Modelling dryland vegetation patterns: Nonlocal dispersal and species coexistence

Workshop on Mathematical Modelling for Biosciences

09 November 2021

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

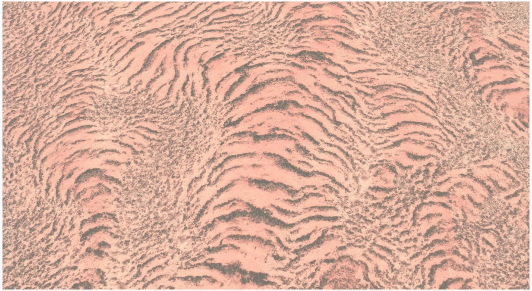
Overview of talk

- 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
  - Spatial self-organisation as a coexistence mechanism.
  - Metastable patterns & transient behaviour

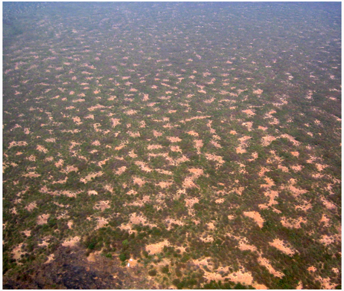
Vegetation patterns

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

Uphill migration due to water gradient.[3]

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

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

Klausmeier model

One of the most basic phenomenological models is the extended Klausmeier reaction-advection-diffusion model.[4]

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

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

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

Klausmeier model

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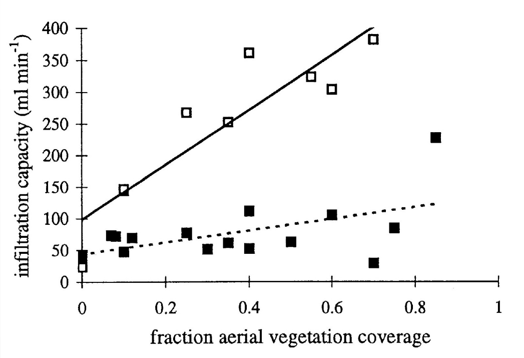
Water uptake



Infiltration capacity increases with plant density[5]

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.

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

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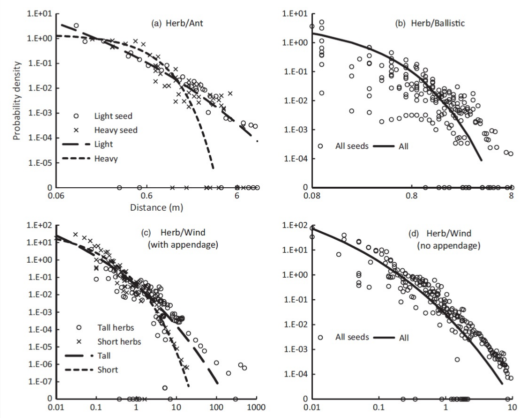
Local Model

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



Data of long range seed dispersal [6]

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

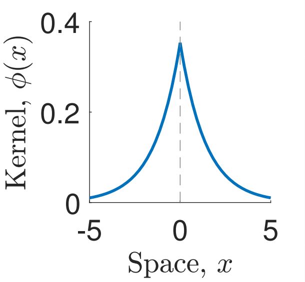
[6] Bullock, J. M. et al.: *J. Ecol.* 105.1 (2017)

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.

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

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



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

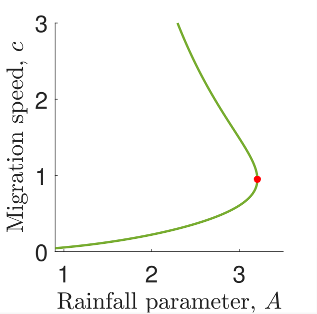
$$\widehat{\phi}(k) = \frac{a^2}{a^2 + k^2}, \quad k \in \mathbb{R}.$$

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 $\Rightarrow$ Periodic travelling waves.
- 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 $A = A_{\mathrm{max}}$, the maximum rainfall level of the Hopf bifurcation loci in the travelling wave ODEs.



Location of the Hopf bifurcation in A-c plane.

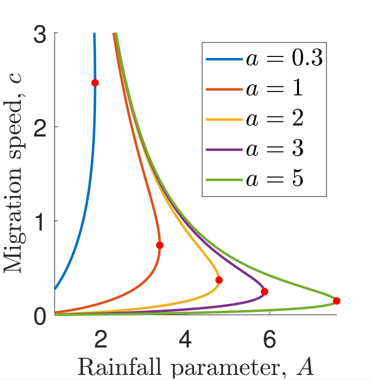
Pattern onset

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 $\nu \to \infty$.

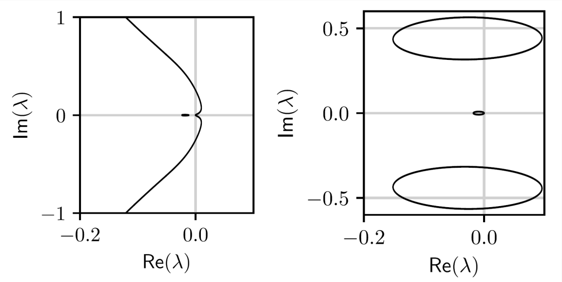
- Note that $A_{\max} = O(\sqrt{\nu})$.
- Decrease in a (i.e. increase in kernel width) causes decrease of $A_{\max}$.
- Increase in dispersal rate C causes decrease of $A_{\max}$.



Locus of Hopf bifurcation for fixed C and varying a.

Pattern stability

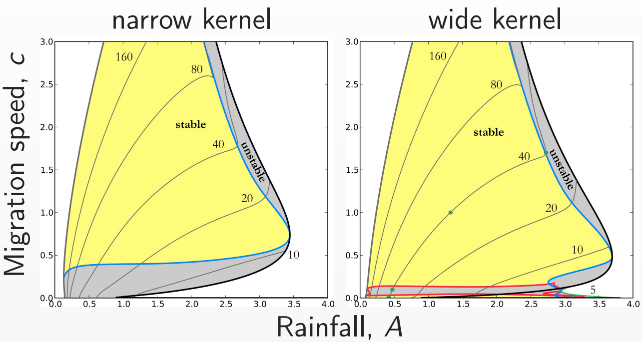
- The essential spectrum of a periodic travelling wave determines the behaviour of small perturbations. ⇒ Tool to determine pattern stability.
- Two different types stability boundaries: Eckhaus-type and Hopf-type.
- Essential spectra and stability boundaries are calculated using the numerical continuation method by Rademacher et al.[7]



Eckhaus-type   Hopf-type

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

Pattern existence and stability

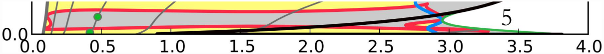


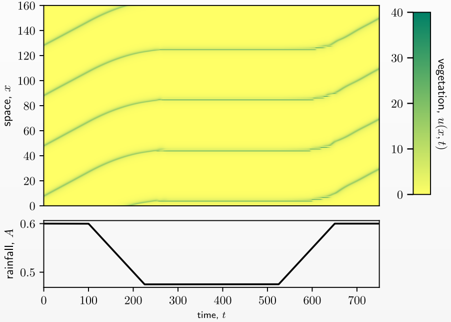
Stability of patterns in the A-c plane.

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[8].
- 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[9].
- Numerical simulations (pattern onset) and space discretisation to avoid nonlocality (calculation of essential spectra) show no qualitative differences for other kernel functions.

[8] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018).

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

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Klausmeier Model

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

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

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Multispecies Model

Multispecies model:

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

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.

Multispecies Model

Multispecies model:

$$\frac{\partial u_1}{\partial t} = \underbrace{w u_1 (u_1 + H u_2) \left(1 - \frac{u_1}{k_1}\right)}_{\text{plant growth}} - \underbrace{B_1 u_1} + \underbrace{\frac{\partial^2 u_1}{\partial x^2}},$$

$$\frac{\partial u_2}{\partial t} = \overbrace{F w u_2 (u_1 + H u_2) \left(1 - \frac{u_2}{k_2}\right)} - \overbrace{B_2 u_2}^{\text{plant loss}} + \overbrace{D \frac{\partial^2 u_2}{\partial x^2}}^{\text{plant dispersal}},$$

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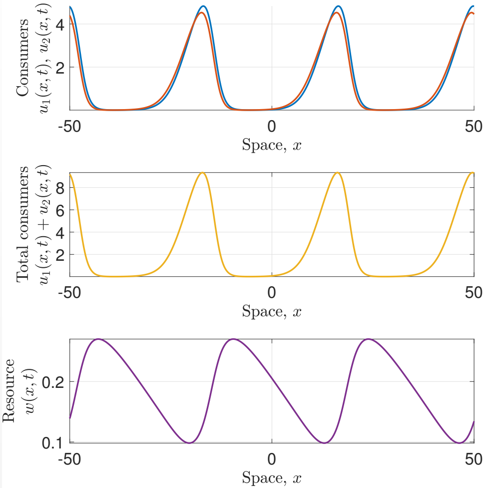
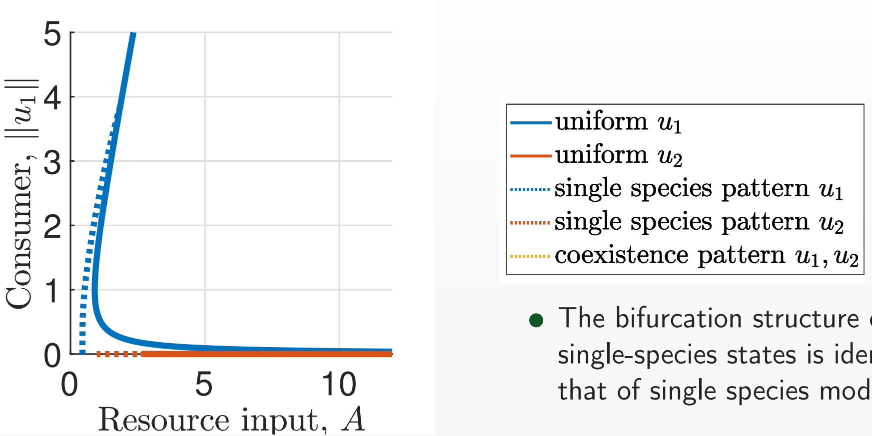
Intraspecific competition is accounted for.

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.

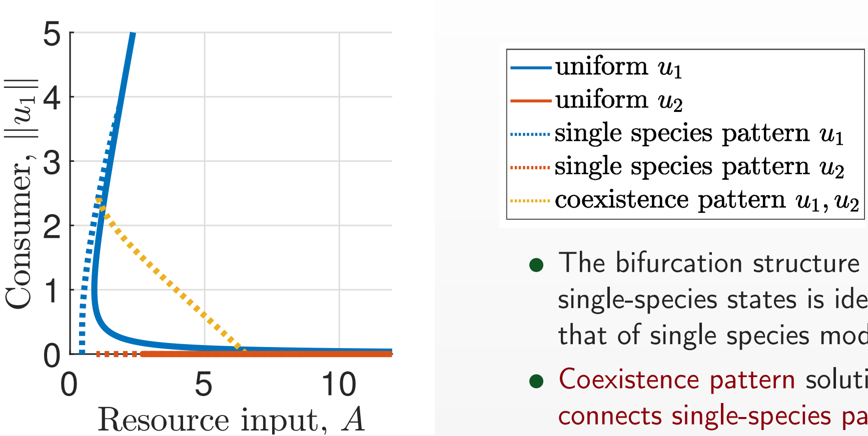
Bifurcation diagram



Bifurcation diagram: one wavespeed only

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

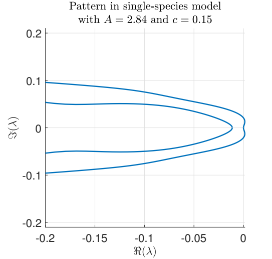
Bifurcation diagram



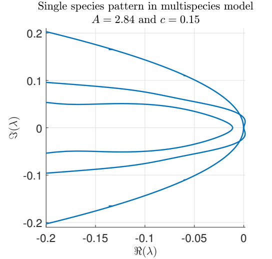
Bifurcation diagram: one wavespeed only

- 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



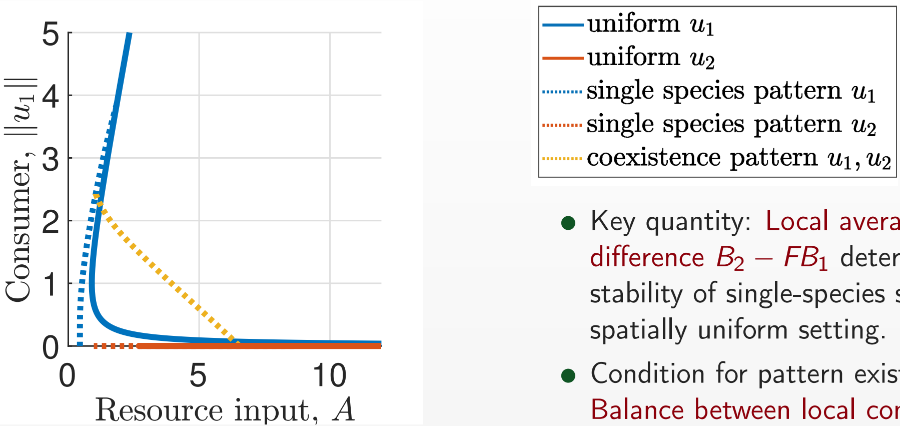
Essential spectrum in single-species model



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.

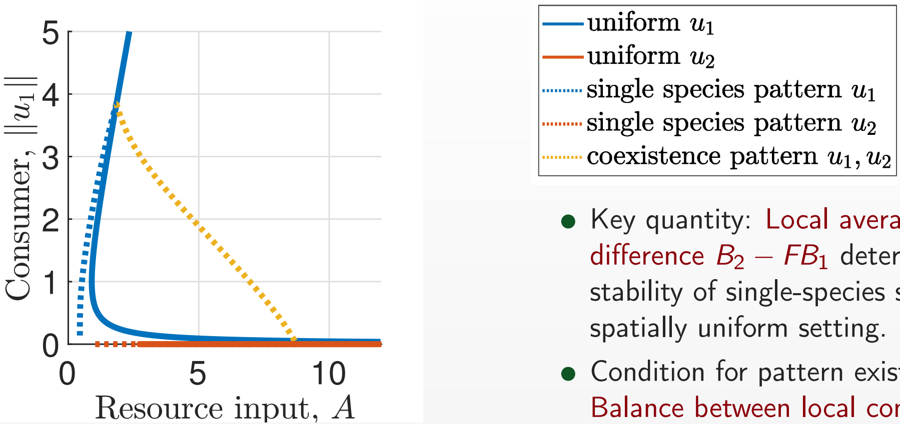
Pattern existence



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

- 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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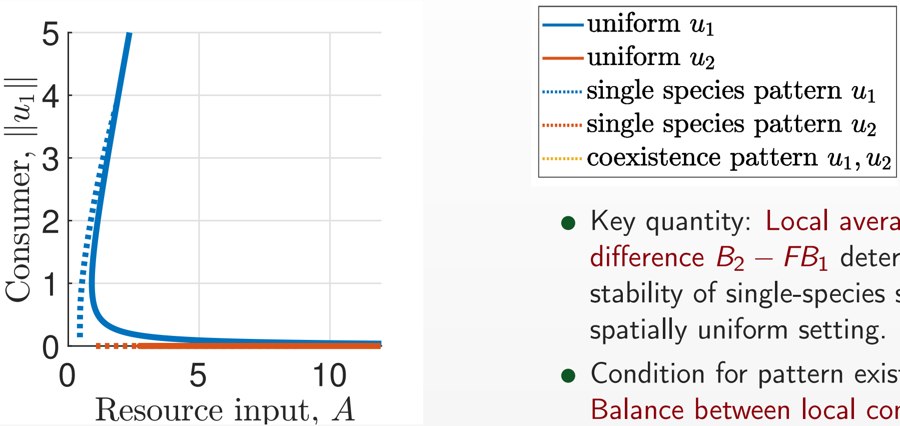
Pattern existence



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

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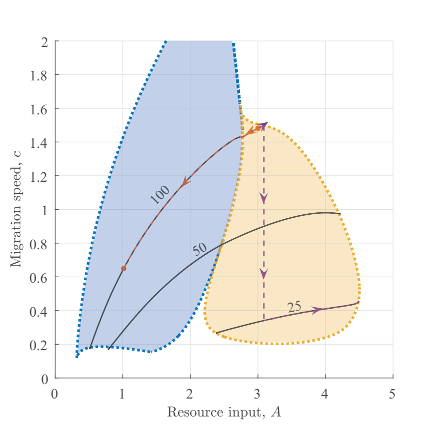
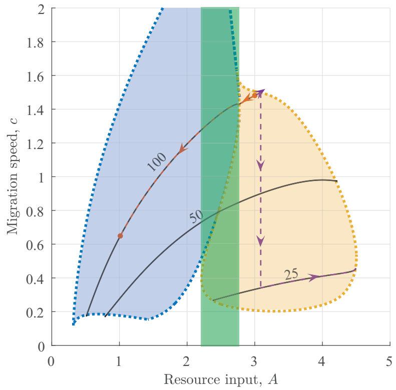
Pattern stability



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.

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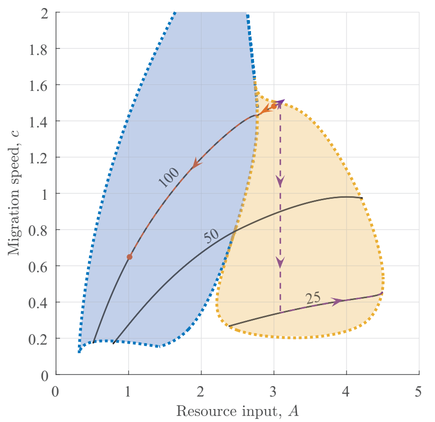
- Bistability of single-species coloniser pattern and coexistence pattern occurs.

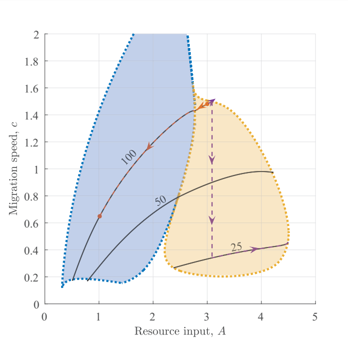
Hysteresis



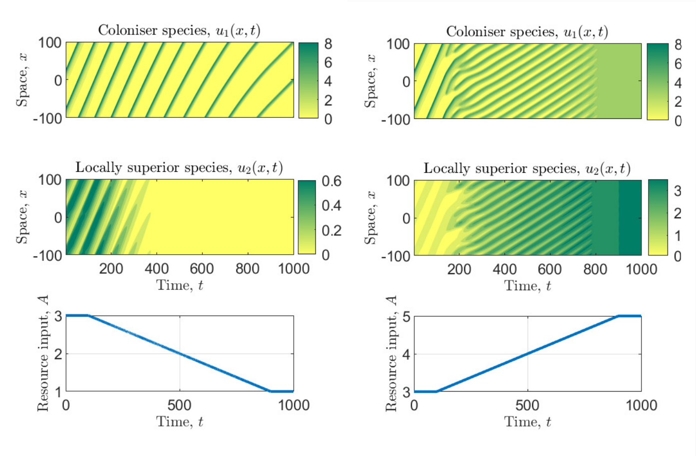
Wavelength contours of stable patterns

- 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.

Hysteresis

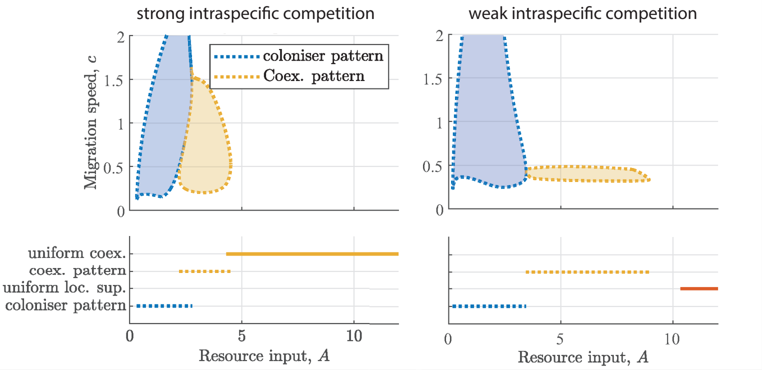


Migration speed, c
Resource input, A
100
50
25



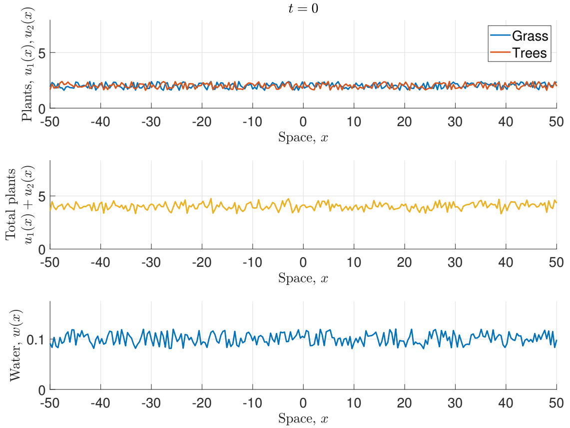
Coloniser species, $u_1(x,t)$
Locally superior species, $u_2(x,t)$
Space, x
Time, t
Resource input, A
Coloniser species, $u_1(x,t)$
Locally superior species, $u_2(x,t)$
Space, x
Time, t
Resource input, A

Intraspecific competition



Lack of intraspecific competition would lead to (a) non-capture of spatially uniform coexistence; and (b) overestimation of pattern resilience.

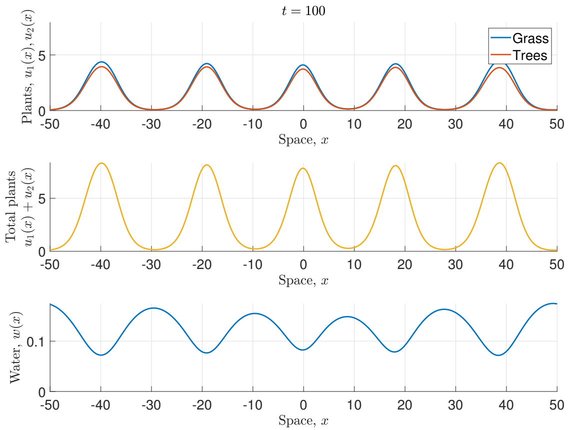
Metastable coexistence



Numerical solution of the multi-species model.

- Coexistence in the model can also occur as a metastable state.
- $t = 1$ corresponds to 3 months

Metastable coexistence



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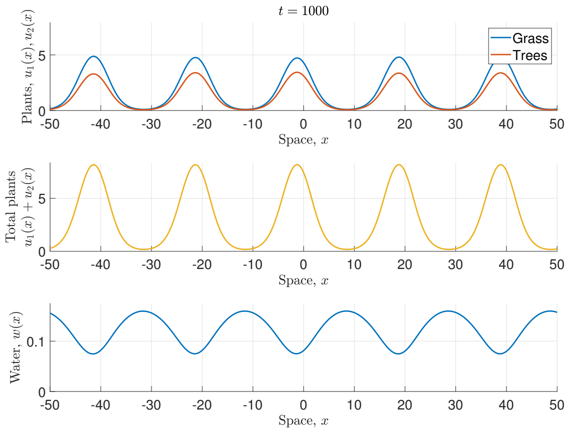
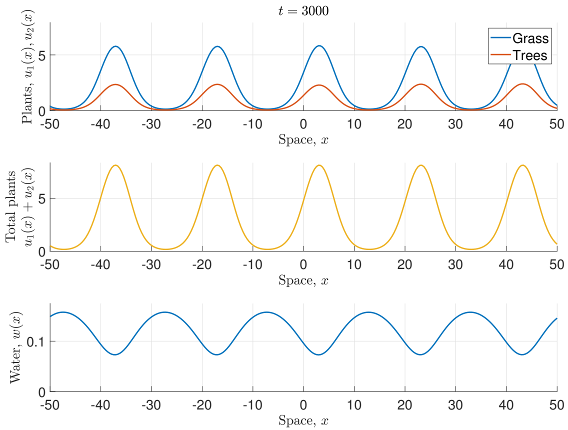


Numerical solution of the multi-species model.

- Coexistence in the model can also occur as a metastable 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.

Metastable coexistence



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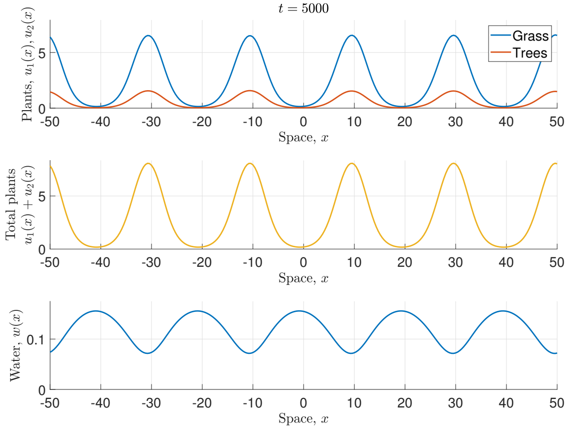

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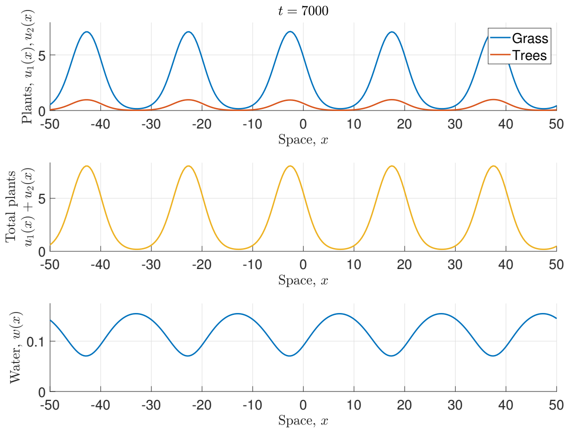

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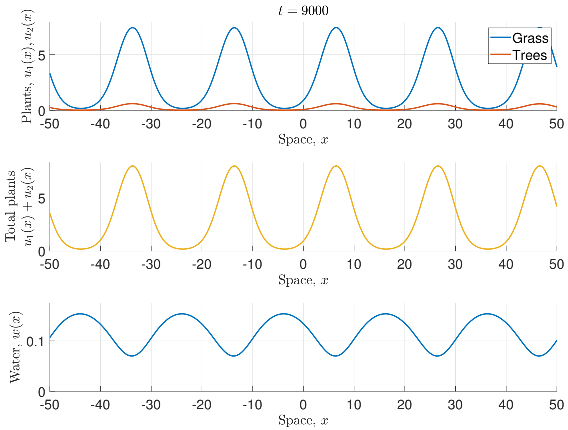

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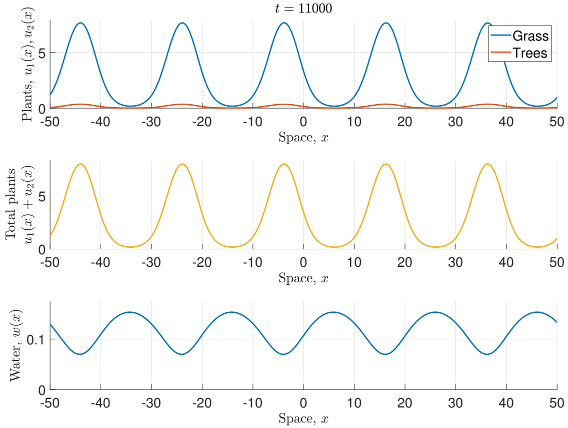

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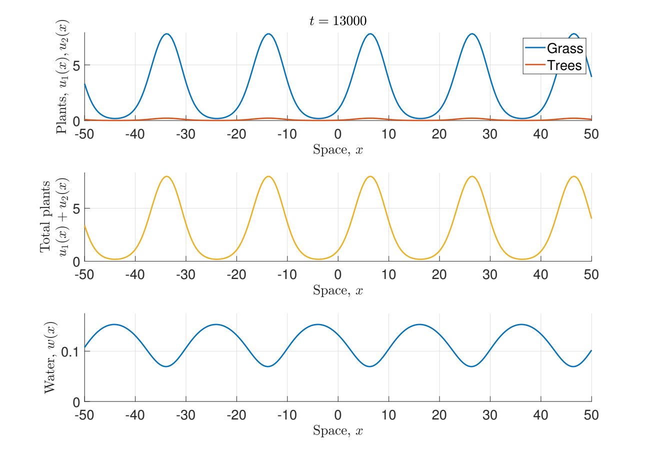

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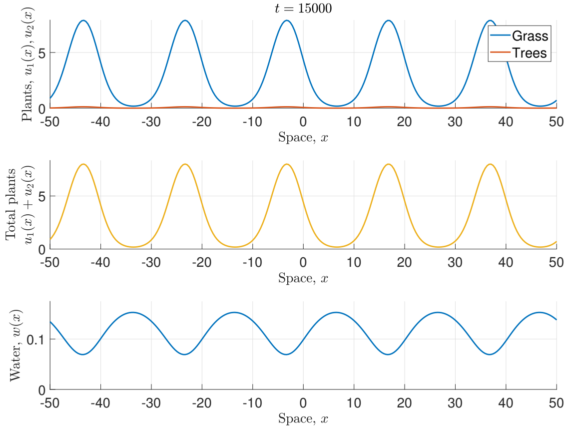
Metastable coexistence



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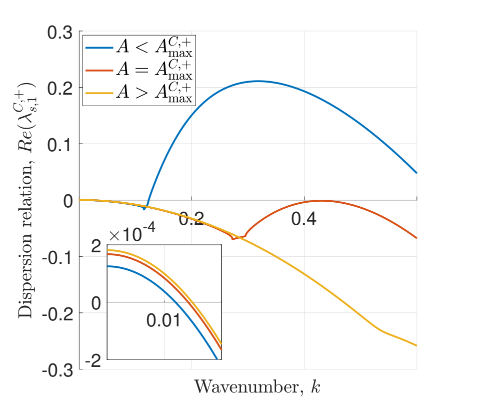


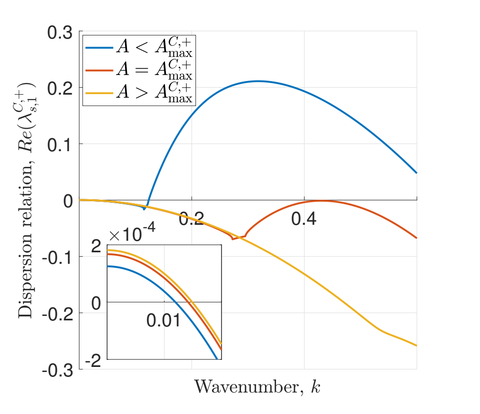
Growth rates of perturbations to equilibrium.

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.

Metastable States



Growth rates of perturbations to equilibrium.

For sufficiently small levels of precipitation $A < A_{\max}^{C}$ 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

- Spatial self-organisation is a coexistence mechanism[10].
- 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 small[11].

[10] EL and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), EL: *Oikos* 130.4 (2021), EL: *Ecol. Complexity* 42 (2020).
[11] EL and Sherratt, J. A.: *Bull. Math. Biol.* 81.7 (2019).

Future Work

- How does nonlocal consumer dispersal affect species coexistence?[12]
- 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 seasonal[13], intermittent[14] and probabilistic resource input regimes on both single-species and multispecies states?

[12] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018).
[13] EL and Sherratt, J. A.: *J. Math. Biol.* 81 (2020).
[14] EL and Sherratt, J. A.: *Physica D* 405 (2020).

References

Slides are available on my website.

`http://lukaseigentler.github.io`

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