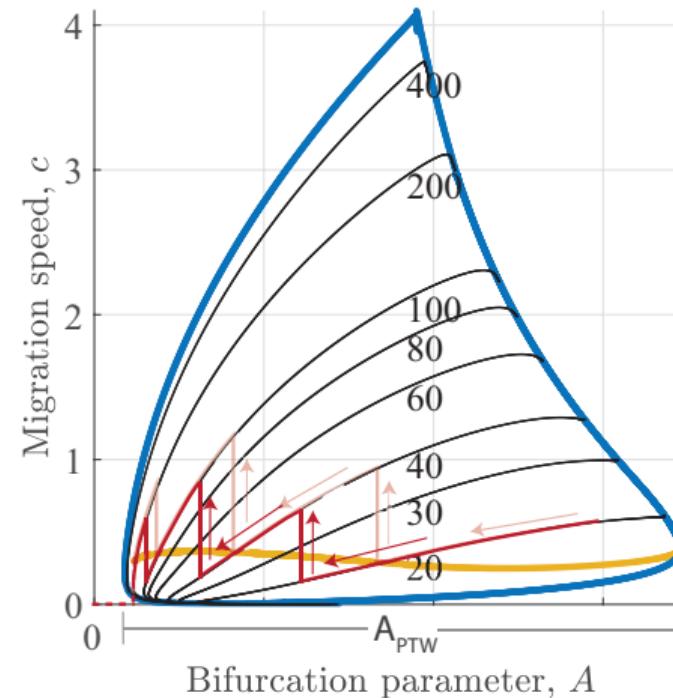
Conclusions 2

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.



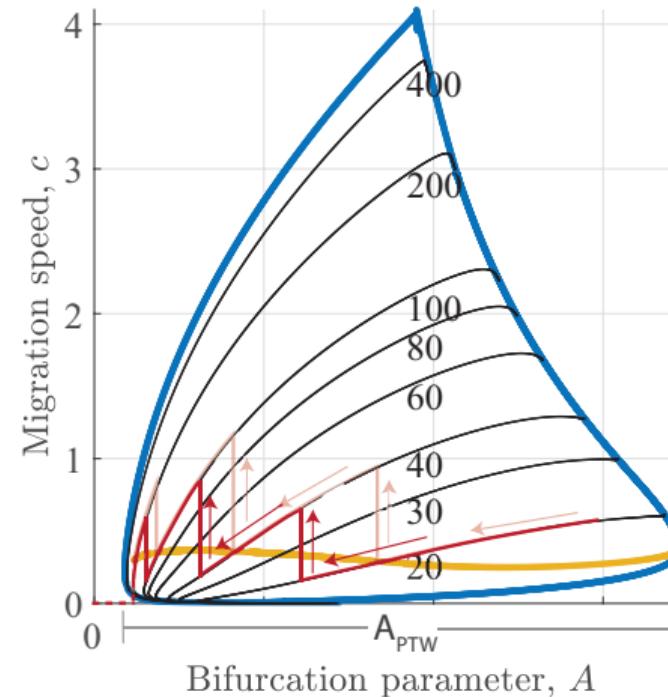
Conclusions 2

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.
- Order of magnitude of the delay can be predicted by tracking the maximum real part of the spectrum of the destabilised pattern over time.



Conclusions 2

- Wavelength changes that occur after crossing a stability boundary are subject to a delay.
- Order of magnitude of the delay can be predicted by tracking the maximum real part of the spectrum of the destabilised pattern over time.
- Open question: What new wavelength is chosen?



Research question 3

- How can species coexist despite competition for one limiting resource?

Klausmeier Model

The **one-species** extended Klausmeier reaction-advection-diffusion model.

$$\begin{aligned}\frac{\partial u}{\partial t} &= \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{\frac{\partial^2 u}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{u^2 w}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$

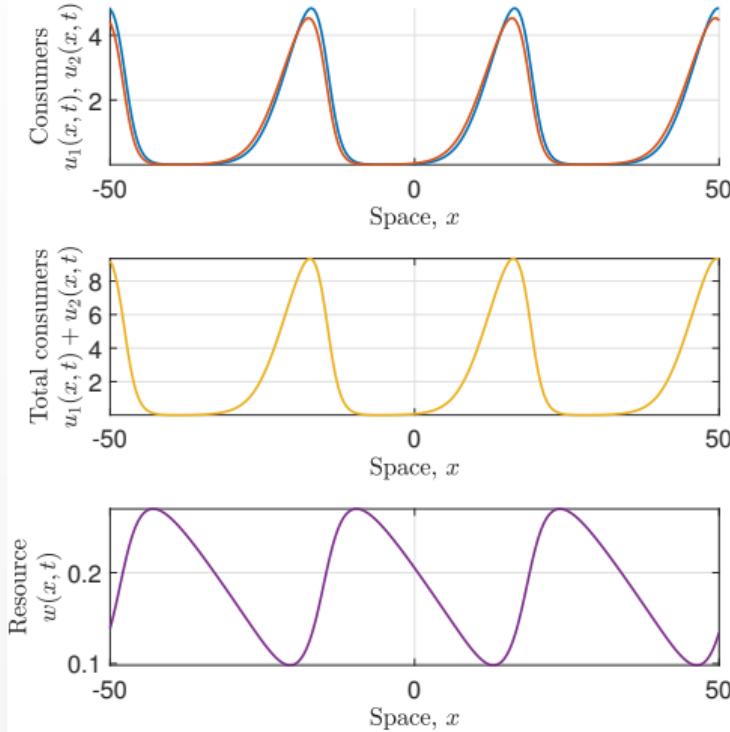
Multispecies Model

Multispecies model:

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= \underbrace{wu_1(u_1 + Hu_2)}_{\text{plant growth}} - \underbrace{B_1 u_1}_{\text{plant loss}} \\ &\quad + \underbrace{\frac{\partial^2 u_1}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial u_2}{\partial t} &= \underbrace{Fwu_2(u_1 + Hu_2)}_{\text{plant growth}} - \underbrace{B_2 u_2}_{\text{plant loss}} \\ &\quad + \underbrace{D \frac{\partial^2 u_2}{\partial x^2}}_{\text{plant dispersal}}, \\ \frac{\partial w}{\partial t} &= \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{w(u_1 + u_2)(u_1 + Hu_2)}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}.\end{aligned}$$

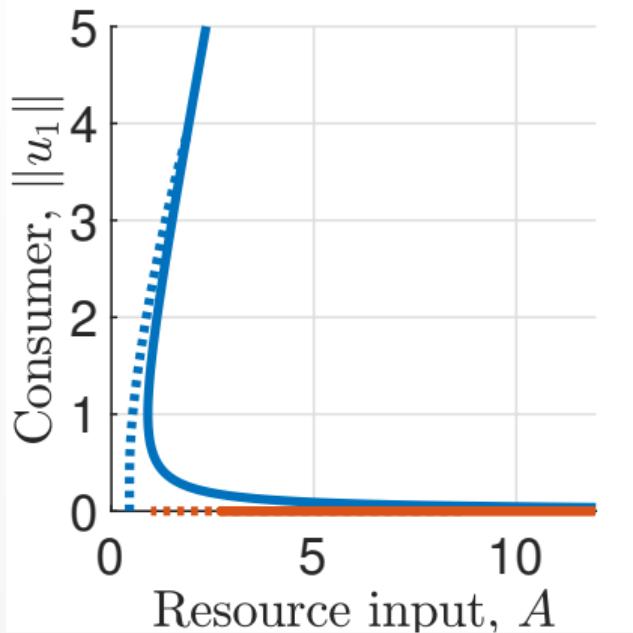
Species only differ quantitatively (i.e. in parameter values) but not qualitatively (i.e. same functional responses).

Simulations



- Consumer species coexist in a spatially patterned solution.
- Coexistence requires a balance between species' local average fitness and their colonisation abilities.
- Solutions are periodic travelling waves and move in the direction opposite to the unidirectional resource flux.

Bifurcation diagram

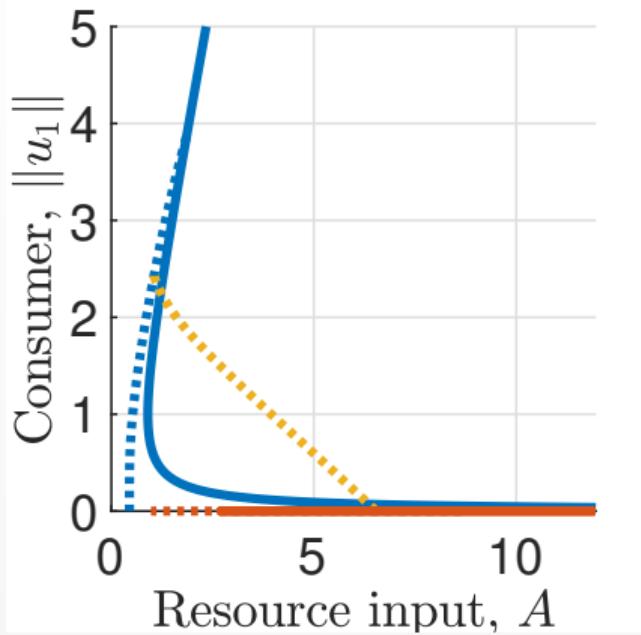


- uniform u_1
- uniform u_2
- single species pattern u_1
- single species pattern u_2
- coexistence pattern u_1, u_2

- The bifurcation structure of single-species states is identical with that of single species model.

Bifurcation diagram: one wavespeed only

Bifurcation diagram

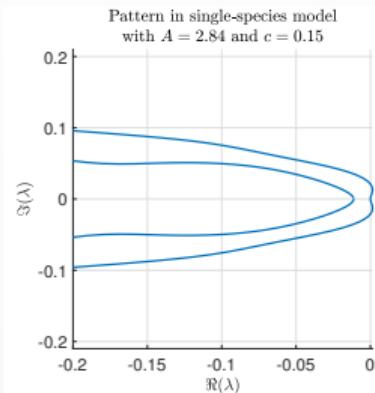


Bifurcation diagram: one wavespeed only

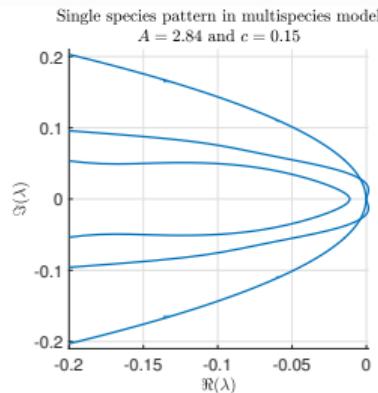
- uniform u_1
- uniform u_2
- single species pattern u_1
- single species pattern u_2
- coexistence pattern u_1, u_2

- The bifurcation structure of single-species states is identical with that of single species model.
- **Coexistence pattern** solution branch connects single-species pattern solution branches.

Pattern onset



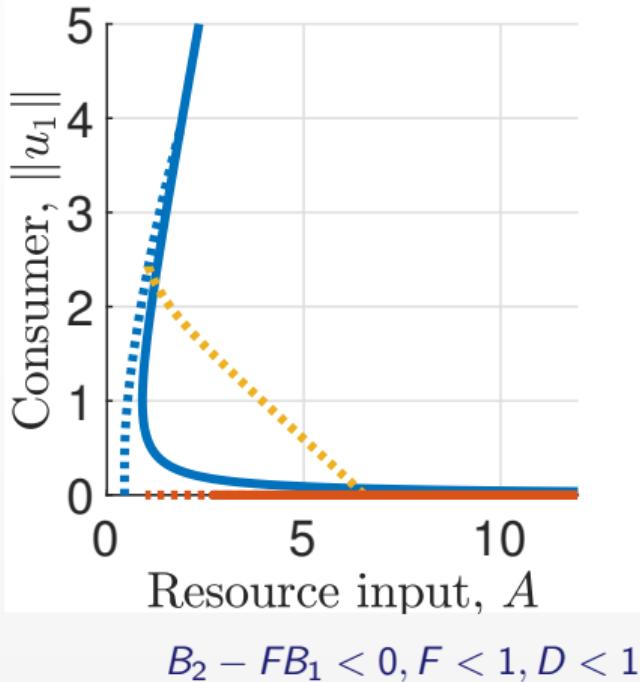
Essential spectrum in single-species model



Essential spectrum in multispecies model

- The key to understand **coexistence pattern onset** is knowledge of single-species pattern's stability.
- Pattern onset occurs as the single-species pattern loses/gains stability to the introduction of a competitor.

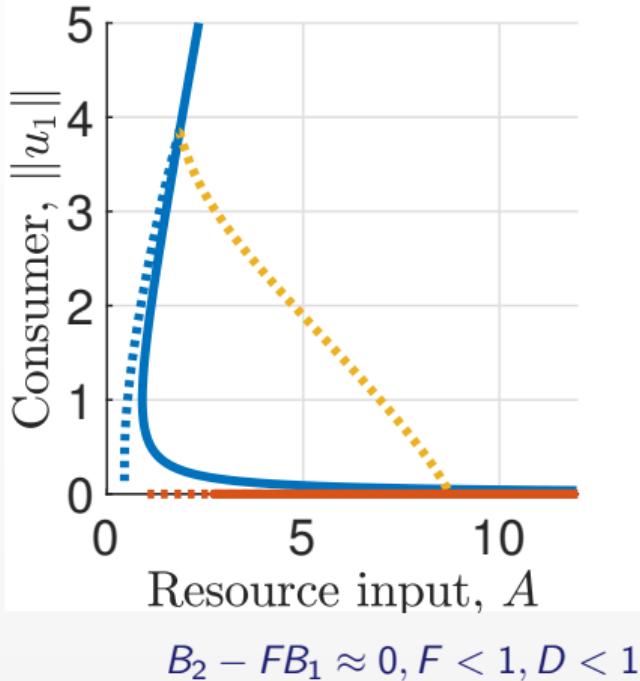
Pattern existence



- uniform u_1
- uniform u_2
- single species pattern u_1
- single species pattern u_2
- coexistence pattern u_1, u_2

- Key quantity: Local average fitness difference $B_2 - FB_1$ determines stability of single-species states in spatially uniform setting.
- Condition for pattern existence: Balance between local competitive and colonisation abilities.

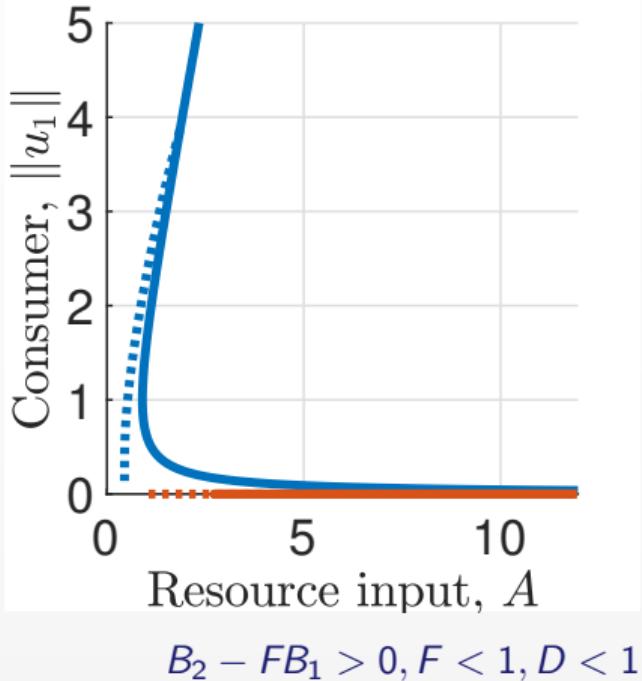
Pattern existence



- uniform u_1
- uniform u_2
- single species pattern u_1
- single species pattern u_2
- coexistence pattern u_1, u_2

- Key quantity: Local average fitness difference $B_2 - FB_1$ determines stability of single-species states in spatially uniform setting.
- Condition for pattern existence: Balance between local competitive and colonisation abilities.

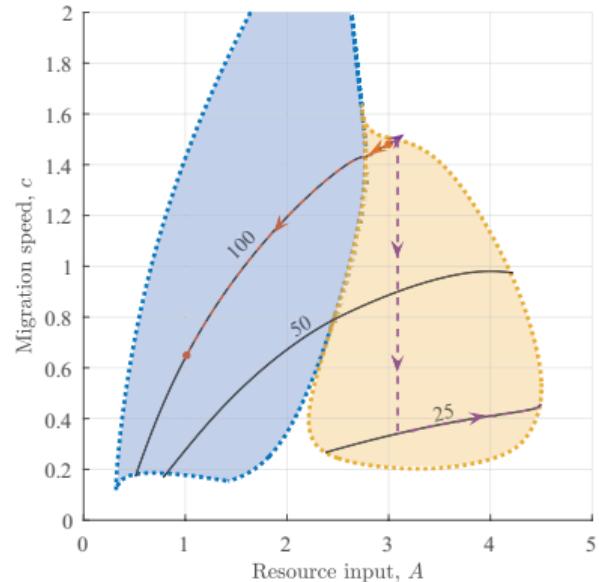
Pattern existence



- uniform u_1
- uniform u_2
- single species pattern u_1
- single species pattern u_2
- coexistence pattern u_1, u_2

- Key quantity: Local average fitness difference $B_2 - FB_1$ determines stability of single-species states in spatially uniform setting.
- Condition for pattern existence: Balance between local competitive and colonisation abilities.

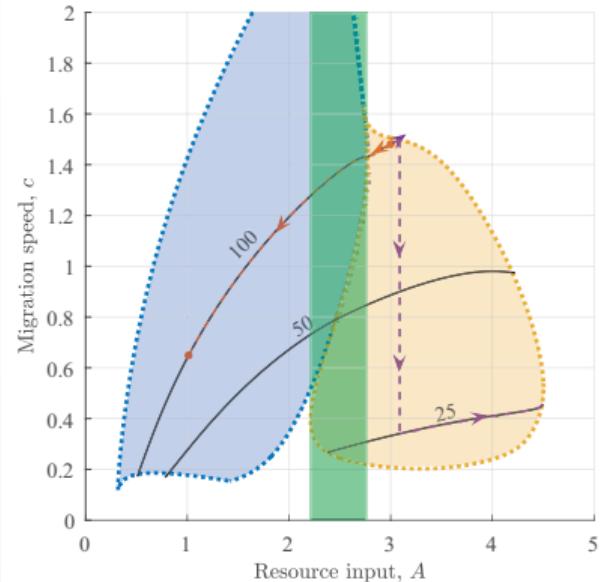
Pattern stability



Stability regions of system states.

- Stability regions of patterned solution can be traced using numerical continuation.
- For decreasing resource input, coexistence state loses stability to single-species pattern of coloniser species.

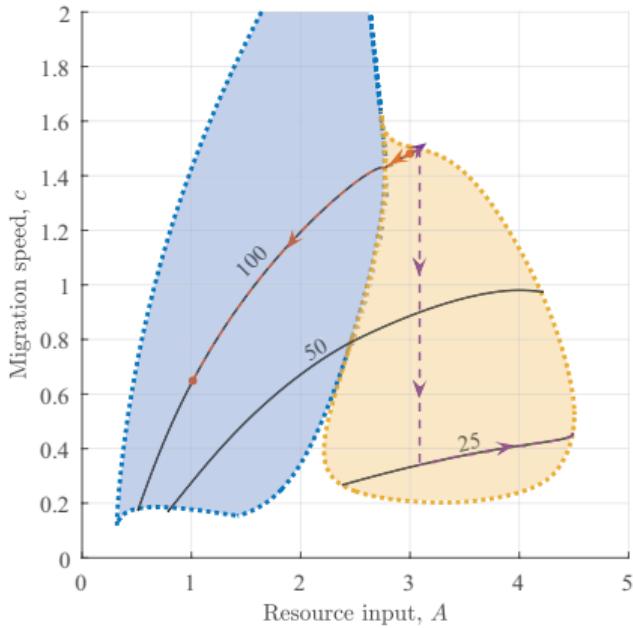
Pattern stability



Stability regions of system states.

- Stability regions of patterned solution can be traced using numerical continuation.
- For decreasing resource input, coexistence state loses stability to single-species pattern of coloniser species.
- **Bistability of single-species coloniser pattern and coexistence pattern occurs.**

Hysteresis



Wavelength contours of stable patterns

- State transitions are affected by **hysteresis**.
- Extinction can occur despite a coexistence state being stable.
- **Ecosystem resilience depends on both current and past states of the system.**

Conclusions II

- Spatial self-organisation is a coexistence mechanism¹⁹.
- Coexistence is enabled by spatial heterogeneities in the resource, caused by the consumers' self-organisation into patterns.
- A balance between species' colonisation abilities and local competitiveness promotes coexistence.

¹⁹ EL and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), EL: *Oikos* 130.4 (2021), EL: *Ecol. Complexity* 42 (2020).

References

Slides are available on my website.

<http://lukaseigentler.github.io>

- [1] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018), pp. 151–161.
- [2] EL: *Ecol. Complexity* 42 (2020), p. 100835.
- [3] EL: *Oikos* 130.4 (2021), pp. 609–623.
- [4] EL and Sensi, M.: *Journal of Theoretical Biology* 595 (2024), p. 111945.
- [5] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018), pp. 739–763.
- [6] EL and Sherratt, J. A.: *J Math Biol* 86.15 (2023).
- [7] EL and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), p. 110122.