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Integrating Theoretical Climate and Fire Effects on Savanna and Forest Systems

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ABSTRACT: The role of fire and climate in determining savanna and forest distributions requires comprehensive theoretical reevaluation. Empirical studies show that climate constrains maximum tree cover and that fire feedbacks can reduce tree cover substantially, but neither the stability nor the dynamics of these systems are well understood. A theoretical integration of rainfall effects with fire processes in particular is lacking. We use simple, well-supported assumptions about the percolation dynamics of fire spread and the demographic effects of climate and fire on trees to build a dynamic model examining the stability of tree cover in savannas and forests. Fire results in the potential for one or possibly two stable equilibria, while the effects of increasing rainfall on tree demography result in (discontinuous) increases in tree cover and in forest tree dominance. As rainfall increases, the system moves from (1) stable low tree cover to (2) bistability of low and high tree cover to (3) stable high tree cover. Thus, theory suggests that tree cover uniquely determined by climate at low and high rainfall but determined by fire feedbacks at intermediate rainfall—as empirical studies suggest—may be a universal feature of systems where fire has strong effects on tree demography.

Keywords: savanna, forest, climate, fire, alternative stable states.

Introduction

Both rainfall and fire are strong predictors of the global distribution of the savanna biome (Bond et al. 2005; Lehmann et al. 2011; Staver et al. 2011a, 2011b) and of tree cover within savannas (Sankaran et al. 2005, 2008; Bucini and Hanan 2007). Experimental work has demonstrated that fire can, in some cases, prevent the formation of closed canopies (Brookman-Amisshah et al. 1980; Swaine et al. 1992; Moreira 2000; Russell-Smith et al. 2003; Andersen et al. 2005; Bond 2008), while in others, fire may affect tree cover but savannas can persist even without regular fires (Higgins et al. 2007; Bond 2008). In large part, this is due to climatic context (Sankaran et al. 2005; Bond 2008; Hirota et al. 2011; Staver et al. 2011a, 2011b): savannas represent the climax biome at low rainfall, while forests

do so at higher rainfall. However, fires can reduce tree cover even where forests are climatically possible, and there is even some evidence that fires maintain savanna as a distinct, open-canopy alternative biome state to forest at intermediate rainfall (Staver et al. 2011a, 2011b).

While empirical evidence highlights the role of both climate and fire in determining tree cover and biome distributions, our understanding of the long-term persistence of savannas in particular is poor. Examination of the distribution of savanna and its drivers in a theoretical context can provide insights into temporal dynamics where data are lacking. For example, models that closely reproduce spatial tree-cover patterns have suggested that fire can maintain savanna as an alternative stable state to forest (Beckage and Ellingwood 2008; Beckage et al. 2009; Staver et al. 2011b). Other models that examine only tree-grass coexistence dynamics, usually in arid areas where savanna is the climax biome, have predicted the potential for multiple stable states in tree cover (Menaut et al. 1990; Higgins et al. 2000, 2010; van Langevelde et al. 2003; D'Odorico et al. 2006, 2007; Scheiter and Higgins 2007; Holdo et al. 2009), although these have generally ignored the potential for the closed-canopy forest that characterizes mesic savannas.

However, an emphasis on the mechanisms that produce tree cover is vital to a useful theoretical evaluation of the stability and dynamics of savanna and forest. In this context, two distinct processes are particularly important in mediating fire and rainfall effects on tree cover in savanna and forest systems: the spread of fire and the effects of fire on the demography of tree populations. That fire and rainfall affect tree cover via their effects on tree populations is well established (Higgins et al. 2000; Hanan et al. 2008). Fire limits tree cover in savannas by preventing the recruitment of savanna tree saplings into adults (Higgins et al. 2000; Bond and Midgley 2001; Hoffmann et al. 2009; Staver et al. 2009; Prior et al. 2010) and in forests primarily by killing both forest saplings and adult trees (Barlow et al. 2003; Fensham et al. 2003). Thus, explicitly considering the population-level processes that determine tree cover

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is fundamental to a mechanistic understanding of the dynamics that characterize savanna and forest.

The mechanisms by which fire spreads are more difficult to simplify, because fire spread is strongly dependent on weather, fuel load, and landscape connectivity (Archibald et al. 2012). Within savanna, trees are not flammable and usually act as barriers to fire spread by interrupting the grass layer, although in pine savannas, highly flammable tree litter may actually contribute to fire spread (Beckage and Ellingwood 2008; Beckage et al. 2009). At a broad scale, however, fire spread depends on the continuity of the grass layer, to which tree cover usually acts as a barrier. In the tropics, tree cover has little effect on fire spread, frequency, or size until it reaches a threshold (45%–50%) above which fire can no longer spread (Hennenberg et al. 2006; Archibald et al. 2009, 2012; Pueyo et al. 2010; Staver et al. 2011*a*, 2011*b*). In this way, fire acts approximately as a percolation process, where either systems are connected and fire can spread or they are not connected and fire cannot spread (Li 2002; Favier 2004; Sullivan 2009). Fire can thus, at least in theory, act as a positive feedback within savannas that maintains open canopies, which in turn promote the spread of fire.

These processes—fire spread and its effects on tree demography—provide a basis on which we can build a much-needed mechanistic framework for integrating savanna dynamics across arid and mesic types. Models within savanna (Menaut et al. 1990; Higgins et al. 2000, 2010; van Langevelde et al. 2003; D’Odorico et al. 2006, 2007; Scheiter and Higgins 2007; Holdo et al. 2009), while valuable for their insights into tree-grass coexistence, tell us little about the distribution of savanna versus forest and the dynamics that characterize mesic savannas. Models that describe savanna-forest transitions have, to date, examined the dynamics of savanna and forest patches at their ecotone, largely ignoring individual-level and tree-grass interactions (Sternberg 2001; Favier et al. 2004). Although these patch-dynamics models are able to capture elements of savanna and forest stability and of transitions between types at their boundary, they are inadequate for a thorough understanding of the processes that shape biome distributions.

Those few models that have attempted to integrate grass, savanna trees, and forest trees have included only a subset of ecologically meaningful processes (Sternberg 2001; Hoffmann et al. 2002; Bond et al. 2005; Beckage and Ellingwood 2008; Beckage et al. 2009; Accatino et al. 2010), ignoring rainfall, fire spread, and/or the demographic characteristics of savanna and forest trees. There remains a need to integrate the dynamics of arid and mesic savannas, including explicit consideration of fire and its mechanistic effects on tree cover. Those effects are a persistent modeling challenge because fire is an ecological process that very differently affects savannas, which are

highly fire adapted, and forests, which are not. Nonetheless, effectively incorporating the ecological effects of fire can hugely affect the qualitative predictions of models (Higgins et al. 2000; Bond et al. 2005; Hanan et al. 2008; Staver et al. 2009).

Here, we examine and synthesize the interactive effects of rainfall and fire on savanna and forest stability dynamics via an analytical and mechanistic model of the interactions among grass, savanna tree saplings and adults, and forest trees. Invoking basic assumptions about the ecology of fire in savannas and forests, we examine the stability of patterns of tree cover with respect to rainfall. The model is an expansion of a simpler model, including only grass cover and savanna tree cover, presented in conjunction with an empirical analysis of tree cover in sub-Saharan Africa by Staver et al. (2011*b*). The inclusion of an additional functional type, forest trees, allows us to explore the dynamics not only of tree-grass coexistence in savannas but also of local interactions among savanna and forest types that may influence the distributions of savanna and forest biomes.

Model Description

We have incorporated the fire feedback mechanism suggested by empirical analyses of fire spread (Archibald et al. 2009; Staver et al. 2011*b*) into a simple model to evaluate the potential for savanna and forest to exist as alternative stable states, especially with respect to rainfall. Although fire spread is very much a spatial process, we have not included space explicitly but rather have used mean field approximations based on the idea that fire spread is a percolation process (Li 2002; Favier 2004; Sullivan 2009; Archibald et al. 2012). To this end, we have accounted for space implicitly by assuming that all space is occupied by either grass or trees of one type or another, so that the proportions of land cover occupied by grass (G), savanna saplings (S), and adult trees (T) and forest trees (F) sum to 1 (fig. 1*A*). We incorporate fire dynamics into the landscape by assuming that fire spread in savannas depends on sufficient grass and that it affects both forest and savanna trees. Savannas with tree cover below ~40% burn frequently, but fire is almost nonexistent in systems with tree cover above ~40% (Hennenberg et al. 2006; Archibald et al. 2009; Pueyo et al. 2010; Staver et al. 2011*b*). This threshold appears to be universal, despite differences in the effects of forest versus savanna trees on the grass layer in their subcanopy. Thus, we assume a threshold response of fire frequency to grass abundance: above a threshold in grass abundance (G_T), fire spreads; below that threshold, it does not.

The different effects of fire on savanna and forest tree demographics determine how fire spread affects demographic rates for savanna and forest trees. In the case of

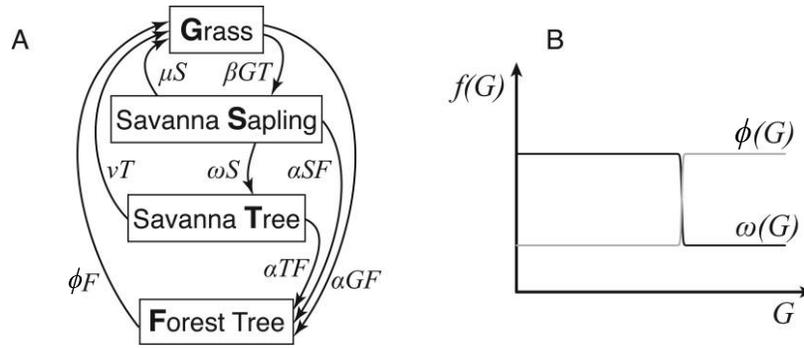


Figure 1: Full model schematic (A) and functional forms for $\omega(G)$ and $\phi(G)$ (savanna sapling-to-tree recruitment and forest tree mortality, respectively; B). Fire spread is assumed to have a threshold response to grass abundance (G). Fire limits the establishment of savanna trees, resulting in fire-limited savanna tree recruitment from saplings (ω) as a function of grass cover (G). In contrast, fire kills forest trees, resulting in the form of forest tree mortality (ϕ) as a function of grass cover (G).

savanna trees, the effects of fire are life stage specific (see Staver et al. 2011b). Fire prevents the establishment of savanna trees by preventing the recruitment of savanna tree saplings (S) into adults (T ; Higgins et al. 2000; Bond and Midgley 2001; Hoffmann et al. 2009; Staver et al. 2009; Prior et al. 2010), but savanna saplings are usually robust resprouters after fires (Hoffmann et al. 2009; Schutz et al. 2009), and adult savanna trees are rarely affected by fire (Hoffmann and Solbrig 2003). Generally, fire seems to affect the establishment, rather than the mortality, of savanna trees. Thus, the ecology of savanna trees as a functional type, combined with assumptions about fire spread, suggests that “intrinsic” (i.e., high) rates of sapling-to-tree recruitment should occur at low grass cover and that fire-limited (i.e., low) rates of recruitment should occur at high grass cover, with a rapid decrease in establishment rate at the threshold in grass abundance required for fire spread (see $\omega(G)$ in fig. 1B).

Forest trees are functionally distinct from savanna trees in their responses to fire. Forest tree saplings resprout much less after a fire than savanna saplings do (Hoffmann et al. 2003, 2009), and fires frequently kill both forest saplings and adult trees (Barlow et al. 2003; Fensham et al. 2003). Generally, fire appears to affect forest trees by increasing their mortality, regardless of size, such that stage structuring of forest trees is unnecessary. Thus, the ecology of forest trees as a functional type, combined with assumptions about fire spread, suggests that “intrinsic” (i.e., low) mortality should occur at low grass cover and that fire-induced (i.e., high) mortality should occur at high grass cover, with a threshold decrease in mortality concurrent with the drop-off in fire spread (see $\phi(G)$ in fig. 1B).

Grass (G) is the default, occupying all areas not explicitly occupied by savanna saplings (S), adult savanna trees (T), or forest trees (F ; fig. 1A); implicit in this assumption is

the idea that grass establishment occurs on a much faster timescale than tree establishment. Savanna saplings establish in proportion to the area of adult savanna trees already in the system, and forest trees similarly establish in proportion to their own area. However, savanna saplings can establish only in areas occupied by grass (rate constant β), while forest trees can establish in areas occupied by grass or by savanna saplings or trees (rate constant α). In effect, this establishes the spatial competitive hierarchy forest trees > savanna trees > grasses (Durrett and Schinazi 1993). The recruitment of savanna saplings (S) into adult savanna trees (T) varies with grass (rate constant $\omega(G)$), because fire, which limits the recruitment of savanna saplings into adult trees, depends on grass cover. Savanna saplings, adult savanna trees, and forest trees die and revert to grass in proportion to their area (rates μ , ν , and $\phi(G)$, respectively; see table 1 for definitions of parameters). The mortalities of savanna saplings and adults are constants, while the mortality of forest trees varies with grass. Fire kills forest trees, in contrast to savanna trees, and fire spread depends on grass cover.

The model is formally described by the following set of coupled differential equations, which always add to 0 (since $G + S + T + F = 1$):

$$\frac{dG}{dt} = \mu S + \nu T + \phi(G)F - \beta GT - \alpha GF \quad (1)$$

$$\frac{dS}{dt} = \beta GT - \omega(G)S - \mu S - \alpha SF \quad (2)$$

$$\frac{dT}{dt} = \omega(G)S - \nu T - \alpha TF \quad (3)$$

$$\frac{dF}{dt} = [\alpha(1 - F) - \phi(G)]F \quad (4)$$

Table 1: Symbology

| Symbol | Ecological interpretation |
|------------------|---|
| State variables: | |
| G | Grass cover |
| S | Savanna sapling cover |
| T | Adult savanna tree cover |
| F | Forest tree cover |
| Demographics: | |
| α | Forest tree birth rate |
| β | Savanna sapling birth rate |
| ω | Savanna sapling-to-adult recruitment rate |
| ϕ | Forest tree mortality rate |
| μ | Savanna sapling mortality rate |
| ν | Adult savanna tree mortality rate |

yielding an effectively three-dimensional system. We also assume that $\omega(G)$ and $\phi(G)$ are, respectively, decreasing and increasing smooth approximations to step functions (fig. 1B), transitioning sharply at the threshold in grass cover required for fire spread (G_T) from ω_0 and ϕ_0 to ω_1 and ϕ_1 .

Model Analysis

The system admits multiple possible boundary equilibria, which include equilibria that include (1) grass only (G); (2) grass and savanna trees and saplings only (GST); and (3) grass and forest trees only (GF). For some parameters, internal equilibria may also exist in which all types ($GSTF$) are present. The system also admits periodic and more complicated dynamic shifts among states. Any stable equilibrium must include grass G , and naturally, savanna saplings S and trees T are either both present or both absent. The analysis of G -only equilibria is simple to interpret graphically from analyses of other boundary and internal equilibria, so we do not separate their analysis from the other sections.

For clarity, we define “conditionally stable” to mean equilibria that are locally asymptotically stable within a boundary (i.e., where either F or S and T are 0). Conditionally stable equilibria that are locally asymptotically stable to invasion are referred to simply as “stable.”

Stable Coexistence of Grass (G) and Savanna Trees (S and T)

In the absence of forest trees (F), the system of equations (1)–(4) defines a dynamic exclusively between grass and savanna trees, already examined in Staver et al. (2011b). From equations (2) and (3), possible equilibria within this GST boundary include one without savanna trees (where $S = T = 0$ and $G = 1$) or with few savanna trees and

another in which grass cover is low and savanna trees abundant. When both exist, they are separated by another nontrivial equilibrium with intermediate grass and tree cover. All nontrivial equilibria satisfy

$$\omega(\hat{G}) = \frac{\mu\nu}{\beta\hat{G} - \nu}. \quad (5)$$

Any such equilibrium is conditionally stable when

$$\omega'(\hat{G}) > \frac{-\beta\mu\nu}{(\beta\hat{G} - \nu)^2}, \quad (6)$$

where the left and right sides of equation (6) are the derivatives of the left and right sides of equation (5), respectively, yielding a convenient graphical analysis of the system (fig. 2A). Clearly, any intermediate tree-cover equilibrium is always unstable. Hence, a sigmoidal response of savanna tree establishment to fire can produce a bistability in tree cover in the absence of forest trees, depending on model parameters (for a more detailed analysis of this boundary equilibrium, see Staver et al. 2011b).

When a boundary equilibrium with G , S , and T is conditionally stable, its invasibility by forest trees determines whether it is stable. Without loss of generality, we substitute $S = 1 - G - T - F$ to obtain a dynamical system in G , T , and F only and determine stability by evaluating the linearization matrix at $F = 0$,

$$\mathbf{J}_{F=0} = \begin{bmatrix} -\mu - \beta\hat{T} & -\mu + \nu - \beta\hat{G} & -\mu + \phi(\hat{G}) - \alpha\hat{G} \\ -\omega(\hat{G}) + \omega'(\hat{G})\hat{S} & -\omega(\hat{G}) - \nu & -\omega(\hat{G}) - \alpha\hat{T} \\ 0 & 0 & \alpha - \phi(\hat{G}) \end{bmatrix}. \quad (7)$$

The 2×2 submatrix defined by the first two rows and columns is the one associated with the conditional stability already assumed. Thus, we see that F can invade if and only if its growth rate exceeds its death rate,

$$\alpha > \phi(\hat{G}). \quad (8)$$

Because α is constant and $\phi(G)$ is always larger at high G than at low G (i.e., $\phi_1 > \phi_0$), GT equilibria with low G are clearly more invasible by F . Ecologically, this means simply that high-savanna tree cover systems (i.e., savanna woodlands) are more likely to be invaded by forest trees than are low-tree cover savannas because fires, which kill forest trees, are more frequent.

Stable Coexistence of Grass (G) and Forest Trees (F)

In the absence of savanna saplings (S) and trees (T), the system of equations (1)–(4) defines a dynamic exclusively

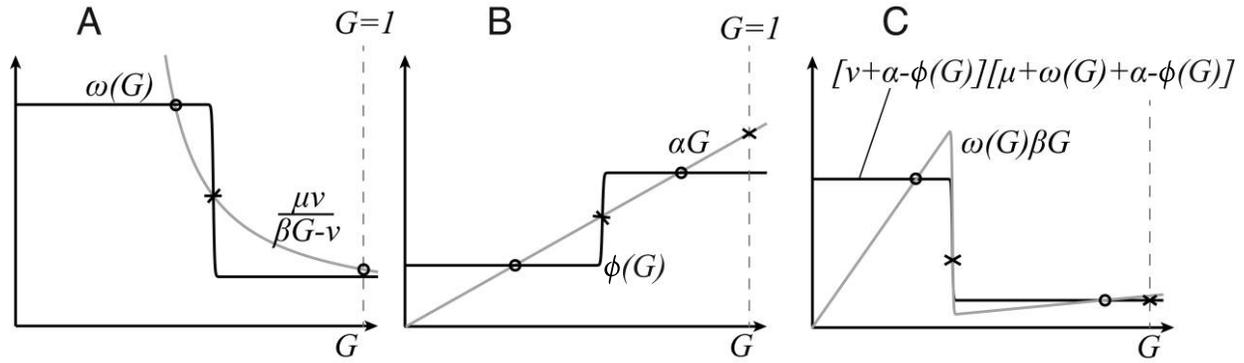


Figure 2: Graphical analysis of boundary equilibria with grass (G), savanna saplings (S), and savanna trees (T ; A), boundary equilibria with grass (G) and forest trees (F ; B), and internal equilibria with all types present, valid when forest tree cover (F) is positive (i.e., when $\alpha > \phi(G)$; C). Equilibria occur at values of G at which isoclines (given by eqq. [5], [9], and [15]) intersect. Stability of all equilibria can be evaluated via graphical analysis of equations (6), (8), (10), (12), and (18). Equilibria marked with circles are conditionally stable, and those marked with crosses are unstable.

between grass and forest trees. With only two components, the system is effectively one-dimensional. From equation (4), equilibria within this GF boundary include one without trees (where $F = 0$ and $G = 1$) and possibly one to three nontrivial boundary equilibria given by

$$\alpha \check{G} = \phi(\check{G}), \quad (9)$$

in which grass and forest trees coexist. Any such equilibrium is conditionally stable when

$$\alpha > \phi'(\check{G}), \quad (10)$$

yielding a convenient graphical analysis of the system (fig. 2B). If $\phi(1) < \alpha$, then $G = 1$ is locally stable, but a second, nontrivial equilibrium with forest trees present may still exist. If $\phi(1) > \alpha$, then $G = 1$ is unstable, but the sigmoidal forest tree mortality response to fire may still produce bistability in tree cover, with one equilibrium at low forest tree cover and one at high cover, even in the absence of savanna trees.

This dynamic indicates that resprouting by trees after fires, which characterizes savanna trees, is not necessary for bistability in tree cover to emerge. However, a strong demographic response of trees to fires is, in this case, a tree-mortality response. Low forest tree cover facilitates fire spread, which induces high tree mortality, thereby maintaining low forest tree cover; high forest tree cover prevents fire spread, resulting in low tree mortality, thereby maintaining high forest tree cover. Empirical evidence of the stable coexistence of forest trees and grasses maintained by fire is scant, but they have coexisted, for instance, for the past 4,000 years in the forest/grassland mosaics in Atlantic Brazil (Behling et al. 2004).

As in the previous case, the stability of an existing con-

ditionally stable boundary equilibrium in which both G and F are present depends on whether savanna trees can invade the system. We analyze the simultaneous invasion of S and T because neither can persist stably without the other. Without loss of generality, we substitute $F = 1 - G$ to obtain a dynamical system in G , T , and F only and determine stability by evaluating the Jacobian matrix for $S = 0$ and $T = 0$:

$$\mathbf{J}_{S=T=0} =$$

$$\begin{bmatrix} (\phi'(\check{G}) - \alpha)(1 - \check{G}) & \mu & \nu - \beta\check{G} \\ 0 & -\omega(\check{G}) - \mu - \alpha(1 - \check{G}) & \beta\check{G} \\ 0 & \omega(\check{G}) & -\nu - \alpha(1 - \check{G}) \end{bmatrix}, \quad (11)$$

where the three eigenvalues of the matrix are given by the term in the upper left and the two eigenvalues of the 2×2 submatrix formed by striking out the first row and the first column. The first eigenvalue is clearly negative for conditionally stable equilibria (see eq. [10]). The other two eigenvalues are negative when the trace of the 2×2 submatrix is negative and its determinant is positive. The condition on the trace is clearly trivially satisfied; therefore, S and T can invade conditionally stable GF boundary equilibria when

$$\omega(\check{G})\beta\check{G} > (\nu + \alpha\check{F})(\mu + \omega(\check{G}) + \alpha\check{F}), \quad (12)$$

or, in effect, when the products of the rates of addition of S and T exceed the products of their removal rates for given values of G and F .

In this case, low-tree cover systems favor savanna tree invasion because of a proliferation of areas available for establishment (i.e., grassy areas), while high-tree cover

systems favor savanna tree establishment because of the absence of fire, which limits sapling-to-tree recruitment. The relative importance of these factors—and the resulting invasibility of low- versus high-tree cover systems—is strongly parameter dependent.

Stable Coexistence of Grass (G), Savanna Trees (S and T), and Forest Trees (F)

In this system, the invasion of stable configurations of grass and savanna saplings and trees by forest trees or of stable configurations of grass and forest trees by savanna trees can result in one of three possible outcomes: (1) the invading functional type of tree replaces the resident functional type in coexistence with grass, (2) stable internal equilibria with grasses, savanna trees, and forest trees all present, or (c) more-complex phenomena, such as limit cycles or strange attractors, with all components present. Analyzing the existence and dynamics of internal equilibria can provide insight into whether stable equilibria with all three types are possible and under what conditions.

Equations (1)–(4) constrain the ratio S/T and values of F for existing internal equilibria,

$$\frac{\bar{S}}{\bar{T}} = \frac{\beta\bar{G}}{\mu + \omega(\bar{G}) + \alpha\bar{F}} = \frac{\nu + \alpha\bar{F}}{\omega(\bar{G})}, \quad (13)$$

$$\bar{F} = \frac{\alpha - \phi(\bar{G})}{\alpha}, \quad (14)$$

where $\bar{S} \neq 0$, $\bar{T} \neq 0$, and $\bar{F} \neq 0$. These can be combined to yield a statement in terms of only G ,

$$\omega(\bar{G})\beta\bar{G} = (\mu + \omega(\bar{G}) + \alpha - \phi(\bar{G})) \times (\nu + \alpha - \phi(\bar{G})), \quad (15)$$

that can then be used, together with equations (13) and (14) and $G + S + T + F = 1$, to solve for all state variables in any feasible equilibrium. This yields a maximum of three possible equilibria (fig. 2C), whose stability can be analyzed as follows.

Because the system is effectively three-dimensional, the Jacobian has three eigenvalues. We invoke the assumption that the curves that give $\omega(G)$ and $\phi(G)$ are either flat or steep and hence that either both

$$\omega'(G) \approx 0 \quad \text{and} \quad \phi'(G) \approx 0 \quad (16)$$

or both

$$\omega'(G) \ll 0 \quad \text{and} \quad \phi'(G) \gg 0, \quad (17)$$

which simplifies an approximate analysis of these conditions. Again, without loss of generality, we substitute $S = 1 - G - T - F$ to obtain a dynamical system in G ,

T , and F only, and we determine stability by evaluating the linearization matrix,

$$\mathbf{J} = \begin{bmatrix} -\mu + \bar{F}\phi'(\bar{G}) - \beta\bar{T} - \alpha\bar{F} & -\mu + \nu - \beta\bar{G} & -\mu + \phi(\bar{G}) - \alpha\bar{G} \\ -\omega(\bar{G}) + \omega'(\bar{G})\bar{S} & -\omega(\bar{G}) - \nu - \alpha\bar{F} & -\omega(\bar{G}) - \alpha\bar{T} \\ -\bar{F}\phi'(\bar{G}) & 0 & -\alpha\bar{F} \end{bmatrix}. \quad (18)$$

In three dimensions, the condition that the dominant (and therefore all) eigenvalues be negative results in three Routh-Hurwitz conditions for stability: (1) the trace is negative, (2) the determinant is negative, and (3) the determinant is greater than the product of the trace and the sum of the determinants of the dominant subminors. When they occur over ranges of G where $\omega(G)$ and $\phi(G)$ are flat (see eq. [16]), all stability conditions are trivially satisfied and equilibria are stable. Equilibria that occur over ranges of G where $\omega(G)$ and $\phi(G)$ are steep (see eq. [17]) are not stable.

The graphical analysis of potential internal equilibria presented in figure 2C demonstrates that grass, savanna trees, and forest trees can all coexist stably and that zero to two stable internal equilibria with persistent coexistence of grass (G), savanna saplings (S) and trees (T), and forest trees (F) are possible.

Analysis of the stability of equilibria under conditions where we relax the assumption that $\omega(G)$ and $\phi(G)$ are nearly step functions remains an open but important challenge; such conditions may give rise to complex behaviors. Even if $\omega(G)$ and $\phi(G)$ are nearly step functions with smooth transitions between the flat and steep parts of their curves, complex (if short-lived) behaviors may arise over those transitional areas. Examining the effects of changing one parameter (α) on the stability dynamics of the system reveals that internal equilibria can lose stability via a Hopf bifurcation, in which one stable equilibrium bifurcates into an unstable equilibrium and a stable limit cycle (fig. 3; note that fig. 3A is a projection of three-dimensional space onto a two-dimensional plane), characterized by a pair of complex eigenvalues whose real part changes from negative to positive. These stable limit cycles can occur only as long as the slopes of $\omega(G)$ and $\phi(G)$ are on the cusps between shallow and steep. If we relax the assumption that $\omega(G)$ and $\phi(G)$ are nearly step functions, the limit cycles can be expected to be more persistent than they are under current model assumptions.

Global System Stability Analysis

Characterizing the overall stability of the system presents a challenge, particularly in view of the analytical intractability of solutions for G . Local stability analysis provides

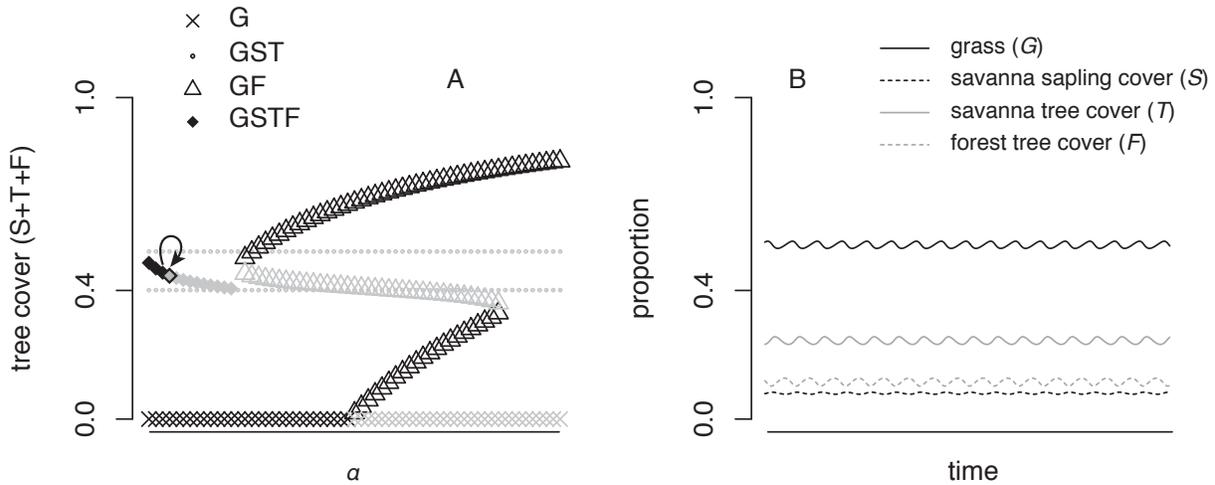


Figure 3: Changing one parameter (in this case, α) can result in changes in the stability of equilibria via Hopf bifurcations, shown by the arrow in A, in which an equilibrium loses stability when the real part of a pair of complex eigenvalues changes sign from negative to positive. A stable limit cycle (B) and an unstable equilibrium emerge. In A, stable equilibria are denoted by black points and unstable ones by gray points; the gray internal equilibrium outlined in black is unstable and is associated with the stable limit cycle depicted in B (where $\alpha \approx 0.1245$, $\beta = 0.5$, $\omega_{G=0} = 0.5$, $\omega_{G=1} = 0.1$, $\mu = 0.3$, $\nu = 0.15$, $\phi_{G=0} = 0.1$, and $\phi_{G=1} = 0.3$). G, GST, GF, and GSTF refer to systems with, respectively, grass only; grass and savanna saplings and trees; grass and forest trees; and all four vegetation types (see fig. 1).

insights into whether those equilibria that do exist are stable or unstable, but it is insufficient to characterize more complex model behaviors, such as stable limit cycles or strange attractors, that may exist far from equilibrium. Nor can local stability analysis tell us about the basins of attraction of equilibria. Via Bendixson's negative criterion, it is easy to show that stable limit cycles are impossible on the boundaries, where one or more system components are absent, but such methods break down in the higher-dimensional interior regions. For example, simulations suggest that stable heteroclinic cycles in the interior, connecting two unstable equilibria, can occur (fig. 4). Further analysis of such behaviors will clearly be of mathematical interest, but the possibility of such behaviors also raises intriguing biological questions. A regular oscillation between savanna and forest systems, with fire as the driver flipping them, such as would be exhibited by the heteroclinic cycles, would be a novel and exciting phenomenon.

An analysis of the local stability of equilibria can nonetheless provide extensive insights into the global stability of the system. A graphical look at boundary and internal equilibria separately revealed that a maximum of two conditionally stable GF equilibria, two conditionally stable GST equilibria, and two stable internal GSTF equilibria are possible (fig. 2). However, a synthesis of some of the conditions for invasion by F or S and T with constraints on parameters given by solutions for G provides some

insights into the potential stable equilibria that characterize the system as a whole.

Combining conditions for invasion by F of GST equilibria (from eq. [8]) with constraints placed on parameters by equilibrium solutions for F (from eqq. [9] and [14]) yields the fairly obvious general result that only stable equilibria with F present can occur and that F must be present at stable equilibria when

$$\alpha > \phi(\bar{G}) \quad (19)$$

or when the birth rate of F exceeds its death rate. Similarly, combining conditions for invasion by S and T of GF equilibria (from eq. [12]) with constraints placed on parameters by equilibrium solutions for G (from eqq. [5] and [15]) yields the result that S and T can invade when

$$\omega(\bar{G})\beta\bar{G} \geq (\nu + \alpha\bar{F})(\mu + \omega(\bar{G}) + \alpha\bar{F}) \quad (20)$$

and that this condition must apply at any equilibrium including S and T.

Between them, these conditions constrain the types of stable equilibria that are possible. The assumption that $\phi(G)$ and $\omega(G)$ are nearly step functions, taking essentially only two values each (respectively, ϕ_0 , ϕ_1 and ω_0 , ω_1) that are separated by the same grass-cover threshold (G_T), places a constraint on maximum number of stable equilibria. For each unique region of $\phi(G)$, equation (19) is either satisfied or it is not, resulting in stable equilibria

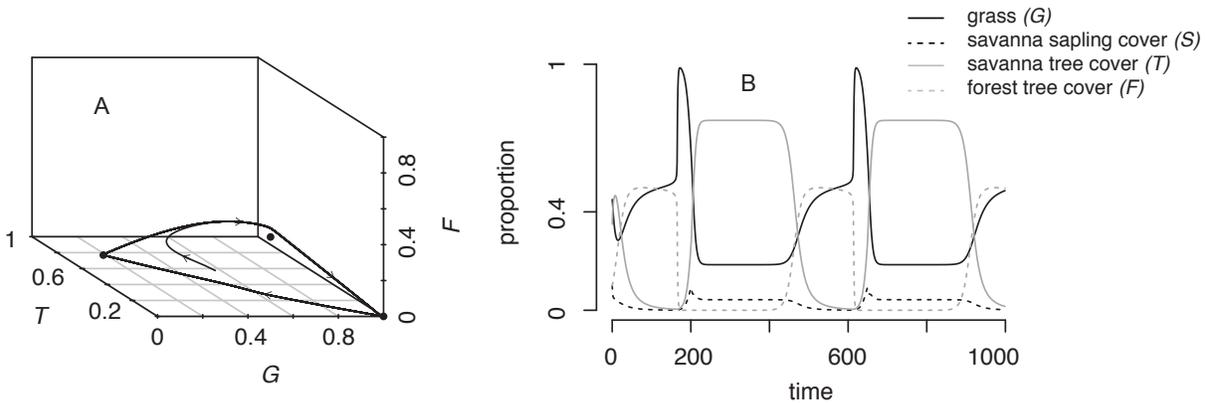


Figure 4: Three-dimensional cycles are possible for some parameter combinations. Here, the same combination ($\alpha = 0.2$, $\beta = 0.3$, $\omega_{G=0} = 0.9$, $\omega_{G=1} = 0.4$, $\mu = 0.1$, $\nu = 0.05$, $\phi_{G=0} = 0.1$, and $\phi_{G=1} = 0.9$) is illustrated both in three dimensions, where the black points denote equilibria, all of which are unstable (A), and as a state variable time series (B). These orbits tend toward a heteroclinic cycle that connects two boundary equilibria that exclude forest trees, one at $G = 1$ and one that includes G , S , and T .

that either include F or do not. For each unique region of $\phi(G)$ and $\omega(G)$, equation (20) can be satisfied or not, resulting in stable equilibria that either include S and T or do not. The result is that for each unique region of $\phi(G)$ and $\omega(G)$, a maximum of one stable equilibrium is possible, resulting in a system with a maximum of two possible stable equilibria.

Whether one or two stable equilibria exist depends on values of G given by equations (5), (9), and (15). The system can have a single equilibrium with low tree cover, a single equilibrium with high tree cover, or two equilibria: one with high and another with low tree cover. The dynamics of any particular system are governed by its demographic rates.

Model Behavior with Parameter Dependence on Rainfall

So far, we have focused on the effects of fire on local savanna-forest dynamics, via a series of well-supported assumptions about fire spread and the effects of fire on the demographics of savanna and forest trees. However, empirical work has demonstrated that the effects of fire on savanna structure (Sankaran et al. 2005, 2008; Bucini and Hanan 2007) and on the distribution of savanna and forest (Staver et al. 2011a, 2011b) depend strongly on climatic context—in particular, on rainfall. In fact, in the tropics and subtropics, savanna and forest appear as fire-driven alternative stable states only at intermediate rainfall (Staver et al. 2011a, 2011b); at low and high rainfall, climate closely constrains tree cover (Hirota et al. 2011; Staver et al. 2011a, 2011b).

In light of this body of empirical work, it makes sense

to evaluate the model presented here in the context of large-scale continental gradients in mean annual rainfall. Given clear relationships of increasing net primary productivity with rainfall (Field et al. 1998), we might expect rainfall to affect model dynamics by either (1) increasing rates of seedling/tree establishment and recruitment or (2) decreasing rates of tree mortality. Within-site temporal studies tend to confirm this expectation; they clearly suggest that droughts frequently result in higher tree mortality (Nepstad et al. 2007; Fensham et al. 2009; Phillips et al. 2009) and that wet years result in higher rates of tree establishment (Kitzberger et al. 2000; Kraaij and Ward 2006), in savannas and forests alike. However, large-scale responses of tree demographics to rainfall have not been synthesized, as far as we know.

The few studies of the responses of tree populations to small-scale spatial variation in rainfall suggest that establishment increases and mortality decreases nonlinearly with rainfall (Condit et al. 2004; Fensham et al. 2009). The simplest assumption would be that rates of establishment (α , β , ω) increase and mortality rates (μ , ν , ϕ) decrease monotonically and continuously with increasing rainfall. However, this may be an oversimplification: grass biomass responses to rainfall and concomitant changes in fire frequency and intensity (Govender et al. 2006; Archibald et al. 2009) may confound this pattern, at least over some ranges of rainfall. This model examines only grass cover, assuming that within a relatively homogeneous environment, grass biomass will not vary substantially. Over continental-scale gradients in rainfall, the grass biomass represented in a unit of grass cover may vary substantially, however, and the potential demographic effects of fire on tree populations may therefore also change.

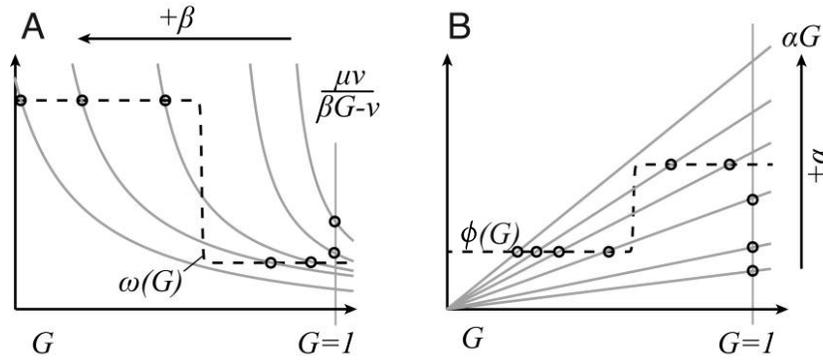


Figure 5: Effects of rainfall-driven increases in establishment rates (α and β) on boundary equilibria with grass (G) and savanna saplings (S) and trees (T) present (A) and on boundary equilibria with grass (G) and forest trees (F) present (B). Stable equilibria occur at circled intersections between isoclines and unstable ones at intersections that are not circled. Grass generally decreases with increasing tree cover, but increases are not linear or continuous.

While increasing rainfall likely results in increasing growth rates and decreasing mortality, fire-induced mortality or limitations on recruitment may therefore increase with increasing rainfall. Thus, we expect that over large rainfall ranges, ω_1 and ϕ_1 will increase and decrease, respectively (as do ω_0 and ϕ_0 ; Lehmann et al. 2011), but over portions of the rainfall range this pattern may be reversed.

Analytically, the most obvious and predictable result of increasing rainfall is increasing forest tree cover (F), which is autonomously defined by the relationship between the establishment (α) and mortality rates (ϕ) of forest tree cover. From equation (6), forest tree cover increases deterministically with the expected effects of rainfall. From equation (5), increasing rainfall also results in an increasing potential for invasion of forest trees, particularly of low-grass cover equilibria, where ϕ_0 is relatively low. When rainfall is low,

$$\alpha < \phi_0 < \phi_1, \quad (21)$$

but as rainfall and α increase, α becomes intermediate,

$$\phi_0 < \alpha < \phi_1, \quad (22)$$

and, depending on the response of ϕ_1 to rainfall, may eventually become dominant,

$$\phi_0 < \phi_1 < \alpha, \quad (23)$$

such that α , the establishment rate of forest trees, increases to exceed their mortality rate (ϕ).

Increases in the prevalence and amount of forest tree cover are not continuous because the response of forest tree mortality (ϕ) to grass cover (G) is sigmoidal (fig. 5B). At low rainfall, when forest tree establishment rates are low and mortality rates are high, only the low-tree cover equilibrium is possible and (at least) conditionally stable.

As α increases and ϕ_0 decreases, a second, high-tree cover equilibrium eventually also becomes possible and at least conditionally stable. Finally, again depending on the response of ϕ_1 to rainfall, the low-tree cover equilibrium may become impossible (fig. 5B), but this will occur only if ϕ_1 eventually decreases to the point that

$$\check{G} = \frac{\phi_1}{\alpha} < G_T. \quad (24)$$

Otherwise, two equilibria will persist even as rainfall becomes very high. However, empirically observed patterns of tree cover with respect to rainfall suggest that at high rainfall, equation (24) is satisfied, because tree cover is bistable only at intermediate rainfall (Hirota et al. 2011; Staver et al. 2011a, 2011b). This has clear implications for expected demographic responses to rainfall over large scales.

Responses of savanna tree cover to increasing rainfall, via increases in birth rates (β), decreases in savanna sapling and tree mortality rates (μ and ν , respectively), and changes in savanna sapling-to-tree recruitment rates (ω), are more complicated to interpret than are forest tree cover responses. Manipulating equations (5) and (15) to solve for \bar{G} ,

$$\bar{G} = \left(\frac{\mu + \alpha \bar{F}}{\omega(\bar{G})} + 1 \right) \left(\frac{\nu + \alpha \bar{F}}{\beta} \right), \quad (25)$$

makes it clear that absent other parameter changes (i.e., when F is constant), grass cover (G) must decrease and savanna tree cover ($S + T$) must increase as β increases, ω_0 increases, or μ and ν decrease. However, note that in low-tree cover equilibria, savanna tree cover may decrease over some ranges of rainfall if ω_1 does. By the same token (from eq. [12]), as rainfall increases and β increases, S and

T are increasingly able to invade boundary equilibria with only G and F present. At low rainfall,

$$\begin{aligned} \beta \check{G} &< (\nu + \alpha \check{F}) \left(\frac{\mu + \alpha \check{F}}{\omega_0} + 1 \right) \\ &< (\nu + \alpha \check{F}) \left(\frac{\mu + \alpha \check{F}}{\omega_1} + 1 \right). \end{aligned} \quad (26)$$

However, as rainfall and β increase (or μ and ν decrease),

$$\begin{aligned} (\nu + \alpha \check{F}) \left(\frac{\mu + \alpha \check{F}}{\omega_0} + 1 \right) &< \beta \check{G} \\ &< (\nu + \alpha \check{F}) \left(\frac{\mu + \alpha \check{F}}{\omega_1} + 1 \right), \end{aligned} \quad (27)$$

and finally, depending on the response of ω_1 to rainfall,

$$\begin{aligned} (\nu + \alpha \check{F}) \left(\frac{\mu + \alpha \check{F}}{\omega_0} + 1 \right) &< (\nu + \alpha \check{F}) \left(\frac{\mu + \alpha \check{F}}{\omega_1} + 1 \right) \\ &< \beta \check{G}. \end{aligned} \quad (28)$$

Hence, S and T can invade low-grass cover equilibria before they can invade high-grass cover equilibria.

Changes in tree cover that result from increasing rainfall eventually result in decreases in G that cross the grass cover threshold for fire spread (G_T), resulting in system-level responses to rainfall that are nonlinear (fig. 5A). Again, at low rainfall, when establishment and recruitment rates are low and mortality rates are high, only a low-tree cover equilibrium is possible and at least conditionally stable. As rainfall increases, a second, high-tree cover equilibrium eventually also becomes possible and at least conditionally stable. Finally, depending on the response of ω_1 to rainfall, the low-tree cover equilibrium may become impossible (fig. 5A), although the region of bistability may persist until high rainfall. Again, empirically observed patterns of tree cover with respect to rainfall (Hirota et al. 2011; Staver et al. 2011a, 2011b) suggest that even where grass cover is high, tree establishment rates probably do generally increase and mortality rates decrease over large ranges of rainfall.

Simultaneous changes in savanna tree and forest tree demographic rates complicate the response of savanna tree cover to increasing rainfall (because forest tree cover is autonomously defined, its responses are unchanged). In this case, the effects of rainfall-related changes in demographic rates on the prevalence and cover of savanna saplings and adult trees are more parameter dependent. Because forest tree cover (F) increases with increasing rainfall, resulting in decreases in grass cover (G), the rate of removal of savanna saplings and adult trees by forest

trees also increases. As a result, the net rate of removal of S and T may actually increase, and their establishment rates may decrease. Notably, because F —like S and T —invades low-grass cover equilibria first, these effects most likely occur where S and T appear at best advantage, at least when F is absent. Thus, while savanna trees undoubtedly benefit from increased rainfall, they may actually lose out to forest trees in more mesic environments.

Numerical analyses of the range of system-level responses to changes in demographic rates with increasing rainfall nonetheless confirm those general trends that emerged from an analytical examination of responses (fig. 6). Tree cover generally increases and grass cover decreases with changes in demographic rates, in line with empirical observations (Staver et al. 2011a, 2011b), although quantitative estimates obviously depend on parameterization. In the examples presented here, demographic responses to rainfall are such that even in the presence of grass, ω_1 generally increases and ϕ_1 generally decreases over large increases in rainfall, although they may do the opposite over portions of the rainfall range. Under these conditions, forest trees become more prevalent and forest tree cover increases as rainfall increases, eventually resulting in dominance by forest trees of all equilibria at high rainfall. Savanna tree responses to increasing rainfall are less predictable; in the absence of forest trees, savanna tree cover increases, but when forest trees can invade, savanna tree cover decreases. Numerical analyses also confirm what graphical analyses of boundary equilibria with increasing rainfall suggest (fig. 5): that the system appears to consistently move through a region of bistability with both low-tree cover and high-tree-cover equilibria at intermediate rainfall, although where this occurs depends on parameterization (fig. 6). Again, these patterns are likely to depend on real large-scale functional responses of tree demographics to rainfall, and this pattern does depend strongly on the assumption that ω_1 generally increases and ϕ_1 generally decreases over large increases in rainfall. However, empirical patterns suggest that savanna can persist only due to fire feedbacks at intermediate rainfall (Hirota et al. 2011; Lehmann et al. 2011; Staver et al. 2011a, 2011b). We expect that data on tree demography will show that tree establishment generally tends to increase and mortality to decrease as rainfall increases, even within grassy savanna systems; unfortunately, such data are not currently available.

Evaluating the model in the context of rainfall effects on tree establishment and mortality reveals that this simple set of assumptions can reproduce patterns of tree cover with rainfall and fire that are closely reflective of real empirical patterns found in sub-Saharan Africa (Staver et al. 2011b) and globally (Staver et al. 2011a). Fire provides a plausible mechanism for limiting tree cover in systems that

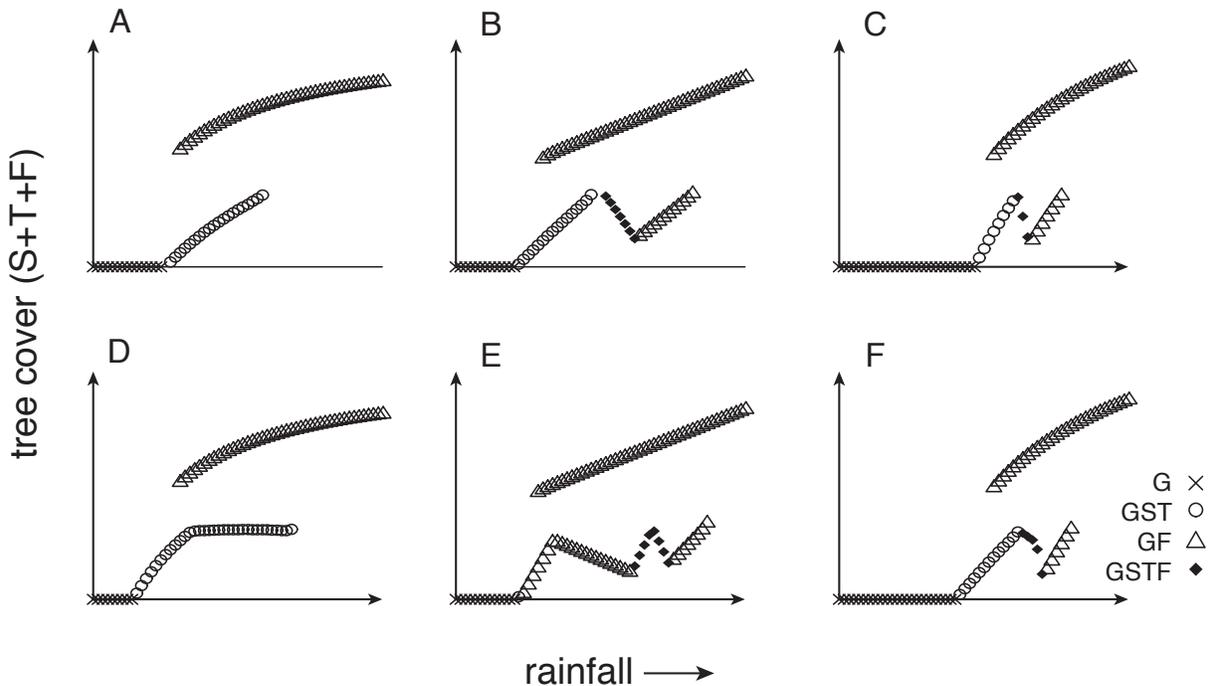


Figure 6: Response of tree cover to increases in rainfall, assuming increases in establishment (α, β) and recruitment (ω ; A); decreases in mortality (ϕ, μ, ν ; B); combined responses from A and B (C); increases in establishment (α, β) and intrinsic recruitment (ω_0) but fire-affected recruitment (ω_f) that increases, then decreases, then increases (D); decreases in intrinsic mortality (ϕ_0, μ, ν) but fire-affected mortality (ϕ_f) that decreases, then increases, then decreases (E); and combined responses from D and E (F). Increasing rainfall characteristically results in increasing tree cover, especially maximum potential tree cover, and a region of bistability in tree cover, with one high- and one low-tree cover equilibrium. G, GST, GF, and GSTF refer to systems with, respectively, grass only; grass and savanna saplings and trees; grass and forest trees; and all four vegetation types (see fig. 1).

are climatically suitable for supporting closed canopies. This mechanism may act as a positive, stabilizing feedback that facilitates the long-term, stable persistence of savannas that do not represent climate maxima. In addition, these patterns of tree cover with response to rainfall are evidently common, even universal, for systems where fire spread responds to grass abundance sharply at a threshold and where fire affects tree demography (although whether it affects tree establishment or mortality is evidently less critical).

Discussion

We have developed a model to examine the fire- and rainfall-mediated interactions of grasses, savanna saplings and trees, and forest trees, hoping to gain insight into the stability dynamics of savanna and forest biomes. The model assumes that fire spread has a threshold response to grass abundance (Hennenberg et al. 2006; Archibald et al. 2009; Pueyo et al. 2010), that fire affects savanna trees by decreasing their establishment and forest trees by increasing

their mortality (Higgins et al. 2000; Barlow et al. 2003; Fensham et al. 2003; Hoffmann et al. 2009), and that rainfall generally increases tree establishment and/or decreases tree mortality.

The model accurately reproduces several empirically supported characteristics of patterns of tree cover: (1) that increasing rainfall results in increasing tree cover, (2) that fire affects tree cover and results in bistability in tree cover at intermediate rainfall, depending on interactions of tree demography with grass biomass and fire frequency, and (3) that forest-type trees dominate closed-canopy systems, while savanna-type trees have a strong relative advantage where tree cover is lower. This last point especially offers an explanation for the persistence of savanna-type trees only in open tree cover systems. In a simpler version of this model, the absence of fire strongly favored savanna-type trees over grasses (Staver et al. 2011b). The expanded model, including two functional types of trees, yields the conclusion that although fire-tolerant savanna trees benefit from the absence of fire, they benefit less than fire-intolerant forest trees and are ultimately less competitive in

environments without fire. They retain a relative advantage only under conditions of frequent fire.

While other models have also reproduced some of these findings (Beckage et al. 2009; Accatino et al. 2010; Higgins et al. 2010), they generally do so with higher dimensionality. This work suggests that a very simple ecological mechanism—a fire-vegetation feedback in which fire limits tree establishment or induces tree mortality and the absence of trees promote fire—may plausibly be responsible for empirically observed bimodalities in tree cover.

Even more notable is the implication that where fire spread has a threshold response to grass cover and strongly affects tree demographics, we should expect to find a range of rainfall for which alternative stable states in tree cover occur. In tropical and subtropical savannas generally, fire does impose strong limitations on savanna tree establishment (Bond and Midgley 2001; Bond 2008; Hoffmann et al. 2009; Staver et al. 2009; Prior et al. 2010) and often kills forest trees (Barlow et al. 2003; Fensham et al. 2003; Hoffmann et al. 2009), and fire spread does have a threshold response to grass cover (Hennenberg et al. 2006; Archibald et al. 2009; Pueyo et al. 2010). Recent analyses have shown that, as expected, across the tropics and subtropics at least, savanna and forest may represent alternative states for areas with intermediate rainfall and without strong rainfall seasonality (Staver et al. 2011*a*, 2011*b*). Nonlinearities in tree cover, bistability of biome types with respect to climate, and historical dependency in biome distributions may actually be the norm.

This model represents a simplified theoretical perspective on the climate and fire mechanisms that produce tree cover and biome distributions. Other processes may shape or modify these dynamics, including spatial patterning that affects fire spread (Zinck and Grimm 2009), intrinsic demographic differences among species independent of climate (Poorter et al. 2008; Rossatto et al. 2009; Martínez-Vilalta et al. 2010) or induced by soils (Davies 2001; Russo et al. 2005; Toledo et al. 2010), exogenous disturbance that favors transient ecosystem dynamics, as in North America (Abrams 2003; Boucher et al. 2006), and the potential effects of herbivory, both on tree cover directly (Bucini and Hanan 2007; Staver et al. 2009) and on the spread of fire (Archibald et al. 2005). Incorporating other ecological interactions into models and into continental analyses of biome distributions will yield additional insights into determinants of vegetation structure.

However, this analysis does suggest that nonlinearities in tree cover and bistability of biome types with respect to climate may be fairly universal, with empirical support for the possibility that bistabilities in tree cover, maintained by fire, are geographically extensive throughout the tropics and subtropics (Hirota et al. 2011; Staver et al. 2011*a*) and possibly beyond. Incorporating these types of

ecosystem dynamics into our understanding of biome distributions will be fundamental to accurately predicting the effects of human-driven global change. Shifts in rainfall and the seasonality of rainfall may have direct effects on the potential distributions of savanna and forest (Kumar et al. 1999; Hirota et al. 2011; Lehmann et al. 2011; Staver et al. 2011*a*). Climate change–associated changes in fire frequency are already resulting in extensive degradation of Amazonian tropical rainforest (Malhi et al. 2009; Phillips et al. 2009; Asner and Alencar 2010). Meanwhile, direct human effects on fire regimes, due to active management and to landscape fragmentation (Archibald et al. 2012), have resulted in widespread woody encroachment into savanna systems (Goetze et al. 2006; Mitchard et al. 2009), possibly aggravated by the effects of increasing CO₂ (Wigley et al. 2010). The persistence of forest trees in savannas, suggested by this model with some empirical support (Rossatto et al. 2009), may further facilitate the encroachment of forest into savanna (Favier et al. 2004) in the face of changes in fire regime, climate, and atmospheric CO₂. The hysteresis implied by these results suggests that both savanna and forest have some limited resilience to global change (Hirota et al. 2011). However, when they do occur, changes in biome state will be sudden and, whether they favor savanna or forest, are likely to be persistent.

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