Heriot-Watt University &
The University of Edinburgh

Modelling dryland vegetation patterns: Nonlocal dispersal and species coexistence

Applied Analysis Seminar University of Strathclyde

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

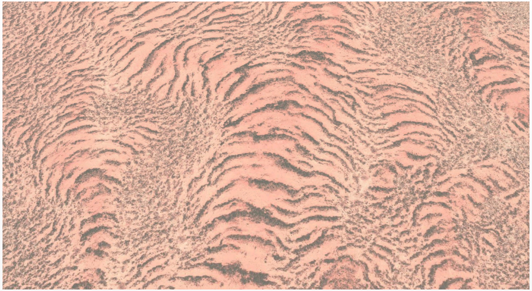
Overview of talk

- Motivation, ecological background & a basic phenomenological mathematical model
- Nonlocal plant (seed) dispersal
  - Pattern onset: Analytic derivation in an asymptotic limit
  - Pattern existence & spectral stability using a numerical continuation method
- Species coexistence
  - Metastable patterns & transient behaviour
  - Stable coexistence in savannas: Insights into pattern onset, existence & stability through their essential spectra.

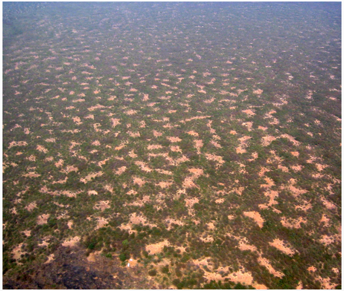
Vegetation patterns

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

Stripe pattern in Ethiopia[1].



Gap pattern in Niger[2].

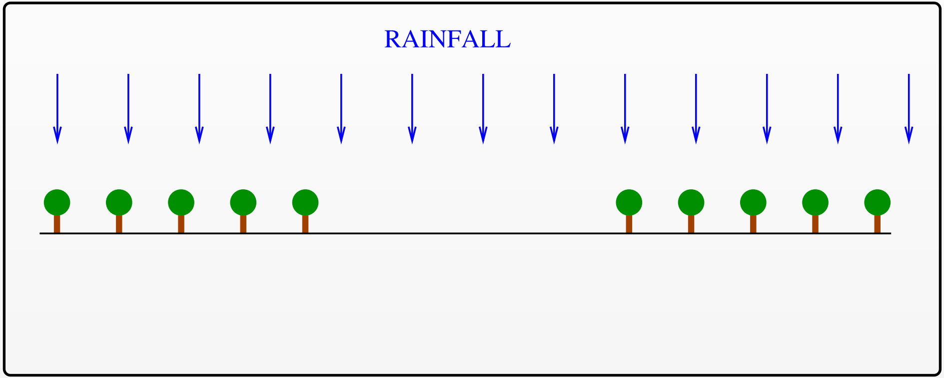


- Plants increase water infiltration into the soil and thus induce a positive feedback loop.

[1] Source: Google Maps
[2] Source: Wikimedia Commons

Vegetation patterns

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



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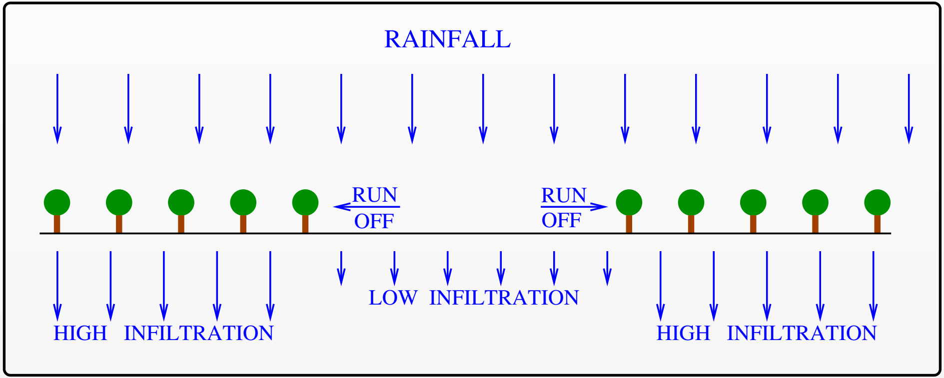

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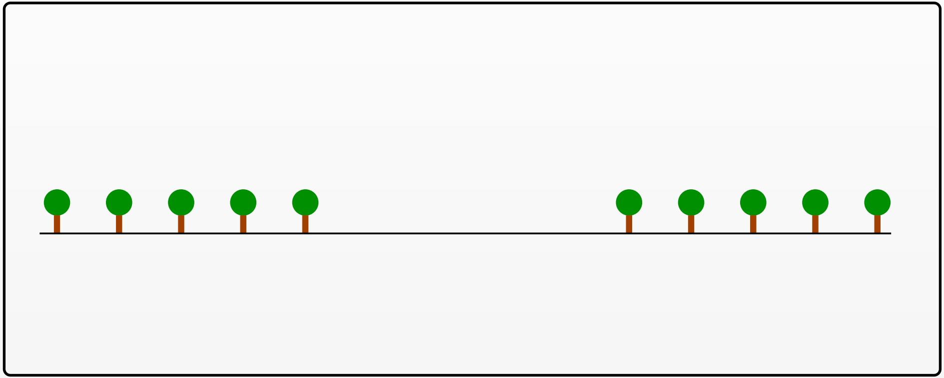

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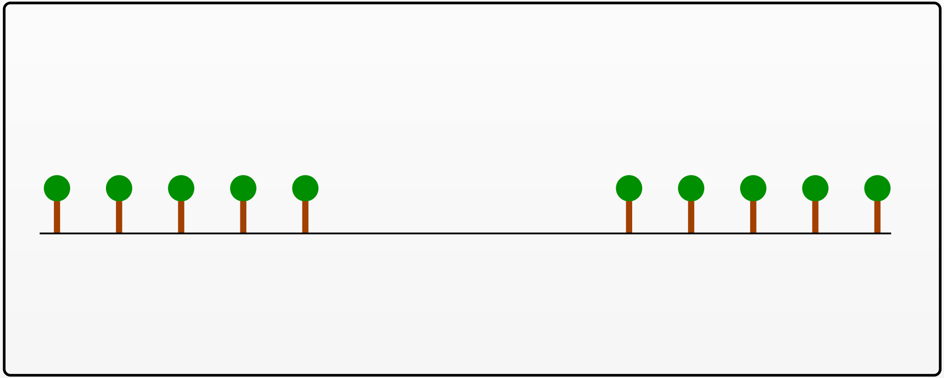

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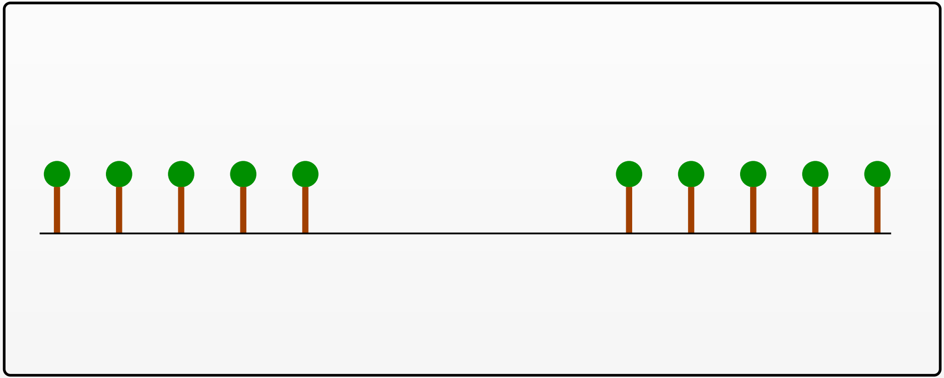

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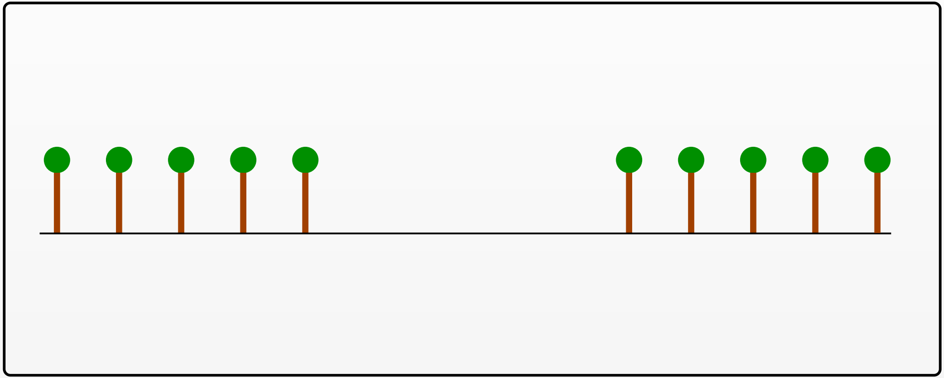

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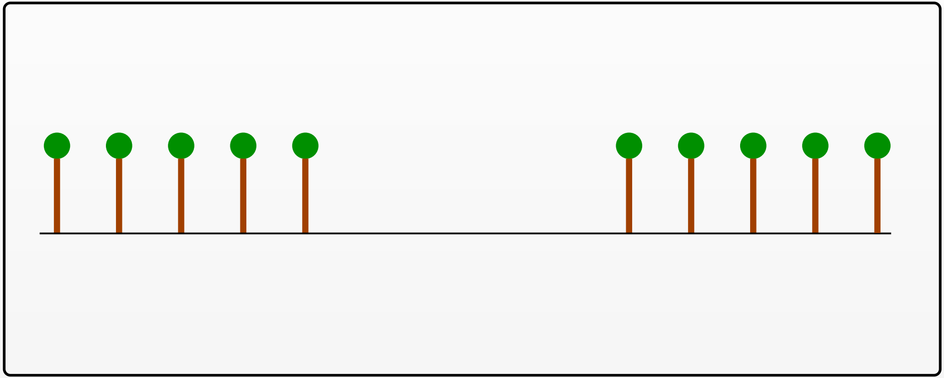

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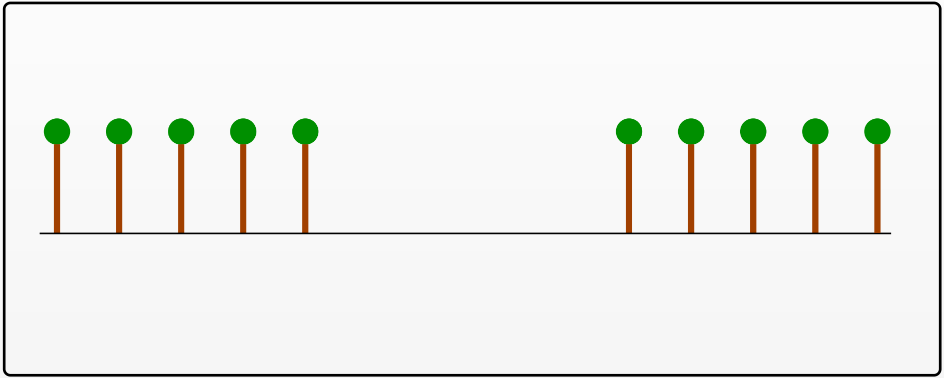

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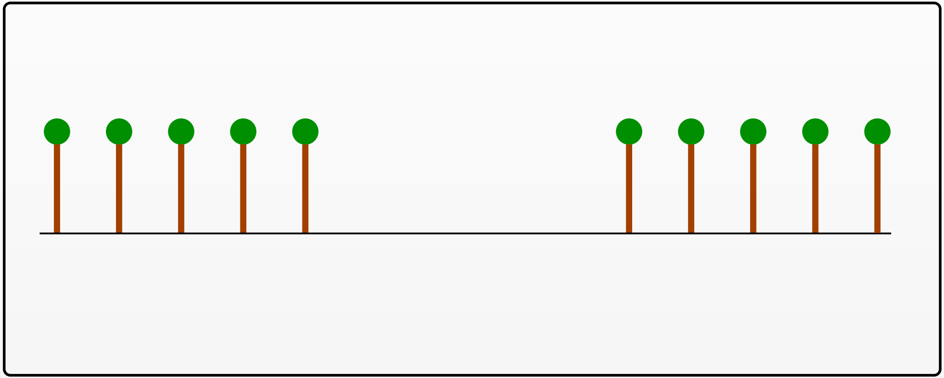

Vegetation patterns

Uphill migration due to water gradient.[3]

Arid savanna in Australia[4]

- On sloped ground, stripes grow parallel to the contours.
- Stripes either move uphill or are stationary.
- Both vegetation patterns and arid savannas are characterised by species coexistence.

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

[4] Source: Wikimedia Commons

Klausmeier model

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

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

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

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

Klausmeier model

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

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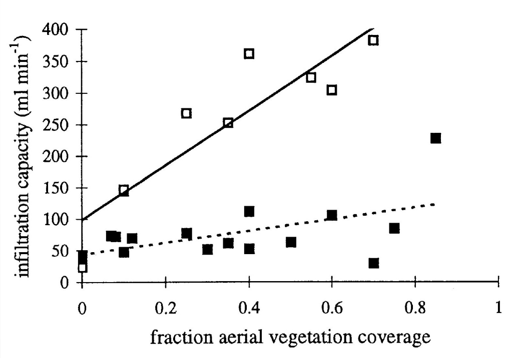
Water uptake



Infiltration capacity increases with plant density[6]

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

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

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

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Local Model

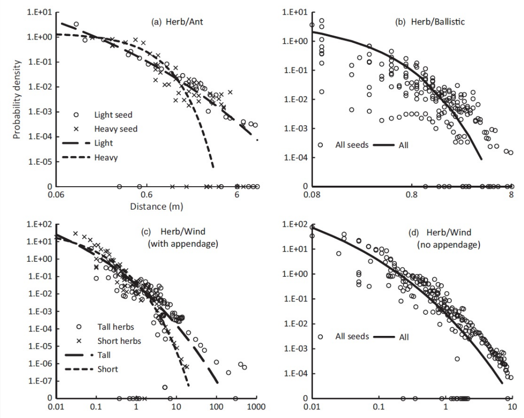
A - rainfall, B - plant loss, d - w. diffusion
ν - w. flow downhill

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

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

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

Nonlocal seed dispersal



Data of long range seed dispersal [7]

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

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

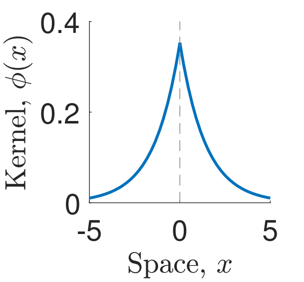
Nonlocal model

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.

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

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



Laplacian kernel

If ϕ decays exponentially as $|x| \to \infty$, 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

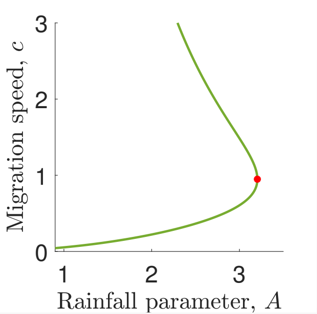
$$\widehat{\phi}(k) = \frac{a^2}{a^2 + k^2}, \quad k \in \mathbb{R}.$$

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

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

Travelling waves

- Numerical simulations of the model on sloped terrain suggest uphill movement of $\Rightarrow$ 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 $A = A_{\text{max}}$, the maximum rainfall level of the Hopf bifurcation loci in the travelling wave ODEs.



Location of the Hopf bifurcation in A-c plane.

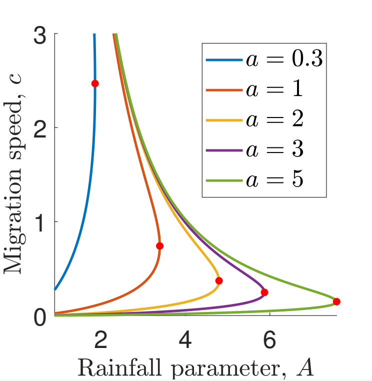
Pattern onset

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 $\nu \to \infty$.

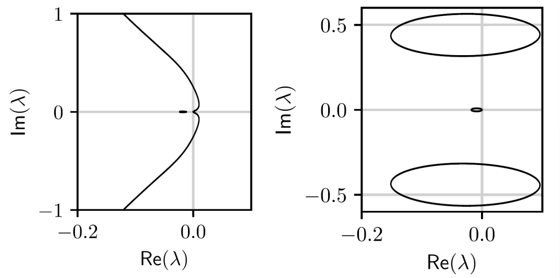
- Note that $A_{\max} = O(\sqrt{\nu})$.
- Decrease in a (i.e. increase in kernel width) causes decrease of $A_{\max}$.
- Increase in dispersal rate C causes decrease of $A_{\max}$.



Locus of Hopf bifurcation for fixed C and varying a.

Pattern stability

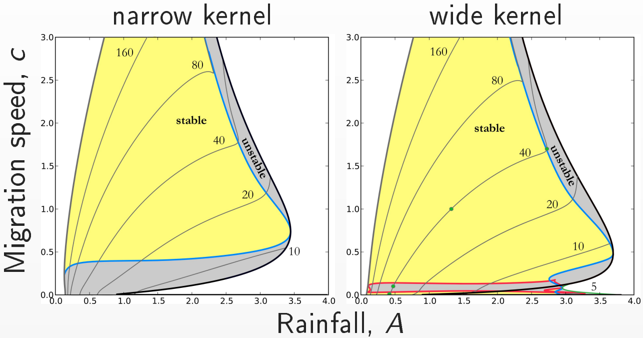
- The essential spectrum of a periodic travelling wave determines the behaviour of small perturbations. $\Rightarrow$ Tool to determine pattern stability.
- Two different types stability boundaries: Eckhaus-type and Hopf-type.
- Essential spectra and stability boundaries are calculated using the numerical continuation method by Rademacher et al.[8]



Eckhaus-type Hopf-type

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

Pattern existence and stability

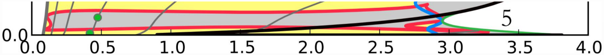


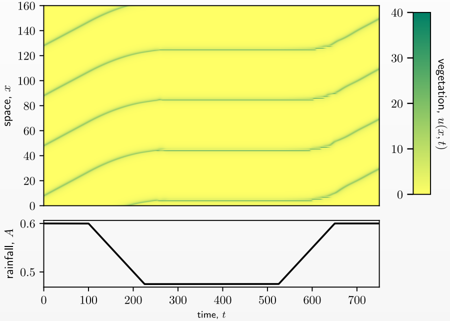
Stability of patterns in the A-c plane.

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,

Pattern existence and stability





Existence of stable (almost) stationary patterns.

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 ($c \ll 1$).

Conclusions I

- The scale difference between plant dispersal and water transport and choice of dispersal kernel allows for an analytical derivation of a condition for pattern onset in an asymptotic limit.
- 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.

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Klausmeier Model

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

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Multispecies Model

A - rainfall, B_i - plant loss, F - plant growth ratio, D - plant diffusion ratio, H - infiltration effect ratio ν - w. flow downhill d - water diffusion

Multispecies model based on the extended Klausmeier model.

$$\frac{\partial u_1}{\partial t} = \overbrace{wu_1\left(u_1 + Hu_2\right)}^{\text{plant growth}} - \overbrace{B_1 u_1}^{\substack{\text{plant}\\ \text{mortality}}} + \overbrace{\frac{\partial^2 u_1}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial u_2}{\partial t} = \overbrace{Fwu_2\left(u_1 + Hu_2\right)}^{\text{plant growth}} - \overbrace{B_2 u_2}^{\substack{\text{plant}\\ \text{mortality}}} + \overbrace{D\frac{\partial^2 u_2}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation}} - \underbrace{w\left(u_1 + u_2\right)\left(u_1 + Hu_2\right)}_{\text{water uptake by plants}} + \underbrace{\nu\frac{\partial w}{\partial x}}_{\substack{\text{water flow}\\ \text{downhill}}} + \underbrace{d\frac{\partial^2 w}{\partial x^2}}_{\substack{\text{water}\\ \text{diffusion}}}.$$

E.g. u_1 is a grass species; u_2 a tree species. $\Rightarrow B_2 < B_1$, $F < 1$, $H < 1$.

Simulations

- Coexistence in the model occurs
  (i) as a stable savanna state.
  (ii) as a metastable vegetation pattern state.

Simulations

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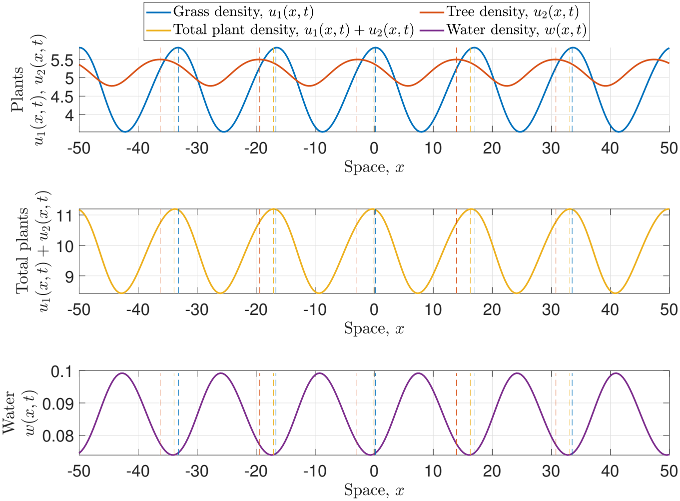
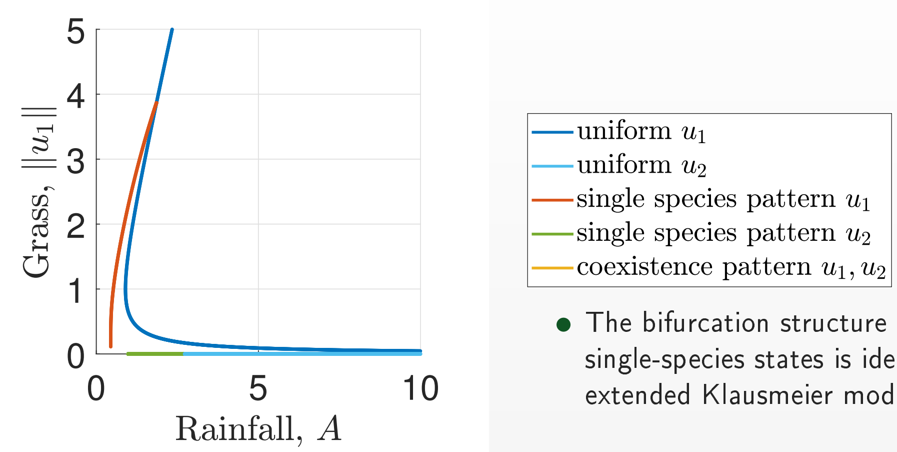


- Coexistence in the model occurs
  - (i) as a stable savanna state.
  - (ii) as a metastable vegetation pattern state.
- Phase difference between plant densities is captured.

Bifurcation diagram

A - rainfall, B_i - plant loss, F - plant growth ratio,
D - plant diffusion ratio, H - infiltration effect ratio
ν - w. flow downhill d - water diffusion



Bifurcation diagram

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

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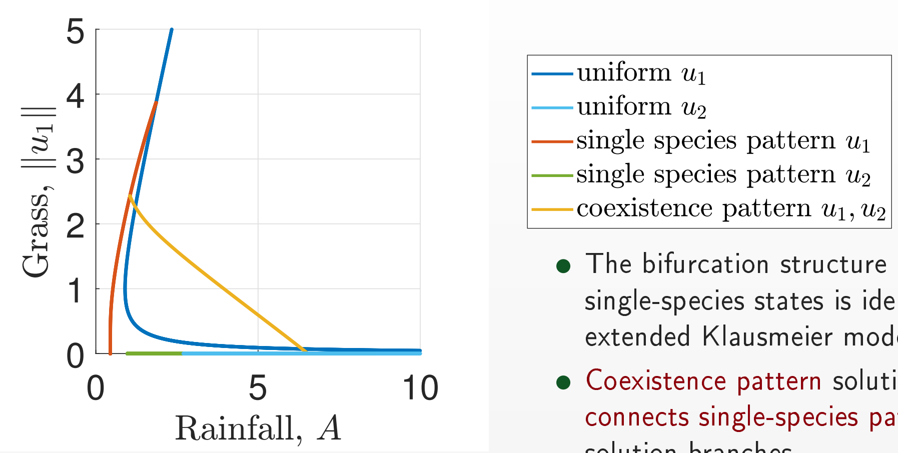

Bifurcation diagram

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

Pattern onset

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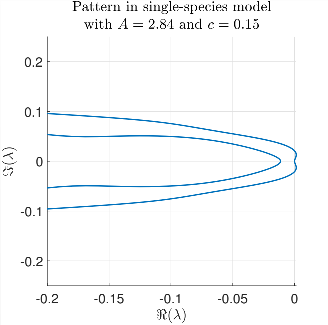
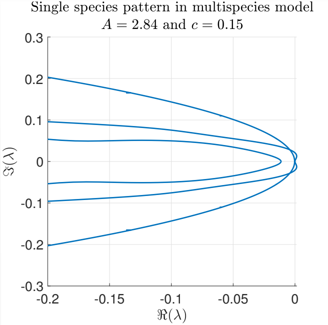


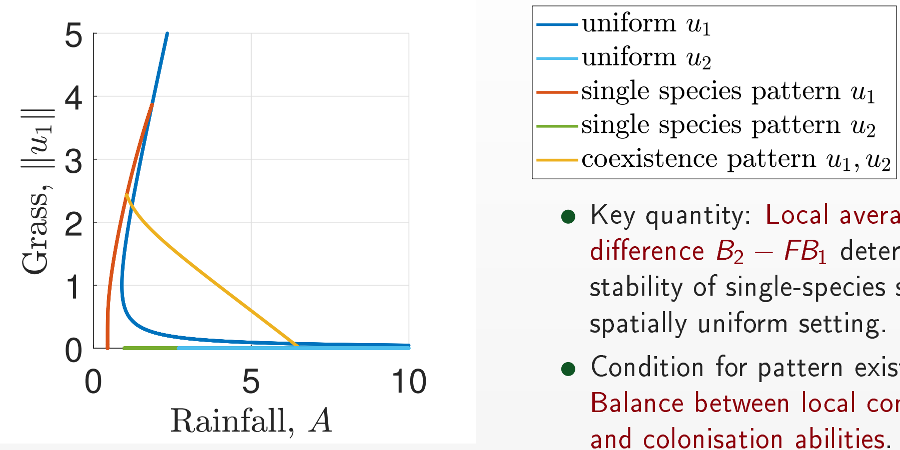
Essential spectrum in single-species model



Essential spectrum in multispecies model

- The key to understand coexistence pattern onset is knowledge of single-species pattern's stability.
- The essential spectrum of a single-species pattern contains additional elements accounting for perturbations in the second species.
- Pattern onset occurs as the single-species pattern loses/gains stability to the introduction of a competitor.

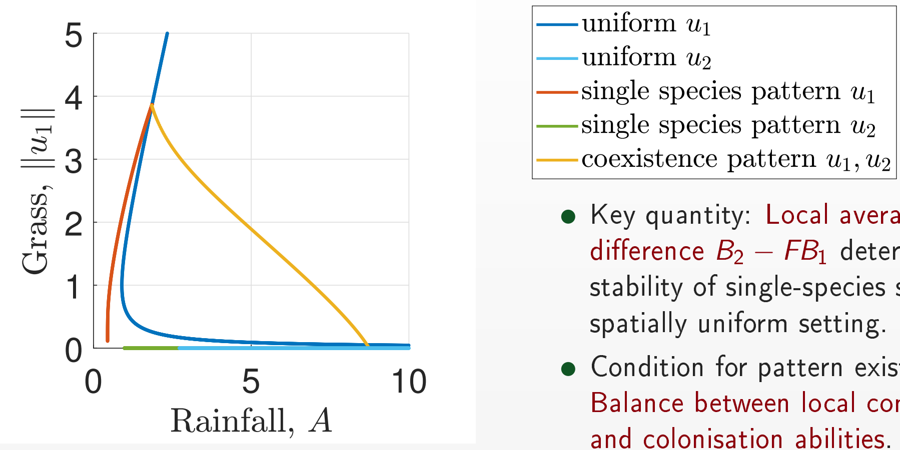
Pattern existence



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

- 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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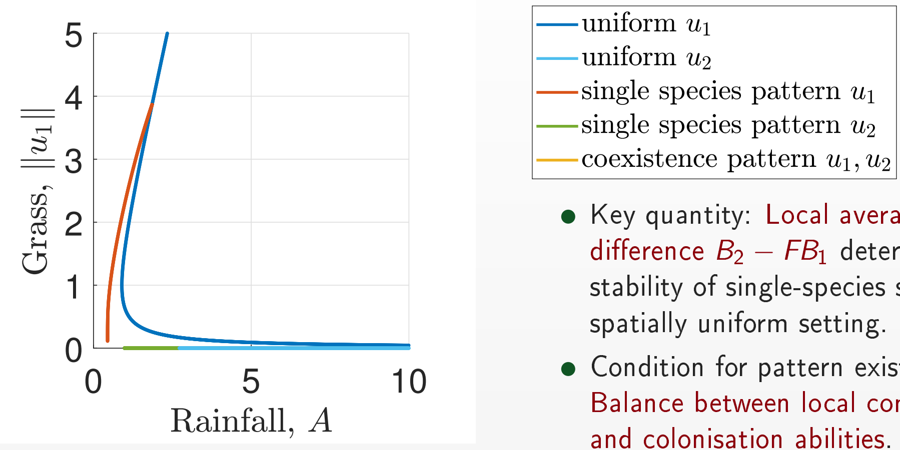

$B_2 - FB_1 > 0, F < 1, D < 1$

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Pattern stability

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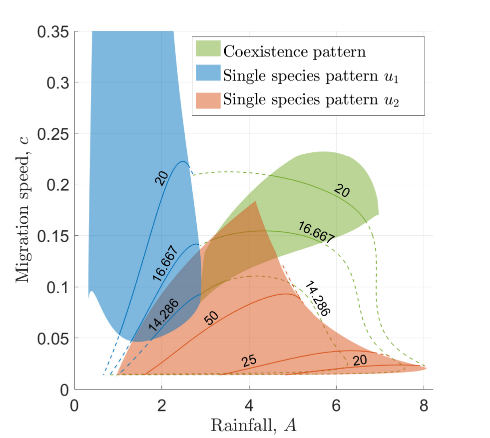

Busse balloons of all pattern types in the system

- Pattern dynamics (wavelength, migration speed) are dominated by properties of coloniser species.
- Busse balloons of coexistence patterns and single-species tree patterns overlap ⇒ potentially significant ecologically (ecosystem engineering).

Simulations

A - rainfall, B_i - plant loss, F - plant growth ratio,
D - plant diffusion ratio, H - infiltration effect ratio
ν - w. flow downhill d - water diffusion

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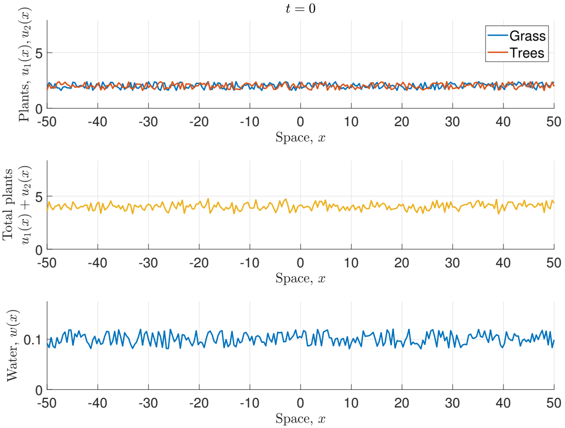

Numerical solution of the multi-species model.

- Coexistence in the model occurs
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- $t = 1$ corresponds to 3 months

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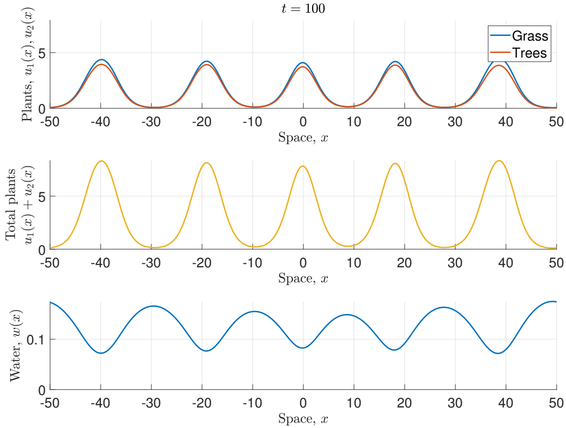

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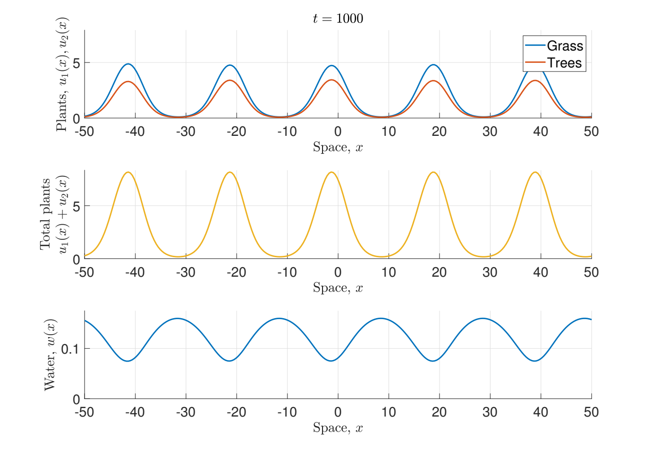

Numerical solution of the multi-species model.

- Coexistence in the model occurs
  - (i) as a stable savanna state.
  - (ii) as a metastable vegetation pattern state.
- $t = 1$ corresponds to 3 months $\Rightarrow$ coexistence of more than 1000 years.
- Coexistence occurs as a long transient to a one-species pattern.

Simulations

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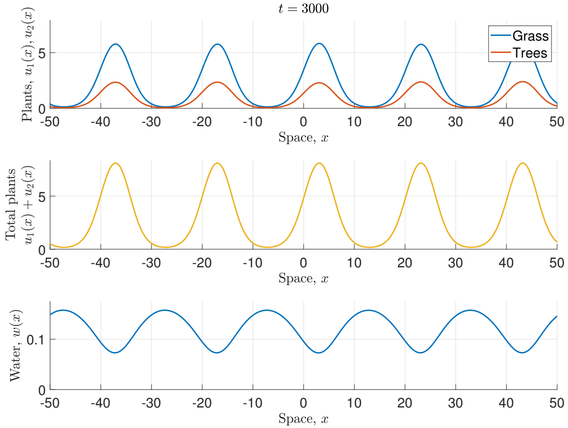
D - plant diffusion ratio, H - infiltration effect ratio
ν - w. flow downhill d - water diffusion



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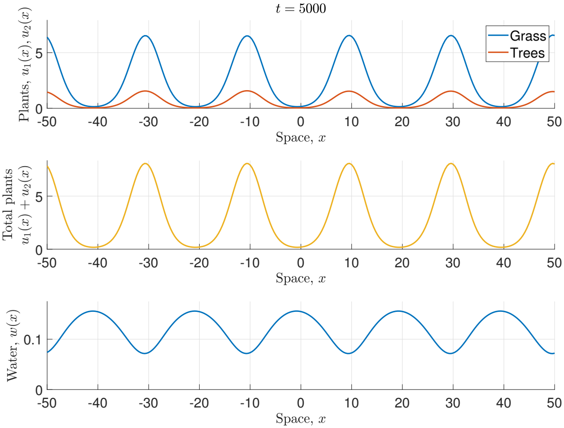
  - (i) as a stable savanna state.
  - (ii) as a metastable vegetation pattern state.
- $t = 1$ corresponds to 3 months $\Rightarrow$ coexistence of more than 1000 years.
- Coexistence occurs as a long transient to a one-species pattern.

A - rainfall, B_i - plant loss, F - plant growth ratio, D - plant diffusion ratio, H - infiltration effect ratio ν - w. flow downhill d - water diffusion



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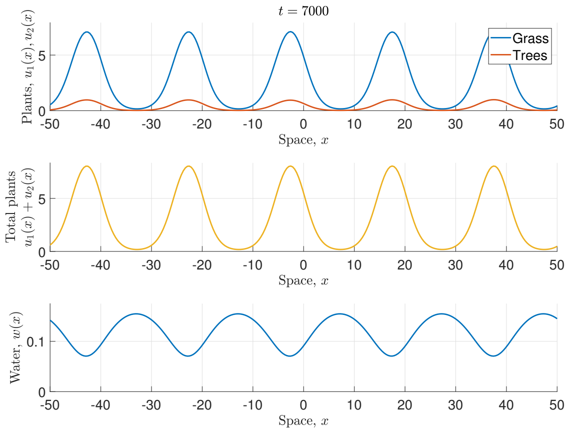

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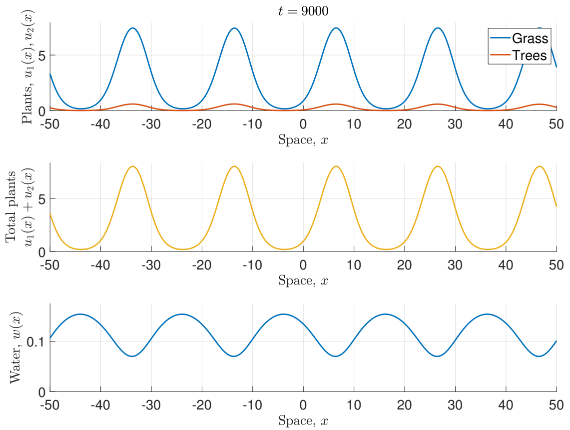

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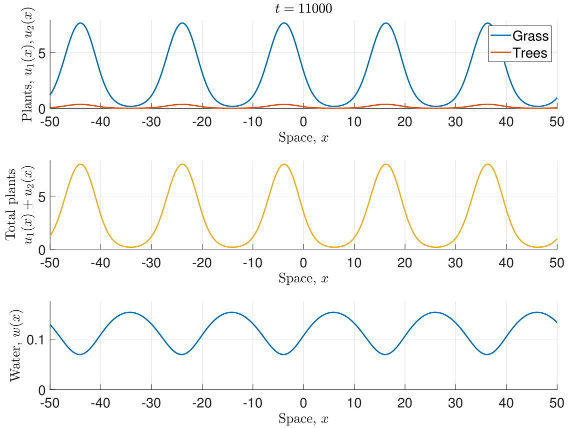

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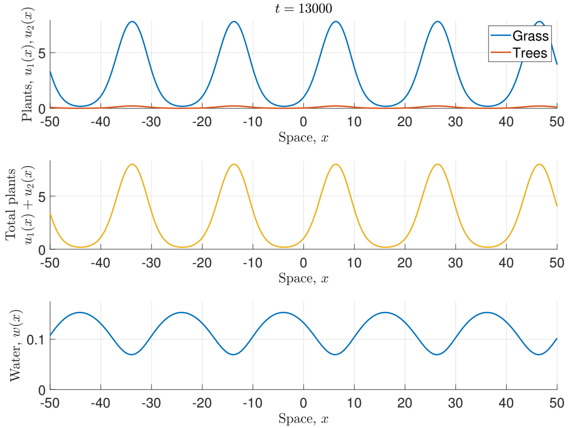

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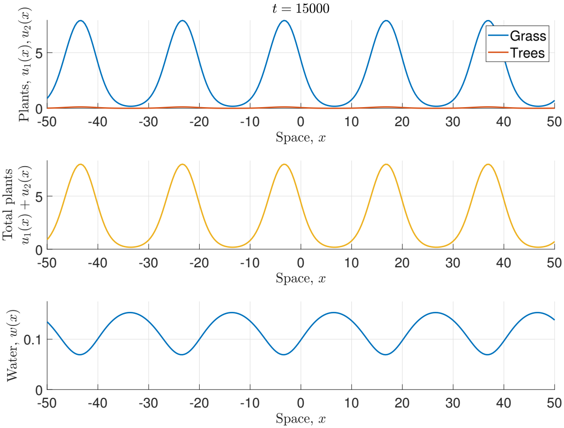

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Metastable States

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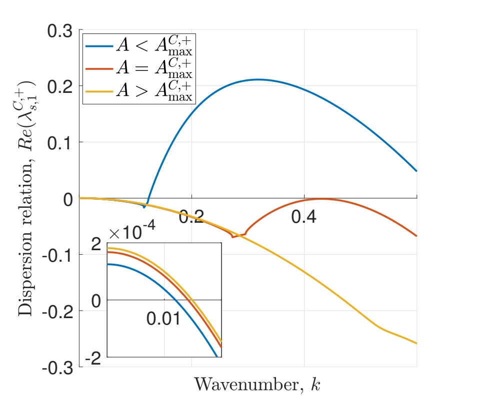
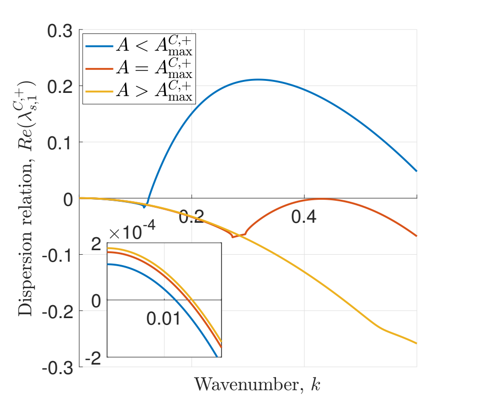


Growth rates of perturbations to equilibrium.

Calculation of the growth rate λ_u of spatially uniform perturbations to the single-species equilibria shows

$$\Re(\lambda_u) = O(B_2 - B_1 F).$$

- If the average fitness difference $B_2 - B_1 F$ is small, then coexistence occurs as a long transient to a stable one-species state.
- Non-spatial property.



Growth rates of perturbations to equilibrium.

For sufficiently small levels of precipitation $A < A^C_{\max}$ the growth rate λ_s of spatially nonuniform perturbations satisfies

$$\max_{k>0} \{\Re(\lambda_s(k))\} \gg \Re(\lambda_u)$$

- Pattern formation occurs on a much shorter timescale.
- The predicted wavelength of the coexistence pattern may differ from that of a singe-species pattern. $\Rightarrow$ Change in wavelength occurs during transient.

Conclusions II

- The basic phenomenological reaction-advection-diffusion system captures species coexistence as
  (i) a metastable state representing patterned vegetation,
  (ii) a stable patterned solution representing a savanna state.
- Stability analyses of spatially uniform solutions and periodic travelling waves (via a calculation of essential spectra) provide insights into existence and stability of coexistence states.
- Plant dispersal bears significant influence on existence of coexistence states. What are the effects of nonlocal plant dispersal?

Future Work

- How does nonlocal seed dispersal affect species coexistence?
- Do results extend to an arbitrary number of species?
- Do stable coexistence patterns exist?
- How do fluctuations in environmental conditions (in particular precipitation) affect coexistence?
- In particular, what are the effects of seasonal[9], intermittent[10] and probabilistic rainfall regimes on both single-species and multispecies states?

[9] EL and Sherratt, J. A.: *An integrodifference model for vegetation patterns in semi-arid environments with seasonality* (submitted).

[10] EL and Sherratt, J. A.: *Effects of precipitation intermittency on vegetation patterns in semi-arid landscapes* (submitted).

References

Slides are available on my website.

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

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- 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.
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- Eigentler, L. and Sherratt, J. A.: 'Spatial self-organisation enables species coexistence in a model for savanna ecosystems'. (Submitted).