

University of Dundee

Modelling dryland vegetation patterns:
Nonlocal dispersal and species coexistence

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joint work with

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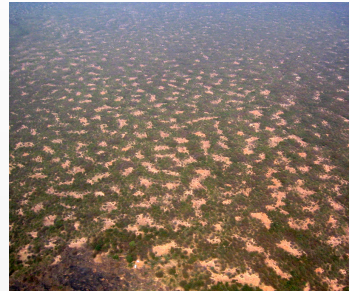
Vegetation patterns

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

Stripe pattern in Ethiopia¹.



Gap pattern in Niger².



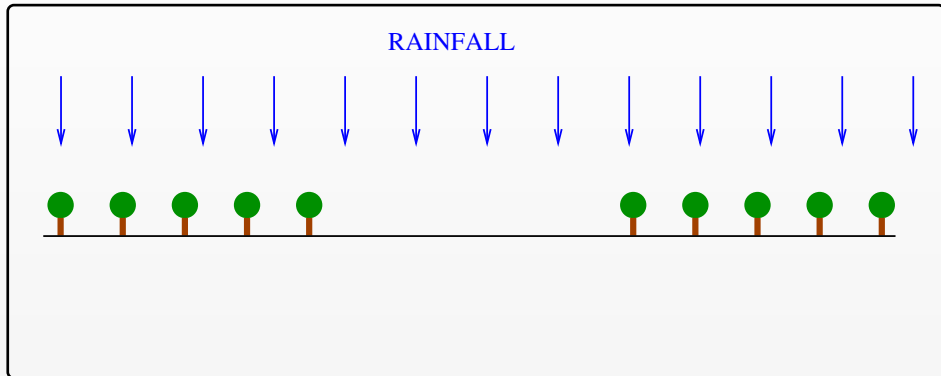
- Plants increase water infiltration into the soil and thus induce a **positive feedback loop**.

¹Source: Google Maps

²Source: Wikimedia Commons

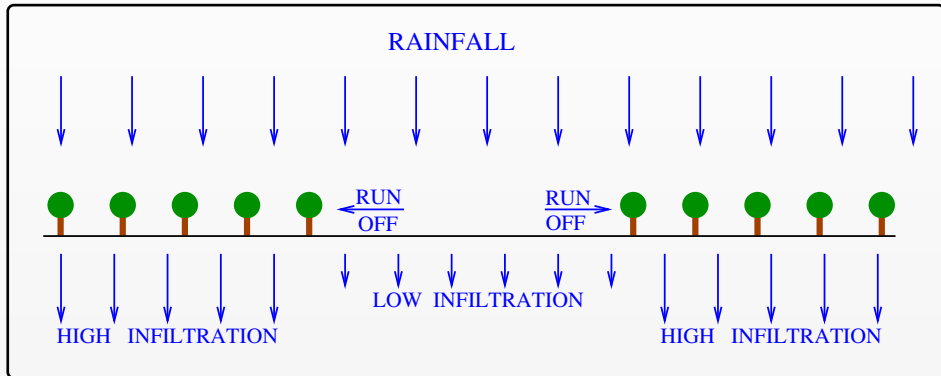
Local facilitation in vegetation patterns

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



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³Source: Google Maps

⁴Source: Wikimedia Commons

Vegetation patterns

Uphill migration due to water gradient.⁵



- On sloped ground, stripes grow **parallel to the contours**.
- Stripes either **move uphill** or are **stationary**.
- **Species coexistence** commonly occurs.

⁵Dunkerley, D.: *Desert* 23.2 (2018).

Klausmeier model

One of the most basic phenomenological models is the **extended Klausmeier reaction-advection-diffusion model**.⁶

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

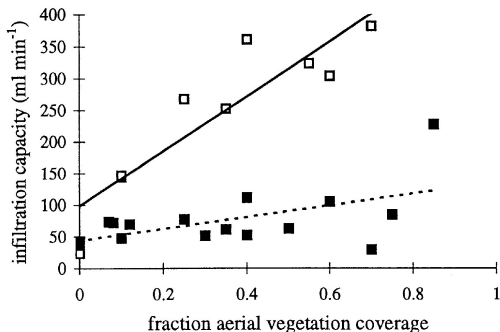
⁶Klausmeier, C. A.: *Science* 284.5421 (1999).

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Water uptake



Infiltration capacity increases with plant density⁷

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.

⁷Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000)

Research questions

- How does nonlocal seed dispersal affect onset, existence and stability of patterns?
- How can species coexist despite competition for one limiting resource?

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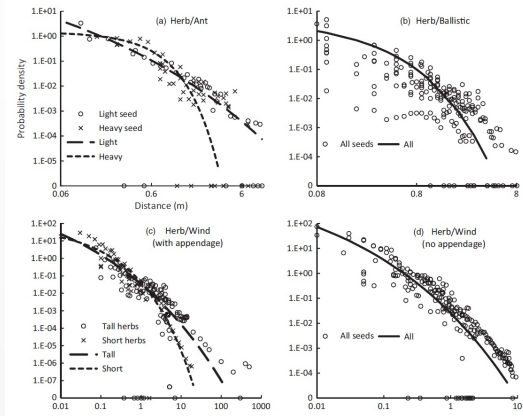
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Local Model

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

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

Nonlocal seed dispersal



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

Data of long range seed dispersal ⁸

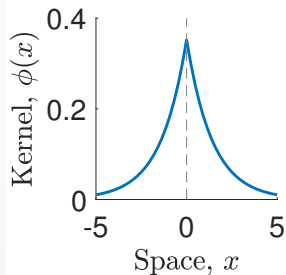
⁸Bullock, J. M. et al.: *J. Ecol.* 105.1 (2017)

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.

$$\frac{\partial u}{\partial t} = \underbrace{u^2 w}_{\text{plant growth}} - \underbrace{Bu}_{\text{plant loss}} + \underbrace{C(\phi(\cdot; a) * u(\cdot, t) - u)}_{\text{nonlocal plant dispersal}},$$

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



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

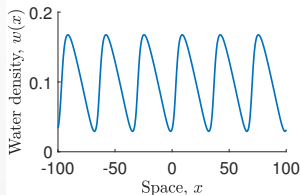
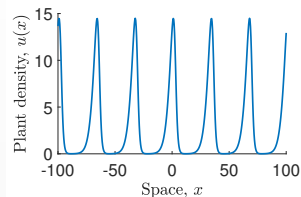
$$\hat{\phi}(k) = \frac{a^2}{a^2 + k^2}, \quad k \in \mathbb{R}.$$

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

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

Travelling waves

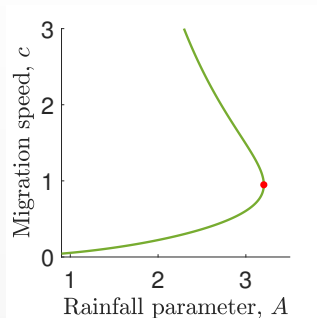
- Numerical simulations of the model on sloped terrain suggest uphill movement \Rightarrow Periodic travelling waves.
- Patterns correspond to **limit cycles** of the travelling wave integro-ODEs.



Numerical simulation.

Travelling waves

- Numerical simulations of the model on sloped terrain suggest uphill movement \Rightarrow Periodic travelling waves.
- Patterns correspond to **limit cycles** of the travelling wave integro-ODEs.
- Numerical continuation shows that **patterns emanate from a Hopf bifurcation** and terminate at a homoclinic orbit.
- In the PDE model, pattern onset occurs at a threshold $A = A_{\max}$, the maximum rainfall level of the Hopf bifurcation loci in the travelling wave ODEs.



Location of the Hopf bifurcation in A - c plane.

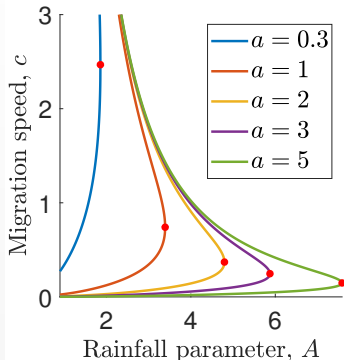
Pattern onset

Using that $\nu \gg 1$,

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

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

- Note that $A_{\max} = O(\sqrt{\nu})$.
- Decrease in a (i.e. increase in kernel width) causes decrease of A_{\max} .
- Increase in dispersal rate C causes decrease of A_{\max} .

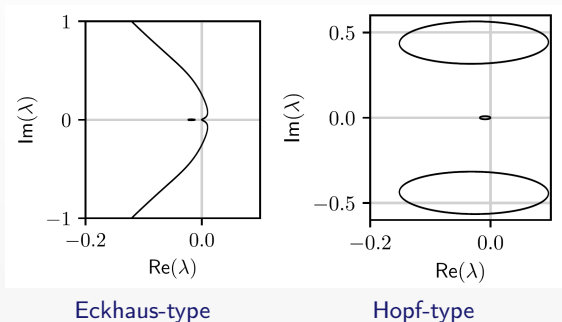


Locus of Hopf bifurcation for fixed C and varying a .⁹

⁹EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018)

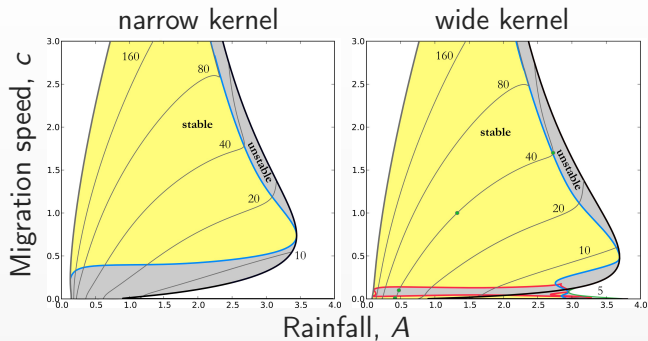
Pattern stability

- 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.¹⁰



¹⁰Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007)

Pattern existence and stability



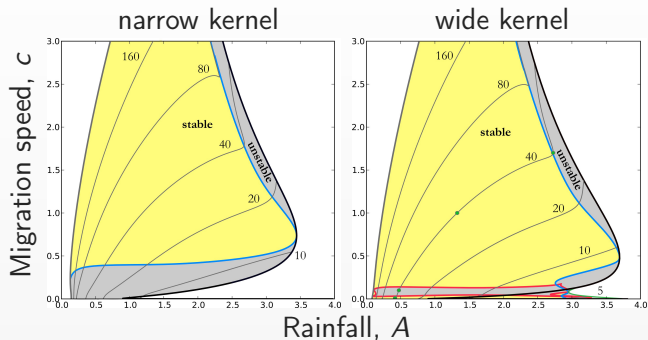
Stability of patterns in the A - c plane.¹¹

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

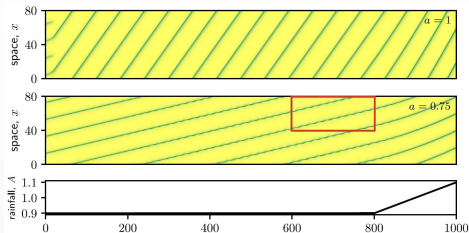
- **increased resilience** due to oscillating vegetation densities in peaks,

¹¹Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Pattern existence and stability



Stability of patterns in the A - c plane.¹²

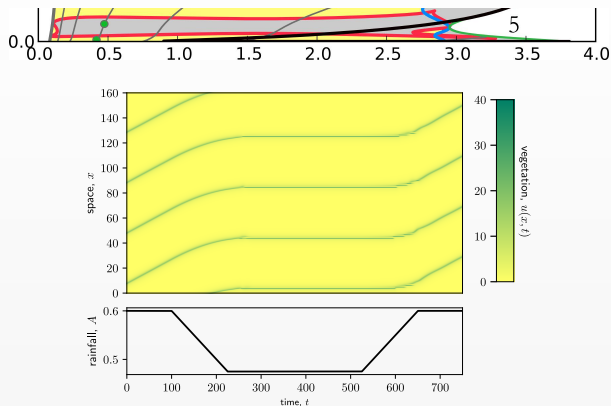


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Pattern existence and stability



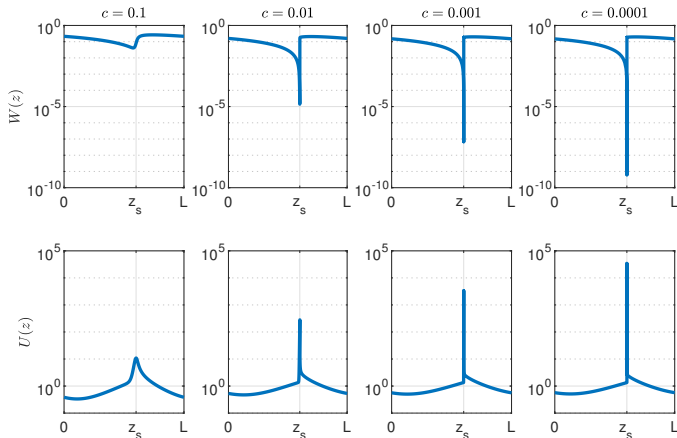
For wide kernels, the stability boundary towards the desert state changes from Eckhaus (sideband) to Hopf-type. This yields

- **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.¹³

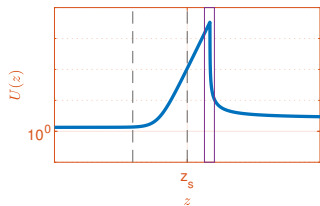
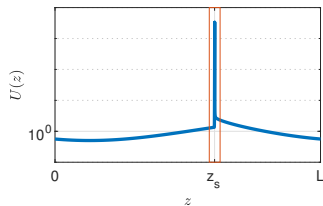
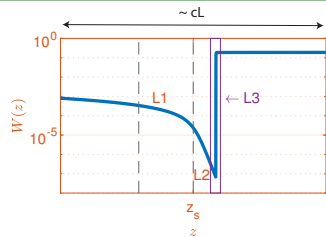
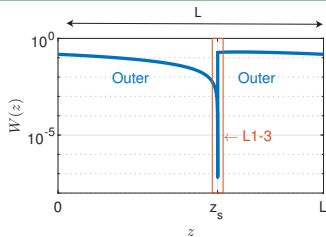
¹³Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Almost stationary spike patterns



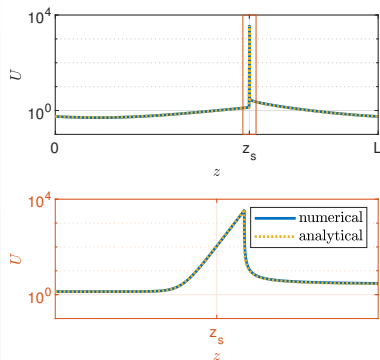
As c decreases, plant density develops a “spike”.

Almost stationary spike patterns



Layered structure of spike solution

Almost stationary spike patterns



Analytical calculation of (almost) stationary patterns.¹⁴

¹⁴EL and Sherratt, J. A.: (submitted)

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

Conclusions I

- **Wider kernels** and **higher dispersal rates** inhibit pattern onset.
- Stability analysis of periodic travelling waves provides ecological insights into pattern dynamics: Long-range seed dispersal **increases** the **resilience** of a pattern and **stabilises** (almost) **stationary patterns**.
- Numerical simulations (pattern onset) and space discretisation to avoid nonlocality (calculation of essential spectra) show **no qualitative differences for other kernel functions**.

Research questions

- How does nonlocal seed dispersal affect onset, existence and stability of patterns?
- How can species coexist despite competition for one limiting resource?

Klausmeier Model

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

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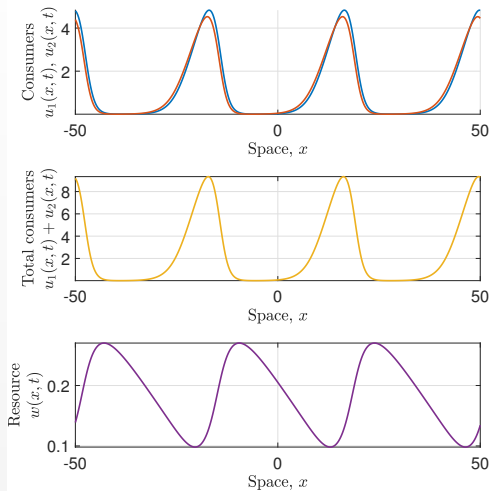
Multispecies Model

Multispecies model:

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

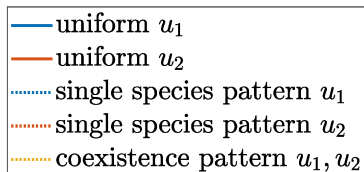
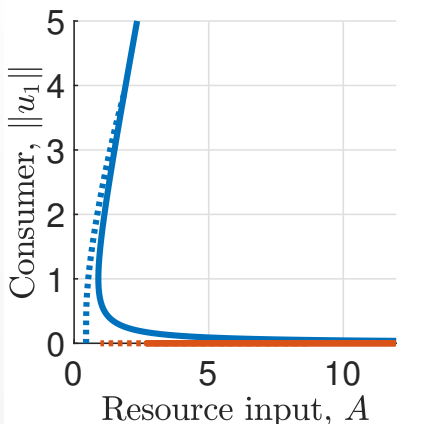
Species only differ quantitatively (i.e. in parameter values) but not qualitatively (i.e. same functional responses). Assume u_1 is superior coloniser; u_2 is locally superior.

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.

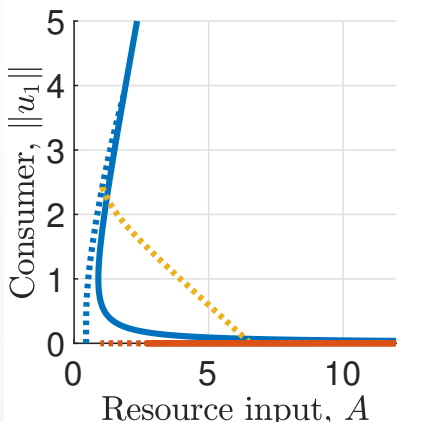
Bifurcation diagram



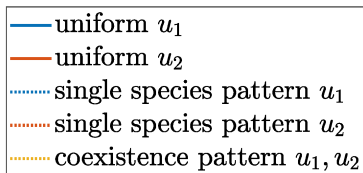
- The bifurcation structure of single-species states is identical with that of single species model.

Bifurcation diagram: one wavespeed only

Bifurcation diagram

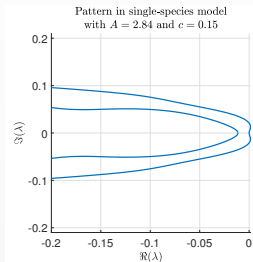


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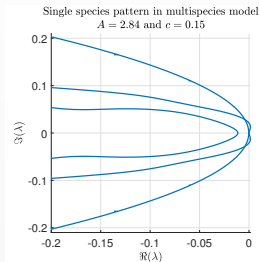


- The bifurcation structure of single-species states is identical with that of single species model.
- **Coexistence pattern** solution branch connects **single-species pattern** solution branches.

Pattern onset



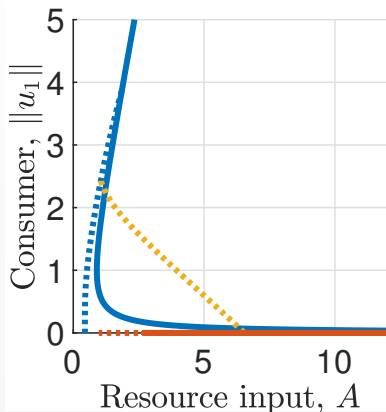
Essential spectrum in
single-species model



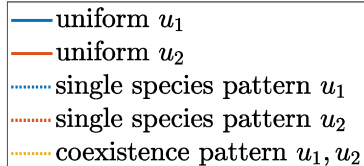
Essential spectrum in
multispecies model

- 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

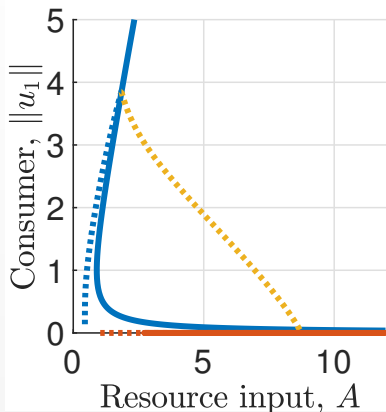


$$B_2 - FB_1 < 0, F < 1, D < 1$$

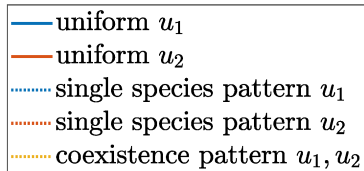


- Key quantity: **Local average fitness difference $B_2 - FB_1$** determines stability of single-species states in spatially uniform setting.
- Condition for pattern existence: **Balance between local competitive and colonisation abilities.**

Pattern existence

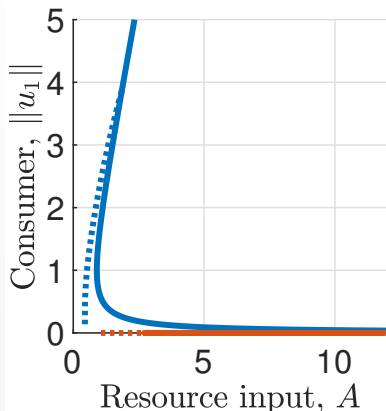


$$B_2 - FB_1 \approx 0, F < 1, D < 1$$

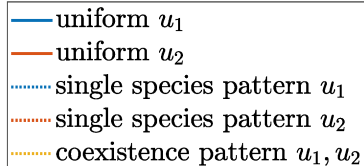


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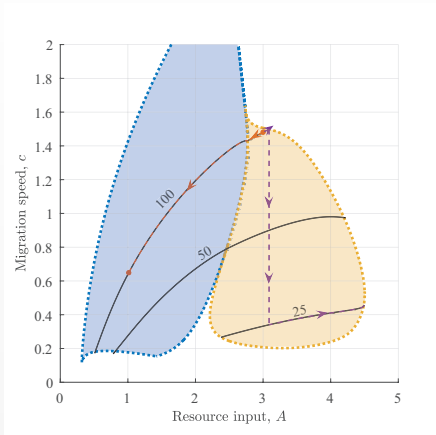


$$B_2 - FB_1 > 0, F < 1, D < 1$$



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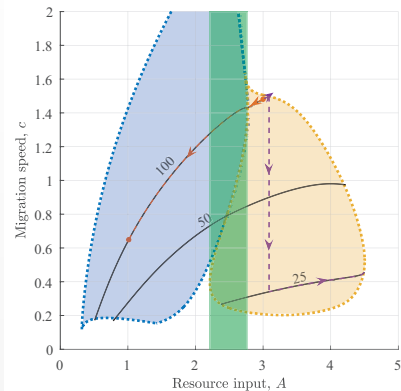
Pattern stability



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.

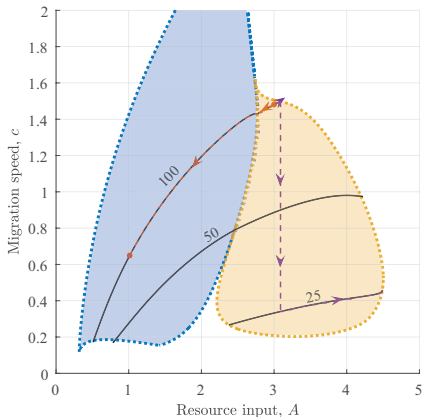
Pattern stability



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 mechanism¹⁵.
- 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 enables coexistence.
- Coexistence may occur as a **metastable state** if the average fitness difference between species is small¹⁶.

¹⁵EL and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), EL: *Oikos* 130.4 (2021), EL: *Ecol. Complexity* 42 (2020).

¹⁶EL and Sherratt, J. A.: *Bull. Math. Biol.* 81.7 (2019).

Future Work

- How does nonlocal consumer dispersal affect species coexistence?¹⁷
- Do results extend to an arbitrary number of species?
- How do fluctuations in environmental conditions (in particular resource input) affect coexistence?
- In particular, what are the effects of seasonal¹⁸, intermittent¹⁹ and probabilistic resource input regimes on both single-species and multispecies states?

¹⁷EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018).

¹⁸EL and Sherratt, J. A.: *J. Math. Biol.* 81 (2020).

¹⁹EL and Sherratt, J. A.: *Physica D* 405 (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] Eigentler, L.: *Oikos* 130.4 (2021), pp. 609–623.
- [3] Eigentler, L.: *Ecol. Complexity* 42 (2020), p. 100835.
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- [7] Eigentler, L. and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), p. 110122.