Heriot-Watt University &
The University of Edinburgh

Metastability as a Coexistence Mechanism in a Model for Dryland Vegetation Patterns

MMEE 2019

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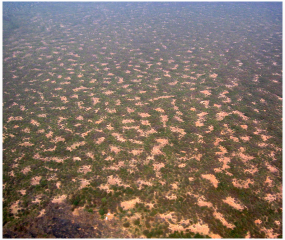
joint work with Jonathan Sherratt

Vegetation Patterns

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

(a) Stripe pattern in Australia.

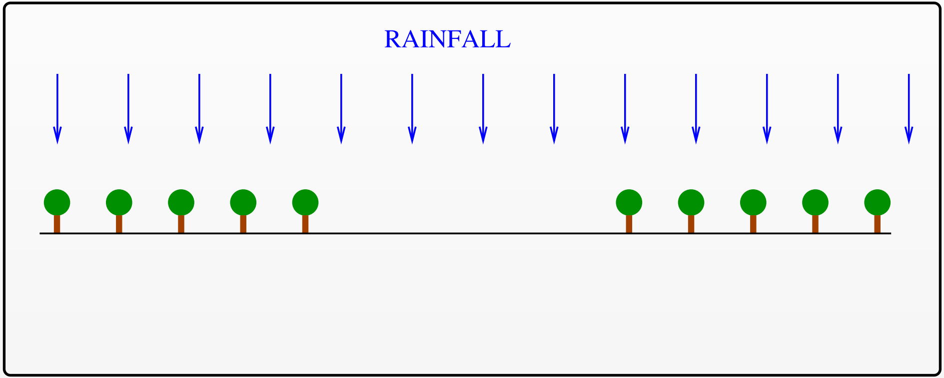


(b) Gap pattern in Niger.

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

Vegetation patterns

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



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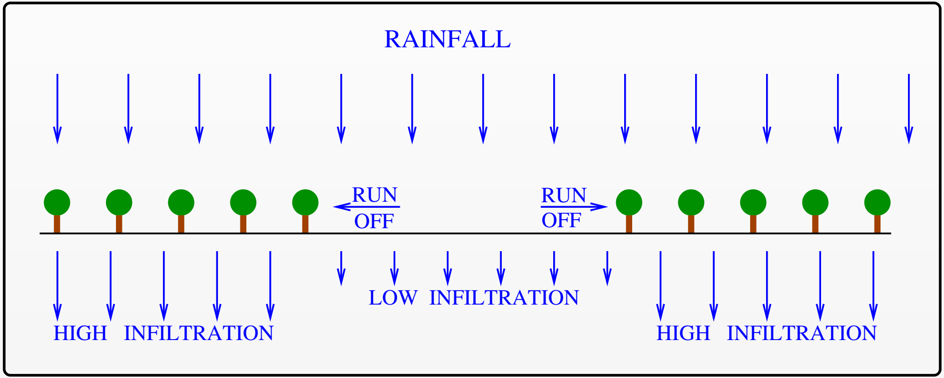

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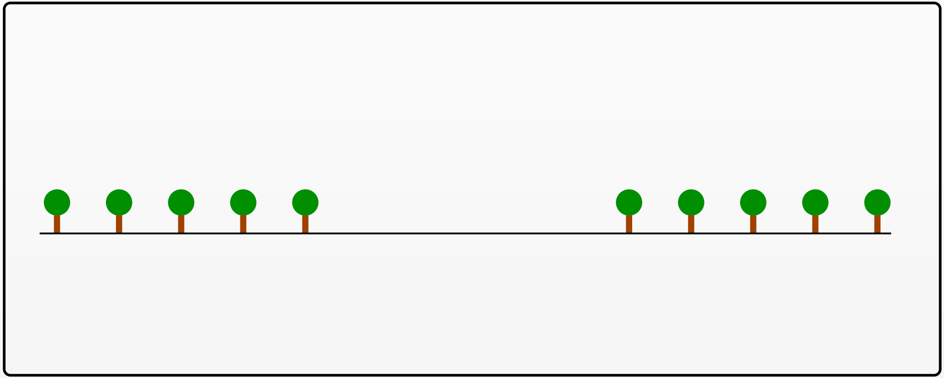

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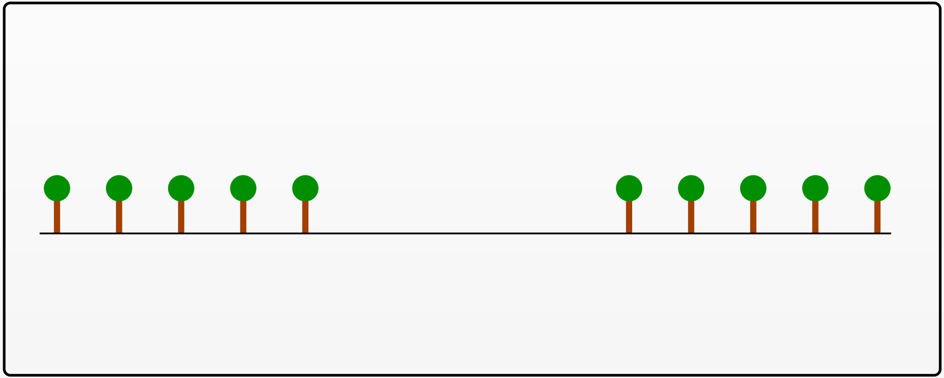

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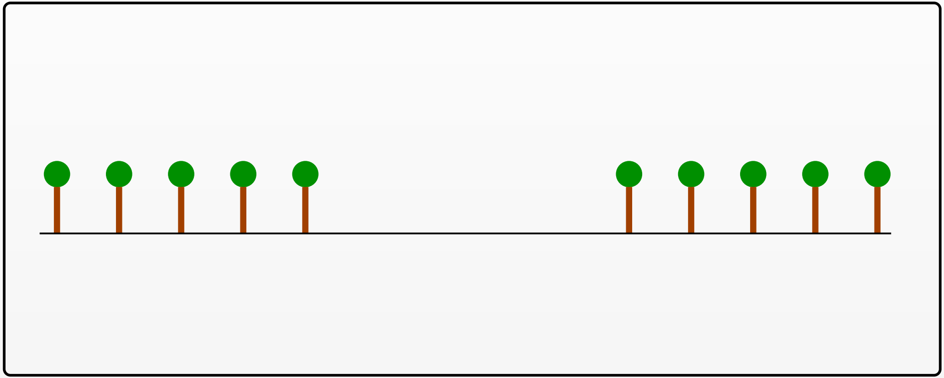

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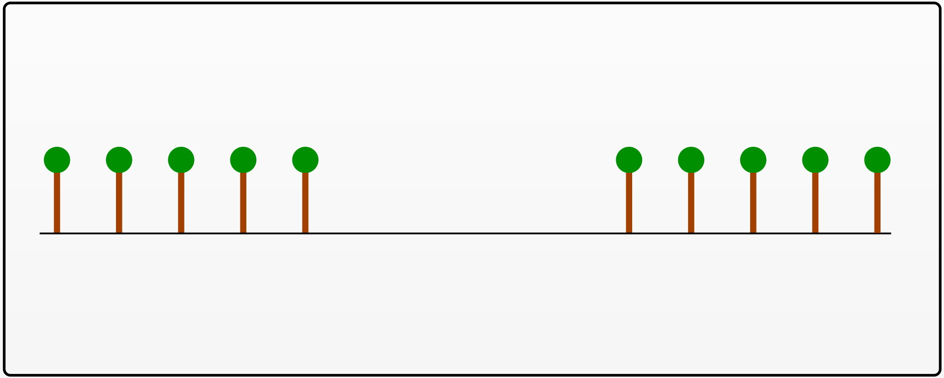

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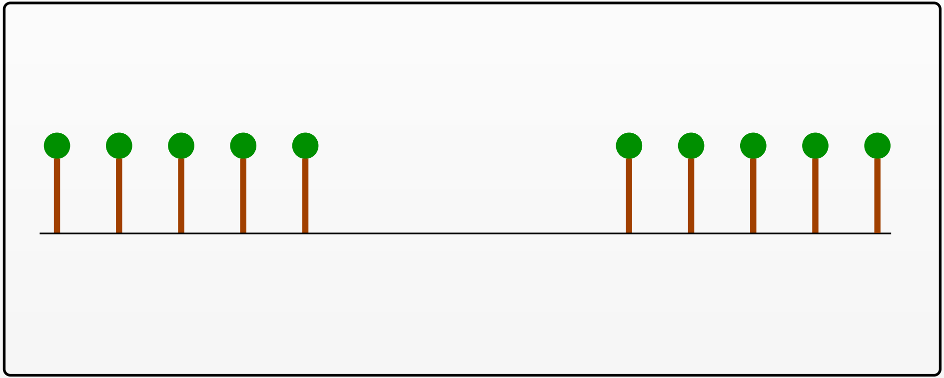

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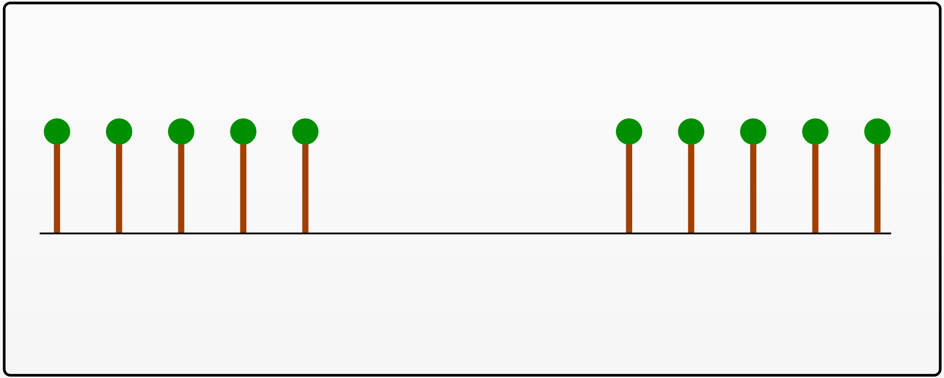

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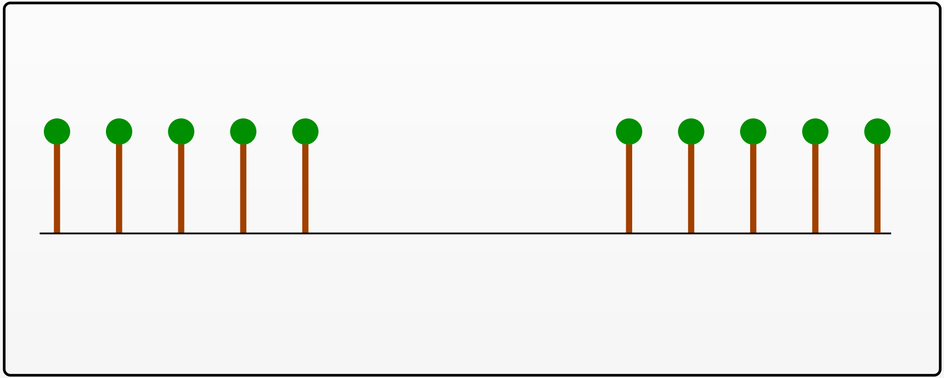

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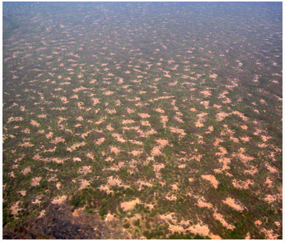

(d) Gap pattern in Niger.

- Plants increase water infiltration into the soil and thus induce a positive feedback loop.
- In general, patterns consist of different plant species (on the level of a single vegetation patch).

Klausmeier Model

One of the most basic phenomenological models for one plant species is the Klausmeier reaction-advection-diffusion model[1].

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

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

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

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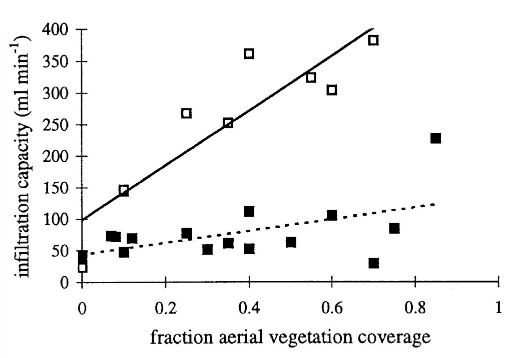
Water Uptake



Infiltration capacity increases with plant density[2]

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.

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

Klausmeier Model

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

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Multispecies Model

A - rainfall, B_i - plant loss, S - shading
F - plant growth ratio, H - infiltration effect ratio
D - plant diffusion ratio, d - water diffusion

Multispecies model with asymmetric direct interspecific competition (e.g. shading).

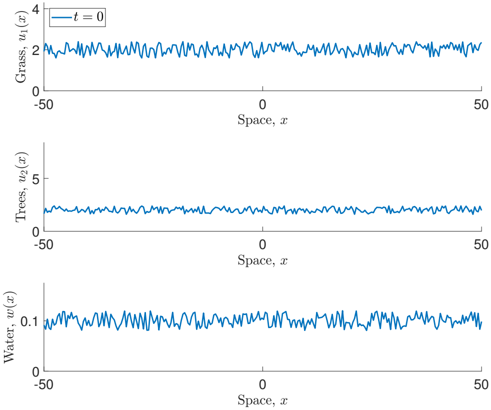
$$\frac{\partial u_1}{\partial t} = \overbrace{wu_1\left(u_1 + Hu_2\right)}^{\text{plant growth}} - \overbrace{B_1 u_1}^{\substack{\text{plant}\\ \text{mortality}}} - \overbrace{Su_1 u_2}^{\substack{\text{interspecific}\\ \text{competition}}} + \overbrace{\frac{\partial^2 u_1}{\partial x^2}}^{\text{plant dispersal}},$$

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

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

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

Simulations



Numerical solution of the multi-species model.

- $t = 1$ corresponds to 3 months

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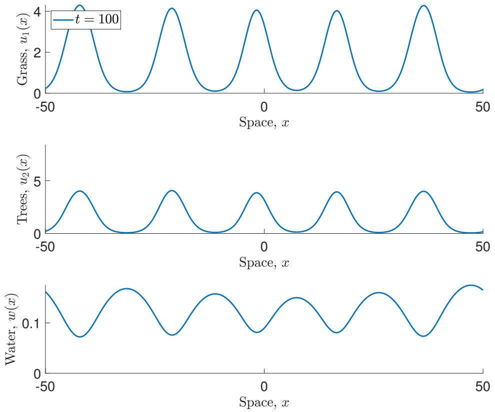

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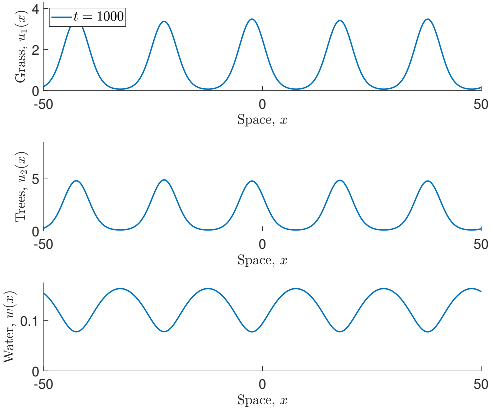

Numerical solution of the multi-species model.

- $t = 1$ corresponds to 3 months $\Rightarrow$ coexistence of more than 1000 years.
- Coexistence occurs as a long transient to a one-species pattern.

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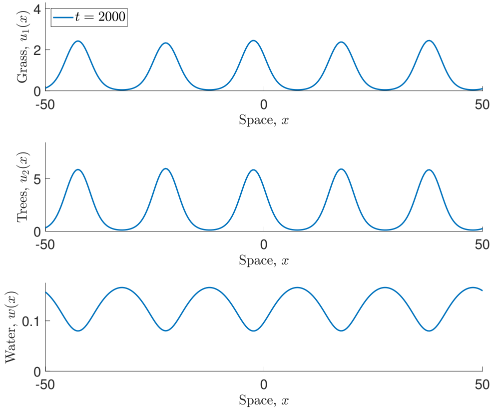

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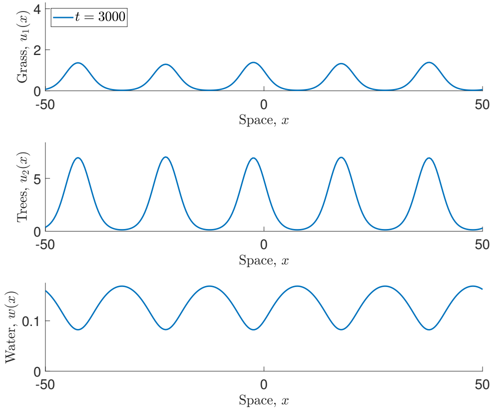

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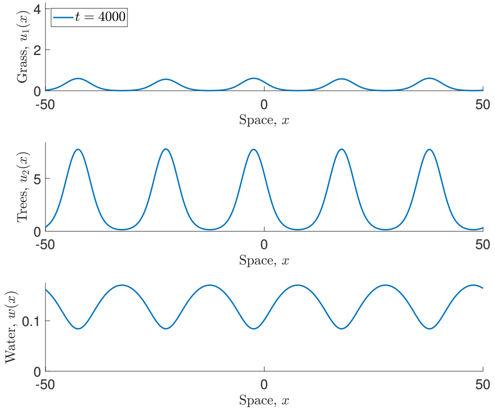

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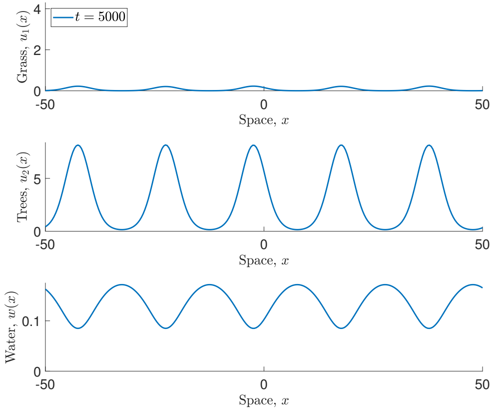

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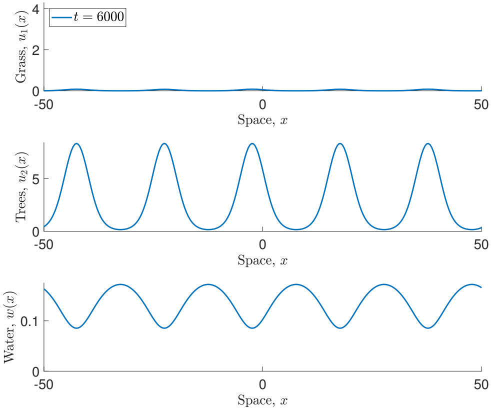

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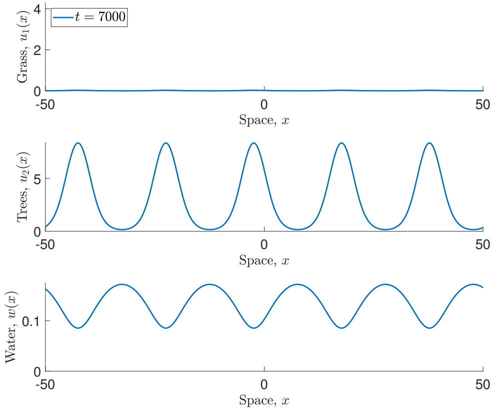

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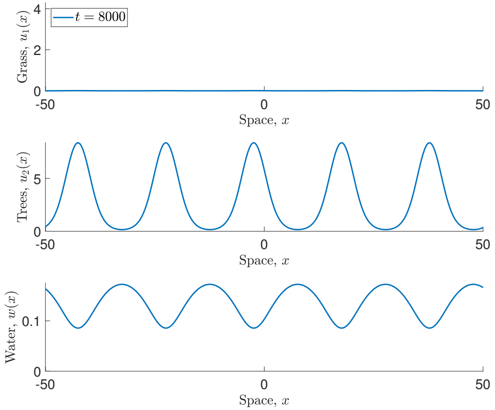

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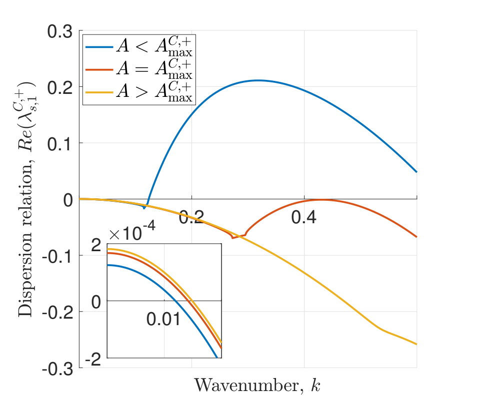
Metastable States

- The metastable state's origin is a unstable coexistence equilibrium $(\overline{u_1}^C, \overline{u_2}^C, \overline{w}^C)$ that exists provided $B_2 - B_1F > 0$ and $A > A^C_{\text{min}}$.
- $B_2 - B_1F$ is the average fitness difference.
- Linear stability analysis yields instability through one eigenvalue $\lambda^C \in \mathbb{C}$ (of the corresponding Jacobian) with positive real part.

Metastable States



Growth rates of perturbations to coexistence equilibrium.

Calculation of the growth rate λ_u^C of spatially uniform perturbations to the coexistence equilibrium shows

$$\text{Re}\left(\lambda_u^C\right) = O(B_2 - B_1 F).$$

- If the average fitness difference $B_2 - B_1 F$ is small, then coexistence occurs as a long transient from $(\overline{u_1}^C, \overline{u_2}^C, \overline{w}^C)$ to a stable one-species state.
- This carries over to a two-dimensional spatial domain.

Metastable States

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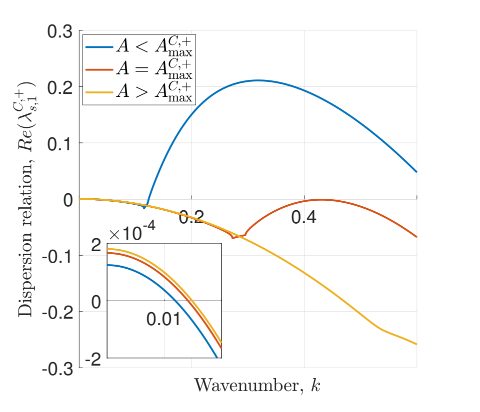


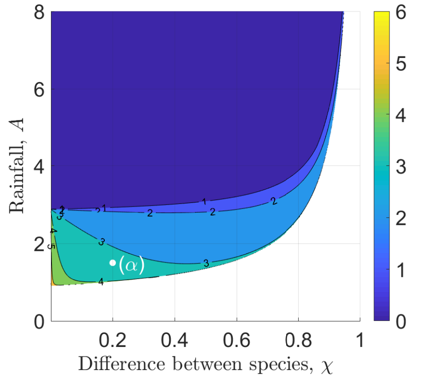
Growth rates of perturbations to coexistence equilibrium.

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

$$\max_{k>0}\left\{\mathrm{Re}\left(\lambda_s^C(k)\right)\right\} \gg \mathrm{Re}\left(\lambda_u^C\right)$$

- 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.

Metastable States



Order of magnitude difference of maximum perturbation growth rate between spatial and non-spatial model.

$0 < \chi < 1$ is the difference between the two species, i.e.

$$
\begin{aligned}
B_2 &= B_1 - \chi(B_1 - b_2), \\
F &= 1 - \chi(1 - f), \\
H &= 1 - \chi(1 - h), \\
S &= s\chi, \\
D &= 1 - \chi(1 - D_0)
\end{aligned}
$$

Coexistence (both in spatially uniform and patterned form) occurs for a wide range of parameters.

Conclusion

- Coexistence of two species competing for the same limiting resource can occur as a long transient state, originating from a unstable coexistence equilibrium.
- Mathematically, this metastability is characterised by the small size of the only positive eigenvalue.
- Ecologically, small differences in the species' average fitness (water to biomass conversion capability to mortality ratio) facilitate the transient state.
- Similar results hold in an invasion-type scenario, in which a single-species pattern is unstable to the introduction of a second species.
- Wavelength of coexistence pattern may change during long transient to single-species pattern. $\Rightarrow$ Potentially a useful tool for prediction of the eventual fate of a pattern.

Future Work

- 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?

References

Slides are available on my website.

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

Eigentler, L. and Sherratt, J. A.: 'Metastability as a coexistence mechanism in a model for dryland vegetation patterns'. *Bull. Math. Biol.* 81.7 (2019), pp. 2290–2322.