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

ECMTB 2018

24 July 2018

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# Vegetation Patterns

Mitchell grass in Australia

Bushes in Niger

- Lack of water causes self-organisation into patterns.
- On sloped ground, stripes grow parallel to the contours.

# Klausmeier Model

Klausmeier reaction-advection-diffusion model.[1]

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

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

[1] Klausmeier, C. A.: *Science* 284.5421 (1999), pp. 1826–1828.

# Klausmeier Model

$A$ - rainfall, $B$ - plant loss, $d$ - w. diffusion
$\nu$ - w. flow downhill

Klausmeier reaction-advection-diffusion model.

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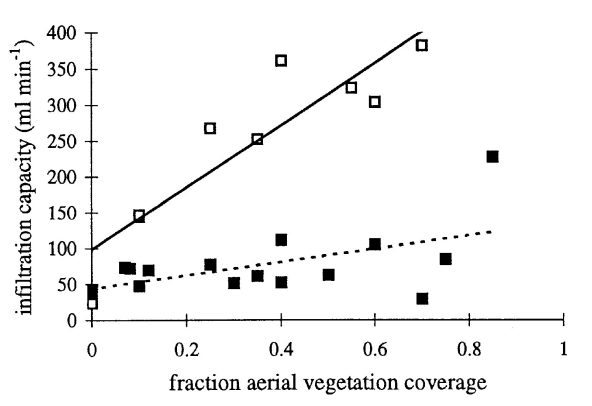
# Water Uptake




Infiltration capacity increases with plant density[2] $\Rightarrow$ Water uptake = Water density x plant density x infiltration rate

[2] Rietkerk, M. et al.: *Plant Ecol.* 148.2 (2000), pp. 207–224.

# Klausmeier Model

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# Local Model

Klausmeier reaction-advection-diffusion model.

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

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

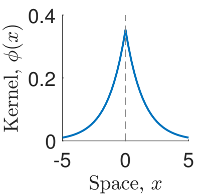
# Nonlocal Model

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

Diffusion is replaced by convolution.

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

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



# Laplacian Kernel

If $\phi$ 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

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

# Steady States



Desert steady state,

$$(0, A) \quad \text{stable.}$$

If $A \geq 2B$, there are two additional steady states

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

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

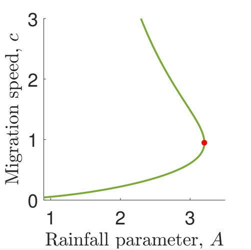
# Travelling Waves

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

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

# Travelling Waves

- Patterns correspond to limit cycles of the travelling wave integro-ODEs.
- Local model: The parameter region supporting patterns is bounded above by a Hopf bifurcation in the $A$-$c$ plane[3].




Location of the Hopf bifurcation in $A$-$c$ plane.

[3] Sherratt, J. A. and Lord, G. J.: *Theor. Popul. Biol.* 71.1 (2007), pp. 1–11.

# Onset of Patterns



For perturbations $\tilde{U}(z)$, $\tilde{W}(z)$ proportional to $e^{\lambda z}$ of a steady state $(\overline{U}, \overline{W})$, $\lambda$ satisfies

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

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 $\omega^2$ gives

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

These need to be positive for $\omega \in \mathbb{R}$.

# Onset of Patterns

$A$ - rainfall, $B$ - plant loss, $d$ - w. diffusion
$\nu$ - 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 $\nu \gg 1$,

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

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

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

# Onset of Patterns

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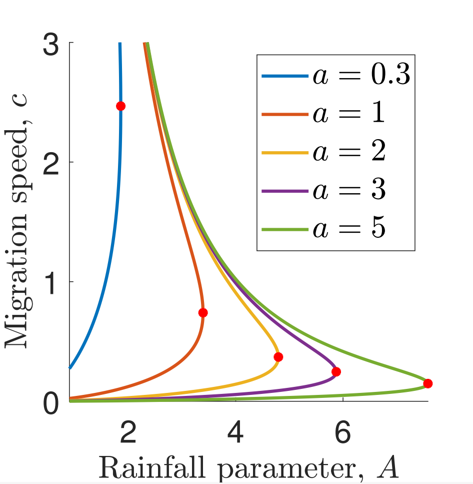



Locus of Hopf bifurcation for fixed $C$ and varying $a$.

# Other Kernel Functions



Gaussian kernel:

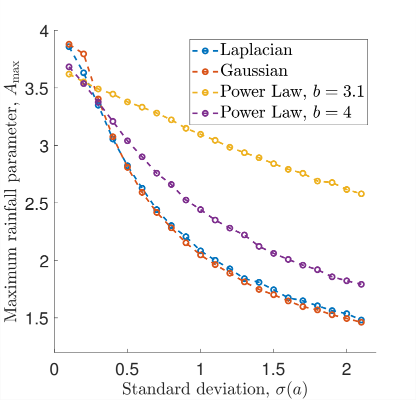
$$\phi(x) = \frac{a_g}{\sqrt{\pi}} e^{-a_g^2 x^2}, \quad x \in \mathbb{R}, a_g > 0.$$

Power law distribution:

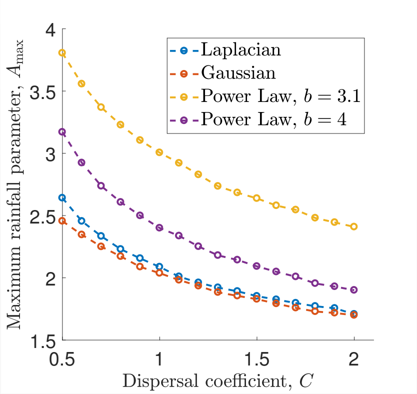
$$\phi(x) = \frac{(b-1)a_p}{2\left(1 + a_p|x|\right)^b}, \quad x \in \mathbb{R}, a_p > 0, b > 3.$$

# Numerical Simulations

$A$ - rainfall, $B$ - plant loss, $d$ - w. diffusion
$\nu$ - 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 $C$.

# Conclusions

- Wider kernels and higher dispersal rates inhibit pattern formation.
- But plants develop a narrow dispersal kernel $\Rightarrow$ 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.

# Extension

- Rainfall events in semi-arid regions are usually short in their duration but high in their intensity and cause a pulse of biological processes.
- Combination of continuous-time processes and such pulses can be described by an impulse-type model: PDEs that are periodically (in time) updated through integrodifference equations.
- Pulse-type dispersal weakens the effects of the dispersal kernel but same parametric trends are observed.
- Less frequent pulses reduce tendency to form patterns but increase water requirements for plants to persist.

# References


- Eigentler, L. and Sherratt, J. A.: 'Analysis of a model for banded vegetation patterns in semi-arid environments with nonlocal dispersal'. *J. Math. Biol.* 77.3 (2018), pp. 739–763.
- Eigentler, L. and Sherratt, J. A.: 'Effects of precipitation intermittency on vegetation patterns in semi-arid landscapes'. (Submitted).