Emergence of nonlinear dynamics from spatial structure in tropical forest-grassland landscapes

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It is thought that tropical forests can exist as an alternative stable state to savanna [1, 2]. Therefore, the cumulative effects of perturbation by climate change or human impact may lead to crossing of a tipping point beyond which there is rapid large-scale forest dieback that is not easily reversed [3, 4]. Empirical evidence for bistability due to fire-vegetation feedbacks relies on tree cover bimodality in satellite-observed data [1, 2], but this may also be explained by spatial heterogeneity [5], or by biases in the data [6, 7]. Most modelling studies of alternative stable tree cover states have so far either relied on mean-field assumptions [5, 8–12] or not included the spatiotemporal dynamics of fire [13], making it hard to compare model results to spatial data. In this work, we analyse a microscopic model of tropical forest dynamics and fire spread, proposed by [14], to show how dynamics of forest area emerge from spatial structure. We find that the relation between forest perimeter and area determines the nonlinearity in forest growth while forest perimeter weighted by adjacent grassland area determines the nonlinearity in forest loss. Together with the linear changes, which are independent of spatial structure, these two effects lead to an emergent relation between forest area change and forest area, defining a single-variable ordinary differential equation. Such a relation between pattern and dynamics offers falsifiable theoretical predictions of the bistability hypothesis that are more closely linked to the underlying mechanism than bimodality and provides a criterion for forest vulnerability.

I. INTRODUCTION

Satellite observations of tropical tree cover show that in a wide range of mean annual rainfall [1, 2], both savanna (low tree cover) and forest (high tree cover) are possible, making the distribution of tree cover bimodal. On the one hand, fire exclusion experiments show that fire can maintain low tree cover [15]. On the other hand, fire occurs almost exclusively below a tree cover threshold of about 40% [1, 5, 16–18], which is consistent with fire being a percolation process [19, 20] on grass patches [9, 21]. Such a highly nonlinear response of fire to grass together with an empirically consistent response of vegetation to fire was shown to be sufficient for inducing bistability in simple models [8]. Taken together, the bimodality, the two-way interaction between fire and vegetation, and the availability of a plausible underlying mechanism provide compelling evidence that forest and savanna are alternative stable states, maintained by a feedback between vegetation and fire [1], and between which transitions would neither be gradual nor easily reversed [3, 4]. This local-scale fire-vegetation feedback may exacerbate the effects of the regional-scale feedback between vegetation and rainfall [22].

Nevertheless, subsequent analysis of the same data showed that at least part of the bimodality can be explained by independent spatial heterogeneity of parameters other than mean annual rainfall [5]. Yet another possibility is that the bimodality results from artificial discontinuities in the data, introduced by its generative machine-learning algorithm [6, 7]. Therefore, the fire-mediated alternative stable state hypothesis is still contested, with some left unconvinced and in favour of other causal mechanisms that distinguish between savanna and forest [23]. Taking into consideration the possible alternative explanations for bimodality, further tests of bistability using remote-sensed data would have to rely on more specific indicators than bimodality. For their specificity, they should ideally be closely tied to the assumed underlying mechanism, while for comparability with spatial data, they should relate to space.

Indicators are provided by theoretical models. Despite the fact that tropical vegetation dynamics is a high-dimensional spatial stochastic process, its conceptual analysis has mostly been concerned with models consisting of a small number of ordinary differential equations (ODE) representing macroscale dynamics [e.g. 8, 24, 25], possibly including a noise [10, 26] or impulsive [e.g. 27–29] term. Such an approach is justified under validity of mean-field assumptions: (i) well mixedness, allowing the probability of interaction between two species to be written as the product of their overall occurrence probability, (ii) large system size and validity of the law of large numbers in the deterministic case or an appropriate limit theorem for the noise term in the stochastic case, (iii) spatial homogeneity. E.g., the Staver-Levin model of tropical tree cover bistability [8] is an ODE in which the variables represent the system-scale fractions of area covered by grass, forest trees, savanna trees or savanna saplings. Species interact through competition for space or through the mediating effect of grass cover on fire occurrence. By the well-mixedness assumption, competition terms involve products of these macroscopic cover fractions and fire effects on tree cover are functions of macroscale grass cover multiplied by macroscale tree cover. Taking account of the threshold dependence of fire on grass cover, with fire affecting forest trees, but not the fire-adapted savanna trees, except for their recruitment from saplings, the Staver-Levin model exhibits tree cover bistability but also oscillatory behaviour [8, 10].
Assuming well-mixedness allows a greatly simplified description, but it comes at the expense of disregard for spatial structure. Therefore, mean-field models cannot provide predictions or indicators that relate to spatial structure. Spatial mean-field models of tree cover bistability, such as reaction-diffusion \cite{5,11,12} and integro-partial-differential \cite{13} equations, partially alleviate this problem by allowing for spatial variation on the mesoscale. They show that, due to stationary fronts in heterogeneous environments, bistability does not necessarily lead to bimodality, unless interfacial effects are large \cite{11} or the forest and savanna components are sufficiently decoupled \cite{12}. However, they still rely on mean-field assumptions between the meso- and microscale, thereby still neglecting the effects of microscopic spatial structure. As trees or forest patches are typically highly clustered in space, this neglect of structure by the well-mixedness assumption is usually unjustified.

Contrary to mean-field models, microscopic spatial simulation models, such as interacting particle systems or cellular automata, capture detailed spatial structure, thereby also allowing them to provide indicators that are testable by spatial data. The interacting particle system of Patterson et al. \cite{13} reproduces many of the behaviours of the Staver-Levin model, to which it was proven to converge under mean-field assumptions, but it also shows front solutions, as in the spatial mean-field models, and finite-size effects, such as extinction after a finite simulation time. However, it did not include fire as a percolation process, even though percolation was assumed to play the key role in inducing nonlinearity and bistability \cite{8,9,21,30}. The cellular automaton of Hébert-Dufresne et al. \cite{14}, which can be considered as a simplified version of \cite{31}, captures the joint dynamics of forest cover and fire percolation. In their model, fires spread rapidly and nearly perfectly on grass but can only burn forests at their edge. Besides bistability of forest cover, they also found that isolated forest patches obtain a steady state shape characterised by a perimeter-area power law relation consistent with fits based on remote-sensed observations in 86 protected areas of the Brazilian Cerrado. Stochastic spatial simulation models are, however, far harder to analyse than mean-field models. In particular, simulations only give access to the stable parts of phase space, unless one is prepared to wait prohibitively long.

In this work, we analyse the nonlinear dynamics of the cellular automaton proposed by \cite{14} without relying on mean-field assumptions. Instead, we start from the observation that fire spreads on grass much faster than forest and assume that it spreads perfectly, reaching the entire perimeter of the ignited grass patch, and damaging the forest at this perimeter. This assumption makes two structural quantities relevant for the long-term evolution of the forest-grass landscape: the forest perimeter for gain from forest spread, and, the grassland-weighted forest perimeter, which counts each part of the forest perimeter weighted by the size of its adjacent grass patch, for loss induced by fire. Via simulations, we test how these perimeter quantities affect the dynamics. We are able to explore the unstable parts of phase space by first obtaining unstable solutions from feedback-controlled simulations. This will show that both perimeter quantities are approximate functions of forest area throughout the dynamics, allowing the evolution of forest area to be written as a single-variable ODE. In this equation, the nonlinear terms emerge from competition of forest and grass patches at their perimeter, while the linear terms arise from spatially independent spontaneous conversions.

II. RESULTS

A. The FGBA probabilistic cellular automaton

The FGBA probabilistic cellular automaton (adapted from \cite{14} – see Methods) models the stochastic dynamics of tropical vegetation and fire on a square lattice and in continuous time. The key empirical facts of tropical forest and fire dynamics captured by the FGBA automaton are: (i) fires only naturally ignite in grasslands but they can spread into forest, (ii) fires spread faster in grassland than in forest, such that forests suppress fires, albeit imperfectly, (iii) forest dynamics occurs on a strongly separated time scale from fire spread and grass regrowth.

This results in the following reaction rules in the cellular automaton. At any time, each lattice cell can be in one of four states: $F$ – forest, $G$ – grass, $B$ – burning, $A$ – ash. Conversions between these states can occur spontaneously or due to spread to neighbouring cells (Fig. 1a and Table M1). The spontaneous conversions are: forest recruitment on grass cells due to long-distance seed dispersal ($G \rightarrow F$ at rate $\beta$), forest mortality ($F \rightarrow G$ at rate $\gamma$), fire ignition on grass cells ($G \rightarrow B$ at rate $\phi$), and grass regrowth on ash cells ($A \rightarrow G$ at rate $\lambda$). The conversions due to spread to neighbours are: forest recruitment due to short-distance seed dispersal on grass or ash cells ($GF \rightarrow FF$, $AF \rightarrow FF$ at rate $\alpha$), fire spread on grass ($GB \rightarrow BB$ at rate $\rho_f$) or on tree cells ($FB \rightarrow BB$ at rate $\rho_f$). Chosen parameters are in the ranges empirically justified by \cite{14} for a square domain of 100x100 cells, with cell size $\Delta x = \Delta y = 30$m. The time scale separation between fire and forest dynamics implies that the rates satisfy $\rho_g, \rho_f, \mu, \lambda \gg \alpha, \beta, \gamma$. In particular, we choose

\begin{align}
\rho_g, \mu \sim 10^6 > \rho_f \sim 10^5 \gg 1y^{-1}, \\
\alpha, \beta, \gamma \sim 10^{[4, -2]} \ll \lambda \sim 1y^{-1}.
\end{align}

So, fire spreading and extinction $\rho_g, \rho_f, \mu$ occurs on the scale of hours, while grass regrows on ash over months ($\lambda$) and forest spread, growth and mortality $\alpha, \beta, \gamma$ occurs over decades. We take fire ignition rate $\phi \sim 1/N$ such that fires spontaneously occur about once per year in the modelled area. Figure 1b–d shows a typical time profile
Figure 1. The FGBA stochastic cellular automaton: (a) state transition diagram (coloured rates: spread to neighbouring cell, black rates: spontaneous conversion within cell), (b) example time series of a simulation starting at zero tree cover, (c,d) 10x and 10^5x zoom of (b), (e-h) snapshots of a simulation at indicated times for low fire ignition rate ($\phi N = 0.075$). The fire in (f) spreads throughout grassland in the whole domain whereas that in (g) went extinct locally because forest splits grassland in clusters (notice the area of ash near the top). Remaining parameters are shown in Table M1. Domain size: 200x200 cells.

Figure 2a shows a bifurcation diagram of steady state forest cover in the FGBA cellular automaton, denoted by $[F]$ (see Eq. M1), versus fire ignition rate $\phi$. Unstable steady states (saddles) were obtained by applying feedback control to the simulations (see Methods). Bistability occurs above a critical ignition rate $\phi$. Simulations initiated at the saddle will tip up or down depending on initial stochasticity (Fig. 2b). Near the lower end of the bistability range, the saddle solution is fairly homogeneous, but for higher $\phi$ values, a single hole of grass in forest arises (insets in Fig. 2a).

B. Fast and slow subprocesses

The time scale separation (Eqs. 1 and 2) permits treatment of the joint vegetation and fire dynamics as a fast-slow system. Fire spread occurs on the fast time scale, where the vegetation landscape is treated as constant. Forest dynamics occurs on the slow time scale, where the effects of fire are a steady state function of the vegetation landscape.

a. Fast process: fires spreading in a given landscape

On the time scale of a single fire event, forest dynamics are negligible ($\alpha, \beta, \gamma \ll 1/\text{day}$) such that we can consider the total landscape of forest patches as fixed. For each ignition event, this results in the following dynamics. A fire ignites on a grass cell, then spreads across its grassland cluster at a rate $\rho_g$ per BG link, after which it reaches the interface with adjacent forest, where it starts spreading.
intruding the forest at a rate \(\rho_f\) per BT link. At any time, burning cells can spontaneously extinguish, converting to ash at a rate \(\mu\). The probabilities of fire spreading into a neighbouring grass or forest cell before the originating cell extinguishes are given by

\[
p_g := \frac{\rho_g}{\rho_g + \mu} = 0.9, \quad p_f := \frac{\rho_f}{\rho_f + \mu} = 0.1, \quad (3)
\]

where we have shown the chosen values in our simulations (adopted from [14]). Since new fires arise and grass regrows only with much lower rates than the fire spreading rate (\(\phi N \lesssim \lambda \ll \rho_f, \mu, \rho_g\), we observe repeated fire waves well separated in time (Fig. 1b).

When a fire in grassland cluster with index \(j\) reaches its interface with adjacent forest, the resulting forest loss due to this single fire event can be approximated as a fraction \(p_f\) of the forest cells at this interface. This leads to the approximate loss of forest per fire event

\[
\Delta_{F,j}^{\text{loss}} = p_f |FG|_j, \quad (4)
\]

where \([FG]_j\) counts the number of forest cells adjacent to grassland cluster \(j\) (with both sides of the equation optionally normalised by \(N\)). This approximation relies on the assumptions that the fire reaches the whole interface with forest (i.e. \(p_g \to 1\)) and only once per fire (i.e. \(\rho_g \gg \lambda \gg \phi N\)), and that burning forest does not pass on fires further to adjacent forest (i.e. \(p_f\) small).

b. **Slow processes: forest demography and fire damage**

Forest demography and loss due to repeated fires occur on the slow time scale. Writing the number of neighbour pairs with \(FG\) as \([FG]\) (divided by \(N\), equivalently the domain perimeter of forest or grass patches, see Eq. M1), the dynamics for tree recruitment and mortality result in an expected rate of change for \([F]\)

\[
\Delta_F^{\text{gain}} := \beta[G] - \gamma[F] + \alpha[FG]. \quad (5)
\]

In Eq. 5, the rates of change are \(\beta[G]\) for spontaneous forest growth on grass, \(\gamma[F]\) for forest mortality, and \(\alpha[FG]\) for spread of forest into grass at its perimeter.

The rate of forest erosion at its perimeter due to fire damage over many fire events is the weighted sum over all grass clusters \(j = 1, \ldots, n_c\), i.e.

\[
\Delta_F^{\text{loss}} := \sum_{j=1}^{n_c} \phi N[G]_j \Delta_{F,j}^{\text{loss}} = \phi N \rho_f \sum_{j=1}^{n_c} [G]_j [FG]_j, \quad (6)
\]

where \([G]_j\) is the fraction of \(G\) cells in grass cluster \(j\) (so, \([G] = \sum_{j=1}^{n_c} [G]_j\), \(\phi N[G]_j\) is the rate at which fires spontaneously ignite in grass cluster \(j\) (\(\phi\) is the rate per cell and \(N[G]_j\) is the area of the cluster), and \(\Delta_{F,j}^{\text{loss}} = p_f |FG|_j\) is the conversion of forest to ash caused by each fire event (see Eq. 4) (note also that \([FG] = \sum_{j=1}^{n_c} [FG]_j\)).

By defining the **grassland-weighted forest perimeter** as

\[
([FG])_{cg} := \sum_{j=1}^{n_c} \frac{[G]_j [FG]_j}{[G]_j}, \quad (7)
\]

Eq. 6 becomes

\[
\Delta_F^{\text{loss}} := \phi \rho_f N[G]([FG])_{cg}. \quad (8)
\]

The grassland-weighted forest perimeter \(([FG])_{cg}\) is the average perimeter of forest clusters weighted by the relative size of their adjacent grass cluster.

C. **Emergent slow dynamics**

We now form the balance between the slow processes discussed above, assuming fire converts trees immediately to grass (i.e. \(\lambda \gg \phi N\)). The resulting expected rate of
forest cover change during a short time interval is
\[
\frac{d[F]}{dt} = \Delta_F^{\text{gain}} - \Delta_F^{\text{loss}},
\]

where we used Eqs. 5 and 8, and assumed on the left-hand side that \( N \) is sufficiently large, such that, via the law of large numbers, \( \langle d[F]/dt \rangle \approx \langle d[F]/dt \rangle. \) Equation 9 can be understood intuitively as forest and grass competing for space within patches (spontaneous terms) and at their interface (interaction terms). A larger interface \( [FG] \) leads simultaneously to faster forest spread (proportional to its perimeter \( [FG] \)), and to increased exposure to fires (proportional to its grassland-weighted perimeter \( \langle [FG] \rangle_{cg} \)).

Fires are most damaging to forest when \( [G] \) forms a single cluster, i.e., \( \langle [FG] \rangle_{cg} = [FG] \), such that each fire reaches the whole interface. Conversely, when forest patches break \( [G] \) into several clusters \( \langle [FG] \rangle_{cg} \) is smaller than \([FG] \), such that several ignitions are required to have the same effect, slowing forest erosion down. Additionally, the total amount of grass \( N[G] \) determines the number of ignitions and hence the rate at which grass spreads into forest. The parameters determine the relative weight of each of the discussed effects.

Figure 3 shows example simulations along trajectories starting from the saddle equilibria of Fig. 2, showing forest area \( [F] \) in space and time (a–d), the gain/loss terms \( \Delta_F^{\text{gain}} \) and \( \Delta_F^{\text{loss}} \) defined in Eqs. 5 and 8 (e–f), and the right-hand side of Eq. 9 (gain minus loss, g–h). The left column of Fig. 3 shows simulations for low fire ignition rate \( \phi \) and low \( [F](0) \), and the right column for high \( \phi \) and high \( [F](0) \). Each column shows two realisations, both starting from the same saddle steady state. One realisation evolves toward high forest cover, shown on axis \( t^+ \) (increasing to the left from \( t = 0 \), the other realisation evolves toward low forest cover, shown on axis \( t^- \) (increasing to the right from \( t = 0 \)). In the stable steady states, gain (green) and loss (red) terms vary around the same mean. On the saddle (at time 0) gain and loss functions cross. This shows that the steady states and changes are accurately captured by Eq. 9. The largest changes in forest cover \( [F] \) occur when there are large changes in forest loss due to fire. The snapshots in Fig. 3a,b show that the high-cover state changes as an expanding/contracting hole in the forest, whereas the low-cover state is more homogeneous.

**D. Emergent nonlinear relations**

Equation 9 explains how the rate of change of \( [F] \) depends on the perimeter quantities \( [FG] \) and \( \langle [FG] \rangle_{cg} \). Figure 4a–c shows a scatterplot of \( [FG](t) \) and \( \langle [FG] \rangle_{cg}(t) \) versus \( [F](t) \) for three different values of \( \phi \), and for an ensemble of simulations starting from the saddle in Fig. 2a, with each point being a value observed at a discrete observation time. Remarkably, we observe that \( [FG] \) and \( \langle [FG] \rangle_{cg} \) lie on a narrow band around some steady state functions \( [FG]^* \) and \( \langle [FG] \rangle_{cg}^* \) of \( [F] \) (and \( \phi \)), which implies that \( [FG]_t, \langle [FG] \rangle_{cg}_t \) are changing on a much faster time scale, making them slaved to \( [F] \). Figure 4d–f shows the terms on the right-hand side of Eq. 9 depending on \( [F] \), splitting between gain and loss terms \( \Delta_F^{\text{gain}}, \Delta_F^{\text{loss}} \), as defined in Eqs. 5 and 8. Steady states occur when gain equals loss (\( \Delta_F^{\text{gain}} = \Delta_F^{\text{loss}} \)). The resulting graph of \( d[F]/dt \) versus \( [F] \) in Fig. 4g–i clearly shows the bistability of \( [F] \).

Replacing the quantities \( [FG] \) and \( \langle [FG] \rangle_{cg} \) by their steady-state functions \( [FG]^* \) and \( \langle [FG] \rangle_{cg}^* \) results in the single-variable ODE for \( [F] \),
\[
\frac{d[F]}{dt} = \beta[G] - \gamma[F] + \alpha[FG]^* - \phi p_f N[G][\langle [FG] \rangle_{cg}^*],
\]

where \( [FG]^*, \langle [FG] \rangle_{cg}^* \) are functions of \( [F] \) and \( \phi \) (as shown in Fig. 4a–c), and \( [G] = 1 - [F] \). With these functions \( [FG]^* \) and \( \langle [FG] \rangle_{cg}^* \), the observed bistability is caused by a classic scalar double-well potential of the gradient system Eq. 10. In this ODE, nonlinearities emerge due to the equilibrium dependence of the interface on forest area (affecting \( [FG]^* \) and \( \langle [FG] \rangle_{cg}^* \) due to the segmentation of grass cells near and below the percolation threshold (affecting \( \langle [FG] \rangle_{cg} \)) and due to dependence of the ignition rate on grass patch size (multiplying \( \langle [FG] \rangle_{cg} \)).

![Figure 4. Emergent relations between key quantities and forest area [F]: (a–c) forest perimeter [FG] and grassland-weighted forest perimeter \( \langle [FG] \rangle_{cg}, \) (d–f) forest gain terms and loss terms in Eqs. 5 and 6, (g–i) forest area rate of change \( \langle [FG] \rangle_{cg} \) from Eq. 9. Columns correspond to vertical dashed lines in Fig. 2 (\( \phi N = 0.257, \phi N = 0.38, \phi N = 1.32 \)). Domain size: 100x100 cells.](image)
with $[G]$). In Fig. S3, we show the roots of Eq. 10 using a nonparametric fit of $[FG]^*[([F];\phi)]$ and $([FG])^*_{cg}([F];\phi)$. These match well with the steady states obtained via control (dot-dashed red).

If there is only one connected component of grass cells, we have $([FG])_{cg} = [FG]$, such that Eq. 10 simplifies to

$$\frac{d[F]}{dt} = \beta[G] - \gamma[F] + (\alpha - \phi p f N[G])[FG]^*. \quad (11)$$

For homogeneous initial conditions (i.e. $[F]$ is about the same in different large subsections of the domain), this approximation is expected to be valid for small $[F]$, where most grass cells belong to the giant component. Figure S3 shows the resulting steady states of Eq. 11 as a function of $\phi$ and $[F]$ when only using the fit of $[FG]^*[([F];\phi)]$ (dashed blue). The approximation is good for landscapes with low forest cover ($[F] \leq 0.2$). Above $[F] \approx 0.2$, it fails because the grassland breaks up into multiple clusters and fires are smaller than in case of a single cluster. Figure 4a–c already indicated that the single-cluster approximation is accurate for low forest cover since $([FG])_{cg} \approx [FG]$ for low $[F]$ in the scatterplots.

### III. DISCUSSION

Using as high-dimensional reference model a continuous-time stochastic cellular automaton, adapted from ref. [14], that includes reaction rules for both forest dynamics and fire percolation, we have shown how low-dimensional nonlinear dynamics of tropical forest emerge from the spatial configuration of forest patches. Taking the assumption on the fast time scale that fire spreads perfectly on grass, reaching the whole perimeter of adjacent forest, makes two macroscopic structural quantities relevant for the evolution of forest area on the slow time scale (Eq. 9): the forest perimeter $[FG]$ for gain from forest spread, and, the grassland-weighted forest perimeter $([FG])_{cg}$ for loss induced by fire. Simulations initiated at the unstable steady states allowed us to explore the whole phase space and revealed that these quantities are evolving on a much faster time scale than forest area, such that on the slow time scale and for given parameters, they are equilibrium functions of forest area. Hence, replacing the perimeter quantities with their steady state functions of forest area reduces the evolution of forest area on the slow time scale to a one-variable ODE, Eq. 10. In this emergent relation between forest change and forest area, nonlinear terms arise due to spatially structured interactions at the forest-grass interface whereas linear terms arise from spontaneous transitions, which are independent of spatial structure.

In the rest of our discussion, we will compare our result to what is obtainable by mean-field models, illustrate the role of finite-size effects in bistability, and consider the implications for empirical tests.

#### a. Inadequacy of mean-field models

Mean-field models fail to capture the role played by forest perimeter and grassland clusters because they neglect spatial structure (by the well-mixedness assumption, point (i) in the introduction). The mean-field approximation for the FGBA process is given in Section S1 (Supporting Information). Mean-field model Eq. S3 assumes absence of pairwise correlations, which permits substitutions such as $[FG] = 4[F][G]$ in Eq. S2 and closure of the system of equations. Such a substitution of counts of larger units by an algebraic expression in terms of counts of smaller units in order to close a system of equations is known as a closure formula [32]. Neglect of structure leads to a well-known bias in the location of steady states compared to the simulations [e.g. 33]. This may be mitigated by mean-field models of higher order, which consider units of larger size than single cells, but for dynamics on the square lattice in regimes with long-range dependence (such as induced by fire or forest spreading) this would require an impractically large number of equations [32], defeating its purpose of low-dimensional approximation.

By exploiting time scale separation of fire and forest dynamics, we arrived at Eq. 10, which respects the spatially structured nature of the dynamics, in contrast to mean-field approximations. In our description, the steady state functions $[FG]^*$ and $([FG])^*_{cg}$ of $[F]$ are closure formulas to obtain Eq. 10 from Eq. 9. Here the closure is observed emerging in simulations instead of derived from an a priori imposed assumption of statistical independence (see also [34]). Closure at low dimension is feasible due to time-scale separation between forest perimeter quantities and forest area.

#### b. Finite sizes and bistability

In simple bistable chemical systems, it is known that bistability converges to an abrupt phase transition in the thermodynamic limit ($N \to \infty$) [35, 36], at a value known as the Maxwell point [e.g. 37], making the macroscopic state of the system deterministically dependent on the parameters (e.g. pressure or temperature). With only forest and grass or provided that savanna and forest components are sufficiently decoupled, the same behaviour occurs in spatial mean-field models of tropical forest, with a front between forest and nonforest that is deterministically dependent on environmental drivers [12]. We do not expect such determinism as $N \to \infty$ to arise in the FGBA cellular automaton. The infinite FGBA cellular automaton possesses grass clusters of arbitrary size, such that, even when assuming that fire spreads instantly on grass, there will always be some parts of the forest perimeter shielded from intruding fires by adjacent ash cells. Were it not for this shielding effect, then there would be a deterministic dependence of the dynamics on fire ignition rate away from the absorbing states: $\phi > 0$ would lead to forest spread while $\phi < 0$ would lead to forest extinction (see Section S2, for the case $\beta = \gamma = 0$). In reality, finite fire spreading rates and, in particular, the effects of heterogeneity in time (e.g. the influence of weather
on spreading rates) or space impose stronger limits on the reach of fires. Hence, while, due to the large size of a typical system of molecules, the thermodynamic limit is usually of practical relevance in context of materials, in case of ecosystems, finite sizes and their effects are the norm. In finite domains, both the FGBA system and scalar reaction-diffusion equations show bistability due to critical patch sizes and dependence on interfacial characteristics [e.g. 11, 38], but this correspondence requires further scrutiny. In realistic scenarios, the amount of bistability then depends (besides the parameters) on a ‘characteristic system size’, which in turn depends on e.g. fire spreading and/or plant dispersal ranges. How this is affected by environmental heterogeneity is subject of future work.

c. Implications for empirical tests By taking the simplest possible model that was able to include fire percolation and forest spread, we were able to obtain structural indicators of bistable forests prone to fire percolation effects. These indicators are theoretical predictions additional to bimodality that can be tested against spatial data. We emphasise here that the perimeter quantities $[FG]$ and $\langle FG \rangle_{cg}$ do not have to be in equilibrium for Eq. 9 to be valid, such that it can also be tested in places where human impact keeps them away from their natural equilibrium. Furthermore, they are in principle easy to determine from observations. In the original treatment of the FGBA cellular automaton [14], a climate-dependent equilibrium perimeter-area relation for isolated forest patches in low-cover simulations was found to be consistent with data of protected areas in the Brazilian Cerrado. The perimeter-area relation at the patch level for given parameters determines the perimeter-area relation at domain level $[FG]^*$ versus $[F]$. Therefore, we expect this consistency with data to hold at the domain level, at least for low cover areas. Inclusion of additional realism, such as environmental heterogeneity, larger neighbourhoods, non-lattice geometry, presence and dynamics of other tree types and life stages, will lead to modified perimeter quantities, but these can be derived and tested in a similar manner. We hope that the additional opportunities that our theoretical predictions offer for falsification lead to a faster rate of progress in the field. If this progress leads to theory with sufficient reliability and validity, it may eventually function as a tool for conservation of existing or restoration of lost tropical forests.

### IV. METHODS

a. Details of the FGBA probabilistic cellular automaton The FGBA probabilistic cellular automaton is a minimal spatial stochastic process that models the joint dynamics of tropical vegetation and fire. It is an adapted version of the BGT(A) model of ref. [14]. The modifications compared to ref. [14] are: (i) it runs in continuous time, (ii) it includes a spontaneous forest mortality rate $\gamma$, (iii) it optionally includes rainfall feedback (for Fig. S1) (iv) species $T$ is labelled as $F$, consistent with other models of tropical vegetation dynamics [8, 12, 13]. Note that according to some definitions, probabilistic continuous-time cellular automata are considered as interacting particle systems. In general, when studying the stochastic dynamics of a number $n$ of interacting species on a square lattice with $N$ cells, the state of the system can be represented as

$$X := (X_1, X_2, ..., X_N),$$

where $X_i$ is the label of the species that occupies cell $i$. Each cell is occupied by exactly one of four possible species: grass, forest, burning and ash, with labels $G$, $F$, $B$ and $A$. Transitions between states (species) occur in continuous time, resulting in a continuous-time Markov chain with $n^N$ possible states. The reaction rules for transitions between states are shown in Table M1, where spontaneous conversions are shown on the left and conversions due to nearest-neighbour interactions on the right (see also Fig. 1a for the state transition diagram). The latter type of interaction occurs over each four nearest-neighbour connections of the indicated type. E.g., fire will spread into a given grass cell with a rate $\rho_F$ for each burning neighbour. For realistic time scales, our parameters satisfy Eqs. 1 and 2, which were empirically justified in [14]. This results in separated time scales for forest spread (slow) and fire spread (fast). We borrow our notation from the moment closure literature [e.g. 32, 33, 39], writing the global fraction of species with label $x$ and the interface between species with label $x$ with label $y$ respectively as

$$[x] := \frac{1}{N} \sum_{i=1}^{N} \delta_{x}(X_i), \quad [xy] := \frac{1}{N} \sum_{i,j=1}^{N} A_{ij} \delta_{x}(X_i) \delta_{y}(X_j),$$

(M1)

where both are normalised by $N$, $\delta$ is the Kronecker delta function ($\delta_{x}(y)=1$ if $x=y$ and 0 otherwise) and $A \in \{0,1\}^{N \times N}$ the adjacency matrix. We simulated the cellular automaton via a Gillespie algorithm [40] and used a domain of $N=100 \times 100$ ($N=200 \times 200$ in Fig. 1) cells with periodic boundary conditions.

b. Noninvasive feedback control To study steady states regardless of their stability in a simulation, we apply noninvasive feedback control, similar to what was

| Spontaneous | Spread |
|-------------|--------|
| $G \xrightarrow{\beta} F$, $\beta = 2 \cdot 10^{-4}$ | $GF \xrightarrow{\alpha} FF$, $\alpha = 3 \cdot 10^{-2}$ |
| $F \xrightarrow{\gamma} G$, $\gamma = 2 \cdot 10^{-2}$ | $AF \xrightarrow{\alpha} FF$, $\alpha = 3 \cdot 10^{-2}$ |
| $G \xrightarrow{\phi} B$, $\phi = [0, 2] \cdot 10^{-4}$ | $GB \xrightarrow{\rho_g} BB$, $\rho_g = 9 \cdot 10^4$ |
| $B \xrightarrow{\mu} A$, $\mu = 10^6$ | $FB \xrightarrow{\rho_f} BB$, $\rho_f = 1.11 \cdot 10^6$ |
| $A \xrightarrow{\lambda} G$, $\lambda = 5$ |   |
rate is the spontaneous conversion rate $\phi$ of the stochastic lattice model. We can use them to plot a 1-parameter bifurcation diagram by coupling it to the species occurrence fraction model. The artificial feedback makes this rate time dependent and introduce an artificial stabilizing feedback loop.

In Eq. M2, $r$ is one of the conversion rates of the lattice model. The artificial feedback makes this rate time dependent by coupling it to the species occurrence fraction $[x](t)$ through the relation (M2). The factor $g$ is called the feedback control gain and is problem specific. The property of noninvasiveness means that the controlled simulations have the same equilibria as regular simulations [45–47]. This implies that if one extracts the equilibrium values of the controlled simulation tips up or down depending on initial perturbations, (c) snapshot of the domain at the saddle for the control indicated in (a) (black: forest, white: grass). Other parameter values are shown in Table M1.

Figure M1 shows an example for which the controlled simulation is in equilibrium (steady part of the blue curve in Fig. M1b), the steady state values of $[x]$ for $x \in \{F, G, B, A\}$ are obtained via taking the time average, i.e.

$$\overline{[x]} = \frac{1}{T} \int_{t_0}^{t_0+T} [x](t)dt,$$

where $t_0$ is the time after which the dynamics have settled to a steady state and $T$ the averaging time. If $n_{G \rightarrow B}$ is the number of ignition events between $t = t_0$ and $t = t_0 + T$, the steady state of $r$ is obtained by calculating the mean ignition rate as $n_{G \rightarrow B}/T$ and dividing this by the mean number of grass cells, such that

$$\overline{\phi} = \frac{n_{G \rightarrow B}/T}{\overline{G}}.$$  

where $\overline{G}$ is obtained as in Eq. M3. When repeating this exercise for many $[F]_{\text{ref}}$ values (with for each an appropriately chosen gain $g$), one can get multiple points on the unstable branch. Points on the stable branches can be obtained with regular simulations. On the final selection of points, we applied Gaussian process regression to obtain smooth curves and used moving block bootstrapping [48] to obtain confidence intervals. One of the advantages of applying control is that one can obtain states for which one would have to wait prohibitively long in a regular simulation due to their instability. The inset in Fig. M1b shows for instance a snapshot of the unstable steady state obtained with the control indicated in Fig. M1a.

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S1. MEAN-FIELD EQUATIONS OF THE FGBA PROCESS ON THE SQUARE LATTICE

Here we show how to obtain the mean-field equations. Note that ref. [14] already analysed the dynamics of the mean-field model (Eq. S3) with \( \gamma = k = 0 \). Writing \( x_i \) as shorthand for \( \delta_x(X_i) \) (equalling 1 if \( X_i = x \) and 0 otherwise) and taking expectations in each cell \( i \), we obtain equations for the rate of change of the expectation that cell \( i \) is occupied by species \( x \in \{ G, F, B, A \} \),

\[
\begin{align*}
\frac{d}{dt} \langle G_i \rangle &= \lambda \langle A_i \rangle - \langle G_i \rangle \left[ \beta + \phi + \sum_{j \in N(i)} (\rho_y B_j + \alpha F_j) \right] + \gamma \langle F_i \rangle, \\
\frac{d}{dt} \langle F_i \rangle &= \beta \langle G_i \rangle + \alpha \langle (A_i + G_i) \sum_{j \in N(i)} F_j \rangle - \rho_f \langle F_i \sum_{j \in N(i)} B_j \rangle - \gamma \langle F_i \rangle, \\
\frac{d}{dt} \langle B_i \rangle &= \phi \langle G_i \rangle - \mu \langle B_i \rangle + \langle (\rho_f F_i + \rho_y G_i) \sum_{j \in N(i)} B_j \rangle, \\
\frac{d}{dt} \langle A_i \rangle &= -\frac{d}{dt} \langle G_i \rangle - \frac{d}{dt} \langle F_i \rangle - \frac{d}{dt} \langle B_i \rangle = \mu \langle B_i \rangle - \lambda \langle A_i \rangle - \alpha \langle A_i \sum_{j \in N(i)} F_j \rangle.
\end{align*}
\] (S1)

One may think of \( \langle \cdot \rangle \) as ensemble averages here. This set of equations can be derived rigorously from the master equation [e.g. 49]. Summing over \( i \), dividing by \( N \) and using Eq. M1, we obtain equations for total frequencies of all four species in the domain (relative to \( N \)):

\[
\begin{align*}
\frac{d}{dt} \langle [G] \rangle &= \lambda \langle [A] \rangle - (\beta + \phi) \langle [G] \rangle - \rho_y \langle [GB] \rangle - \alpha \langle [FG] \rangle + \gamma \langle [F] \rangle, \\
\frac{d}{dt} \langle [F] \rangle &= \beta \langle [G] \rangle + \alpha \langle [FA] \rangle + \alpha \langle [FG] \rangle - \rho_f \langle [FB] \rangle - \gamma \langle [F] \rangle, \\
\frac{d}{dt} \langle [B] \rangle &= \phi \langle [G] \rangle - \mu \langle [B] \rangle + \rho_f \langle [FB] \rangle + \rho_y \langle [GB] \rangle, \\
\frac{d}{dt} \langle [A] \rangle &= \mu \langle [B] \rangle - \lambda \langle [A] \rangle - \alpha \langle [FA] \rangle,
\end{align*}
\] (S2)

where \( [xy] \) is the total number of neighbouring \( xy \) pairs divided by \( N \), which will later be referred to as the \( xy \) interface or \( xy \) perimeter. Equation S2 is not a closed system. To close the system, we need to determine all undetermined terms \( [xy] \) on the right-hand side without creating new unknowns. The simplest way to do this is to assume absence of pairwise correlations, i.e. \( \langle [xy] \rangle = 4 \langle [x] \rangle \langle [y] \rangle \). We take the additional assumption of \( N \to \infty \), such that the law of large numbers applies and \( [x] \to \langle [x] \rangle \). Taking these assumptions leads to the simple mean-field approximation of the cellular automaton model:

\[
\begin{align*}
\frac{d}{dt} [G] &= \lambda [A] - (\beta + \phi)[G] - 4\rho_y [G][B] - 4\alpha [F][G] + \gamma [F], \\
\frac{d}{dt} [F] &= \beta [G] + 4\alpha [F][A] + 4\alpha [F][G] - 4\rho_f [F][B] - \gamma [F], \\
\frac{d}{dt} [B] &= \phi [G] - \mu [B] + 4\rho_f [F][B] + 4\rho_y [G][B], \\
\frac{d}{dt} [A] &= \mu [B] - \lambda [A] - 4\alpha [F][A],
\end{align*}
\] (S3)

In the main text we focus exclusively on the fire-vegetation feedback due to percolation effects but here we also test the effect of a rainfall feedback that works globally, by taking a linear dependence of forest spreading rate on total forest area, i.e.

\[
\alpha([F]) = \alpha_0 + k[F].
\] (S4)

The mean field assumes spatial homogeneity, well-mixedness and large system size. These assumptions are valid when the dynamics occur on a large complete graph and interactions occur at contact rates of order \( 1/N \).
FIG. S1. FGBA process (Table M1 for simulations and Eq. S3 for mean field): (a) mean-field steady states of forest cover $[F]$ as a function of fire ignition rate $\phi$ and rainfall feedback strength $k$ (blue: steady state manifold, green: contours at fixed $k$ values, red: saddle-node bifurcations), (b) steady states of $[F]$ in the simulations versus $\phi$ (see legend for parameter values, shading: two-standard deviation confidence interval of the mean). The curves in (b) were obtained via a Gaussian process regression on the output of a finite number of simulations (regular for the stable and controlled for the unstable branches).

The FGBA cellular automaton exhibits bistability of tree cover (first shown by ref. [14]) in ranges of all parameters that are expected to show considerable spatial heterogeneity in a given ecosystem: $\alpha, \beta, \gamma, \phi$. The bistability range is widened by the rainfall feedback, as shown in Fig. S1b (red versus blue curve). Yet, for the mean-field model at low rainfall feedback gain $k$, bistability can also be decreased (Fig. S1a). Hence, the effect may not be monotonic. That bistability of tree cover occurs even without rainfall feedback shows that both fire and rainfall feedbacks can cause it independently. Note that the mean field shows significant bias.

S2. EVOLUTION OF FRONTS — HETEROGENEOUS STATES

Here, we illustrate the case where grass and forest are initially separated into two contiguous areas with their interface extending along a straight line. Because for this type of initial conditions the single-cluster approximation (Eq. 11) is valid, we can focus on the evolution of the interface. As spontaneous conversion between forest and grass (with rates $\beta$ and $\gamma$) increases mixing and promotes homogeneity at large scale, we expect the effects of heterogeneous initial conditions to be most persistent when the spontaneous conversion rates $\beta$ and $\gamma$ are small. Therefore, we will set $\beta = \gamma = 0$, for which Eq. 9 becomes

$$\frac{d[F]}{dt} = (\alpha - \phi p_f N[G])[FG].$$

(S5)

Hence, the precise shape of the interface $[FG]$ does not affect the location of the steady states, only the rate at which they are approached or receded from. The trivial steady states of Eq. S5 (for $[FG] = 0$) are $[F] = 0$ and $[F] = 1$, which are stable, and between them, there is the (unstable) saddle

$$[F]^* = 1 - \frac{\alpha}{\phi N p_f}.$$  

(S6)

As seen in Fig. S4, this analytical prediction (solid black) matches the controlled simulations with $p_g = 0.9999$ (shaded blue). For $p_g = 0.9$ (shaded red), which we used before, there is a small bias. In the limit of $N \to \infty$, Eq. S6 converges to $[F]^*_\infty = 1$, implying that in an infinite domain, any positive fire rate leads to extinction of forest below $[F]^* = 1$. When ignoring the effect of ash, this would also occur for heterogeneous initial conditions. That is, considering an infinite domain with many grass clusters of which the size is a random variable (with support $[0, \infty)$), there will be initial grass clusters of arbitrarily large size, which will expand and eventually drive forest extinct. However, such determinism does not occur in the simulations because at high fire rates, patches with ash start to block fires, and
the rate of exposure of the forest interface to fire becomes limited by the rate at which ash is converted back into grass. As a first correction for this, one can multiply $p_f$ with the average proportion of grass sites that are in the ash state after the expected waiting time between fires $1 - \exp(-\lambda/\phi N)$, such that $[F]_\infty^* = 1 - \alpha/\lambda p_f$. Keeping in mind that we are focusing on heterogeneous states, the analysis here implies that for $\gamma = \beta = 0$, there is a critical patch size above which the forest patch expands and below which it contracts. The intuition is that above the critical forest patch size, there is not enough grass area to reach the minimum number of ignitions required to erode the forest.

In Fig. S2, we show how the dynamics and steady states arise from $[FG]$, as we did in Fig. 3 and Fig. 4, but now starting with separated patches of grass and forest that interface on a line on both sides (showing for $[F](0) = 0.57$). From $[FG](0) = 2L/N = 2N^{-1/2} = 0.02$, the interface quickly gains roughness due to the dynamics, until it reaches a steady state of $[FG]^* \approx 6L/N = 6N^{-1/2} = 0.06$ (see Fig. S2a–c), which appears independent of $\phi$ (not shown). Figure S2b confirms that $\langle [FG] \rangle_{cg} \approx [FG]$ (except when forest cover approaches $[F] = 0$ or $[F] = 1$), confirming that the single-cluster approximation is valid. Away from $[F] = 0$ and $[F] = 1$, $[FG]$ stays about constant as the forest interface moves (Fig. S2b–c). Therefore the gain and loss terms (as defined in Eqs. 5 and 8) are now, respectively, constant and linearly decreasing with $[F]$ (Fig. S2e), such that $d[F]/dt$ increases linearly with $[F]$ (Fig. S2g), except near $[F] = 0$ and $[F] = 1$, where it connects to 0, as here $[FG] = 0$.
S3. SUPPLEMENTARY FIGURES

FIG. S3. Steady states of Eq. 10 (multicluster – dot-dashed red) and of Eq. 11 (single cluster – dashed blue) compared to controlled simulations (solid black with shading indicating two-standard deviation confidence interval of the mean). Parameters in the cellular automaton: $\gamma=0.02, \alpha=0.03, \beta=2 \cdot 10^{-4}, \rho_g=9 \cdot 10^6, \rho_f=1.11 \cdot 10^5, \mu=10^6, \lambda=5$.

FIG. S4. Saddle of Eq. S5 via Eq. S6 (single cluster – solid black) compared to controlled simulations (shaded red: $p_0 = \rho_g / (\rho_g + \mu) = 0.9$, shaded blue: $p_0 = 0.9999$) in case of heterogeneous initial conditions and without spontaneous interactions ($\beta=\gamma=0$). Other parameters: $\alpha=0.03, \rho_f=1.11 \cdot 10^5, \mu=10^6, \lambda=5$. 