Pattern formation can enable species coexistence in resource-limited ecosystems

XL Dynamic Days - 25/08/2021

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Patterned ecosystems

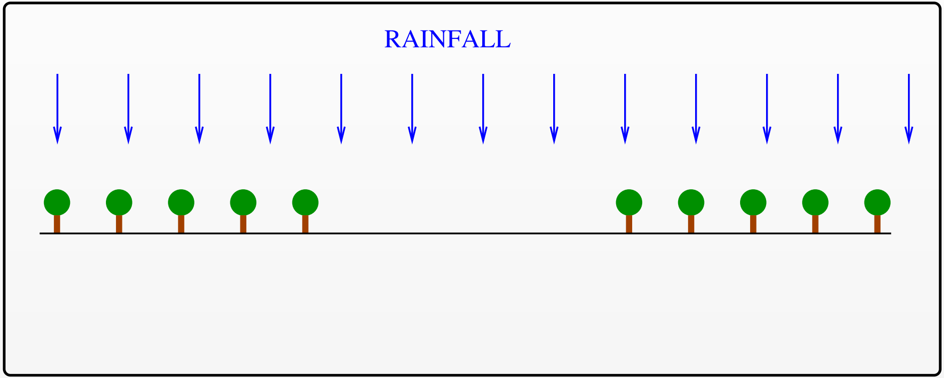
- Scale dependent feedback loops cause pattern formation in ecological systems.
- Local facilitation: e.g. increased water infiltration in vegetated areas, ...
- Long-range competition: e.g. competition for a limiting resource.
- Self-organisation into colonised and uncolonised areas is typically associated with high environmental stress.
- Unidirectional resource flux leads to stripe patterns.

Vegetation pattern & mussel beds.

Ribbon forest

Local facilitation in vegetation patterns

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



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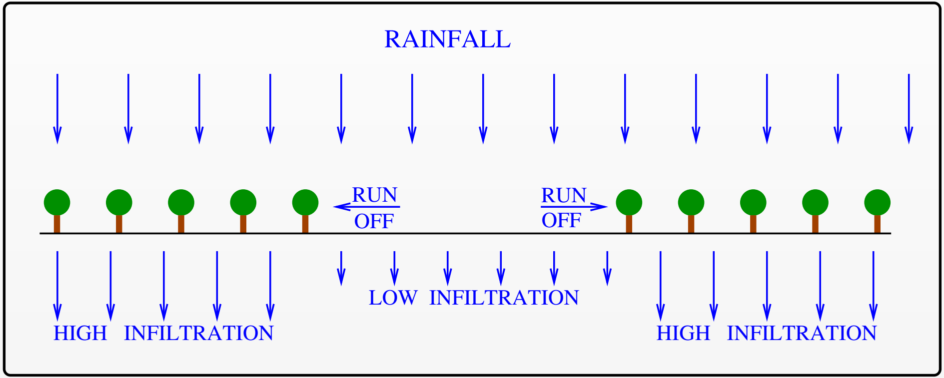

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Patterned ecosystems

- Coexistence typically occurs despite competition for a single limiting resource.
- Coexistence occurs on the scale of a single stripe (i.e. no spatial segregation).
- What mechanisms cause coexistence?

Vegetation pattern & mussel beds.

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Klausmeier model

One of the most basic phenomenological models is the extended Klausmeier reaction-advection-diffusion model.[1]

$$\frac{\partial u}{\partial t} = \overbrace{u^2 w \left(1 - \frac{u}{k}\right)}^{\text{consumer growth}} - \overbrace{Bu}^{\text{consumer death}} + \overbrace{\frac{\partial^2 u}{\partial x^2}}^{\text{consumer dispersal}},$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\substack{\text{resource}\\\text{input}}} - \underbrace{w}_{\substack{\text{natural resource}\\\text{depletion}}} - \underbrace{u^2 w}_{\substack{\text{resource consumption}\\\text{by consumers}}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\substack{\text{unidirectional}\\\text{resource flux}}} + \underbrace{d \frac{\partial^2 w}{\partial x^2}}_{\substack{\text{resource}\\\text{diffusion}}}.$$

The model describes interactions between the limiting resource and a single consumer species.

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

Multispecies Model

Multispecies model:

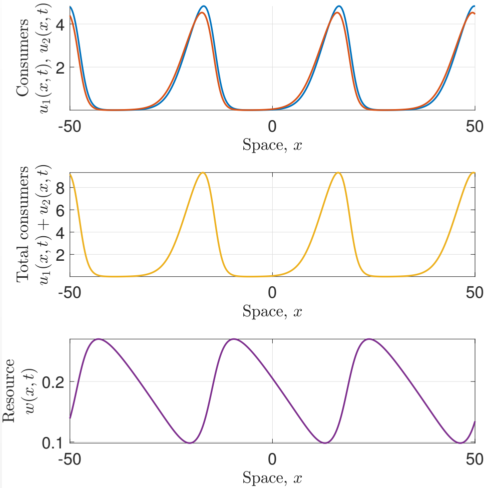
$$\frac{\partial u_1}{\partial t} = \underbrace{wu_1\left(u_1 + Hu_2\right)\left(1 - \frac{u_1}{k_1}\right)}_{\text{consumer growth}} - \underbrace{B_1 u_1}_{\text{consumer mortality}} + \underbrace{\frac{\partial^2 u_1}{\partial x^2}}_{\text{consumer dispersal}},$$

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

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{resource input}} - \underbrace{w}_{\text{natural resource depletion}} - \underbrace{w\left(u_1 + u_2\right)\left(u_1 + Hu_2\right)}_{\text{resource consumption by consumer}} + \underbrace{\nu\frac{\partial w}{\partial x}}_{\text{unidirectional resource flux}} + \underbrace{d\frac{\partial^2 w}{\partial x^2}}_{\text{resource diffusion}}.$$

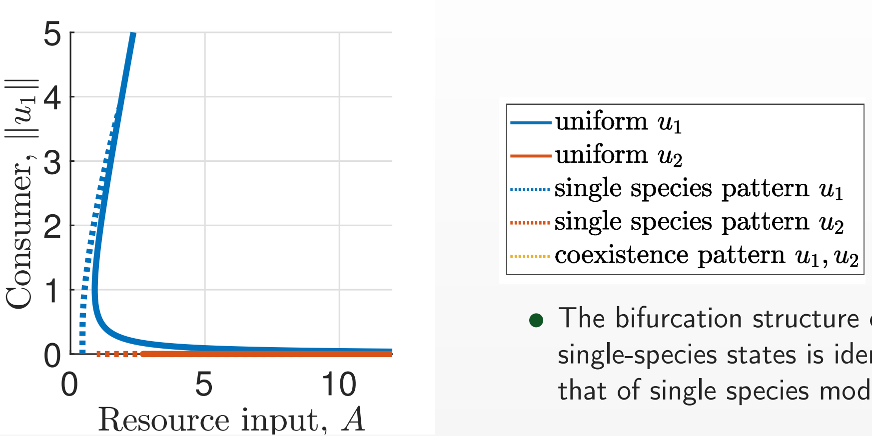
Species only differ quantitatively (i.e. in parameter values) but not qualitatively (i.e. same functional responses). Assume u_1 is superior coloniser; u_2 is locally superior.

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.

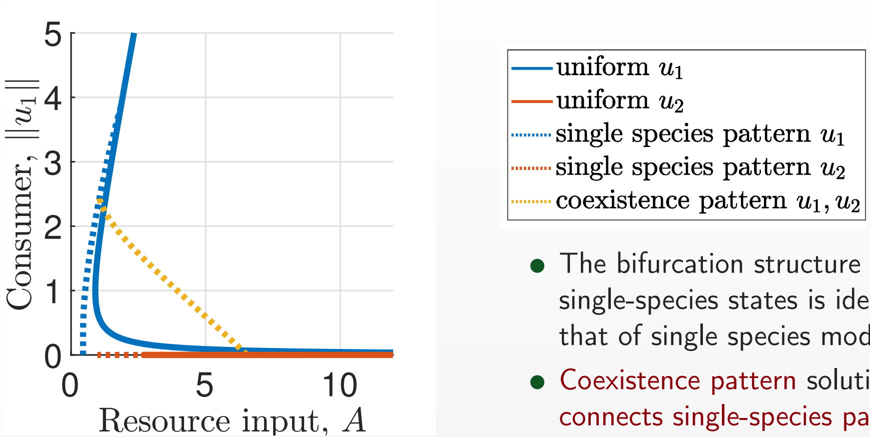
Bifurcation diagram



Bifurcation diagram: one wavespeed only

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

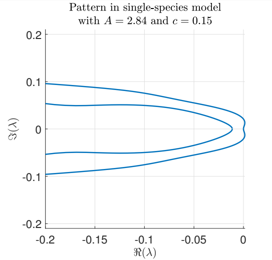
Bifurcation diagram



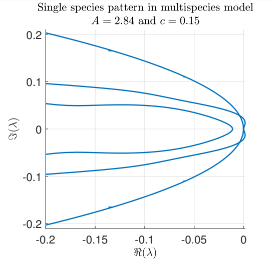
Bifurcation diagram: one wavespeed only

- 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

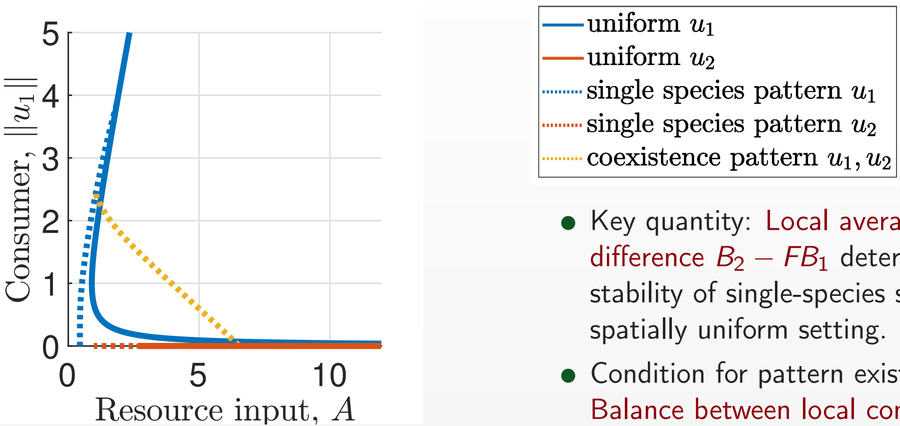


Essential spectrum in multispecies model

- 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.[2]
- Pattern onset occurs as the single-species pattern loses/gains stability to the introduction of a competitor.

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

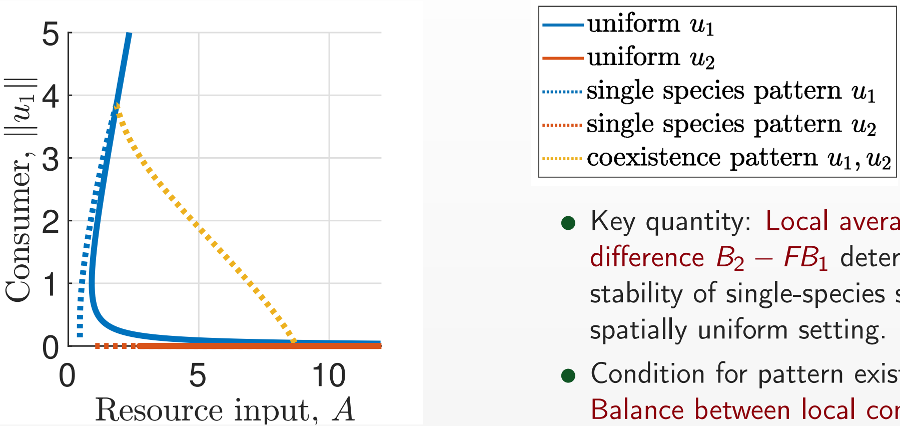
Pattern existence



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

- 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



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

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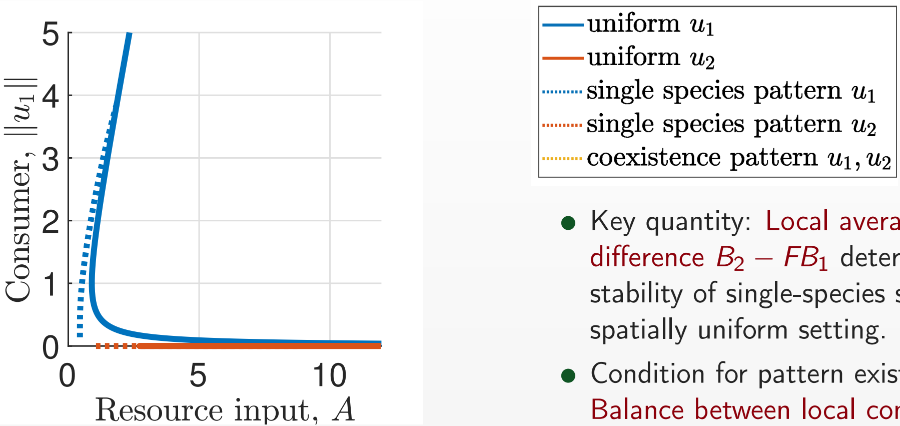
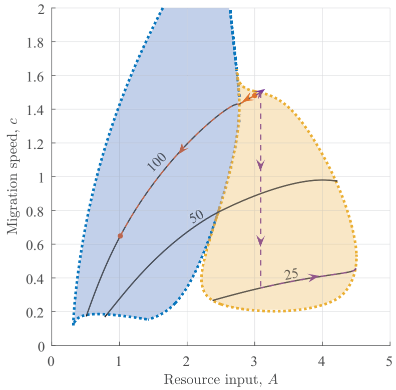
Pattern existence



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

- 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.

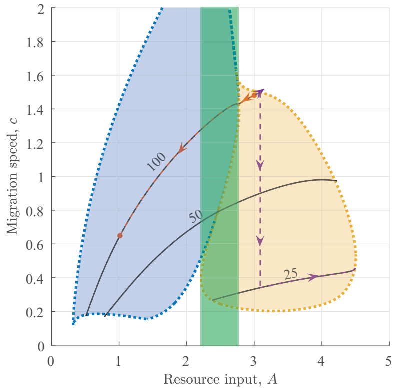
Pattern stability



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.

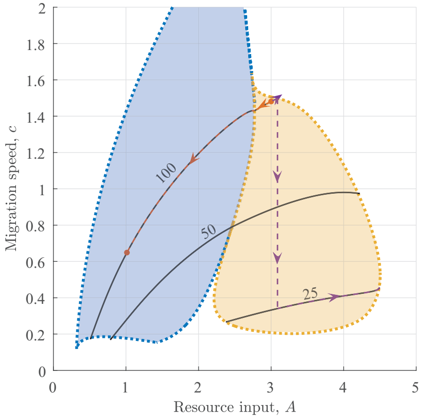
Pattern stability



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.

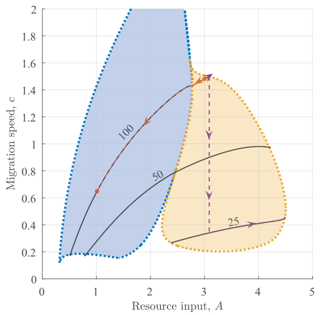
Hysteresis



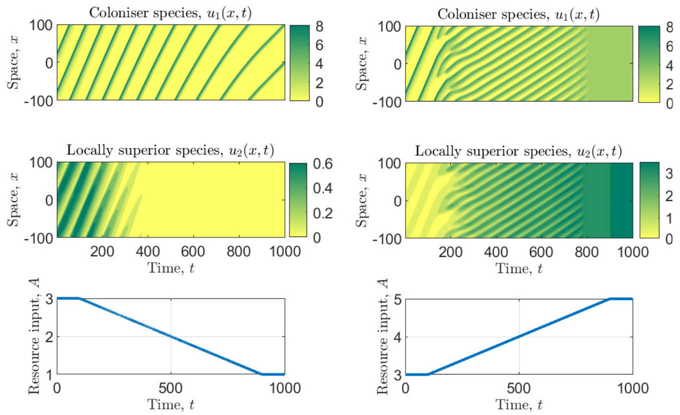
Wavelength contours of stable patterns

- 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

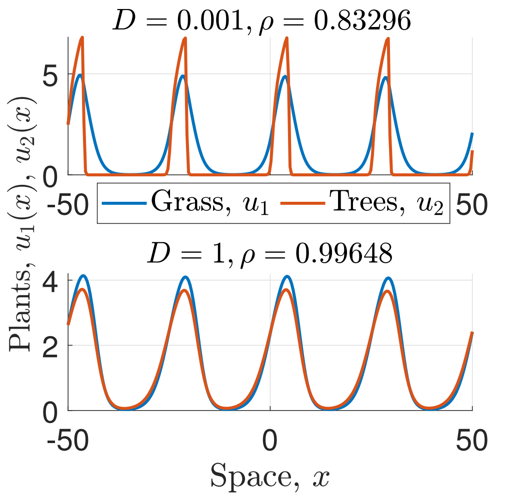


Migration speed, c
Resource input, A
100
50
25



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

Spatial species distribution



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

Conclusions

- Spatial self-organisation is a coexistence mechanism.
- 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[3].

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

Future Work

- How does nonlocal consumer dispersal affect species coexistence?[4]
- 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[5], intermittent[6] and probabilistic resource input regimes on both single-species and multispecies states?

[4] EL and Sherratt, J. A.: *J. Math. Biol.* 77.3 (2018).
[5] EL and Sherratt, J. A.: *J. Math. Biol.* 81 (2020).
[6] EL and Sherratt, J. A.: *Physica D* 405 (2020).

References

Slides are available on my website.
https://lukaseigentler.github.io

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