Heriot-Watt University &
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How Does Long-Range Dispersal Affect Pattern Formation in Semi-Arid Vegetation?

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joint work with Jamie Bennett (Ben Gurion Univ.), Jonathan Sherratt (Heriot-Watt Univ.)

Vegetation Patterns

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

Bushes in Niger.

More water reaches the top edge of a stripe.[1]

- Plants increase water infiltration into the soil and thus induce a positive feedback loop.
- On sloped ground, stripes grow parallel to the contours.
- Stripes either move uphill or are stationary.

[1] Dunkerley, D.: *Desert* 23.2 (2018).

Klausmeier Model

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill

One of the most basic phenomenological models is the Klausmeier reaction-advection-diffusion model.[2]

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

[2] Klausmeier, C. A.: *Science* 284.5421 (1999).

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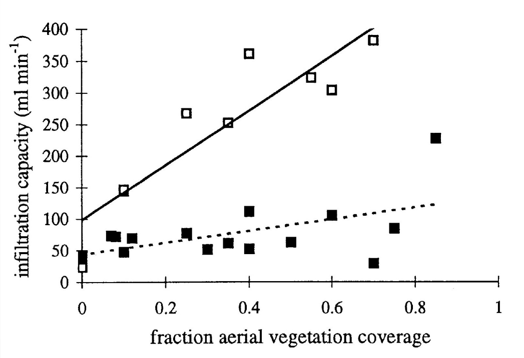
Water Uptake

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill



Infiltration capacity increases with plant density[3]

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

$\Rightarrow$Water uptake = Water density x plant density x infiltration rate.

[3] Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000)

Local Model

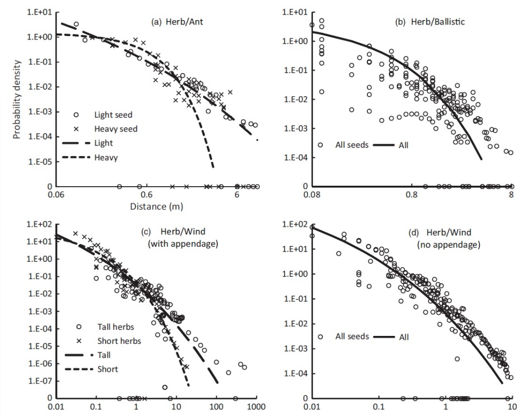
The Klausmeier model models plant dispersal by a diffusion term, i.e. a local process.

$$\frac{\partial u}{\partial t} = \overbrace{u^2 w}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{\frac{\partial^2 u}{\partial x^2}}^{\text{local plant dispersal}},$$

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

Nonlocal Seed Dispersal

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill



Data of long range seed dispersal [4]

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

[4] Bullock, J. M. et al.: *J. Ecol.* 105.1 (2017)

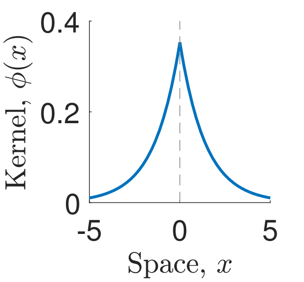
Nonlocal Model

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill, $1/a$ - kernel width
C - dispersal rate

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.

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

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



Laplacian Kernel

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

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

Useful because

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

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

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

Spatially Constant Equilibria

Desert steady state:

$$(\overline{U}_d, \overline{W}_d) = (0, A) \quad \text{stable.}$$

If $A \geq 2B$, there are two additional spatially uniform equilibria:

$$(\overline{U}_-, \overline{W}_-) = \left(\frac{2B}{A - \sqrt{A^2 - 4B^2}}, \frac{A - \sqrt{A^2 - 4B^2}}{2}\right) \quad \text{stable if } B < 2,$$

$$(\overline{U}_+, \overline{W}_+) = \left(\frac{2B}{A + \sqrt{A^2 - 4B^2}}, \frac{A + \sqrt{A^2 - 4B^2}}{2}\right) \quad \text{unstable.}$$

Travelling Waves

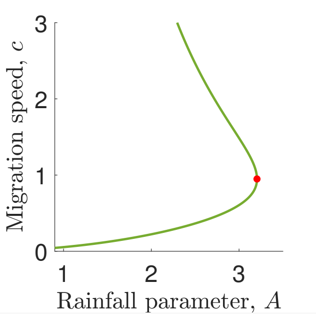
A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill, $1/a$ - kernel width
c - migration speed, C - dispersal rate

- On sloped ground (some) patterns slowly move uphill.
- Travelling wave ansatz $u(x,t) = U(z)$, $w(x,t) = W(z)$, $z = x - ct$ gives the corresponding first-order travelling waves integro-ODE system

$$\begin{aligned}
\frac{\mathrm{d}U}{\mathrm{d}z} &= -\frac{1}{c}\left(U^2W - BU + C\left(\phi(\cdot;a) * U(\cdot) - U(z)\right)\right),\\
\frac{\mathrm{d}W}{\mathrm{d}z} &= W_1,\\
\frac{\mathrm{d}W_1}{\mathrm{d}z} &= -\frac{1}{d}\left(A - W - U^2W + (c+\nu)W_1\right).
\end{aligned}$$

Travelling Waves

- Patterns correspond to limit cycles of the travelling wave integro-ODEs.
- Local model: Patterns emanate from a Hopf bifurctaion. In the A-c plane, the parameter region supporting patterns is bounded above by a Hopf bifurcation.[5]



Location of the Hopf bifurcation in A-c plane.

[5] Sherratt, J. A. and Lord, G. J.: *Theor. Popul. Biol.* 71.1 (2007)

Onset of Patterns

The growth rate $\lambda \in \mathbb{C}$ of perturbations $\tilde{U}(z)$, $\tilde{W}(z)$, $\tilde{W}_1(z)$ to $(\overline{U}_-, \overline{W}_-, \overline{W_1}_-)$, satisfies (after linearisation)

$$\lambda^5 + \alpha\lambda^4 + \beta\lambda^3 + \gamma\lambda^2 + \delta\lambda + \varepsilon = 0,$$

A Hopf bifurcation requires $\lambda = i\omega$, $\omega \in \mathbb{R}$. This yields

$$\alpha\omega^4 - \gamma\omega^2 + \varepsilon = 0,$$
$$\omega^5 - \beta\omega^3 + \delta\omega = 0.$$

Solving for, and eliminating ω^2 gives

$$\frac{\gamma \pm \sqrt{\gamma^2 - 4\alpha\varepsilon}}{2\alpha} = \frac{\beta \pm \sqrt{\beta^2 - 4\delta}}{2}.$$

Onset of Patterns

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill, $1/a$ - kernel width
c - migration speed, C - dispersal rate

$$\alpha = \frac{d(B-C)+c(c+\nu)}{cd},$$

$$\beta = \frac{-2B^2\left(a^2cd-(B-C)(c+\nu)\right)-Ac\left(A+\sqrt{A^2-4B^2}\right)}{2B^2cd},$$

$$\gamma = \frac{-2B^2a^2\left(d+c(c+\nu)\right)+A(B+C)\left(A+\sqrt{A^2-4B^2}\right)-4B^3}{2B^2cd},$$

$$\delta = \frac{a^2\left(-2B^3(c+\nu)+Ac\left(A+\sqrt{A^2-4B^2}\right)\right)}{2B^2cd},$$

$$\varepsilon = \frac{a^2\left(-A\left(A+\sqrt{A^2-4B^2}\right)+4B^2\right)}{2B^2cd}.$$

Onset of Patterns

Using that $\nu \gg 1$,

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

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

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

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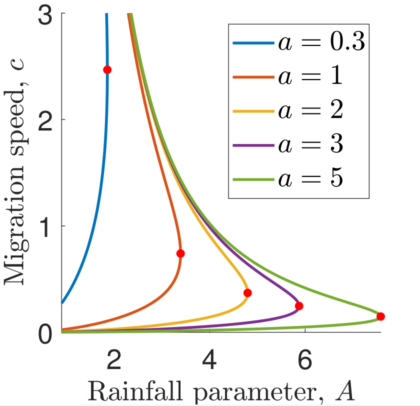


Locus of Hopf bifurcation for fixed C and varying a.

Other Kernel Functions

Gaussian kernel:

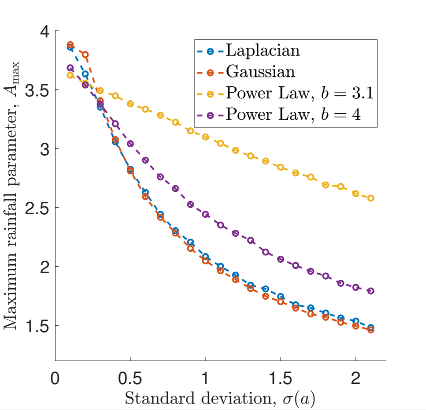
$$\phi(x) = \frac{a_g}{\sqrt{\pi}} e^{-a_g^2 x^2}, \quad x \in \mathbb{R}, a_g > 0.$$

Power law distribution:

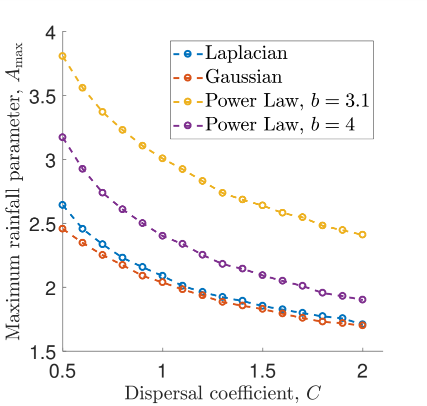
$$\phi(x) = \frac{(b-1)a_p}{2\left(1 + a_p|x|\right)^b}, \quad x \in \mathbb{R}, a_p > 0, b > 3.$$

Numerical Simulations

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill, $1/a$ - kernel width
c - migration speed, C - dispersal rate



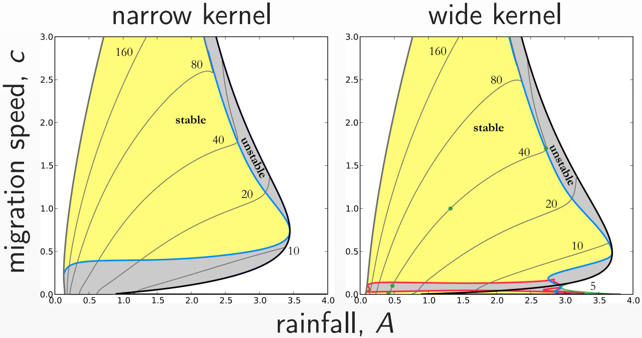
Maximum rainfall parameter under changes to kernel width a.



Maximum rainfall parameter under changes to the dispersal rate C.

Stability of Patterns

A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill, $1/a$ - kernel width
c - migration speed, C - dispersal rate



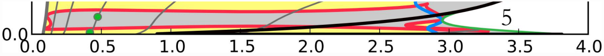
Stability of patterns in the A-c plane [6].

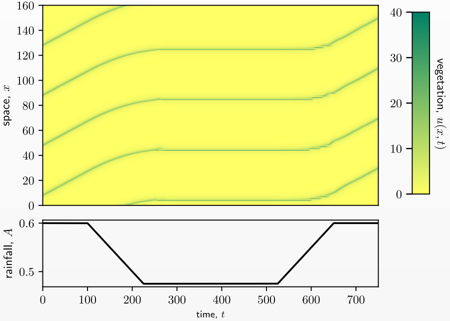
Stability of patterns is calculated using the numerical continuation method by Rademacher et al. [7]
For wide kernels, the stability boundary towards the desert state changes from Eckhaus to Hopf-type. This yields

- increased resilience due to oscillating vegetation densities in peaks,

[6] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* (2018)
[7] Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007)

Stability of Patterns





Existence of stable (almost) stationary patterns [8].

Stability of patterns is calculated using the numerical continuation method by Rademacher et al. [9]

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 ($c \ll 1$).

[8] Bennett, J. J. R. and Sherratt, J. A.: *J. Theor. Biol.* (2018)
[9] Rademacher, J. D., Sandstede, B. and Scheel, A.: *Physica D* 229.2 (2007)

Conclusions

- Wider kernels and higher dispersal rates inhibit pattern onset.
- But plants develop a narrow dispersal kernel $\Rightarrow$ possible trade-off?
- Mathematically motivated form of trade-off: $C = 2/\sigma(a)^2$. Model tends to the local reaction-advection-diffusion system as $\sigma(a) \to 0$.
- Tendency to form patterns depends on the kind of decay of the dispersal kernel.
- Long-range seed dispersal increases the resilience of a pattern and stabilises (almost) stationary patterns.

References

Slides are available on my website.

`http://www.macs.hw.ac.uk/~le8/`

Bennett, J. J. R. and Sherratt, J. A.: 'Long-distance seed dispersal affects the resilience of banded vegetation patterns in semi-deserts'. *J. Theor. Biol.* (2018), in press.

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