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An Analysis of Vegetation Stripe Formation in Semi-Arid Landscapes

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Abstract. Vegetation stripes ("tiger bush") are a characteristic feature of semi-arid environments. The stripes typically lie along the contours of gentle slopes, and some authors report a gradual uphill migration. A previous mathematical model (Klausmeier, *Science*, 284:1826, 1999) has shown that this phenomenon can be explained relatively simply by the downhill flow of rainwater coupled with the diffusive spread of the plant population. This paper presents a detailed analysis of pattern formation in the Klausmeier model. The author derives formulae for the wavelength and migration speed of the predicted patterns, and systematically investigates how these depend on model parameters. The results make new predictions and suggest possible approaches to testing the model.

1. Introduction

Banded patterns of vegetation are a characteristic feature of many semi-arid areas. They occur in regions of low woodlands or tall shrublands, on gentle slopes of about 0.25% gradient. Vegetation is concentrated into bands running along the contours of the hill, typically 100m–250m wide. These stripes of vegetation are separated by gaps, typically of width 200m–1km, in which vegetation is sparse or absent. This phenomenon is often undetectable on the ground, and its initial identification was via aerial photography in Africa (MacFadyen, 1950; Hemming, 1965; Wickens & Collier, 1971), where it is known as "tiger bush". Subsequently, vegetation stripes were also discovered in semi-arid regions of Australia (Mabbutt & Fanning, 1987; Dunkerley & Brown, 2002) and Mexico (Montaña *et al.*,, 1990; Montaña, 1992). Some authors report a slow uphill migration of the bands (Worrall, 1959; Hemming, 1965; Montaña, 1992), although this aspect of vegetation stripes remains controversial (Dunkerley & Brown, 2002), due primarily to the limited long-term data.

There is a continuing debate on the mechanism responsible for vegetation stripes; however, it is generally agreed that competition for water is a key factor. In simple terms, rainfall onto an area without vegetation runs downhill into a region with vegetation, where it is absorbed. This enables vegetation stripes to be maintained, and the moist soil on the uphill side of a stripe creates a tendency for the stripes to gradually migrate uphill. Various computer-based simulation models representing this process were developed in the 1990s (Thiéry *et al.*,, 1995; Mauchamp *et al.*,, 1994; Dunkerley, 1997). Klausmeier (1999) then proposed a

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relatively simple partial differential equation model, with equations for vegetation $U(X, Y, T)$ and surface water $W(X, Y, T)$:

$$\partial U/\partial T = \overbrace{k_1 U^2 W}^{\substack{\text{plant}\\\text{growth}}} - \overbrace{k_2 U}^{\substack{\text{plant}\\\text{loss}}} + \overbrace{k_3 \left(\partial^2 U/\partial X^2 + \partial^2 U/\partial Y^2\right)}^{\text{dispersal}} \tag{1a}$$

$$\partial W/\partial T = \underbrace{k_4}_{\text{rainfall}} - \underbrace{k_5 W}_{\text{evaporation}} - \underbrace{k_6 U^2 W}_{\substack{\text{uptake}\\\text{by plants}}} + \underbrace{k_7 \left(\partial W/\partial X\right)}_{\substack{\text{flow}\\\text{downhill}}} . \tag{1b}$$

Here $k_1, \ldots , k_7$ are positive constants. By numerical solution of these equations, Klausmeier (1999) showed that the model predicts both vegetation stripe formation and the uphill migration of the stripes, for appropriate parameter values.

More recently, a number of authors have proposed expanded versions of this model. HilleRisLambers *et al.* (2001) incorporated the diffusion of water within the soil, with separate variables for water on the surface and in the soil. Rietkerk *et al.* (2002) performed a detailed numerical bifurcation study on a minor variant of the HilleRisLambers model, showing that the bifurcations leading to patterning are subcritical, and van de Koppel *et al.,* (2002) added herbivore grazing to Klausmeier's (1999) model, showing that this can significantly modulate the patterning potential. The model of von Hardenberg *et al.,* (2001) and Meron *et al.* (2004) also focusses on ground water, in this case without a variable for surface water. They include a more complex term for ground water flow, based on Darcy's Law, which yields patterns even on flat ground. An alternative modelling approach has been developed by Lejeune and coworkers (Lefever & Lejeune, 1997; Lejeune & Tlidi, 1999; Couteron & Lejeune, 2001). They have developed a more generic modelling framework of "propagation–inhibition" type, in which the slope of the hill acts as a selector of the spatial pattern, rather than the initiator.

In this paper, I return to the original model of Klausmeier (1999), and investigate its potential for pattern formation analytically, for the first time. The main objective is to determine how patterning varies with model parameters. To facilitate this, I rescale the system (1a) as follows:

$$u = U k_6^{1/2}/k_5^{1/2} \quad w = W k_1/k_5^{1/2} k_6^{1/2} \quad x = X k_5^{1/2}/k_3^{1/2} \quad y = Y k_5^{1/2}/k_3^{1/2} \quad t = T k_5$$
$$A = k_4 k_1/k_5^{3/2} k_6^{1/2} \quad B = k_2/k_5 \quad \nu = k_7/k_3^{1/2} k_5^{1/2} .$$

These rescalings are taken from Klausmeier (1999), although my notation is different. The resulting dimensionless equations are

$$\partial u/\partial t = w u^2 - B u + \partial^2 u/\partial x^2 + \partial^2 u/\partial y^2 \tag{2a}$$
$$\partial w/\partial t = A - w - w u^2 + \nu \partial w/\partial x. \tag{2b}$$

In applications, the main dimensional parameters of interest are the rainfall k_4, plant loss k_2 and gradient of slope k_7; note that plant loss will vary depending on the extent of grazing. These three parameters appear (linearly) in the dimensionless quantities A, B and ν respectively. Therefore in the remainder of the paper I study the dimensionless equations (2a), focussing on the conditions for patterning, and the way in which the patterns vary with these three parameters. An indication of the typical values of these parameters is given by Klausmeier's(1999) estimates, which are $\nu = 182.5$ for a typical slope with vegetation stripes, with $A = 0.077-0.23$, $B = 0.045$ for trees, and $A = 0.94-2.81$, $B = 0.45$ for grass.

In §2 I use linear analysis to determine conditions for stripe formation. In §3 I calculate the predicted wavelength of the stripes, and how this varies with model parameters, and in §4 I investigate the speed of migration of the stripes.

2. Conditions for Pattern Formation

The first step in investigating the pattern-forming potential of the model (2) is to determine the spatially homogeneous steady states. Straightforward calculation shows that when $A < 2B$, the only steady state is $u = 0$, $w = A$ (no plants), which is linearly stable. Intuitively, plants cannot survive in this parameter regime because the rainfall is too low in comparison to plant loss. When $A \geq 2B$, two other steady states develop, one of which is linearly unstable to homogeneous perturbations. The other is given by

$$u = u_s \equiv \frac{2B}{A - \sqrt{A^2 - 4B^2}}, \qquad w = w_s \equiv \frac{A - \sqrt{A^2 - 4B^2}}{2}$$

which is linearly stable whenever $B < 2$, and for A sufficiently large when $B > 2$. Intuitively, this means that the rainfall is large enough to sustain plant growth. Realistic parameter values for plant growth in semi-arid environments imply $B < 2$, and we assume henceforth that $u = u_s$, $w = w_s$ is linearly stable to homogeneous perturbations. This raises the possibility of Turing-type patterns. Linearizing the model equations (2) about this steady state gives

$$\begin{aligned} \tilde{u}_t &= a\tilde{u} + b\tilde{w} + \tilde{u}_{xx} + \tilde{u}_{yy} \\ \tilde{w}_t &= c\tilde{u} + d\tilde{w} + \nu\tilde{w}_x \end{aligned}$$

where $\tilde{u} = u - u_s$, $\tilde{w} = w - w_s$, and the linear coefficients a, b, c, d are given by

$$a = B \tag{3a}$$

$$b = \frac{A + \sqrt{A^2 - 4B^2}}{A - \sqrt{A^2 - 4B^2}} \tag{3b}$$

$$c = -2B \tag{3c}$$

$$d = \frac{-2A}{A - \sqrt{A^2 - 4B^2}}\,. \tag{3d}$$

Klausmeier's (1999) parameter estimates, given at the end of the introduction, imply that for trees $a = 0.045$, $b = 1-24$, $c = -0.09$, $d = (-2)-(-25)$, while for grass $a = 0.45$, $b = 1.8-37$, $c = -0.9$, $d = (-2.8)-(-38)$. In the former case, these ranges for b and d exclude the smallest values of A, which are less than $2B$. Note that b and $(-d)$ are both increasing functions of A, so that their absolute values vary in parallel.

To consider pattern formation, we look for solutions proportional to $\exp(ikx + ily + \lambda t)$; here the wavenumbers k and l are real, but the growth rate λ may be complex. Nontrivial solutions of this form are possible provided

$$\lambda^2 + \lambda\left(k^2 + l^2 - a - ik\nu - d\right) + (a - k^2 - l^2)(ik\nu + d) - bc = 0$$

which gives the dispersion relation

$$\lambda = \tfrac{1}{2}\left[(a - l^2 + d + ik\nu - k^2) \pm \sqrt{\alpha + i\beta}\right] \tag{4}$$

where $\alpha = (a - l^2 + d - k^2)^2 - k^2\nu^2 - 4(a - l^2 d - bc - dk^2)$ and $\beta = 2k\nu(k^2 - a - l^2 + d)$. Straightforward manipulation of (4) yields

$$\operatorname{Re}\lambda = \tfrac{1}{2}\left[a - l^2 + d - k^2 + j\left\{\tfrac{1}{2}\left(\sqrt{\alpha^2 + \beta^2} + \alpha\right)\right\}^{1/2}\right] \tag{5}$$

$$\operatorname{Im}\lambda = \tfrac{1}{2}\left[k\nu + j\,\operatorname{sign}(\beta)\left\{\tfrac{1}{2}\left(\sqrt{\alpha^2 + \beta^2} - \alpha\right)\right\}^{1/2}\right] \tag{6}$$

where $j = \pm 1$.

The condition for a spatial mode (defined by k and l) to be unstable and thus grow into a pattern is that $\operatorname{Re}\lambda > 0$. Therefore, pattern formation will occur if $\operatorname{Re}\lambda > 0$ for any values of k and l. For general advection-diffusion equations this was first investigated by Jorné (1974), with a number of subsequent studies. In particular, Perumpanani *et al.,* (1995) showed that patterning occurs if the advection rate (ν in (2a)) is above a critical value, but were unable to obtain an analytical expression for this critical value. However for the particular problem of vegetation stripes, a significant simplification can be achieved by making use of the large (dimensionless) value of ν in comparison to the other parameters: recall that Klausmeier (1999) estimates $\nu = 182.5$ for a typical slope with vegetation stripes, with $A = 0.077 - 0.23$, $B = 0.045$ for trees, and $A = 0.94 - 2.81$, $B = 0.45$ for grass. Therefore I expand (5) as a power series in $\nu \gg 1$. In due course I will consider both $k = O_s(1/\nu)$ and $k = O_s(1/\nu^{1/2})$, but to begin with I assume that $k = O_s(1)$. (The notation $k = O_s(1)$ means that $k = O(1)$ and $k \neq o(1)$.) For any given k and l, the fastest growth rate has $j = +1$, and is given by

$$\operatorname{Re}\lambda = a - l^2 - k^2 + O(1/\nu^2) \tag{7}$$

when $k^2 < a - l^2 - d$, with $\operatorname{Re}\lambda < 0$ for all $k^2 > a - l^2 - d$. Since $d < 0$, this shows that any mode with $0 < k^2 + l^2 < a$ is unstable for sufficiently large ν.

There is an apparent discrepancy between (7) and my earlier statement that the steady state $u = u_s$, $v = v_s$ is stable to homogeneous perturbations, since (7) implies that $\operatorname{Re}\lambda > 0$ at $k = l = 0$. This is because (5) has boundary layer type behaviour near $k = 0$, which is revealed by assuming $\nu \gg 1$ with $k = O_s(1/\nu)$, say $k = \hat{k}/\nu$. Expanding (5) as a power series in ν under this assumption and with $j = +1$ gives

$$\operatorname{Re}\lambda = \tfrac{1}{2}\left[a - l^2 + d + \left\{\tfrac{1}{2}\left(\left(\left[\left\{(a - l^2 - d)^2 + 4bc - \hat{k}^2\right\}^2 + 4\hat{k}^2(a - l^2 - d)^2\right]^{1/2}\right.\right.\right.\right.$$

$$\left.\left.\left.\left. + (a - l^2 - d)^2 + 4bc - \hat{k}^2\right)\right)\right\}^{1/2}\right]. \tag{8}$$

This is an increasing function of $\hat{k}$, negative at $\hat{k} = 0$, and approaching $a - l^2$ asymptotically as $\hat{k} \to \infty$. Figure 1 illustrates the comparison between (7), (8) and the full expression (5) for $\operatorname{Re}\lambda$.

On their own, neither (7) or (8) are very informative about the pattern forming potential of (2a). It is possible to combine them into a "composite" approximation for $\operatorname{Re}\lambda$, but this is not much simpler algebraically than the full expression (5). In order to obtain a more informative approximation to (5), an intermediate expansion is needed, in which $\nu \gg 1$ with $k = O_s(1/\nu^{1/2})$, say $k = \tilde{k}/\nu^{1/2}$. Expanding (5) as a power series in ν, again with $j = +1$, this gives

$$\operatorname{Re}\lambda = a - l^2 - \frac{1}{\nu}\left\{\frac{(-bc)(a - l^2 - d)}{\tilde{k}^2} + \tilde{k}^2\right\} + o(1/\nu)\,. \tag{9}$$

This has its largest value when $l = 0$ and when

$$\tilde{k} = \tilde{k}_{max} \equiv [(-bc)(a - d)]^{1/4} \tag{10}$$

$$\text{with}\quad \operatorname{Re}\lambda = \Lambda_{max} \equiv a - \frac{2}{\nu}\sqrt{(-bc)(a - d)}\,. \tag{11}$$

The condition for diffusion driven instability is that $\Lambda_{max} > 0$. Since $a > 0$, this will clearly occur for any values of a, b, c and d, provided that ν is sufficiently large. However, in applications to vegetation stripes, not only is ν large, but $|d|$ and $|bc|$ can also be large, while a is typically small. Therefore, diffusion driven instability is not automatic for realistic parameters, and requires investigation.

The formulae (10) and (11) were derived under the assumption that $\nu \gg 1$ with all other parameters $O_s(1)$. However, the derivation is unaffected if in addition $(-d) \gg 1$ and/or $(-bc) \gg 1$ and/or $a \ll 1$, provided that $\nu \gg (bc/d)^{1/2}$ and $\nu \gg (d^3/bc)^{1/2}$; details of this are given in Appendix A. These conditions are reasonable for realistic parameters for vegetation stripe formation. For example the parameter estimates of Klausmeier (1999), discussed previously, imply that for trees $(bc/d)^{1/2} = 0.2$–0.3 and $(d^3/bc)^{1/2} = 9.4$–85 while for grass $(bc/d)^{1/2} = 0.76$–0.94 and $(d^3/bc)^{1/2} = 3.7$–41; these compare with $\nu = 182.5$. The formula (11) implies that the condition for vegetation stripe formation is

$$\nu > 2\sqrt{(-bc)(a - d)}/a\,.$$

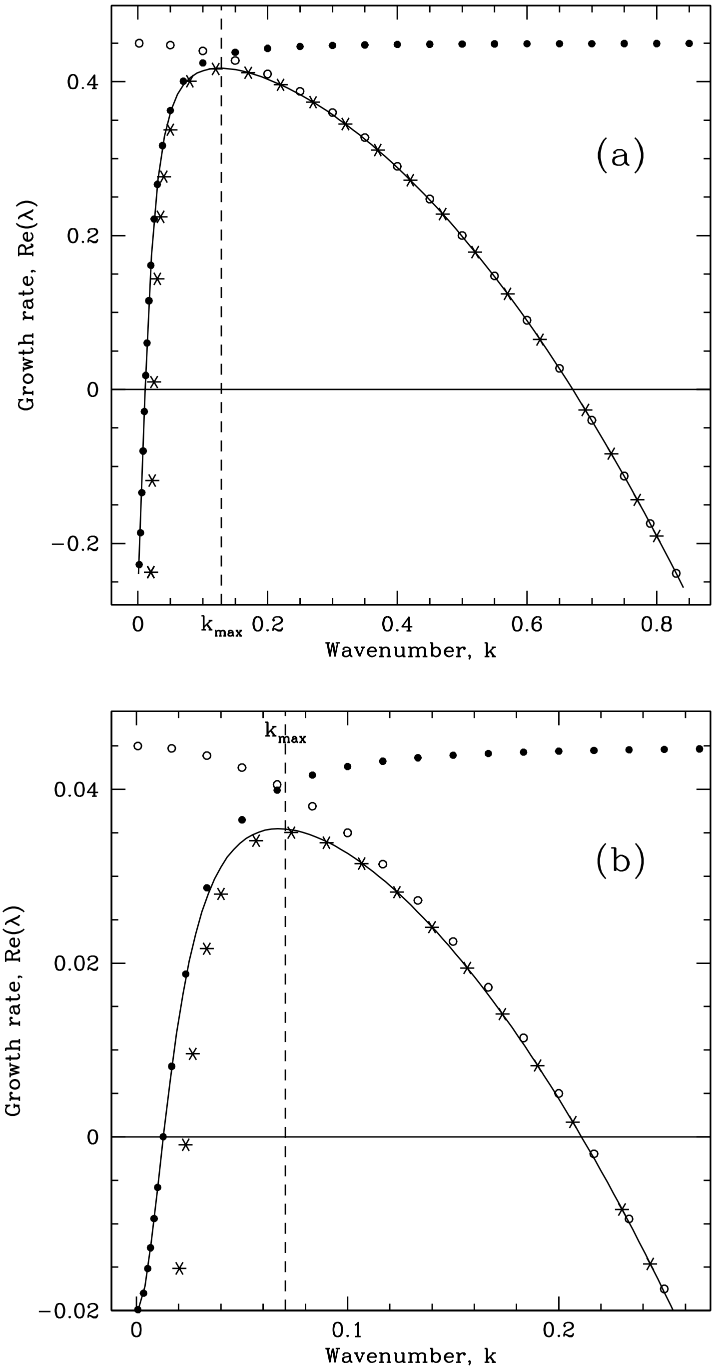

Fig. 1. Caption on next page

Fig. 1. An illustration of the dispersion relation and various approximations to it, for parameter values corresponding to (a) grass and (b) trees, based on the parameter estimates of Klausmeier (1999). The solid curve is (5), the actual dispersion relation. The open circles ($\circ$) show the approximation (7), given by assuming $\nu \gg 1$ with $k = O(1)$. The filled circles ($\bullet$) show the approximation (8), given by assuming $\nu \gg 1$ with $k = O(1/\nu)$. Finally the stars ($*$) show (9), given by assuming $\nu \gg 1$ with $k = O(1/\nu^{1/2})$. The position of k_{max}, given in (10) is also shown. The parameter values are $\nu = 182.5$ and (a) $A = 1$, $B = 0.45$; (b) $A = 0.1$, $B = 0.045$

Substituting (3) into this gives

$$\begin{aligned}\nu^2 &> 8\,\frac{A+\sqrt{A^2-4B^2}}{A-\sqrt{A^2-4B^2}} + \frac{16}{B}\,\frac{A^2+A\sqrt{A^2-4B^2}}{(A-\sqrt{A^2-4B^2})^2}\\ &= 8\left(\psi^2/B - \psi/B + \psi - 1\right) \qquad (12)\\ &\text{where}\quad \psi = 2\Big/\left(1-\sqrt{1-4B^2/A^2}\right).\end{aligned}$$

In applications to vegetation stripe formation, ν^2 is usually much greater than $1/B$. For example, Klausmeier (1999) estimates $1/B = 22$ for trees and $1/B = 2.2$ for grass, while $\nu^2 = 3.3 \times 10^4$. Therefore condition (12) is always satisfied unless $\psi \gg 1$, which requires $B \ll A$. The right hand side of (12) will then be dominated by $8\psi^2/B$, so that to leading order (12) simplifies to

$$\nu > \sqrt{8}A^2/B^{5/2}\,. \qquad (13)$$

This condition is satisfied throughout the parameter range estimated by Klausmeier (1999) for grass, with $\sqrt{8}A^2/B^{5/2} = 18-164$, while $\nu = 182.5$; however for trees, his estimates imply $\sqrt{8}A^2/B^{5/2} = 39 - 348$ (again $\nu = 182.5$), predicting that stripes will only form at lower levels of rainfall.

The model (2a) predicts that vegetation stripes will occur when A is small enough to satisfy condition (13), but larger than $2B$. Specifically, the (approximate) condition for pattern formation is

$$2B < A < 8^{-1/4}\nu^{1/2}B^{5/4}\,. \qquad (14)$$

Figure 2 illustrates the comparison between the approximate condition (14) and a numerical calculation of stability, obtained by computing the maximum of $\mathrm{Re}\,\lambda$ directly from the formula (5). The comparison is very good for a large value of ν such as that estimated by Klausmeier (1999) ($\nu = 182.5$), and is fairly good even for a lower value of ν such as 50. Intuitively, one expects a condition of the form (14) for stripe formation. Recall that A reflects the rainfall, while B is a measure of plant loss, and ν indicates the steepness of the slope. If the rainfall A is too small compared to plant loss B, then vegetation will simply die out. On the other hand, if rainfall A is sufficiently large, then the competition amongst plants for water will not be very strong, resulting in homogeneous vegetation. However, for intermediate levels of rainfall, vegetation can survive but with a strong competition

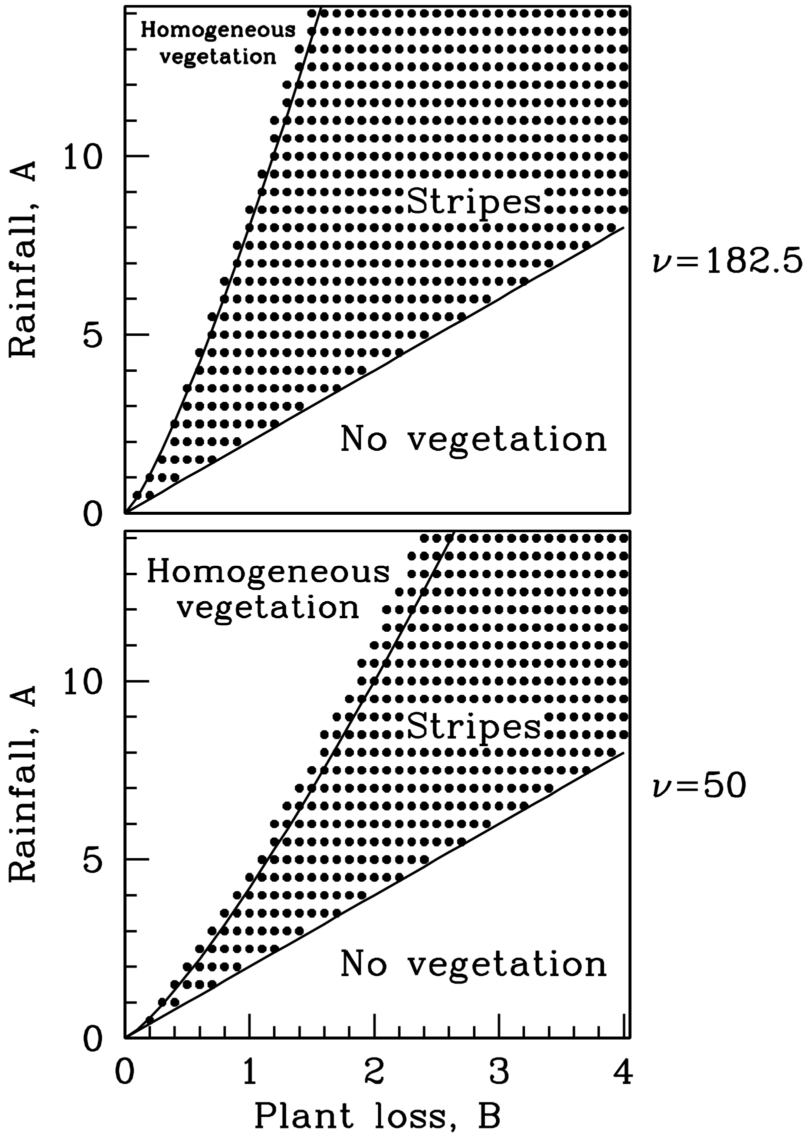

Fig. 2. An illustration of the comparison between the approximate condition (14) for vegetation stripe formation, and a numerical calculation of stability. The condition (14) implies stripe formation for parameters between the two solid curves (—). Numerical calculation of Re λ from (5) implies that stripes will form for parameters indicated by a filled circle (●). Therefore the figure shows that (14) is a very good approximation for the value of $\nu = 182.5$ estimated by Klausmeier (1999) as being typical for vegetation striping, and the approximation remains fairly good even for smaller values of ν. As indicated in the figure, when the rainfall is too low for vegetation stripe formation, vegetation is absent; when the rainfall is too high for stripes, there is a homogeneous level of vegetation

amongst plants for water, leading to vegetation stripes. The dependence of the upper threshold on ν occurs because on steeper slopes rainfall will run off more quickly, increasing the competitive advantage of areas of high plant density over those of lower density. However the whole model assumes that the slope is not too steep, otherwise the water will not flow downhill as a sheet, and instead will form gullies.

3. The Wavelength of Vegetation Stripes

A key issue for vegetation stripes is to determine their wavelength, and the way in which this varies with model parameters. This is a property of the nonlinear system (2), and detailed investigation would require nonlinear analysis that is beyond the scope of this paper. However some insight into the wavelength can be obtained from the linear analysis in the previous section. When patterns occur, one expects that these will be dominated by the fastest growing mode – this will hold sufficiently close to the Turing bifurcation curve defined by (12). Because the fastest growing mode has $l = 0$, the corresponding pattern will have the form of stripes along the contours of the slope (i.e. parallel to the y-axis), with wavelength

$$2\pi/k_{max} = 2\pi\nu^{1/2}/[(-bc)(a-d)]^{1/4}. \tag{15}$$

This leading order approximation to the fastest growing mode compares well with numerical plots of (5), as illustrated in Figure 1.

From an ecological viewpoint, a key issue is the way in which the predicted spatial wavelength (15) varies with the model parameters A and B. Klausmeier (1999) hypothesises that the wavelength is a decreasing function of water input A and an increasing function of mortality B; I investigate this systematically using (15). Substituting (3) into (10) gives the following expression for the fastest growing wavenumber:

$$\tilde{k}_{max} = \left\{\left[A^4 + A^2B^3 - 3A^2B^2 - 2B^5 + A(A^2 - B^2 + B^3)\sqrt{A^2 - 4B^2}\right]/B^3\right\}^{1/4}. \tag{16}$$

Explicit differentiation, followed by extensive algebraic simplification, gives

$$\begin{aligned}\frac{\partial \tilde{k}_{max}}{\partial A} = \frac{1}{2\tilde{k}^3_{max}B^3\sqrt{A^2 - 4B^2}} & \Big[A\sqrt{A^2 - 4B^2}\left\{2(A^2 - 4B^2) + B^2(B + 5)\right\} \\ & + (A^2 - 4B^2)(2A^2 + B^2 + B^3) + 2B^4(B + 3)\Big]\end{aligned}$$

and
$$\begin{aligned}\frac{\partial \tilde{k}_{max}}{\partial B} = \frac{-1}{4\tilde{k}^3_{max}B^4\sqrt{A^2 - 4B^2}} & \Big[\sqrt{A^2 - 4B^2}\Big\{3(A^2 - 4B^2)(A^2 + 3B^2) \\ & + 4B^4(B + 9)\Big\} + A\left\{3(A^2 - 4B^2)(A^2 + B^2) + 4B^4(B + 3)\right\}\Big].\end{aligned}$$

Recall that $A > 2B$ is a necessary condition for the existence of the steady state (u_s, w_s), which is required for spatial patterning. Therefore pattern wavelength decreases with A and increases with B, as hypothesised by Klausmeier (1999) and as illustrated in Figure 3. Note that because this prediction comes from linear

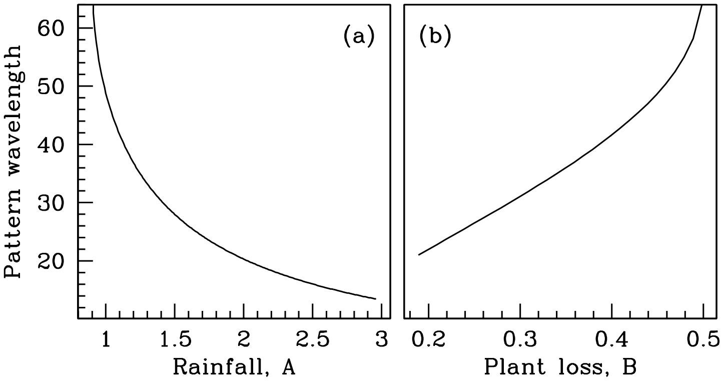

Fig. 3. An illustration of the variation in pattern wavelength with (a) rainfall A and (b) plant loss B. As shown in the main text, my linear analysis predicts that the wavelength decreases with A and increases with B. The wavelength is calculated using the formula (15). The parameter values are $\nu = 182.5$ and (a) $B = 0.45$, (b) $A = 1$. In both (a) and (b), the plots cover the full parameter ranges giving pattern formation; these are defined by the conditions $A < 2B$ and (13)

analysis, it only applies sufficiently close to the Turing bifurcation curve; nevertheless, both of the parameter variations are supported by the limited field data that is available (White, 1971; Wickens & Collier, 1971; Mabbutt & Fanning, 1987).

4. Pattern Speed

The fact that λ is a complex number means that the striped pattern predicted by the above calculations is not stationary, but rather moves over time. Some field studies report such movement, with typical speeds being $0.15-0.3\,\mathrm{m\,yr}^{-1}$ for trees, and $0.3-1.5\,\mathrm{m\,yr}^{-1}$ for grass. The speed of movement predicted by my linear analysis is $|\mathrm{Im}\,\lambda|/k$. To simplify this, I expand (6) as a power series in ν, again with $k = \tilde{k}/\nu^{1/2}$ and $j = +1$: note that (9) implies that $\beta < 0$ whenever pattern formation occurs. This implies that the speed s is given by

$$s = (-bc)/\tilde{k}^2 + o(1)\,. \tag{17}$$

Thus to leading order when $\nu \gg 1$, the fastest growing mode has speed

$$\begin{aligned} s_{max} &= \sqrt{(-bc)/(a-d)} \\ &= \left\{ \frac{B\left[A^2(1+B) - 2B^3 + A(1+B)\sqrt{A^2-4B^2}\right]}{A^2(1+B)+B^4} \right\}^{1/2} . \end{aligned} \tag{18}$$

Here I have used the formulae (3) for the linear coefficients a, b, c and d.

One immediate implication of (16) is that to leading order, the speed is independent of ν, and thus of the gradient of the slope. I am not aware of field data addressing this issue, but it provides a natural test for the model. There is also ecological interest in the way in which the speed varies with the parameters A and B. Direct differentiation of (16) gives

$$\begin{aligned}\frac{\partial s_{max}}{\partial A} &= \frac{B^3(1+B)}{s_{max}\left[A^2(1+B)+B^4\right]^2\sqrt{A^2-4B^2}}\Big\{(A^2-4B^2)(B^2+2B+2)\\ &\quad +2B^2(B+2)^2+AB(B+2)\sqrt{A^2-4B^2}\Big\}\\ \frac{\partial s_{max}}{\partial B} &= \frac{A}{2s_{max}\left[A^2(1+B)+B^4\right]^2\sqrt{A^2-4B^2}}\Big\{(A^2-4B^2)^2(B+1)^2\\ &\quad -(A^2-4B^2)B^4(2B+3)-4B^4(B+1)(B+2)^2\\ &\quad +A\Big[(A^2-4B^2)(B+1)^2-B^2(2B^3+5B^2-4)\Big]\sqrt{A^2-4B^2}\Big\}\ .\end{aligned}$$

Recalling that $A > 2B$ for patterning to be possible, these show that s_{max} is an increasing function of the water input A (illustrated in Figure 4a), but that the dependence on mortality B may be increasing or decreasing, depending on parameters (Figure 4b).

In Appendix B, I show that $\partial s_{max}/\partial B > 0$ if and only

$$\Leftrightarrow A > A_{crit} \equiv \frac{2B(B+2)}{\sqrt{2B+3}}\ . \tag{19}$$

The parameter estimates of Klausmeier (1999) imply that for trees $A_{crit} = 0.1$, which compares with $A = 0.077$–0.23; for grass $A_{crit} = 1.1$, with $A = 0.94$–2.81.

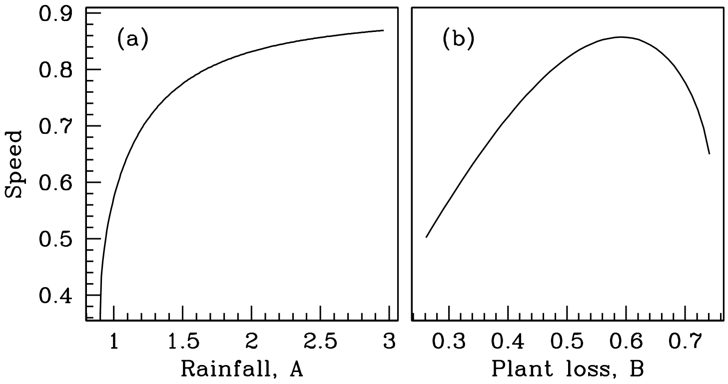

Fig. 4. An illustration of the variation in the speed of vegetation stripe migration with rainfall A and plant loss B, as predicted by linear analysis. As shown in the main text, the speed increases with A; as B increases, the speed initially increases, reaches a maximum, and then decreases. The speed is calculated using the formula (16).The parameter values are (a) $B = 0.45$, (b) $A = 1.5$. In both (a) and (b), the plots cover the full parameter ranges giving pattern formation; these are defined by the conditions $A < 2B$ and (13)

This suggests that as plant loss increases, both increases and decreases in the speed of pattern migration may occur. However, because the decrease in wave speed with plant loss occurs for parameters some distance from the Turing bifurcation curve, it requires confirmation by nonlinear analysis, which is outside the scope of this paper.

5. Discussion

Vegetation stripes are an intriguing natural phenomenon, widespread in semi-arid regions. Using a model proposed previously by Klausmeier (1999), I have presented the first systematic analysis of the dependence of these striped patterns on key ecological parameters. I have determined an approximate condition on parameters for vegetation stripes to form. Further, I have shown that pattern wavelength is a decreasing function of rainfall, and an increasing function of plant loss and of the gradient of the slope on which the stripes form. These dependencies are expected intuitively and are consistent with the numerical simulations of Klausmeier (1999). Finally I have shown that an uphill migration of the stripes is expected, at a speed that decreases with rainfall, and can increase or decrease with plant loss, according to parameter values.

From the viewpoint of testing the model, the most significant predictions concern the variation with ν, which is approximately proportional to the gradient of the hill. My analysis predicts that the wavelength of the vegetation stripes is proportional to the square root of the gradient, with their speed of migration unaffected by the slope. Because any geographical area will typically contain slopes of different gradients but with broadly similar vegetation and grazing levels, these predictions are definitely testable; however I am not aware of suitable existing data. Three caveats must be added to these predictions. Firstly, like the model itself, my prediction assumes gentle slopes (gradient less than about 1%). On steeper gradients, the water does not flow as a sheet but rather gullies form, leading to different behaviour. Vegetation stripe formation is a phenomenon associated primarily with gentle slopes. Secondly, the movement of the stripes remains a controversial aspect of the phenomenon, with very limited data, some of which appears to show a static pattern (Dunkerley & Brown, 2002). One possible explanation for this is that when the soil is of certain types, its structure may be altered in the presence/absence of vegetation in a manner that immobilises the patterns. However, this effect would not depend on gradient, and thus the independence of migration speed on gradient would remain true. The final caveat is that my predictions are based on linear analysis. Therefore, one expects them to hold for parameters close to the Turing bifurcation curve, where the patterns will be of low amplitude. However for larger amplitude patterns, nonlinear effects will be important and may alter the parameter dependencies.

Pattern formation caused by the combination of diffusion and advection has been best studied in the context of chemical systems. Here it is usually known as “differential flow-induced instability” (Jorné, 1974; Rovinsky & Menzinger, 1993; Satnoianu *et al.,*, 2001), and the advection term is due simply to fluid flow in the aqueous system of reactants. The approach used in this paper would apply equally to these chemical systems at large flow speeds. Moreover, because these systems are more amenable to systematic experiment, the resulting predictions would be relatively easy to test. In the context of vegetation stripes, however, experiments are not possible, so that one must rely on the gathering of additional field data in order to test model predictions.

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Appendix A

In this Appendix, I give the derivation of the intermediate expansion for $\operatorname{Re}\lambda$, from which I have calculated leading order approximations for the fastest growing mode (10) and the conditions for diffusion driven instability (13). Specifically, I derive an approximation to the formula (5) for $\operatorname{Re}\lambda$ when $\nu \gg 1$, with $1 = O(-d)$, $1 = O(-bc)$, and $a = O(1)$, subject to the conditions $\nu \gg (bc/d)^{1/2}$ and $\nu \gg (d^3/bc)^{1/2}$. For notational ease, I write $p = a - d$ and $q = -bc$, so that $\nu \gg 1$, $1 = O(p)$ and $1 = O(q)$, with $\nu \gg (q/p)^{1/2}$ and $\nu \gg (p^3/q)^{1/2}$. Further I assume that $k = O_s(p^{1/4}q^{1/4}/\nu^{1/2})$, say $k^2 = \kappa p^{1/2}q^{1/2}/\nu$. Then

$$\begin{aligned}
\alpha &= \left(\kappa p^{1/2}q^{1/2}/\nu - p\right)^2 - \kappa\nu p^{1/2}q^{1/2} - 4q \\
\beta^2 &= 4\kappa\nu p^{1/2}q^{1/2}\left(\kappa p^{1/2}q^{1/2}/\nu - p\right)^2 .
\end{aligned}$$

From these, $\alpha^2 + \beta^2$ can easily be determined. It contains 16 terms, but it will become clear later in the calculation that terms smaller than p^2q can be neglected. This leaves 6 significant terms:

$$\begin{aligned}
\alpha^2 + \beta^2 &= \kappa^2\nu^2 pq + 2\kappa\nu p^{5/2}q^{1/2} + 8\kappa\nu p^{1/2}q^{3/2} + p^4 + 16q^2 \\
&\quad -(4\kappa^2 + 8)p^2q + o(p^2q) \\
&= \kappa^2\nu^2 pq\left[\left(1 + \frac{p^{3/2}}{\kappa\nu q^{1/2}} + \frac{4q^{1/2}}{\kappa\nu p^{1/2}}\right)^2 - \frac{4p(\kappa^2+4)}{\nu^2\kappa^2} + o(p/\nu^2)\right] \\
\Rightarrow (\alpha^2+\beta^2)^{1/2} &= \left(\kappa\nu p^{1/2}q^{1/2} + p^2 + 4q\right)\left[1 - \frac{4p(\kappa^2+4)}{\kappa^2\nu^2} + o(p/\nu^2)\right]^{1/2} \\
&= \kappa\nu p^{1/2}q^{1/2} + p^2 + 4q - 2p^{3/2}q^{1/2}\nu^{-1}(\kappa + 4/\kappa) + o(p^{3/2}q^{1/2}/\nu).
\end{aligned}$$

Therefore

$$\begin{aligned}
\alpha + \left(\alpha^2+\beta^2\right)^{1/2} &= 2p^2 - \frac{p^{3/2}q^{1/2}}{\nu}(4\kappa + 8/\kappa) + o(p^{3/2}q^{1/2}/\nu) \\
\Rightarrow \left\{\tfrac{1}{2}\left[\alpha + \left(\alpha^2+\beta^2\right)^{1/2}\right]\right\}^{1/2} &= p\left[1 - \frac{q^{1/2}(2\kappa^2+4)}{\kappa\nu p^{1/2}} + o(q^{1/2}/p^{1/2}\nu)\right]^{1/2} \\
&= p\left[1 - \frac{q^{1/2}(\kappa^2+2)}{\kappa\nu p^{1/2}} + o(q^{1/2}/p^{1/2}\nu)\right] .
\end{aligned}$$

Finally, this gives

$$\mathrm{Re}\,\lambda = a - \frac{p^{1/2}q^{1/2}}{\nu}\left(\kappa + \frac{1}{\kappa}\right) + o(p^{1/2}q^{1/2}/\nu)\,.$$

Therefore to leading order, $\mathrm{Re}\,\lambda$ has a maximum value of $a - 2p^{1/2}q^{1/2}/\nu$, when $\kappa = 1$.

Appendix B

In this Appendix, I determine the conditions for the speed s_{max} of the fastest growing mode (defined in (16)) to be increasing or decreasing as a function of B. To investigate this, it is convenient to work in terms of $\xi \equiv A^2 - 4B^2$ rather than A; note that $\xi > 0$ is necessary for patterns. In terms of ξ and B,

$$\begin{aligned}
&\partial s_{max}/\partial B|_{A\ \mathrm{const}} > 0 \Leftrightarrow f(\xi, B) > g(\xi, B)\\
&\qquad \text{where } f(\xi, B) = (\xi^2 + 4B^2\xi)^{1/2} \cdot \left[\xi(B+1)^2 - B^2(2B^3 + 5B^2 - 4)\right]\\
&\qquad \text{and } g(\xi, B) = -\xi^2(B+1)^2 + \xi B^4(2B+3) + 4B^4(B+1)(B+2)^2\,.
\end{aligned}$$

It is easy to see that $f(\xi = 0, B) < g(\xi = 0, B)$, while $f(\xi = \infty, B) > g(\xi = \infty, B)$. Therefore there is at least one positive ξ for which $f = g$. Moreover, $f^2 = g^2$ is a cubic in ξ that can be solved exactly, and has a unique positive root at $\xi = 4B^2(B+1)^2/(2B+3)$. Therefore $\partial s_{max}/\partial B|_{A\ \mathrm{const}} > 0$ if and only if

$$\begin{aligned}
&\xi > 4B^2(B+1)^2/(2B+3)\\
\Leftrightarrow\ &A > A_{crit} \equiv \frac{2B(B+2)}{\sqrt{2B+3}}\,.
\end{aligned}$$

This is the condition given in (19).

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