

REVIEW SUMMARY

ECOLOGY

Evasion of tipping in complex systems through spatial pattern formation

Max Rietkerk*, Robbin Bastiaansen, Swarnendu Banerjee, Johan van de Koppel, Mara Baudena, Arjen Doelman

BACKGROUND: In the Anthropocene, there is a need to better understand the catastrophic effects that climate and land-use change may have on ecosystems, Earth system components, and the whole Earth system. The concept of critical transitions, or tipping from one state to another, contributes to this understanding. Tipping occurs in a system when it is forced outside the basin of attraction of the original equilibrium, resulting in a critical transition to an alternative, often less-

desirable, stable state. In this context, the search for early warning signals for such imminent critical transitions has become a focus of research. In particular, spatial self-organization in ecosystems, such as the spontaneous formation of regular vegetation patterns—so-called Turing patterns—has been suggested as a prominent early warning signal.

ADVANCES: However, recent findings indicate that such spatial self-organization should

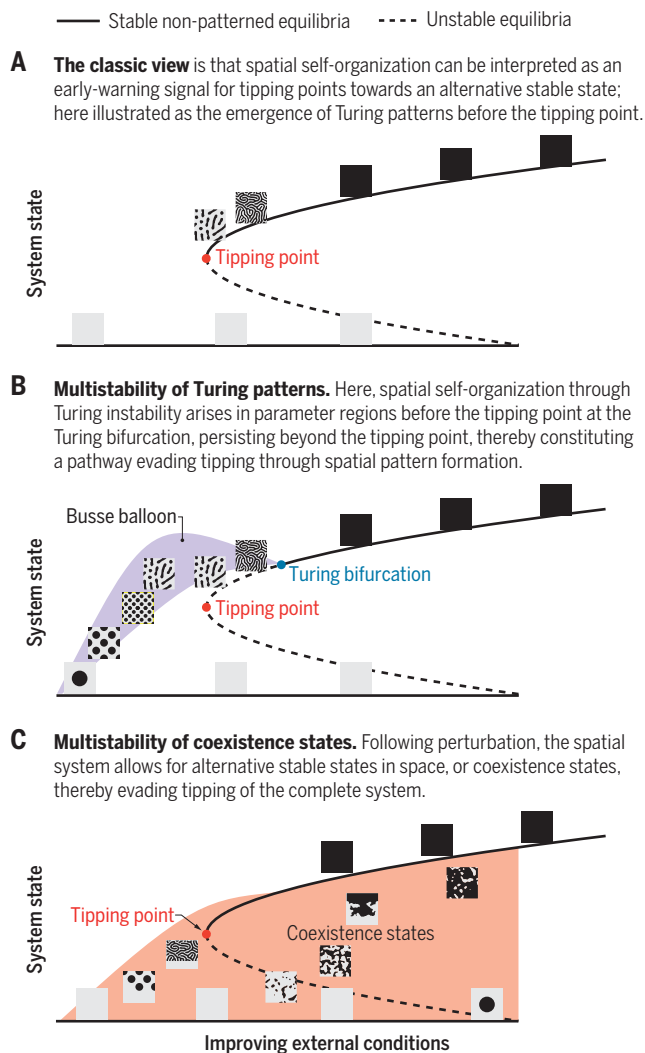
Evasion of tipping points.

We illustrate the response of complex systems to changes in external conditions (i.e., a bifurcation diagram). Homogeneous dark gray squares depict high density of the system state variable, and homogeneous light gray squares illustrate low density.

(A) Classic view. (B) Multistability of Turing patterns.

Recent model analysis has revealed multistability of Turing patterns in Busse balloons, supported by satellite observations of real ecosystems. A Busse balloon is the region in parameter space in mathematical models where multistability of patterned equilibria occurs.

(C) Multistability of coexistence states. Evading tipping can also be the result of multistability of coexistence states. These spatial patterns originate in the bistability region before the tipping point; the evolving spatial patterns can also persist beyond the tipping point with worsening external conditions, thereby constituting an alternative pathway to evade tipping points.



not necessarily be interpreted as an early warning signal for critical transitions. Instead, spatial self-organization can cause ecosystems to evade tipping points and can thereby be a signal of resilience. These findings are based on recent mathematical analyses of spatial models and on observations of real ecosystems. Both have revealed multistability, meaning that many different spatial patterns can co-occur under the same environmental conditions, and each of these patterns can stay stable for a wide range of conditions. This enables complex system states to persist beyond tipping points through spatial self-organization. Moreover, if a complex system with tipping properties experiences a perturbation, subsequent change of the system does not necessarily lead to tipping of the complete system. Instead, the change can stay localized because the system allows for alternative states to coexist in space—thus referred to as coexistence states. These spatial patterns can also persist beyond tipping points with worsening conditions through this alternative pathway. We refer to both Turing patterns and coexistence states as spatial pattern formation. Evasion of tipping through these various pathways of spatial pattern formation may be relevant for many ecosystems and Earth system components that were hitherto interpreted as prone to tipping, including for Earth as a whole.

OUTLOOK: To further study how complex systems evade tipping through spatial pattern formation, savanna ecosystems can be considered as a concrete archetypal example because of the alternative states and spatial patterns observed for them. Moreover, universal conditions for evading tipping points in both ecosystems and Earth system components can be derived by mathematical analyses. Scenarios can be revealed by which Turing patterns with small amplitudes can grow and form large-scale localized interacting structures, thereby aiding complex systems to evade tipping. The effects that global change has on the spatial boundaries between coexistence states should be studied, and the impacts of restrictions of spatial domain and localized and nonlocal homogenizing effects by humans should be revealed. This approach will advance our understanding and predictions of critical transitions in nature and reveal how these may be avoided or reversed. ■

The list of author affiliations is available in the full article online.
*Corresponding author. Email: m.g.rietkerk@uu.nl
Cite this article as M. Rietkerk et al., *Science* 374, eabj0359 (2021). DOI: 10.1126/science.abj0359

S READ THE FULL ARTICLE AT
<https://doi.org/10.1126/science.abj0359>

REVIEW

ECOLOGY

Evasion of tipping in complex systems through spatial pattern formation

Max Rietkerk^{1*}, Robbin Bastiaansen², Swarnendu Banerjee^{1,3,4}, Johan van de Koppel^{5,6}, Mara Baudena^{1,7}, Arjen Doelman⁸

The concept of tipping points and critical transitions helps inform our understanding of the catastrophic effects that global change may have on ecosystems, Earth system components, and the whole Earth system. The search for early warning indicators is ongoing, and spatial self-organization has been interpreted as one such signal. Here, we review how spatial self-organization can aid complex systems to evade tipping points and can therefore be a signal of resilience instead. Evading tipping points through various pathways of spatial pattern formation may be relevant for many ecosystems and Earth system components that hitherto have been identified as tipping prone, including for the entire Earth system. We propose a systematic analysis that may reveal the broad range of conditions under which tipping is evaded and resilience emerges.

The concept of critical transitions and tipping points contributes to our understanding of planetary changes in the Anthropocene (1–3). This idea is that ecosystems or Earth system components undergoing global change can typically persist and stay in a similar equilibrium state. The impending danger, however, is that this is only the case until a tipping point is reached, at which time this (often desired) stable state disappears, and the system undergoes a critical or catastrophic transition toward an alternative equilibrium (1, 2, 4). The latter is a state that will also prevail if the external change goes back to its original value, thus displaying hysteresis (1, 5). Classic examples of ecosystems thought to exhibit critical transitions with tipping points between alternative stable states include clear lakes becoming turbid because of nutrient overloading (6); barren deserts replacing vegetated areas in dry savannas, or drylands in general, because of drought or overgrazing (5, 7); and savannas replacing tropical forests because of deforestation associated with fire, possibly combined with less rainfall (8–10).

Mechanisms that cause such tipping dynamics are positive feedbacks—i.e., processes

that amplify change imposed on complex systems. In the above-mentioned ecosystems, the positive feedbacks are increased turbidity in lakes leading to less macrophyte plants, which hinders nutrient uptake, leading to even more turbidity (6); reduced vegetation cover resulting in less water infiltration into the soil in dry savannas, which in turn leads to even less vegetation (5, 7); and fewer forest trees in tropical forests because of deforestation and fires allowing more grass growth, fueling more fires, and preventing forest tree establishment, thereby leading to even fewer forest trees (10–12). At tipping points, positive reinforcing feedbacks overwhelm the negative balancing feedback processes that maintain the desired state of ecosystems, often leading to the catastrophic loss of ecosystem services to humans.

There are many possible ways that positive feedbacks may overtake negative feedbacks and tipping can be triggered. Tipping occurs as a result of the loss of resilience, which is interpreted as the amount of environmental change or the strength of perturbation that a system can withstand before it tips to another basin of attraction (13). Three of the most prominent possibilities have been classified as follows (14): Bifurcation-induced tipping (B-tipping) happens when a parameter shift (e.g., a change in environmental conditions) reduces the basin of attraction of the original stable state to zero; noise-induced tipping (N-tipping) occurs when a perturbation of the system state—e.g., as the result of environmental noise or disturbance—knocks the system outside the basin of attraction of the original state; and rate-induced tipping (R-tipping) arises when an environmental (parameter) change is faster than the restorative attraction to the original state. The restorative attraction to the original state, or the speed after

which an equilibrium state is restored, is called engineering resilience, or stability, in the ecological literature (13).

This idea of tipping or critical transitions is important not only for ecosystems at a local scale but also for many regional-scale Earth system components (15, 16). Two examples include tipping of the Arctic ice sheets because of warming, inducing changes of surface albedo, leading to more warming (17–19), and tipping of the Atlantic Ocean circulation induced by changes in surface water fluxes (20–22). The same notion of tipping points also underlies the concept of hazardous planetary boundaries at the global scale (23) and has similarly been applied to Earth's biosphere as a whole, as a response to climate and land-use changes (3, 24). This concept is therefore relevant for all spatial scales, ranging from ecosystems to the entire complex Earth system.

For spatially extended ecosystems, such as drylands, savannas, and peatlands, it has been highlighted that critical transitions are associated with the formation of self-organized spatial patterns of vegetation (2, 25). In these systems, as environmental conditions worsen, a uniform coverage becomes unstable to non-uniform (spatial) disturbances, as a result of the spatial processes, which leads to the formation of regular spatial patterns. Such spatial destabilization of a uniform state is called a Turing instability or a Turing bifurcation after Alan Turing, who first studied this in reaction-diffusion systems (26). After a Turing instability, so-called Turing patterns emerge that can have various spatial forms depending on environmental conditions. This has previously been interpreted as preceding a tipping point to an alternative ecosystem state (25). Most notably in drylands, the following vegetation patterns are observed (listed here in the order in which they appear with worsening environmental conditions, such as increasing drought or grazing): bare gaps in homogeneous vegetation cover, labyrinthine or striped vegetation cover, and spotty vegetation in homogeneous bare soil (25, 27–30).

The mechanistic base of Turing instability is that the positive feedback mentioned earlier is scale dependent in spatially extended systems: The positive feedback dampens and is subsequently replaced by a negative feedback further away in space, generating scale-dependent feedbacks as a result of spatial processes (31). The crucial spatial effects of these processes leading to scale-dependent feedbacks are typically neglected when assuming that systems are homogeneous. In drylands, for example, the scale-dependent feedback relates to increased infiltration of water into the soil and larger soil water uptake at places where vegetation is growing. This generates surface and soil water flows toward the vegetation at the cost of available water further

¹Copernicus Institute of Sustainable Development, Utrecht University, 3508 TC, Utrecht, Netherlands. ²Department of Physics, Institute for Marine and Atmospheric Research Utrecht, Utrecht University, 3508 TA, Utrecht, Netherlands. ³The Institute of Mathematical Sciences, CIT Campus, Taramani, Chennai 600113, India. ⁴Indian Statistical Institute, Agricultural and Ecological Research Unit, Kolkata 700108, India. ⁵Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, 4400 AC, Yerseke, Netherlands. ⁶Groningen Institute for Evolutionary Life Sciences, Conservation Ecology Group, University of Groningen, 9700 CC, Groningen, Netherlands. ⁷National Research Council of Italy, Institute of Atmospheric Sciences and Climate (CNR-ISAC), 10133 Torino, Italy. ⁸Mathematical Institute, Leiden University, 2300 RA, Leiden, Netherlands. *Corresponding author. Email: m.g.rietkerk@uu.nl

away (28, 29), ultimately resulting in spatial patterns of concentrated vegetation in some places and bare soil in others.

Evading tipping points through Turing patterns

The regular spatial patterns resulting from Turing instability have been understood until now as early warning signals for tipping points or critical transitions toward an alternative state (B-tipping) in various ecosystems (2, 25). However, recent mathematical analyses, combined with satellite observations of real ecosystems, have revealed a drastic alternative view (32–34). These analyses have exposed the existence of pattern-driven multistability described by Busse balloons, after F. H. Busse (32, 33, 35). The Busse balloon (Fig. 1) indicates a region of the parameter space in mathematical models for which a large range of wavelengths of regular spatial patterns (vegetation in the dry savanna example) are possible and stable. Also, when conditions or parameters in the model are changed, a specific spatial organization can remain stable, which means

that the wavelength does not change for a wide range of environmental conditions until the edge of the Busse balloon is reached. Here, the spatial organization and ecosystem state variable, such as ecosystem productivity, may adjust in a noncritical or noncatastrophic way (Fig. 1). This can be at parameter values for which, in the nonspatial model, the homogeneous vegetation state may still exist or may have already collapsed to bare soil.

The alternative view mentioned above stems from the fact that earlier analysis of the ecosystem models only considered the stability of uniform states. Such analysis concealed the many possible responses of spatially patterned states, overlooking the existence of Busse balloons. Studies beyond the conventional analysis (32) have also considered the stability of patterned states, exposing the Busse balloons, implying qualitatively new model predictions, and inspiring new observations in real ecosystems.

These model predictions, including the existence of multistability and the notion of

Busse balloons, have lately been supported by observations in real ecosystems (33). Satellite observations have shown regular spatial vegetation patterns that occur in vast areas in different regions in dry savannas in Africa. These observations have shown that many spatial patterns with different wavelengths co-occur next to each other in one and the same area with similar environmental conditions, and for different areas within the same larger region, supporting the Busse balloon theory. Moreover, the wavelengths of the patterns in specific areas within those regions have remained stable in time for decades, despite changes in environmental conditions. Once again, we refer to these two phenomena combined as multistability, which is illustrated by the Busse balloon (Fig. 1) (32, 33). Also, recent model analyses have revealed that at the edge of the Busse balloon, ecosystems adjust their spatial organization in such a way that they stay within the Busse balloon. In other words, the dominant variable generating the spatial pattern (ecosystem productivity in our example) does not change drastically in the way that it would with a critical or catastrophic transition, but more gradually instead (34). Moreover, in the patterned state, vegetation persists for environmental conditions beyond the tipping point (Fig. 1B). This therefore demonstrates a case where the system shows spatial pattern formation at the Turing bifurcation before the tipping point is reached, which then extends beyond the tipping point, essentially constituting a pathway evading it (Fig. 1).

Thus, a phenomenon once considered to be an illustrative early warning signal of imminent critical transitions now appears to be a sign of resilience instead. In this case, the patterns originate from a Turing instability, leading to multistability of patterns and subsequent gradual change of the system. Similarly, in mussel beds, multistability of patterned states has been found in models and real systems (36, 37). It is noteworthy that the predicted size and number of ecosystem shifts can vary; these depend on the magnitude and rate of environmental change (32, 34).

There are now strong indications that evading tipping points through spatial self-organization may be very common for ecosystems and Earth system components. This is based on earlier work on regular pattern formation in real ecosystems (31), combined with the recent insights outlined here, and a mathematical analysis (Box 1) of a class of models. This is also underpinned by other observations—tipping points and alternative stable states (bistability) have been suggested on the basis of simple, nonspatial models for at least the following ecosystems: drylands or dry savannas (5, 7), savannas (10, 11, 38), peatlands (39), mussel beds (40), intertidal mudflats (41), barrier islands (42),

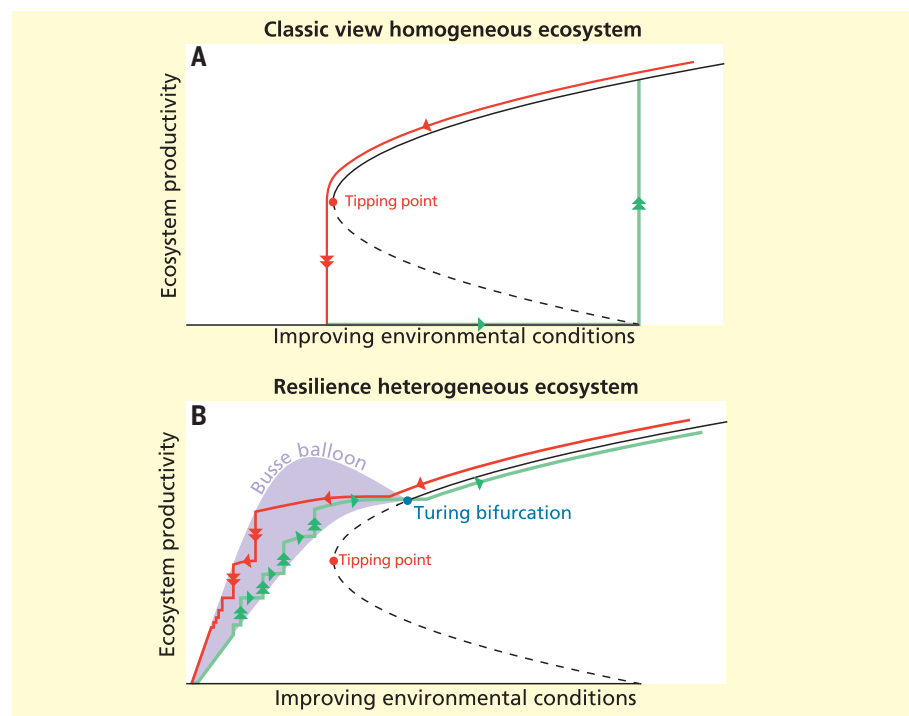


Fig. 1. Resilience in homogeneous and heterogeneous ecosystems. Solid lines denote stable non-patterned equilibria, and dashed lines indicate unstable equilibria. Double arrows indicate ecosystem shifts, and single arrows indicate minor ecosystem adjustments. Typical trajectories for ecosystem degradation (red) and recovery (green) are given, showing the narrowed hysteresis loop for heterogeneous, spatially self-organized ecosystems. **(A)** Classic view of a homogeneous ecosystem. Classically, worsening environmental conditions correspond to a minor adjustment of the ecosystem state or ecosystem productivity, until these drive the system over a tipping point, and a critical or catastrophic transition (B-tipping) occurs. **(B)** Resilience heterogeneous ecosystem. In multistable spatial ecosystems, every set of environmental conditions beyond the Turing bifurcation allows for multiple stable, spatially self-organized states, indicated by the purple area, named the Busse balloon. Here, instead of one critical transition, multiple smaller ecosystem shifts from one spatially patterned state to another occur, which have minor effects on the function or productivity of the ecosystem as a whole (32, 34).

Box 1. Turing-before-tipping.

In mathematical models, B-tipping takes place when an equilibrium state loses its attraction and disappears in response to a parameter, for example A , passing through a critical value, A^* . At that moment, the system has to shift to an alternative equilibrium state. In the literature (10, 38, 39), the models in which tipping occurs typically are spatially homogeneous—i.e., not spatially extended. However, the associated modeled systems are almost without exception spatially extended, and it is thus natural and necessary to model the spatial effects. The main idea underlying the concept of Turing-before-tipping is as follows: For tipping, it is necessary that the (initial) equilibrium state stays stable until it tips. Therefore, it is self-evident to ask the question, is the homogeneous equilibrium state that precedes tipping also stable against spatial effects? If not, a spatially extended version of the model will not exhibit tipping; spatial patterns emerge before parameter A has reached its critical (tipping) value A^* . In that case, the modeled ecosystem will not tip but instead will evade the critical transition by forming spatial patterns.

As a general and relatively simple example of how one can determine whether Turing-before-tipping occurs (or not), we consider the dynamics of a biological quantity $b(t)$ in interaction with a (typically limited) resource $r(t)$ and assume that this is described by the model $\frac{db}{dt} = F(b, r)$, and $\frac{dr}{dt} = G(b, r)$, in which $F(b, r)$ and $G(b, r)$ represent various growth, decay, and interaction effects that vary with parameter A . For example, in the (nondimensionalized) model for vegetation dynamics in drylands of Bastiaansen *et al.* (33), $b(t)$ is the biomass of the vegetation, $r(t)$ is the available water, and $F(b, r) = -Mb + rb^2$, $G(b, r) = A - r - rb^2$, where M models the vegetation mortality rate and A the rainfall. Tipping occurs when, as a function of parameter A , two equilibrium states merge into one, the threshold state (b^*, r^*) at $A = A^*$, and subsequently disappear. To guarantee that one of these equilibrium states is stable, and thus observable, until it tips, it is necessary that $\frac{\partial F}{\partial b}(b^*, r^*) + \frac{\partial G}{\partial r}(b^*, r^*) < 0$. To consider the question whether Turing-before-tipping may occur, one therefore needs to incorporate spatial effects into the homogeneous model. A simple way to do so is to extend the model for $b(t)$ and $r(t)$ into a system of reaction-diffusion equations for biomass $B(x, t)$ and resource $R(x, t)$: $\frac{\partial B}{\partial t} = d_B \Delta B + F(B, R)$, $\frac{\partial R}{\partial t} = d_R \Delta R + G(B, R)$, in which Δ models (spatial) diffusion, and d_B and d_R are the diffusion coefficients that govern the diffusive spreading speeds of $B(x, t)$ and $R(x, t)$. It can be obtained that only if $d_R \frac{\partial F}{\partial b}(b^*, r^*) + d_B \frac{\partial G}{\partial r}(b^*, r^*) < 0$ the threshold state (b^*, r^*) is stable against spatial perturbations. In other words, Turing-before-tipping occurs if $\frac{\partial F}{\partial b}(b^*, r^*) + \frac{\partial G}{\partial r}(b^*, r^*) < 0$ and $d_R \frac{\partial F}{\partial b}(b^*, r^*) + d_B \frac{\partial G}{\partial r}(b^*, r^*) > 0$. This condition therefore determines whether an ecosystem can evade collapse by forming patterns (or not) and can be checked explicitly in any given model. For example, in the dryland model of Bastiaansen *et al.* (33), these conditions are given by $M < 2$ and $eM > 2$ [at $(b^*, r^*) = (1, M)$ with $A^* = 2M$, $d_R = e$, and $d_B = 1$]. In Bastiaansen *et al.* (33), the following realistic choices for M and e were made: $M = 0.45$, $e = 500$ (32). Thus, Turing-before-tipping takes place as is also exhibited by the observations reported. Explicit conditions for Turing-before-tipping can also be deduced for multicomponent models and/or for models with spatial effects beyond (linear) diffusion.

and sea grasses (43). Most notably, for all of these model ecosystems, spatial self-organization, or Turing patterns, have been observed in their real counterpart systems, which are always spatially extended (31, 44–47).

The evasion of tipping points may not be restricted to the case of Turing patterns in Busse balloons, but rather may include more comprehensive spatial pattern formation, as we will outline below. Apart from spatial pattern formation, there are also other mechanisms through which tipping may be evaded. For example, sufficiently fast reset of the changing parameters as compared with the rate of the changing state variable may repair the overshooting of a tipping point (that is, put the state variable back into the original basin of attraction) in simple Earth system component models (48). We expect that both spatial patterns and time delay of the state variable will not only affect B-tipping but also have a very similar effect on N-tipping and R-tipping—that is, evasion of (complete) tipping of the

system. In this context, it is also interesting to note that thresholds related to tipping points are generally rarely detectable from empirical data (49).

Evading tipping points through coexistence states

The ranges of conditions and mechanisms for which complex systems can evade tipping through spatial pattern formation are not restricted to those leading to Turing patterns in Busse balloons—they include more comprehensive spatial pattern formation. Although nonspatial complex systems can respond to disturbances or perturbations only with a system-wide response that leads either to complete tipping to an alternative stable state (N-tipping) or to full recovery, this is not the case for real systems, which are always spatially extended. In those systems, localized or random disturbances that are omnipresent can lead to spatial pattern formation in which only part of the spatial domain transitions to

the alternative state, and system-wide N-tipping is evaded. Such spatial patterns consist of the coexistence of alternative stable states in space and are herein referred to as coexistence states. Multistability of different spatial patterns of those coexistence states can occur for given environmental conditions (50, 51). Spatial boundaries, or interfaces, necessarily arise between alternative states in space. These boundaries can range from very simple, in the form of a single front, to a rich patterned structure of alternative stable states. For example, presence and absence of ice are two alternative stable states that can occur in the spatial domain of the whole Earth system; these states coexist on a global scale. Ice only appears at the polar latitudes, and no ice occurs in between, with a simple spatial boundary between them named the ice line or grounding line (52, 53). At smaller scales, such spatial boundaries between ice and no-ice states can consist of much more complex structures of alternative stable states (54).

The spatial boundaries separating the coexisting states may themselves become unstable, which might lead to one alternative state invading the other, thereby providing a mechanism for evolving such a rich and complex patterned structure of alternative stable states (51, 55). Furthermore, reorganization of spatial patterns may take place as a result of environmental change, without any abrupt change in system characteristics at the global system scale. Therefore, the system can evade critical transitions, and a smoother and much more gradual response can be expected instead (50, 51). In this manner, the spatial patterns can also persist beyond the tipping point with worsening environmental conditions. This constitutes another essential pathway for ecosystems and Earth system components to evade tipping points through spatial pattern formation and multistability. Unexpectedly, such spatial organization could even lead to nonforced reversed transitions in which a state counterinvades, or (in other words) the automatic and spontaneous recovery of the original state from the alternative one (55).

These coexistence states may also form in ecosystems because of the aggregation of organisms into self-organized patchiness (56), as was observed in the clustering of mussels in mussel beds (57). Here, there is an interesting parallel with the physical theory of phase separation. This theory describes the dynamics of spatial interfaces of phases (i.e., spatial boundaries between coexistence states in our terminology) and explains a rich variety of possibly very slow transient spatial patterns. These include maze or labyrinths patterns, spot patterns, and viscous fingering, which may cause very gradual transitions when conditions are changed. Phase separation dynamics leading to coexistence states can be present

in ecosystems and Earth system components as well (58). For instance, some of the spatial aggregation of organisms and resources can be interpreted as such. Comparisons with phase segregation mechanisms have been made already for other ecosystems besides mussels (57)—e.g., for the aggregation of vegetation in fingering patterns (55).

New theories and procedures need to be developed to distinguish spatial pattern formation from patterns originating from preexisting heterogeneity, because real systems are generally a mixture of both (59). One example of preexisting heterogeneity that could falsify the mechanism of spatial pattern formation in the specific context of vegetation patterns could be preexisting drainage patterns governed by topography explaining tree distribution patterns.

Toward a theory on spatial pattern formation and multistability

The insights described above highlight how spatial pattern formation in complex systems can lead to evasion of tipping and increased resilience. We highlight a few illustrative examples in Box 2 and Box 3. However, some complex systems may still exhibit tipping even though they are spatially extended. So when does the classical nonspatial framework of tipping points break down and need to be supplemented by a new theory on spatial pattern formation? For what ecosystems and Earth system components, including the complex Earth system as a whole, is this relevant? And for what conditions and at which spatial scales is this the case? Currently, these questions are not fully resolved. In the text below, we provide a synthesis of the current understanding, based on analysis of model and real patterned systems, in which we also explicitly point out missing pieces of knowledge.

An archetypical system: Evading savanna tipping

Savannas are defined by the coexistence of grasses and trees, spread over one-eighth of the land surface worldwide, and are an important source of livelihood for many (60). The expected changes in climate and land use can lead to substantial alteration of vegetation characteristics and global savanna distributions (61, 62). Tree cover is highly variable and notoriously difficult to predict; it has been suggested that space could be a main element elucidating this, which is missing in many studies of savannas (63). Savannas can be considered as a model ecosystem to derive and validate conditions for evading tipping points because of the following two main reasons. First, observations in models and real ecosystems show multiple alternative states and tipping phenomena. The ecosystem may change between a system with no trees (barren desert or grassland), open savanna with grasses and scattered trees, closed

Box 2. Spatial pattern formation evading tipping in local-scale ecosystems.

Savanna ecosystems are characterized by the coexistence of trees and grasses. Most homogeneous models reproduce this coexistence. They show that, depending on rainfall, fire intensity, and level of herbivory, open savannas (with dispersed trees) may generally switch between multiple alternative homogeneous states (Fig. 2): no trees; either barren desert or grassland, closed tree cover of mainly savanna trees; savanna woodland, or closed tree cover of mainly forest trees; or tropical forest (5, 10, 11, 38, 64, 65, 75). In other words, neglecting spatial effects, these models predict that savanna ecosystems can exhibit alternative states and critical transitions with tipping between them. However, when spatially extended, the models instead show a rich variety of spatial patterns through the emergence of Turing patterns (71, 104) and because of the coexistence of alternative stable states in space (51, 73) (Fig. 2). The system may, or may not, evade tipping by the appearance of spatial patterns, as analysis (Box 1) indicates that both situations may occur. Whether a tropical forest or savanna collapses or increases its resilience by the multistability associated with spatial pattern formation depends on local, but system-wide, conditions—i.e., the parameters in the model.

Box 3. Multistability evading tipping in regional- and global-scale Earth systems.

Tipping behavior and critical transitions are attributed to many Earth system components (3, 15). However, even for these systems, the framework of tipping points may be too limited, and multistability may play a more important role than previously thought.

As a classic example, we consider how spatial effects lead to the introduction of coexistence states and thereby change the tipping behavior related to the ice-albedo feedback in an Earth's global climate model (52, 53, 105, 106). Changes in Earth's temperature are directly related to changes in the energy budget, which is computed as incoming solar radiation minus reflected and outgoing (Planck) radiation. The temperature dependency of the albedo is the ice-albedo feedback: As long as temperatures are low, Earth is covered in ice, which reflects much of the solar radiation. However, when temperatures rise, the ice melts and consequently less radiation is reflected, which leads to further temperature increase. If one does not take spatial effects into account, as is commonly done, this feedback mechanism leads to two alternative Earth states in this model: An Earth fully covered in ice ("snowball earth") or an Earth with no ice ("no-ice Earth"). There is a bistable region where both of these states exist, and critical transitions and tipping points between those states occur when one stable state vanishes.

However, in reality, we are clearly not in either of those two Earth states because ice is present only at the polar regions. That is because spatial effects that play an important role in the real Earth's global energy budget are ignored in such a model. For example, incoming solar radiation is latitude dependent, and meridional heat flow forms an integral part of energy distribution. When adding such spatial mechanisms, the models also predict coexisting states of ice and no-ice in addition to the alternative snowball and no-ice Earth states. In the coexistence states, ice is present in only part of Earth—near a pole there is ice, while simultaneously there is no ice at the equator, with a spatial boundary between these alternative states occurring at some intermediate latitude. The presence of these additional states changes the classical tipping properties of the nonspatial system: When a fully (un)covered Earth state disappears, a less-critical transition to a system with coexistence states might happen, and more gradual transitions are possible.

In addition to this example of coexistence states, there is multistability attributed to Earth system components. In fact, the Busse balloon finds its origin in the study of thermal convection (35), which is closely related to turbulence in fluid mechanics and thus relevant also for the global atmosphere and the ocean circulation of Earth. However, in the example of the Atlantic meridional overturning circulation mentioned above, when using box models with relatively few boxes, tipping is observed (107), whereas multistability of coexistence states is not detected. We suggest that, despite taking into account spatial processes between the boxes, homogenizing within only a restricted number of boxes severely limits the many emergent spatial responses that the system may unfold. Increasing the spatial resolution, by adding more boxes, increases the number and nature of stable states (108, 109) and gradually brings back the multistability. In this context, an interesting line of research is to investigate whether such tipping of Earth system components in general (15) persists in higher-resolution models, such as in the state-of-the-art global climate models (16), or is replaced by multistability of coexistence states including more gradual transitions. If the latter is the case, this may be a possible explanation why the full-complexity global climate models seem more stable than the simple or intermediate-complexity ones (110).

savanna woodland covered with savanna trees and shrubs, and closed tropical forest with forest trees (5, 8–12, 38, 64–68) (Fig. 2). Savanna trees are more fire tolerant and less shade tolerant than forest trees (69). This, together with the flammability and fire resistance of grasses that can easily regrow after fires, is the key of the positive feedback mentioned earlier, generating alternative stable states between open savanna and tropical forests. Second, both types of spatial pattern formation as we outlined, namely Turing patterns and coexistence states, have been observed in real and model systems (12, 25, 68, 70–76) (Fig. 2). Therefore, studying savanna ecosystems is an excellent opportunity to obtain results that are of general interest and applicability.

Toward a unified spatial savanna model

To the best of our knowledge, no unified savanna model exists that explains all of the possible ecosystem states including spatial Turing patterns and coexistence states. To develop a unified spatially explicit savanna

model, existing savanna models (71, 76, 77) could be combined in such a way that the new model consists of (at least) the state variables water, grass biomass, savanna tree biomass, and forest tree biomass. Savanna and forest trees should be distinguished by their different fire responses and shade tolerance (78, 79). Nonspatial models that consider rain, fire, and herbivory may aid in the development of such a unified framework (64, 80), and studies of savanna-forest transitions may also prove useful (10, 81). The new model could include positive feedbacks between water infiltration into the soil and biomass and between fire and grass biomass (11). Herbivory (grazing and browsing) could be added as an extra negative term (82), or possibly as an extra dynamic equation (83). It could then be analyzed to address the following questions along a rainfall gradient (Fig. 2): Under which conditions do sharp or gradual spatial boundaries exist between open savanna on the one hand and tropical forest, savanna woodland, or desert on the other? How are those bound-

aries evolving, bifurcating, or moving with respect to (changes in) climate, herbivory, and fire? Under which conditions do spatial patterns occur, either Turing patterns or coexistence states? Answers to these questions can be obtained by a combination of simulations, mathematical bifurcation analyses, and numerical continuation (84, 85).

General new predictions based on the theory that could be tested with such a unified model are as follows (Fig. 2): (i) At the humid end of the rainfall gradient, at the tropical forest–savanna boundaries, where fire is generally assumed to drive alternative stable states between tropical forests and open savannas, we expect to discover coexistence states (68, 86) evading tipping. (ii) In the mesic range, where a combination of fire and herbivory drives alternative states between closed savanna woodland and open savanna, we expect to find both coexistence states and Turing patterns (70, 73, 74) evading tipping. (iii) At the dry end of the gradient, where dryness drives alternative stable states between open savanna on the one hand and desert on the other, we suppose that the occurrence of Turing patterns associated with Busse balloons (33, 34) leads to the evasion of tipping points. (iv) Increased fire intensity will lead to movement of the tropical forest–savanna boundary toward tropical forest (humid savannas replacing forest) (81). A decrease in fire or herbivory will lead to savanna woodland invading mesic open savanna, and decreased rainfall will lead to desert replacing dry savanna.

Observations of spatial patterns evading tipping points

Toward the wet end of the rainfall gradient, sharp tropical forest–savanna fronts (87) without spatial pattern formation could be interpreted as spatial substitutions of critical transitions (88). However, it is not clear for which conditions tropical forest–savanna boundaries are sharp or gradual, whether they are moving, and whether patterned structures of alternative stable states (coexistence states) occur. Therefore, the same questions as those for the model analyses described above can be addressed through observations. After being tested by model analyses, the predictions mentioned above can be validated, focusing on fire and dryness as main drivers. Spatial signatures of sharp vegetation boundaries (88) between tropical forests and open savannas can be explored worldwide from satellite data (87, 89). This can be done at multiple spatial resolutions to create time series for multiple years or decades (90) to detect vegetation boundaries at both coarser and finer resolutions necessary to screen boundaries of spatial patterned structures of coexistence states (68, 86) and Turing patterns, which could both be easily overlooked by only using coarser



Fig. 2. Savannas along a rainfall gradient. Open savannas with dispersed trees can be classified into three broad ranges according to annual rainfall (67): humid, mesic, and dry (blue bar indicates rainfall decreasing from humid to dry, from right to left). The humid range potentially demonstrates bistability with tropical forest. The mesic range shows possible bistability with savanna woodland, and the dry end shows possible bistability with barren desert (or grassland, which is not shown). Fire and herbivory play an important role in savanna dynamics, determining varying tree cover given a certain amount of rainfall. The importance of fire (illustrated by the red shade in the fire bar) decreases from humid toward dry ranges, where water availability is the main limiting factor and driving force. We compare the expected spatial structures with symbolic Google Earth image examples, from right to left with decreasing rainfall, namely: coexistence states between forests and humid savannas (Gabon 1°16'1.06" S to 13°56'18.63" E, 2000 m by 2000 m), coexistence states as well as Turing patterns between savanna woodland and mesic open savanna (Kenya 1°28'8.83" S to 34°53'55.60" E, 1200 m by 1200 m; Mali 13°03'15.09" N to 6°40'50.86" W, 800 m by 800 m), and Turing patterns between dry savannas and desert (Sudan 11°26'47.53" N to 27°53'30.07" E, 1500 m by 1500 m). There is no unifying model explaining all savanna states and spatial patterns observed. We suggest that developing and analyzing such a unifying savanna model is needed by incorporating relevant state variables and parameters, making the model spatially explicit, and using a combination of mathematical bifurcation analyses, simulations, and numerical continuation methods (84, 85).

spatial resolutions. The same approach can be followed for open savanna–savanna woodland boundaries for the mesic ranges of the rainfall gradient and for dry savanna–desert boundaries at the dry end of the gradient.

Such findings can be related to the main drivers, such as dryness and fire as mentioned above, through change indicators (91, 92). Metrics of spatial boundaries can also be correlated to annual burned area maps (93). This would allow for tests of the predictions of how these drivers determine the sharpness of vegetation boundaries, whether patterned structures of coexistence states and Turing patterns occur, and how moving the boundaries is associated with a change of the main drivers. This is important in the light of expected changes in climate and land use, and it will provide insight into the conditions for which tipping points may be evaded or not.

Universal conditions for spatial pattern formation and multistability

A major part of the mathematical literature on spatial pattern formation focuses on the onset of Turing patterns close to homogeneous equilibria (94). However, real ecosystems and Earth system components in their natural state typically are not close to such an onset at which the patterns first emerge, but rather are far from equilibrium, where the spatial patterns are fully developed. There can only be limited mathematical insight into many of the spatial patterns in real systems, unless the governing system shows a sufficient large-scale separation—the condition in which spatial transport of the components of the system plays out on vastly different spatial and temporal scales. A system for which this occurs is called singularly perturbed in the mathematical literature. Notably, the spatially extended models and real systems considered here typically are singularly perturbed, where the singularly perturbed nature stems from observations that pattern formation in ecosystems is in fact driven by counteracting feedback mechanisms on widely different spatial scales (37). Therefore, the realistic, far-from-equilibrium patterns considered here can be studied in mathematical detail by the methods of singular perturbation theory (95). Moreover, the most relevant patterns commonly exhibited by ecosystems and Earth system components (including the examples of Box 2 and 3) have the nature of interacting localized structures, such as areas with vegetation bands surrounded by areas with bare soil (33), the boundaries mentioned above between open savanna and savanna woodlands (73), and the grounding line of glaciers (54). Resilience by multistability (33, 34) is directly coupled to the very rich variety of patterns associated with interacting localized structures like localized stripes and spatial boundaries.

Therefore, the formation of these fundamental spatial patterns and multistability provide mechanisms by which spatial ecosystems (Box 2) or Earth system components (Box 3), including the complex Earth system as a whole, may evade tipping in general. Whether this occurs or not will depend on local (but system-wide) conditions in real systems, or parameter combinations in models. For various classes of systems, there will be universal conditions that lead to the evasion of tipping points through spatial pattern formation and multistability, such as for savanna ecosystems. These are classes of ecosystems and Earth system components for which tipping points are currently predicted.

Turing-before-tipping

Preliminary analyses of spatially extended ecosystems, such as dry savannas, modeled by activator-inhibitor-type reaction-diffusion equations (27, 75, 76), show that tipping may or may not be preceded by a pattern-forming Turing bifurcation (Box 1 and Fig. 1). The conditions for which this may or may not happen can be explicitly expressed in terms of model parameters (Box 1). However, the Turing bifurcation only gives insight into the onset of spatial patterns, not into their behavior beyond onset (far from equilibrium), where the patterns become more developed and observable. Moreover, it is the dynamics beyond onset that determine if and how these Turing patterns lead to evasion of tipping. An explicit scenario has been unraveled within the literature on dry savannas (32, 34) where Turing patterns evolved beyond the onset in such a way that tipping is evaded in the system. The crucial question now is whether this scenario may also play a role in other types of systems and whether there are alternative scenarios through which small-amplitude Turing patterns may evolve into large-scale interacting localized structures that enable the system to evade tipping. Because of the singularly perturbed nature of the models, it is possible to study the basic localized structures and their interactions mathematically (96–98). To make the crucial connection between these localized patterns and those that appear from the Turing bifurcation, a further analysis of the Busse balloon—and especially the nature of its boundary—by a combination of bifurcation analyses, simulations, and numerical continuation (32, 84, 85) is necessary.

Such analyses will also reveal the dynamics of systems preceding bifurcation points, thereby leading to better early warning signs. The classical theory of tipping, predominantly based on nonspatial models, led to the creation of generic early warning signs before such tipping occurs (2, 99), mainly associated with critical slowing down of recovery after perturbation. In spatial systems, this idea becomes more complicated because this may now cru-

cially depend on the nature of the different spatial perturbations; critical slowing down will only show for perturbations that have a specific spatial structure (74), which may be hard or even impossible to detect in spatially averaged data. Simultaneously, the form of the perturbation that does show critical slowing down can help to determine the type of bifurcation before onset—i.e., whether a system will tip or evade tipping by forming spatial patterns. After the system is exposed to some generic perturbation (that might be random or localized) before a bifurcation is reached, the system will restore during a transient restoration period, and temporarily, either a patterned or a nonpatterned state may emerge. The form of this emerging transient state could now be distinctive, and the type of bifurcation it precedes could be identified. Leading up to Turing bifurcation, such emerging transient state may be some spatially periodic pattern. By contrast, tipping bifurcation could be preceded by emerging transient states that are either spatially homogeneous or extremely localized. This would make it possible to distinguish between both types of bifurcations from spatial time series before they occur. Of course, one main challenge is the extraction of these spatial perturbations from data, but existing so-called mode decomposition algorithms (100) may be a viable option.

Destabilizations of interfaces between coexistence states

Isolated interfaces between coexistence states, such as the open savanna–savanna woodland boundary, the tropical forest–savanna boundary (Box 2 and Fig. 2), and the interfaces between ocean and ice (Box 3), are necessary for the multistability by which tipping of the whole spatial system through perturbation of the stable state may be evaded. However, for the spatial coexistence patterns to persist beyond the tipping point with worsening external conditions, an additional mechanism is required and likely. Similarly to how homogeneous states can be destabilized by Turing bifurcations, spatial fronts between coexistence states may typically also bifurcate and may thus be the origin of a multitude of evolving localized spatial patterns. These patterns subsequently may provide the ecosystem or Earth system component with further multistability and with various gradual routes it may follow beyond the tipping point—i.e., with evasion of the tipping point when environmental conditions worsen. These bifurcations can be traced numerically (51, 55). But more importantly, the singular perturbed nature of the models allows for the development of a fundamental understanding of the underlying destabilizing mechanisms (98, 101). For instance, conditions can be derived for which an invading front that leaves a homogeneous stable state

behind triggers a counterinvasion of an alternative patterned state, which comprises multistability and thus a gradual route, thereby circumventing tipping points.

The impact of domain, localized, and nonlocal homogenizing effects

Most mathematical studies of spatial pattern formation in spatially extended complex systems take place assuming a highly idealized domain—a sufficiently large open space or volume in which environmental conditions do not change throughout the domain. In real systems, however, such idealized domains do not exist, and it is not evident if and how results carry over from idealized domains to more realistic ones. For example, if the spatial domain in which a system can evolve is too small for spatial pattern formation, evasion of tipping cannot work anymore. A prominent example could be alternative stable states and tipping of the spatially confined and shallow lakes (6). This implies there is a minimum domain size for complex systems to form spatial patterns and enhance resilience; this minimum size would depend on the spatial scale of the dominant mechanisms and resulting spatial patterns of the specific system under consideration.

Moreover, localized effects—e.g., those produced by human interventions—can have a strong impact on the formation, stability, and dynamics of patterns (102). Examples of this include logging in tropical forests and imposed fixing of sand dunes or building dikes in coastal dune systems. Such human perturbation, albeit localized, may substantially reduce the flexibility and thus the resilience of the patterned system as a whole. Similarly, and probably more importantly, the same can happen if humans homogenize spatial patterns characteristic of pristine systems nonlocally, because the mechanisms outlined here enhancing resilience will not function anymore. Examples of this include large-scale agriculture in terrestrial ecosystems, spatially homogeneous restoration efforts combating desertification, and destructive bottom trawling in marine ecosystems. Therefore, the study of resilience through spatial pattern formation in complex systems should be embedded in a thorough analysis of the impact of spatial restrictions of the domain and the effects of localized and nonlocal homogenizing, human-induced effects. A relevant approach would be a combination of computational and analytical studies to determine the effects of such spatial (in)homogeneities on pattern dynamics and resilience (103). This is important for ecosystem restoration and mitigating the effects of land use and climate change.

Conclusions

Here, we have shown how spatial self-organization and multistability resulting from Turing pat-

terns may help complex systems evade tipping points and enhance resilience. Additionally, we have outlined that the ranges of conditions and mechanisms for which tipping is evaded are supposed to be much broader than those leading to Turing patterns, owing to more comprehensive spatial pattern formation and multistability, including the occurrence of coexistence states. We highlighted that both types of spatial pattern formation originate before and can persist beyond tipping points, demonstrating various pathways evading tipping while strongly enhancing the resilience. We emphasized that such spatial pattern formation and multistability have also been observed recently for real ecosystems, and we argued that this may be relevant for many ecosystems and Earth system components, including for the complex Earth system as a whole. Savannas can be considered an archetypal ecosystem to further investigate this because of observations of tipping phenomena together with spatial pattern formation. A better understanding of the dynamics of spatial pattern formation in general is needed to determine how these patterns respond to external changes of various magnitudes and rates and to localized and nonlocal homogenizing perturbations. Such an understanding will help determine which conditions and spatial patterns lead to the evasion of tipping and which do not. We expect that identifying these in the many ecosystems and Earth system components that are supposedly tipping prone will reveal that some are actually much more resilient than currently thought.

REFERENCES AND NOTES

1. M. Scheffer, S. Carpenter, J. A. Foley, C. Folke, B. Walker, Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001). doi: [10.1038/35098000](https://doi.org/10.1038/35098000); pmid: [11595939](https://pubmed.ncbi.nlm.nih.gov/11595939/)
2. M. Scheffer et al., Early-warning signals for critical transitions. *Nature* **461**, 53–59 (2009). doi: [10.1038/nature08227](https://doi.org/10.1038/nature08227); pmid: [19727193](https://pubmed.ncbi.nlm.nih.gov/19727193/)
3. W. Steffen et al., Trajectories of the Earth System in the Anthropocene. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 8252–8259 (2018). doi: [10.1073/pnas.1810141115](https://doi.org/10.1073/pnas.1810141115); pmid: [30082409](https://pubmed.ncbi.nlm.nih.gov/30082409/)
4. J. van de Koppel, M. Rietkerk, F. J. Weissing, Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol. Evol.* **12**, 352–356 (1997). doi: [10.1016/S0169-5347\(97\)01133-6](https://doi.org/10.1016/S0169-5347(97)01133-6); pmid: [21238102](https://pubmed.ncbi.nlm.nih.gov/21238102/)
5. M. Rietkerk, F. van den Bosch, J. van de Koppel, Site-specific properties and irreversible vegetation changes in semi-arid ecosystems. *Oikos* **80**, 241–252 (1997). doi: [10.2307/3546592](https://doi.org/10.2307/3546592)
6. M. Scheffer, S. H. Hosper, M.-L. Meijer, B. Moss, E. Jeppesen, Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* **8**, 275–279 (1993). doi: [10.1016/0169-5347\(93\)90254-M](https://doi.org/10.1016/0169-5347(93)90254-M); pmid: [21236168](https://pubmed.ncbi.nlm.nih.gov/21236168/)
7. M. Rietkerk, J. van de Koppel, Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* **79**, 69–76 (1997). doi: [10.2307/3546091](https://doi.org/10.2307/3546091)
8. M. Hirota, M. Holmgren, E. H. Van Nes, M. Scheffer, Global resilience of tropical forest and savanna to critical transitions. *Science* **334**, 232–235 (2011). doi: [10.1126/science.1210657](https://doi.org/10.1126/science.1210657); pmid: [21998390](https://pubmed.ncbi.nlm.nih.gov/21998390/)
9. A. C. Staver, S. Archibald, S. A. Levin, The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**, 230–232 (2011). doi: [10.1126/science.1210465](https://doi.org/10.1126/science.1210465); pmid: [21998389](https://pubmed.ncbi.nlm.nih.gov/21998389/)
10. A. C. Staver, S. A. Levin, Integrating theoretical climate and fire effects on savanna and forest systems. *Am. Nat.* **180**, 211–224 (2012). doi: [10.1086/666648](https://doi.org/10.1086/666648); pmid: [22766932](https://pubmed.ncbi.nlm.nih.gov/22766932/)
11. F. Van Langevelde et al., Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**, 337–350 (2003). doi: [10.1890/0012-9658\(2003\)084\[0337:EFOFAH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0337:EFOFAH]2.0.CO;2)
12. J. C. Aleman et al., Floristic evidence for alternative biome states in tropical Africa. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 28183–28190 (2020). doi: [10.1073/pnas.2011515117](https://doi.org/10.1073/pnas.2011515117); pmid: [33109722](https://pubmed.ncbi.nlm.nih.gov/33109722/)
13. C. S. Holling, in *Engineering Within Ecological Constraints*, P. E. Schulze, Ed. (National Academy Press, 1996), pp. 31–43.
14. P. Ashwin, S. Wieczorek, R. Vitolo, P. Cox, Tipping points in open systems: Bifurcation, noise-induced and rate-dependent examples in the climate system. *Phil. Trans. R. Soc. A* **370**, 1166–1184 (2012). doi: [10.1098/rsta.2011.0306](https://doi.org/10.1098/rsta.2011.0306); pmid: [22291228](https://pubmed.ncbi.nlm.nih.gov/22291228/)
15. T. M. Lenton et al., Tipping elements in the Earth's climate system. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1786–1793 (2008). doi: [10.1073/pnas.0705414105](https://doi.org/10.1073/pnas.0705414105); pmid: [18258748](https://pubmed.ncbi.nlm.nih.gov/18258748/)
16. S. Drifftout et al., Catalogue of abrupt shifts in Intergovernmental Panel on Climate Change climate models. *Proc. Natl. Acad. Sci. U.S.A.* **112**, E5777–E5786 (2015). doi: [10.1073/pnas.1511451112](https://doi.org/10.1073/pnas.1511451112); pmid: [26460042](https://pubmed.ncbi.nlm.nih.gov/26460042/)
17. P. Huybrechts, J. de Wolde, The dynamic response of the Greenland and Antarctic ice sheets to multiple-century climatic warming. *J. Clim.* **12**, 2169–2188 (1999). doi: [10.1175/1520-0442\(1999\)012<2169:TDR0TG>2.0.CO;2](https://doi.org/10.1175/1520-0442(1999)012<2169:TDR0TG>2.0.CO;2)
18. F. Pattyn, M. Morlighem, The uncertain future of the Antarctic ice sheet. *Science* **367**, 1331–1335 (2020). doi: [10.1126/science.aaz5487](https://doi.org/10.1126/science.aaz5487); pmid: [32193321](https://pubmed.ncbi.nlm.nih.gov/32193321/)
19. J. Garbe, T. Albrecht, A. Levermann, J. F. Donges, R. Winkelmann, The hysteresis of the Antarctic ice sheet. *Nature* **585**, 538–544 (2020). doi: [10.1038/s41586-020-2727-5](https://doi.org/10.1038/s41586-020-2727-5); pmid: [32968257](https://pubmed.ncbi.nlm.nih.gov/32968257/)
20. T. F. Stocker, D. G. Wright, Rapid transitions of the ocean's deep circulation induced by changes in surface water fluxes. *Nature* **351**, 729–732 (1991). doi: [10.1038/351729a0](https://doi.org/10.1038/351729a0)
21. S. Rahmstorf, A. Ganopolsky, Long-term global warming scenario's computed with an efficient coupled climate model. *Clim. Change* **43**, 353–367 (1999). doi: [10.1023/A:1005474526406](https://doi.org/10.1023/A:1005474526406)
22. J. Lohmann, P. D. Ditlevsen, Risk of tipping the overturning circulation due to increasing rates of ice melt. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e20179891 (2021). doi: [10.1073/pnas.2017989118](https://doi.org/10.1073/pnas.2017989118); pmid: [33619095](https://pubmed.ncbi.nlm.nih.gov/33619095/)
23. J. Rockström et al., A safe operating space for humanity. *Nature* **461**, 472–475 (2009). doi: [10.1038/461472a](https://doi.org/10.1038/461472a); pmid: [19779433](https://pubmed.ncbi.nlm.nih.gov/19779433/)
24. A. D. Barnosky et al., Approaching a state shift in Earth's biosphere. *Nature* **486**, 52–58 (2012). doi: [10.1038/nature11018](https://doi.org/10.1038/nature11018); pmid: [22678279](https://pubmed.ncbi.nlm.nih.gov/22678279/)
25. M. Rietkerk, S. C. Dekker, P. C. de Ruiter, J. van de Koppel, Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**, 1926–1929 (2004). doi: [10.1126/science.1101867](https://doi.org/10.1126/science.1101867); pmid: [15448261](https://pubmed.ncbi.nlm.nih.gov/15448261/)
26. A. M. Turing, The chemical basis of morphogenesis. *Bull. Math. Biol.* **52**, 153–197 (1990). doi: [10.1007/BF02459572](https://doi.org/10.1007/BF02459572); pmid: [2185858](https://pubmed.ncbi.nlm.nih.gov/2185858/)
27. C. A. Klausmeier, Regular and irregular patterns in semiarid vegetation. *Science* **284**, 1826–1828 (1999). doi: [10.1126/science.284.5421.1826](https://doi.org/10.1126/science.284.5421.1826); pmid: [10364553](https://pubmed.ncbi.nlm.nih.gov/10364553/)
28. J. von Hardenberg, E. Meron, M. Shachak, Y. Zarmi, Diversity of vegetation patterns and desertification. *Phys. Rev. Lett.* **87**, 198101 (2001). doi: [10.1103/PhysRevLett.87.198101](https://doi.org/10.1103/PhysRevLett.87.198101)
29. M. Rietkerk et al., Self-organization of vegetation in arid ecosystems. *Am. Nat.* **160**, 524–530 (2002). doi: [10.1086/342078](https://doi.org/10.1086/342078); pmid: [18707527](https://pubmed.ncbi.nlm.nih.gov/18707527/)
30. K. Gowda, H. Riecke, M. Silber, Transitions between patterned states in vegetation models for semiarid ecosystems. *Phys. Rev. E* **89**, 022701 (2014). doi: [10.1103/PhysRevE.89.022701](https://doi.org/10.1103/PhysRevE.89.022701); pmid: [25353503](https://pubmed.ncbi.nlm.nih.gov/25353503/)
31. M. Rietkerk, J. van de Koppel, Regular pattern formation in real ecosystems. *Trends Ecol. Evol.* **23**, 169–175 (2008). doi: [10.1016/j.tree.2007.10.013](https://doi.org/10.1016/j.tree.2007.10.013); pmid: [18255188](https://pubmed.ncbi.nlm.nih.gov/18255188/)
32. K. Siteur et al., Beyond Turing: The response of patterned ecosystems to environmental change. *Ecol. Complex.* **20**, 81–96 (2014). doi: [10.1016/j.ecocom.2014.09.002](https://doi.org/10.1016/j.ecocom.2014.09.002)
33. R. Bastiaansen et al., Multistability of model and real dryland ecosystems through spatial self-organization. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 11256–11261 (2018). doi: [10.1073/pnas.1804771115](https://doi.org/10.1073/pnas.1804771115); pmid: [30322906](https://pubmed.ncbi.nlm.nih.gov/30322906/)
34. R. Bastiaansen, A. Doelman, M. B. Eppinga, M. Rietkerk, The effect of climate change on the resilience of ecosystems with adaptive spatial pattern formation. *Ecol. Lett.* **23**, 414–429 (2020). doi: [10.1111/ele.13449](https://doi.org/10.1111/ele.13449); pmid: [31912954](https://pubmed.ncbi.nlm.nih.gov/31912954/)

35. F. H. Busse, Non-linear properties of thermal convection. *Rep. Prog. Phys.* **41**, 1929–1967 (1978). doi: [10.1088/0034-4885/41/12/003](#)
36. R. H. Wang, Q. X. Liu, G. Q. Sun, Z. Jin, J. van de Koppel, Nonlinear dynamic and pattern bifurcations in a model for spatial patterns in young mussel beds. *J. R. Soc. Interface* **6**, 705–718 (2009). doi: [10.1098/rsif.2008.0439](#); pmid: [18986965](#)
37. Q. X. Liu *et al.*, Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. *Nat. Commun.* **5**, 5234 (2014). doi: [10.1038/ncomms6234](#); pmid: [25335554](#)
38. E. H. van Nes, M. Hirota, M. Holmgren, M. Scheffer, Tipping points in tropical tree cover: Linking theory to data. *Glob. Change Biol.* **20**, 1016–1021 (2014). doi: [10.1111/gcb.12398](#); pmid: [24106057](#)
39. J. Pastor, B. Peckham, S. Bridgman, J. Weltzin, J. Chen, Plant community dynamics, nutrient cycling, and alternative stable equilibria in peatlands. *Am. Nat.* **160**, 553–568 (2002). doi: [10.1086/342814](#); pmid: [18707507](#)
40. M. J. Donahue, R. A. Desharnais, C. D. Robles, P. Arriola, Mussel bed boundaries as dynamic equilibria: Thresholds, phase shifts, and alternative states. *Am. Nat.* **178**, 612–625 (2011). doi: [10.1086/662177](#); pmid: [22030731](#)
41. J. Van de Koppel, P. M. J. Herman, P. Thoolen, C. H. R. Heip, Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology* **82**, 3449–3461 (2001). doi: [10.1890/0012-9658\(2001\)082\[3449:DASSO\]2.0.CO;2](#)
42. O. D. Vinent, L. J. Moore, Barrier island bistability induced by biophysical interactions. *Nat. Clim. Change* **5**, 158–162 (2015). doi: [10.1038/NCLIMATE2474](#)
43. T. Van der Heide *et al.*, Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. *Ecosystems* **10**, 1311–1322 (2007). doi: [10.1007/s10021-007-9099-7](#)
44. T. van der Heide *et al.*, Spatial self-organized patterning in seagrasses along a depth gradient of an intertidal ecosystem. *Ecology* **91**, 362–369 (2010). doi: [10.1890/0891-1517.1001.0362](#); pmid: [20392001](#)
45. E. D. Lazarus, S. Armstrong, Self-organized pattern formation in coastal barrier washover deposits. *Geology* **43**, 363–366 (2015). doi: [10.1130/G36329.1](#)
46. D. Ruiz-Reynés *et al.*, Fairy circle landscapes under the sea. *Sci. Adv.* **3**, e1603262 (2017). doi: [10.1126/sciadv.1603262](#); pmid: [28782035](#)
47. V. Reijers, “A song of sand and mud: How plant-mediated feedbacks dictate landscape formation and dynamics of barrier islands,” thesis, Radboud University, Nijmegen (2019).
48. P. D. L. Ritchie, J. J. Clarke, P. M. Cox, C. Huntingford, Overshooting tipping point thresholds in a changing climate. *Nature* **592**, 517–523 (2021). doi: [10.1038/s41586-021-03263-2](#); pmid: [33883733](#)
49. H. Hillebrand *et al.*, Thresholds for ecological responses to global change do not emerge from empirical data. *Nat. Ecol. Evol.* **4**, 1502–1509 (2020). doi: [10.1038/s41559-020-1256-9](#); pmid: [32807945](#)
50. G. Bel, A. Hagberg, E. Meron, Gradual regime shifts in spatially extended ecosystem. *Theor. Ecol.* **5**, 591–604 (2012). doi: [10.1007/s12080-011-0149-6](#)
51. Y. R. Zelnik, E. Meron, Regime shifts by front dynamics. *Ecol. Indic.* **94**, 544–552 (2018). doi: [10.1016/j.ecolind.2017.10.068](#)
52. M. Ghil, Climate stability for a Sellers-type model. *J. Atmos. Sci.* **33**, 3–20 (1976). doi: [10.1175/1520-0469\(1976\)033<0003:CSFAST>2.0.CO;2](#)
53. T. Bódi, V. Lucarini, F. Lunkeit, R. Boschi, Global instability in the Ghil–Sellers model. *Clim. Dyn.* **44**, 3361–3381 (2015). doi: [10.1007/s00382-014-2206-5](#)
54. S. H. R. Rosier *et al.*, The tipping points and early-warning indicators for Pine Island Glacier, West Antarctica. *Cryosphere* **15**, 1501–1516 (2021). doi: [10.5194/tc-15-1501-2021](#)
55. C. Fernandez-Oto, O. Tzok, E. Meron, Front instabilities can reverse desertification. *Phys. Rev. Lett.* **122**, 048101 (2019). doi: [10.1103/PhysRevLett.122.048101](#); pmid: [30768298](#)
56. M. E. Cates, J. Tailleur, Motility-induced phase separation. *Annu. Rev. Condens. Matter Phys.* **6**, 219–244 (2015). doi: [10.1146/annurev-conmatphys-031214-014710](#)
57. Q.-X. Liu *et al.*, Phase separation explains a new class of self-organized spatial patterns in ecological systems. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 11905–11910 (2013). doi: [10.1073/pnas.1222339110](#); pmid: [23818579](#)
58. Q.-X. Liu *et al.*, Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns. *Phys. Life Rev.* **19**, 107–121 (2016). doi: [10.1016/j.plrev.2016.07.009](#); pmid: [27478087](#)
59. E. Sheffer, J. von Hardenberg, H. Yizhaq, M. Shachak, E. Meron, Emerged or imposed: A theory on the role of physical templates and self-organisation for vegetation patchiness. *Ecol. Lett.* **16**, 127–139 (2013). doi: [10.1111/ele.12027](#); pmid: [23157578](#)
60. R. J. Scholes, S. R. Archer, Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* **28**, 517–544 (1997). doi: [10.1146/annurev.ecolsys.28.1.517](#)
61. J. D. Anadon, O. E. Sala, F. T. Maestre, Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas. *J. Ecol.* **102**, 1363–1373 (2014). doi: [10.1111/1365-2745.12325](#)
62. M. Garcia Criado, I. H. Meyers-Smith, A. D. Bjorkman, C. E. R. Lehman, N. Stevens, Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Glob. Ecol. Biogeogr.* **29**, 925–943 (2020). doi: [10.1111/geb.13072](#)
63. A. C. Staver, Prediction and scale in savanna ecosystems. *New Phytol.* **219**, 52–57 (2018). doi: [10.1111/nph.14829](#); pmid: [29027662](#)
64. F. Accatino, C. De Michele, R. Vezzoli, D. Donzelli, R. J. Scholes, Tree-grass co-existence in savanna: Interactions of rain and fire. *J. Theor. Biol.* **267**, 235–242 (2010). doi: [10.1016/j.jtbi.2010.08.012](#); pmid: [20708629](#)
65. M. Baudena, F. D’Andrea, A. Provenzale, An idealized model for tree-grass coexistence in savannas: The role of life stage structure and fire disturbances. *J. Ecol.* **98**, 74–80 (2010). doi: [10.1111/j.1365-2745.2009.01588.x](#)
66. V. de L. Dantas, M. Hirota, R. S. Oliveira, J. G. Pausas, Disturbance maintains alternative biome states. *Ecol. Lett.* **19**, 12–19 (2016). doi: [10.1111/ele.12537](#); pmid: [26493189](#)
67. D. D’Onofrio, J. von Hardenberg, M. Baudena, Not only trees: Grasses determine African tropical biome distributions via water limitation and fire. *Glob. Ecol. Biogeogr.* **27**, 714–725 (2018). doi: [10.1111/geb.12735](#)
68. A. W. Cardoso *et al.*, A distinct ecotonal tree community exists at central African forest-savanna transitions. *J. Ecol.* **109**, 1170–1183 (2021). doi: [10.1111/1365-2745.13549](#)
69. T. Charles-Dominique, G. F. Midgley, K. W. Tomlinson, W. J. Bond, Steal the light: Shade vs fire adapted vegetation in forest-savanna mosaics. *New Phytol.* **218**, 1419–1429 (2018). doi: [10.1111/nph.15117](#); pmid: [29604213](#)
70. T. A. Groen, “Spatial matters: How spatial patterns and processes affect savanna dynamics,” thesis, Wageningen University (2007).
71. M. Baudena, M. Rietkerk, Complexity and coexistence in a simple spatial model for arid savanna ecosystems. *Theor. Ecol.* **6**, 131–141 (2013). doi: [10.1007/s12080-012-0165-1](#)
72. R. Martínez-García, J. M. Calabrese, C. López, Spatial patterns in mesic savannas: The local facilitation limit and the role of demographic stochasticity. *J. Theor. Biol.* **333**, 156–165 (2013). doi: [10.1016/j.jtbi.2013.05.024](#); pmid: [23747988](#)
73. T. A. Groen, C. A. D. M. van de Vijver, F. van Langevelde, Do spatially homogenizing and heterogenizing processes affect transitions between alternative stable states? *Ecol. Modell.* **65**, 119–128 (2017). doi: [10.1016/j.ecolmodel.2017.10.002](#)
74. S. Eby, A. Agrawal, S. Majumder, A. P. Dobson, V. Guttal, Alternative stable states and spatial indicators of critical slowing down along a spatial gradient in a savanna ecosystem. *Glob. Ecol. Biogeogr.* **26**, 638–649 (2017). doi: [10.1111/geb.12570](#)
75. L. Eigentler, J. A. Sherratt, Metastability as a coexistence mechanism in a model for dryland vegetation patterns. *Bull. Math. Biol.* **81**, 2290–2322 (2019). doi: [10.1007/s11538-019-00606-z](#); pmid: [31012031](#)
76. O. Tzok, H. Uecker, E. Meron, The role of spatial self-organization in the design of agroforestry systems. *PLOS ONE* **15**, e0236325 (2020). doi: [10.1371/journal.pone.0236325](#); pmid: [32692773](#)
77. B. Wuyts, A. R. Champneys, N. Verschueren, J. I. House, Tropical tree cover in a heterogeneous environment: A reaction-diffusion model. *PLOS ONE* **14**, e0218151 (2019). doi: [10.1371/journal.pone.0218151](#); pmid: [31246968](#)
78. V. Yatat, P. Couteron, J. J. Tewa, S. Bowong, Y. Dumont, An impulsive modelling framework of fire occurrence in a size-structured model of tree-grass interactions for savanna ecosystems. *J. Math. Biol.* **74**, 1425–1482 (2017). doi: [10.1007/s00285-016-1060-y](#); pmid: [27659304](#)
79. V. Yatat, P. Couteron, Y. Dumont, Spatially explicit modelling of tree–grass interactions in fire-prone savannas: A partial differential equations framework. *Ecol. Complex.* **36**, 290–313 (2018). doi: [10.1016/j.ecocom.2017.06.004](#)
80. C. De Michele, F. Accatino, R. Vezzoli, R. J. Scholes, Savanna domain in the herbivores–fire parameter space exploiting a tree–grass–soil water dynamic model. *J. Theor. Biol.* **289**, 74–82 (2011). doi: [10.1016/j.jtbi.2011.08.014](#); pmid: [21875600](#)
81. Q. Li, A. C. Staver, E. Weinan, S. A. Levin, Spatial feedbacks and the dynamics of savanna and forest. *Theor. Ecol.* **12**, 237–262 (2019). doi: [10.1007/s12080-019-0428-1](#)
82. E. Siero *et al.*, Grazing away the resilience of patterned ecosystems. *Am. Nat.* **193**, 472–480 (2019). doi: [10.1086/701669](#); pmid: [30794443](#)
83. R. M. Holdo, R. D. Holt, J. M. Fryxell, Herbivore-vegetation feedbacks can expand the range of savanna persistence: Insights from a simple theoretical model. *Oikos* **122**, 441–453 (2013). doi: [10.1111/j.1600-0706.2012.20735.x](#)
84. J. Sherratt, Numerical continuation methods for studying periodic travelling wave (wavetrain) solutions of partial differential equations. *Appl. Math. Comput.* **218**, 4684–4694 (2012). doi: [10.1016/j.amc.2011.11.005](#)
85. S. Van der Steit, A. Doelman, G. M. Hek, J. Rademacher, Rise and fall of periodic patterns for a generalized Klausmeier–Gray–Scott model. *J. Nonlinear Sci.* **23**, 39–95 (2013). doi: [10.1007/s00332-012-9139-0](#)
86. A. Staal, S. C. Dekker, C. Xu, E. Van Nes, Bistability, spatial interactions and the distribution of tropical forests and savannas. *Ecosystems* **19**, 1080–1091 (2016). doi: [10.1007/s10021-016-0011-1](#)
87. J. C. Aleman, A. C. Staver, Spatial patterns in the global distributions of savanna and forest. *Glob. Ecol. Biogeogr.* **27**, 792–803 (2018). doi: [10.1111/geb.12739](#)
88. D. R. Uden *et al.*, Spatial imaging and screening for regime shifts. *Front. Ecol. Evol.* **7**, 407 (2019). doi: [10.3389/fevo.2019.00407](#)
89. A. C. Staver, G. P. Asner, I. Rodriguez-Iturbe, S. A. Levin, I. P. J. Smit, Spatial patterning among savanna trees in high-resolution, spatially extensive data. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 10681–10685 (2019). doi: [10.1073/pnas.1819391116](#); pmid: [31085650](#)
90. W. Zhang *et al.*, From woody cover to woody canopies: How Sentinel-1 and Sentinel-2 data advance the mapping of woody plants in savannas. *Remote Sens. Environ.* **234**, 111465 (2019). doi: [10.1016/j.rse.2019.111465](#)
91. G. Xanthopoulos, G. Maheras, V. Gourma, M. Gouvás, Is the Keetch–Byram drought index (KBDI) directly related to plant water stress? *For. Ecol. Manage.* **234**, S27 (2006). doi: [10.1016/j.foreco.2006.08.043](#)
92. L. Wang, J. J. Qu, Satellite remote sensing applications for surface soil moisture monitoring: A review. *Front. Earth Sci. China* **3**, 237–247 (2009). doi: [10.1007/s11707-009-0023-7](#)
93. T. Long *et al.*, 30 m Resolution Global Annual Burned Area Mapping Based on Landsat Images and Google Earth Engine. *Remote Sens.* **11**, 489 (2019). doi: [10.3390/rs11050489](#)
94. R. B. Hoyle, *Pattern Formation: An Introduction to Methods* (Cambridge Univ. Press, 2006).
95. A. Doelman, in *Complexity Science*, M. Peletier, R. van Santen, E. Steur, Eds. (World Scientific, 2019), pp. 129–192.
96. R. Bastiaansen, A. Doelman, The dynamics of disappearing pulses in a singularly perturbed reaction-diffusion systems with parameters that vary in time and space. *Physica D* **388**, 45–72 (2019). doi: [10.1016/j.physd.2018.09.003](#)
97. R. Bastiaansen, P. Carter, A. Doelman, Stable planar vegetation stripe patterns on sloped terrain in dryland ecosystems. *Nonlinearity* **32**, 2759–2814 (2019). doi: [10.1088/1361-6544/ab1767](#)
98. O. Jaibi, A. Doelman, M. Chirilus-Brukner, E. Meron, The existence of localized vegetation patterns in a systematically reduced model for dryland vegetation. *Physica D* **412**, 132637 (2020). doi: [10.1016/j.physd.2020.132637](#)
99. M. Scheffer *et al.*, Anticipating critical transitions. *Science* **338**, 344–348 (2012). doi: [10.1126/science.1225244](#); pmid: [23087241](#)
100. J. N. Kutz, S. L. Brunton, B. W. Brunton, J. L. Proctor, *Dynamic Mode Decomposition: Data-Driven Modeling of Complex Systems* (Society for Industrial and Applied Mathematics, 2016).
101. P. Van Heijster, B. Sandstede, Bifurcations to travelling planar spots in a three-component FitzHugh–Nagumo system. *Physica D* **275**, 19–34 (2014). doi: [10.1016/j.physd.2014.02.001](#)
102. B. Wuyts, A. R. Champneys, J. I. House, Correction: Author Correction: Amazonian forest-savanna bistability and human impact. *Nat. Commun.* **9**, 16179 (2018). doi: [10.1038/ncomms16179](#); pmid: [29465082](#)
103. A. Doelman, P. van Heijster, J. Shen, Pulse dynamics in reaction–diffusion equations with strong spatially localized

- impurities. *Phil. Trans. R. Soc. A* **376**, 20170183 (2018). doi: [10.1098/rsta.2017.0183](https://doi.org/10.1098/rsta.2017.0183); pmid: [29507168](https://pubmed.ncbi.nlm.nih.gov/29507168/)
104. L. Eigentler, J. A. Sherratt, Spatial self-organisation enables species coexistence in a model for savanna ecosystems. *J. Theor. Biol.* **487**, 110122 (2020). doi: [10.1016/j.jtbi.2019.110122](https://doi.org/10.1016/j.jtbi.2019.110122); pmid: [31862451](https://pubmed.ncbi.nlm.nih.gov/31862451/)
 105. M. I. Budyko, The effect of solar radiation variations on the climate of the Earth. *Tellus* **21**, 611–619 (1969). doi: [10.3402/tellusa.v21i5.10109](https://doi.org/10.3402/tellusa.v21i5.10109)
 106. W. D. Sellers, A global climatic model based on the energy balance of the earth-atmosphere system. *J. Appl. Meteorol.* **8**, 392–400 (1969). doi: [10.1175/1520-0450\(1969\)008<0392:AGCMBO>2.0.CO;2](https://doi.org/10.1175/1520-0450(1969)008<0392:AGCMBO>2.0.CO;2)
 107. H. Stommel, Thermohaline convection with two stable regimes of flow. *Tellus* **13**, 224–230 (1961). doi: [10.1111/j.2153-3490.1961.tb00079.x](https://doi.org/10.1111/j.2153-3490.1961.tb00079.x)
 108. H. Gildor, E. Tziperman, Physical mechanisms behind biogeochemical glacial-interglacial CO₂ variations. *Geophys. Res. Lett.* **28**, 2421–2424 (2001). doi: [10.1029/2000GL012571](https://doi.org/10.1029/2000GL012571)
 109. H. M. Alkhayoun, P. Ashwin, L. C. Jackson, C. Quinn, R. A. Wood, Basin bifurcation, oscillatory instability and scale-induced thresholds for Atlantic meridional overturning circulation in a global box model. *Proc. R. Soc. A* **475**, 20190051 (2019). doi: [10.1098/rspa.2019.0051](https://doi.org/10.1098/rspa.2019.0051)
 110. P. Valdes, Built for stability. *Nat. Geosci.* **4**, 414–416 (2011). doi: [10.1038/ngeo1200](https://doi.org/10.1038/ngeo1200)

ACKNOWLEDGMENTS

M. te Beest and A. Staal critically reviewed earlier versions of this manuscript. M. Eppinga, J. Rademacher, E. Siero, K. Siteur, and S. van der Stelt contributed to research that led to new insights

leading to this paper. We thank T. Markus for designing figures.

Funding: The research leading to this paper was funded by the Netherlands Organization of Scientific Research, NWO Complexity and NWO Mathematics of Planet Earth programs. This project is TİPES contribution no. 83. This project has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement 820970. **Author contributions:** All authors contributed to the conceptualization and research ideas. M.R., A.D., and R.B. wrote the original draft, and all authors contributed to reviewing and editing the paper. M.R., R.B., S.B., J.v.d.K., and M.B. prepared visual materials. **Competing interests:** The authors declare no competing interests.

[10.1126/science.abj0359](https://doi.org/10.1126/science.abj0359)