Winter School – Patterns of Vegetation in Water Controlled Ecosystems

Group Work Proposal by Jonathan A. Sherratt

Colonisation on Hillslopes in Arid Environments: A Spanish Case Study

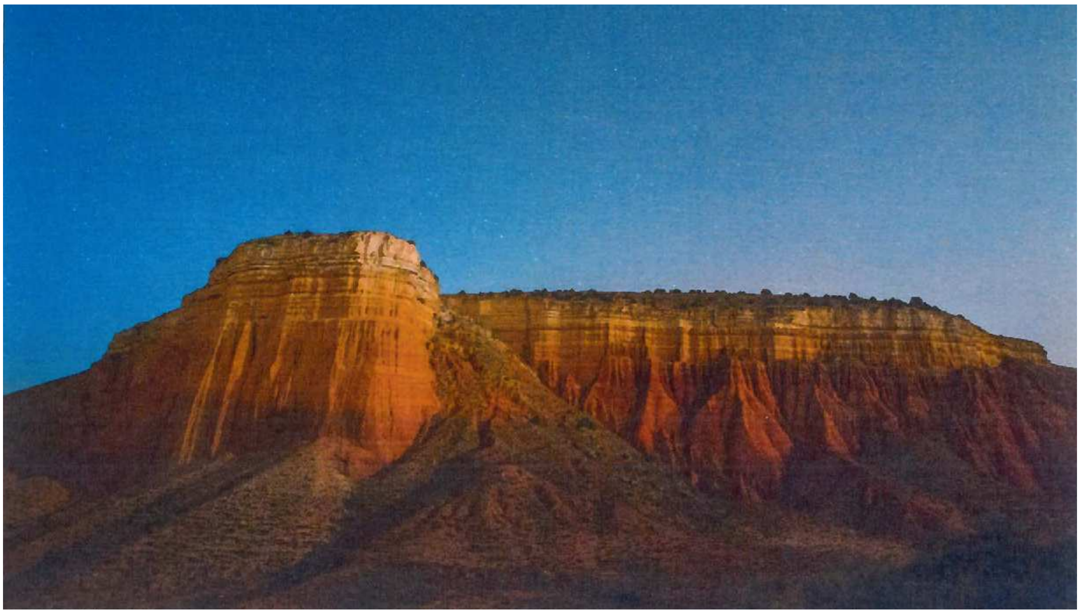

Figure 1: Photograph of terrain in the Teruel province in eastern Spain.

Field data from a wide range of environments shows that there are threshold levels of slope angle above which plants cannot colonise bare ground. A case study demonstrating this is described in Bochet *et al.* (2009). In this paper the authors present data on the Alfambra River basin, which is in Teruel province in eastern Spain. They deduce from the data that there is a critical slope angle above which plant colonisation is not possible; the critical angle depends on latitude and on slope aspect (north, south, east or west). This group work proposal concerns mathematical modelling aimed at obtaining greater insight into these field data. The proposal is divided into three parts, which are independent of one another. Thus the group could focus on one part only; alternatively different individuals could study different parts and then combine their results / conclusions.

The modelling background to the proposal are the Klausmeier equations for semi-arid vegetation (Klausmeier, 1999), which was introduced in my lectures. Water is the limiting resource for plants in dryland environments. Therefore one can reasonably assume that the rate of plant growth is proportional to water uptake. Denoting by $u(t)$ and $w(t)$ the plant and water densities respectively, this suggests the model

$$\begin{aligned} du/dt &= \overbrace{\mathcal{F}(u)\,wu}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} && \text{(1a)} \\ dw/dt &= \underbrace{A}_{\text{rain-fall}} - \underbrace{w}_{\text{evap-oration}} - \underbrace{\mathcal{F}(u)\,wu}_{\text{uptake by plants}}\,. && \text{(1b)} \end{aligned}$$

This is a dimensionless version of the model, in which t denotes time and the (dimensionless) parameters A and B can be most usefully interpreted as reflecting rainfall and plant loss (which includes herbivory), although they actually represent a combination of ecological quantities. The function $\mathcal{F}(u)$ represents the rate at which rainwater infiltrates into the soil. Ecological data indicates that this infiltration rate is positively correlated with vegetation biomass (Figure 2).

On bare ground, much of the water that falls as rain simply runs off, but higher levels of organic matter in the soil, and the presence of roots, increases the proportion of rain water infiltrating into the soil. Figure 2 shows field data supporting this positive correlation, showing an approximately linear relationship between $\mathcal{F}$ and u. A typical estimate for the plant loss parameter is $B = 0.45$ (Klausmeier, 1999).

As a simple representation of plant dispersal, we add a diffusion term to (1a). On a hillslope, we must also add a term reflecting the downhill flow of water, giving

$$\begin{aligned} \partial u/\partial t &= \overbrace{wu^2}^{\text{plant growth}} - \overbrace{Bu}^{\text{plant loss}} + \overbrace{\partial^2 u/\partial x^2}^{\text{plant dispersal}} && \text{(2a)} \\ \partial w/\partial t &= \underbrace{A}_{\text{rain-fall}} - \underbrace{w}_{\text{evap-oration}} - \underbrace{wu^2}_{\text{uptake by plants}} + \underbrace{\nu\,\partial w/\partial x}_{\text{water flow downhill}}\,. && \text{(2b)} \end{aligned}$$

The plant and water densities u and w are now functions of time t and the one-dimensional space variable x, which is measured in the uphill direction. The parameter ν reflects the slope of the hillside.

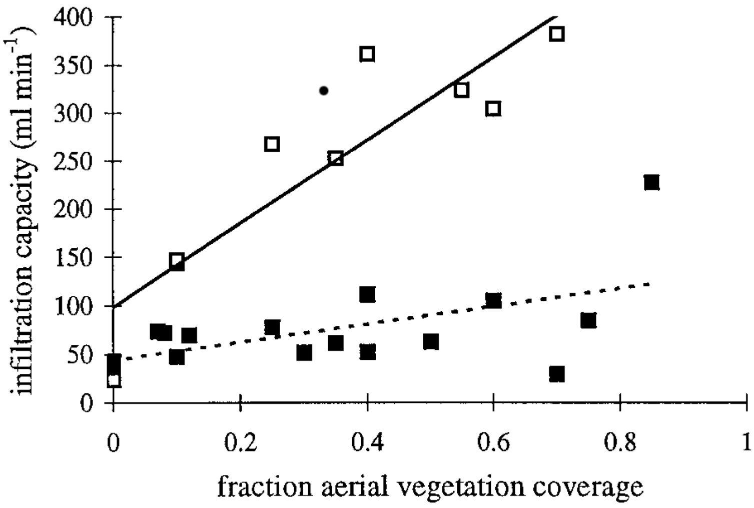

Figure 2: Empirical data for the dependence of rainwater infiltration into soil on vegetation coverage. Data were obtained using a rainfall simulator on 0.25m×0.25m plots in Burkina Faso (West Africa). For data points marked with filled squares, vegetation consisted only of annual grasses. In the case of open squares, vegetation consisted of perennial grasses, annual grasses and litter, but the horizontal axis shows only the fractional coverage by perennial grasses. This figure is reproduced from Rietkerk et al (2000).

Part 1: Mathematical analysis of colonisation in the Klausmeier model

Exercise 1.1: Using pen and paper, calculate the steady states of the model.
You should find that there are either 1 or 3 steady states, depending on the values of A and B. What is the ecological interpretation of the three steady states? Henceforth we will assume that the values of A and B are such that there are 3 steady states.

Exercise 1.2: Investigate the stability of the steady states.
The issue here is stability to spatially homogeneous perturbations, so the relevant equations are (1). It is possible to determine stability using standard methods: calculate the stability matrix and find its trace and determinant. For stability, the trace must be negative and the determinant must be positive.

Exercise 1.3: What are the travelling wave equations satisfied by invasion so-

lutions of (2)? What are the (simpler) equations satisfied when the invasion speed is zero?
The case of zero invasion speed corresponds to the critical value of A below which desertification occurs – explain why this is the case.

Exercise 1.4: Consider the case of flat ground ($\nu = 0$). Using pen and paper, eliminate the water density from the zero-speed travelling wave equations, to give a single differential equation for the plant density. Use this to find an algebraic equation satisfied by (A/B) at the onset of desertification.
Using MATLAB or other software, write a program to solve this equation numerically, and plot the critical value of A for desertification against the plant loss parameter B. These results are for flat ground – what can you infer about colonisation on slopes? Are your results consistent with the field data concerning the dependence of critical slope angle on latitude and on slope aspect?

Exercise 1.5: Calculate the conversion from the dimensionless rainfall parameter A to a dimensional rainfall in mm per year.
To do this, you will need the nondimensionalisation used to obtain (2), which is given in footnote 17 of Klausmeier (1999), and also the parameter estimates, which are given in footnote 21. What is the dimensional value of your critical rainfall for $B = 0.45$, which is a typical and widely used estimate? Search the internet to check how this compares with the mean annual rainfall levels in the Teruel region of eastern Spain.

Part 2: Numerical investigation of colonisation in the Klausmeier model

Exercise 2.1: As in part 1, use pen and paper to calculate the steady states of the model.
You should find that there are either 1 or 3 steady states, depending on the values of A and B. What is the ecological interpretation of the three steady states? Henceforth we will assume that the values of A and B are such that there are 3 steady states.

Exercise 2.2: Investigate numerically the stability of the steady states.
The issue here is stability to spatially homogeneous perturbations, so the relevant equations are (1). The procedure is as follows:

(i) Choose a value of A between 1.5 and 3.0, and fix $B = 0.45$ which is a typical and widely used estimate.

(ii) Using a calculator, find the three steady states for your chosen value of A.

(iii) With this value of A, solve (1) numerically for different initial values of u and w. By observing how the solutions evolve, deduce the stability of the three steady states.

To avoid you having to write your own computer code, I am providing the `matlab` program `sherrattlabodes.m`; you can download this from `www.macs.hw.ac.uk/∼jas/venice/` and use it if you have the `matlab` package on your laptop. Note that your results only apply to one value of A, but in fact the stability structure is the same for all A such that there are 3 steady states. (You do not need to prove this).

One issue that can be studied using the model (2) is the movement of the interface between vegetation and bare ground. Suitable initial conditions are to set u and w to the steady state corresponding to vegetation in one half of the domain, and to the steady state corresponding to bare ground in the other half. I am providing the `matlab` program `sherrattlabpdes.m`, which solves (2) subject to these initial conditions; you can download this from `www.macs.hw.ac.uk/∼jas/venice/` and use it if you have the `matlab` package on your laptop.

Exercise 2.3: Investigate the way in which the interface moves as the rainfall

parameter A varies, on flat ground.
With B fixed at 0.45, set the slope parameter ν to zero. Start with $A = 1.5$, and gradually decrease A towards the minimum value for which there are three steady states. How does the invasion of the desert by vegetation vary?

In answering the last Exercise you will have noticed that for A sufficiently small (but still large enough for three steady states), the region occupied by vegetation shrinks: it is invaded by desert rather than the other way round. Conversely, for large A the vegetated region expands, invading the desert.

Exercise 2.4: Fix $A = 1.2$, and use numerical simulations of (2) to investigate the effect on the desert invasion of varying ν between -10 and 10.
How does the slope affect the invasion speed? Explain your findings ecologically. Can your results explain the observation in the Spanish field data of a critical slope gradient for colonisation?

Exercise 2.5: By doing additional simulations, investigate the dependence of the critical slope gradient on latitude and slope aspect.
Again, can your results explain the Spanish field data?

Part 3: Formulation of a more realistic model.

The Klausmeier model is intentionally generic. The objective of this part of the project is to develop a model that is oriented more specifically towards the Alfambra River basin ecosystem.

Exercise 3.1: List some simplifications made (deliberately) by Klausmeier when formulating his model.
There are a number of such simplifications, made in the interests of mathematical convenience, and indeed the ability to mathematically study the model in detail has led to it being widely used. However these simplifications may limit the value of the model when considering field data in detail. You may find the following papers helpful as you formulate your list of simplifications: Guttal & Jayaprakash (2007), Meron *et al.* (2004), Rietkerk *et al.* (2002), Siteur *et al.* (2014), Ursino (2005).

Exercise 3.2: List some specific aspects of the Spanish case study that are poorly represented in the Klausmeier model.

The issue here is whether there are particular and perhaps unusual features of the Alfambra River basin ecosystem that should be included in a model that is intended for application to this specific case.

Exercise 3.3: With these two lists in mind, formulate a more realistic and more specific model.

This first improved model should use advection and diffusion terms to represent plant dispersal and water movement: attention should be focussed on the birth and death of plants, and on water inputs and losses.

Exercise 3.4: Consider whether alternative representations of movement terms would be more realistic.

When modelling plant populations, many authors use integral-based terms to represent dispersal. Such terms are able to reflect occasional long-range dispersal events, which can be very important for plant populations. This would cause (2) to be replaced by an integrodifferential equation. The following model derivation is based on Pueyo *et al.* (2008). Seed production can reasonably be taken as proportional to plant density u, and we denote by s_0 the average rate of seed production per plant. Seed dispersal from a plant to a given point in space will be a function K of distance from the plant; it is convenient to normalise K so that $\int K(x)\,dx = 1$. (This and the subsequent integrals are over all space). Therefore the overall rate of seed production is $S(x,t) = s_0 \int K(|x-y|)u(y)\,dy$. The rate at which seeds germinate into seedlings depends on water density, with a suitable form being $S \cdot g_1 w/(g_2 + w)$. Combining these gives the following term for plant dispersal, which could replace the diffusion term in (2a):

$$\frac{s_0 g_1 w}{g_2 + w} \int K(|x-y|)u(y)\,dy\,.$$

Consider whether this type of integral term would give an improved model in the case of the Alframbra River basin. If so, what type of data would be needed in order to accurately estimate a form for the kernel $K(.)$? Would a nonlocal term be appropriate for water movement?

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