Research Statement

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Please note that in the interest of brevity, I only refer to my own papers and omit any other references.

1 Motivation & background

Vegetation patterns are a ubiquitous feature of dryland ecosystems, occurring on all continents except Antarctica. Such mosaics of alternating patches of biomass and bare soil develop as a consequence of a self-organisation principle induced by a positive feedback between local vegetation growth and water redistribution to areas of high biomass.

A detailed understanding of the dynamics of vegetation patterns is of considerable socio-economic importance as they hold valuable information on the health of ecosystems. In particular, changes to a pattern's properties may act as an early warning signal of desertification, a major threat to economies of countries in arid regions.

Data acquisition for vegetation patterns is notoriously difficult due to the spatial and temporal scales associated with the ecosystem dynamics. In particular, their recreation in laboratory settings is infeasible. Thus, a powerful tool to overcome these challenges is the use of mathematical models. The theoretical study of dryland ecosystems, in particular continuum approaches utilising PDEs, has thrived over the last two decades.

In the following, I outline several topics that I have addressed in my research to contribute to the development of a better understanding of the complex ecosystem dynamics in semi-arid environments. All work is based on the Klausmeier model, a reaction-advection-diffusion system describing the ecohydrological dynamics of drylands.

2 Nonlocal seed dispersal

For mathematical simplicity, plant dispersal is modelled by diffusion in many theoretical models. In [6], I replace plant diffusion by a convolution term to account for nonlocal effects, backed up by empirical data. An asymptotic analysis of the model is possible, due to a scale difference between plant dispersal and water transport. Using a specific dispersal kernel, a condition for pattern onset can be found analytically, valid to leading order in a large parameter describing water flow downhill on sloped terrain. Assuming an evolutionary trade-off between dispersal distance and dispersal rate, a convergence result allows for a comparison to results for the model with local plant diffusion. Finally, numerical schemes can be utilised to show that results remain qualitatively unaffected by the choice of kernel function.

The main finding is that both longer dispersal distances and faster dispersal rates inhibit the onset of spatial patterns by stabilising a spatially uniform vegetated state for lower precipitation volumes. Auxiliary results include information on the patterns' properties, such as wavelength or migration speed in the uphill direction, close to onset. Some limited empirical data exists for both pattern wavelength and uphill migration, and thus theoretical results may provide useful complements to future empirical studies.

3 Species coexistence

Herbaceous and woody species generally coexist in dryland ecosystems (both in patterned vegetation and arid savannas), despite their competition for the same limiting resource. This presents an apparent mismatch to the principle of competitive exclusion, which can be addressed through the use of mathematical models. In my work, I present several multispecies models to propose potential mechanisms that can enable species coexistence in both savannas [1] and vegetation patterns [2, 5].

In the context of arid savannas, model solutions are still characterised by spatial patterns, but in stark contrast to solutions representing a vegetation pattern, they oscillate between two nonzero biomass densities [1]. As a consequence, tools and methods from pattern formation theory can also be applied to solutions representing a savanna biome. I utilise this by applying numerical continuation techniques using AUTO-07p to investigate the onset, existence and stability of coexistence states in a mathematical model. Coexistence is facilitated by spatial heterogeneities in the environmental conditions (water density), induced by the positive feedback between local plant growth and water redistribution. A crucial condition for the occurrence of coexistence states is a balance between the species' local competitive abilities and their dispersal behaviours. In other words, species coexistence between two species requires the superior local competitor to be inferior in its colonisation abilities. Ecologically, my results may be of crucial importance to better understand species interactions in resource-limited ecosystems, as a comparison with results of the corresponding one-species models suggest that the coloniser species facilitates the superior local competitor under precipitation volumes that would not allow the latter to exist on its own. This is an example of ecosystem engineering, a modification of environmental conditions by one species that facilitates the growth of a competitor species.

For lower precipitation volumes, the same model captures coexistence solutions that represent patterned vegetation (i.e. the oscillation of biomass between a vegetated and a bare soil state). In contrast to the savanna-type solutions discussed above, these patterns are not stable solutions. Instead, coexistence patterns occur as long transient states. In [5], I derive that such metastable states are characterised by small growth rates of spatially uniform perturbations to equilibria and occur if the average fitness difference between two species is small. The formation of spatial patterns on a much shorter timescale occurs due to the existence of a spatial mode for which growth rates of perturbations are much larger. These results emphasise an important issue often ignored in the analysis of mathematical models, but regarded as highly important by ecologists. In many ecosystems, it may be insufficient to only consider equilibrium dynamics. Instead, the understanding of transient states is of utmost importance as many ecosystems never reach an equilibrium state due to frequent disturbances, such as changes in environmental conditions.

On the other hand, coexistence patterns occur as a stable model solution if intraspecific competition is considered. In [2], I show that both patterned and spatially uniform stable species coexistence occur if intraspecific competition is stronger than the interspecific competition for water. In particular, the strength of the intraspecific competition of the coloniser species is singled out as a significant factor, as it keeps the superior coloniser at sufficiently low densities which can be invaded by a competitor. Moreover, this approach allows for a statistical analysis of the spatial distribution of both species under changes to the system's parameters, based on the numerical continuation of model solutions. This provides more insight into the dynamics between the coloniser species and its competitor, and may become a valuable testable hypothesis in case data acquisition techniques (e.g. image processing) improve in the future.

4 Rainfall intermittency and seasonality

Most continuum approaches of modelling vegetation patterns are based on PDEs and thus assume that rainfall occurs continuously and uniformly in time. In reality, however, precipitation in drylands is seasonal, intermittent or a combination thereof. The temporal non-uniformity in precipitation regimes also has significant effects on other biological processes. For example, seed dispersal typically occurs in the latter stages of the dry season or is synchronised with a rainfall event, while plant growth processes predominantly occur during and shortly after precipitation occurrences. Experiments with small numbers of individual plants show that such rainfall regimes have a significant impacts on the plants, but its effects on an ecosystem-wide scale have not been addressed in detail using theoretical models before.

In [3], I describe seasonality of precipitation (with no intermittency during the wet season) and seed dispersal using a discrete integrodifference system to show that such an approach is insufficient to capture effects of nonuniformity in precipitation on vegetation patterns. Motivated by this, I investigate the effects of rainfall intermittency, by proposing a model of impulsive differential equations in [4]. The idea of using such a hybrid model is to combine processes occurring continuously in time (e.g. plant mortality, water transpiration) with pulse-type processes triggered by high-intensity precipitation events (e.g. plant growth, seed dispersal). The focus lies on a derivation of conditions for pattern onset, which can be found analytically under strict assumptions on the plant dispersal kernel and functional responses in the system. The effects of those assumptions can be further investigated using numerical simulations. The main finding is that a detailed knowledge about a plant species' response to low soil moisture levels is key in understanding the effects of intermittent precipitation on the ecohydrological dynamics. If plant growth is only triggered under sufficiently high water levels, a low frequency of high-intensity rainfall events inhibits pattern onset compared to a more frequent addition of water under the same total annual precipitation volume.

References

[1] L. Eigentler and J. Sherratt. "Spatial self-organisation enables species coexistence in a model for savanna ecosystems". *J. Theor. Biol.* 487 (2020), p. 110122. DOI: `10.1016/j.jtbi.2019.110122`.

[2] L. Eigentler. "Intraspecific competition can generate species coexistence in a model for dryland vegetation patterns". *bioRxiv preprint* (2020). DOI: `10.1101/2020.01.13.903179`.

[3] L. Eigentler and J. A. Sherratt. "An integrodifference model for vegetation patterns in semi-arid environments with seasonality" (2019). arXiv: `1911.10964 [q-bio.PE]`.

[4] L. Eigentler and J. A. Sherratt. "Effects of precipitation intermittency on vegetation patterns in semi-arid landscapes" (2019). arXiv: `1911.10878 [q-bio.PE]`.

[5] L. Eigentler and J. A. Sherratt. "Metastability as a coexistence mechanism in a model for dryland vegetation patterns". *Bull. Math. Biol.* 81.7 (2019), pp. 2290–2322. DOI: `10.1007/s11538-019-00606-z`.

[6] L. Eigentler and J. A. Sherratt. "Analysis of a model for banded vegetation patterns in semi-arid environments with nonlocal dispersal". *J. Math. Biol.* 77.3 (2018), pp. 739–763. DOI: `10.1007/s00285-018-1233-y`.