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Spatial self-organisation enables species coexistence in a model for dryland vegetation patterns

eSMB 2020

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joint work with Jonathan Sherratt

Vegetation patterns

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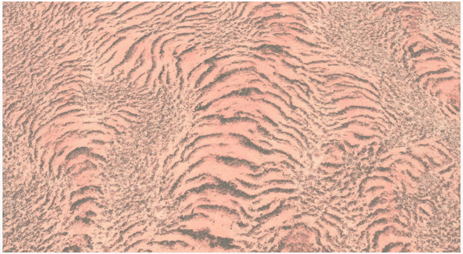
Vegetation patterns are a classic example of a self-organisation principle in ecology.

Vegetation band in Austrialia.[1]

Stripe pattern in Ethiopia[2].



- Plants increase water infiltration into the soil and induce a positive feedback loop.
- On sloped ground, stripes grow parallel to the contours.

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

[2] Source: Google Maps

Vegetation patterns

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Transition from vegetation patterns to arid savannas along the precipitation gradient.

Vegetation pattern.[3]

Arid savanna.[4]

- Both vegetation patterns and arid savannas are characterised by species coexistence.

[3] Dunkerley, D.: *Desert* 23.2 (2018).
[4] Source: Wikimedia Commons

Klausmeier model

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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

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Water uptake

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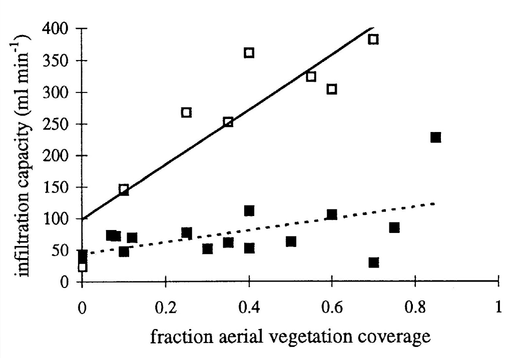

Infiltration capacity increases with plant density[6]

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)

Klausmeier Model

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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

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Multispecies model based on the extended Klausmeier model.

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

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

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

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

Multispecies Model

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Intraspecific competition may be considered.

$$\frac{\partial u_1}{\partial t} = \overbrace{wu_1\left(u_1 + Hu_2\right)\left(1 - \frac{u_1}{k_1}\right)}^{\text{plant growth}} - \overbrace{B_1 u_1}^{\substack{\text{plant}\\\text{mortality}}} + \overbrace{\frac{\partial^2 u_1}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial u_2}{\partial t} = \overbrace{Fwu_2\left(u_1 + Hu_2\right)\left(1 - \frac{u_2}{k_2}\right)}^{\text{plant growth}} - \overbrace{B_2 u_2}^{\substack{\text{plant}\\\text{mortality}}} + \overbrace{D\frac{\partial^2 u_2}{\partial x^2}}^{\text{plant dispersal}},$$

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Simulations

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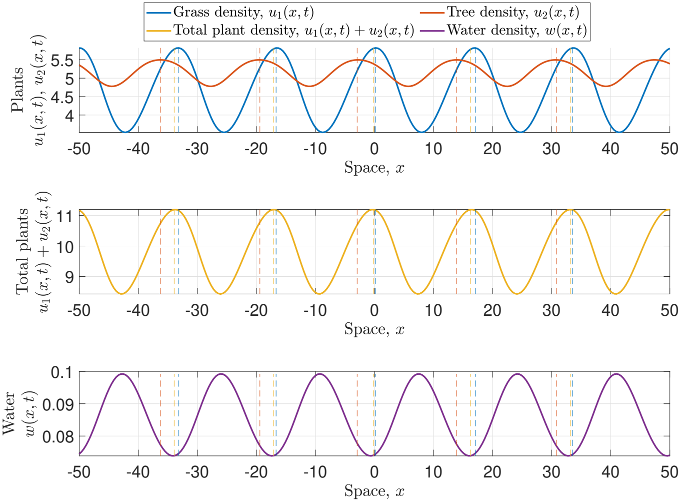

- In the absence of intraspecific competition, coexistence in the model occurs as a stable savanna state.

Bifurcation diagram

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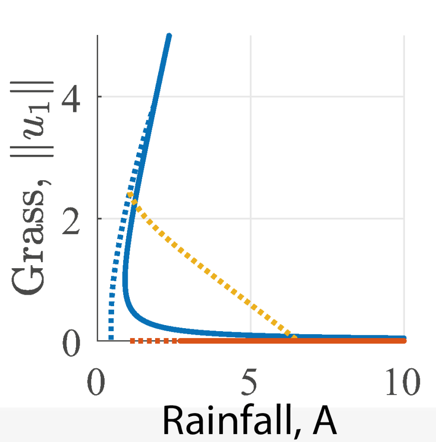

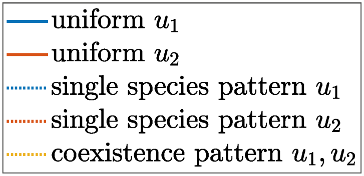

Bifurcation diagram: one wavespeed only

- 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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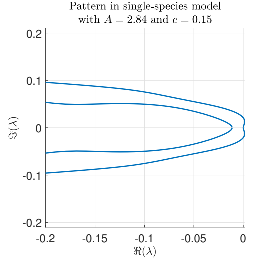
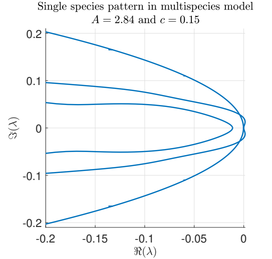


Essential spectrum in single-species model



Essential spectrum in multispecies model

- The key to understand coexistence pattern onset is knowledge of single-species pattern's stability.
- Tool: essential spectra of periodic travelling waves, calculated using the numerical continuation method by Rademacher et al.[7]
- Pattern onset occurs as the single-species pattern loses/gains stability to the introduction of a competitor.

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

Pattern existence

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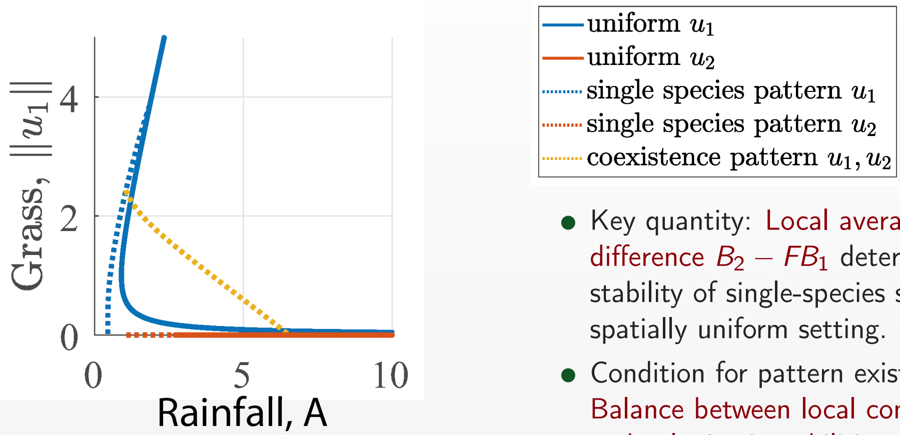

$B_2 - FB_1 < 0, F < 1, D < 1$

- 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

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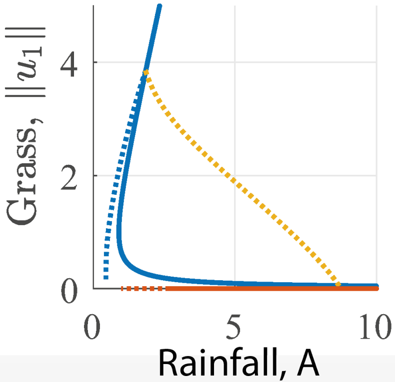
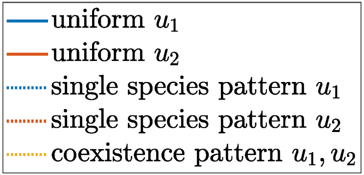


$B_2 - FB_1 \approx 0, F < 1, D < 1$



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Pattern existence

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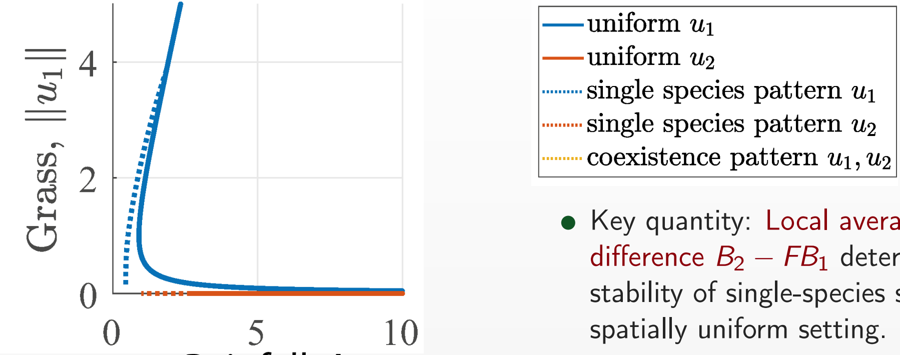

Rainfall, A

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

- Key quantity: Local average fitness difference $B_2 - FB_1$ determines stability of single-species states in spatially uniform setting.
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Pattern stability

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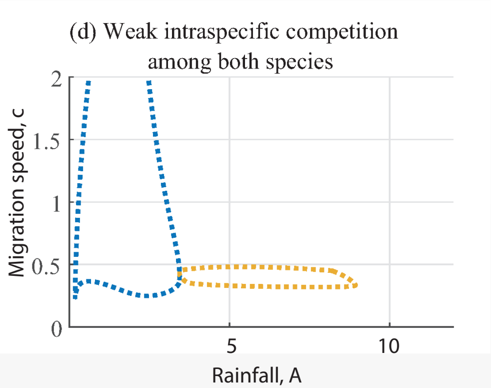

Busse balloons of all pattern types in the system

- For decreasing rainfall, coexistence savanna state loses stability to single-species grass pattern.
- Transition occurs at moderate environmental stress $\Rightarrow$ Coexistence only possible in savanna state.

Effects of intraspecific competition

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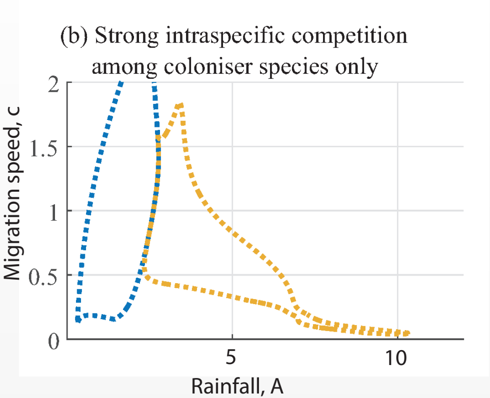

Busse balloons of all pattern types in the system

- Intraspecific competition among colonisers stabilise coexistence in vegetation pattern state.
- Intraspecific competition among locally superior species enables spatially uniform coexistence (not shown).
- Omission of intraspecific competition leads to overestimation of single-species pattern resilience.

Effects of intraspecific competition

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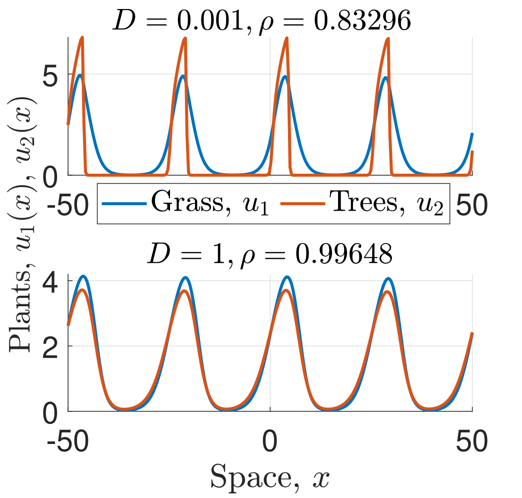

- The model captures the spatial species distribution of grasses and trees in a pattern.
- The faster the coloniser's dispersal, the more pronounced is its presence at the top edge of each stripe.

Conclusions

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- The basic phenomenological reaction-advection-diffusion system captures species coexistence as
  - (i) a stable patterned solution representing a savanna state.
  - (ii) a stable vegetation pattern state if intraspecific competition among the superior coloniser is sufficiently strong.
  - (iii) a metastable state if the average fitness difference between species is small[8].
- Coexistence is enabled by spatial heterogeneities in the resource, caused by the plants' self-organisation into patterns.
- 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.

[8] EL and Sherratt, J. A.: *Bull. Math. Biol.* 81.7 (2019).

Future Work

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- How does nonlocal seed dispersal affect species coexistence?
- Do results extend to an arbitrary number of species?
- 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.: *arXiv:1911.10964* (2019).
[10] EL and Sherratt, J. A.: *Physica D* 405 (2020).

References

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Slides are available on my website.

`https://lukaseigentler.github.io`

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