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<http://lukaseigentler.github.io>

Pattern migration (or not?) of dryland vegetation stripes

MODIS, ICMS

15 September 2023

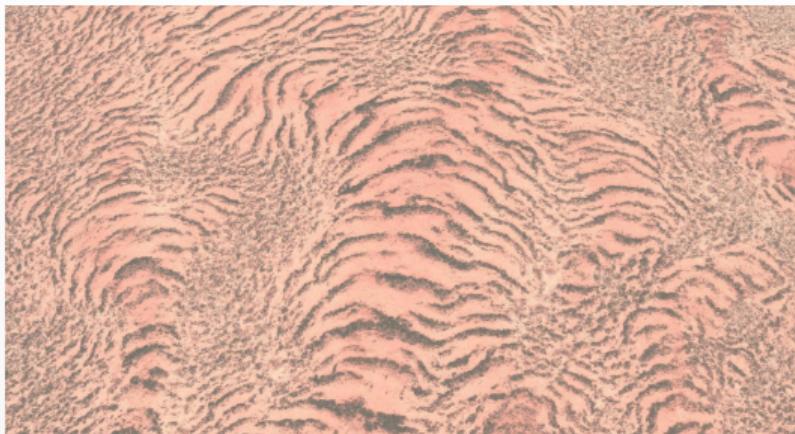
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joint work with Jonathan A Sherratt (Heriot-Watt Univ.)

Vegetation patterns

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

Stripe pattern in Ethiopia¹.



Gap pattern in Niger².



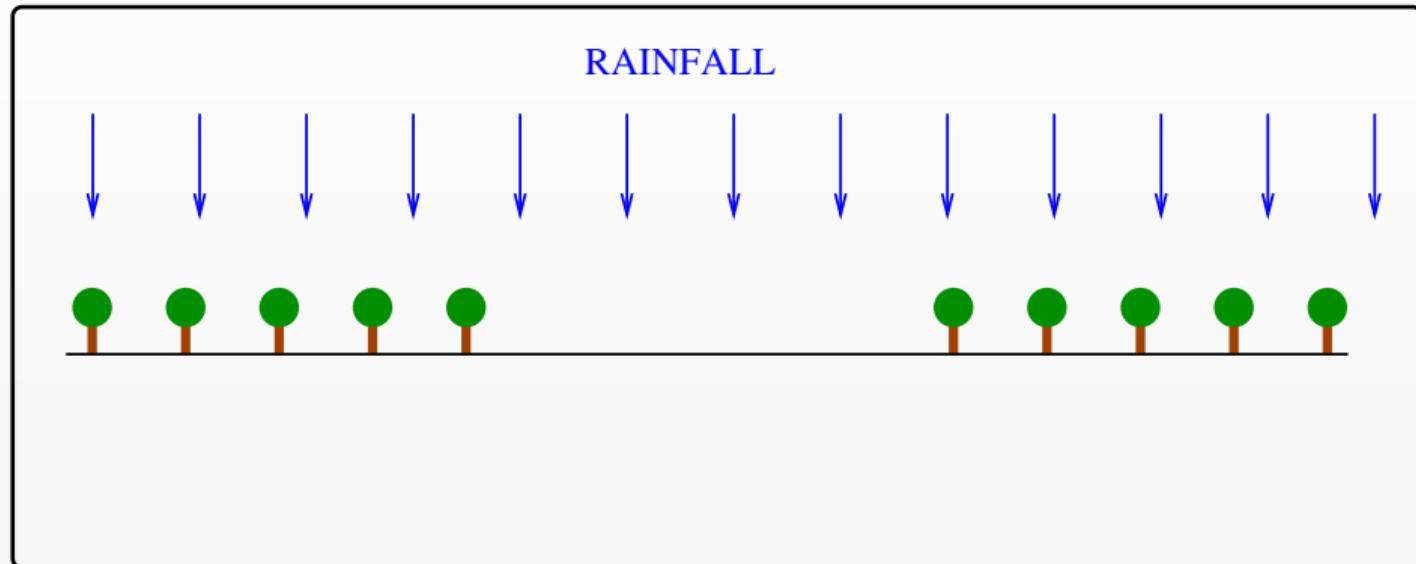
- Plants increase water infiltration into the soil and thus induce a **positive feedback loop**.

¹Source: Google Maps

²Source: Wikimedia Commons

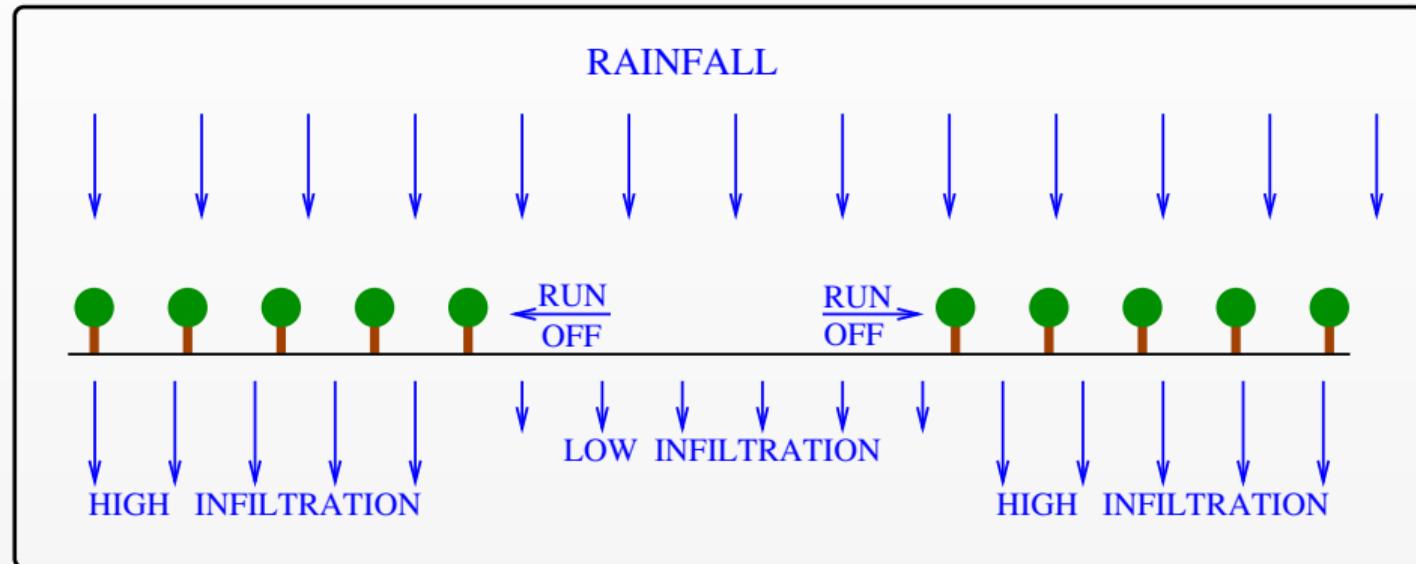
Local facilitation in vegetation patterns

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



Local facilitation in vegetation patterns

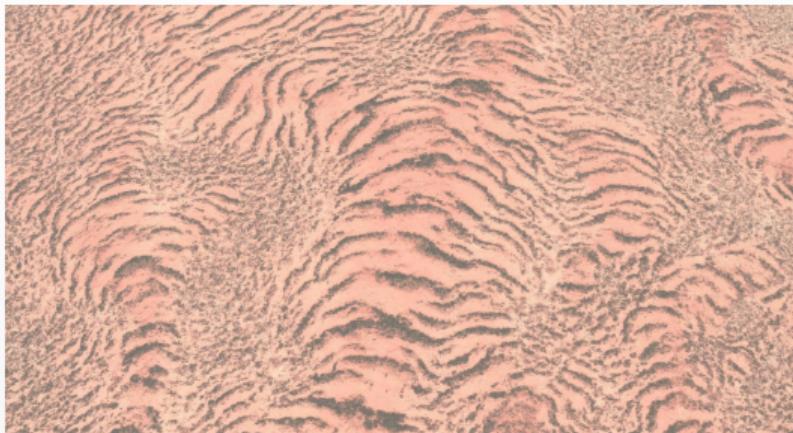
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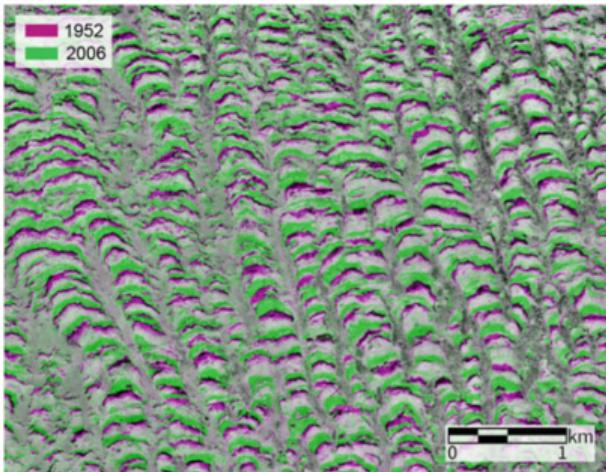
- On sloped ground, stripes grow **parallel to the contours**.

³Source: Google Maps

⁴Source: Wikimedia Commons

Vegetation patterns

Timeseries data.⁵



Uphill migration due to water gradient.⁶



- Contrasting field data: stripes either **move uphill** (< 1m per year) or are **stationary**⁷.
- **No reports of downhill movement.**

⁵Gandhi, P. et al.: *Dryland ecohydrology*. Springer International Publishing, 2019, pp. 469–509.

⁶Dunkerley, D.: *Desert* 23.2 (2018).

⁷Deblauwe, V. et al.: *Ecol. Monogr.* 82.1 (2012).

Klausmeier model

One of the most basic phenomenological models is the **extended Klausmeier reaction-advection-diffusion model**.⁸

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

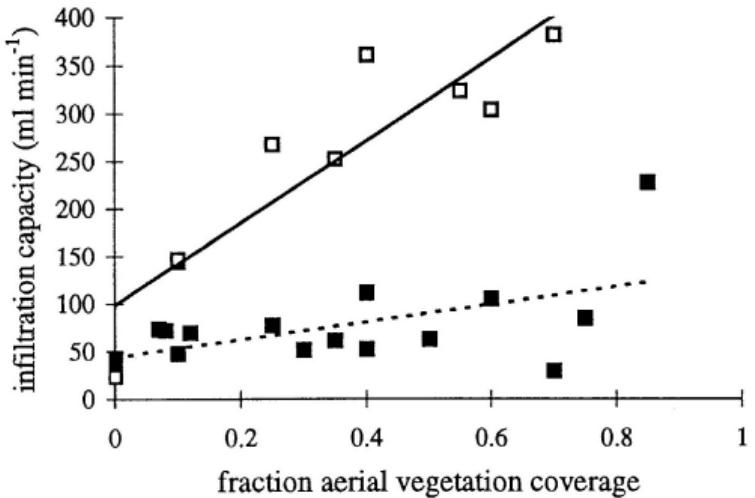
⁸Klausmeier, C. A.: *Science* 284.5421 (1999).

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Water uptake



Infiltration capacity increases with plant density⁹

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.

⁹Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000)

Research question

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

Main research question

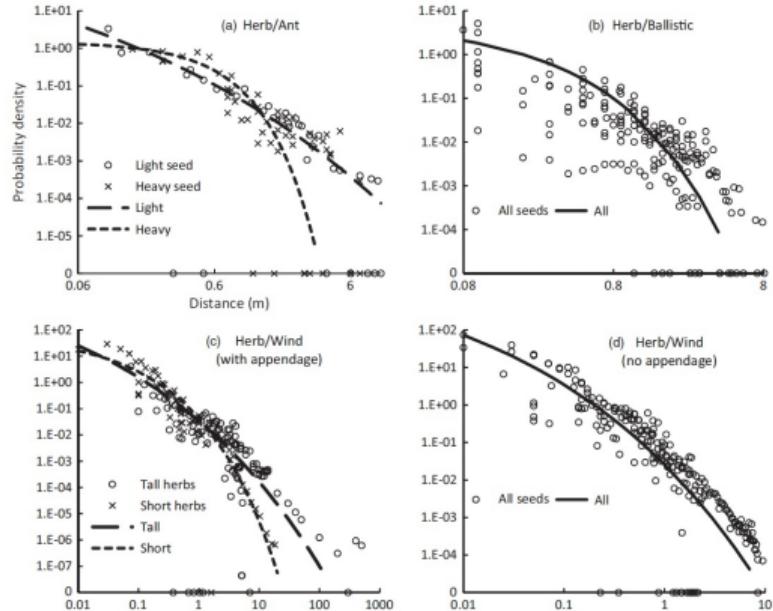
- How does nonlocal seed dispersal affect onset, existence and stability of patterns?
⇒ How can the contrasting field data on uphill movement be explained?

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 dispersal¹⁰

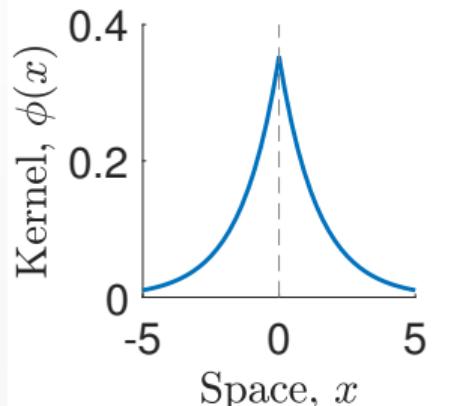
¹⁰Bullock, J. M. et al.: *J. Ecol.* 105.1 (2017)

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

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

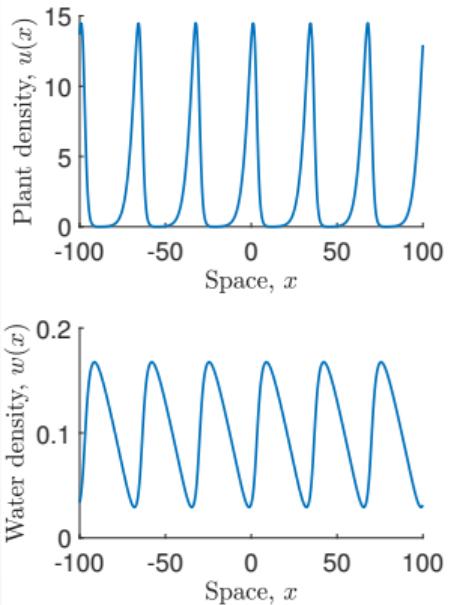
$$\hat{\phi}(k) = \frac{a^2}{a^2 + k^2}, \quad k \in \mathbb{R}.$$

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

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

Travelling waves

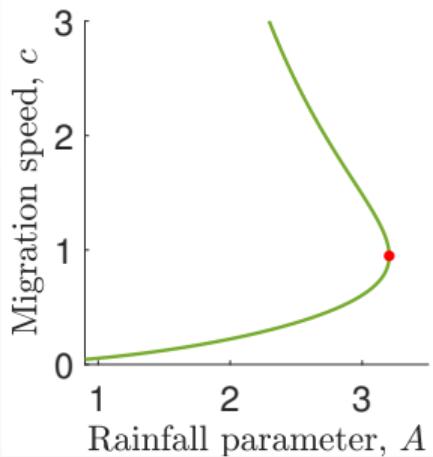
- Numerical simulations of the model on sloped terrain suggest uphill movement \Rightarrow Periodic travelling waves.
- Patterns correspond to **limit cycles** of the travelling wave integro-ODEs.



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.

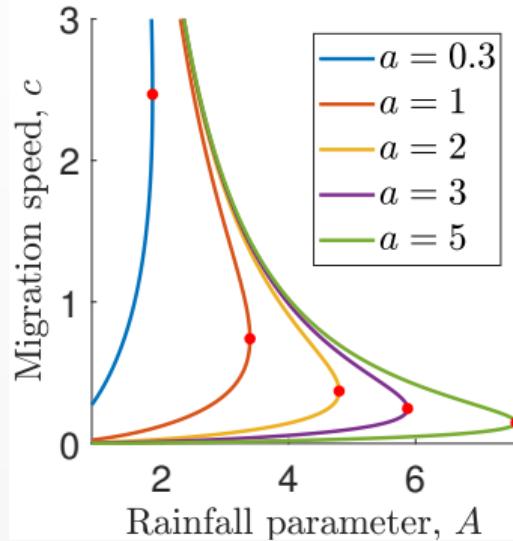
Pattern onset

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} .

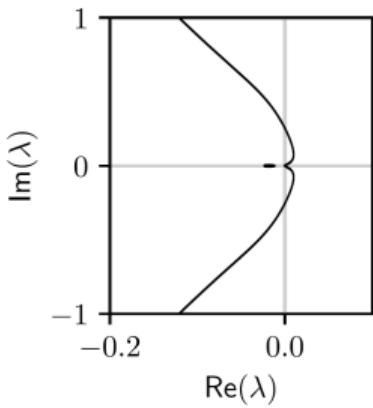


Locus of Hopf bifurcation for fixed C and varying a .¹¹

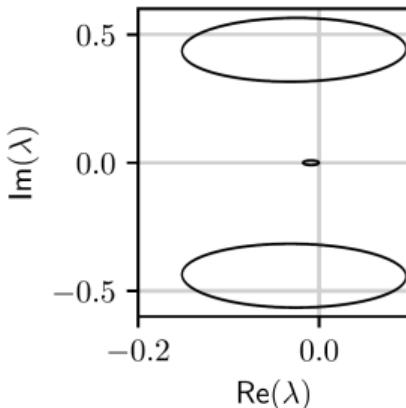
¹¹EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018)

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.¹²



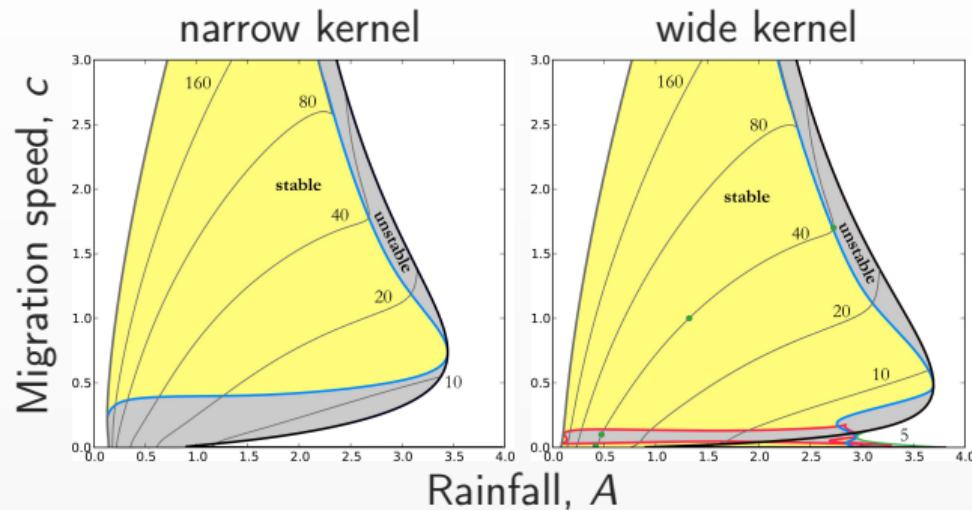
Eckhaus-type



Hopf-type

¹²Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007)

Pattern existence and stability



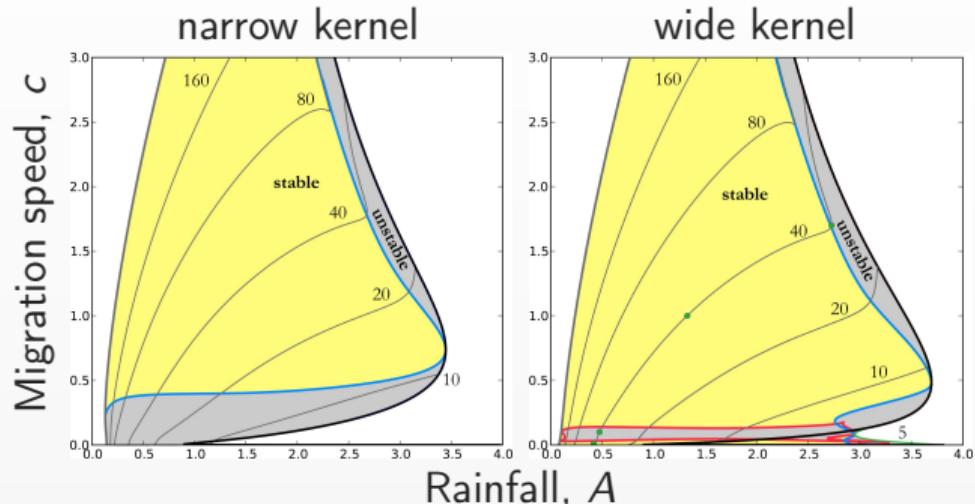
Stability of patterns in the A - c plane.¹³

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

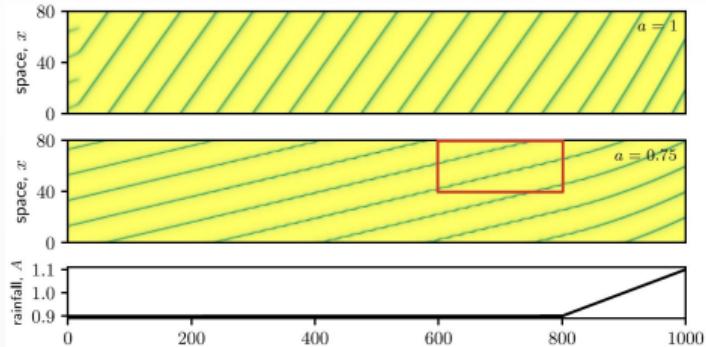
- increased resilience due to oscillating vegetation densities in peaks,

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

Pattern existence and stability



Stability of patterns in the A - c plane.¹⁴

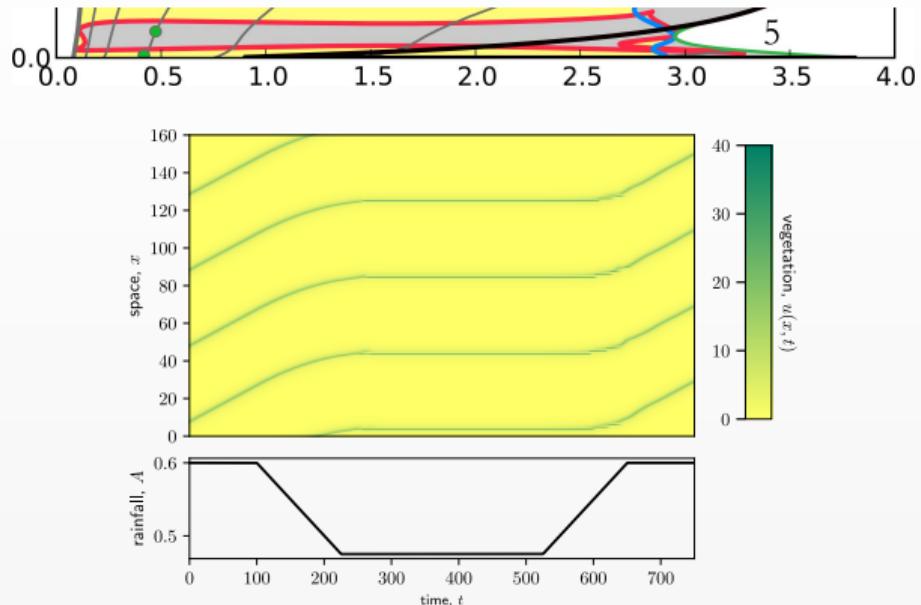


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Pattern existence and stability



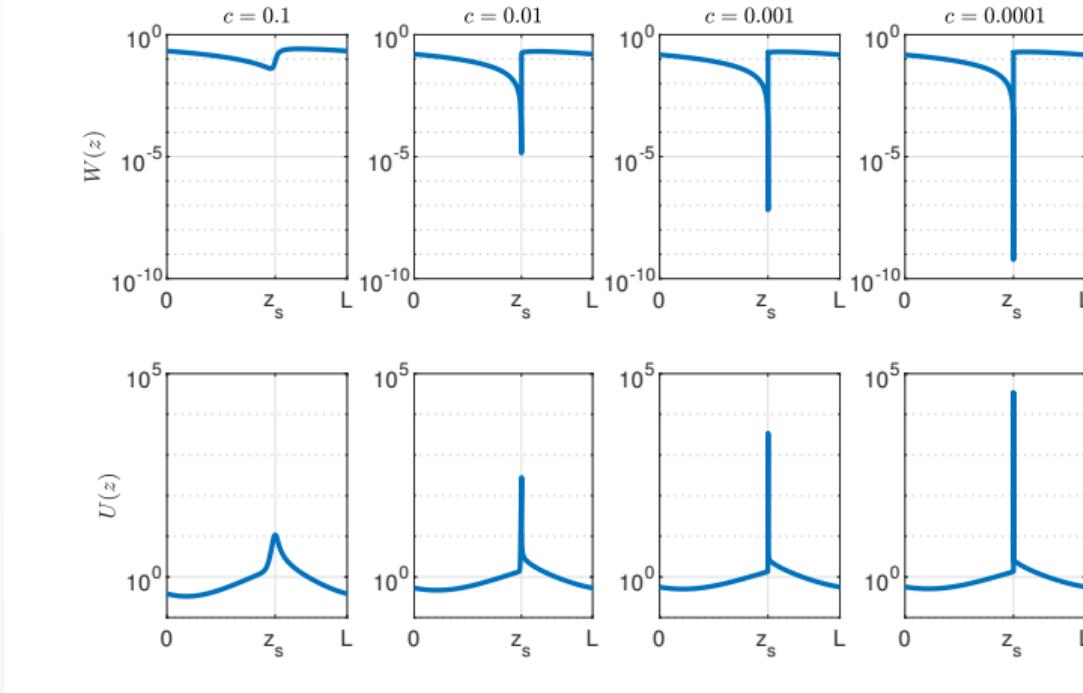
For wide kernels, the stability boundary towards the desert state changes from Eckhaus (sideband) to Hopf-type. This yields

- 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.¹⁵

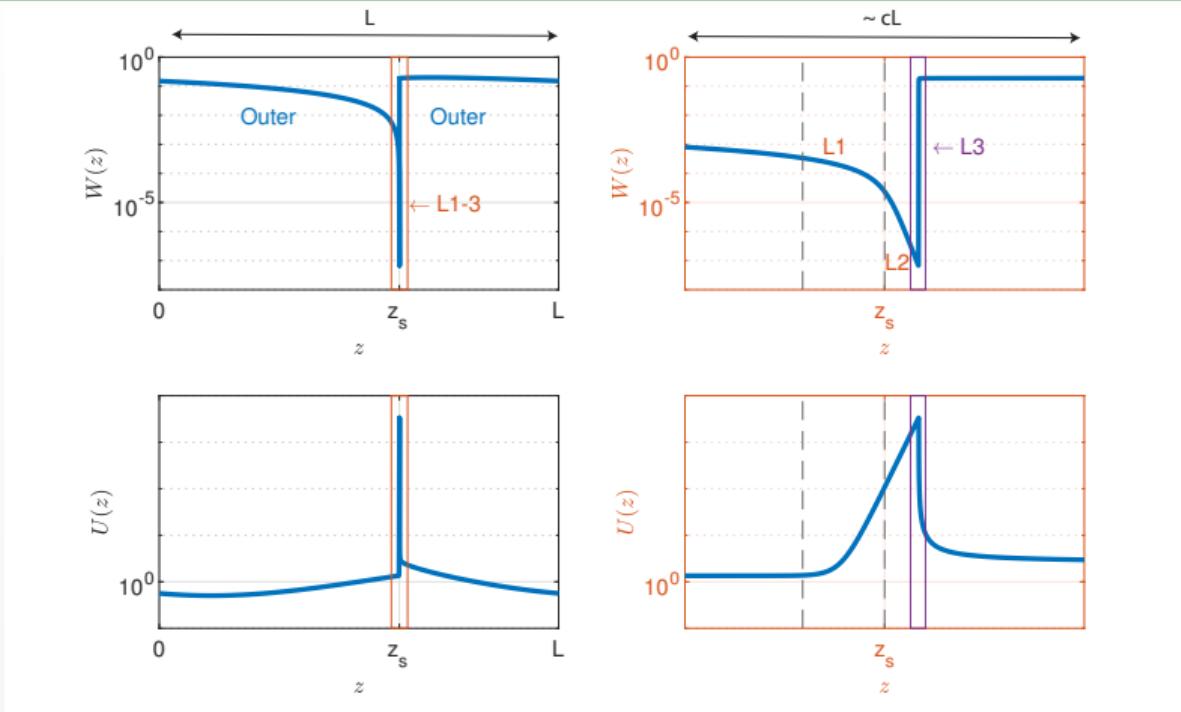
¹⁵ Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018)

Almost stationary spike patterns



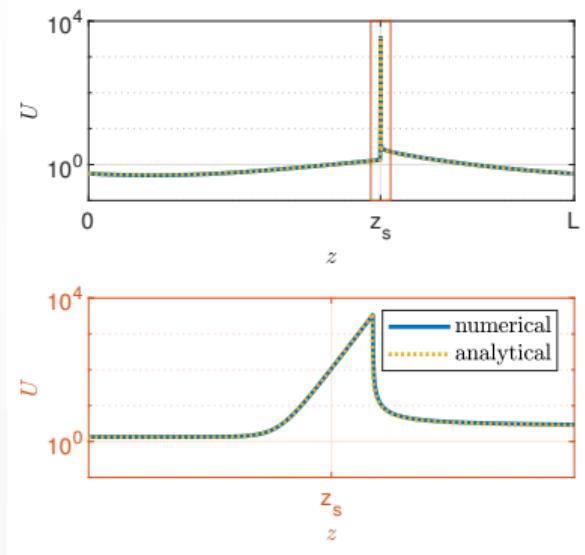
As c decreases, plant density develops a “spike”.

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.¹⁶

¹⁶EL and Sherratt, J. A.: *J Math Biol* 86.15 (2023)

Conclusions

- 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.

Future Work

- Empirical tests of these hypotheses?
- How can a system reach a non-migration state?
- How resilient are non-migration states to environmental change?

References

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- [1] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* 481 (2018), pp. 151–161.
- [3] Eigentler, L. and Sherratt, J. A.: *J. Math. Biol.* 77 (2018), pp. 739–763.
- [4] Eigentler, L. and Sherratt, J. A.: *J. Math. Biol.* 86.15 (2023).