Effects of precipitation intermittency on semi-arid 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.

Dense plant patches increase the soil's water infiltration capacity and therefore act as sinks and deplete soil water in regions of bare ground. This redistribution of the limiting resource drives further growth in vegetation patches and thus closes the feedback loop.

Rainfall in semi-arid regions occurs intermittently, seasonally or as a combination of both. Under intermittent rainfall regimes only a small number of short-lasting precipitation events per year provide a sufficiently large amount of water to affect vegetation growing in these regions. If such rainfall events are sufficiently separated, they cause a pulse of biological processes (in particular plant growth) before processes associated with dry spells take over. Plants in semi-arid regions are sensitive to quantity, frequency and temporal spread of intermittent precipitation events.

The model

The Klausmeier model [2] is a frequently used model describing pattern formation in dryland ecosystems as its simplicity provides a rich framework for mathematical analysis. Based on this reaction-diffusion system we propose an impulsive model to account for the combination of mechanisms occurring continuously in time with pulse-type processes caused by rainfall events. After a suitable nondimensionalisation the model for the plant density u_n and water density w_n after $n \in \mathbb{N}$ rainfall pulses is

$$\begin{aligned}
\frac{\partial u_n}{\partial t} &= \overbrace{-Bu_n}^{\text{plant mortality}}, \\
\frac{\partial w_n}{\partial t} &= \overbrace{-w_n}^{\text{evaporation}} + \overbrace{d\frac{\partial^2 w_n}{\partial x^2}}^{\text{water diffusion}}, \\
u_{n+1}(x,0) &= \underbrace{u_n(x,T)}_{\text{existing plants}} + \underbrace{\phi(\cdot) * \left(\left(\frac{u_n(\cdot,T)}{1+u_n(\cdot,T)}\right)^2 (w_n(\cdot,T)+TA)\right)}_{\text{dispersal of new biomass}}, \qquad \text{(M)} \\
w_{n+1}(x,0) &= \underbrace{w_n(x,T)}_{\text{existing water density}} + \underbrace{TA}_{\text{rainfall}} - \underbrace{\left(\frac{u_n(x,T)}{1+u_n(x,T)}\right)^2 (w_n(x,T)+TA)}_{\text{water uptake by plants}},
\end{aligned}$$

in an infinite space domain $x \in \mathbb{R}$. The model is split into two stages:

- Time-continuous processes (plant loss, water evaporation, water diffusion) modelled by PDEs for $nT < t < (n+1)T$.
- Pulse-type processes (rainfall, water uptake, plant growth, dispersal of new biomass) occurring at $t = nT$ described by integrodifference equations.

Parameter	A	B	d	T
Description	Annual rainfall	Plant loss rate	Water diffusion rate	Interpulse time
Estimates	0-15	0.45	500	0-4

Main assumptions:

- All rainfall events are of the same intensity and occur periodically in time with period T.
- A denotes the total amount of rainfall over a fixed period of time; TA the amount of rainfall per rain pulse.
- Plant growth and dispersal are synchronised with rainfall pulses.
- Plant (seed) dispersal is described by a nonlocal process with dispersal kernel ϕ.

Equilibria of (M) are time-periodic solutions with period T. A non-trivial equilibrium $(\overline{u}, \overline{w})$ in which the plant density is non-zero exists provided precipitation is sufficiently high, i.e. $A > A_{\min}$.

Choice of dispersal kernel

The Laplace kernel

$$\phi(x) = \frac{a}{2}e^{-a|x|}, \quad a > 0, x \in \mathbb{R}. \qquad \text{(L)}$$

provides a significant simplification due to the algebraically simple form of its Fourier transform and thus facilitates an analytical study of pattern existence in (M).

References

[1] Eigentler, L, et al. *J Math Biol* 77(3):739 2018

[2] Klausmeier, CA *Science* 284(5421):1826 1999

Results on pattern existence

In the Klausmeier reaction-diffusion model, on which our impulsive model is based, a sufficiently large ratio of water diffusion rate to plant diffusion rate yields a pattern-forming instability for any precipitation level (diffusion-driven instability). Linear stability analysis of the impulsive model (M) with dispersal kernel (L) about $(\overline{u}, \overline{w})$ yields a different behaviour (Fig. 2).

- In general, no diffusion-driven instability occurs.
- Exceeding a diffusion threshold is necessary but not sufficient for pattern existence.
- If $d \to \infty$, there exists $A_{\max}(T) < \infty$ such that patterns exist for $A_{\min} < A < A_{\max}$.

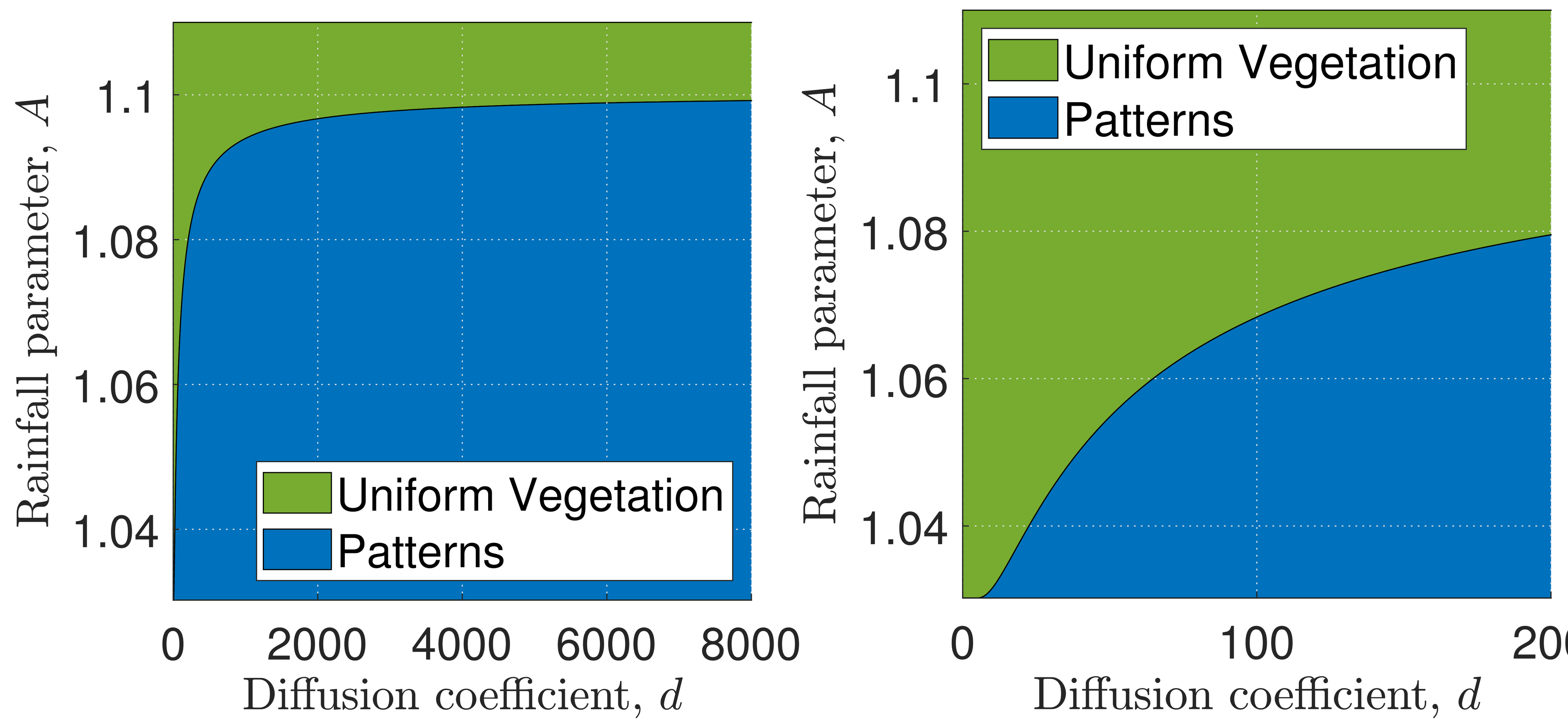

Fig. 2: Pattern existence in the A-d parameter plane for $T = 0.5$ and $B = 0.45$, with ϕ being the Laplacian kernel.

The T dependence of $A_{\max}$ suggests a closer investigation of effects caused by changes to the interpulse time T on the existence of patterns. In the limiting case $d \to \infty$, the threshold $A_{\max}$ can be derived and the T-A parameter plane is split into three regions (Fig. 3); a region supporting no plants, a region of pattern existence and a region in which uniform vegetation is stable. This yields

- Both $A_{\min}$ and $A_{\max}$ increase with the interpulse time T.
- The relative size $\varepsilon_{\max}$ of the interval $[A_{\min}, A_{\max}]$ decreases with the length of drought periods T and is proportional to e^{-2T} as $T \to \infty$.
- Maximum biomass occurs at intermediate interpulse time T.

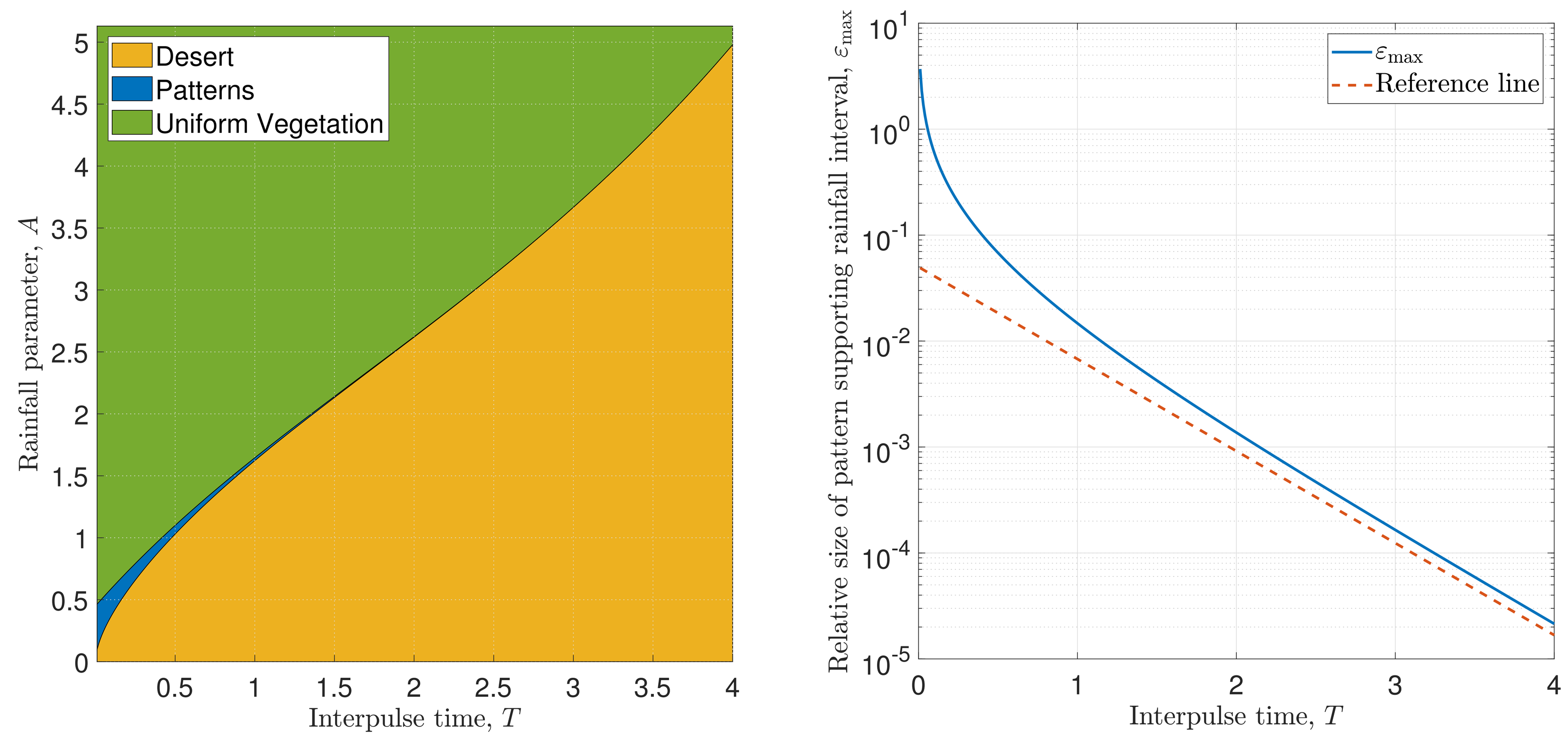

Fig. 3: Classification of the A-T parameter plane and the relative size of the rainfall interval supporting pattern formation as $d \to \infty$ with a reference line of slope -2.

Conclusions

Our model analysis investigates effects of rainfall intermittency on pattern existence in dryland ecosystems.

- It is essential to consider a model such as (M) that captures the combination of processes occurring continuously in time with pulse-type events. A purely discrete integrodifference model cannot provide any information on effects caused by variations in the interpulse time.
- Longer interpulse times reduce the tendency to form patterns as high-intensity rain events weaken the pattern-inducing vegetation-infiltration feedback.
- Diffusion alone cannot cause pattern formation as long drought periods yield low water densities and cause the homogenising effect of diffusion to be negligible.
- A more realistic description of rainfall pulses would be a Poisson process with exponentially distributed intensities. The period T and precipitation A used in (M) can be seen as the respective expected values of such a process.
- Investigation of pattern existence for other kernel functions relies on numerical simulations. We find that longer dispersal distances inhibit pattern formation (in agreement with a previous study [1]) but effects caused by variations in the kernel functions are small compared to those caused by changes in the interpulse time.

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