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Spatial self-organisation enables species coexistence in a model for savanna ecosystems

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Introduction

The savanna biome is characterised by a continuous vegetation cover, comprised of herbaceous and woody plants. The coexistence of species in arid savannas, where water availability is the main limiting resource for plant growth, provides an apparent contradiction to the classical principle of competitive exclusion. Previous theoretical work on species coexistence in savannas has focussed on nonspatial models and has been based on strong assumptions on the differences between species (e.g. different functional responses to fires).

Fig. 1: Arid savanna in Australia (source: Wikimedia commons).

Here, we investigate the effects of a spatial self-organisation principle, induced by a positive feeback between local vegetation growth and water redistribution towards patches of dense biomass, on coexistence of herbaceous and woody species in savannas. To solely focus on the effects of the spatial dynamics, species are assumed to only differ in their basic parameters (e.g. growth rate), but not in any of their functional responses.

The model

We propose a reaction-advection-diffusion model to describe the ecohydrological dynamics of a savanna ecosystem. Suitably nondimensionalised, the model is

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

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

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

Main assumptions of the model:

- $x \in \mathbb{R}$ increases in the uphill direction if the terrain is assumed to be sloped.
- Vegetation-infiltration feedback loop: Plants increase water infiltration into the soil $\Rightarrow$ Water consumption $=$ water density (w) $\times$ total plant density $(u_1 + u_2)$ $\times$ soil's infiltration capacity $(u_1 + Hu_2)$.
- u_1 is a herbaceous (grass) species and assumed to be superior in its colonisation abilities $(D < 1,\ F < 1)$.
- u_2 is a woody (tree, shrub) species and assumed to be locally superior, i.e. of higher local average fitness $(B_2 - FB_1 < 0)$ - The condition for this is determined by linear stability analysis in a spatially uniform setting.

Parameter	Description
A	Rainfall
B_i	Plant mortality
F	Ratio of water to biomass conversion rates $(u_2 : u_1)$
H	Ratio of soil modification effects $(u_2 : u_1)$
D	Ratio of diffusion rates $(u_2 : u_1)$
ν	Speed of water flow downhill
d	Ratio of diffusion rates $(w : u_1)$

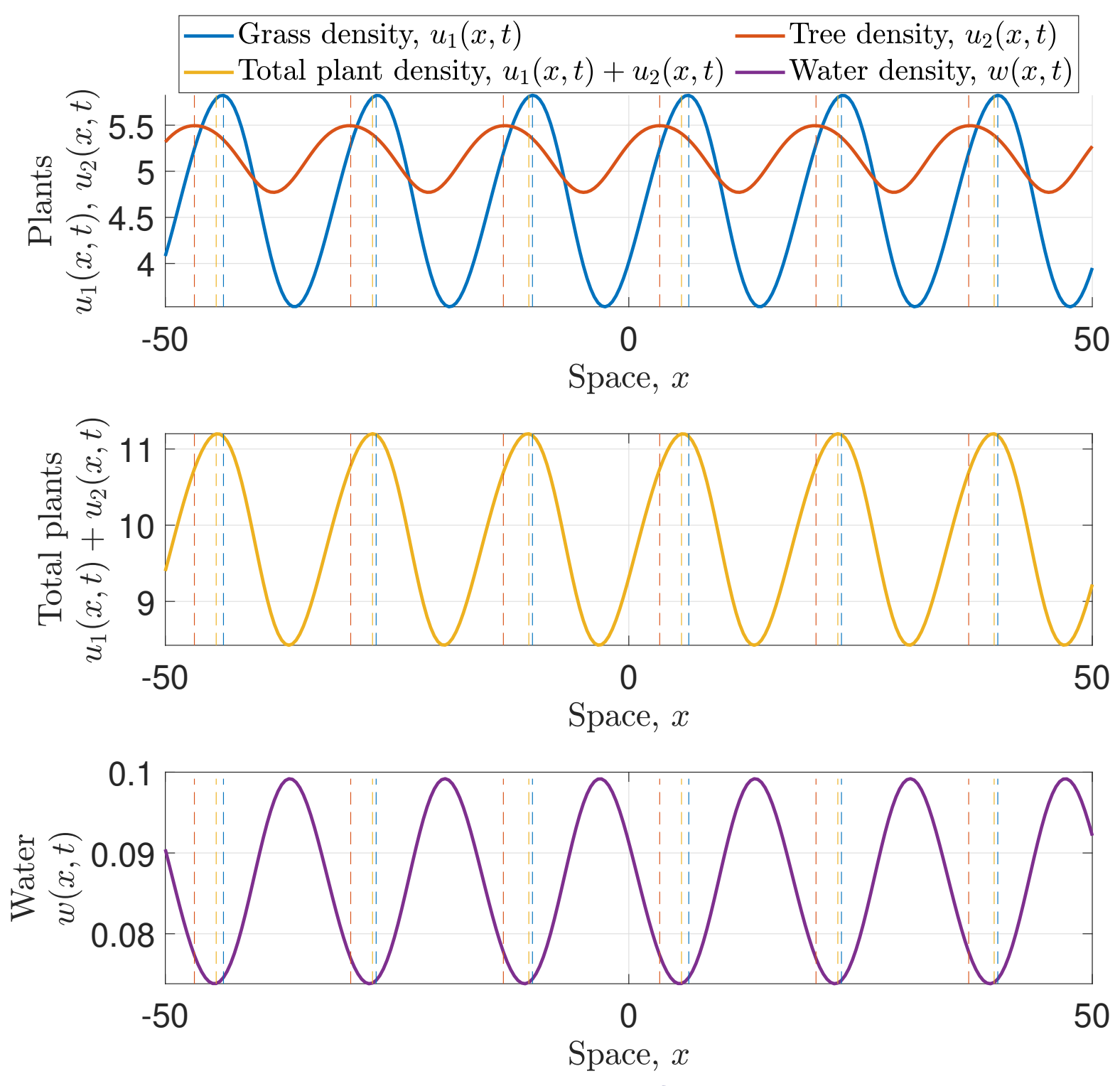

Fig. 2: Numerical solution of the multispecies model showing species coexistence in a savanna state.

Simulation results

- Patterned solutions are periodic travelling waves, i.e. periodic in space and move in the uphill direction of the domain at a constant speed c.
- Single-species solutions represent a vegetation pattern, i.e. oscillations between a high level of biomass and zero.
- Coexistence solutions represent a savanna biome; plant densities oscillate between two nonzero levels with low relative amplitude (Fig. 2).

References

[1] L. Eigentler and J.A. Sherratt. Metastability as a coexistence mechanism in a model for dryland vegetation patterns. *Bull. Math. Biol.*, 81(7):2290–2322, 2019.

[2] L. Eigentler and J.A. Sherratt. Spatial self-organisation enables species coexistence in a model for savanna ecosystems. *J. Theor. Biol.*, 487:110122, 2020.

Pattern onset

- Branches of coexistence patterns connect both single-species pattern branches (Fig. 4).
- Onset of coexistence patterns occurs as a single-species pattern loses/gains stability to the introduction of a second species.
- Stability of single-species patterns is investigated through a comparison of their essential spectra (calculated using a numerical continuation method) in the multispecies model and the corresponding single-species model (Fig. 3).
- Spectra in the multispecies model include additional elements that correspond to the introduction of a second species.

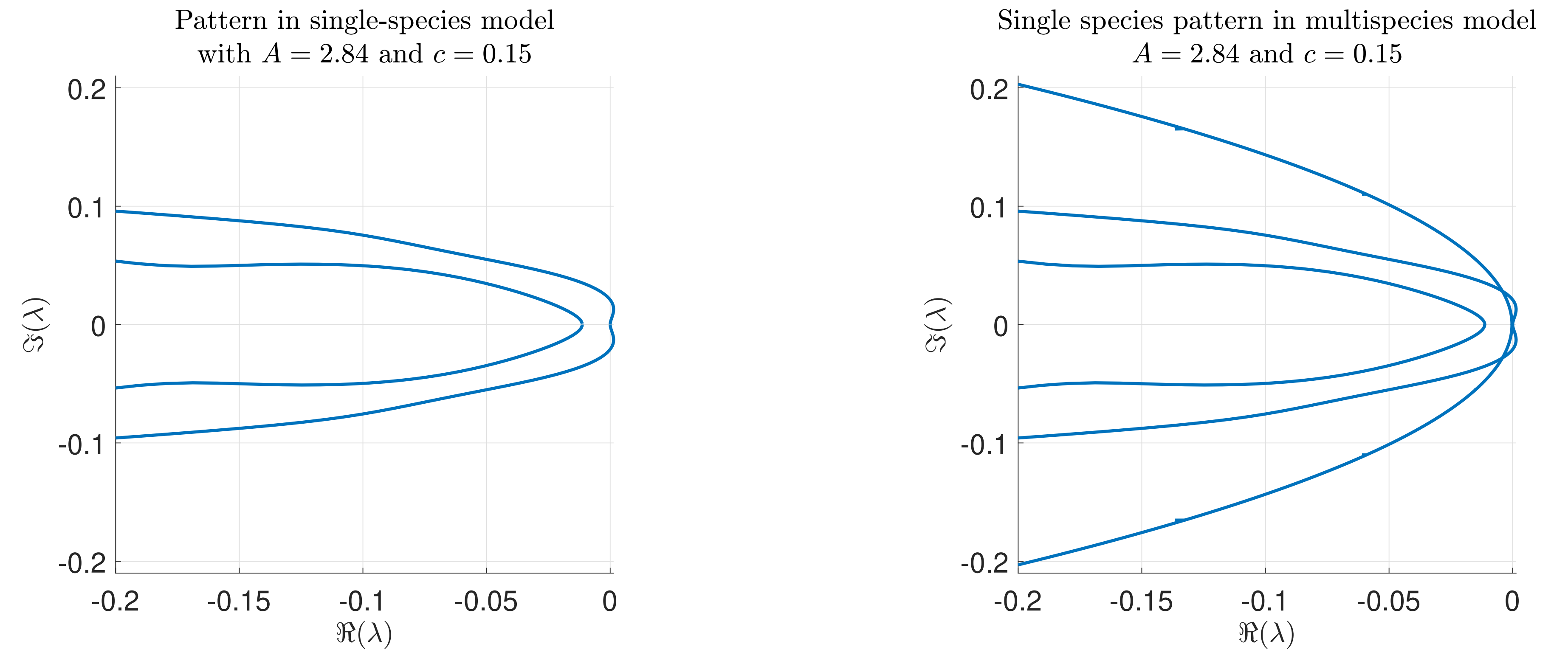

Fig. 3: Spectra of single-species patterns. The visualisations compare the spectrum of a patterned solution in the single-species Klausmeier model to that of the identical periodic travelling wave in the multispecies model. The latter contains additional components corresponding to perturbations in the plant density absent in the single species pattern.

Pattern existence

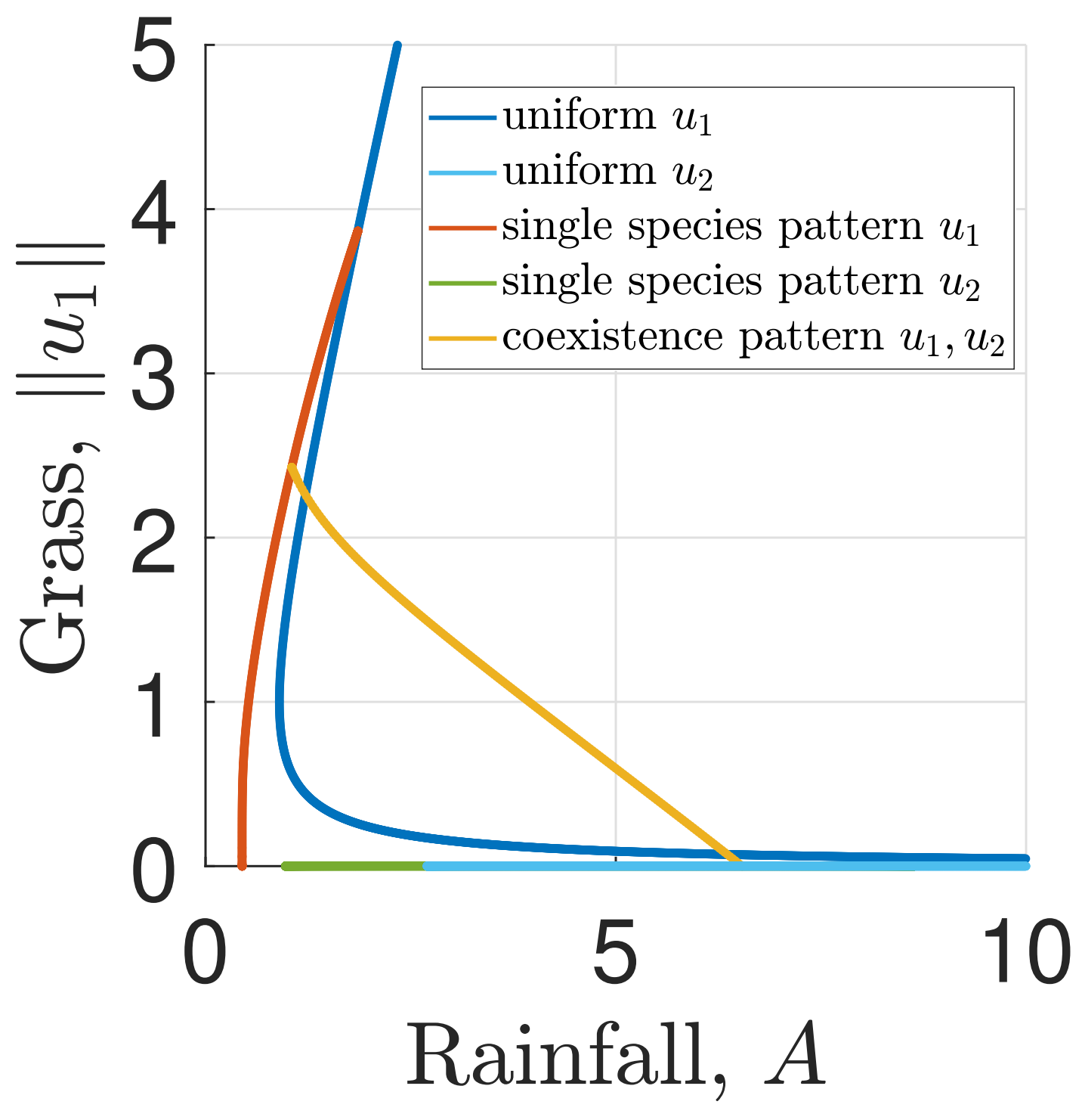

Fig. 4: A typical bifurcation diagram (for species u_1 only) is shown. Multiple branches of patterned solutions exist, but only those for one fixed wavespeed are shown.

- Single-species patterns originate at a Hopf-bifurcation on the corresponding spatially uniform equilibrium and terminate at a homoclinic orbit.
- Coexistence patterns connect both single-species pattern branches and bifurcations occur where the single-species solutions undergo a stability change due to the introduction of the competitor species.
- Pattern existence requires the locally inferior species to be superior in its colonisation abilities.

Pattern stability

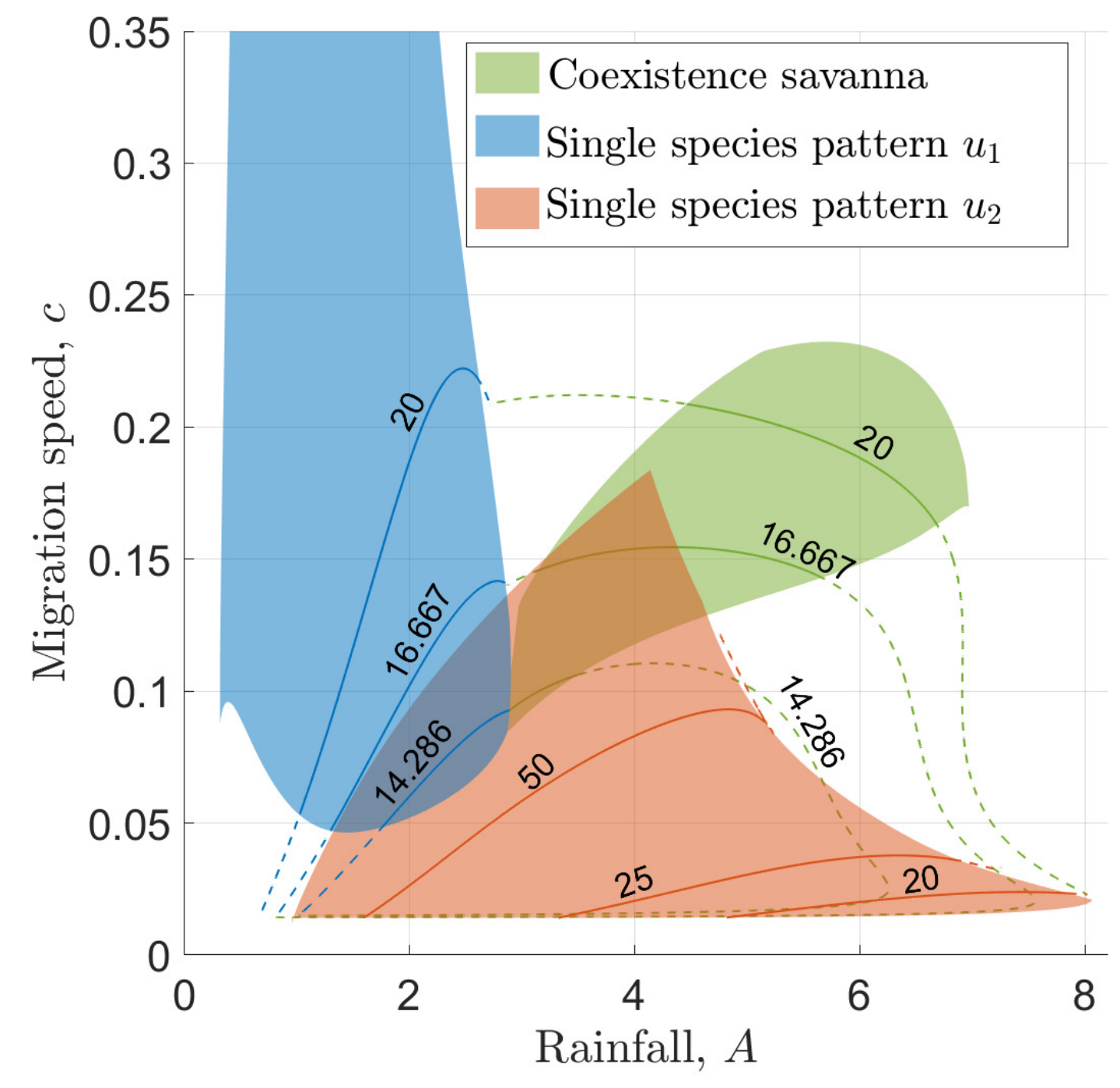

Fig. 5: Busse balloons of all pattern types in the system and wavelength contours. Solid (dashed) lines show wavelength contours of stable (unstable) patterns of each state.

- Busse balloons (parameter regions of stable patterns) are computed through tracking of stability boundaries based on features of the patterns' essential spectra.
- Coexistence patterns' properties (e.g. wavelength) are determined by the superior coloniser.
- Stability regions overlap. This points towards ecosystem engineering.

Conclusions

- Species coexistence in savannas is enabled by a self-organisation principle, induced by a positive feedback between local vegetation growth and water redistribution towards areas of high biomass.
- A balance between species' local competitiveness and their colonisation abilities stabilises coexistence.
- The superior coloniser can utilise spatial heterogenieties in resource availability, caused by spatial self-organisation, to quickly colonise bare soil, before being locally outcompeted by the locally superior species.
- Results on pattern stability suggest that grasses act as ecosystem engineers. Trees can exist in a continuous coexistence state (savanna) for parameters for which they can only occur in a spatially intermittent state (vegetation pattern) in the absence of a competitor species.
- Coexistence states representing vegetation patterns (alternating patches of biomass and bare soil) are not stable but occur as long transient states [1].

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