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Geometry of vegetation patterns: understanding patterns in dryland ecosystems and beyond

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Outlook

At first glance, Chapter 2 and Chapter 3 do not appear connected in a cohesive way, but together they certainly endeavor to lay the foundations of understanding the mathematical mechanisms driving the formation and nonlinear evolution of ecosystems and the observations thereof. While achieving this, they consolidate the universality of distinct features that bridge the gap between mathematics and ecology.

This thesis constitutes a constant interplay and wavering between two parallel, yet complementary worlds: a fundamental and a realistic one. Both Chapter 2 and Chapter 3 have shown the importance of ecological background in understanding the nature of patterns exhibited by reaction-diffusion models. Additionally, the scope of patterns we were initially interested in was broadened. By posing the relevant ecological questions, the underlying mathematical mechanisms unrolled themselves into a realm of expected and unexpected patterns and geometrical constructions. Rigorous analysis of reaction-diffusion models in return demarcates the possible outcomes and sceneries an ecosystem can have as well as its spatio-temporal evolution. A real ecosystem is typically not close to onset, i.e., features parameters μ that are not close to the critical parameter value μ_c , thereby yielding patterns exhibited by (1.20–1.21–2.1–3.1) that are ‘far-from-equilibrium’. This allows for these patterns to be studied by the methods of geometric singular perturbation theory (as has been done in this thesis).

This is a mere recapitulation of the longer call we have stated in the introduction, that, trying to understand natural complex phenomena such as climate change and soil degradation, requires the fusing of these two fields of research. It has become clear throughout this thesis that in the study of ecosystem dynamics the knowledge of both ecology and mathematics needs to be combined in order to optimize the posed research questions and the models that are used in order to describe the processes at play. As data acquisition and sampling methods develop and expand by the minute, the areas of ecosystem modeling and model

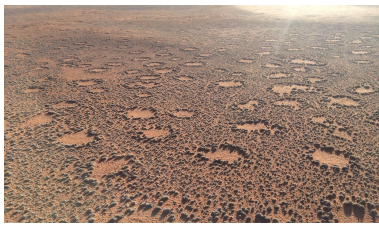
assessment are just set out. Along this development, a multitude of follow-up research questions arise from the studies done in this thesis, from the establishment of the Busse balloon in Chapter 2 to the geometric singular perturbation theory tools of Chapter 3.

As outlined in Chapter 1.2, the models studied differ in their approach by their different ecological settings, one being more conceptual and the other trying to include more realistic parameters and environmental constraints. Studying the most conceptual model, the extended-Klausmeier model, and its Busse balloon in Chapter 2, and laying it next to real state-of-the-art acquired dryland vegetation data, confirmed that ecological systems are more resilient on a fundamental level than previously thought and that various patterns can co-exist simultaneously for the same parameter values. In an analogous way, in Chapter 3, we have found the Turing bifurcation in model (3.1) and we have constructed by means of geometric singular perturbation theory several classes of spatially periodic far-from equilibrium patterns as seen in Figures (3.17a,3.18a) of Chapter 3.6. These represent sections of the Busse balloon of the model of Chapter 3, and form a basis to build upon in completing the Busse balloon in parameter-space and thus for the existence of the Busse balloon and the multistability of periodic patterns for this model.

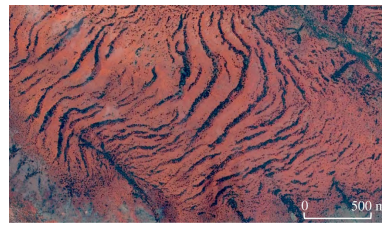
Along the lines of parameter-space and parameters, the more realistic model of Chapter 3, may also have been used to analyze the data of Chapter 2 from a quantitative perspective. With the abundance of ecological parameters within this model, this would have gone beyond qualitatively establishing the fundamental phenomenon of increased resilience through multistability. Thus, this may be a relevant extension of the study of these sites, by providing a more qualitative interpretation of the latter. For this, a meticulous study of the ecological literature is required to acquire realistic values of the parameters present. In model (3.1), the Busse balloon of the model of Chapter 3 can be determined explicitly. The model of Chapter 3 can also easily incorporate an advection term to account for the topological variations (which was initially done in the 3D Gilad et al. version [61]) that were present on site. This would be an interesting next step: to put both models side by side in order to analyze and compare their predictions. Actual model comparison, to my knowledge, has not been done systematically as the parameters' choices of each model are often hard to retrace, therefore making one-on-one correlation a challenge. Nevertheless, a qualitative comparison of both models and their predictions with respect to actual observations would be a natural follow-up, in order to also fine-tune the ecological parameters that have been worked with for years within Klausmeier-type models.

A fundamental challenge that we did not touch upon is, of course, the direct relevance of the 1D model analyses of Chapters 2 and 3 in the realistic setting

2-dimensional (spatial) domains. Naturally, extrapolating the patterns found in the one dimensional case to the 2-dimensional case using the symmetry in the y -direction results in trivial straight stripes. Moreover, perfectly circular symmetric patterns can also be studied by the 1D-methods of this thesis – see for instance [158] and the references therein. However, these idealized two dimensional shapes are, for example, very different from the realistic ecological case, where we have a broad range of patterns that are far from being perfectly symmetric: fairy circles, labyrinths, gaps, curved stripes as can be seen in Figure 4.1. Thus, a mere extension of the 1D analysis of our models to a two dimensional space is too simplistic (in fact, it should even be noted that the precise nature of the interaction terms in the model may be different in 2-space dimensions – see Chapter 3, and [106]). However, the patterns exhibited in Figure 4.1 also suggest that the analysis of realistic patterns may be developed by a perturbative approach that starts out from perfectly symmetrical intrinsically 1D patterns. Moreover, even if one would restrict oneself to perhaps the most simple start-up problem, the evolution of curved interfaces, a problem that has been extensively studied in the mathematical literature (see for instance [23] and the references therein), the mathematical challenge should not be underestimated: unlike the evolving interfaces generally considered in the literature, ecologically relevant stripes and interfaces may be destabilized by their evolution or through their interactions with other stripes/interfaces – see for instance [11] for examples in one space dimension. Nevertheless, we may conclude that the 1D analysis applied and further developed in this thesis does provide a first stepping stone towards understanding the evolution and dynamics of ecologically relevant patterns in 2D.



(a) Fairy circles in the Namibian desert [1].



(b) A site displaying curved banded vegetation patterns in the Western Creek Basin southwest of Newman, Australia ($-23.5^{\circ}N, 119.5^{\circ}E$). Picture taken from [60].

Figure 4.1: Two dimensional vegetation patterns in nature.

The dimensionality of an ecosystem model is not the only place where space and spatial coordinates play a key role in the type of patterns exhibited and their behavior. A research question that has not yet been thoroughly explored is the

role of topography and its effect, even on a small scale, on the family of patterns that the models can exhibit and that can be observed. Model predictions in Chapter 2 regarding the role of slope with respect to migration speed was not corroborated by the empirical data analyzed, suggesting that the inclusion of small-scale topographical heterogeneities is a promising avenue for future model analysis, something that was further researched in [10]. Including slope into model of Chapter 3 would be a next step into incorporating the topographical effect into the analysis of ecosystem dynamics. The curvature of the slow manifolds has played a crucial role in the asymmetrical type of connections that we encountered, starting with the 'basic' connections between bare soil and vegetated state. Including advection into the model, that is, breaking of the reversibility symmetry $(u(x, t), v(x, t)) \rightarrow (u(-x, -t), v(-x, -t))$ of the system will at the very least affect the profile of the connections established, if not completely reshape the family of periodic patterns found on the slow manifolds, as these are symmetric stationary solutions and breaking of the reversibility symmetry would disrupt these constructions. Such modifications have, for example, been researched in [9] for a 2-component extended Klausmeier-type model, the basic connections between bare soil and vegetated state will be altered from being completely symmetric in the case of a pulse and a gap to the new patterns that can be seen in Figure 4.2.

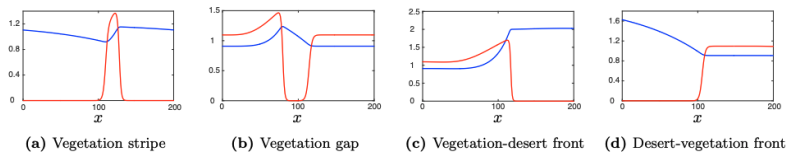


Figure 4.2: Shown are the different patterned solutions of an extended Klausmeier-type model. Presented figures show 1D cross-sections $u(x)$ (blue) and $v(x)$ (red) of direct numerical simulations. Figures from [9] – where water diffusion has been omitted for simplicity.

Aside from the possible model extensions and further ecological applications, a natural next step building on the existence proofs of Chapter 3 is to study the stability of the new found orbits and connections in both one and two dimensions. This is, besides its mathematical importance, of high relevance to the ecological community as the only observable patterns in nature are those that are mathematically stable. As the model of Chapter 3 encapsulates a ‘new’ variety of slow localized patterns, that are completely embedded in a slow manifold of the singularly perturbed spatial dynamical system, further stability analysis is required, by performing the corresponding spectral stability analysis. In [40], a very first step in this direction has been taken.

One overall clear takeaway from this thesis is that the practical applicability of geometrical singular perturbation theory transcends specific model formulation. Given a reaction-diffusion system that incorporates spatial scale separation, a successful geometric singular perturbation analysis will make clear which patterns exist, what they look like, what their period is (if present), and how these properties depend on the model parameters [41, 44]. Given that patterns in real ecosystems are singularly perturbed by definition [113], as biomass and water diffuse with very different speeds, geometric singular perturbation theory is an excellent tool to go with in order to investigate the different vegetation patterns exhibited. The existence and properties of orbits are directly related to the shape and transversal intersection of the geometrical objects (stable and unstable manifolds) introduced in Chapter 1 and Chapter 3 in phase space. This has, from a model perspective, two consequences. First, recent insight shows that the existence and properties of several important types of special orbits can be established [31, 40, 46] using only general properties of the reaction terms $f(u) : \mathbb{R}^m \rightarrow \mathbb{R}^m$ in (1.8) – that is, patterns such as pulses or periodic orbits, and their properties, can be found for general classes of reaction-diffusion systems. For a specific reaction-diffusion system, one only needs to check whether its reaction terms obey certain (mild) conditions; if so, the pattern properties are explicitly given in terms of integrals involving the reaction terms, and certain solutions to lower-dimensional differential equations. A second, and related, consequence of the geometric approach is that because the specific functional form of the reaction terms $f(u)$ is not important, the reaction terms can be directly defined for instance through an (experimentally obtained) response curve. Only the geometric shape of this curve determines the existence and properties of pattern solutions, not the specific algebraic implementation of this shape. Therefore, patterns obtained by a geometric singular perturbation construction are structurally stable. Thus, geometric singular perturbation theory is an extremely suitable ‘tool’ by which we can understand ecosystem models – even the more realistic and thus complex ones. However, the present state-of-the-art theory is still insufficiently developed (especially concerning the stability of patterns): ecology will keep on driving the development of the theory for quite a number

of years.