Pattern formation can enable species coexistence in resource-limited plant ecosystems

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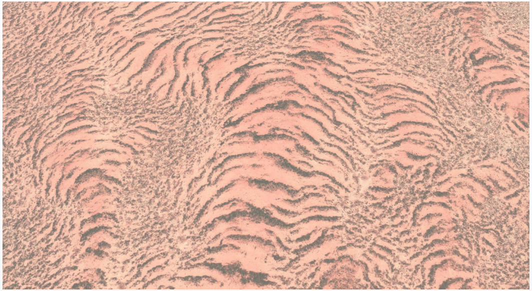
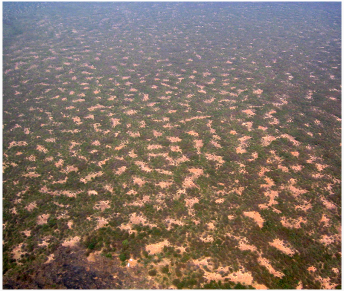
Vegetation patterns

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.
- 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).

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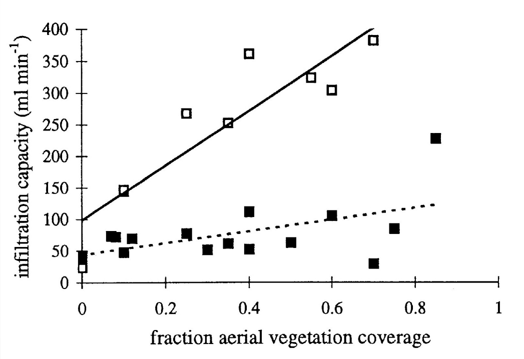
Water uptake



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)

Klausmeier Model

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

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

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

Multispecies Model

Multispecies model:

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

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

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

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:

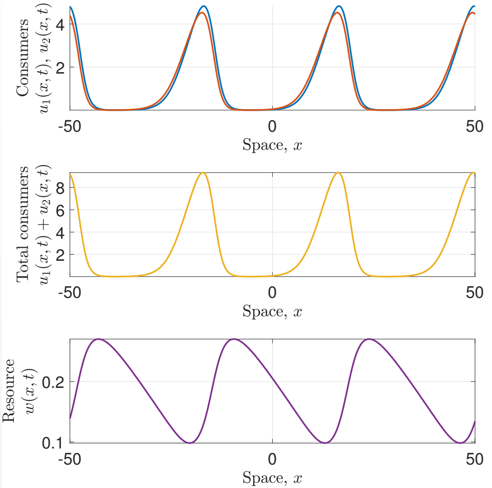
$$\frac{\partial u_1}{\partial t} = \underbrace{w u_1 (u_1 + H u_2) \left(1 - \frac{u_1}{k_1}\right)} - \underbrace{B_1 u_1} + \underbrace{\frac{\partial^2 u_1}{\partial x^2}},$$

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

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

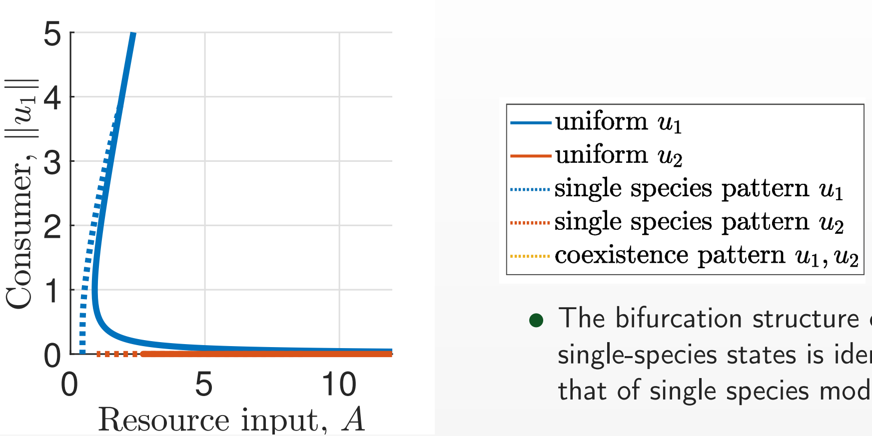
Intraspecific competition is accounted for.

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.

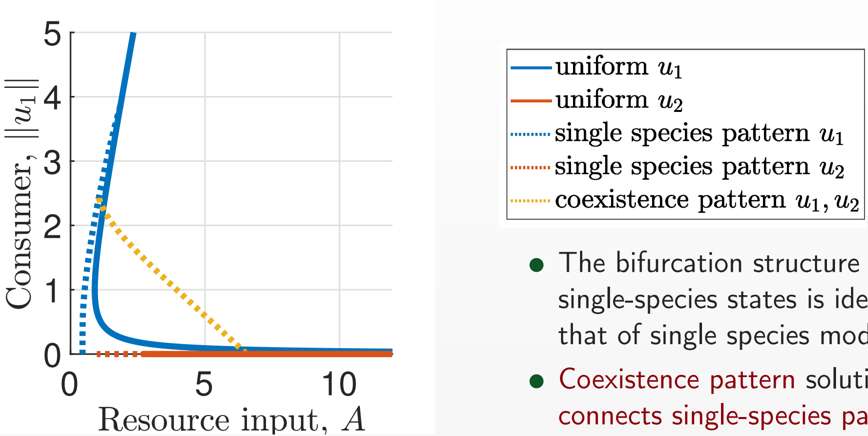
Bifurcation diagram



Bifurcation diagram: one wavespeed only

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

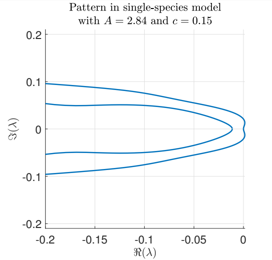
Bifurcation diagram



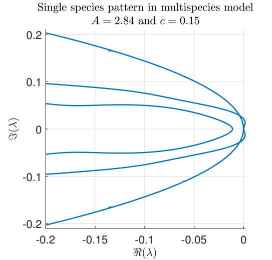
Bifurcation diagram: one wavespeed only

- 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

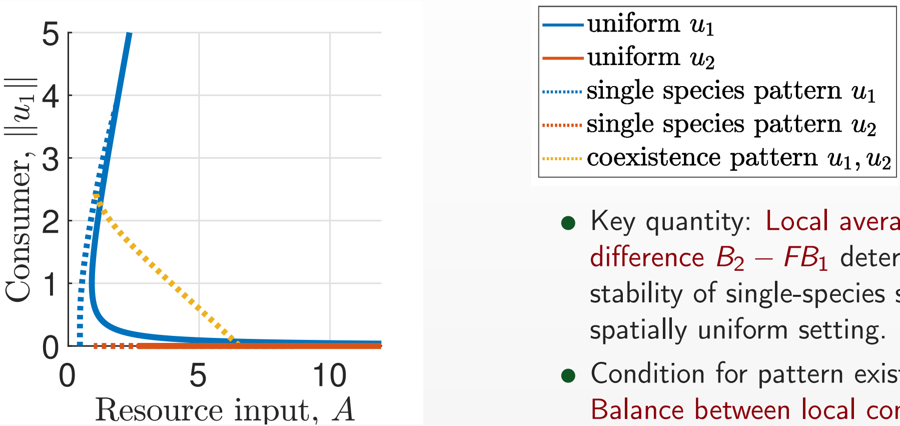


Essential spectrum in multispecies model

- The key to understand coexistence pattern onset is knowledge of single-species pattern's stability.
- Tool: essential spectra of periodic travelling waves, calculated using the numerical continuation method by Rademacher et al.[6]
- Pattern onset occurs as the single-species pattern loses/gains stability to the introduction of a competitor.

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

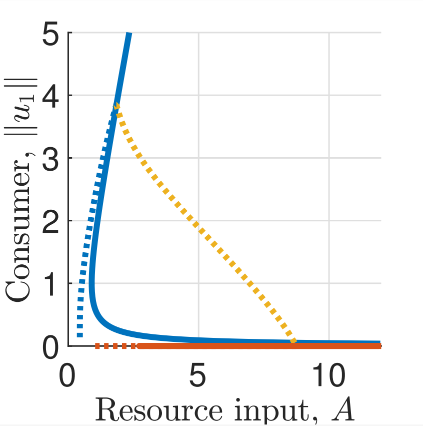
Pattern existence



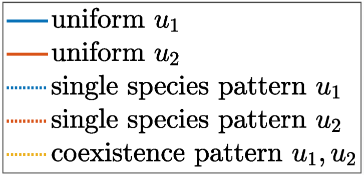
$B_2 - FB_1 < 0, F < 1, D < 1$

- 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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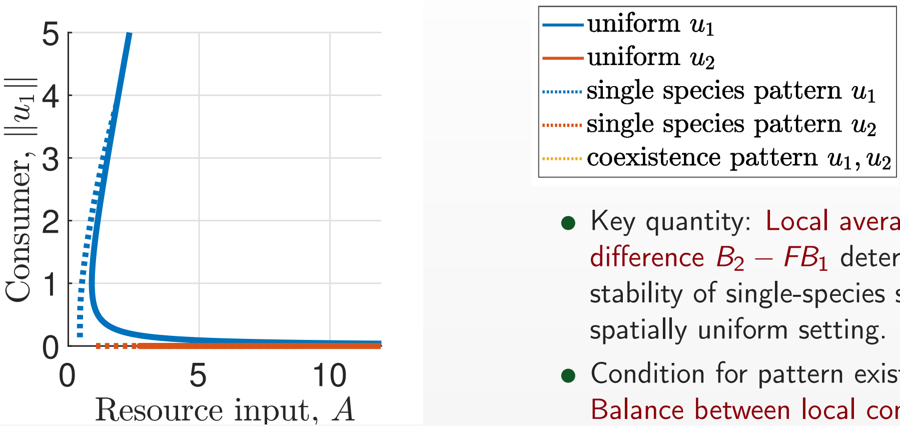
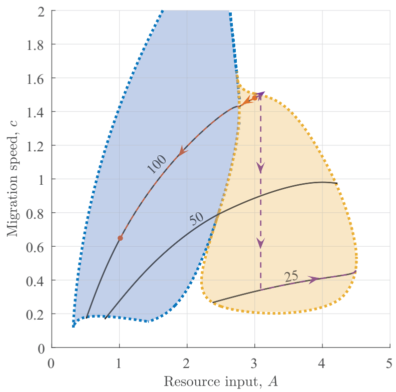


$B_2 - FB_1 > 0, F < 1, D < 1$

- 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.

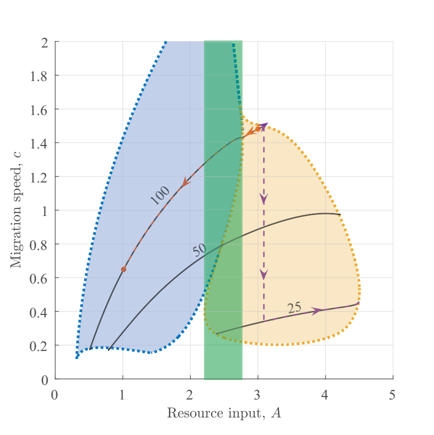
Pattern stability



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.

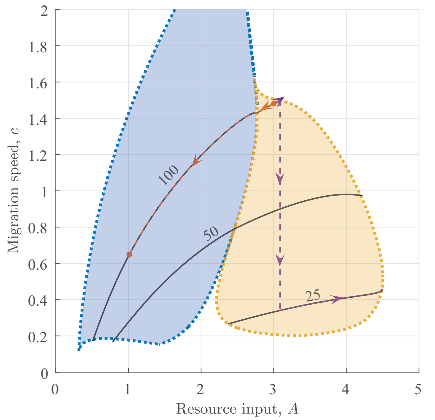
Pattern stability



Stability regions of system states.

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

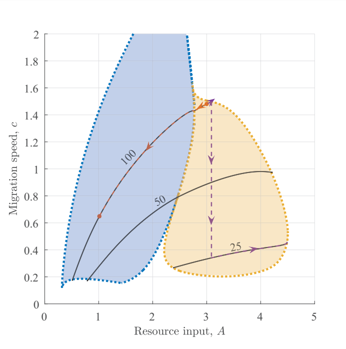
Hysteresis



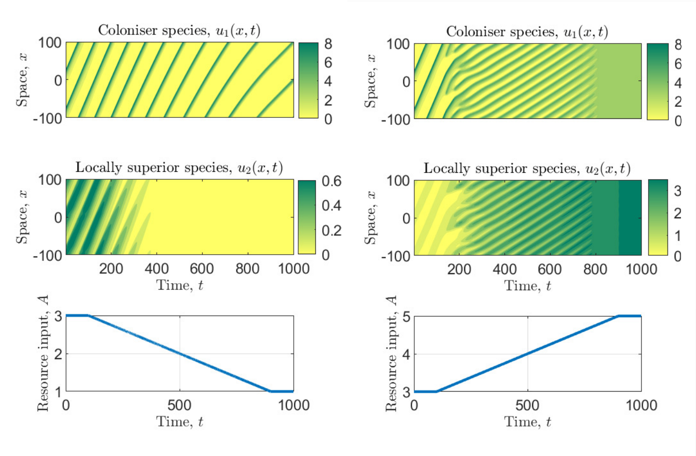
Wavelength contours of stable patterns

- 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

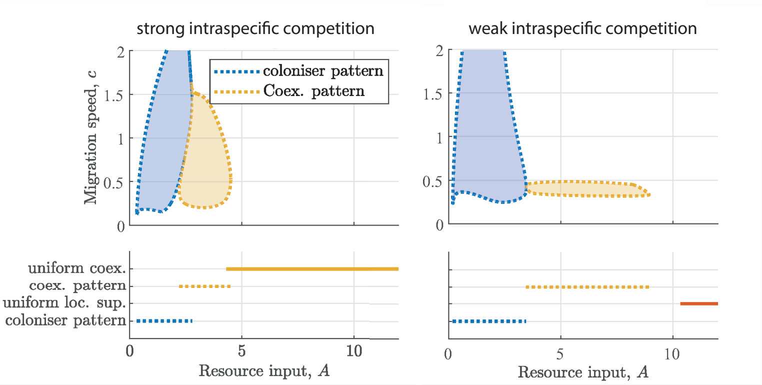


Migration speed, c
Resource input, A
100
50
25



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.

Conclusions

- Spatial self-organisation is a coexistence mechanism[7].
- 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[8].

[7] EL and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), EL: *Oikos* 130.4 (2021), EL: *Ecol. Complexity* 42 (2020).

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

Future Work

- How does nonlocal consumer dispersal affect species coexistence?[9]
- 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[10], intermittent[11] and probabilistic resource input regimes on both single-species and multispecies states?

[9] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018).
[10] EL and Sherratt, J. A.: *J. Math. Biol.* 81 (2020).
[11] EL and Sherratt, J. A.: *Physica D* 405 (2020).

References

Slides are available on my website.

`http://lukaseigentler.github.io`

[1] Eigentler, L.: *Oikos* 130.4 (2021), pp. 609–623.

[2] Eigentler, L.: *Ecol. Complexity* 42 (2020), p. 100835.

[3] Eigentler, L. and Sherratt, J. A.: *J. Theor. Biol.* 487 (2020), p. 110122.