Rethinking tipping points in spatial ecosystems

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Abstract

The theory of alternative stable states and tipping points has garnered a lot of attention in the last decades. It predicts potential critical transitions from one ecosystem state to a completely different state under increasing environmental stress. However, typically ecosystem models that predict tipping do not resolve space explicitly. As ecosystems are inherently spatial, it is important to understand the effects of incorporating spatial processes in models, and how those insights translate to the real world. Moreover, spatial ecosystem structures, such as vegetation patterns, are important in the prediction of ecosystem response in the face of environmental change. Models and observations from real savanna ecosystems and drylands have suggested that they may exhibit both tipping behavior as well as spatial pattern formation. Hence, in this paper, we use mathematical models of humid savannas and drylands to illustrate several pattern formation phenomena that may arise when incorporating spatial dynamics in models that exhibit tipping without resolving space. We argue that such mechanisms challenge the notion of large scale critical transitions in response to global change and reveal a more resilient nature of spatial ecosystems.

Keywords: alternative stable states, vegetation patterns, resilience, Turing instability, front dynamics, coexistence states

1. Introduction

The idea that alternative stable states may exist in ecosystems has prevailed in ecological literature for almost half a century now (Holling, 1973; May, 1977; Noy-Meir, 1975). This directly relates to the theory of tipping points, which contributes to our understanding of

ecosystem functioning (Scheffer et al., 2009; Scheffer et al., 2001; van Nes et al., 2016). With increasing stress, an ecosystem persists in one of its stable states until a critical point (also called a tipping point) is reached and a critical transition (or tipping) to another stable state occurs (Fig. 1a). Once the system has crossed a tipping point, decreasing stress to the original value does not restore the system to the original state. This phenomenon of history dependence is called *hysteresis*. The ecological significance of such a phenomenon is that a tiny change in environmental conditions can result in irreversible change of the system to another state with completely different characteristics. The theory of alternative stable state has been used by ecologists to explain, for instance, the process of clear lakes rapidly turning turbid (Banerjee et al., 2021; Scheffer et al., 1993), desertification of vegetated lands (Rietkerk & van de Koppel, 1997; Rietkerk et al., 1997) and the co-occurrence of tropical forests and savannas for the same climatic conditions (Hirota et al., 2011; Staver et al., 2011).

To understand ecosystems with multiple alternative states, often the ball in a landscape analogy is used (Fig. 1b). Here, a ball represents the current ecosystem state and the landscape represents its stability properties (its 'stability landscape'). When there is only one stable state, the landscape has one valley where the ball rests. With increasing environmental stress, the landscape changes shape and has two valleys, each representing an alternative stable state. The peak in between these two valleys represents a third equilibrium that is unstable. For further increase in stress levels, the landscape changes such that the original valley disappears and the ball rolls to the alternative valley. The mathematical phenomenon by which valleys form or disappear in the landscape is known as a bifurcation. This is the underlying cause for critical transition or (bifurcation-induced) tipping.

A common mechanism that drives ecosystems to undergo such critical transitions are positive feedbacks (DeAngelis, 1986; van Nes et al., 2016). For instance, in the case of shallow lakes, nutrient overloading causes water turbidity, which leads to decrease in density of macrophyte plants, which in turn leads to even lesser nutrient uptake and so more turbidity (Scheffer et al., 1993). Similarly, in the case of dryland ecosystems, a decrease in vegetation reduces water infiltration into the soil, which in turn leads to further vegetation decrease (Rietkerk et al., 1997). In recent years, the changing global environment due to climate change led to a renewed resurgence of these ideas whereby the concept of critical transitions has been linked to ecosystems as well as climate system elements (Lenton et al., 2008).

Alternative stable states

Fig 1. A. **Classical theory of tipping points**: *with increasing environmental stress the ecosystem undergoes a critical transition to the alternative stable state at T_1 and the stress has to decrease below T_2 before the ecosystem returns to the original state via another critical transition. The blue shaded region indicates the environmental conditions under which alternative stable states may exist. The solid and dotted lines represent stable and unstable ecosystem states respectively. B. Changes in stability landscape with increasing environmental stress (from top to bottom). Numbered balls in A and B correspond to the same ecosystem state for the same environmental stress levels.*

Typically, the vulnerability of ecosystems to critical transitions has been predicted by analyzing simple non-spatial models, which do not take into account important spatial processes, such as dispersal or lateral flows. Such mechanisms can lead to spatially structured ecosystem states, with spatial boundaries or fronts between alternative states; this has been shown to be important to assess ecosystem responses to global change (Goel et al., 2020; Zelnik et al., 2017). In this paper, we demonstrate the role of spatial processes for (ecosystem) models exhibiting alternative stable states without resolving space. When non-spatial models are extended by the inclusion of spatial processes, completely new behaviors can be found, leading to new predictions of the ecosystem dynamics and resilience. Although some spatial mechanisms of transitions that are relevant to spatially extended systems have been studied in ecological context, a comprehensive understanding is still lacking. So, it is important to summarize relevant knowledge in this area and integrate it with state-of-the-art ecological understanding. In this study, we demonstrate with examples various types of ecosystem behavior that can be found once we spatially extend non-spatial bistable models that are tipping-prone.

We have chosen savannas and drylands as archetypical ecosystems for this study (Rietkerk et al., 2021), because of two main reasons. First, model predictions and observations suggest that savanna ecosystems may exhibit tipping. For instance, at the wetter end of its

range of existence, the savanna-forest transition zone could be bimodal, i.e., for the same climatic conditions, both savanna and forest are observed (Aleman et al., 2020; D'Onofrio et al., 2018; Dantas et al., 2016; Hirota et al., 2011; Staver et al., 2011). Further in drylands, with arid and semi-arid conditions, it is predicted that desertification could occur via critical transitions or tipping (Rietkerk & van de Koppel, 1997; Rietkerk et al., 1997). Second, for both savannas and drylands, spatial patterns have been observed (Groen, 2007), and their importance has been acknowledged. At the savanna-forest boundary, the role of spatial scale and heterogeneity has been stressed upon recently (Aleman & Staver, 2018; Staver, 2018; Wuyts et al., 2017). In semi-arid ecosystems, various kinds of vegetation patterns such as gaps, labyrinth, stripes and spots are well documented in the literature (Deblauwe et al., 2008; Rietkerk & van de Koppel, 2008; Rietkerk et al., 2002), which highlights the importance of spatial processes.

In this paper we represent drylands and humid savannas with two spatially explicit models. We use the reaction diffusion framework, as it is mathematically tractable and commonly used in ecology (Rietkerk et al., 2002; Zelnik et al., 2015). We demonstrate spatial pattern formation in these models due to diverse dynamics, such as interacting spatial feedbacks, spatial heterogeneity and behavior of spatial boundaries (also called fronts or interfaces) between alternative stable states. We identify the mechanisms that might be more relevant for each biome and argue that these mechanisms make ecosystems more resilient than earlier thought on the basis of non-spatial frameworks.

The rest of the manuscript is organized in the following manner. First, we introduce non-spatial models of humid savannas and drylands and study the change in equilibrium properties as environmental conditions change. Subsequently, we incorporate spatial dynamics in these models and demonstrate how this can fundamentally and qualitatively change the model predictions. Further, we elaborate on the differences in predictions that might be observed under dry and humid conditions depending on the driving force in that region. Finally, we discuss the implications of these new developments and delineate future perspectives for studies contributing towards consequences of global change.

2. Model description

To model humid savannas and drylands, we use two conceptual models, each with two interacting state variables. We choose this level of complexity for the following reasons. While single component models, which have been used earlier to model these ecosystems (Bastiaansen et al., 2022; Goel et al., 2020), are easier to analyze, they do not accommodate the richness and variety of behaviors that may be possible due to spatial effects. However, for the ease of analysis, we also refrain from incorporating more state variables, the likes of which are also prevalent in the literature (e.g. Gilad et al (2004); Rietkerk et al. (2002); Staver & Levin (2012); Wuyts et al. (2017)). Using models of similar complexity for both cases allows us to compare the two models with each other and generate new hypothesis about the mechanisms which may lead to different kinds of behavior when models exhibiting alternative stable states are spatially extended.

a. Humid savanna model

Here, we introduce a new modelling framework (hereafter referred to as "humid savanna model") that considers two plant functional types: grasses, which fundamentally define savannas and its vegetation (Lehmann et al., 2011; Parr et al., 2014), and forest trees. For simplicity, we do not explicitly model savanna trees, but we cluster them together with grasses into the savanna vegetation variable, since the savanna trees have similar responses to shade and fire as grasses (Charles-Dominique et al., 2018). Grasses are shade intolerant, fire resistant and have good resprouting abilities, which thus results in minimal loss and quick regrowth after fire (Hoffmann et al., 2012). Further, grasses act as fuel for fires enabling them to spread, thus playing a significant role in fire mediated destruction of the forest trees (Lehmann et al., 2011). Conversely, tropical forest trees can tolerate shade well but do not generally have any trait conferring them fire resistant (Charles-Dominique et al., 2018).

We denote savanna biomass density by S (kg m^{-2}) and forest biomass by F (kg m^{-2}), and model their dynamics as:

$$\frac{dS}{d\tau} = r_S S \left(1 - \frac{S}{K_S}\right) - cFS - (\eta f_S S + d_S)S$$

$$\frac{dF}{d\tau} = r_F F \left(1 - \frac{F}{K_F}\right) - \eta f_F SF - d_F F$$

$$\text{---------------------- (1)}$$

Here, logistic growth is considered, which allows the forest and savanna biomass to increase until their carrying capacity is reached. r_S and r_F are the growth rate of savanna vegetation and forest trees respectively. K_S and K_F are their carrying capacities. d_F and d_S are the removal rate of the forest trees and of the savanna vegetation, resulting from various factors, such as natural mortality and herbivory. f_S and f_F represent the sensitivity of savanna vegetation and forest trees to fire, with $f_F > f_S$ since savanna vegetation is more fire-resistant than forest trees. Savanna vegetation acts as a fuel to the fires, which occur at a frequency η. Thus, the rate at which savanna biomass is lost is proportional to the savanna plant biomass and can be modeled as $-\eta f_S S$. Further, fire also causes destruction and loss of forest biomass and the rate at which such loss occurs is modeled with $-\eta f_F S$. Forest trees with closed canopy have a negative influence on the shade-intolerant savanna vegetation which is modeled with $-cFS$. τ is time expressed in years. The dimensionless version of the model can be expressed as follows (see Supplementary material Section A.1 for details):

$$\frac{ds}{dt} = s(1 - s) - bfs - ns$$

$$\frac{df}{dt} = \mu f(1 - f) - asf - mf$$

$$\text{---------------------- (2)}$$

Here, s and f are the dimensionless state variables and μ, a, b, m, n are the dimensionless parameters of the model. In order to explore the equilibrium properties of the humid-savanna model, we carry out a bifurcation analysis of the nonspatial model (Eqs. (2)). Water availability, mostly due to rainfall, is expected to be an important bifurcation parameter as tropical forests ultimately dominate when water availability is very large, while savannas are observed at lower mean annual rainfall (e.g. (Lehmann et al., 2011)) . As we are not modelling water availability explicitly, we represent, the changing climatic condition along the rainfall gradient in this transition zone by changing the forest tree growth rate (r_F in the dimensional model (1)). This is justified as precipitation increases the forest tree growth rate, while it has negligible impact on the growth of the savanna vegetation in mesic and humid savannas, where the prevailing humid conditions are sufficient so that the grasses are not limited by water (D'Onofrio et al., 2018). Since $\mu = \frac{r_F}{r_S}$ (see Supplementary material Section A.1), we choose μ as the bifurcation parameter (Fig 2.A,B). The choices of the rest of the parameters are motivated from ecological literature (see Supplementary material Section A.5).

In an intermediate range of forest tree growth rate, μ, the forest and savanna states exist as alternative stable states. On decreasing μ, if the system is in the savanna state, it continues to persist in the same state, while if the system is in the forest state it undergoes an abrupt transition to the savanna state when the rainfall is low enough. The opposite happens on increasing μ. It is interesting to note here that the tipping behavior demonstrated in this model is due to two transcritical bifurcations (see Supplementary material Section A.2, A.3 for analytical expression of the steady states and their stability conditions and Section A.5, Fig S1 for the complete bifurcation diagram), and not fold bifurcations (Fig. 1), which are encountered in many other similar models (Staver & Levin, 2012; van de Leemput et al., 2015).

Fig. 2. Bifurcation diagrams of the two dimensionless non-spatial models. (A,B) Humid savanna model (Equation 2), forest tree (A) and savanna vegetation (B) biomass as a function of forest tree growth rate (μ). The green lines represent forest-only state and the yellow lines represent savanna-only state. The solid lines represent stable equilibria while the dashed lines represent unstable equilibria. For clarity, other biologically non-feasible equilibria are not shown here (see Supplementary material Section A.5, Fig S1, for the complete bifurcation diagram). Parameter values: a=1.3, b=1.8, m=0.02, n=0.4. (C) Dryland model (Equation 4), vegetation biomass as a function of rainfall (p). The dark brown line represents the vegetated state and the light brown line represent the barren state. Parameter values: u=1.2, k=1. The red lines denote time series simulations with the respective equilibria as initial conditions and a gradual decrease in bifurcation parameters, i.e., dμ/dt=0.0005 and dp/dt=-0.0005.

b. Dryland model

To represent the vegetation dynamics in drylands, we consider a modified version of the commonly used Klausmeier model (Bastiaansen et al., 2019; Eigentler, 2021; Klausmeier, 1999). Although this model has been largely used in the spatial context, we start with a non-spatial variant here to highlight the differences in behavior predicted from the spatial and the non-spatial version. The non-spatial (i.e., "reaction") part of the model (hereafter referred to as "dryland model"), which describes the water-plant interactions in drylands, is given as follows:

$$\frac{dW}{d\tau} = q - lW - rWV^2$$

$$\frac{dV}{d\tau} = rjWV^2\left(1 - \frac{V}{K}\right) - dV$$

---------------------- (3)

Here, W represents surface water and V represents vegetation biomass. q represents rainfall, l represents the water evaporation rate and rWV is the uptake rate of water which depends on both the water and the vegetation biomass present. The conversion of water into biomass is assumed to only occur until the vegetation reaches a carrying capacity K. Hence, it can be expressed as $j(1-V/K)$ which is a decreasing function of V until it reaches zero at the carrying capacity, $V=K$. d represents natural mortality of the vegetation.

The model can then be non-dimensionalized (see Supplementary material Section B.1) as follows:

$$\frac{dw}{dt} = p - w - wv^2$$

$$\frac{dv}{dt} = wv^2\left(1 - \frac{v}{k}\right) - uv$$

---------------------- (4)

where w and v are the dimensionless state variables and p, u, and k are positive parameters. Since water limitation drives the system dynamics, the rainfall parameter, 'q', is the appropriate choice for the bifurcation parameter. In the dimensionless model, this corresponds to 'p'. All other parameters are adapted from earlier literature (see Supporting information, section 2.5). The model possesses two alternative stable states that exist for a certain parameter range, namely (i) a bare soil state and (ii) a vegetation state (Fig. 2.C). As rainfall decreases, vegetation biomass decreases slowly until it reaches a threshold where vegetation can no longer persist and the system undergoes a critical shift to the barren state. This shift is irreversible as on increasing rainfall, the system can no longer go back to the vegetated state.

3. Spatially extended ecosystems

Spatial processes play a vital role in ecosystem functioning and biome distributions. Therefore we now spatially extend these two models and demonstrate how the predictions of alternative stable state theory change when incorporating spatial effects. We consider the evolution of the two dynamical variables in each model, $\binom{s}{f}$ in case of the humid savanna model or $\binom{w}{v}$ in case of the dryland model, on a unbounded spatial domain with

coordinates $(x, y) \in \mathbb{R}^2$ (or only $x \in \mathbb{R}$ in case of one dimension). In addition to the local dynamics, spatial transport between locations now also plays a role. The simplest way to implement spatial transport is to add (linear) diffusion. Thus, new spatial models describing the vegetation dynamics in the humid savanna and drylands over time and space are given by the partial differential equations given by the following.

Humid savanna model:

$$\frac{\partial s}{\partial t} = s(1 - s) - bfs - ns + \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 s}{\partial y^2}\right)$$

$$\frac{\partial f}{\partial t} = \mu f(1 - f) - asf - mf + \delta\left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2}\right)$$

-------------------(5)

Dryland model:

$$\frac{\partial w}{\partial t} = p - w - wv^2 + \delta_w\left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right)$$

$$\frac{\partial v}{\partial t} = wv^2\left(1 - \frac{v}{k}\right) - uv + \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2}\right)$$

-------------------(6)

Here, δ represents the ratio of the diffusion coefficient of the forest and savanna vegetation and δ_w represents the ratio of the diffusion coefficient of water and dryland vegetation (see Supplementary material Section A.1. and B.1 for non-dimensionalization of the full spatial models). This type of models, known as reaction-diffusion equations, consist of a reaction part which describes the local dynamics and a diffusion part which describes the spatial transport. Such models are important in the context of spatial dynamics because they are mathematically tractable. Furthermore, a relatively simple class of such models can exhibit rich patterns (Klausmeier, 1999; Rietkerk et al., 2002; Wuyts et al., 2017; Zelnik et al., 2015), which are comparable to what is observed in real ecosystems. In the following sections, we discuss the various mechanisms of spatial pattern formation that may be observed when models with alternative stable states are spatially extended. We discuss regular pattern formation which are known to occur in many models of drylands. Furthermore, patterns could also be formed due to local disturbances – which we discuss in the context of both humid savanna and drylands and then compare the two cases. We discuss the implications of such pattern formations in the context of transitions between alternative stable ecosystem states. The emergence of coexistence states, rather than tipping, as a result of spatially heterogeneous environment and front instabilities are also described. All simulations in the following sections have been carried out using MATLAB.

a. Turing before tipping

In the non-spatial models, the forest-only state as well as the savanna-only state, in case of humid savanna, and the vegetated state, in case of drylands, remain stable under small perturbations until a particular threshold of environmental pressure. However, such spatially uniform equilibria in models with two or more components may become unstable to spatially heterogeneous perturbations. This is the most well-known and largely studied Turing bifurcation and results in regular spatial patterns (HilleRisLambers et al., 2001; Turing, 1952). On investigating the models (5) and (6) for Turing bifurcations, we see that the humid savanna model does not exhibit such instability (for details see Han (2011) and Supplementary material Section A.4). So if a spatial domain is homogeneously covered with either of the forest or savanna state, then changing μ may lead to tipping of the domain to the alternative stable state. However, for the dryland model, the onset of Turing patterns could be seen easily (Fig. 3 and Supplementary material Section B.4, Fig. S2) and patterns observed in many real drylands are often explained by this phenomenon (Rietkerk & van de Koppel, 2008; Rietkerk et al., 2002). Further, we observe in the dryland model that the Turing bifurcation occurs before the threshold of environmental pressure where tipping is predicted to occur in the non-spatial version of the model (Fig 3, Supplementary material Section B.4 and Fig S2). This phenomenon has been referred to as "Turing before tipping" (Rietkerk et al., 2021). So, essentially this implies that, when considering spatial dynamics, on decreasing rainfall there is onset of pattern formation before the system reaches the tipping point.

Fig 3.   Turing before tipping. (A) Turing bifurcation occurs for larger values of rainfall (p_{Turing}) compared to the tipping point (p_T) in the dryland model. The ecosystem could then persist in patterned states beyond the tipping point within the Busse balloon (a conceptual diagram is

presented). With decreasing rainfall, the patterned state retains its wavelength until the edge of the Busse balloon (minor ecosystem adjustments are indicated by single arrows) where the ecosystem could shift (indicated by double arrows) to a pattern of different wavelength. There could be multiple such ecosystem shifts instead of a single catastrophic state shift when the rainfall parameter, p, changes gradually over time. Pathway for ecosystem degradation is indicated by the red lines and for ecosystem recovery is indicated by the green lines. The dark brown line (solid: stable; dashed: unstable) represents the vegetated state and the light brown line represent the barren state. (B) Vegetation biomass across one-dimensional spatial domain on decreasing the rainfall parameter gradually, i.e., $dp/dt=-1.25\text{x}10^{-6}$, with randomly perturbed homogeneous vegetation state for $p<p_{Turing}$ as initial condition. Patterns of different wavelengths can be observed for $p_1=5.825>p_T$ (C) and for $p_2=5.7625<p_T$ (D). Parameter values: $\delta_w=200$, other parameter values are the same as in Fig 2.

Ecologically, such pattern formation can be explained by a combination of short-range facilitation and long-range inhibition due to vegetation. Vegetation patches increase water infiltration, which in turn increases vegetation locally thus resulting in a positive feedback. Water taken up by the vegetation leads to diffusion of water from nearby areas to the patch. Hence, there is less water further away from the patch, leading to decrease in vegetation which is a negative feedback. This feedback, which changes from positive to negative at different spatial scales is known as scale dependent feedback, and it explains the regular spatial pattern formation (Rietkerk & van de Koppel, 2008). Although the emergence of such patterns in ecosystem were earlier believed to be an early warning to the upcoming abrupt transitions, recent developments suggest that the behavior and stability of such patterns determines whether the ecosystem will undergo a critical transition to an alternative stable state. It has been shown in similar dryland models that the patterns can remain stable for a large range of environmental conditions. Also, for a particular environmental condition, there could be multiple stable patterns of different wavelengths. Moreover, it is possible to define a region in the parameter wave-number (number of patches per unit distance) space, also called "Busse balloon" comprising all the stable patterns (Bastiaansen et al., 2018; Siteur et al., 2014). In fact, on changing environmental conditions, the patterns remain stable up to the edge of this region where they typically adapt to a new wavelength. This mechanism leads to small transitions between patterns of different wavelength, which help ecosystems evade large critical transitions or tipping as predicted by alternative stable states theory. While we do not specifically define the Busse balloon for this particular model, in Fig. 3A, we illustrate a conceptual diagram of the general mechanism by which such a stability region helps evade tipping.

b. Patterns due to local disturbances

Although scale-dependent feedbacks (or Turing bifurcations) are probably the most well studied mechanism of pattern formation in ecosystems, patterns could also be formed due to spatially localized disturbances to the system state, such as grazing and local deforestation. The disturbances, here, refer to a change in ecosystem state in an otherwise homogeneous landscape rather than change in model parameters, which represents environmental condition. In models exhibiting alternative stable states, a range of environmental conditions (parameters) exists where the whole domain can be in one of the two possible states. In such an environment, if only a part of the domain is disturbed and transformed into the other ecosystem state, then the two alternative states can coexist in

space, in a transient way, while they are connected via a spatial boundary, which is also called 'front' in the mathematical literature. Front dynamics are not fully understood yet, except for so-called potential systems (see Box 1). In the case of single component models that represent potential systems, such a front always exists in the bistable regime of the model. The fronts propagate in one of the directions, resulting in either a gradual recovery from initial disturbance or a gradual but complete transition to the alternative stable state (Bel et al., 2012; van de Leemput et al., 2015). They always travel towards the state with lowest potential or in other words the deepest well in the ball in landscape picture (see Fig. 1).

However, most two- or multi-component models representative of ecosystems are often not potential systems. In such a case, the above framework does not necessarily hold true and the direction of front propagation can only be explained by environmental conditions represented by model parameters. To demonstrate this, we study the spatial version of the humid savanna model equations (5) in one-dimension, under conditions where there is bistability between forest-only and savanna-only state in the non-spatial model. When the landscape is initially divided into forest and savanna, we see that either the forest biome invades the savanna biome or vice versa depending on the parameter values – similar to the case explained in Box 1. Moreover, when all other parameters are appropriately chosen, the parameter μ, representing forest growth rate, can govern the direction of propagation of the traveling wave (see Fig. 4). For parameters corresponding to Fig. 2, when $\mu = 0.4$, the savanna invades the forests and eventually covers the whole landscape and when $\mu = 0.5$, the opposite happens. Since forest growth rates are expected to increase with water availability, ecologically this implies that changing climatic conditions could govern whether savanna invades the forest or vice versa.

Box 1

Direction of front propagation

The intuition behind front propagation can be understood with the help of relatively simple models that are so-called potential systems. A system which describes time evolution of a state variable *v*, can be defined as a potential system if it is possible to define a function *U(v)* such that it always decreases with time (Strogatz, 1994). While this in general does not hold for most two- or multicomponent ecosystem models, single component non-spatial models are always potential systems. Hence, we consider such a model to illustrate this

$$\frac{dv}{dt} = F(v)$$

U is called a potential function and can be defined such that the following holds:

$$\frac{dU}{dv} = -F(v)$$

Here, the function *U* depends on *v* which in turn depends on *t*. So, *U* has implicit dependence on time. Now,

$$\frac{dU}{dt} = \frac{dU}{dv}\frac{dv}{dt} = -\left(F(v)\right)^2 \leqslant 0$$

So, the potential function U either remains constant with time or decreases. This implies that the system always approaches a local minimum of its potential. Such a minimum represents a stable state where any perturbation which is sufficiently small must decay in time. This is the mathematical reasoning behind the potential landscape being representative of the stability properties of a system, as demonstrated in Fig. 1. In case the system displays alternative stable states, say a state v_A and a state v_B, the states represent local minima, i.e., minimum with respect to local surroundings in the potential landscape.

Using the potential function, and adding diffusion with coefficient D, a spatially extended model can be written as the following partial differential equation

$$\frac{\partial v}{\partial t} = -\frac{dU}{dv} + D\frac{\partial^2 v}{\partial x^2}$$

For simplicity, we restrict ourselves to one spatial dimension. When one part of the spatial domain is in state v_A and the other is in v_B, there is a front connecting the two. Letting ξ denote the constant velocity at which the front propagates, we may define a new spatial coordinate that follows the location of the front $z=x-\xi t$. We consider a front which asymptotically converges to v_A when $z \to -\infty$ and v_B when $z \to \infty$, then the velocity, ξ, can be expressed as (see Bel et al. (2012) and full derivation, see Supplementary material Section C)

$$\xi = A^{-1}[U(v_B) - U(v_A)]$$

$$\text{where, } A = \int_{-\infty}^{\infty}(v')^2 dz$$

It can be observed from above that the front velocity depends on the difference between the potential U at the two alternative stable states. In the potential landscape, this process of front propagation converts areas of high potential to areas of low potential. In other words, this means the deeper well in Fig. 1 invades the other. The specific value (or values) of the parameter at which the potentials corresponding to the two alternative states are the same is called the Maxwell point, and for these parameter values the front is stationary, i.e. its velocity $\xi = 0$ (Bel et al., 2012; Pismen, 2006).

Interestingly, there is a parameter value at which the front remains stationary, i.e., neither of the states invade the other, which is called "Maxwell point" (Pismen, 2006). At this point, in other words, the velocity of the front propagation becomes zero and thus the part of the landscape covered by each of the ecosystem states remains the same in size. Although the term "Maxwell point" has been coined in the case of potential systems (and before that in physics, see Clerk-Maxwell (1875)), we will further extend this notion to stationary fronts in other systems as well. The Maxwell point in the above case will be $0.4 < \mu_M < 0.5$ and can numerically be approximated to be $\mu_M \sim 0.4489$ (Fig 4.B). It is noteworthy that any slight deviation from that environmental condition at the Maxwell point would lead to a transition

of the whole spatial domain to either of the ecosystem states, thereby exhibiting a characteristic of an unstable state. Similar analysis was also carried out for the dryland system where larger precipitation (p=6.4) leads to vegetation invading the barren land and a lower precipitation (p=6.3) results in the movement of the front in the opposite direction (Fig. 4. D-F). The "Maxwell point" in this case is approximately $p_M \sim 6.3513$ (Fig. E).

Fig 4: Front propagation over time in one dimensional space. Direction of front propagation is indicated by the arrows. (A-C) Fronts connecting the savanna and the forest states. The savanna invades the forest when $\mu=0.4<\mu_M$, and the forest invades the savanna when $\mu=0.5>\mu_M$. For $\mu=\mu_M(\sim0.4489)$, the front remains approximately stationary. Green and yellow lines denote forest and savanna biomass respectively, close to the initial condition where half of the spatial domain is in the savanna state and the other half is in the forest state. The shaded regions indicate their respective biomass after a time t. Parameter values: $\delta=0.01$, the other parameters are the same as in Fig 2. (D-F) Front connecting vegetation and the barren states. Vegetation invades barren land when p=6.4, and barren land invades vegetation when p=6.3. For $p=p_M$ (~6.3513), the front remains approximately stationary. The brown line indicates vegetation biomass close to the initial condition where half of the spatial domain is in the barren state and the other half is in the vegetated state. Parameter values: $\delta_w=100$, the other parameters are the same as in Fig 2.

The above-described behavior can lead to stable spatial patterns when multiple localized disturbances form localized domains of the alternative stable states in the landscape. This could happen when a homogeneous landscape is disrupted by, for instance, changes in land use. For example, multiple large patches of bare soil could form within an otherwise vegetated landscape in drylands. Mathematically, this results in the creation of multiple fronts. The dynamics of these multiple fronts is a bit more subtle than that of a single front. The fronts (i.e. the edges of the patches) may move towards each other, leading the vegetation patches or the barren areas to merge, depending on the direction of front

propagation (Bel et al., 2012). However, a different behavior can also be observed, because, importantly, the presence of one front influences the movement of the other. In the case of two- or multicomponent systems, this can result in stationary fronts (Jaïbi et al., 2020; Zelnik & Meron, 2018). Such multiple stationary fronts may lead to domains of alternative stable states positioned next to each other, so they can coexist in a stable way. So, for environmental conditions where the barren state can invade the vegetated state, such multiple stationary fronts created via, for instance, local disturbances can lead to coexistence states, thus making the ecosystem more resilient. We show this with the 1D spatially-extended dryland model (6) (see Figure 5. A-C). When initially one part of the landscape is disturbed and converted to barren land, the whole landscape gradually evolves to a barren state (Fig. 5.A). On the other hand, when the initial disturbance produces multiple patches of barren land in the landscape, the same environmental conditions (i.e. the same model parameters) could yield stable vegetation patches (Fig 5.B). The barren state invades the vegetation in both directions until both fronts interact with each other leading to the stable vegetation patch (Fig. 5.C). It is interesting to note that we do not find such type of stable patterns for the humid savanna model. In order to find that, an additional condition of environmental spatial heterogeneity is necessary, which is discussed in the following section (see Fig 5D-F)

Fig.5: Coexistence states. (A) Barren state invading the vegetated state in the dryland ecosystem. (B) Stable vegetation patch in drylands due to multiple stationary fronts. (C) Propagation of the fronts in the dryland when there are multiple barren patches in the landscape. The brown line indicates vegetation biomass close to the initial condition while the shade indicates the biomass after a long time (t=1200). Parameters: $p=6.2<p_M$, other parameters are the same as Fig. 4. (D) The forest state invades the savanna state in the humid savanna system ($\mu= \mu_0$). (E-F) Stable patterns of alternate savanna(s) and forest (f) patches due to (environmental) spatial heterogeneity of water availability, expressed as variation in the forest growth rate, $\mu= \mu_0 + 0.025 \sin (0.16x)$, where x is the 1D spatial coordinate. The green and yellow shades in (F) indicate forest and savanna biomass at the end simulation time (t=11000). Parameters: $\mu_0=0.46>\mu_M$, other parameters are the same as Fig 4.

c. Spatially heterogeneous environment

Front propagation in ecosystems will depend on local environmental conditions. Although it is common in model studies to assume that the dynamics arising from interactions between the system components remains the same throughout the whole domain, in real ecosystems conditions are typically heterogenous. Thus, local interactions can vary across the landscape with the spatial location. For example, water availability could vary quite a bit across a landscape, due to e.g. variations in topography and/or soil types. We incorporate such spatial heterogeneity of environmental conditions in the humid savanna model by assuming that the water availability determines variations in the forest growth rate, μ, across the domain. We specifically use two forms of spatial variation in μ: (i) small changes around a mean and (ii) monotonically decreasing across the domain. For the former, we assume small sinusoidal variations in the forest growth rate, μ, across the domain, and simulate over a one dimensional spatial domain with $\mu(x)= 0.46 + 0.025 \sin (0.16x)$, where x is 1D dimensionless spatial coordinate (Fig 5 E-F). We stress that the spatial variation in μ is thus relatively small. Noticeably, we now observe stable alternate patches or "coexistence states" of savanna and forest if there are multiple localized domains of savanna in a homogeneous forest landscape. This could potentially explain the savanna-forest mosaics often observed at the transition zone between the two biomes (Charles-Dominique et al., 2018; Charles-Dominique et al., 2015). It is important to note that without spatial heterogeneity (i.e., for $\mu=0.46$ in Fig. 5D), the whole landscape would be covered only with forest. In other words, incorporation of spatial heterogeneity made the propagating fronts stationary. So, for environmental condition where forest could invade the savanna, spatial heterogeneity can lead to stable coexistence states, thus making the ecosystem more resilient. This result is in accordance to earlier findings where spatial heterogeneity in environmental conditions has been shown to explain stable savanna-forest boundaries (Goel et al., 2020; Wuyts et al., 2017; Wuyts et al., 2019) .

Fig. 6: Tipping to intermediate coexistence states when forest growth rate, $\mu(x)=\mu_{max} e^{-0.02x}$. Mean biomass of savanna (A) and forest (B) vegetation with respect to changing μ_{max}. The green lines indicate forest-only state while the yellow lines indicate the savanna only state. The blue line indicates the intermediate coexistence states where part of the landscape is covered with savanna and the rest with forest. The dashed black lines represent the unstable states. The red lines denote time series simulations with savanna state as initial condition and a gradual increase in the bifurcation parameter, i.e., $d\mu_{max}/dt=0.0002$. The circles marked on the blue lines indicate the three values of μ_{max} for which the coexistence states are demonstrated in (C). The coexistence state for $\mu_{max1}=0.7$ indicates multistability of the ecosystem; the coexistence states for $\mu_{max2}=1.5$ and $\mu_{max3}=2.8$ are far beyond the tipping point in the non-spatial system in Fig. 2. Parameters values are same as Fig. 3.

So, the non-spatial model, which exhibits tipping behavior, when extended with spatial effects shows either gradual transitions from one state to another or stable coexistence of forest and savanna states with boundaries separating the two states. Now, it is important to ask how these coexistence states respond to changing climatic conditions. It has been shown by Bastiaansen et al. (2022) that if the environmental condition varies within the landscape, i.e., the model parameters varies spatially, then that may lead to existence of multiple stable coexistence states for the same climatic condition. This is true in case of different single component ecosystem and climate system element models. These authors

have argued that this may lead to the so-called "fragmented tipping", i.e., the system will only tip to such intermediate coexistence states rather than undergoing one large scale critical transition to the alternative stable state. This leads us to testing this prediction within our two-component humid savanna model. For this, we use a second form of spatial heterogeneity of the forest growth rate parameter and assume $\mu(x) = \mu_{max} \, e^{-0.02x}$ (see Fig 6). This essentially implies that the forest growth rate is at its maximum at one end of the landscape *(x=0),* and it decreases monotonically along the landscape with a minimum at the other end *(x=L).* We observe that changing the parameter μ_{max}, which amounts to change in the forest growth rate on the whole landscape, will not amount to tipping of the savanna-only state to the forest only state but instead the system will switch to an intermediate stable coexistence state where only a part of the domain will transition to the new state. On changing the environmental condition μ_{max}, further, then system gradually changes along this intermediate stable state thus making the process less critical and more easily reversible. It is important to note that these coexistence states can remain stable for environmental conditions much beyond the tipping point predicted by the non-spatial model. This demonstrates that spatial processes in the ecosystems combined with small environmental heterogeneity makes them much more resilient than that predicted by non-spatial models.

d. Front instabilities

Although till now we only discussed front dynamics in one spatial dimension, even richer behavior can be observed when extending in two spatial dimensions. When the fronts are not stationary, local processes that occur at the front zone determine the nature of the global transitions. Boundaries or fronts separating different ecosystem states are spatial structures that can go through instabilities much like uniform states can go through Turing instabilities in response to perturbations. When that happens, the spatial interface between alternative states or coexistence states can deform and self-organize giving rise to so called "finger-like patterns". Similar patterns of coexistence states arising out of front invasion have been studied in the past in the context of predator-prey models, including three species Lotka-Volterra models (Mimura & Tohma, 2015; Petrovskii et al., 2005; Petrovskii et al., 2002), models of bacterial growth (Giverso et al., 2015) and dryland ecosystem models (Fernandez-Oto et al., 2019). A recent study by Carter et al. (2023) showed that the dryland model (Equation (6)) also exhibits front instabilities, which can in turn lead to spatial patterns. In that study, the authors established a mathematical criterion for the instability of fronts in two-component reaction diffusion models in two spatial dimensions. In particular, for activator-inhibitor-type systems, such as the dryland model (6), fronts between stable homogeneous states are typically unstable when the ratio of the diffusion coefficients of the components is suitably large, a reasonable assumption in the case of the dryland model (as water diffuses much faster than vegetation). This instability can lead to regular pattern formation: one observes "finger-like patterns" emerging from the interface in such models (Figure 7). In contrast to the corresponding system in one (spatial) dimension, a traveling front between stable homogeneous states is unstable in such activator-inhibitor-type models in two spatial dimensions, with instabilities giving way to alternating stable states

which can self-organize into labyrinthine structures resembling Turing patterns. Ecologically such pattern formation is of potential profound significance: while one ecosystem state invades the other, simultaneously the latter is able to invade the former. This could even lead to reverse transitions of biomes, for example reversing desertification (Fernandez-Oto et al., 2019). However, in the humid savanna model, which does not have a strict activator-inhibitor structure, we were unable to find any front instability, in spite of extensive numerical exploration. In fact, this is in accordance to the criterion introduced by Carter et al. (2023) which indicates that interfaces in such models may be stable also in two spatial dimensions so that no spatial patterns – fingers or labyrinths – will be formed.

Fig. 7: The time evolution of front instabilities in the dryland model. Vegetation density is indicated by the color bar. Dark brown represents the vegetated state and light brown represents barren state. Simulations are initialized with vegetation covering (A) half of the landscape (B) a circular patch within the landscape. Parameter values: p=6.2, δ_w=400. Other parameters are the same as in Fig 2.

4. Discussion

Distinct ways of spatial pattern formation may be pathways for ecosystems to avoid critical transitions or tipping. While non-spatial systems with alternative stable states predict that the system can exists in only one of the states, including spatial dynamics leads to qualitatively different behavior. A common scientific hypothesis currently is that humid savannas are bistable with forests, with these two biomes thus linked to tipping as theoretical framework (Hirota et al., 2011; Staver et al., 2011). Further, in drylands, desertification is also believed to be a result of ecosystem tipping (Rietkerk et al., 1997). We have shown that incorporation of relatively simple spatial dynamics in these ecosystem

models can give rise to spatial patterns, which may lead to intermediate states and gradual transitions from one of the alternative ecosystem states to the other.

In the drylands, scale-dependent feedbacks can lead to formation of Turing patterns before the environmental condition where tipping is predicted to occur. This phenomenon is known as "Turing before tipping". Although patterns formed due to such instability were earlier believed to be early warning signs for tipping points, new mathematical analyses now indicate otherwise. Such patterns, in fact, indicate that multiple stable intermediate states exist in the ecosystems. On increasing pressure on the ecosystem, the patterns can adapt to a new wavelengths, thus undergoing small transitions instead of one large critical transition or tipping.

Although much of the studies regarding pattern formation in ecosystems have been linked to scale-dependent feedbacks, other mechanisms of pattern formation, e.g., due to local disturbances, may be equally relevant. A simple spatial extension of non-spatial models displaying tipping indicate that the spatial boundary separating the two states or biomes can move laterally in space on a slow time scale, leading to gradual transition of one of the states to the other. In other words, the two stable states can form coexistence states in a transient manner. Whether the forest invades the savanna or barren land invades the vegetation, or the other way around, is determined by environmental conditions. Further, if there are multiple patches of one stable state embedded in a landscape of the alternative stable state, such as e.g. patches of vegetation in barren land, there could be multiple fronts, whose movements are influenced by each other. These can lead to stationary fronts resulting in patterns of alternative states positioned next to each other. In other words, the two stable states could form coexistence states in a stable way.

The above-described stationary fronts may not be a characteristic of some ecosystems, for instance in the humid savannas. In such a case, however, a small spatial heterogeneity, due to, for example, topography or soil type, can give rise to stationary fronts resulting in coexistence states of savanna and forest (see also Bastiaansen et al. (2022); Goel et al. (2020)). So, additionally, if there are multiple localized disturbances in the spatial domain, these may result in stable savanna-forest mosaics, much often observed at the savanna-forest boundary (Charles-Dominique et al., 2018; Charles-Dominique et al., 2015). Furthermore, such heterogeneity can be responsible for the system undergoing fragmented tipping. In this case, a part of the landscape tips to the alternative ecosystem state on changing climatic condition. Further change may result in only gradual transitions between the stable coexistence states. Such coexistence states can also exist much beyond the tipping point of the non-spatial system, making the ecosystem much more resilient than earlier believed.

Even without spatial heterogeneity, these propagating spatial boundaries between two ecosystem states can destabilize to form finger-like patterns of alternative stable states situated next to each other, also referred to as coexistence states. In ecosystems with activator-inhibitor mechanisms playing an important role, such patterns eventually in the long run self-organize into labyrinth like structures resembling Turing patterns. It is important to note, however, that such a phenomenon may occur at much larger annual

rainfall far from the point when Turing instability sets in. This underlines yet another mechanism by which ecosystems self-organize and may evade tipping.

5. Conclusion

Our study highlights the role of spatial pattern formation in ecosystem tipping and showcases that distinct mechanisms underlying pattern formation are relevant when there exists alternative stable states. While both dryland and humid savanna ecosystems may show gradual transitions from one stable state to the other, the drylands can exhibit stable patterns due to multiple localized disturbances. Such disturbances can also form patterns in the humid savannas but only under spatially heterogeneous environmental conditions. In fact, depending on the type of such heterogeneity, these stable coexistence of savanna and forest can exist much beyond the tipping point predicted by the non-spatial framework. Additionally, the drylands can also demonstrate spatial patterns due to Turing instability or front instability before the tipping point which were not observed in the case of humid savannas. The differences in the possible pathways of evading tipping can be attributed to the key mechanisms at play in the two biomes which are also reflected in the model structure. While the drylands are driven by an activator-inhibitor mechanism, in the humid savannas, the negative effect of the two vegetation types on each other is the dominant factor. The models used in this paper provide meaningful insights, but nevertheless it is important to acknowledge that they are quite simple and the realistic spatial effects are more complicated, probably leading to even more intricate dynamics in the real world. Hence, it is important to appreciate the spatial complexity of ecosystems while predicting its response and resilience to global change. Future research should be focused on identifying spatial patterns in real ecosystems which are believed to be tipping-prone and analyzing data from observations and remote sensing to understand the mechanisms behind such pattern formation and their resilience to changing climatic conditions. This can help in validation of the prediction from this study, and allow better understanding of ecosystem response thus enabling us to identify the ecosystems most vulnerable to the ongoing climate and land use change.

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Supplementary text for "Rethinking tipping points in spatial ecosystems"

A The humid savanna model

The forest-savanna boundary, which is at the wet end of the rainfall gradient, can be represented by the following set of equations where the biomass density of the savannas ($S\ kgm^{-2}$) and the forest($F\ kgm^{-2}$) are the state variables. τ is the time in years and $\tilde{x}$ and $\tilde{y}$ are the dimensional spatial coordinates (in m).

$$\frac{\partial F}{\partial \tau} = r_F F \left(1 - \frac{F}{K_F}\right) - \eta f_F S F - d_F F + D_F \left(\frac{\partial^2 F}{\partial \tilde{x}^2} + \frac{\partial^2 F}{\partial \tilde{y}^2}\right) \tag{1a}$$

$$\frac{\partial S}{\partial \tau} = r_S S \left(1 - \frac{S}{K_S}\right) - cFS - \eta f_S S^2 - d_S S + D_S \left(\frac{\partial^2 S}{\partial \tilde{x}^2} + \frac{\partial^2 S}{\partial \tilde{y}^2}\right) \tag{1b}$$

A.1 Non-dimensionalisation

To reduce the number of parameters in the above model, we introduce the dimensionless variables:

$$s = S\left(\frac{1}{K_S} + \frac{\eta f_S}{r_S}\right), f = \frac{F}{K_F}, t = r_S \tau$$

and dimensionless parameters:

$$\mu = \frac{r_F}{r_S}, b = \frac{cK_F}{r_S}, m = \frac{d_F}{r_S}, n = \frac{d_S}{r_S}, a = \frac{\eta f_F}{r_S\left(\frac{1}{K_S} + \frac{\eta f_S}{r_S}\right)}, \delta = \frac{D_F}{D_S}$$

and dimensionless spatial coordinates:

$$x = \tilde{x}\sqrt{\frac{r_S}{D_S}}, y = \tilde{y}\sqrt{\frac{r_S}{D_S}}$$

Replacing the state variables in the diffusion term of equation (1a), we find:

$$D_F \frac{\partial^2 F}{\partial \tilde{x}^2} = D_F \frac{\partial}{\partial \tilde{x}} \left(\frac{\partial F}{\partial \tilde{x}} \right) = D_F K_F \frac{\partial}{\partial \tilde{x}} \left(\frac{\partial f}{\partial x} \frac{\partial x}{\partial \tilde{x}} \right) = D_F K_F \sqrt{\frac{r_S}{D_S}} \frac{\partial^2 f}{\partial x \partial \tilde{x}}$$

$$= D_F K_F \sqrt{\frac{r_S}{D_S}} \frac{\partial^2 f}{\partial x^2} \frac{\partial x}{\partial \tilde{x}} = r_S K_F \frac{D_F}{D_S} \frac{\partial^2 f}{\partial x^2}$$

Similarly, $D_F \dfrac{\partial^2 F}{\partial \tilde{y}^2} = r_S K_F \dfrac{D_F}{D_S} \dfrac{\partial^2 f}{\partial y^2}$

Substituting the above and all other state variables in equation (1a), we have:

$$K_F \frac{\partial f}{\partial t} \frac{\partial t}{\partial \tau} = r_S K_F \frac{\partial f}{\partial t}$$

$$= r_F K_F f (1 - f) - \frac{\eta f_F K_F}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} sf - d_F K_F f + r_S K_F \frac{D_F}{D_S} \left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right)$$

Dividing both sides of the above equation by $r_S K_F$, we have:

$$\frac{\partial f}{\partial t} = \frac{r_F}{r_S} f (1 - f) - \frac{\eta f_F}{\dfrac{1}{r_S} \left(\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S} \right)} sf - \frac{d_F}{r_S} f + \frac{D_F}{D_S} \left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right)$$

Hence, substituting the dimensionless parameters, we have:

$$\frac{\partial f}{\partial t} = \mu f (1 - f) - asf - mf + \delta \left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right)$$

Replacing the state variables in the diffusion term of equation (1b), we find:

$$D_S \frac{\partial^2 S}{\partial \tilde{x}^2} = D_S \frac{\partial}{\partial \tilde{x}} \left(\frac{\partial S}{\partial \tilde{x}} \right) = \frac{D_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \frac{\partial}{\partial \tilde{x}} \left(\frac{\partial s}{\partial x} \frac{\partial x}{\partial \tilde{x}} \right)$$

$$= \frac{D_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \sqrt{\frac{r_S}{D_S}} \frac{\partial^2 s}{\partial x \partial \tilde{x}} = \frac{D_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \sqrt{\frac{r_S}{D_S}} \frac{\partial^2 s}{\partial x^2} \frac{\partial x}{\partial \tilde{x}} = \frac{r_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \frac{\partial^2 s}{\partial x^2}$$

$$= \frac{D_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \sqrt{\frac{r_S}{D_S}} \frac{\partial^2 s}{\partial x^2} \frac{\partial x}{\partial \tilde{x}} = \frac{r_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \frac{\partial^2 s}{\partial x^2}$$

Similarly, $D_S \dfrac{\partial^2 S}{\partial \tilde{y}^2} = \dfrac{r_S}{\dfrac{1}{K_S} + \dfrac{\eta f_S}{r_S}} \dfrac{\partial^2 s}{\partial y^2}$

Now, equation (1b) can be rearranged as:

$$\frac{\partial S}{\partial t} \frac{\partial t}{\partial \tau} = r_S \frac{\partial S}{\partial t}$$

$$= r_S S \left(1 - S \left(\frac{1}{K_S} + \frac{\eta f_S}{r_S} \right) \right) - cFS - d_S S + D_S \left(\frac{\partial^2 S}{\partial \tilde{x}^2} + \frac{\partial^2 S}{\partial \tilde{y}^2} \right)$$

Replacing the state variables, the above equation can be rewritten as:

$$\frac{r_S}{\frac{1}{K_S} + \frac{\eta f_S}{r_S}} \frac{\partial s}{\partial t}$$

$$= \frac{r_S s}{\frac{1}{K_S} + \frac{\eta f_S}{r_S}}(1 - s) - \frac{cK_F f s}{\frac{1}{K_S} + \frac{\eta f_S}{r_S}} - \frac{d_S s}{\frac{1}{K_S} + \frac{\eta f_S}{r_S}} + \frac{r_S}{\frac{1}{K_S} + \frac{\eta f_S}{r_S}} \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 s}{\partial y^2} \right)$$

Dividing both sides by $\dfrac{r_S}{\frac{1}{K_S} + \frac{\eta f_S}{r_S}}$, we have:

$$\frac{\partial s}{\partial t} = s(1 - s) - \frac{cK_F f s}{r_S} - \frac{d_S s}{r_S} + \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 s}{\partial y^2} \right)$$

Hence, substituting the dimensionless parameters,

$$\frac{\partial s}{\partial t} = s(1 - s) - bfs - ns + \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 s}{\partial y^2} \right)$$

So the dimensionless version of equation (1) indeed becomes

$$\frac{\partial f}{\partial t} = \mu f(1 - f) - asf - mf + \delta \left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right) \tag{2a}$$

$$\frac{\partial s}{\partial t} = s(1 - s) - bfs - ns + \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 s}{\partial y^2} \right) \tag{2b}$$

A.2 Equilibria

The above system (2) can be rewritten as:

$$\frac{\partial f}{\partial t} = f(\alpha - \mu f - as) + \delta \left(\frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right)$$

$$\frac{\partial s}{\partial t} = s(\beta - s - bf) + \left(\frac{\partial^2 s}{\partial x^2} + \frac{\partial^2 f}{\partial y^2} \right) \tag{3}$$

where we define, $\alpha = \mu - m$ and $\beta = 1 - n$ and assume $\alpha, \beta > 0$. Then the system can have the following equilibria: $E_0 = (0, 0)$, $E_f = (\frac{\alpha}{\mu}, 0)$, which is the forest-only state and $E_s(0, \beta)$, which is the savanna-only state. The coexistence

equilibrium, $E_{fs}(\hat{f}, \hat{s})$, is given by the following two equations:

$$\alpha - \mu\hat{f} - a\hat{s} = 0$$
$$\beta - \hat{s} - b\hat{f} = 0 \tag{4}$$

so that $\alpha - \mu\hat{f} = a\beta - ab\hat{f} \implies \alpha - a\beta = \mu\hat{f} - ab\hat{f} \implies \hat{f} = \dfrac{\alpha - a\beta}{\mu - ab}$

Substituting the value of $\hat{f}$ in (4) yields

$$a\hat{s} = \alpha - \mu\left(\frac{\alpha - a\beta}{\mu - ab}\right) = \frac{\alpha(\mu - ab) - \mu(\alpha - a\beta)}{\mu - ab} = \frac{\mu a\beta - ab\alpha}{\mu - ab}$$
$$\implies \hat{s} = \frac{\mu\beta - b\alpha}{\mu - ab}$$

E_{fs} is biologically feasible (i.e., both $\hat{s}$ and $\hat{f}$ are non-negative) only when either of the following conditions hold:

$$\mu - ab > 0, \mu\beta - b\alpha > 0, \alpha - a\beta > 0$$
$$\mu - ab < 0, \mu\beta - b\alpha < 0, \alpha - a\beta < 0 \tag{5}$$

A.3 Stability of the steady states

To determine the stability of an equilibrium, $E_*(f_*, s_*)$, against homogeneous perturbations, the system (3) is linearized around the equilibria by setting $(f, s)(x, t) = (f_*, s_*) + e^{\lambda t}(\bar{f}, \bar{s})$, where (f_*, s_*) is the equlibria of the system. This yields the eigen value problem, $\lambda\begin{pmatrix}\bar{f}\\\bar{s}\end{pmatrix} = J(f_*, s_*)\begin{pmatrix}\bar{f}\\\bar{s}\end{pmatrix}$, where $J(f_*, s_*)$ is the Jacobian matrix corresponding to system (3) evaluated at the equilibrium, (f_*, s_*). Now, the Jacobian matrix for the system (3) can be written as:

$$J(f, s) = \begin{pmatrix} \alpha - 2\mu f - as & -af \\ -bs & \beta - 2s - bf \end{pmatrix}$$

So to determine stability of the equlibrium, E_0, we evaluate the Jacobian at the equilibrium:

$$J(0,0) = \begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix}$$

The eigenvalues of the matrix are $\lambda = \alpha > 0$ and $\lambda = \beta > 0$. Since both the eigenvalues are positive, $E_0(0, 0)$ is unstable. The Jacobian evaluated at E_f is given by:

$$J(\frac{\alpha}{\mu}, 0) = \begin{pmatrix} -\alpha & -\dfrac{a\alpha}{\mu} \\ 0 & \beta - \dfrac{b\alpha}{\mu} \end{pmatrix}$$

The eigenvalues of the matrix are $\lambda = -\alpha < 0$ and $\lambda = \beta - \dfrac{b\alpha}{\mu}$. So the forest-only state, $E_f(\dfrac{\alpha}{\mu}, 0)$, is stable when $\mu\beta - b\alpha < 0$ and a saddle when $\mu\beta - b\alpha > 0$. The Jacobian evaluated at E_s is given by:

$$J(0, \beta) = \begin{pmatrix} \alpha - a\beta & 0 \\ -b\beta & -\beta \end{pmatrix}$$

The eigenvalues of the matrix are $\lambda = \alpha - a\beta$ and $\lambda = -\beta < 0$. So the savanna-only state, $E_s(0, \beta)$, is stable when $\alpha - a\beta < 0$ and a saddle when $\alpha - a\beta > 0$. The Jacobian evaluated at E_{fs} is given by:

$$J(\hat{f}, \hat{s}) = \begin{pmatrix} -\mu\hat{f} & -a\hat{f} \\ -b\hat{s} & -\hat{s} \end{pmatrix}$$

$\text{Tr}(J(\hat{f}, \hat{s})) = -\mu\hat{f} - \hat{s} < 0$ and $\text{Det}(J(\hat{f}, \hat{s})) = \hat{s}\hat{f}(\mu - ab)$. The savanna-forest mixed state, E_{fs}, is stable when $\text{Det}(J(\hat{f}, \hat{s})) > 0$ which implies $\mu - ab > 0$ (since $\hat{s}\hat{f} > 0$). In that case, from (5), it follows, $\mu\beta - b\alpha > 0$ and $\alpha - a\beta > 0$ which implies that both E_f and E_s are unstable. When either or both E_f and E_s are stable, from (5), it follows that if E_{fs} exists, then $\mu - ab < 0$. This implies E_{fs} is unstable. Hence, the savanna-forest mixed state cannot exist together as a stable state with either or both of the stable savanna-only or forest-only state.

A.4 Turing analysis

To determine the stability of the equilibria against spatially heterogeneous perturbations, the system (3) is again linearized around the equilibria, this time by setting $(f, s)(x, t) = (f_*, s_*) + e^{\lambda t + i\kappa x}(\overline{f}, \overline{s})$, where (f_*, s_*) is the equilibria of the system, λ is the growth rate and κ is the wave number of the perturbation. This yields the eigenvalue problem, $\lambda \begin{pmatrix} \overline{f} \\ \overline{s} \end{pmatrix} = M(f_*, s_*) \begin{pmatrix} \overline{f} \\ \overline{s} \end{pmatrix}$, where $M(f_*, s_*) = J(f_*, s_*) - D$, $J(f_*, s_*)$ is the Jacobian evaluated at the equilibria (f_*, s_*) and $D = \begin{pmatrix} \kappa^2\delta & 0 \\ 0 & \kappa \end{pmatrix}$. So at the equilibrium E_f,

$$M(\dfrac{\alpha}{\mu}, 0) = \begin{pmatrix} -\alpha - \kappa^2\delta & -\dfrac{a\alpha}{\mu} \\ 0 & \beta - \dfrac{b\alpha}{\mu} - \kappa^2 \end{pmatrix}$$

$\text{Tr}(M(\dfrac{\alpha}{\mu}, 0)) = -\alpha - \beta - \dfrac{b\alpha}{\mu} - \kappa^2(\delta + 1) < 0$ as $\delta > 0$ and $\text{Det}(M(\dfrac{\alpha}{\mu}, 0)) = (-\alpha - \kappa^2\delta)(\beta - \dfrac{b\alpha}{\mu} - \kappa^2)$. From section , one can see that for the equilibrium

E_f to be stable without diffusion, $\beta - \dfrac{b\alpha}{\mu} < 0$ which implies Det $(M(\dfrac{\alpha}{\mu}, 0))$ can never be negative. So Turing instability cannot occur.

At the equilibrium E_s,

$$M(0, \beta) = \begin{pmatrix} -\alpha - a\beta - \kappa^2\delta & 0 \\ -b\beta & -\beta - \kappa^2 \end{pmatrix}$$

So Tr$(M(0,\beta))= -\alpha - a\beta - \beta - \kappa^2(\delta+1) < 0$ as $\delta > 0$ and Det$(M(0,\beta))=(-\alpha - a\beta - \kappa^2\delta)(-\beta - \kappa^2) > 0$. So Turing instability cannot occur.

Lastly, at the equlibrium E_{fs},

$$M(\hat{f}, \hat{s}) = \begin{pmatrix} -\mu\hat{f} - \kappa^2\delta & -a\hat{f} \\ -b\hat{s} & -\hat{s} - \kappa^2 \end{pmatrix}$$

Now, Tr$(M(\hat{f}, \hat{s}))= -\mu\hat{f} - \hat{s} - \kappa^2(\delta + 1) < 0$ as $\delta > 0$ and Det$(M(\hat{f}, \hat{s}))= (-\mu\hat{f} - \kappa^2\delta)(-\hat{s} - \kappa^2) - ab\hat{s}\hat{f} = (\mu - ab)\hat{s}\hat{f} + \kappa^2(\delta\hat{s} + \mu\hat{f}) + \kappa^4\delta$. From section A.3, it is clear that for the equilibrium, E_{fs}, to be stable without the diffusion, the condition, $\mu - ab > 0$, needs to be satisfied. This implies Det$(M(s,f))$ can never be negative. Turing instability cannot occur.

A.5 Parameterization and bifurcation diagram

The model (1) is parameterized using ecologically realistic values which are provided in Table 1. The rationale behind choosing each value is explained below the table.

Table 1 Description of parameters of model (1) and their values

Par.	Values (Units)	Description	Notes/References
r_F	0.25 yr^{-1}	growth rate of the forest biomass	Iuorio et al (2023)
r_S	0.5 yr^{-1}	growth rate of the savanna biomass	(i)
d_F	0.01 yr^{-1}	death rate of the forest biomass	(ii)
d_S	0.1-0.5 yr^{-1}	death rate of the savanna biomass	(ii)
η	0.85 yr^{-1}	Fire frequency	(iii)
K_F	30 kgm^{-2}	carrying capacity of the forest biomass	Chave et al (2003)
K_S	3 kgm^{-2}	carrying capacity of the savanna biomass	(iv)
c	0.03 $kg^{-1}m^2yr^{-1}$	shading effect of the forest limiting savanna	(v)
f_F	0.3 $kg^{-1}m^2$	sensitivity of forest trees to fire	(vi)
f_S	0.033 $kg^{-1}m^2$	sensitivity of savanna biomass to fire	(vii)
D_F	3.65-36.5 m^2yr^{-1}	diffusion coefficient of the forest	assumed
D_S	365-3650 m^2yr^{-1}	diffusion coefficient of the savanna	$100 \times D_F$

(i) The savanna biomass includes grass and trees and is assumed to grow at twice the rate equal of the forest biomass. (ii) Forest trees live approximately 100 years. Hence, $d_F = 1/100$ (Accatino et al, 2010) and combined life expectancy of savanna tree and grass is assumed 10-50 years (Accatino et al, 2010). (iii) It is assumed that there could be fire maximum once a year.

(iv) The carrying capacity of biomass of forest trees is taken from Chave et al (2003) and for savanna biomass we assumed it to be lower by a factor of 5-10. (v) We assumed that when the forest reaches it carrying capacity, then its negative effect on the savanna vegetation is large. So if we assume cK_F=0.9 yr^{-1} , it implies c=0.03 $kg^{-1}m^2yr^{-1}$. (vi) Similarly, when the savanna biomass reaches its carrying capacity, then its negative impact on the forest is large. So if we assume f_FK_S=0.9, which implies f_F=0.3 $kg^{-1}m^2$. (vii) Under similar conditions, i.e., when savanna biomass is at its carrying capacity, the negative impact of fire on savanna biomass is relatively much less. So if we assume f_FK_S=0.1, it implies f_S=0.033 $kg^{-1}m^2$.

The above parameters are used to calculate the values of the dimensionless parameters in the model (3). So the ratio of the diffusion coefficients can also be calculated as $\delta = 0.01$. The spatial coordinates x and y can also be calculated assuming $D_S = 500$. $x = 100$ is equivalent to approximately 3100 m. The values for other dimensionless parameters are used to demonstrate a bifurcation diagram for the nonspatial version of model (3), with respect to μ (see Fig. S1, parameters provided in the caption). We have used the numerical continuation software, Matcont, for this bifurcation diagram (Dhooge et al, 2008).

Figure S1 Bifurcation diagram, with respect to μ, for the humid savanna model. (A) savanna biomass (B) forest biomass. The green and the yellow lines indicate forest-only equilibrium (E_f) and savanna-only euilibrium (E_s) respectively. Dotted lines indicate unstable equilibria. TB denotes transcritical bifurcation. The black solid lines indicate equilibria which are not ecologically feasible as either savanna (s) or forest (f) is negative. In the inset, although there exist a stable branch but the value of savanna biomass is negative. H denotes Hopf bifurcation. E_0, which is always unstable, is not shown. Parameter values: $a = 1.3$, $b = 1.8$, $m = 0.02$ and $n = 0.4$

B The dryland model

To represent the drylands, where rainfall is very limited, a modified version of the Klausmeier model is used where the vegetation biomass (V kgm^{-2}) and the rainfall (W mm) are the state variables. τ is the time (day^{-1}) and $\tilde{x}$ and $\tilde{y}$ are the dimensional spatial coordinates (in m).

$$\frac{\partial W}{\partial \tau} = q - lW - rWV^2 + D_W \left(\frac{\partial^2 W}{\partial \tilde{x}^2} + \frac{\partial^2 W}{\partial \tilde{y}^2} \right) \tag{6a}$$

$$\frac{\partial V}{\partial \tau} = rjWV^2(1 - \frac{V}{K}) - dV + D_V \left(\frac{\partial^2 V}{\partial \tilde{x}^2} + \frac{\partial^2 V}{\partial \tilde{y}^2} \right) \tag{6b}$$

B.1 Non-dimensionalisation

To reduce the number of parameters in the above model, we introduced the dimensionless variables:

$$w = \frac{r^{\frac{1}{2}}}{l^{\frac{1}{2}}} jW, \, v = \frac{r^{\frac{1}{2}}}{l^{\frac{1}{2}}} V, \, t = l\tau,$$

the dimensionless parameters:

$$p = \frac{r^{\frac{1}{2}} j}{l^{\frac{3}{2}}} q, \, k = \frac{r^{\frac{1}{2}}}{l^{\frac{1}{2}}} K, \, u = \frac{d}{l}, \, \delta_w = \frac{D_W}{D_V},$$

and the dimensionless spatial coordinates:

$$x = \frac{l^{\frac{1}{2}}}{D_V^{\frac{1}{2}}} \tilde{x} \text{ and } y = \frac{l^{\frac{1}{2}}}{D_V^{\frac{1}{2}}} \tilde{y}$$

Replacing the state variables, the diffusion term of (6a) becomes:

$$D_W \frac{\partial^2 W}{\partial \tilde{x}^2} = D_W \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}} j} \frac{\partial}{\partial \tilde{x}} \left(\frac{\partial w}{\partial \tilde{x}} \right) = D_W \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}} j} \frac{\partial}{\partial \tilde{x}} \left(\frac{\partial w}{\partial x} \frac{\partial x}{\partial \tilde{x}} \right)$$

$$= D_W \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}} j} \frac{l^{\frac{1}{2}}}{D_V^{\frac{1}{2}}} \frac{\partial^2 w}{\partial \tilde{x} \partial x} = D_W \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}} j} \frac{l^{\frac{1}{2}}}{D_V^{\frac{1}{2}}} \frac{\partial^2 w}{\partial x^2} \frac{\partial x}{\partial \tilde{x}} = \delta_w \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}} j} \frac{\partial^2 w}{\partial x^2}$$

Similarly, $D_W \frac{\partial^2 W}{\partial \tilde{y}^2} = \delta_w \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}} j} \frac{\partial^2 w}{\partial y^2}$

Replacing all the state variables of (6a), we have:

$$\frac{\partial W}{\partial t} \frac{\partial t}{\partial \tau} = \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}} j} \frac{\partial w}{\partial t}$$

$$= q - \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}j}w - r\frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}j}\frac{l}{r}wv^2 + \delta_w \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}j}\left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right)$$

Dividing both sides by $\dfrac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}j}$ yields,

$$\frac{\partial w}{\partial t} = \frac{r^{\frac{1}{2}}j}{l^{\frac{3}{2}}}q - w - wv^2 + \delta_w\left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right)$$

Substituting the dimensionless parameters gives:

$$\frac{\partial w}{\partial t} = p - w - wv^2 + \delta_w\left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right)$$

Replacing the state variables, the diffusion term of equation (6b) can be expressed as:

$$D_V \frac{\partial^2 V}{\partial \tilde{x}^2} = D_V \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}}\frac{\partial}{\partial \tilde{x}}\left(\frac{\partial v}{\partial \tilde{x}}\right) = D_V \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}}\frac{\partial}{\partial \tilde{x}}\left(\frac{\partial v}{\partial x}\frac{\partial x}{\partial \tilde{x}}\right)$$

$$= D_V \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}}\frac{l^{\frac{1}{2}}}{D_V^{\frac{1}{2}}}\frac{\partial^2 v}{\partial \tilde{x}\partial x} = D_V \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}}\frac{l^{\frac{1}{2}}}{D_V^{\frac{1}{2}}}\frac{\partial^2 v}{\partial x^2}\frac{\partial x}{\partial \tilde{x}} = \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}}\frac{\partial^2 v}{\partial x^2}$$

Similarly, $D_V \dfrac{\partial^2 V}{\partial \tilde{y}^2} = \dfrac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}}\dfrac{\partial^2 v}{\partial y^2}$

Replacing all the state variables of Equation (6b), we have:

$$\frac{\partial V}{\partial t}\frac{\partial t}{\partial \tau} = \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}}\frac{\partial v}{\partial t}$$

$$= rj\frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}j}\frac{l}{r}wv^2(1 - \frac{vl^{\frac{1}{2}}}{r^{\frac{1}{2}}K}) - \frac{l^{\frac{1}{2}}}{r^{\frac{1}{2}}}dv + \frac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}}\left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2}\right)$$

Dividing both sides by $\dfrac{l^{\frac{3}{2}}}{r^{\frac{1}{2}}}$ and substituting the dimensionless parameters gives:

$$\frac{\partial v}{\partial t} = wv^2(1 - \frac{v}{k}) - uv + \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2}\right)$$

Hence, the dimensionless version of the system (6) becomes

$$\frac{\partial w}{\partial t} = p - w - wv^2 + \delta_w\left(\frac{\partial^2 w}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right) \tag{7a}$$

$$\frac{\partial v}{\partial t} = wv^2(1 - \frac{v}{k}) - uv + \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 w}{\partial y^2}\right) \tag{7b}$$

B.2 Equilibria

The system can have one barren state, $E_w = (p, 0)$, and two vegetated states, $E_{wv}(w_{1,2}, v_{1,2})$, determined by the following equation:

$$p - w - wv^2 = 0 \tag{8a}$$

$$wv(1 - \frac{v}{k}) - u = 0 \tag{8b}$$

From above, setting $h = \dfrac{1}{k}$, the equibria, $E_{wv}(w_{1,2}, v_{1,2})$, are (see Bastiaansen et al (2019)):

$$w_{1,2} = u(\frac{p}{u} - \frac{v_{1,2}}{1 - hv_{1,2}}) = u\frac{\dfrac{p}{u} + 2\dfrac{p}{u}h^2 + 2h \pm \sqrt{\left(\dfrac{p}{u}\right)^2 - 4(1 + \dfrac{p}{u}h)}}{2(1 + h^2)}$$

$$v_{1,2} = \frac{\dfrac{p}{u} \mp \sqrt{\left(\dfrac{p}{u}\right)^2 - 4(1 + \dfrac{p}{u}h)}}{2\left(1 + \dfrac{p}{u}h\right)} \tag{9}$$

The two equilibria exists only if the term within the square root is positive, i.e.,

$\left(\dfrac{p}{u}\right)^2 - 4\left(1 + \dfrac{p}{u}h\right) > 0$ which implies $\left(\dfrac{p}{u} - 2h\right)^2 > 4 + 4h^2$

or, $\dfrac{p}{u} > 2(h + \sqrt{1 + h^2})$. The two equilibria coincides at $\dfrac{p}{u} = 2(h + \sqrt{1 + h^2})$. So this value, $p = 2u(h + \sqrt{1 + h^2}) = p_T$ is said to be the tipping point of the system. For lesser rainfall, when $p < p_T$, no vegetated state can exist.

B.3 Stability of the equilibria

To determine the stability of the equilibria, E_*, against homogeneous perturbations, the system (7) is linearized around the equilibria by setting $(w, v)(x, t) = (w_*, v_*) + e^{\lambda t}(\overline{w}, \overline{v})$, where (w_*, v_*) is the equlibria of the system. This yields the eigenvalue problem, $\lambda \begin{pmatrix} \overline{w} \\ \overline{v} \end{pmatrix} = J(w_*, v_*) \begin{pmatrix} \overline{w} \\ \overline{v} \end{pmatrix}$, where $J(w_*, v_*)$ is the Jacobian matrix corresponding to system (7) evaluated at the equilibrium, (w_*, v_*). Now, the Jacobian matrix for the system (7) can be written as:

$$J(w, v) = \begin{pmatrix} -1 - v^2 & -2wv \\ v^2(1 - hv) & -u + (2 - 3hv)wv \end{pmatrix}$$

So, to check the stability of the equlibria, we evaluate the Jacobian at the equilibrium, E_w:

$$J(p, 0) = \begin{pmatrix} -1 & 0 \\ 0 & -u \end{pmatrix}$$

Since $u > 0$, both the eigen values are negative. Hence, $E_w(p, 0)$ is always stable.

Further, we evaluate the Jacobian at E_{wv}:

$$J(w_{1,2}, v_{1,2}) = \begin{pmatrix} -1 - v_{1,2}^2 & -2w_{1,2}v_{1,2} \\ v_{1,2}^2(1 - hv_{1,2}) & -u + (2 - 3hv_{1,2})w_{1,2}v_{1,2} \end{pmatrix}$$

$\text{Tr(J)} = -1 - v_{1,2}^2 - u + (1 - 2hv_{1,2} + 1 - hv_{1,2})w_{1,2}v_{1,2}$

$= -1 - v_{1,2}^2 - u + (1 - hv_{1,2})w_{1,2}v_{1,2} + (1 - 2hv_{1,2})w_{1,2}v_{1,2}$

$= -1 - v_{1,2}^2 + (1 - 2hv_{1,2})w_{1,2}v_{1,2}$ (using (8b))

Again replacing $w_{1,2}v_{1,2}$ using (8b), we have,

$\text{Tr(J)} = -1 - v_{1,2}^2 + u\dfrac{1 - 2hv_{1,2}}{1 - hv_{1,2}}$

Using 8(b), we have,

$\text{Det(J)} = (-1 - v_{1,2}^2)(1 - 2hv_{1,2})w_{1,2}v_{1,2} + 2w_{1,2}v_{1,2}(1 - hv_{1,2})v_{1,2}^2$

$= -w_{1,2}v_{1,2}((1 + v_{1,2}^2)(1 - 2hv_{1,2}) - 2(1 - hv_{1,2})v_{1,2}^2)$

$= -w_{1,2}v_{1,2}((1 + v_{1,2}^2) - 2hv_{1,2}(1 + v_{1,2}^2) - 2v_{1,2}^2 + 2hv_{1,2}^3)$

$= w_{1,2}v_{1,2}(-1 + v_{1,2}^2 + 2hv_{1,2})$

Again replacing $w_{1,2}v_{1,2}$ using (8b),

$\text{Det(J)} = \dfrac{u}{1 - hv_{1,2}}(-1 + v_{1,2}^2 + 2hv_{1,2})$

E_{wv} is stable when $\text{Tr}(J(w, v)) < 0$ and $\text{Det}(J(w, v)) > 0$. It is easy to see from above, $\text{Det}(J) > 0$ implies $(-1 + v_{1,2}^2 + 2hv_{1,2}) > 0$ or, $v_{1,2} > -h + \sqrt{(1 + h^2)}$ and $\text{Det}(J) < 0$ implies $v_{1,2} < -h + \sqrt{(1 + h^2)}$. It can be shown from (9) that $v_1 < -h + \sqrt{1 + h^2}$ and $v_2 > -h + \sqrt{1 + h^2}$ (see (Bastiaansen et al, 2019)). So the uniform state (u_2, v_2) is stable and (u_1, v_1) is unstable.

B.4 Turing analysis

To determine the stability of the equilibria against spatially heterogeneous perturbations, the system (3) is again linearized around the equilibria, this time by setting $(w, v)(x, t) = (w_*, v_*) + e^{\lambda t + i\kappa x}(\overline{w}, \overline{v})$, where (w_*, v_*) is the equilibria of the system, λ is the growth rate and κ is the wave number of the perturbation. This yields the eigen value problem, $\lambda \begin{pmatrix} \overline{w} \\ \overline{v} \end{pmatrix} = M(w_*, v_*) \begin{pmatrix} \overline{w} \\ \overline{v} \end{pmatrix}$, where $M(w_*, v_*) = J(w_*, v_*) - D$, $J(w_*, v_*)$ is the Jacobian evaluated at the

equilibrium, (w_*, v_*) and $D = \begin{pmatrix} \kappa^2 \delta_w & 0 \\ 0 & \kappa \end{pmatrix}$. Since (w_2, v_2) is the only stable vegetated state, we evaluate the matrix M at $E_{wv}(w_2, v_2)$,

$$M(w_2, v_2) = \begin{pmatrix} -1 - v_2^2 - \kappa^2 \delta_w & -2w_2 v_2 \\ v_2^2(1 - hv_2) & -u_2 + (2 - 3hv_2)w_2 v_2 - \kappa^2 \end{pmatrix}$$

$\text{Tr}(M) = -1 - v_2^2 - u + (1 - 2hv_2 + 1 - hv_2)w_2 v_2 - \kappa^2(\delta_w + 1)$

$= \text{Tr}(J) - \kappa^2(\delta_w + 1) < 0$

$\text{Det}(M) = (-1 - v_2^2 - \kappa^2 \delta_w)((1 - 2hv_2)w_2 v_2 - \kappa^2) + 2w_2 v_2(1 - hv_2)v_2^2$

$= \kappa^4 \delta_w - \kappa^2(\delta_w(1 - 2hv_2)w_2 v_2 - (1 + v_2^2)) + Det J = H(\kappa^2)$

Turing instability occurs only when the largest real part of the eigenvalues, λ, are positive, or $\text{Det}(M) = H(\kappa^2) < 0$. Since $H(\kappa^2)$ is a parabola in κ^2, the minimum value is attained at $\kappa^2 = \kappa_c^2$ for which $\dfrac{dH(\kappa^2)}{d\kappa^2} = 0$. Solving this yields $\kappa_c^2 = \dfrac{\delta_w(1 - 2hv_2)w_2 v_2 - (1 + v^2)}{2\delta_w}$. Substituting the value of k_c above, the condition for Turing instability is $H(k_c^2) < 0$. For parameter values used throughout the main text and described in the following section, we plot the largest real part of the eigen values, λ and $H(\kappa^2)$ for different values of p and κ (Fig S2). The Turing bifurcation occurs around $p = 5.91$. For the same parameter values, it is easy to see that tipping from vegetated state to barren state occurs at $p_T = 5.794$. This phenomenon is referred to as Turing before tipping.

Figure S2 (A)The largest real part of the eigen values, λ and (B) $H(\kappa^2)$ with changing κ^2. The different curves represent different values of p. The yellow curve touches the zero line and so turing bifurcation occurs around p=5.91. Other parameter values $\delta_w = 200$, $u = 1.2$, $k = 1$

B.5 Parameterization

All the parameters for the dryland model have been selected in the range described in Klausmeier (1999).

Table 2 Description of parameters of model (6)

Parameters	Units	Description
q	400-750 $mm\ yr^{-1}$	precipitation rate
l	1.5 yr^{-1}	water evaporation rate[i]
r	30 $yr^{-1}\ kg\ m^{-2}$	uptake rate of water
j	0.003 $kg\ m^{-2}\ mm^{-1}$	plant biomass yield per unit water consumed
K	0.225 $kg\ m^{-2}$	carrying capacity of vegetation[ii]
d	1.8 yr^{-1}	natural moratlity of vegetation
D_V	1 $m^2 yr^{-1}$	diffusion coefficient of vegetation
D_W	100-400 $m^2 yr^{-1}$	diffusion coefficient of water[iii]

(i) same order of magnitude as (Klausmeier, 1999), (ii) same order of magnitude as equilibrium plant biomass in (Klausmeier, 1999), (iii) assumed to be in the range (100-400) $\times D_V$. The above parameters are used to calculate the dimensionless parameters of the dryland model (given in caption of Fig. S2). Also, the spatial coordinates, x and y can be calculated for the above model. $x = y = 100$ is equivalent to approximately 81 m.

C Front propagation

To understand the notion of front propagation, we consider the following simple reaction-diffusion equation. We restrict ourselves to one spatial dimension for simplicity.

$$\frac{\partial v(x,t)}{\partial t} = F(v) + \frac{\partial^2 v(x,t)}{\partial^2 x} \tag{10}$$

We consider the system described by the time evolution of v to be a potential system. Further, we also assume that in the absence of diffusion, the model exhibits alternative stable states, v_A and v_B, i.e., $F(v_A) = F(v_B) = 0$ and $F'(v_A), F'(v_B) < 0$. Let a front connecting two states v_A and v_B in the spatial domain move with a velocity ξ. A new co-moving frame of reference, $z = x - \xi t$ can be introduced. So the front will asymptotically converge to v_A when $z \to -\infty$ and v_B when $z \to +\infty$. Substituting $v(x) = v(z)$ in the above equation (10) gives:

$$\frac{\partial v(z)}{\partial t} = \frac{dv(z)}{dz}\frac{dz}{dt} = -\xi\frac{dv}{dz} \text{ and } \frac{\partial^2 v(z)}{\partial x^2} = \frac{d^2 v(z)}{dz^2}$$

Therefore, the above equation (10) can be written as $-\xi\dfrac{dv}{dz} = F(v) + \dfrac{d^2 v}{d^2 z}$.

Multiplying $\dfrac{dv}{dz}$ on both sides, we have:

$$-\xi \left(\frac{dv}{dz} \right)^2 = F(v)\frac{dv}{dz} + \frac{d^2 v}{d^2 z}\frac{dv}{dz}$$

Since the system is a gradient system, there is a potential function $U(v)$ such that $F(v) = -\dfrac{dU}{dv}$. Substituting this in the equation above, we have:

$$-\xi \left(\frac{dv}{dz} \right)^2 = \frac{d}{dz} \left(\frac{1}{2} \left(\frac{dv}{dz} \right)^2 - U \right)$$

Integrating both sides over the whole spatial domain, we have:

$$-\xi \int_{-\infty}^{+\infty} \left(\frac{du}{dz} \right)^2 dz = \left[\frac{1}{2} \left(\frac{du}{dz} \right)^2 - U \right]_{-\infty}^{+\infty}$$

Using boundary conditions, $v(z \to -\infty) = v_A$, $v(z \to +\infty) = v_B$ and $\dfrac{dv}{dz} \to 0$ as $z \to \pm\infty$, from the above equation, it can be readily seen that

$$\xi = A^{-1}[U(v_B) - U(v_A)] \text{ where } A = \int_{-\infty}^{+\infty} \left(\frac{dv}{dz} \right)^2 dz$$

So the front velocity depends on the difference between the potential, U, at the two alternative stable states.

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