Species coexistence in resource-limited patterned ecosystems is facilitated by the interplay of spatial self-organisation and intraspecific competition

Virtual Asilomar 2021 - 11/01/2021

Lukas Eigentler - leigentler001@dundee.ac.uk

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

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?
- Classical result: intraspecific competition.
- More recent: spatial self-organisation (i.e. local facilitation)
- What is the impact of these two contrasting processes on coexistence?

Vegetation pattern & mussel beds.

Ribbon forest

Multispecies Model

Multispecies model based on the extended Klausmeier model[1].

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

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

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

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.

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

Multispecies Model

Intraspecific competition (other than that for the resource) may be considered.

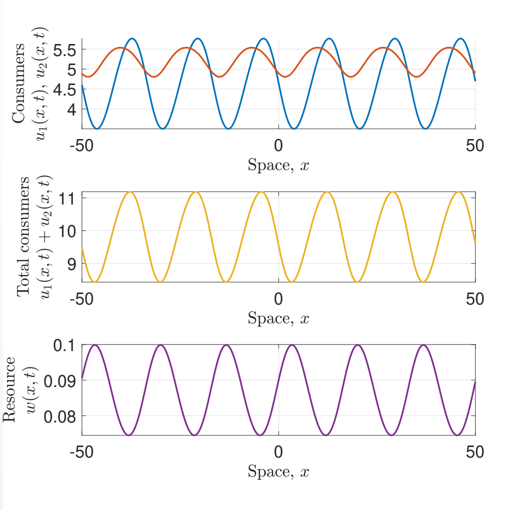
$$\frac{\partial u_1}{\partial t} = \underbrace{w u_1 \left(u_1 + H u_2\right) \left(1 - \frac{u_1}{k_1}\right)}_{\text{consumer growth}} - \underbrace{B_1 u_1} + \underbrace{\frac{\partial^2 u_1}{\partial x^2}},$$

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

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

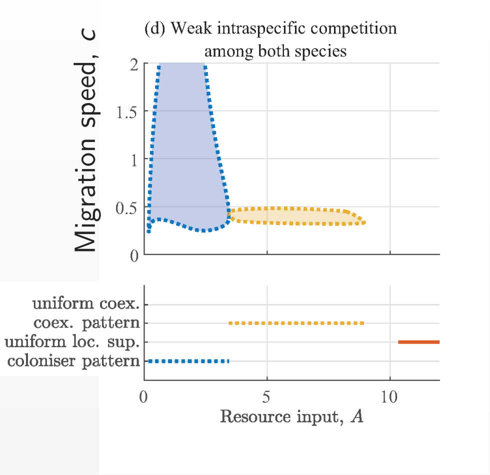
Species only differ quantitatively (i.e. in parameter values) but not qualitatively (i.e. same functional responses). Assume u_1 is superior coloniser; u_2 is locally superior.

Simulations



- In the absence of intraspecific competition, coexistence coexistence is captured, but not under high environmental stress.
- Coexistence requires a balance between local average fitness and their colonisation abilities.
- Patterns move in the direction opposite to the unidirectional resource flux.

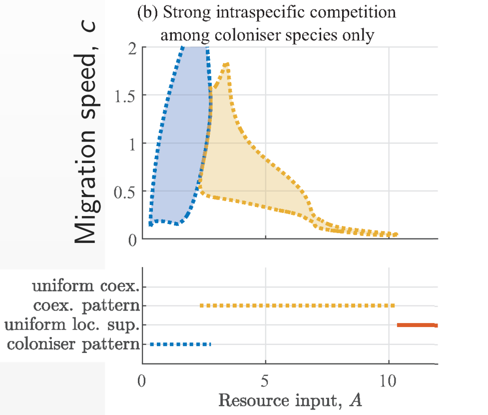
Pattern stability



Stability regions of system states.

- For decreasing resource input, coexistence state loses stability to single-species pattern of coloniser species.
- Transition occurs at moderate environmental stress ⇒ no coexistence in the sense of a patterned ecosystem.

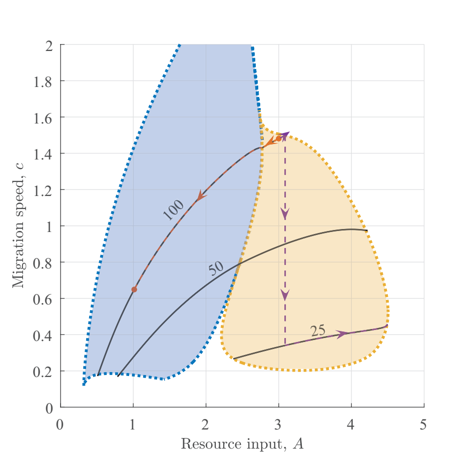
Effects of intraspecific competition



Stability regions of system states.

- Intraspecific competition among colonisers stabilise coexistence in patterned 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.

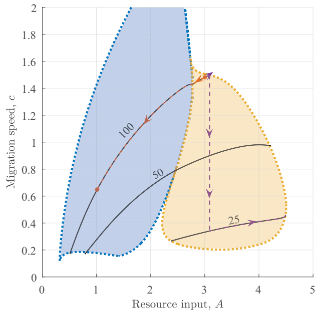
Hysteresis

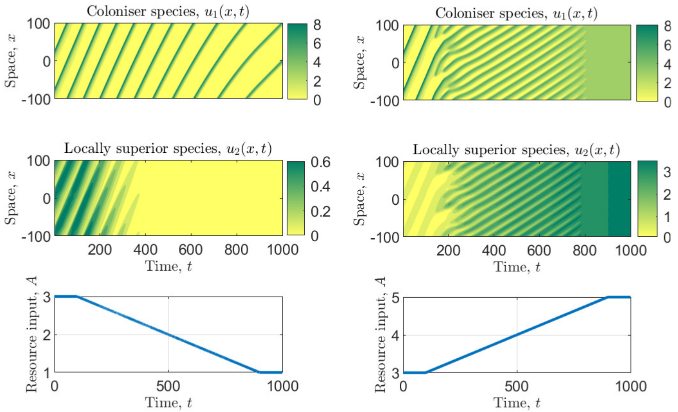


Wavelength contours of stable patterns

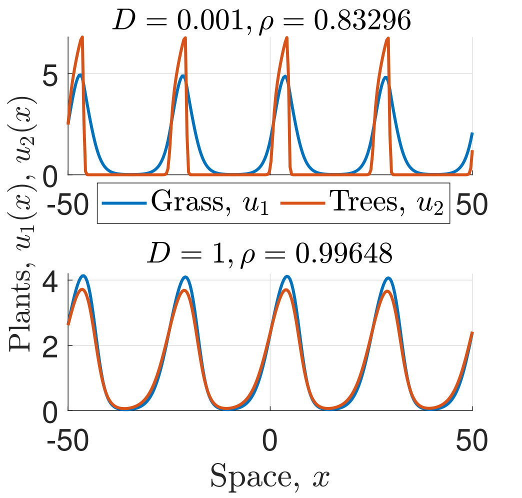
- State transitions are affected by hysteresis.
- Extinction can occur despite a coexistence state being stable.
- Ecosystem resilience depends on both current and past states of the system.

Hysteresis


Migration speed, c
Resource input, A
100
50
25
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8 2
0 1 2 3 4 5


Coloniser species, $u_1(x,t)$
Locally superior species, $u_2(x,t)$
Space, x
Time, t
Resource input, A
100
0
-100
200 400 600 800 1000
0 500 1000

Effects of intraspecific competition



- 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

- The basic phenomenological reaction-advection-diffusion system captures species coexistence as
  (i) a stable patterned solution representing a continuously colonised state.
  (ii) a stable patterned state if intraspecific competition among the superior coloniser is sufficiently strong.
  (iii) a metastable state if the average fitness difference between species is small[2].
- Coexistence is enabled by spatial heterogeneities in the resource, caused by the consumers' self-organisation into patterns.
- Intraspecific competition stabilises coexistence under severe environmental stress.

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

Future Work

- How does nonlocal consumer dispersal affect species coexistence?[3]
- 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[4], intermittent[5] and probabilistic resource input regimes on both single-species and multispecies states?

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

References

Slides are available on my website.

https://lukaseigentler.github.io

- Eigentler, L.: ‘Intraspecific competition in models for vegetation patterns: decrease in resilience to aridity and facilitation of species coexistence’. *Ecol. Complexity* 42 (2020), p. 100835.
- Eigentler, L.: ‘Species coexistence in resource-limited patterned ecosystems is facilitated by the interplay of spatial self-organisation and intraspecific competition’. *bioRxiv preprint* (2020).
- 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.
- Eigentler, L. and Sherratt, J. A.: ‘Spatial self-organisation enables species coexistence in a model for savanna ecosystems’. *J. Theor. Biol.* 487 (2020), p. 110122.