

Pattern selection and hysteresis in the Rietkerk model for banded vegetation in semi-arid environments

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Banded vegetation is a characteristic feature of semi-arid environments. It occurs on gentle slopes, with alternating stripes of vegetation and bare ground running parallel to the contours. A number of mathematical models have been proposed to investigate the mechanisms underlying these patterns, and how they might be affected by changes in environmental conditions. One of the most widely used models is due to Rietkerk and co-workers, and is based on a water redistribution hypothesis, with the key feedback being that the rate of rainwater infiltration into the soil is an increasing function of plant biomass. Here, for the first time, we present a detailed study of the existence and stability of pattern solutions of the Rietkerk model on slopes, using the software package WAVETRAIN (WWW. ma.hw.ac.uk/wavetrain). Specifically, we calculate the region of the rainfall-migration speed parameter plane in which patterns exist, and the sub-region in which these patterns are stable as solutions of the model partial differential equations. We then perform a detailed simulation-based study of the way in which patterns evolve when the rainfall parameter is slowly varied. This reveals complex behaviour, with sudden jumps in pattern wavelength, and hysteresis; we show that these jumps occur when the contours of constant pattern wavelength leave the parameter region giving stable patterns. Finally, we extend our results to the case in which a diffusion term for surface water is added to the model equations. The parameter regions for pattern existence and stability are relatively insensitive to small or moderate levels of surface water diffusion, but larger diffusion coefficients significantly change the subdivision into stable and unstable patterns.

1. Introduction

In 1950, the geologist William MacFadyen published aerial photographs taken over British Somaliland (now northern Somalia) which provided the first documented evidence of striped patterns of vegetation alternating with bare ground [1]. It is now known that self-organized vegetation patterns are a characteristic feature of semi-arid regions in many parts of the world, particularly Africa [2,3], Australia [4,5] and North America [2,6,7]. On slopes, these patterns consist of stripes running parallel to the contours [8–11]. Many different plant types can be involved in this 'banded vegetation', and trees often interact with grasses within the bands [12]. Wavelengths are typically in the range 50-300 m (see table 2 of [8]).

There are no laboratory replicates of banded vegetation, and fieldwork is difficult because of the remoteness and physical harshness of potential study sites. Therefore, most empirical work has been restricted to remote sensing, most recently using satellite images. This has provided much valuable information; however, it has clear limitations, for instance being unable to make predictions about how patterns might change in response to



Table 1. A list of the ecological interpretations of the various parameters in the Rietkerk model (1.1). We also list the units of the parameters and the values used in this paper; apart from *R* (which we vary), these are the values given in Rietkerk *et al.* [37]. Note that there is a typo in the units for g_{max} in [37]; the correct units are given in table 1 of [36].

parameter	value	units	interpretation
С	10	${\rm g}~{\rm mm}^{-1}~{\rm m}^{-2}$	conversion of water uptake into new biomass
g _{max}	0.05	mm $g^{-1} m^{-2} d^{-1}$	maximum water uptake per unit of biomass
<i>k</i> ₁	5	mm	half-saturation constant for water uptake
D _p	0.1	$m^2 d^{-1}$	plant dispersal coefficient
α	0.2	d ⁻¹	maximum infiltration rate
k ₂	5	$\mathrm{g}~\mathrm{m}^{-1}$	saturation constant for water infiltration
W ₀	0.2	no units	water infiltration rate without plants
r _w	0.2	d ⁻¹	specific rate of evaporation and drainage
D _w	0.1	$m^2 d^{-1}$	diffusion coefficient of soil water
D	0.25	d ⁻¹	per capita death rate of plants
ν	10	$m d^{-1}$	advection coefficient for downslope water flow
R	varied	mm d^{-1}	mean rainfall

environmental variations. In view of this, and also as a result of the long space and time scales involved in vegetation pattern formation, mathematical models have emerged as a key research tool. Early models involved either cellular automata [13,14] or large systems of coupled ordinary differential equations [15]. However, partial differential equations are now established as the dominant modelling framework. An early model of this type that has been very influential was due to Klausmeier [16] and is based on the empirical observation that in semi-arid regions, the infiltration of rain water into the soil is positively correlated with vegetation biomass [8,17-19]. This results in greater water availability per unit of biomass, and thus increased plant growth, at higher vegetation densities-a positive feedback that has the potential to generate spatial patterns [20]. Klausmeier's model [16] explores this potential in a mathematical framework consisting of coupled reaction-diffusionadvection equations for plant biomass and water density. This model and small extensions of it have been explored in very great detail in both simulation-based research [21-24] and analytical studies [25-32].

Although the Klausmeier model is a valuable tool, it is by construction very simplistic. Perhaps its most pronounced simplification is the use of a single water variable. In reality, water dynamics in semi-arid regions are complex. Rainfall contributes directly to surface water, which must then infiltrate into the soil before becoming accessible to plants; and water uptake within the soil is complicated by spatiotemporal variability in rooting depth [33-35]. Most models building on the Klausmeier equations take some account of this complexity by including separate variables for soil and surface water. An important example of this is the Rietkerk model [36,37], which has been used as the basis for many modelling studies of banded vegetation. The model involves three variables: plant biomass P (gm⁻²), soil water W (mm) and surface water O (mm), which are functions of space x(m) and time t (days). Note that although the model in

[36,37] is formulated in two space dimensions, our work is restricted to one dimension. The equations have the form

plant
biomass
$$\frac{\partial P}{\partial t} = \underbrace{\frac{\partial P}{\partial p \partial^2 P}}_{\text{fow}} + \underbrace{\frac{\partial P}{\partial x^2}}_{\text{of surface water}} + \underbrace{\frac{\partial W}{W + k_1}P}_{\text{fow}} - \underbrace{\frac{\partial W}{\partial t}}_{\text{fow}} + \underbrace{\frac{\partial P}{\partial x^2}}_{\text{fow}} + \underbrace{\frac{\partial P}{\partial x^2}}_{W + k_2} + \underbrace{\frac{\partial W}{\partial t}}_{W + k_2} - \underbrace{\frac{\partial W}{W + k_1}P}_{\text{fow}} - \underbrace{\frac{\partial W}{W + k_1}P}_{\text{fow}} + \underbrace{\frac{\partial W}{\partial t}}_{W + k_1} + \underbrace{\frac{\partial W}{\partial t}}_{W + k_2} + \underbrace{\frac{\partial W}{\partial$$

and surface
$$\frac{\partial O}{\partial t} = \underbrace{\frac{\nu \partial O}{\partial x}}_{\text{flow}} - \underbrace{\alpha O \frac{P + k_2 W_0}{P + k_2}}_{\text{infiltration}} + \underbrace{R}_{\text{rainfall}}.$$
 (1.1c)

Table 1 lists the interpretation of the various parameters. Infiltration of surface water into the soil is taken to be an increasing function of plant biomass. As mentioned above, this variation is observed empirically; it results from higher levels of organic matter in the soil, and the alteration in soil structure caused by the increasing density of roots. The uptake of soil water by plants is assumed to have a Michaelis-Menten-type dependence on soil water, and the plant growth rate is assumed to be proportional to this uptakethis is reasonable for a semi-arid environment where water is the limiting resource. Soil water loss will occur due to both evaporation and drainage (leakage), and for simplicity these processes are assumed to be linear functions of water availability and are combined into a single term. Rainfall is assumed to be constant, but note that Guttal & Jayaprakash [38] have performed a detailed modelling studying on an adapted version of (1.1) that includes seasonal variation in rainfall. The use of linear diffusion to model soil water flow is deliberately simple; more detailed representations of ground water flow are used in the models of von Hardenberg et al. [39] and Meron et al. [40] for vegetation patterning. For plant dispersal, diffusion is again used for reasons of simplicity; a more realistic non-local dispersal term is used in the model of Pueyo *et al.* [41]. The one-dimensional spatial coordinate *x* runs in the uphill direction, so that the advection term in (1.1c) represents the downhill flow of surface water. Again some subsequent models have used more detailed terms; in particular, in footnote 18 of [42], Gilad *et al.* derive a representation of surface water flow using shallow water theory.

Most previous studies using the Rietkerk model (1.1) have considered pattern formation on flat ground, but in this paper we will focus on banded vegetation patterns on slopes. We will vary the rainfall parameter R, and we fix all other parameters at the values given in Rietkerk *et al.* [37], which are listed in table 1. The parameter d merits specific mention because Rietkerk *et al.* [37] give a range of values: between 0 and 0.5 d⁻¹. This is because the plant loss term includes any herbivory, the extent of which will vary greatly between sites. We fix d in the middle of this range. For the rainfall parameter R, Rietkerk *et al.* [37] again give a range of values: between 0 and 3 mm d⁻¹.

The model (1.1) has two spatially uniform steady states: a 'desert' state

$$(P, W, O) = \left(0, \frac{R}{r_{w}}, \frac{R}{(\alpha W_{0})}\right)$$

and a 'vegetated' state (P_s , W_s , O_s), where

$$W_{\rm s} = \frac{dk_1}{Cg_{\rm max} - d}, \quad P_{\rm s} = \frac{R - r_{\rm w} W_{\rm s}}{g_{\rm max} W_{\rm s}} (W_{\rm s} + k_1)$$

and $O_{\rm s} = \frac{R}{\alpha} \frac{P_{\rm s} + k_2}{P_{\rm s} + k_2 W_0}.$ (1.2)

For the parameter values given in table 1, these two steady states meet in a transcritical bifurcation at $R = 1 \text{ mm d}^{-1}$. For R > 1, the vegetated steady state is stable to homogeneous perturbations, whereas the desert steady state is unstable. For R < 1, the desert steady state is stable, whereas the vegetated steady state is unstable; also $P_s < 0$ for R < 1 so that this state is not ecologically relevant.

Patterned solutions of (1.1) arise for $R > 1 \text{ mm d}^{-1}$ when the vegetated steady state is unstable to spatially inhomogeneous perturbations. This is illustrated in figure 1, which shows large time solutions for R = 1.05, 1.1 and 1.25 mm d^{-1} on a domain of length 500 m with periodic boundary conditions and with initial conditions consisting of small inhomogeneous perturbations applied to $(P_{s_{\ell}}, W_{s_{\ell}}, O_{s})$. In each case, a periodic spatial pattern develops. The patterns are not stationary: rather they move at a constant speed in the uphill direction. Mathematically, this movement is a consequence of the advection term in (1.1c). In the field, such movement is indeed observed in many cases (see [2] and table 5 of [8]) and is due to moisture levels being higher on the uphill edge of vegetation bands than on their downhill edge; this is reflected in lower levels of plant death and higher seedling densities [43,44]. However, some field studies also report stationary banded patterns [2,45,46]. This has been attributed to complicating factors including inhibition of seed germination by long-term changes in soil structure in non-vegetated regions [45], and preferential dispersal of seeds in the downslope direction, due to transport in run-off [47,48].



Figure 1. Plots against x of pattern solutions of (1.1) for R = 1.05, 1.10 and 1.25 mm d^{-1} , showing plant density (red), soil water (green) and surface water (blue). These solutions correspond to banded vegetation patterns. As R increases from 1.05 to 1.25 mm d⁻¹, the width of the vegetation bands grows larger and the bare interbands become narrower. Our starting solutions were set at the vegetated steady state (1.2), perturbed randomly by +5%. The model (1.1) was solved numerically on the domain 0 < x < 500 up to $t = 200\ 000$ days for $R = 1.05\ \text{mm}\ \text{d}^{-1}$ and t = 800000 days for R = 1.1 and 1.25 mm d⁻¹. These long solution times allow transients to fully dissipate. In each case, the patterns move in the uphill (positive x) direction, and we estimated the migration speed to be (a) 0.053 m d^{-1} , (b) 0.052 m d^{-1} and (c) 0.039 m d^{-1} . We used a semi-implicit finite difference method with periodic boundary conditions at both ends; we chose a grid spacing of $\delta x = 0.5$ and a time step of $\delta t = 0.025$ so that the CFL (Courant – Friedrichs – Lewy) number $\nu \delta t / \delta x = 0.5$. The standard criterion for numerical convergence in simple reaction-advection equations is that the CFL number is less than 1. (Online version in colour.)



Figure 2. Plots of the region in the R-c plane in which pattern solutions exist. (*a*) The full region, which is bounded by a locus of Hopf bifurcations of the vegetated steady state (plotted in orange) and a locus of homoclinic solutions (plotted in red). (*b*) A close-up for small *c*. This shows that there is a small region to the right of the Hopf bifurcation locus in which patterns exist. This region is bounded by a locus of folds (plotted in blue) and is too small to be visible in (*a*). Note that there are also pattern solutions with c < 0 for R < 1 mm d⁻¹, but these involve negative values of *P* and are therefore not ecologically relevant. (Online version in colour.)

2. Existence and stability of pattern solutions

The uphill migration of pattern solutions means that they are periodic travelling waves, with the form $P(x, t) = \tilde{P}(z)$, $W(x, t) = \tilde{W}(z)$ and $O(x, t) = \tilde{O}(z)$, where z = x - ct and c is the migration speed. Substituting these solution forms into (1.1) gives a fifth-order system of travelling wave ordinary differential equations. Pattern solutions of (1.1) correspond to limit cycle (periodic) solutions of these equations. Note that our restriction to one space dimension means that the patterns we consider would correspond to stripes running parallel to the contours in a two-dimensional setting. The specification in table 1 fixes all of the parameters in the travelling wave equations except two: the rainfall R and the migration speed c. Our initial objective is to determine the region of the R-c parameter plane in which patterns exist. General theory implies that this region will be bounded by segments of three types of loci: Hopf bifurcations, homoclinic (infinite period) solutions and folds in a limit cycle solution branch. We calculated these loci using WAVETRAIN (www.ma. hw.ac.uk/wavetrain) [49], which is a software package based on numerical continuation [50] that is specifically designed for the study of periodic travelling wave solutions of partial differential equations.

Figure 2 illustrates the region of the R-c plane in which patterns exist, determined using WAVETRAIN. It extends to values of the migration speed c that are much too large for ecological realism (up to 14 m d⁻¹) and are also very much larger than those observed in simulations such as figure 1, for which we measured speeds less than 0.1 m d^{-1} for each of the three values of *R*. This led us to consider the stability of patterns as solutions of (1.1), which can also be studied using WAVETRAIN. Rademacher et al. [51] proposed a method for determining the stability of periodic travelling waves by numerical continuation of the spectrum, and this is implemented in WAVETRAIN [52]. Using this approach, we found that patterns are unstable in almost all of the region illustrated in figure 2, with stable patterns only occurring for *c* less than about 0.2 m d^{-1} . Therefore, we focused attention on that part of the parameter region. We found that there were stable patterns for *R* between about 0.4 and 1.4 mm d^{-1} , and c between about 0.02 and 0.2 m d^{-1} . At the lower



Figure 3. An illustration of the part of the R-c parameter plane giving stable patterns, which is shaded. The locus of Hopf bifurcations is plotted in orange, the stability boundary in green, a homoclinic locus in pink and the locus of folds in blue. The homoclinic locus is actually an approximation, given by the locus of periodic travelling waves of fixed period 1000 m. We also plot in grey the locus of waves of fixed periods 100, 250 and 500 m. To improve clarity, we omit from this plot a small closed loop of fold loci, which is shown in figure 6. The units of rainfall are millimetres per day, and speed is measured in metres per day. (Online version in colour.)

boundary of this region of stable patterns, there is a stability change of Eckhaus (sideband) type, meaning that there is a change in the sign of the curvature of the spectrum at the origin. This stability boundary is a locus of Eckhaus points, which can again be traced using WAVETRAIN [52]. The R-c parameter region giving stable patterns is illustrated in figure 3, in which we also plot several contours of fixed pattern wavelength. This division of the parameter plane into regions giving stable and unstable patterns is of key importance in applications, because only stable patterns will be observed



Figure 4. (*a*) The period as a function of *R* for c = 0.04 m d⁻¹. Note that there are two different waves, wave 1 (period 133 m) and wave 2 (period 104 m) at R = 1.29 mm d⁻¹. The red square indicates a Hopf bifurcation point. (*b*,*c*) Spectra for wave 1 (unstable) and wave 2 (stable). (Online version in colour.)



Figure 5. Bifurcation diagram for $c = 0.02 \text{ m d}^{-1}$, plotting the pattern wavelength as a function of the rainfall parameter *R* (mm d⁻¹). (*a*) The whole bifurcation diagram: there are two Hopf points for this *c* value (red squares), at *R* = 1 and *R* = 1.27 mm d⁻¹. (*b*) Detail of the solution branch emanating from the second Hopf point. Our numerical continuation of this branch failed at a period of about 1500 m, but we speculate that this solution branch actually extends to arbitrarily large periods. (Online version in colour.)

as spatially extensive model solutions, although 'convectively unstable' patterns can arise as long-term spatio-temporal transients (see §5).

To consider the parameter region illustrated in figure 3 in more detail, it is helpful to consider the solutions as R varies, with the migration speed c fixed. For values of c above about 0.037 m d^{-1} , and also below about 0.015 m d^{-1} , the pattern solution branch connects the Hopf bifurcation at $R \approx 1.25$ mm d⁻¹ to the homoclinic (infinite period) solution at the left-hand edge of the parameter region giving patterns. For smaller values of *c*, the Hopf bifurcation is subcritical, meaning that the solution branch initially proceeds in the direction of increasing R and then folds. The locus of these folds forms the boundary of the parameter region in which patterns exist: to the right of this locus there are no patterns. Figure 4 shows detail near the fold for $c = 0.04 \text{ m d}^{-1}$ and includes plots of the spectra for the two different patterns that coexist at a single value of *R*. The solutions with larger/ smaller period are unstable/stable, respectively. Thus as one moves along the solution branch, there is a change in stability at the fold.

For *c* between about 0.015 and 0.037 m d^{-1} , the structure is more complicated. There is then a solution branch connecting two homoclinic loci, which folds just beyond the right-most homoclinic locus: the fold and homoclinic loci are very close and cannot be resolved in figure 3. There is also a separate solution branch that emanates from the Hopf bifurcation at $R \approx 1.25$ mm d⁻¹. This branch has a snaking form, with a tortuous variation in the period (figure 5). Snaking solution branches have been studied in great detail for localized patterns in the Swift-Hohenberg equation [53,54]; in that context, additional peaks are added to the pattern pulse as one moves up the twists of the snaking branch. By contrast, the snaking branch shown in figure 5 consists entirely of periodic (i.e. non-localized) solutions. The part of the R-cplane in which this snaking behaviour occurs is clarified by plotting the loci of the initial folds along the branch, which form a closed loop in the R-c plane (figure 6). The snaking behaviour occurs for values of *c* within this loop. Calculation of the spectra suggests that all of the many solutions along these snaking branches are unstable as solutions of (1.1) (figure 7). From these investigations, we conclude that the 5

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Figure 6. Detail of the R-c parameter plane to illustrate the region in which the snaking behaviour shown in figure 5 occurs. As in figure 3, the locus of Hopf bifurcations is plotted in orange and the locus of folds is plotted in blue. The closed loop of fold loci, which was omitted from figure 3 for clarity, corresponds to the initial folds along the snaking solution branch. Therefore, this loop indicates the parameter region in which the snaking behaviour occurs. The units of rainfall are millimetres per day, and speed is measured in metres per day. (Online version in colour.)

snaking branches do not have ecological relevance, and those patterns that are stable for *c* in this range ($0.015-0.037 \text{ m d}^{-1}$) lie on the solution branch connecting the two homoclinic loci.

Finally, we comment that for all values of *c*, there is also a second solution branch that emanates from the part of the Hopf bifurcation locus running through the middle of the pattern region (at $R \approx 1 \text{ mm d}^{-1}$). This branch is very tightly localized in *R* and involves only patterns with extremely large periods (see figure 5); it is therefore of no practical relevance.

The basic conclusion of this section is that there is a single stable pattern solution in the shaded region of the parameter plane in figure 3. There are additional patterns in some other parts of this region, but they are all unstable. This information is of considerable value in understanding and interpreting the results of model simulations. To illustrate this, we will consider in §3 the way in which the vegetation patterns predicted by (1.1) change as the rainfall parameter is gradually varied. We will show that there are abrupt changes in pattern wavelength which can be explained by the results in figure 3.

3. Pattern evolution for variable rainfall

The model idealization of constant parameter values is of course a simplification. In reality, vegetation dynamics are strongly affected by environmental changes, and as a case study we consider the response to variations in rainfall. We performed a series of long numerical simulations on a domain with periodic boundary conditions. We chose a wavelength compatible with these boundary conditions, i.e. (domain length)/N for some integer N. As an initial condition, we used a pattern of this wavelength (a mode N pattern). To reduce computation time, we chose an initial value of R such that the pattern is relatively close to the stability boundary, on the stable side; our results are not sensitive to the initial choice of R. We calculated the initial pattern using WAVETRAIN. We solved for 20 000 days, which is about 55 years. We then made a small change in R and solved for another 20 000 days. We repeated this process, recording the pattern speed and wavelength immediately before each change in R. We varied the increments in R slightly in order to improve the clarity of the results. Note that we do not add noise or any other external perturbation when we change the value of R. Typical results are shown in figure 8, for two different initial values of R. As R varies, the pattern remains on the period contour until this crosses the stability boundary, when it jumps to a new value. Further changes in R cause the pattern to remain on the new period contour, even when the variation in R is reversed. Simulations starting with patterns of other mode numbers N give similar results.

These results imply that the pattern wavelength depends not only on environmental parameters, but also on their values at previous times. Hysteresis between patterned vegetation and bare ground has been noted in a number of previous modelling papers [9,39,40]. Our results show a different type of hysteresis, between patterns of different wavelength. This type of historydependence has been noted previously in simulations of the Klausmeier model for banded vegetation [21,55]. Its occurrence in the more realistic Rietkerk model argues strongly that it should also be expected in real ecosystems with banded vegetation if the patterns arise because of water redistribution, because this mechanism is the common assumption underlying both the Klausmeier and Rietkerk models. However, it should be noted that our results are all for finite domains with periodic boundary conditions, and their robustness to changes in boundary conditions have not been investigated. There are very few data against which the prediction of hysteresis can be tested, because it would require measurements of wavelength at a series of time points spanning several decades for a single study site. There are a number of examples of such data for two different time points, which have been collected to assess the extent of uphill migration. Older studies of this type measure pattern location relative to ground benchmarks [56,57] while most recent research is based on satellite images [2,11]. The only dataset that we are aware of involving multiple wavelength estimates over several decades is in [58]. This paper studied banded vegetation at several sites in Niger on six occasions between 1950 and 1995. Rainfall varied significantly over this period, and this was reflected in variations in the band : interband width ratio, but the wavelength of the patterns remained constant. This is consistent with our simulation results and suggests that larger variations in rainfall would be needed to induce shifts in pattern wavelength. Climate change means that such large fluctuations in rainfall and other environmental parameters are increasingly likely, and the high volume and easy availability of satellite images will make any resulting pattern change easy to detect over the coming years.

Our work shows that plots of parameter regions giving patterns are very helpful for understanding results from model simulations, with the boundary between stable and unstable patterns being particularly significant. We do not know how to predict the new wavelength that develops when the current period contour crosses the stability boundary. However, we have found that the new value depends on the increments made in the rainfall parameter *R*. As an example, the contour of period 50 m crosses the stability boundary at $R = 0.705 \text{ mm d}^{-1}$. We started with a (stable) pattern of wavelength 50 m (mode 10) with $R = 0.73 \text{ mm d}^{-1}$, again on a domain of length 500 m with periodic boundary conditions. Decreasing *R* to 0.61 mm d⁻¹ leads to a change in wavelength, with a mode 3 pattern (wavelength 166.7 m) developing between 5000 and 10 000 time units (days) after



Figure 7. (*a*) Detail of the solution branch emanating from the Hopf bifurcation at $R = 1.27 \text{ mm d}^{-1}$ and $c = 0.02 \text{ m d}^{-1}$ (indicated by a red square). We plot the period as a function of *R*. Within our chosen limits on the period axis, there are six different patterns for $R = 1.286 \text{ mm d}^{-1}$, and in (*b*) we plot their spectra. All six solutions are unstable. Note that there is a stable pattern for $R = 1.286 \text{ mm d}^{-1}$ and $c = 0.02 \text{ m d}^{-1}$, but this lies on a different solution branch that connects two homoclinic solutions (see figure 5). (Online version in colour.)

the change in *R*. If instead *R* is reduced to only 0.64 mm d⁻¹, then the solution still resembles a mode 10 pattern after 20 000 time units (days). This is probably due to the very slow growth of the unstable linear modes; a further decrease in *R* quickly induces a shift to a mode 3 pattern. Conversely, when a larger change in *R* is applied, to 0.57 mm d⁻¹, vegetation disappears entirely to give the desert steady state, which is stable for $R < 1 \text{ mm d}^{-1}$. This is a significant result for real vegetation patterns, suggesting that sufficiently large changes in the environment can eradicate vegetation even at rainfall levels that are high enough to support it.

4. Model extension: lateral spread of surface water

In (1.1), the flow of surface water is assumed to be due entirely to the slope. The surface water variable O is simply the height (mm) above ground of the surface water

layer, and if this varies in space then there will be flow even on flat ground, due to pressure differences. In their original model (which assumed flat ground), HilleRisLambers *et al.* [36] included a diffusion term for *O* as a simple representation of this process. When Rietkerk *et al.* [37] applied the model to vegetation dynamics on a slope, they removed the diffusion term and replaced it with the advection term that is in (1.1*c*), on the basis that downhill flow will be dominant. We now consider the effect of including the diffusion term, as well as the advection term, in the equation for surface water. Thus, we add the term $D_O \partial^2 O / \partial x^2$ to the right-hand side of (1.1*c*). Again we restrict attention to one space dimension.

With the other parameters fixed at the values given in table 1, we investigated the existence and stability of pattern solutions in the R-c plane as D_O is varied (figure 9). Note that the units of D_O are m² d⁻¹. For $D_O = 1$, there is no visible difference from the $D_O = 0$ case (compare figure 9*a* with figure 3). Increasing D_O to 25 has little effect: just a slight

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Figure 8. Numerical solutions of (1.1) on a domain of length 2000 m with periodic boundary conditions and with initial conditions consisting of a wave on the period contour of period 62.5 (=2000/32) m. The green curve shows the boundary between stable and unstable patterns. The insert shows details of how patterns are affected as the rainfall increases above the stability threshold for large *R*; the range on the vertical axis is 0.012 < c < 0.04, while that on the horizontal axis is 1.21 < R < 1.39. The black dots represent the wavelength and speed obtained as R is varied and the arrows indicate the direction of this variation. The partial differential equations (1.1) were solved numerically using a finite difference scheme with periodic boundary conditions. The rainfall parameter *R* was changed every 20 000 days, and the wavelength and speed were recorded immediately before each change in R. We used a spatial grid spacing of 0.25 and fixed the CFL (Courant-Friedrichs-Lewy) number at 0.8 by using a time step of 0.02. The units of rainfall are millimetres per day, and speed is measured in metres per day. (Online version in colour.)

shift in the stability boundary. However, for D_O above about 35, there is a significant difference. The region in which periodic travelling waves exist is little changed (at least within the part of the R-c plane we are considering) but the stability boundary changes shape completely. Note in particular that the minimum speed for stable patterns decreases significantly. At large D_O , the advection term in the O equation is dominated by lateral diffusion, so that our finding of stable patterns that move very slowly is consistent with Rietkerk *et al.*'s [37] original observation of stationary patterns on flat ground.

As D_O is increased from 50 to 100, the stability change on one part of the stability boundary changes from Eckhaus to Hopf type, meaning that it is associated with eigenvalues away from the origin (see figure 10). This change has major implications for the way in which patterns respond to changes in rainfall. In §3, we showed that as rainfall varies with $D_O = 0$, patterns remain of constant wavelength until the wavelength contour crosses a stability boundary (of Eckhaus type), when there is an abrupt transition to a new wavelength. Corresponding simulations for $D_O = 100$ show that there is no such abrupt transition when the wavelength contour crosses the stability boundary of Hopf type (figure 11). Instead, the pattern remains approximately periodic with the same spatial wavelength, but becomes oscillatory in time. Of course, the pattern is intrinsically oscillatory in time, being a periodic travelling wave, but there are now additional oscillations of higher frequency. Figure 12a,b shows plots of plant density against space and time when R = 1.15 during the simulation used for figure 11. The time course clearly involves a superposition of different oscillations, and this is clarified by calculation of the power spectrum (figure 12*c*). The dominant temporal period is that associated with the underlying periodic travelling wave, which is equal to the wavelength divided by the wave speed. The power series also shows a second significant period, which corresponds approximately to the most unstable part of the spectrum for the underlying periodic travelling wave.

5. Discussion

Among the various mathematical models that have been proposed for vegetation patterning in semi-arid environments, the Rietkerk model [36,37] is probably the most widely used, both as a research tool for ecologists and as the basis for model extensions. Despite this very widespread usage, all work on this model has to our knowledge been simulation-based, except for the numerical bifurcation diagrams presented in Rietkerk et al.'s [37] original paper. Here, we have performed a systematic study of pattern existence and stability. We have also shown that these results provide a straightforward explanation for the complex, history-dependent changes in pattern that occur in response to variations in rainfall. Finally, we considered the way in which our results are affected by the inclusion of a diffusion term in the equation for surface water. This showed that abrupt changes in wavelength only occur when the wavelength contour crosses stability boundaries of Eckhaus type. When the surface water diffusion coefficient is sufficiently large, one of the stability boundaries is of Hopf type, and a crossing of this boundary results in a gradual change in pattern form and the onset of more complicated temporal oscillations, rather than an abrupt transition to a different pattern. All of our work is in one space dimension, so that the patterns that we consider correspond to stripes running parallel to the contours. Extension of our work to two space dimensions is an important but challenging goal for future research.

A key aspect of our work is the classification of patterns into those that are stable/unstable as solutions of (1.1). It is important to emphasize that unstable patterns are not necessarily irrelevant for real instances of banded vegetation. Unstable solutions of a partial differential equation subdivide according to whether the instability is 'convective' or 'absolute' [59-61]. In the former case, the solutions can occur as persistent spatio-temporal transients [62,63]. Unfortunately, the numerical procedures currently available to distinguish convective and absolute instabilities apply only to very special types of partial differential equation that do not include (1.1). However, we can say definitely that both types of instability do occur in the Rietkerk model. General theory implies that patterns sufficiently close to the stability boundary (and on the unstable side) will be convectively unstable [59]. Moreover, if the spectrum of the pattern contains an isola to the right of its unbounded part and in the right-hand half of the complex plane, then it is known that the solution is absolutely unstable; this was proved by Rademacher [64] and his paper contains a precise statement of the result. Thus, for example, 'wave 1' in figure 4 is absolutely unstable, as are all six solutions on the snaking branch shown in figure 7. Numerical methodology for determining



Figure 9. (a-f) Illustrations of the part of the R-c parameter plane giving stable patterns for $D_0 = 1, 25, 34, 35, 50, 100 \text{ m}^2 \text{ d}^{-1}$. The locus of Hopf bifurcations is plotted in orange, a homoclinic locus in pink and the locus of folds in blue. The stability boundary is plotted in green when it is of Eckhaus type and cyan when it is of Hopf type. The homoclinic locus is actually an approximation, given by the locus of patterns of wavelength 1200 m. Contours of constant wavelength 100, 250 and 500 m are also shown, in grey. The plots in this figure should be compared with figure 3 which shows the corresponding results for $D_0 = 0$. The units of rainfall are millimetres per day, and speed is measured in metres per day. (Online version in colour.)



Figure 10. Eigenvalue spectra of patterns near the stability boundary in the cases $D_0 = 50$ and $100 \text{ m}^2 \text{ d}^{-1}$. The left-/right-hand columns show spectra of patterns that are stable/unstable. For $D_0 = 50 \text{ m}^2 \text{ d}^{-1}$, the stability change is associated with a change in the sign of the curvature of the spectrum at the origin (stability change of Eckhaus type). For $D_0 = 100 \text{ m}^2 \text{ d}^{-1}$, the spectrum passes through the imaginary axis away from the origin as the stability boundary is crossed: this is a stability change of Hopf type. The units of rainfall are millimetres per day, and speed is measured in metres per day. (Online version in colour.)



Figure 11. Numerical solutions of (1.1) on a domain of length 500 m, with periodic boundary conditions, and with two different initial conditions, each consisting of a wave of period 100 m. The black dots represent the wavelength and speed obtained as *R* is varied and the black arrows indicate the direction of this variation. The red dot and vertical arrow indicate the point used for figure 12. When the period contour crosses the part of the stability boundary of Eckhaus type (green; at $R \approx 0.5$ mm d⁻¹), there is an abrupt transition to a pattern with a different wavelength, as discussed in §3. However, when the period contour crosses the part of the stability boundary of Hopf type (cyan; at $R \approx 1.01 \text{ mm d}^{-1}$), the pattern remains approximately periodic with spatial period 100 m, but acquires a complex spatio-temporal form involving multiple temporal frequencies (see figure 12 for details). The partial differential equations (1.1) were solved numerically using a finite difference scheme with periodic boundary conditions. The rainfall parameter R was changed every 20 000 days, and the wavelength and speed were recorded immediately before each change in *R*. We used a spatial grid spacing of 0.5 and a time step of 0.001. The units of rainfall are millimetres per day, and speed is measured in metres per day. (Online version in colour.)

absolute stability is an active research area, and if suitable methods become available then a systematic subdivision of the parameter region giving unstable waves would be a valuable study.

Vegetation patterns in semi-arid environments have been studied for more than 60 years. Within the last 10-15 years, it has become clear that they are just one example of selforganized patterns at the landscape scale. A comprehensive survey of such patterns is given in Rietkerk & van de Koppel [65], and we discuss here a few examples. Many savannah ecosystems comprise localized patches of trees in a grassy background [66]. These patterns arise primarily from interactions between rainfall and fire; the former is often erratic and its impact depends on both soil structure and local topography [67], while the frequency of fires has a strong negative correlation with tree cover [68]. The result is a complex and dynamically evolving vegetation structure [69]. In peatlands, one commonly observes patterns of ridges and hollows, with the latter sometimes containing water pools [70-72]. The ridges contain a layer of aerobic peat (the 'acrotelm') that contains peat-forming plants and mosses, and which is thin or absent in the hollows. There is a positive feedback between acrotelm thickness and the rate of peat formation [73], and the observed patterns are thought to arise from the combination of this feedback, a scaledependent accumulation of nutrients in the ridges [74] and water-ponding due to lower hydraulic conductivity in the ridges compared with the hollows [75].

In subalpine forests, strong and consistent winds can cause trees to self-organize into linear patterns [76]. The key mechanism here is that one tree shelters another on its downwind side. The resulting linear patterns can run either parallel or perpendicular to the prevailing wind direction. The former pattern type is known as 'hedges' and is widespread, having been documented in North America, Japan and New Zealand [77]. Lines of trees running perpendicular to the wind direction and separated by unforested gaps are known as 'ribbon forests' [78]; they appear to be restricted to the Rocky Mountains. Snow drifting along the lines of trees is thought to be an important factor in the persistence of these patterns [79,80]: the deep parts of snow drifts prevent seedling 10



Figure 12. Detail of the simulation used in figure 11 when R = 1.15 (indicated by the red dot and vertical arrow in figure 11). This point is chosen as being a moderate distance beyond the stability boundary of Hopf type, so that the instability of the pattern is clearly visible. We show the plant density as a function of space at t = 20000 years (*a*), and as a function of time at x = 100 m (*b*). The temporal behaviour is suggestive of multiple frequencies, and we confirmed this by calculating the power spectrum ('periodogram') (*c*). The dominant period is that associated with the underlying periodic travelling wave, which is the ratio of the wavelength (100 m) and the wave speed (0.038 m d⁻¹). Note that this differs by about 0.3% from the period reported in the power spectrum, due to numerical errors in the simulations. There is also a second significant peak in the power spectrum, which corresponds approximately to the most unstable point in the eigenvalue; this occurs at Im(eigenvalue) ≈ 0.0058 and therefore corresponds to a period of $2\pi/0.0058 \approx 1080$. The power spectru was calculated from a time series of one plant density per year over 20 000 years, as the average of 100 individual power spectra. Each of these spectra used $2^{13} = 8192$ consecutive data points, with the 100 starting points distributed evenly across the first 11 808 points of the time series. The fast Fourier transforms were calculated using the double precision version of the routine fftf from the software package FFTPACK (www.netlib.org/fftpack). (Online version in colour.)

establishment, whereas shallower parts are beneficial since they provide shelter during the winter. Geomorphology is also thought to play an important role in the formation of some ribbon forests, with trees lying along geological ridges [81]. 'Wave regenerated forests' (a.k.a. 'Shimagare') are a different type of linear tree pattern, also running perpendicular to the prevailing wind direction [82,83]. Here, there are alternating bands of live and dead trees; in the former, tree height and age increases in the upwind direction up to an abrupt interface, while extensive regeneration occurs among the dead and dying trees. The bands gradually move in the windward direction, on the timescale of the tree generation time. Patterns of this type occur in Japan, USA and Argentina [76]. As a final example, we mention mussel beds in the Wadden Sea, a large intertidal region bordering the Netherlands, Germany and Denmark. These are self-organized into stripes perpendicular to the tidal flow, with a wavelength of 6-10 m [84]. Two different mechanisms have been proposed for this type of pattern formation. Van de Koppel et al. [85] argue that the binding of mussels to one another, via byssal threads, could cause reduced losses from predation and wave dislodgement at higher mussel densities. Their model has been studied in great detail by Wang et al. [86]. Van Leeuwen *et al.* [84] suggest that the greater deposition of sediment under large clumps of mussels could provide an alternative explanation: the increased elevation gives mussels greater access to algal food in higher water layers. Liu *et al.* [87] present a detailed model demonstrating the feasibility of this mechanism, and comparing its implications with the reduced losses hypothesis.

Some of these landscape-scale patterns are more amenable to empirical study than banded vegetation in semi-arid landscapes. For example, van de Koppel *et al.* [88] successfully achieved self-organized patterning of mussel beds in laboratory tanks, although the patterns were labyrinthine rather than banded. But in all cases, the predictive ability of experiments is severely limited, and mathematical modelling has a vital role to play in understanding how the patterns will be affected by changing environmental conditions. Our work suggests that detailed mathematical investigations of pattern formation in such models will provide a key framework for the understanding of simulation-based studies.

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References

- MacFadyen WA. 1950 Vegetation patterns in the semi-desert plains of British Somaliland. *Geogr. J.* 116, 199–211. (doi:10.2307/1789384)
- Deblauwe V, Couteron P, Bogaert J, Barbier N. 2012 Determinants and dynamics of banded vegetation pattern migration in arid climates. *Ecol. Monogr.* 82, 3–21. (doi:10.1890/11-0362.1)
- Müller J. 2013 Floristic and structural pattern and current distribution of tiger bush vegetation in Burkina Faso (West Africa), assessed by means of belt transects and spatial analysis. *Appl. Ecol. Environ. Res.* 11, 153–171.
- Berg SS, Dunkerley DL. 2004 Patterned mulga near Alice Springs, central Australia, and the potential threat of firewood collection on this vegetation community. *J. Arid Environ.* 59, 313–350. (doi:10. 1016/j.jaridenv.2003.12.007)
- Moreno-de las Heras M, Saco PM, Willgoose GR, Tongway DJ. 2012 Variations in hydrological connectivity of Australian semiarid landscapes indicate abrupt changes in rainfall-use efficiency of vegetation. J. Geophys. Res., 117, G03009. (doi:10. 1029/2011JG001839)
- Montaña C. 1992 The colonization of bare areas in two-phase mosaics of an arid ecosystem. *J. Ecol.* 80, 315–327. (doi:10.2307/2261014)
- McDonald AK, Kinucan RJ, Loomis LE. 2009 Ecohydrological interactions within banded vegetation in the northeastern Chihuahuan Desert, USA. *Ecohydrology* 2, 66–71. (doi:10.1002/eco.40)
- Valentin C, d'Herbès JM, Poesen J. 1999 Soil and water components of banded vegetation patterns. *Catena* 37, 1–24. (doi:10.1016/S0341-8162(99) 00053-3)
- Rietkerk M, Dekker SC, de Ruiter PC, van de Koppel J. 2004 Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**, 1926–1929. (doi:10.1126/science.1101867)
- Deblauwe V, Barbier N, Couteron P, Lejeune O, Bogaert J. 2008 The global biogeography of semi-arid periodic vegetation patterns. Glob. Ecol. Biogeogr. 17, 715–723. (doi:10.1111/j.1466-8238.2008.00413.x)
- Deblauwe V, Couteron P, Lejeune O, Bogaert J, Barbier N. 2011 Environmental modulation of selforganized periodic vegetation patterns in Sudan. *Ecography* 34, 990–1001. (doi:10.1111/j.1600-0587.2010.06694.x)
- Baudena M, Rietkerk M. 2013 Complexity and coexistence in a simple spatial model for arid savanna ecosystems. *Theor. Ecol.* 6, 131–141. (doi:10.1007/s12080-012-0165-1)
- Thiéry JM, D'Herbès J-M, Valentin C. 1995 A model simulating the genesis of banded vegetation patterns in Niger. J. Ecol. 83, 497–507. (doi:10. 2307/2261602)
- Dunkerley DL. 1997 Banded vegetation: development under uniform rainfall from a simple cellular automaton model. *Plant Ecol.* **129**, 103–111. (doi:10.1023/A:1009725732740)
- 15. Mauchamp A, Rambal S, Lepart J. 1994 Simulating the dynamics of a vegetation mosaic: a spatialized

functional model. *Ecol. Modell.* **71**, 107–130. (doi:10.1016/0304-3800(94)90078-7)

- Klausmeier CA. 1999 Regular and irregular patterns in semiarid vegetation. *Science* 284, 1826–1828. (doi:10.1126/science.284.5421.1826)
- Callaway RM. 1995 Positive interactions among plants. *Botanical Rev.* **61**, 306–349. (doi:10.1007/ BF02912621)
- Hills RC. 1971 The influence of land management and soil characteristics on infiltration and the occurrence of overland flow. *J. Hydrol.* 13, 163–181. (doi:10.1016/0022-1694(71)90213-7)
- Rietkerk M, Ketner P, Burger J, Hoorens B, Olff H. 2000 Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. *Plant Ecol.* **148**, 207–224. (doi:10.1023/A:1009828432690)
- Rietkerk M, Van de Koppel J. 1997 Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* 79, 69–76. (doi:10.2307/3546091)
- Sherratt JA, Lord GJ. 2007 Nonlinear dynamics and pattern bifurcations in a model for vegetation stripes in semi-arid environments. *Theor. Pop. Biol.* 71, 1–11. (doi:10.1016/j.tpb.2006.07.009)
- Liu Q-X, Jin Z, Li BL. 2008 Numerical investigation of spatial pattern in a vegetation model with feedback function. *J. Theor. Biol.* **254**, 350–360. (doi:10.1016/j.jtbi.2008.05.017)
- Borthagaray AI, Fuentes MA, Marquet PA. 2010 Vegetation pattern formation in a fog-dependent ecosystem. J. Theor. Biol. 256, 18–26. (doi:10. 1016/j.jtbi.2010.04.020)
- Ursino N, Contarini S. 2006 Stability of banded vegetation patterns under seasonal rainfall and limited soil moisture storage capacity. *Adv. Water Resour.* 29, 1556–1564. (doi:10.1016/j.advwatres. 2005.11.006)
- van der Stelt S, Doelman A, Hek G, Rademacher JDM.
 2013 Rise and fall of periodic patterns for a generalized Klausmeier – Gray – Scott model. J. Nonlinear Sci. 23, 39 – 95. (doi:10.1007/s00332-012-9139-0)
- Sherratt JA. 2005 An analysis of vegetation stripe formation in semi-arid landscapes. J. Math. Biol. 51, 183–197. (doi:10.1007/s00285-005-0319-5)
- Sherratt JA. 2010 Pattern solutions of the Klausmeier model for banded vegetation in semiarid environments. I. *Nonlinearity* 23, 2657–2675. (doi:10.1088/0951-7715/23/10/016)
- Sherratt JA. 2011 Pattern solutions of the Klausmeier model for banded vegetation in semiarid environments. II. Patterns with the largest possible propagation speeds. *Proc. R. Soc. A* 467, 3272–3294. (doi:10.1098/rspa.2011.0194)
- Sherratt JA. 2013 Pattern solutions of the Klausmeier model for banded vegetation in semiarid environments. III. The transition between homoclinic solutions. *Phys. D* 242, 30–41. (doi:10. 1016/j.physd.2012.08.014)
- 30. Sherratt JA. 2013 Pattern solutions of the Klausmeier model for banded vegetation semi-arid

environments. IV. Slowly moving patterns and their stability. *SIAM J. Appl. Math.* **73**, 330–350. (doi:10. 1137/120862648)

- Sherratt JA. 2013 Pattern solutions of the Klausmeier model for banded vegetation in semiarid environments. V. The transition from patterns to desert. *SIAM J. Appl. Math.* **73**, 1347–1367. (doi:10.1137/120899510)
- Kealy BJ, Wollkind DJ. 2012 A nonlinear stability analysis of vegetative Turing pattern formation for an interaction 'diffusion plant – surface water model system in an arid flat environment. *Bull. Math. Biol.* 74, 803–833. (doi:10.1007/s11538-011-9688-7)
- Schwinning S. 2010 The ecohydrology of roots in rocks. *Ecohydrology* 3, 238–245.
- Nippert JB, Knapp AK. 2007 Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos* **116**, 1017–1029. (doi:10.1111/j. 0030-1299.2007.15630.x)
- Nippert JB, Knapp AK. 2007 Linking water uptake with rooting patterns in grassland species. *Oecologia* 153, 261–272. (doi:10.1007/s00442-007-0745-8)
- HilleRisLambers R, Rietkerk M, van de Bosch F, Prins HHT, de Kroon H. 2001 Vegetation pattern formation in semi-arid grazing systems. *Ecology* 82, 50-61. (doi:10.1890/0012-9658(2001)082[0050: VPFISA]2.0.C0;2)
- Rietkerk M, Boerlijst MC, van Langevelde F, HilleRisLambers R, van de Koppel J, Prins HHT, de Roos A. 2002 Self-organisation of vegetation in arid ecosystems. *Am. Nat.* **160**, 524–530. (doi:10.1086/ 342078)
- Guttal V, Jayaprakash C. 2007 Self-organisation and productivity in semi-arid ecosystems: implications of seasonality in rainfall. *J. Theor. Biol.* 248, 290–500. (doi:10.1016/j.jtbi.2007.05.020)
- von Hardenberg J, Meron E, Shachak M, Zarmi Y. 2001 Diversity of vegetation patterns and desertification. *Phys. Rev. Lett.* 87, 198101. (doi:10.1103/PhysRevLett.87.198101)
- Meron E, Gilad E, von Hardenberg J, Shachak M, Zarmi Y. 2004 Vegetation patterns along a rainfall gradient. *Chaos Solitons Fractals* 19, 367–376. (doi:10.1016/S0960-0779(03)00049-3)
- Pueyo Y, Kéfi S, Alados CL, Rietkerk M. 2008 Dispersal strategies and spatial organization of vegetation in arid ecosystems. *Oikos* **117**, 1522– 1532. (doi:10.1111/j.0030-1299.2008.16735.x)
- Gilad E, von Hardenberg J, Provenzale A, Shachak M, Meron E. 2004 Ecosystem engineers: from pattern formation to habitat creation. *Phys. Rev. Lett.* **93**, 098105. (doi:10.1103/PhysRevLett.93. 098105)
- Montaña C, Seghieri J, Cornet A. 2001 Vegetation dynamics: recruitment and regeneration in two-phase mosaics. In *Banded vegetation patterning in arid and semi-arid environments* (eds DJ Tongway, C Valentin, SJ Seghieri), pp. 132–145. New York, NY: Springer.
- 44. Tongway DJ, Ludwig JA. 2001 Theories on the origins, maintainance, dynamics, and functioning of

banded landscapes. In *Banded vegetation patterning in arid and semi-arid environments* (eds DJ Tongway, C Valentin, SJ Seghieri), pp. 20–31. New York, NY: Springer.

- Dunkerley DL, Brown KJ. 2002 Oblique vegetation banding in the Australian arid zone: implications for theories of pattern evolution and maintenance. *J. Arid Environ.* 52, 163–181. (doi:10.1006/jare.2001. 0940)
- Couteron P, Mahamane A, Ouedraogo P, Seghieri J. 2000 Differences between banded thickets (tiger bush) at two sites in West Africa. *J. Veg. Sci.* 11, 321–328. (doi:10.2307/3236624)
- Saco PM, Willgoose GR, Hancock GR. 2007 Ecogeomorphology of banded vegetation patterns in arid and semi-arid regions. *Hydrol. Earth Syst. Sci.* 11, 1717–1730. (doi:10.5194/hess-11-1717-2007)
- Thompson S, Katul G. 2009 Secondary seed dispersal and its role in landscape organization. *Geophys. Res. Lett.* 36, L02402. (doi:10.1029/ 2008GL036044)
- Sherratt JA. 2012 Numerical continuation methods for studying periodic travelling wave (wavetrain) solutions of partial differential equations. *Appl. Math. Comput.* 218, 4684–4694. (doi:10.1016/j. amc.2011.11.005)
- Doedel EJ. 1981 Auto, a program for the automatic bifurcation analysis of autonomous systems. *Cong. Numer.* 30, 265–384.
- Rademacher JDM, Sandstede B, Scheel A. 2007 Computing absolute and essential spectra using continuation. *Phys. D* 229, 166–183. (doi:10.1016/ j.physd.2007.03.016)
- Sherratt JA. 2013 Numerical continuation of boundaries in parameter space between stable and unstable periodic travelling wave (wavetrain) solutions of partial differential equations. *Adv. Comput. Math.* **39**, 175– 192. (doi:10.1007/s10444-012-9273-0)
- Burke J, Knobloch E. 2007 Snakes and ladders: localized states in the Swift-Hohenberg equation. *Phys. Lett. A* 360, 681–688. (doi:10.1016/j. physleta.2006.08.072)
- Beck M, Knobloch J, Lloyd DJ, Sandstede B, Wagenknecht T. 2009 Snakes, ladders, and isolas of localized patterns. *SIAM J. Math. Anal.* 41, 936–972. (doi:10.1137/080713306)
- Sherratt JA. 2013 History-dependent patterns of whole ecosystems. *Ecol. Complexity* 14, 8–20. (doi:10.1016/j.ecocom.2012.12.002)
- Worrall GA. 1959 The Butana grass patterns. J. Soil Sci. 10, 34–53. (doi:10.1111/j.1365-2389.1959. tb00664.x)
- Leprun JC. 1999 The influences of ecological factors on tiger bush and dotted bush patterns along a gradient from Mali to northern Burkina Faso. *Catena* 37, 25–44. (doi:10.1016/S0341-8162(98)00054-X)
- Valentin C, d'Herbès JM. 1999 Niger tiger bush as a natural water harvesting system. *Catena* 37, 231–256. (doi:10.1016/S0341-8162(98)00061-7)
- 59. Sandstede B, Scheel A. 2000 Absolute and convective instabilities of waves on unbounded and

large bounded domains. *Phys. D* **145**, 233–277. (doi:10.1016/S0167-2789(00)00114-7)

- Smith MJ, Rademacher JDM, Sherratt JA. 2009 Absolute stability of wavetrains can explain spatiotemporal dynamics in reaction – diffusion systems of lambdaomega type. *SIAM J. Appl. Dyn. Syst.* 8, 1136–1159. (doi:10.1137/090747865)
- Sherratt JA, Dagbovie AS, Hilker FM. 2014 A mathematical biologist's guide to absolute and convective instability. *Bull. Math. Biol.* 76, 1–26. (doi:10.1007/s11538-013-9911-9)
- Sherratt JA, Smith MJ, Rademacher JDM. 2009 Locating the transition from periodic oscillations to spatiotemporal chaos in the wake of invasion. *Proc. Natl Acad. Sci. USA* **106**, 10 890–10 895. (doi:10. 1073/pnas.0900161106)
- Dagbovie AS, Sherratt JA. 2014 Absolute stability and dynamical stabilisation in predator – prey systems. J. Math. Biol. 68, 1403 – 1421. (doi:10. 1007/s00285-013-0672-8)
- Rademacher JDM. 2006 Geometric relations of absolute and essential spectra of wavetrains. *SIAM J. Appl. Dyn. Syst.* 5, 634–649. (doi:10.1137/050635390)
- 65. Rietkerk M, van de Koppel J. 2008 Regular pattern formation in real ecosystems. *TREE* 23, 169–175.
- Lejeune O, Tlidi M, Couteron P. 2002 Localized vegetation patches: a self-organized response to resource scarcity. *Phys. Rev. E* 66, 010901. (doi:10. 1103/PhysRevE.66.010901)
- Ben Wu X, Archer SR. 2005 Scale-dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes. *Landscape Ecol.* 20, 733–742. (doi:10.1007/s10980-005-0996-x)
- Staver AC, Levin SA. 2012 Integrating theoretical climate and fire effects on savanna and forest systems. *Am. Nat.* 180, 211–224. (doi:10.1086/666648)
- 69. Bai E, Boutton TW, Wu XB, Liu F, Archer SR. 2009 Landscape-scale vegetation dynamics inferred from spatial patterns of soil δ^{13} C in a subtropical savanna parkland. *J. Geophys. Res.* **114**, G01019. (doi:10.1029/2008JG000839)
- Belyea LR, Lancaster J. 2002 Inferring landscape dynamics of bog pools from scaling relationships and spatial patterns. *J. Ecol.* **90**, 223–234. (doi:10. 1046/j.1365-2745.2001.00647.x)
- Eppinga MB, Rietkerk M, Borren W, Lapshina ED, Bleuten W, Wassen MJ. 2008 Regular surface patterning of peatlands: confronting theory with field data. *Ecosystems* **11**, 520–536. (doi:10.1007/ s10021-008-9138-z)
- Eppinga MB, Rietkerk M, Wassen MJ, De Ruiter PC. 2009 Linking habitat modification to catastrophic shifts and vegetation patterns in bogs. *Plant Ecol.* 200, 53-68. (doi:10.1007/s11258-007-9309-6)
- Belyea LR, Clymo RS. 2001 Feedback control of the rate of peat formation. *Proc. R. Soc. Lond. B* 268, 1315–1321. (doi:10.1098/rspb.2001.1665)
- Rietkerk M, Dekker SC, Wassen MJ, Verkroost AWM, Bierkens MFP. 2004 A putative mechanism for bog patterning. *Am. Nat.* 163, 699–708. (doi:10.1086/ 383065)

- Eppinga MB, De Ruiter PC, Wassen MJ, Rietkerk M. 2009 Nutrients and hydrology indicate the driving mechanisms of peatland surface patterning. *Am. Nat.* **173**, 803–818. (doi:10.1086/598487)
- Bekker MF, Malanson GP. 2008 Linear forest patterns in subalpine environments. *Prog. Phys. Geog.* 32, 635–653. (doi:10.1177/030913330 8101384)
- Holtmeier F-K. 2009 Mountain timberlines: ecology, patchiness, and dynamics. Dordrecht, The Netherlands: Kluwer.
- Bekker MF, Clark JT, Jackson MW. 2009 Landscape metrics indicate differences in patterns and dominant controls of ribbon forests in the Rocky Mountains, USA. *Appl. Veg. Sci.* 12, 237–249. (doi:10.1111/j.1654-109X.2009.01021.x)
- Billings WD. 1969 Vegetational pattern near alpine timberline as affected by fire – snowdrift interactions. *Vegetatio* 19, 192 – 207. (doi:10.1007/ BF00259010)
- Hiemstra CA, Liston GE, Reiners WA. 2006 Observing, modelling, and validating snow redistribution by wind in a Wyoming upper treeline landscape. *Ecol. Modell.* **197**, 35–51. (doi:10.1016/j.ecolmodel. 2006.03.005)
- Butler DR, Malanson GP, Bekker MF, Resler LM.
 2003 Lithologic, structural, and geomorphic controls on ribbon forest patterns in a glaciated mountain environment. *Geomorphology* 55, 203–217. (doi:10.1016/S0169-555X(03)00140-5)
- Sato K, Iwasa Y. 1993 Modeling of wave regeneration in subalpine *Abies* forests: population dynamics with spatial structure. *Ecology* 74, 1538–1550. (doi:10.2307/1940081)
- Suzuki SN, Kachi N, Suzuki J-I. 2012 Variability of local spatial structure in a wave-regenerated *Abies* forest. *Ecol. Res.* 27, 893–901. (doi:10.1007/ s11284-012-0966-0)
- Van Leeuwen B, Augustijn DCM, van Wesenbeeck BK, Hulscher SJMH, de Vries MB. 2010 Modeling the influence of a young mussel bed on fine sediment dynamics on an intertidal flat in the Wadden Sea. *Ecol. Eng.* 36, 145–153. (doi:10.1016/j.ecoleng. 2009.01.002)
- van de Koppel J, Rietkerk M, Dankers N, Herman PMJ. 2005 Scale-dependent feedback and regular spatial patterns in young mussel beds. *Am. Nat.* 165, E66–E77. (doi:10.1086/428362)
- Wang RH, Liu Q-X, Sun GQ, Jin Z, van de Koppel J. 2009 Nonlinear dynamic and pattern bifurcations in a model for spatial patterns in young mussel beds. J. R. Soc. Interface 6, 705–718. (doi:10.1098/rsif. 2008.0439)
- Liu Q-X, Weerman EJ, Herman PMJ, Olff H, van de Koppel J. 2012 Alternative mechanisms alter the emergent properties of self-organization in mussel beds. *Proc. R. Soc. B* 279, 2744–2753. (doi:10. 1098/rspb.2012.0157)
- van de Koppel J, Gascoigne JC, Theraulaz G, Rietkerk M, Mooij WM, Herman PMJ. 2008 Experimental evidence for spatial self-organisation and its emergent effects in mussel bed ecosystems. *Science* 322, 739–742. (doi:10.1126/science.1163952)