

Vegetation patterns in semi-arid environments

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Introduction

There is no need to point out the beauty and complexity of patterns that can be found in nature (at all scales).

Mathematical and theoretical biology, have developed different types of models that try to explain the formations of such patterns. One of the first, and maybe most famous, examples was proposed by A.M. Turing in his work [7] in 1952. In which, with a relatively simple PDE model, described the spontaneous formation of non-homogeneous patterns in chemical reactions.

Based on his work, researchers started to use similar models to describe the formation of many patterns in vegetation, among them: the distribution of grass in water-limited environments, which displays non-homogeneous regular patterns like labyrinths, lattices or tiger stripes [4].

The interest for these types of models is not only academic, and goes beyond the explanation of the mechanism that formed the pattern, in fact they can also be used to predict whether a particular territory, will undergo a phase of desertification in the near future.

Semi-Arid Ecosystems

Semi-arid climate conditions can be found all around the globe: in the middle and southern part of Africa, in Mexico and the U.S., Australia, Spain and many other places. Places in which the average amount of rainwater is particularly low, but not completely absent (like deserts), allowing only few types of plants to survive.

The main types of patterns that can be found in semi-arid ecosystems are:

- Random: where no general underlying structure can be found
- Segregated: where single plants arrange themselves in lattices with more or less equally distanced neighbours (the main causes are usually competition and interference between plants)
- Aggregated: where plants group in separated patches

The mechanisms, based on the principle of plants' self-organization, proposed to explain the spontaneous formation of aggregated patterns, are all based on the

interaction that a plant has with the others nearby. The two main behaviours are:

- (Purely Competitive Feedbacks): a plant will always have a negative effect on all the nearby plants (such as reducing the necessary nutrients from the soil or reducing the oxygen intake, like pine needles do if not removed)
- (Scale Dependent Feedbacks): a plant will help the nearby plants to survive, and have negative effects on more distant ones (this can happen in many different ways, such as making it easier for the water to penetrate into the soil which facilitates the absorption for plants nearby but also reduces the water for farther away ones)

SDF

Klausmeier model

The most famous example of a reaction-diffusion SDF was described by Klausmeier [3] in 1999:

Let $W(t, x, y)$ ($N(t, x, y)$) be the amount of water (biomass) at a given point at a give time:

$$\begin{cases} \partial_T W = A_0 - L_0 W - R_0 W N^2 + V_0 \partial_X W \\ \partial_T N = J(R_0 W N^2) - M_0 N + D \Delta_{XY} N \end{cases} \quad (1)$$

the model takes in account: the rainwater (A_0), water evaporation ($-L_0 W$), plant absorption of water ($-R_0 W N^2$), downhill flow of water ($V_0 \partial_X W$), biomass death ($-M_0 N$) and biomass' diffusion ($D \Delta N$).

The model is meant on some rectangular patch of a hill or plain, depending on the V_0 value which is proportional to the (assumed) constant slope of the field (we decrease the altitude by moving in the positive x direction; actually also a $V_0 = V_0(x, y)$ could be considered).

The system can be nondimensionalized and transformed into:

$$\begin{cases} \partial_t w = a_0 - w - w n^2 + \nu_0 \partial_x w \\ \partial_t n = w n^2 - m_0 n + \Delta_{xy} n \end{cases} \quad (2)$$

We can study now whether there are homogeneous stable solutions ($\partial_{x_j}(\dots) = 0$). It's easy to see that the solution ($w = a, n = 0$) always exists and is always stable (for the reduced system). Then depending on the constants at play ($a > 2m$) we can have two additional equilibria. One always unstable, for the other one it can vary (Klausmeier suggests that for some realistic values of the constants there can be stability).

To analyse whether the first equilibria $u_0 = (a, 0)$ might display some sort of Turing instability we can use the standard approach: let $u = u(t, x, y) = u_0 + \varepsilon(t, x, y)$ (where $|\varepsilon|_\infty < \delta$) be a solution (perturbed around u_0), let's plug it in the approximated system:

$$\partial_t u \approx F(u_0) + JF(u_0)\varepsilon + \hat{D}\Delta\varepsilon + \begin{pmatrix} \nu_0 \partial_x u_1 \\ 0 \end{pmatrix} \quad (3)$$

lets also consider the Fourier decomposition of ε such that the basis is a set of eigenfunctions (ϕ_k) of Δ (spatial):

$$\begin{cases} \sum_k (a_k)' \phi_k = -\sum_k a_k \phi_k - \nu_0 \sum_k a_k \partial_x \phi_k \\ \sum_k (b_k)' \phi_k = -m \sum_k b_k \phi_k - \sum_k b_k \lambda_k \phi_k \end{cases}$$

since they are decoupled, we can solve the set of ODEs in the second one, and see that they all die out with $t \rightarrow \infty$. So no plant pattern will form (actually it makes perfect sense since all the rainwater evaporates, so even if we start with some plants those will dry).

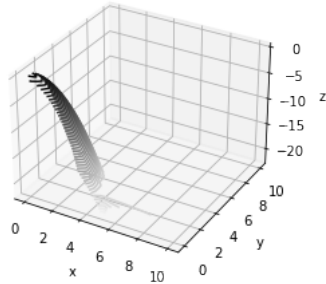
To study the Turing-like instability of the other solutions $(w_+, n_+), (w_-, n_-)$ we need the explicit expression for the eigenfunctions. Following Klausmeier we assume periodic BCs (we assume that the domain is the $(0, L)^2$ square), hence one mode $(M, N) \in \mathbb{N}^2$ of the Fourier's series will be:

$$\begin{pmatrix} \varepsilon_1(t, x, y) \\ \varepsilon_2(t, x, y) \end{pmatrix} = e^{i \frac{2\pi}{L}(Mx+Ny)} \begin{pmatrix} \varepsilon_1(t) \\ \varepsilon_2(t) \end{pmatrix}$$

lets rename M and N (with the same letters) such that they take values in $\frac{2\pi}{L}\mathbb{N}^2$. Now by if we plug it in 3, we obtain:

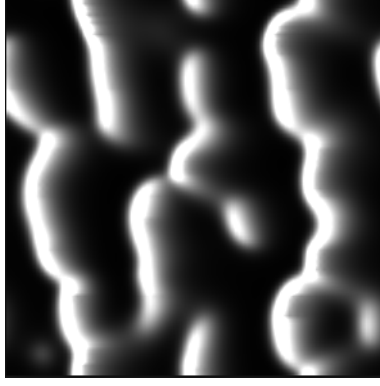
$$\begin{aligned} e^{i(Mx+Ny)} \begin{pmatrix} \varepsilon_1(t)' \\ \varepsilon_2(t)' \end{pmatrix} &= \\ &= e^{i(Mx+Ny)} \begin{pmatrix} -1 - n_+^2 + i\nu_0 M & -2w_+n_+ \\ n_+^2 & -m_0 + 2w_+n_+ - (M^2 + N^2) \end{pmatrix} \begin{pmatrix} \varepsilon_1(t) \\ \varepsilon_2(t) \end{pmatrix} \end{aligned}$$

Now we can compute the eigenvalues of the matrix, that will depend on the variables at play: $\lambda(a_0, m_0, M, N)$ ($\nu_0 > 0$ is fixed now). Plotting the maximum of the real part of the eigenvalues (with respect to M and N), it's possible to see that there exist positive values (for some values of a_0 and m_0 , like the ones suggested by Klausmeier: $a_0 = 2, m_0 = 0.45$), hence we have a Turing-like instability.



(the peak is 0.2616)

In fact, by running simulations with realistic values for the constants, we can actually see the formation of striped patterns:



But the difference with classical Turing stability, is that there also is a negative imaginary part associated to those eigenvalues that cause instability, this makes the solution move uphill over time. The explanation given by Klausmeier of this additional feature is: when rainwater falls on a hill, it gradually gets absorbed as it flows downward, so the lowest plants in a patch will get less water, and over time will eventually die out.

For flat territories ($\nu_0 \approx 0$) a similar analysis shows that no pattern formation can happen (at least for realistic constants).

Now an interesting phenomena that can be observed when running the simulations is: when a_0 decreases the distance between the stripes gets bigger. So if we find some relationship between the distance and the rainfall, we can read the environment back and estimate whether the region is becoming more/less arid. To do so lets first consider the simplified model ($w = w(t, x), n = n(t, x)$):

$$\begin{cases} \partial_t w = a_0 - w - wn^2 + \nu_0 \partial_x w \\ \partial_t n = wn^2 - m_0 n + \partial_{x^2}^2 n \end{cases} \quad (4)$$

Since we are in one spatial dimension the striped patterns will form a train of pulses, so we'll consider a solution of the form:

$$\begin{aligned} w &= \omega(x - ct) \\ n &= \pi(x - ct) \end{aligned}$$

So that the system becomes:

$$\begin{cases} -c\dot{\omega} = a_0 - \omega - \omega\pi^2 + \nu_0 \dot{\omega} \\ -c\dot{\pi} = \omega\pi^2 - m_0\pi + \ddot{\pi} \end{cases} \quad (5)$$

by making a change of variable to get rid off the ν_0 :

$$\begin{cases} -(1 + \frac{c}{\nu_0})\omega' = a_0 - \omega - \omega\pi^2 \\ -\frac{c}{\nu_0}\pi' = \omega\pi^2 - m_0\pi + \frac{1}{\nu_0^2}\ddot{\pi} \end{cases} \quad (6)$$

So if $\nu_0 \gg 1$ we can ignore the second derivative in the second equation, which leaves us with a first order ODE system. Now we can find its equilibria, and we would get the same results as we did before for the homogeneous system. While the jacobian (we got rid off a ν_0 since it multiplies both derivatives):

$$J(\omega, \pi) = \begin{pmatrix} \frac{1+\pi^2}{c+\nu_0} & \frac{2\omega\pi}{c+\nu_0} \\ -\frac{\pi}{c} & \frac{m-2\omega\pi}{c} \end{pmatrix}$$

This is useful since the periodic patterns would form a cycle in the (ω, π) space, so one of the equilibria must be a center (so the model has a Hopf bifurcation). One of the conditions for this to happen is:

$$\text{Tr}(J(\omega_{eq}, \pi_{eq})) = 0$$

by substituting the equilibria and noticing that $\omega_{eq}\pi_{eq} = m$, we can get a relationship for c namely:

$$c \approx \frac{\nu_0 m^3}{a^2}$$

So we can actually use the distance between stripes, as an indicator for the aridity of the land!

Beyond Klausmeier

Besides Klausmeier's work other SDF models have been proposed, such as:

- The Rietkerk model: it's still a reaction-diffusion model (also the water diffuses) that somehow extends Klausmeier's one. Here water gets split in two distinct variable, one for surface water and one for underground water (which are then linked in the PDE).
- Kernel-based: $\partial_t v(\mathbf{x}, t) = h(v) + \int G(\mathbf{x}, \mathbf{x}') (v(\mathbf{x}', t) - v_0) d\mathbf{x}'$ this model takes in account non-local biomass (v) interaction (thanks to the integral). A common choice for the kernel G is a gaussian shape that after some distance from the center becomes negative and eventually vanishes at ∞ (this to ensure positive feedback close to the center and negative otherwise). Unfortunately it can also generate negative (unrealistic) solutions.
- Lefever-Lejeune model: which is a multiplicative non-local interaction model (as opposed to the previous which is additive). This already fixes the problem of the kernel-based of having negative solutions. The non-local interaction mechanism is implemented thanks to 3 different convolutions that act on different distance scales.

All these models produce some kind of spontaneous pattern formation (for some choices of the parameters).

PCF

The simplest way to model a PCF is similar to the SDF's Kernel-based approach.

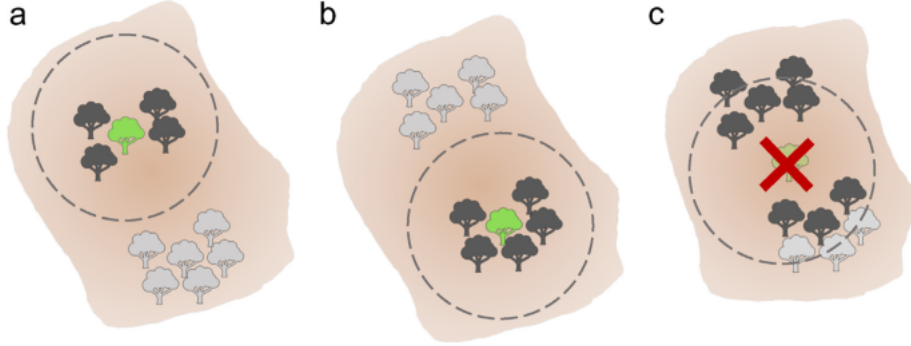
$$\partial_t v(\mathbf{x}, t) = P_E(\tilde{v}, \delta) \beta v(\mathbf{x}, t) \left(1 - \frac{v(\mathbf{x}, t)}{K}\right) - \eta v(\mathbf{x}, t) \quad (7)$$

$$\text{where } \tilde{v} = (\mathbf{x}, t) = \int \omega(|\mathbf{x}' - \mathbf{x}|) v(\mathbf{x}', t) d\mathbf{x}' \quad (8)$$

The model takes in account: dispersion through seeds ($P_E(\tilde{v}, \delta)$ which represents the probability of the seeds to overcome the competition in an already populated area), local logistic growth ($(1 - \frac{v(\mathbf{x}, t)}{K})$ with K local-maximum carrying capacity), biomass death ($\eta v(\mathbf{x}, t)$).

The parameter δ is proportional to the competition that plants/seeds face ($\delta \approx 0$ low competition which means that seeds can easily establish new plants, while $\delta \rightarrow +\infty$ means high competition).

This, intentionally, minimal model already gives rise to patched and labyrinth-like patterns, in which the bare/almost bare spaces are explained by the fact that the competition is higher compared to inside a single patch, since multiple patches exert competitive pressure in it.

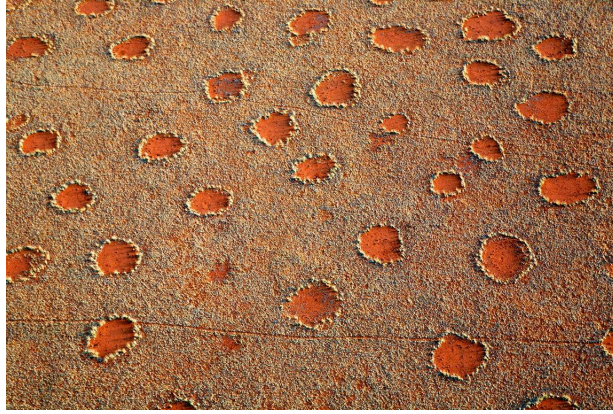


inside the circle the plants are competing with each other (source:[5])

Beyond self-organization

To explain some kind of pattern formations other mechanisms, besides plants' self-organization, have been proposed.

An example where researchers started to doubt that self-organization could be the cause, is the case of the Namibian fairy circles (FCs): strange, circular and grass-bare spots present in the grasslands of the Namib desert.



(source: wikipedia)

In fact, some scientists, think that the formation of these patterns, is caused by termite's engineering (for example [1],[2]).

Both approaches have received criticisms by the other faction. For example: the self-organization supporters, pointed out that most FCs usually have six neighbours, and form large scale structures that insects cannot come up with. While self-organization, has been criticised of completely ignoring the interaction of the insects with the ecosystem, despite evidences.

Truth lies in the middle

But besides these disputes, there really is no reason to think at them as mutually exclusive mechanisms.

In fact, one of the best approaches to describe the formation of FCs merges the two views together: Tarnita et al. model [6].

This model consists of:

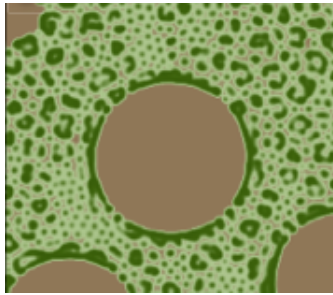
- INSECT MODEL (IM): a cellular automata-like model that simulates the termites' dynamic. This includes termites's foraging, colony growth (in biomass and in size), reproduction and dispersal of the offspring, war between colonies etc.
- PLANT MODEL (PM): a kernel-based SDF model with 3 variables (surface water, underground water and biomass). In which the death of the plants' biomass is increased (in a switch-like manner) by the presence of termites in the area.

The domain of the PM is some square in \mathbb{R}^2 (representing some square patch of flat land in the Namib desert). Overlying this square there is a finite lattice on which the IM works (with the appropriate rules). At the start of the simulation, a small colony is placed on a random point on the lattice, and then left to evolve with all the IM-rules. While a more or less homogeneous distribution of grass

is selected, as the initial condition for the PM. At every iteration the IM uses the plants' biomass distribution (obtained by the PM) to update the termites' dynamic (how many resources does a colony have access to), and the PM gets updated consequently, as mentioned before.

The simulation gives rise to FCs (created by dead colonies) and also shows a higher concentration of plant's biomass, on the border of the FCs (given by the higher moisture present in the FCs) that has been observed in reality (FCs' perennial belts), but never obtained with pure SDF models before. The simulated FCs's life-cycle is also in good accordance with empirical data.

The researchers also focused on a new aspect: namely the grass distribution between FCs after wet seasons, which displayed temporary formations of large grass clumps (randomly distributed), which later have been observed in reality.



grass clumps (source:[6])

Conclusion

Tarnita et al. invite all the researches, that work in this field, to embrace mixed models to get more accurate descriptions of reality. From this case we can also remind ourselves that, despite liking a theory more than another one, we'll always have to face reality at the end.

As a new related (more or less) topic to focus on: I propose the investigation of the patterns formed by mushrooms' distribution in fields. Possible reasons why some kind of self-organizing mechanism may be at work are:

- some types usually come in clusters, forming strips or spots
- often the grass around them has a darker color, hence it would be worth studying the interaction between grass/water/mushrooms
- some spots are more or less constant over a period of about a year, but appear to move over longer periods of time

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