Metastability as a coexistence mechanism in a model for dryland vegetation patterns

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Introduction

Vegetation patterns are a ubiquitous feature of water-deprived ecosystems and are a prime example of a self-organising principle in ecology. One of the main mechanisms that creates such a mosaic of biomass and bare soil is a modification of soil properties by plants that induces a water redistribution feedback loop.

Fig. 1: Striped vegetation ("tiger bush") in Niger.

Most models in this context only consider a single plant species or combine several species into one single variable. However, vegetation patches often consist of a mix of herbaceous and woody species. Previous simulation-based studies of dryland ecosystem models were able to reproduce patterns in which two species coexist by considering a variety of different mechanisms that enable diversity in ecosystems, such as niche adaptation to different soil moisture levels or facilitative feedbacks between two species. However, the possible effects caused by differences in basic plant properties such as mortality rates and water to biomass conversion capabilities have not yet been addressed in this context.

The model

We propose a reaction-diffusion system for the water density w, a herbaceous species u_1 and a woody species u_2, which in nondimensional form is

$$\frac{\partial u_1}{\partial t} = \overbrace{wu_1\left(u_1+Hu_2\right)}^{\text{plant growth}} - \overbrace{B_1u_1}^{\substack{\text{plant}\\\text{mortality}}} - \overbrace{Su_1u_2}^{\substack{\text{interspecific}\\\text{competition}}} + \overbrace{\frac{\partial^2 u_1}{\partial x^2}}^{\text{plant dispersal}},$$

$$\frac{\partial u_2}{\partial t} = \overbrace{Fwu_2\left(u_1+Hu_2\right)}^{\text{plant growth}} - \overbrace{B_2u_2}^{\substack{\text{plant}\\\text{mortality}}} + \overbrace{D\frac{\partial^2 u_2}{\partial x^2}}^{\text{plant dispersal}},$$

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

Main assumptions of the model:

- Vegetation-infiltration feedback loop: Plants increase water infiltration into the soil ⇒ Water consumption = water density (w) × total plant density (u_1+u_2) × soil's infiltration capacity (u_1+Hu_2).
- Shading: Trees (u_2) impose an additional mortality effect on the grass (u_1).
- Plant mortality (excluding shading), water evaporation and rainfall occur at constant rates.

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 ($u_2:u_1$)
S	Shading intensity
D	Ratio of diffusion rates ($u_2:u_1$)
d	Ratio of diffusion rates ($w:u_1$)

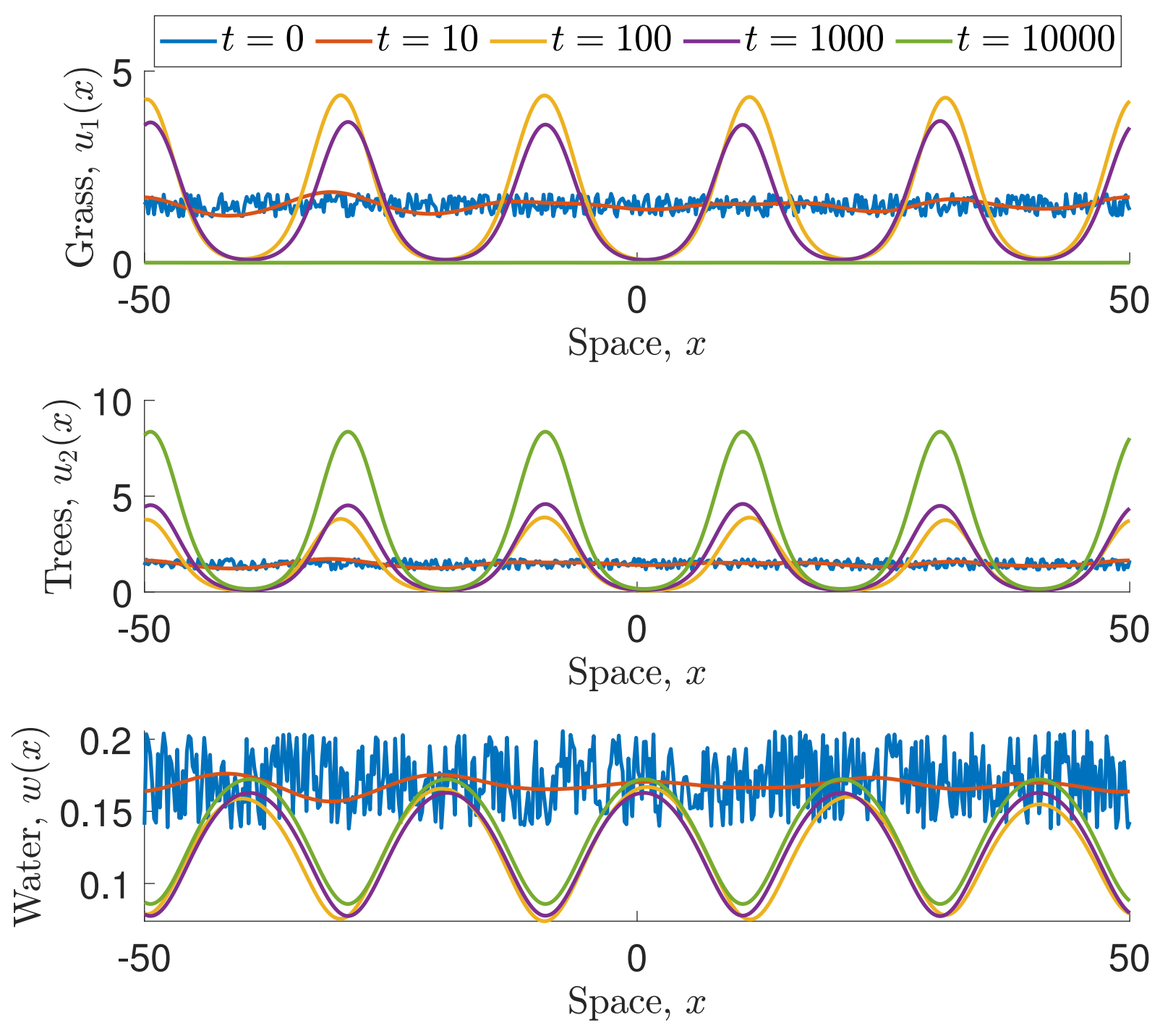


Fig. 2: Numerical solution of the multispecies model showing metastable patterns of species coexistence. Parameter values correspond to (α) in Fig. 3.

To define a measure of species difference we introduce the one parameter family

$$B_2 = B_1 - \chi(B_1-b_2), \quad F = 1-\chi(1-f), \quad H = 1-\chi(1-h),$$
$$S = s\chi, \quad D = 1-\chi(1-D_0),$$

where B_1 and b_2 are set to typical mortality rates of a herbaceous and tree species, respectively; s is set to a typical shading intensity imposed on grass by trees; f, h and D_0 are typical respective ratios between a grass species and a tree species; and $\chi \in [0,1]$ quantifies the difference between the species.

Simulation results

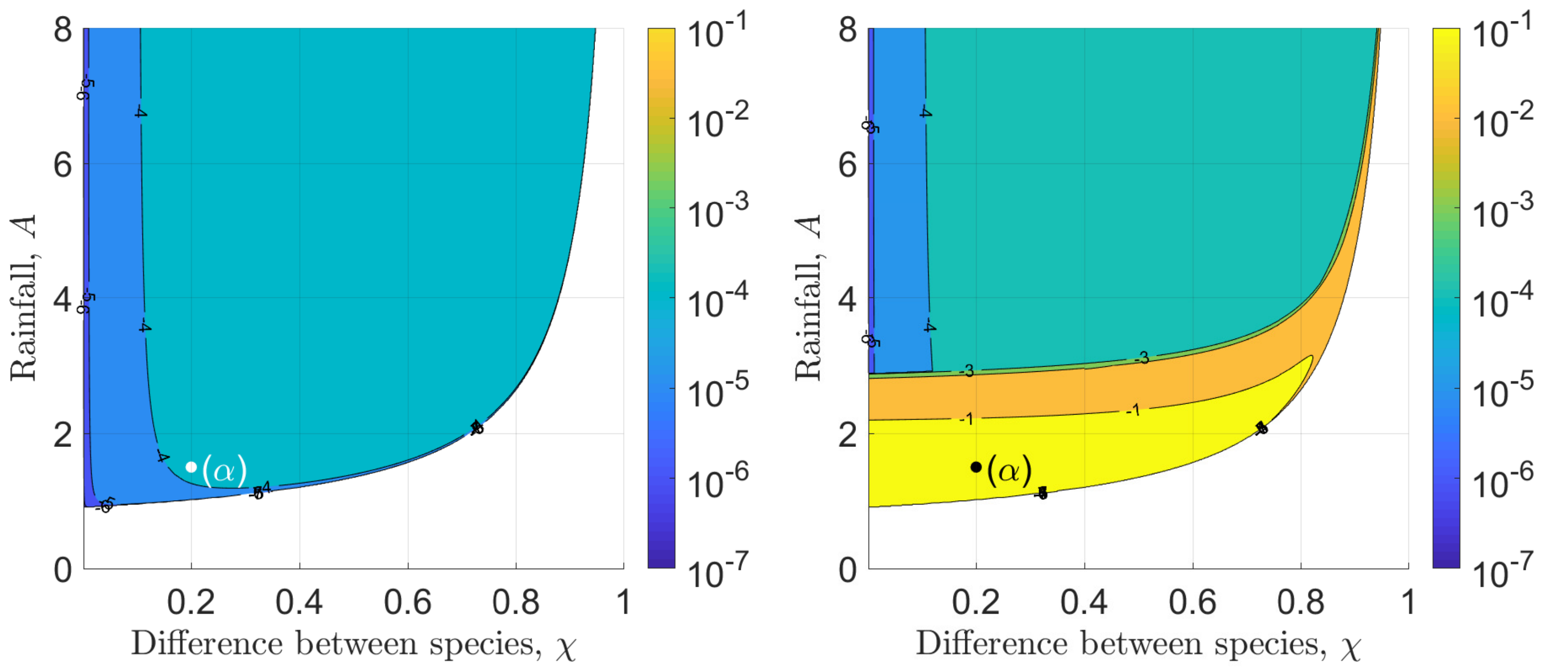
- Species coexistence occurs as a metastable state, i.e. a long transient (exceeding 1000 years) to a single species state (Fig. 2).
- For sufficiently low precipitation levels A, patterns form on a much shorter timescale (Fig. 2).

References

[1] Lukas Eigentler and Jonathan A. Sherratt. Metastability as a coexistence mechanism in a model for dryland vegetation patterns. *Bull. Math. Biol.*, in press.

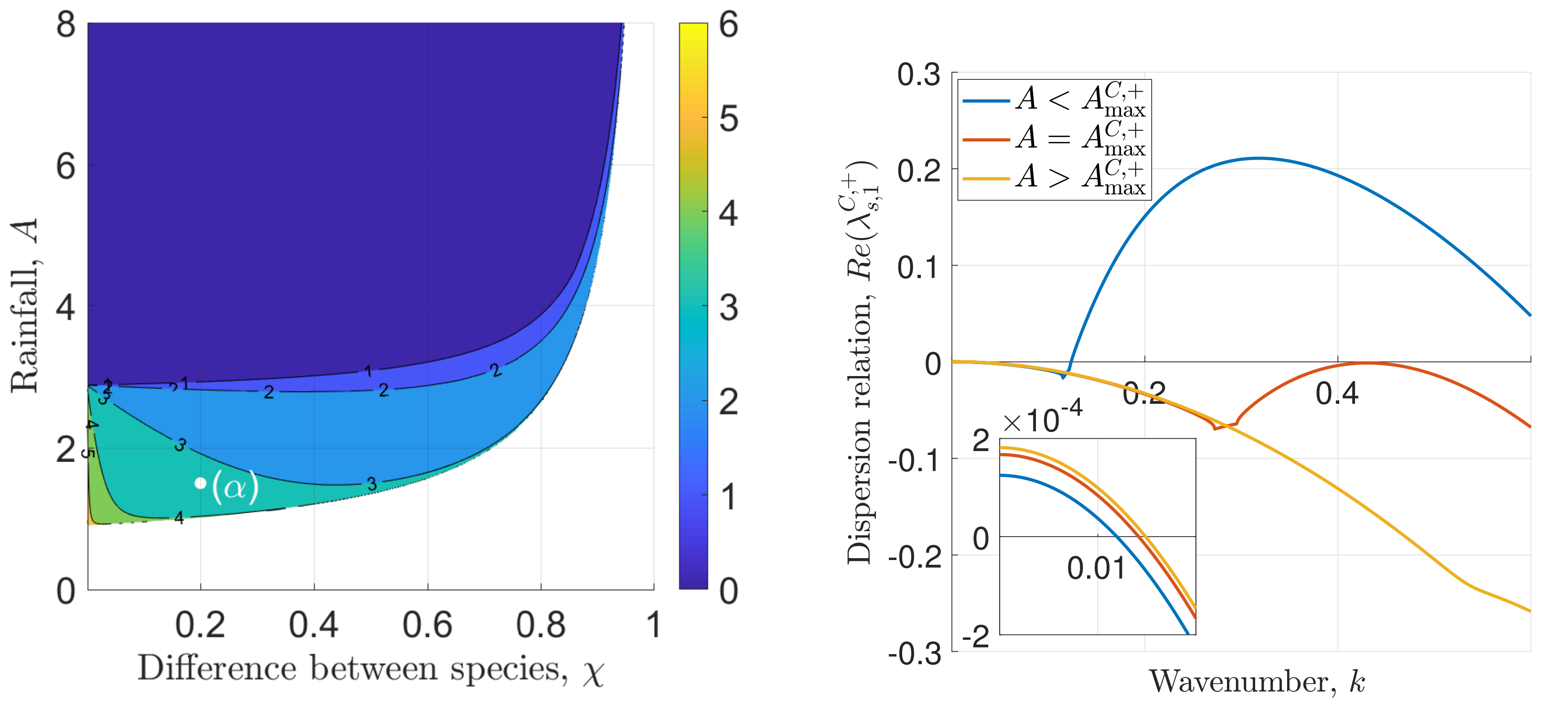
Metastable behaviour

- Metastability is characterised by the small size of the growth rate λ_u of spatially uniform perturbations to a coexistence equilibrium (Fig. 3a), obtained through a linear stability analysis. The growth rate satisfies
$$\mathrm{Re}\left(\lambda_u\right) = O(B_2 - B_1F).$$
The quantity B_2-B_1F is the average fitness difference between the species.
- The onset of a spatial pattern on a much shorter timescale under sufficiently low precipitation levels A occurs if
$$\max_{k>0}\left\{\lambda_s(k)\right\} \gg \mathrm{Re}\left(\lambda_u\right),$$
where $\lambda_s(k)$ is the growth rate of a spatially non-uniform perturbation with mode $k>0$ (Fig. 3b, 3c and 3d).
- Similar considerations hold in an invasion-type scenario. If a stable single-species state becomes unstable due to the introduction of a competitor, coexistence as a metastable state occurs if $|B_2-B_1F| \ll 1$, and is patterned if precipitation A is sufficiently low. This also holds if no direct interspecific competition ($S=0$) is present, while the existence of a coexistence equilibrium considered above requires $S \neq 0$.



(a) Growth rate of spatially uniform perturbations.

(b) Maximum growth rate of spatially heterogeneous perturbations.



(c) Order of magnitude difference between growth rates in (a), (b).

(d) Typical dispersion relations.

Fig. 3: Largest real part of eigenvalues determining stability of the coexistence steady state and examples of the dispersion relation. The (α) marker corresponds to the parameter values used in Fig. 2.

Conclusions

- Metastability enables coexistence of two plant species competing for the same limiting resource (water) in a dryland ecosystem as a transient state.
- Metastability occurs if plant species have a similar average fitness, here quantified by the ratio of a species' water to biomass conversion capabilities to its mortality rate. Thus coexistence can occur even if the species differ significantly (such as grass and trees).
- The understanding of transient states is of utmost importance as many ecosystems never reach an equilibrium state. Disturbances such as changes to grazing patterns or climate change interrupt the convergence to a steady state on a frequent basis, and thus keep systems in perpetual transients.
- A pattern's properties such as its wavelength can provide useful tools to predict the outcome of the transient behaviour. If, for example, the wavelength of a coexistence pattern differs from that of a single-species pattern, then the wavelength changes during the transient, providing an indication on the eventual fate of the pattern.
- The metastability property is not specific to the two species model. Numerical simulations of models accounting for plant communities with more than two plant types also show coexistence patterns as metastable transients provided the species' average fitness difference is small.

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