Davis Math Lab Project Report, Spring 2026
Ecosystem Spatial Pattern Formation

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Contents

1. Introduction

Arid ecosystems found around the globe are characterized by limited water availability where yearly evaporation rate may exceed the annual rainfall. This correlates with formation of various vegetation patterns such as bands, spots, labyrinths, gaps, and rings (Rietkirk 2002; Meron 2007). They are of interest to spatial ecology as they serve as the key to understanding the underlying mechanisms and feedbacks that dictate plant growth. In particular, the paper written by Rietkirk et al. highlights the activation-inhibition mechanism between soil water and plant density, and the resulting spatial self-organization, as the driving process for pattern formation. It goes as such: presence of plants increases the infiltration capability of the soil at that spot, which in turn results in even more plant growth (activation). On the other hand, the lack of plants decreases their growth at that spot by lowering the infiltration rate (inhibition). These ecosystems can be modeled with a set of reaction-diffusion partial equations that at the very minimum must have variables for plant density and soil-water that are dependent on linear on non-linear parameters. These equations can then be studied via linear stability analysis in order to determine the stability of the different vegetated states to perturbations at different parameter values. Especially of interest is the stability of those systems under varying rainfall conditions that, among other things, can emulate extended dry seasons caused by climate change. Furthermore,

more complex models can be used to simulate the effect of adding a vegetation patch in a given region as a remedial measure in order to determine whether it will help the ecosystem be more resilient to change (see Bastiaansen et al.). Overall, these studies can help us better understand what affects ecosystem resilience and potentially open opportunities for us to proactively intervene in order to make sure that the ecosystems stay robust to human-caused environmental changes.

2. Progress

We successfully recreated the results of the Rietkirk paper including the 2D and 1D results as well as the bifurcation graph, which tells us about the stability of the spatial patterns.

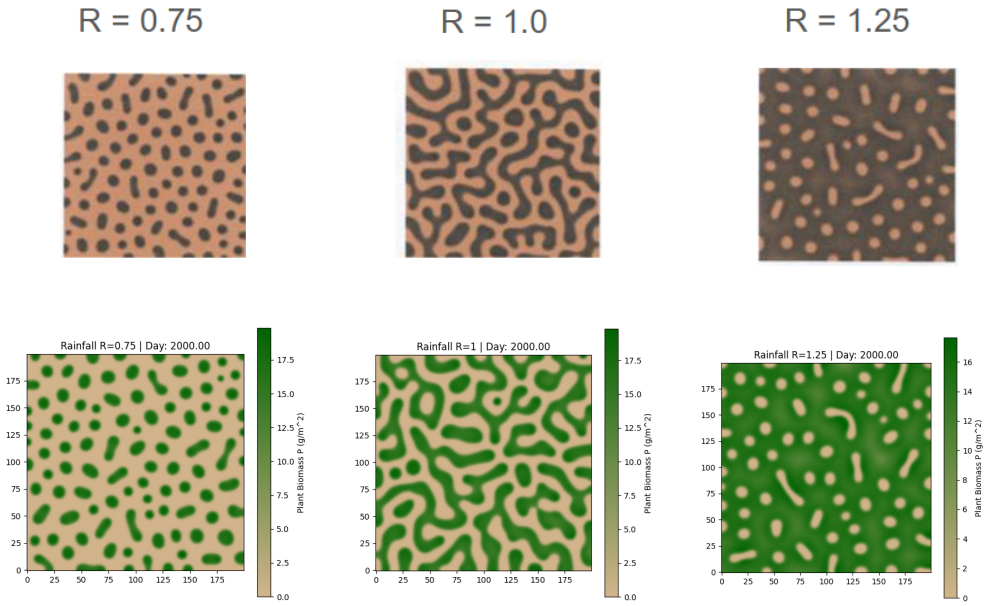


Fig. 1 – Comparison of Rietkirk 2D results (top) and our 2D results (bottom)

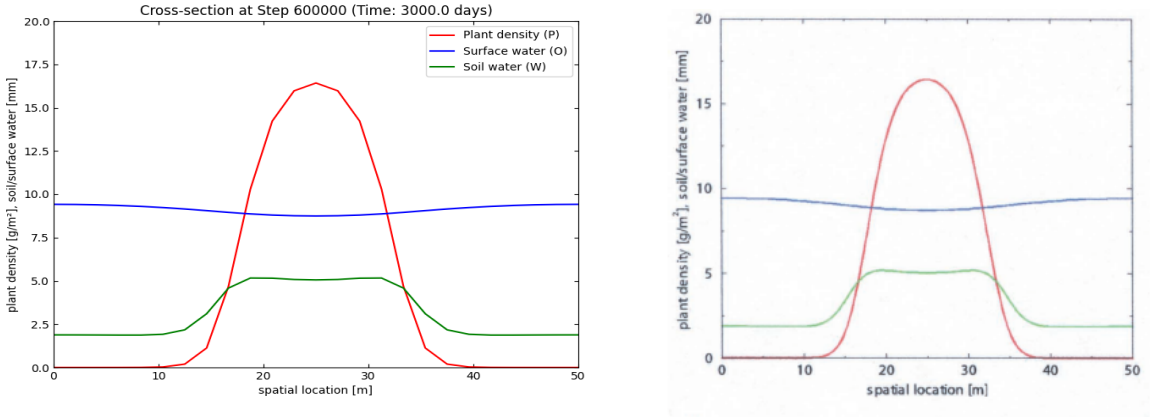


Fig. 2 – Comparison of Rietkirk 1D result of a stable heterogeneous plant peak at R = 0.75 (right) and ours (left); R is the rainfall parameter in units of mm d^{-1}

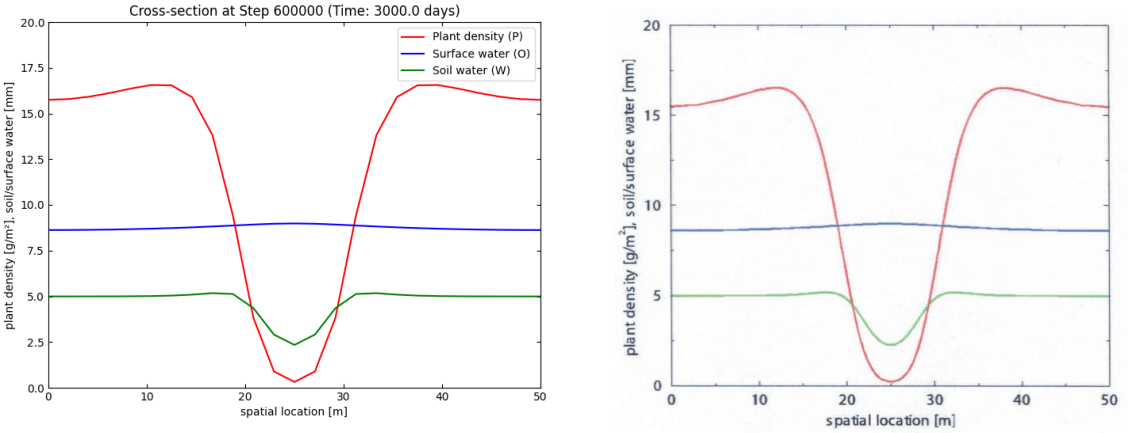


Fig. 3 – Comparison of Rietkirk 1D result of a stable heterogeneous plant gap at R = 1.25 (right) and ours (left)

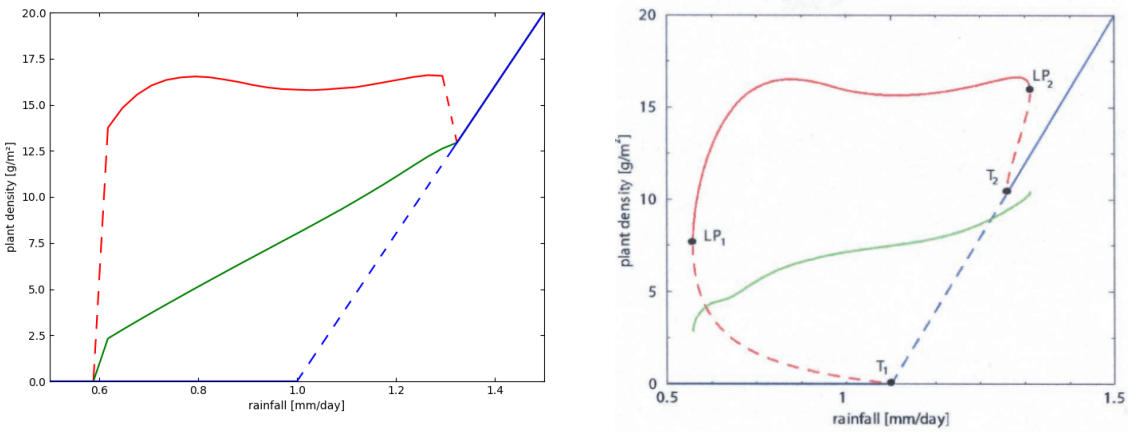


Fig. 4 – Comparison of Rietkirk bifurcation graph (right) and ours (left); blue – homogeneous equilibrium, red – heterogeneous equilibrium, green – average plant density; solid line – stable, dashed line – unstable; T1 and T2 – Turing instability points, LP1 and LP2 – limit points

Furthermore, basing off the Rietkirk model, we made 3 extensions in order to explore pattern formation under varying rainfall and mortality rates as well as the slope of the terrain. Slope, periodic rainfall, and mortality are explored by Kimi (Yuzhe), Ekaterina, and Alice (Ziyu) respectively.

2.1 Slope Model

We also explore the pattern formation in the slope. The level of the slope or the speed of the water flow is controlled by the variable v, and the direction of downhill is left. In the flat ground, we use central difference to simulate the water distribution, however in a slope, we can assume water only flows downhill. Based on the surface water equation, we replace the water diffusion in the flat ground term with the water diffusion in the slope. ($D_o \Delta O \quad \rightarrow -\partial O / \partial x$)

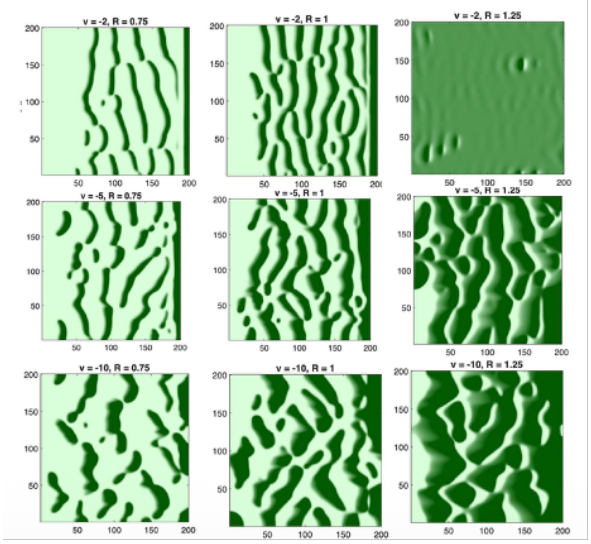


Fig. 5

Originally, surface water only spreads by diffusion, but in the slope model we replaced that with an advection term, so water is transported downhill to the left.

2.2 Stochastic Rainfall in the flat ground

We compare different rainfall values R and slope strengths v. As rainfall increases from 0.75 to 1.25, vegetation becomes denser. It starts with a stripe pattern, and gradually covers the whole area as R increases. (It can be explained by the positive effect of rainfall to the plant density) .

As |v| increases, the downhill flow becomes stronger and we observe that each stripe shaped plant density pattern becomes wider.

2.2.1 Use Markov Chain to simulate rainfall in the real world.

For a 3 by 3 transition matrix, **State1** represent rainfall at 0.75; **State2** represent rainfall at 1; **State 3** represent rainfall at 1.25.

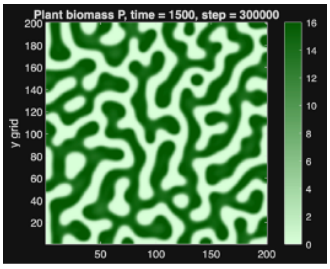
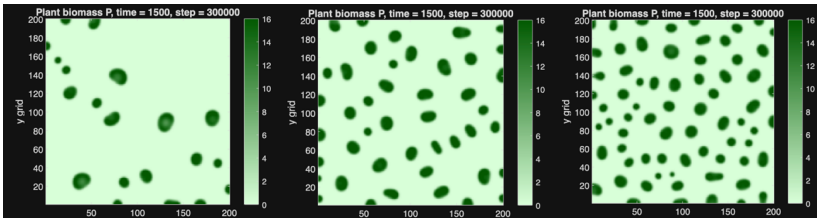


Fig. 6

We observe that the main patterns are labyrinth, rings and spots

For a 4 by 4 transition matrix, **State 2**: Rainfall = 0; **State3**: Rainfall = 0; **State4**: Rainfall = 1.25;



State 1: R = 0.75 R = 1 R = 1.25

Fig. 7

Keeping state 2,3,4 in the same level, we increase rainfall from 0.75 to 1 and to 1.25. Observation1: the main pattern is the spot pattern. As rainfall increases, the number of spots increase simultaneously. Observation2: if the rainfall is too low such as R = 0.75 in plot 1, the pattern of the plant density will start with a spot pattern and gradually evolve to the moon shape/ petal shape pattern. (plant density is higher in the edge of each petal).

1x1 (1.25)	3x3 (1.25 0 1.25)	5x5 (1.25 0 1.25 0 1.25)

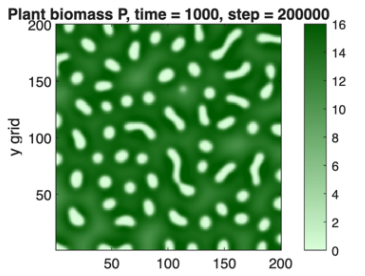
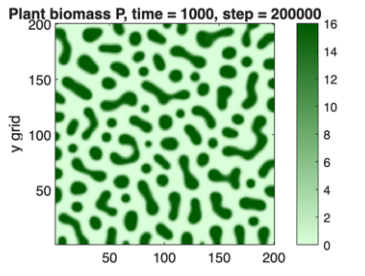
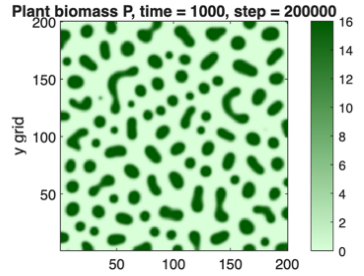
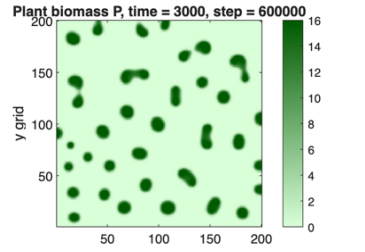
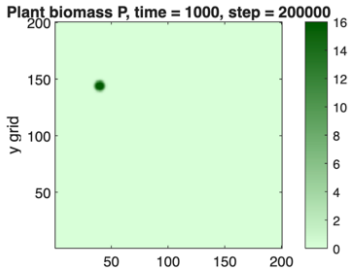
		
7x7 (1.25 0 0 1.25 0 0 1.25)	9x9 (1.25 0 0 0 1.25 0 0 0 1.25)	11x11 (1.25 0 0 0 0 1.25 0 0 0 0 1.25)
		Die out completely

Fig. 8

Note: (xx) is the State of rainfall. Since 0 represents no rainfall, so as the size of the Transition matrix increases oddly, the probability of no rainfall increases. If rainfall is constant throughout the whole time interval, we can guarantee to get a Gap Pattern. As long as there is a probability of getting no rainfall stage(State(n) → 0), the pattern is mainly formed by the Spot Pattern.

2.2.2 Periodic rainfall

Here we model periodic rainfall with a cosine function keeping all of the other attributes of the 2D Rietkirk model the same as in the original. While we tried sweeping different rainfall ranges between R=0.5 and R=1.5, the most notable vegetation pattern occurred in the range between LP1 (R = 0.557) and LP2 (R = 1.312) (see Fig. 4) with a period of rainfall of 300 days. While at other periods and rain ranges the pattern eventually stabilized to either gap or spot pattern, at 300 days the pattern seemed to progress from spot to ring to crescent shape throughout the rain cycle. In addition, the cores of the vegetation patches appeared to migrate as time went on (see Fig. 8).

This behavior is characteristic of a feedback not explicitly captured by this model: the uptake feedback. This is a negative feedback between the amount of soil water at a particular spot and the number of plant roots that extend to this spot. A model with such a feedback was proposed in a paper by Meron et al. where the strength of the effect of root length is controlled by the parameter η. According to this paper, species associated with a large enough η will deplete

the soil water at the borders of a vegetable patch faster thus inhibiting the patch's growth outwards and resulting in a stabilized spot. On the other hand, species with smaller η values, corresponding to those with compact root systems, do not deplete as much soil water at the borders, allowing the patch to expand. At the same time, the core of the patch experiences the most water stress which results in it eventually drying up, producing a ring shape.

In the context of this paper, the periodic rainfall that we added in this extension of the model may 'simulate' the effect that the root system plays otherwise if we hypothesize that at lower rainfall values the negative feedback between plant density and water amount (and thus resulting plant growth) overpowers positive feedback between plant density and plant growth ensured by diffusion. During the periods of high rainfall, the dry patches have enough soil water that the plants can expand uniformly outwards onto them. As the rainfall starts to decrease and the water supply becomes more limited, the cores of the vegetation patches with greatest plant density have the most competition for water (captured by the $-g_{max} \times \frac{W}{W + k_1} \times P$ term in the reaction diffusion equation for soil water in the Rietkirk model), which overpowers diffusion to those spots due to increased infiltration, and results in inhibition of plant growth, leading to formation of ring-like and crest-like shapes. From then on, as rainfall starts increasing again, the activation mechanism and diffusion become more prevalent again, ensuring active vegetation growth around the remaining patches.

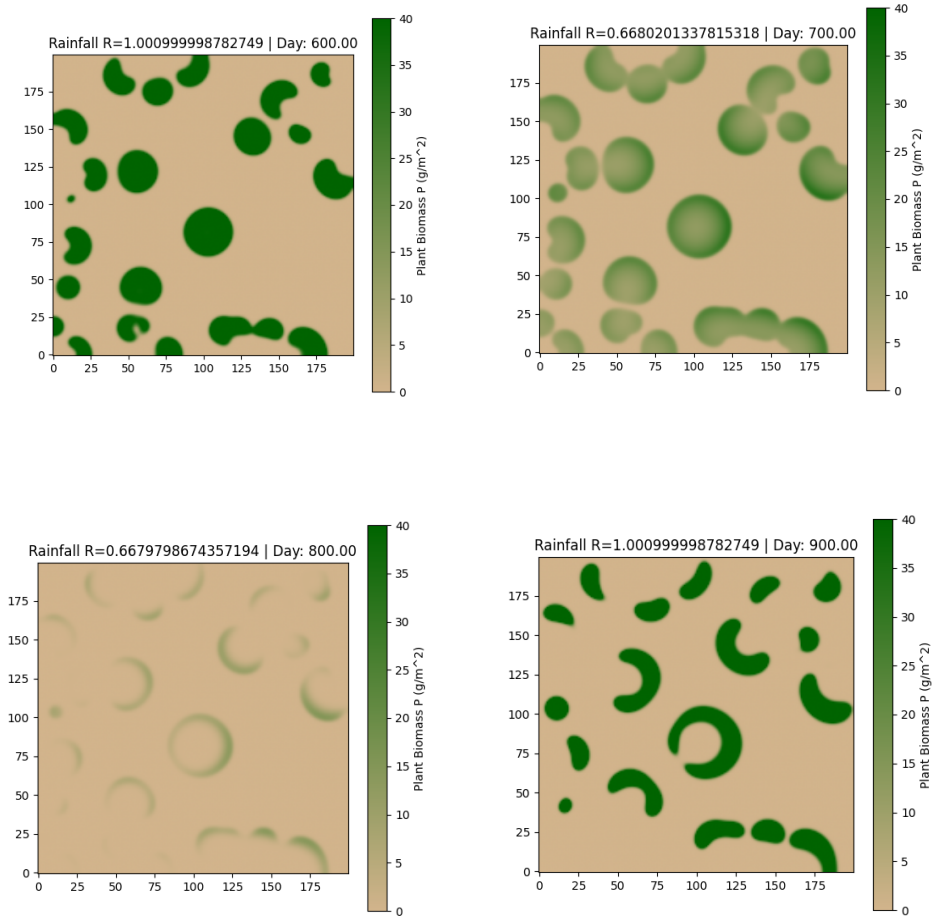


Fig. 8 One period (300 days) evolution of a 2D vegetation patch with 0.557<R<1.312

2.3 Mortality-Based Extensions

2.3.1 Controlled Mortality Experiments

To isolate the effect of plant mortality on spatial self-organization, we performed an additional controlled-parameter experiment based on the original Rietkerk-type vegetation-water model. Rainfall was fixed at (R=1.0), the terrain was treated as flat, and no stochastic perturbation was added to either rainfall or mortality. Therefore, the plant mortality rate (d) was used as the only independent bifurcation parameter, while all other ecological and numerical parameters were held constant.

All simulations were run on the same (200 times 200) spatial grid with the same initial water equilibrium and the same random seed distribution, where 1% of grid points were

initialized as vegetation peaks. This setup allowed us to compare the long-term vegetation patterns under different mortality levels while minimizing the influence of initial randomness or other changing variables. Plant biomass was visualized as a continuous density field, and vegetation cover was also tracked using a biomass threshold.

The results show that increasing mortality does not simply reduce vegetation density in a linear way. Instead, the system passes through several qualitatively different spatial states.

At d=0.26, the vegetation persisted and developed into a connected labyrinth-like pattern. This suggests that, at this mortality level, the positive feedback between plant growth and water infiltration was still strong enough to support spatial self-organization across the domain.

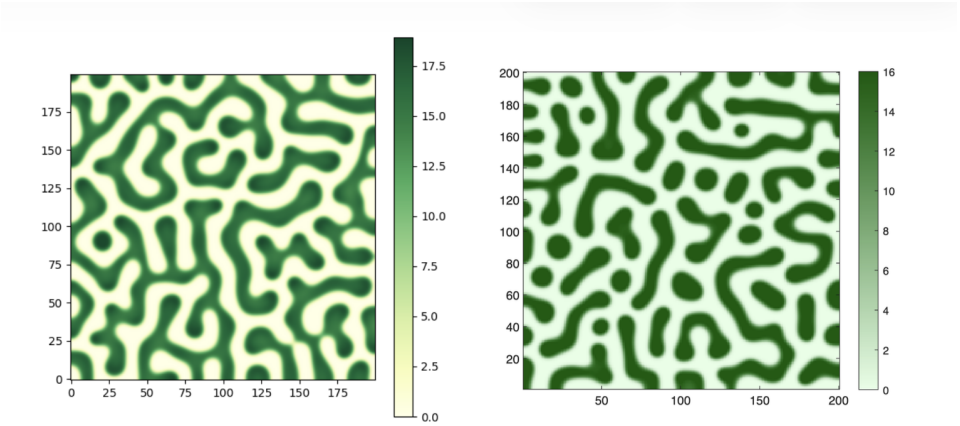
When mortality was increased to d=0.32, the extended labyrinth structure no longer persisted. During the early stage of the simulation, vegetation cover dropped sharply, reaching only about 0.2%–0.3% around Day 80–100. At this point, the system appeared close to complete collapse, with only a tiny isolated green patch remaining. However, this surviving patch did not disappear. Instead, it began to expand slowly, suggesting that a localized plant-water feedback was still able to persist even after most vegetation had died out. As the simulation continued, the small patch enlarged and reorganized. Around Day 500, when vegetation cover had recovered to approximately 2.18%, the biomass in the center of the patch started to thin out and disappear, creating a hollow region. After this interior collapse, the remaining vegetation formed a localized ring-shaped structure. Over longer times, this ring continued to expand and gradually became less circular, developing a rounded-square or weakly diamond-like shape with four more pronounced sides or corners.

This behavior is interesting because d=0.32, did not lead directly to a bare-soil state. Instead, the system passed through a near-collapse stage, recovered from a tiny remnant patch, and then reorganized into a localized ring-shaped pattern. This suggests that near the mortality threshold, the ecosystem may not transition smoothly from vegetation to desert. Instead, it can pass through an intermediate localized survival state before complete desertification.

The values near this transition are also tested. At d=0.325, the system initially appeared close to collapse, leaving only a tiny isolated vegetation patch with very low cover. However, this remaining patch did not disappear immediately; instead, its cover slowly increased over time. This behavior suggests that d=0.325 may still lie on the survival side of the transition, but extremely close to the tipping threshold. In contrast, when mortality was increased slightly to d=0.33, vegetation collapsed rapidly, reaching nearly zero cover by approximately Day 95.

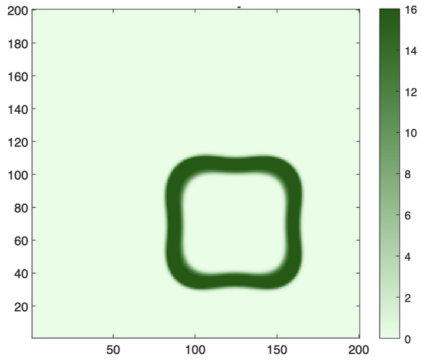
Overall, these simulations indicate a narrow mortality-induced tipping interval between approximately d=0.325 and d=0.33 for the chosen parameter set, grid size, and initial condition.

Ecologically, this result suggests that once mortality becomes large enough, even a small additional increase can destroy the self-organized vegetation-water feedback and push the system toward a bare-soil state.

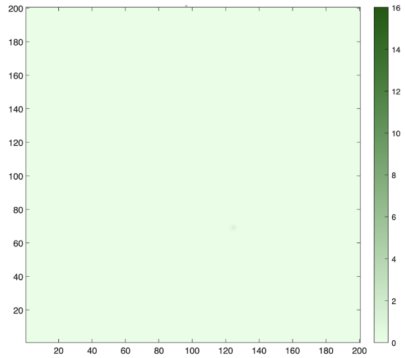


(a) d = 0.25, Day 3000

(b) d = 0.26, Day 3000



(c) d = 0.32, Day 3000



(d) d = 0.33, Day 95

2.3.2 Additive Periodic Mortality Forcing

After testing constant mortality values, I next considered a time-dependent mortality term while still keeping the rest of the system controlled. In this experiment, rainfall was fixed at R=1.0, the terrain remained flat, and no stochastic noise or rainfall variation was included. The only time-dependent forcing was added to the plant mortality rate. Specifically, mortality was modeled as an additive cosine function

$$d(t)=d_{base}+A\cos(2\pi t / T)$$

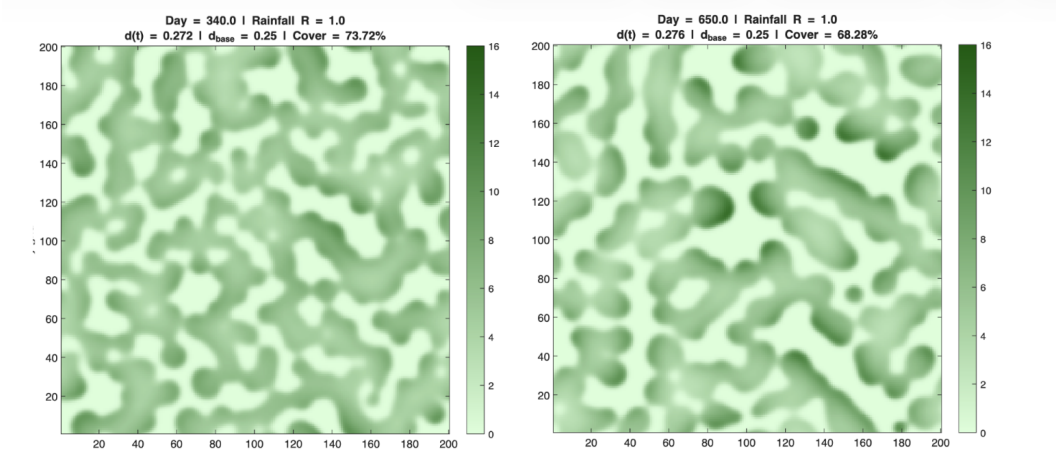
where d_{base}=0.25, A=0.03, and T=300 days. Therefore, the mortality rate oscillated approximately between 0.22 and 0.28, centered around the original Rietkerk mortality value $d=0.25$.

The resulting vegetation pattern did not converge to one fixed spatial endpoint. Instead, the system showed a periodically forced response in which plant biomass expanded and

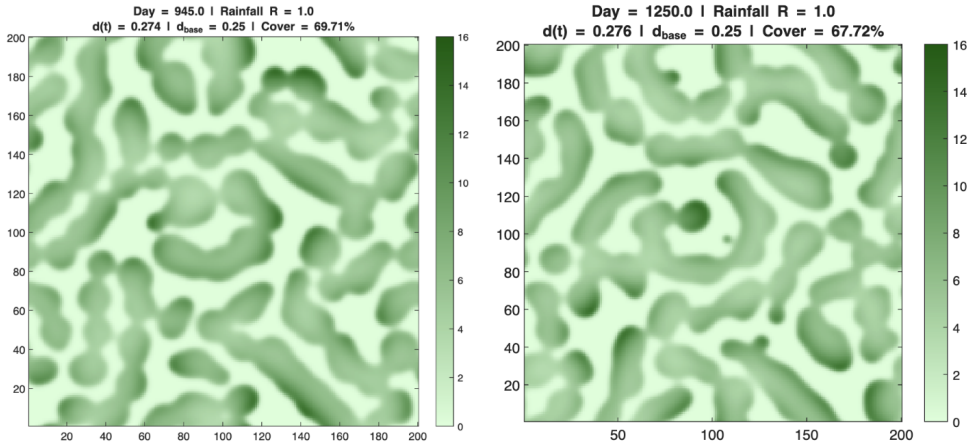
weakened over time as $d(t)$ changed. When mortality was lower, vegetation density increased and the patches became thicker. When mortality became higher, parts of the pattern thinned and became less connected. However, the response was not completely reversible. The spatial structure after each cycle did not fully return to the previous pattern.

To compare the long-term effect of repeated mortality cycles, snapshots at similar phases of the cosine cycle were selected, with $d(t) \approx 0.27$. At Day 340, the vegetation pattern was still relatively connected and resembled a broad labyrinth or gap-like structure. By Day 650 and Day 945, the pattern had become less connected, with longer separated regions and weaker bridges between neighboring patches. By Day 1250, the vegetation still maintained a high overall cover, but the spatial structure appeared more fragmented and divided into larger elongated blocks rather than one continuous network.

This result suggests that additive periodic mortality can produce cumulative structural degradation even when the total vegetation cover remains relatively high. In selected snapshots, vegetation cover stayed within a similar range, approximately 67%–74%, but the connectivity of the vegetation pattern decreased over repeated cycles. Ecologically, this indicates that periodic plant stress may weaken spatial organization before causing a major drop in total vegetation coverage. In other words, the pattern structure may degrade earlier than the average biomass or cover would suggest.



(a) day 340 (b) Day 650



(c) Day 945 (d) Day 1250

2.3.3 Multiplicative Periodic Mortality Forcing

A multiplicative version of periodic mortality forcing was also tested. In this experiment, the mortality rate was modeled as

$$d(t)=d_{base}+[1+q\ cos(2\pi t / T)]$$

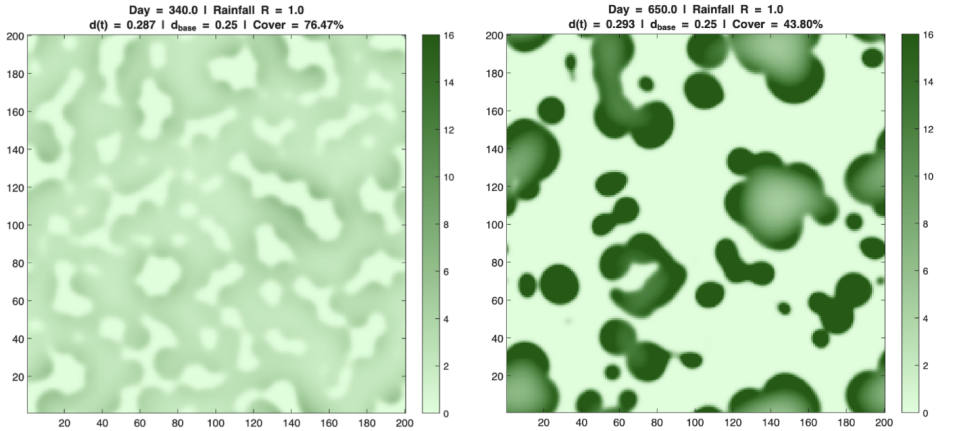
with d_{base}=0.25, q=0.20, and T=300 days. Under this choice, the mortality rate oscillated between approximately 0.20 and 0.30, producing a stronger forcing range than in the additive case.

At early times, the vegetation pattern still retained some resemblance to the additive mortality case, with a broad and partially connected labyrinth-like structure. However, the multiplicative forcing produced a more strongly cycle-dependent response. During high-stress stages of the mortality cycle, the connected vegetation network broke into separated high-biomass clumps and compact patch-like regions. For example, the Day 650 snapshot shows a

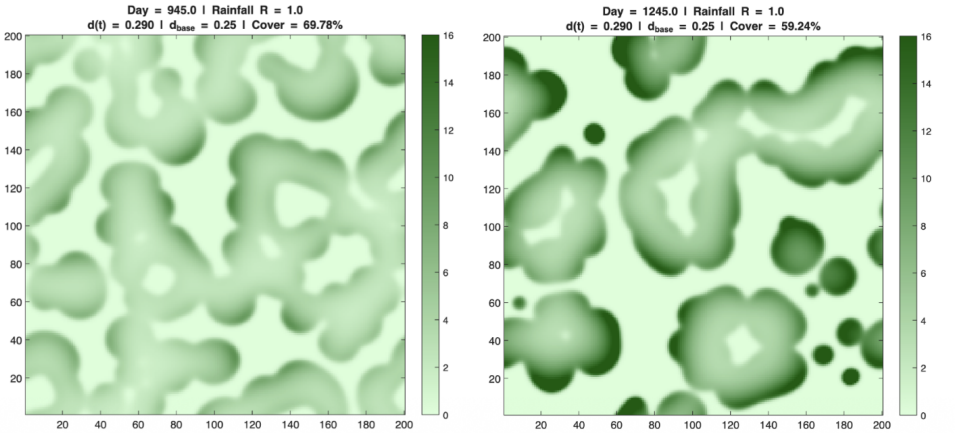
noticeably fragmented state, where vegetation is organized into discrete dark-green patches rather than continuous elongated bands.

The later snapshots suggest that this fragmentation was not simply monotonic. After periods of stronger mortality, vegetation could partially recover and reconnect, as shown by the Day 945 pattern. However, this recovery did not restore the original labyrinth-like network. Instead, the pattern reorganized into larger, block-like patches with weaker connections between regions. By the later stage, the vegetation appeared less like one continuous self-organized network and more like a mosaic of compact clusters, separated patches, and partially hollow block-like structures.

Compared with the additive periodic mortality experiment, the multiplicative case produced stronger spatial segregation. Additive forcing mainly weakened the connectivity of an existing labyrinth-like framework, while multiplicative forcing caused more pronounced fragmentation and reorganization into discrete vegetation clusters. This difference is consistent with the stronger effective forcing range in the multiplicative case. Because mortality fluctuations scaled proportionally with the baseline mortality, the vegetation experienced larger periodic stress, which appears to have weakened the recovery of long connected structures and promoted the formation of separated patch clusters.



(a) day 340 (b) Day 650



(c) Day 945 (d) Day 1245

3. Future Plans

For each extension there are various possibilities for further exploration. In the case of the periodic rainfall extension, we still have yet to explain the asymmetric nature of the rings/ crescents and check the hypothesis about their formation proposed in the section above.

Another route for exploration could be to try introducing more variables in order to model certain ecosystem parameters more explicitly and check whether they play an independent role in the formation of vegetation patterns. An example of this could be introducing two variables for plant density representing two different kinds of plants that have significantly different properties/interactions within the ecosystem. We could also consider another factor: a dead plant will contribute nutrition to the soil and positively affect the growth rate; this contribution can be quantified by a new variable that represents the death of the plant or the

decrease of plant density. We could make both the growing term and surface water equation depend on this variable.

4. References

Bastiaansen, R., Doelman, A., Eppinga, M. B., & Rietkerk, M. (2020). The effect of climate change on the resilience of ecosystems with adaptive spatial pattern formation. Ecology letters, 23(3), 414–429. https://doi.org/10.1111/ele.13449

Meron, E., Yizhaq, H., Gilad, E.; Localized structures in dryland vegetation: Forms and functions. Chaos 1 September 2007; 17 (3): 037109. https://doi.org/10.1063/1.2767246

Rietkerk, M., Boerlijst, M. C., van Langevelde, F., HilleRisLambers, R., de Koppel, J. van, Kumar, L., Prins, H. H. T., de Roos, A. M., & Associate Editor: Mark Westoby. (2002). Self-Organization of Vegetation in Arid Ecosystems. The American Naturalist, 160(4), 524–530. https://doi.org/10.1086/342078