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Author(s): Brian Beckage, William J. Platt, Louis J. Gross
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Vegetation, Fire, and Feedbacks: A Disturbance-Mediated Model of Savannas

Brian Beckage,[1,*] **William J. Platt,**[2] **and Louis J. Gross**[3]

1. Department of Plant Biology, University of Vermont, Burlington, Vermont 05405; 2. Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803; 3. National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, Tennessee 37996

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abstract: Savanna models that are based on recurrent disturbances such as fire result in nonequilibrium savannas, but these models rarely incorporate vegetation feedbacks on fire frequency or include more than two states (grasses and trees). We develop a disturbance model that includes vegetation-fire feedbacks, using a system of differential equations to represent three main components of savannas: grasses, fire-tolerant savanna trees, and fire-intolerant forest trees. We investigate the stability of savannas in the presence of positive feedbacks of fire frequency with (1) grasses, (2) savanna trees, and (3) grasses and savanna trees together while also allowing for negative feedbacks of forest trees on fire frequency. We find that positive feedbacks between fire frequency and savanna trees, alone or together with grasses, can stabilize savannas, blocking the conversion of savannas to forests. Negative feedbacks of forest trees on fire frequency shift the range of parameter space that supports savannas, but they do not generally alter our results. We propose that pyrogenic trees that modify characteristics of fire regimes are ecosystem engineers that facilitate the persistence of savannas, generating both threshold fire frequencies with rapid changes in community composition when these thresholds are crossed and hystereses with bistable community states.

Keywords: disturbance, ecosystem engineer, fire, forest, grassland, savanna.

Introduction

Proposed mechanisms that maintain savannas as a mixture of a graminoid-dominated groundcover and a discontinuous overstory of trees fall broadly into two classes. These include niche-partitioning and disturbance-mediated demographic-bottleneck models (hereafter, disturbance models; e.g., Scholes and Walker 1993; Higgins et al. 2000; Jeltsch et al. 2000; House et al. 2003; Sankaran et al. 2004; D'Odorico et al. 2006; Gilliam et al. 2006), although some savanna models contain aspects of both mechanisms (e.g., van Langevelde et al. 2003; Scheiter and Higgins 2007). Each class of models relates to relationships between dominant functional groups, but their mechanisms result in fundamentally different outcomes: niche-partitioning mechanisms generate equilibrium steady states, while disturbance-related mechanisms generate nonequilibrium transient states.

Niche-partitioning models predict coexistence of graminoids and trees that arises from differential access to soil water. Grasses are proposed to be better competitors for shallow soil water, while woody vegetation has exclusive access to deep soil water (e.g., Walter 1971; Walker et al. 1981; Walker and Noy-Meir 1982; Casper and Jackson 1997). These soil water–partitioning models, which have been developed largely with reference to arid savannas, may not be broadly applicable to all savannas, which span a range of hydrologic conditions from xeric to seasonally hydric (e.g., Sarmiento 1984; Huber 1987; Platt 1999; Higgins et al. 2000; Drewa et al. 2002). In addition, savannas can occur where soils are shallow or there are pronounced wet and dry seasons, and where differential rooting depths of graminoids and trees may not be possible (Sarmiento and Monasterio 1975; Sarmiento 1984; Doren et al. 1993; Platt et al. 2000).

Disturbance models are based on environmental limits on the ability of competitive dominants (large-stature trees and shrubs) to suppress the graminoid understory. Disturbances (e.g., browsing, fires, hurricanes, droughts) are hypothesized to depress particular life-cycle stages of trees in ways that limit tree density, producing an unsaturated canopy beneath which a graminoid understory can flourish (e.g., Platt et al. 2000; Bond et al. 2003). These disturbances, which are similar only in that they limit the density of trees (Werner 1991; Sankaran et al. 2004; Beckage et al. 2006; Scheiter and Higgins 2007), are postulated to generate savannas over wide ranges of return intervals and under a wide range of environmental conditions as long as effects are noncatastrophic (Platt and Connell 2003). Long-term reductions in frequency of recurrent disturbances are predicted to shift savannas toward forests as

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[*] Corresponding author; e-mail: brian.beckage@uvm.edu.

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closed canopies form and the ground cover becomes suppressed (e.g., Beckage and Stout 2000; Jeltsch et al. 2000; Gilliam et al. 2006). Likewise, long-term increases in frequencies of disturbances that remove trees are predicted to shift savannas toward grasslands (e.g., Beckage et al. 2006; Beckage and Ellingwood 2008). Thus, disturbance models predict that persistence of savannas is facilitated by any recurrent environmental mechanism that negatively but noncatastrophically affects trees and is sensitive to long-term variation in recurrence of disturbance.

Disturbances that change in frequency or intensity as savannas shift toward extremes of grasslands or forests could bound savannas away from alternate grassland or forest states. For example, savannas are predicted to be persistent if external climate maintains disturbance frequency within some bounds, such that savannas are not converted to forest or grassland (e.g., Beckage et al. 2005*a*, 2006; D'Odorico et al. 2006). Extrinsically determined disturbance regimes seem unlikely, however, to maintain such bounds, especially over long time intervals (i.e., millennia or longer) as climate fluctuates (Rahmstorf 2002; Pierce et al. 2004; Schoennagel et al. 2007). Instead, any processes intrinsic to savannas that influence trees in a density-dependent manner (e.g., "density vague" in Strong 1984, 1986; also Stiling 1988; Dayton et al. 1999) might reduce variation in intervals between disturbances and thereby facilitate persistence of savannas (e.g., DeAngelis et al. 1986; Gilliam et al. 2006). Plant species that modify disturbance regimes in a density-dependent way that generates open-canopy conditions favorable for persistence of savannas over long timescales would act as ecosystem engineers (sensu Jones et al. 1994, 1997; Wilby et al. 2001; Reichman and Seabloom 2002; Gutiérrez et al. 2003).

Savanna plant species could act as ecosystem engineers by influencing fire frequency. Fire regimes are not simply an extrinsically determined aspect of the environment (e.g., Simard et al. 1985; Brenner 1991; Beckage and Platt 2003), because the likelihood of fire is influenced by the composition and condition of the vegetation, which provides the fuel for fire (e.g., Platt 1999; van Wilgen et al. 2003; Mermoz et al. 2005). Fire-adapted plant species have life-history traits that protect them from damage. As such, they survive fires, often increasing in abundance as fire frequency increases (e.g., Platt et al. 1988; Brewer and Platt 1994; Beckage and Stout 2000). Some species adapted for fire also have characteristics that facilitate the initiation and spread of fire (Mutch 1970; Rundel 1981; Williamson and Black 1981; Platt et al. 1988; Zedler 1995; Platt 1999; Schwilk 2003; Behm et al. 2004). Thus, increases in abundance of fire-adapted and fire-facilitating species could engineer landscapes toward savannas. Such fire facilitation might maintain savannas by reducing the likelihood of transition to forest, but they might also destabilize savannas by increasing the likelihood of transition to grassland unless self-inhibition occurs as savannas transition toward grasslands.

Not all plants in landscapes that experience fire are fire adapted. Fire-sensitive plant species are susceptible to damage during fires, and these species tend to decline in abundance as fire frequency increases (e.g., D'Antonio and Vitousek 1992; Bond and Midgley 1995; Keeley et al. 2005). Such plant species can also have characteristics that inhibit fire spread; these species are even sometimes referred to as "fire fighting" species (Williamson and Black 1981; Streng and Harcombe 1982; Platt and Schwartz 1990; Cole et al. 1992). Thus, increases in abundance of a fire-intolerant but also fire-inhibiting species could engineer landscapes toward forests. Fire inhibition might stabilize savannas by reducing the transition to grasslands, but it might also destabilize savannas by increasing the transition to forest unless fire-facilitating species are also present.

We investigate effects of vegetation-fire feedbacks on savanna communities, using a system of differential equations. We specifically address two questions: Does facilitation or depression of fire by vegetation stabilize or destabilize savannas? If they stabilize savannas, which feedbacks (i.e., between fire and which vegetation components) increase/decrease persistence of savannas? We consider cases where fire disturbance is facilitated or inhibited through density-dependent vegetation-fire feedbacks. One study of grass-fire feedbacks in a two-state (e.g., grass and trees) demographic savanna model has indicated that vegetation-fire feedbacks might destabilize savanna equilibria (D'Odorico et al. 2006). We expand on these results by exploring a variety of fire-vegetation feedbacks in a three-state model system that includes grass, fire-facilitating savanna trees, and fire-inhibiting forest trees. We specifically examine effects of feedbacks between fire and grass, savanna trees, and forest trees on savanna stability.

Model Description

We represent the dynamics of savannas mathematically, using a set of differential equations. These equations are based on the Lotka-Volterra model of species competition (Kot 2001; van Langevelde et al. 2003; Beckage et al. 2006). We use one differential equation to represent the state of each component of the savanna system: grass, savanna trees, or forest trees. We explore the effects of fire and fire-vegetation feedbacks on the dynamics of the savanna system for this three-state model. We examine positive feedbacks of fire-facilitating vegetation such as grass, savanna trees, or grass and savanna trees considered together, as well as negative feedbacks of fire-inhibiting vegetation—namely, forest trees—on fire frequency (fig. 1). Thus, our designation of trees as fire-facilitating or fire-inhibiting differs from other

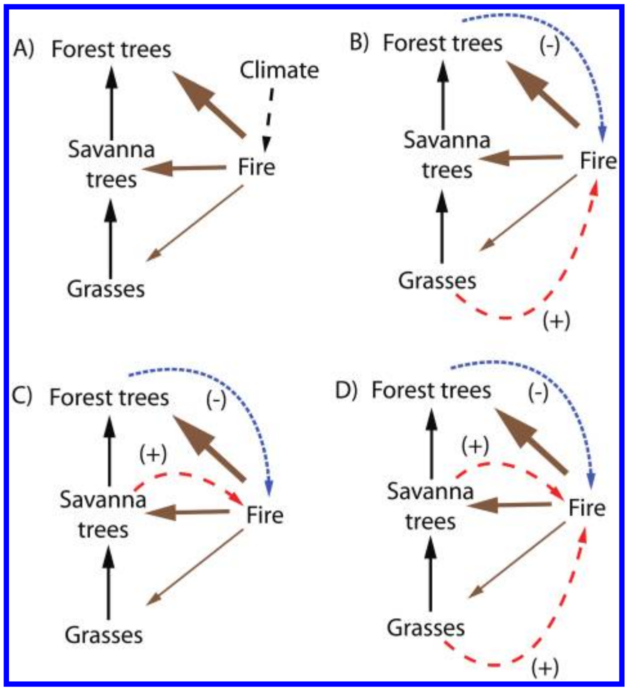

Figure 1: Conceptual model of relationships between fire and vegetation for a three-state system composed of grasses, savanna trees, and forest trees. *A*, Fire frequency is externally determined by climate. *B*–*D*, Fire frequency is determined by positive feedbacks (*red arrows*) with grasses (*B*), savanna trees (*C*), or grasses and savanna trees together (*D*). Forest trees can exert a negative effect (*blue arrows*) on fires in each of the latter three cases. The solid black arrows represent the direction of change in the absence of fire. The brown arrows indicate a negative effect of fire on the given state variable, with the width of the arrow proportional to the strength of the effect. The dashed black arrow in *A* indicates climatic control of fire.

categorizations of trees that are based on resistance or susceptibility to fire (e.g., Gill 1981; Vesk and Westoby 2004).

Our model contains state variables for aboveground biomass of grass, savanna trees, and forest trees. Different combinations of these three components are possible: grass only (grassland); grass and savanna trees (savanna); grass and forest trees (forest savanna); grass, savanna trees, and forest trees (mixed savanna); savanna trees and forest trees (mixed forest); savanna trees only (savanna forest); and forest trees only (forest).

First, we represent the dynamics of the forest trees with the equation

$$\frac{dF}{dt} = r_f F\left(1 - \frac{F}{K_f}\right) - M_f FL(\ ). \tag{1}$$

The left-hand side of equation (1) represents the instantaneous rate of change of aboveground forest tree biomass F (mass/area) in the savanna ecosystem. The right-hand side of equation (1) consists of a growth term where growth of forest tree biomass is described by r_f, which is the intrinsic rate of increase in biomass (1/time), and K_f (mass/area), which is the maximum amount of forest tree biomass that can occur on a given site, that is, the carrying capacity. The growth of forest tree biomass is assumed to be logistic (e.g., Weiner and Thomas 2001; Beckage et al. 2006). The second term on the right-hand side of equation (1) describes the loss of forest tree biomass resulting from the fire frequency $L(\ )$ (in units of 1/time), which may be a function of grass, savanna trees, and/or forest trees. We describe the specific forms of $L(\ )$ below. The variable M_f is a dimensionless constant that represents the proportion of biomass loss with respect to fire for forest trees.

The dynamics of the savanna trees are described by the equation

$$\frac{dS}{dt} = r_s S\left(1 - \frac{S}{K_s} - \frac{F}{K_f}\right) - M_s SL(\ ). \tag{2}$$

The left-hand side of equation (2) again represents the instantaneous rate of change in savanna tree biomass S (mass/area), while the right-hand side contains terms for the growth and loss of savanna tree biomass. Increases in savanna trees are inhibited by the accumulation of forest tree biomass, just as forest trees inhibit forest tree growth in equation (1). In addition, savanna tree growth is also reduced by forest trees, that is, the term F/K_f. The inclusion of this term represents the hierarchical nature of the competitive relationship between savanna and forest trees as observed in savannas of different regions. In the southeastern United States, forest trees are more shade tolerant than savanna trees, and, in the absence of fire, they eventually displace the savanna trees, which are largely unable to regenerate beneath a closed canopy (Veno 1976; Williamson and Black 1981; Gilliam and Platt 1999; Beckage and Stout 2000). Savannas in Africa and Australia are similarly invaded by forest trees in the absence of fire (e.g., Swaine et al. 1992; Luger and Moll 1993; Russell-Smith et al. 2004), and fire prevents the invasion of Brazilian savannas by forest trees (e.g., Hoffman 2000). Forest trees are better competitors for light than are savanna trees; forest trees in some regions, for instance, are twice the height of savanna trees and have greater leaf area and greater allocation to leaves than savanna trees (e.g., Hoffman and Franco 2003). Savanna trees are, in turn, more tolerant of fire than are forest trees because of thicker bark and/or a greater likelihood of resprouting (e.g., William et al. 1998; Platt 1999; Beckage and Stout 2000; Fensham et al. 2003; Hoffman et al. 2003; Bowman 2005). These observations are supportive of a trade-off between competitive ability in low light conditions and fire tolerance, such that forest trees are expected to displace savanna trees in the absence of fire in savannas of North America, South American, Africa, and Australia (Bond et al. 2005).

We do not include a multiplicative factor, α, in F/K_f to modify the strength of the forest tree influence on the savanna trees. Values of α that are <1 would ensure that forest trees could not drive the growth rate of savanna trees to 0. The stability analysis of savanna states performed below would be modified in detail, but not in general form, if an α term were included. The right-hand side of equation (2) also includes a loss term $L(\ )$ that is proportional to fire frequency (described below) and M_s, which is the proportion of biomass loss with respect to fire for savanna trees.

The dynamics of the understory grass layer are described by the equation

$$\frac{dG}{dt} = r_g G\left(1 - \frac{G}{K_g} - \frac{S}{K_s} - \frac{F}{K_f}\right) - M_g GL(\ ). \tag{3}$$

This equation is analogous to equations (1) and (2). Increases in grass biomass are inhibited by grass biomass as well as by savanna tree and forest tree biomass. The inclusion of terms for savanna and forest tree biomass represents a hierarchical ordering of competition between the overstory and the groundcover, where trees shade groundcover vegetation but the groundcover exerts comparatively little effect on the tree layer. For example, the competitive effect of grasses is not strong enough to prevent rapid recruitment of trees into savannas when fire is excluded (Scholes and Archer 1997; Beckage et al. 2006; Gilliam et al. 2006).

We simplified the analysis of this three-state system by first nondimensionalizing the equations, reducing the number of parameters before investigating their behavior (Kot 2001). We made four substitutions into equations (1)–(3) ($T = tr_g$, $g = G/K_g$, $s = S/K_s$, and $f = F/K_f$) to arrive at the following simplified system of equations:

$$\frac{df}{dT} = R_c f(1 - f) - K_A fl(\ ), \tag{4}$$

$$\frac{ds}{dT} = R_b s(1 - s - f) - K_B sl(\ ), \tag{5}$$

$$\frac{dg}{dT} = g(1 - g - s - f) - K_C gl(\ ), \tag{6}$$

where $R_b = r_s/r_g$, $R_c = r_f/r_g$, $K_A = cM_f/r_g$, $K_B = cM_s/r_g$, and $K_C = cM_g/r_g$. (Note that this includes a rescaling of the $L(\ )$ terms to $l(\ )$, as described further below.) The left-hand sides of equations (4)–(6) now represent the rescaled rates of change of forest trees, savanna trees, and grasses, respectively, with the state variables f, s, and g varying on the range (0, 1). This rescaling reduces the number of model parameters, simplifying the analysis. All terms in the rescaled equations (4)–(6) are dimensionless. We present results from the simplified system or the untransformed scales, as appropriate.

We consider forms of the fire frequency function $L(\ )$ to represent hypotheses about the nature of fire-vegetation feedbacks (fig. 1). We use $L(\ )$ terms to represent positive feedbacks on fire frequency as a function of grass, savanna tree, and combined grass and savanna tree biomass, as well as negative feedbacks between forest trees and fire frequency. The five different forms of the fire frequency term $L(\ )$ used in our analyses are as follows:

Climatic control on fire. We consider the case of no feedbacks on fire; in this case, fire regimes are strictly determined by external climatic control (fig. 1*A*). Fire frequency is externally determined from outside the ecological system by a forcing agent such as climate. In this case, $L(\ )$ is a constant ν on the range (0, 1) that represents the frequency of fire with units 1/time.

Grass feedback on fire. Fire frequency is determined by a feedback between fire and grass abundance (fig. 1*B*). In this case, $L(\ )$ is a function of grass biomass only, and we model the loss as $c(G/K_g)$, where c is the fire frequency multiplier, a constant with units 1/time that can increase or decrease the fire frequency associated with a given amount of grass. In this function, fire frequency increases linearly with grass biomass and is bounded by 0 and c, where 0 corresponds to the absence of fire and 1 represents annual fires (assuming the underlying time scale is a year).

Savanna tree feedback on fire. Fire frequency is determined by a feedback between fire and savanna tree biomass (fig. 1*C*). Fire frequency $L(\ )$ is given by $c(S/K_s)$ in a manner analogous to the grass feedback on fire outlined above. Fire frequency is again bounded by 0 and c.

Grass–savanna tree feedback on fire. Fire frequency is determined by a feedback between fire and joint grass–savanna tree biomass (fig. 1*D*). In this case, we assume that $L(\ )$ is proportional to the product of the grass and savanna tree biomasses, for example, $c[(G/K_g)(S/K_s)]$, and we again include a fire frequency multiplier c. Fire frequency reaches a maximum in a savanna site where both grasses and savanna trees are present at intermediate values relative to their carrying capacities.

Forest tree feedback on fire. We allow forest trees to exert a negative effect on fire frequency by modifying the feedback between fire and grass and savanna trees. We include the effect of forest trees on the fire-vegetation feedbacks above by multiplying each $L(\ )$ described above by the additional term $1 - F/K_f$, so that fire frequency declines with increasing forest tree biomass. Thus, fire frequency approaches 0 as $F \rightarrow K_f$.

Table 1: Predicted stable savanna states for different vegetation-fire feedbacks

Positive feedback of fire with	Stable savanna state	Other stable states
No feedback	$(g^*, s^*, f^*) = (\nu(M_s/r_s - M_g/r_g), 1 - (\nu M_s/r_s), 0)$	Grassland, mixed savanna, forest savanna, mixed forest, and forest
Grass	Not present	Grassland: $(g^*, s^*, f^*) = (r_g/(cM_g + r_g), 0, 0)$; forest: $(g^*, s^*, f^*) = (0, 0, 1)$
Savanna tree	$(g^*, s^*, f^*) = (c(M_s r_g - M_g r_s)/r_g(cM_s + r_s), r_s/(cM_s + r_s), 0)$	Savanna forest: $(g^*, s^*, f^*) = (0, r_s/(cM_s + r_s), 0)$; forest: $(g^*, s^*, f^*) = (0, 0, 1)$
Grass + savanna tree	$(g^*, s^*, f^*) = (1 - r_s(cM_g + r_g)/cM_s r_g, r_g r_s/c(M_s r_g - M_g r_s), 0)$	Forest[a]

Note: All equilibria are locally stable. We do not show trivial equilibria that lack any vegetation.

[a] We were unable to find any regions of parameter space that supported a mixture of grasses, savanna trees, and forest trees, but we were not able to exclude this possibility.

We analyzed the resulting systems of equations to determine the local stability of equilibrium solutions when grass and savanna trees coexist, which is our definition of a savanna. The local stability of an equilibrium indicates whether the system will tend to return to that equilibrium if the system is slightly perturbed or, instead, continue to move farther away. The equilibria of the three-state system are first found by setting $dG/dt = 0$, $dS/dt = 0$, and $dF/dt = 0$ and then solving for all three state variables. The local stability of the equilibria is determined by the eigenvalues of the Jacobian $\mathbf{J}$:

$$\mathbf{J} = \begin{bmatrix} \dfrac{\partial(dG/dt)}{\partial G} & \dfrac{\partial(dG/dt)}{\partial S} & \dfrac{\partial(dG/dt)}{\partial F} \\ \dfrac{\partial(dS/dt)}{\partial G} & \dfrac{\partial(dS/dt)}{\partial S} & \dfrac{\partial(dS/dt)}{\partial F} \\ \dfrac{\partial(dF/dt)}{\partial G} & \dfrac{\partial(dF/dt)}{\partial S} & \dfrac{\partial(dF/dt)}{\partial F} \end{bmatrix},$$

which is evaluated at each of i equilibrium points (G^i, S^i, F^i; Kot 2001). The eigenvalues are calculated by solving the characteristic equation corresponding to $\det(\mathbf{J}_i^* - \lambda\mathbf{I}) = 0$, where $\mathbf{J}_i^*$ is the Jacobian evaluated at equilibrium point i. An equilibrium solution is stable when the real component of all three eigenvalues is <0, unstable if the real component of any of the eigenvalues is >0, and of ambiguous stability if some of the eigenvalues have a negative real part while others have a 0 real part. In the third case, we examined the phase plane to ascertain stability of the equilibrium. Purely imaginary eigenvalues indicate neutrally stable equilibria. We illustrate model results by indicating conditions for stable solutions and displaying regions of parameter space that lead to locally stable solutions in a savanna state. In cases where the analytical solutions were complicated, we numerically integrated the system of equations to determine the final system state after 1,000 years (assuming the underlying timescale is a year).

All of the model formulations considered here are competitive dynamical systems (Hirsch 1988), and, thus, any solution approaches an equilibrium point (e.g., no limit cycles or strange attractors exist). Multiple equilibria do exist, however, so that the long-term behavior (e.g., which equilibrium is approached) can depend on initial conditions. We provide analytical conditions on parameters that lead to stability of a single equilibrium and explore sensitivity to initial conditions using numerical simulations.

Results

Our model system results in a stable forest without grasses or savanna trees in the absence of fire. In the presence of fire, we predict multiple stable states that depend on the feedback involved. We provide the stable savanna states, as well as stable grassland and forest states, for each of the four determinants of fire frequency: no feedback plus feedbacks of grass, savanna trees, and grass and savanna trees together (table 1).

No Feedback

The addition of extrinsically driven fires, without vegetation-fire feedbacks, can produce a stable savanna with co-occurring grasses and savanna trees. The savanna equilibrium is stable as long as

$$\frac{r_f}{M_f} < \nu < \frac{r_s}{M_s} < \frac{r_g}{M_g}. \tag{7}$$

This condition indicates that (1) the ratio of intrinsic growth to mortality for forest trees must be less than the fire frequency ν, (2) the same ratio for savanna trees must be greater than the fire frequency, and (3) this ratio for grasses must be greater than that for savanna trees. We found no evidence of sensitivity to initial conditions or any resulting hysteresis for this model system. More frequent fire results in a shift toward a grassland state, and less frequent fire moves the system to a mixed savanna and then toward a mixed forest (fig. 2). A forest without savanna trees is not reached in our model when $r_f/M_f < r_s/M_s < r_g/M_g$, as in equation (7), as long as fires occur (however infrequently). Persistence of savanna trees in landscapes at very low fire frequencies would require some spatial refuge or long-term source of seeds to be maintained. For example, if fire occurred at intervals longer than the biological life spans of forest trees but not longer than those of savanna trees, then seed sources of the savanna trees could be maintained even at low fire frequencies (Platt 1999).

Grass Feedbacks on Fire Frequency

A feedback in which grasses increase fire frequency does not result in a stable savanna in our three-state system. Instead, stable equilibria occur in either a grassland or forest state (table 1), and the system transitions abruptly from a grassland to a forest with changes in fire frequency (fig. 3). The rapid community transition found in this model system, compared with the more gradual changes in community state associated with strict climatic control of fire frequency (e.g., fig. 2), result from the grass-fire feedback: increasing fire frequency leads to more grass that, in turn, results in a higher frequency of fire. This feedback loop results in a nonlinear transition from a forest to a grassland. The location of the threshold fire frequency, across which the system changes state, is dependent on initial conditions (fig. 3*A*, 3*C*, 3*E*): the threshold occurs at lower fire frequencies with an initial state dominated by grass than with one dominated by forest trees. The inclusion of a negative feedback of forest trees on fire, in addition to the positive grass-fire feedback, does not result in a savanna, but it does have a strong influence on the location of the threshold (fig. 3*B*, 3*D*, 3*F*). The negative feedback of forest trees on fire shifts the threshold between grassland and forest to higher fire frequency; the magnitude of this shift in threshold to higher fire frequency increases with the relative fraction of forest trees in the initial community (fig. 3*B*, 3*D*, 3*F*).

The sensitivity to initial conditions creates a hysteresis and the potential for alternative stable states at the same fire frequency. The ecological state of the system, represented as the grass fraction, is dependent not only on fire frequency but also on initial conditions and direction of change in fire frequencies. If the system begins in a grassland state, then fire frequency must be reduced to low levels before the ecosystem will convert to a forest with a low grass frac-

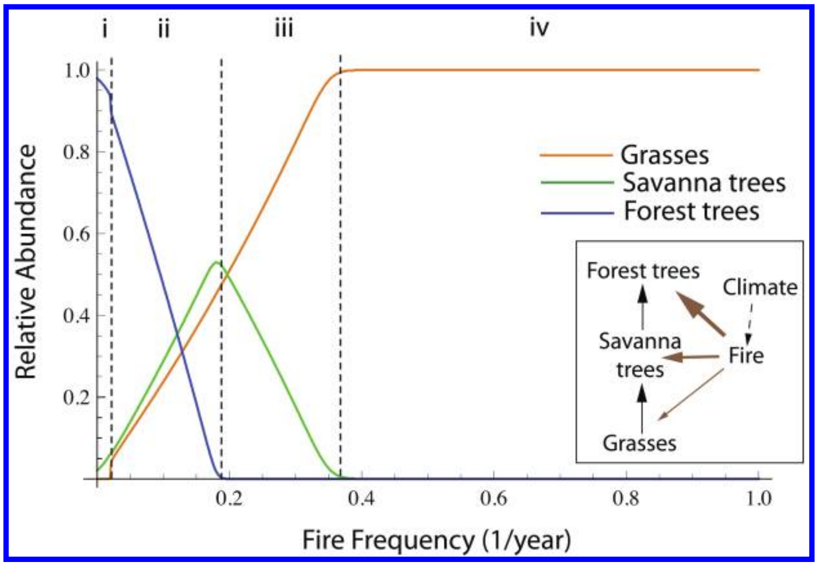

Figure 2: Relative biomass of grass, savanna trees, and forest trees at equilibrium as a function of fire frequency in the absence of vegetation-fire feedbacks, as predicted in our model. Fire frequency (year^{-1}) varies along the *X*-axis from no fire (*left*; 0 year^{-1}) to annual fires (*right*; 1 year^{-1}), with corresponding changes in relative abundance of grasses, savanna trees, and forest trees along the *Y*-axis. Grasslands occur at high fire frequencies (region *iv*), savannas (e.g., grasses + savanna trees) are found at intermediate fire frequencies (region *iii*), and mixed savannas (e.g., grasses + savanna trees + forest trees) occur at lower fire frequencies (region *ii*). As fire frequency approaches 0, grasses disappear and savanna trees decline (region *i*). The relative abundances shown were calculated from numerical integrations of the system of differential equations to 1,000 years using the following parameters: $r_g = 1.5$, $M_g = 0.95$, $r_s = 0.7$, $M_s = 0.2$, $r_f = 0.09$, and $M_f = 0.5$. These parameter values satisfy equation (7) for a fire frequency that is between 0.18 and 0.35. The nondimensionalized state variables (g, s, and f) were then normalized to sum to 1 and are reported as relative abundances. The inset corresponds to the appropriate conceptual model from figure 1 that describes fire frequency.

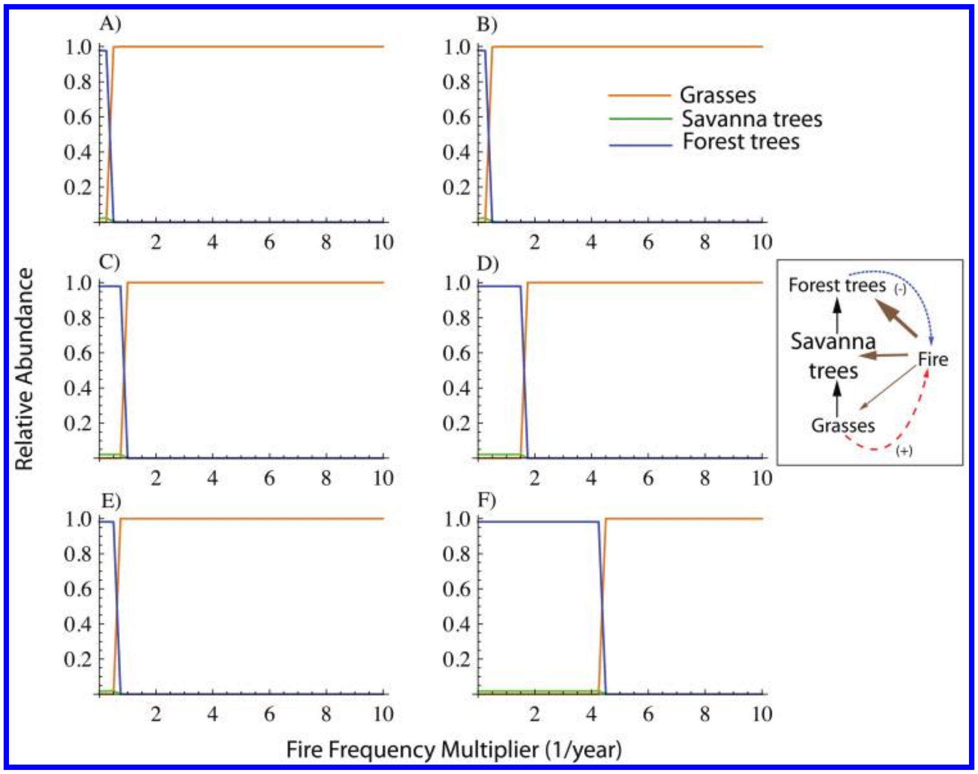

Figure 3: Relative biomass of grass, savanna trees, and forest trees when fire frequency is determined by a feedback with grass alone (*A*, *C*, *E*) or with a negative forest tree feedback (*B*, *D*, *F*). The initial state of the simulations was varied across the three rows of panels: *A* and *B* began with a grassland initial state (the initial values of (g, s, f) were (0.9, 0.1, 0.1)), *C* and *D* had a mixed initial state ((g, s, f) were (0.5, 0.5, 0.5)), and *E* and *F* had a forest tree initial state ((g, s, f) were (0.1, 0.1, 0.9)). The value of the fire frequency multiplier (i.e., c in the loss terms outlined in "Model Description") is varied on the *X*-axis: higher values of the fire frequency multiplier correspond to a higher fire frequency. The relative abundances shown were calculated with the same parameter values as in figure 2, and the nondimensionalized state variables were normalized to show relative abundances. The inset corresponds to the appropriate conceptual model from figure 1 that describes fire frequency.

tion. This is because the high fraction of the grass component facilitates the occurrence of fire. In contrast, if the initial condition is a forest state that does not facilitate fire, higher fire frequencies are required to convert the system to grassland. Both grassland and forest states can occur at intermediate fire frequencies between the two bounding fire frequencies that define the ecological thresholds.

Savanna Tree Feedbacks on Fire Frequency

A positive feedback of savanna trees on fire frequency can result in a stable equilibrium in a savanna state in addition to grassland and forest states (table 1). The savanna is stable as long as $cM_g r_s/r_g^2 < cM_s/r_g < cM_f r_s/r_g r_f - r_s/r_g$. The savanna tree component of the savanna gradually increases and the grass component declines with decreasing fire frequency until an ecological threshold is reached, at which point the community is abruptly transformed into a closed forest (fig. 4). The location of the threshold fire frequency is again dependent on initial conditions (fig. 4*A*, 4*C*, 4*E*), which occur at lower fire frequencies with an initial state dominated by grass than with one dominated by forest trees, creating the potential for a hysteresis and alternative stable states. The addition of a negative feedback of forest trees on fire still allows for the stable equilibrium in a savanna state, changing neither the location nor the criteria for stability of the equilibrium but influencing the location of the ecological threshold (fig. 4*B*, 4*D*, 4*F*): higher relative abundances of forest trees move the threshold to higher fire frequencies, particularly with a negative feedback of forest trees on fire.

Grass–Savanna Tree Feedbacks on Fire Frequency

A stable equilibrium in a savanna state is also possible when fire frequency is determined jointly by a feedback with grass and savanna trees (table 1). We did not establish the analytical conditions for the stability of this solution,

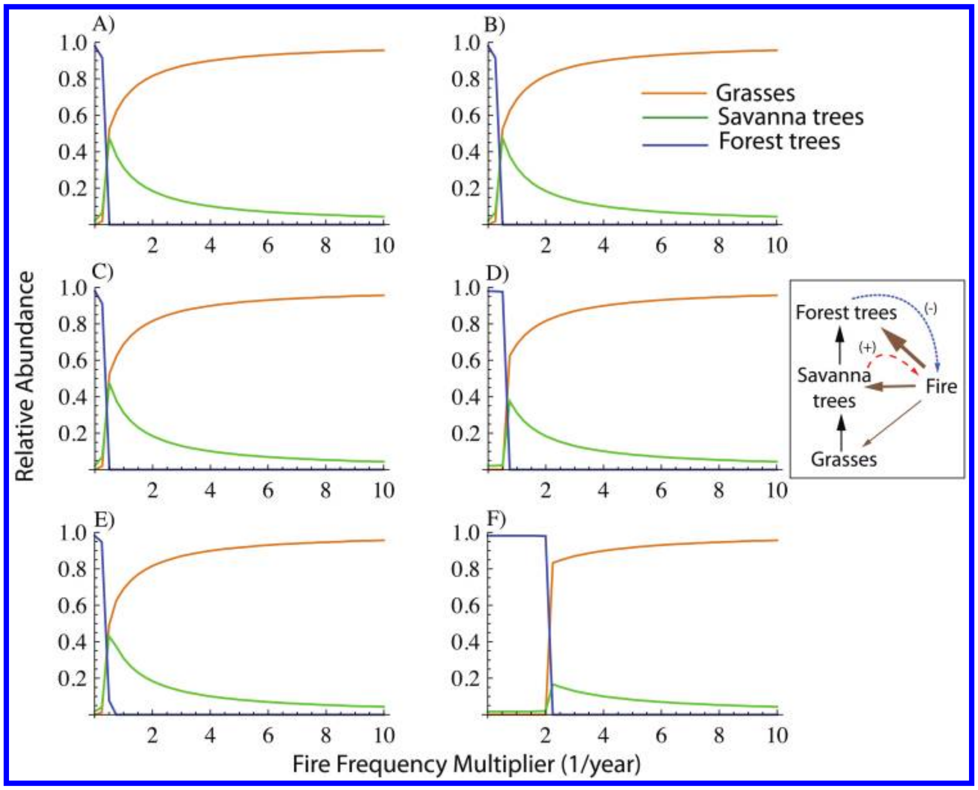

Figure 4: Relative biomass of grass, savanna trees, and forest trees when fire frequency is determined by a feedback with savanna trees alone (*A*, *C*, *E*) or with an additional negative forest tree feedback (*B*, *D*, *F*). The initial condition of the simulated community was grassland (*A*, *B*), mixed (*C*, *D*), or forest (*E*, *F*), as described in figure 3. A savanna tree–fire feedback can result in a savanna, but the savanna abruptly transitions to a forest with decreasing fire frequency. The location of the threshold is sensitive to the initial system state: the threshold shifts to higher fire frequencies as the initial grass component declines and the forest tree component increases. This shift in threshold location with increasing forest tree fraction is particularly pronounced in the presence of the negative feedback of forest trees on fire (*B*, *D*, *F*). The inset corresponds to the appropriate conceptual model from figure 1 that describes fire frequency.

but we were able to numerically explore the range of parameter space leading to a savanna as well as establish the sensitivity to initial conditions (fig. 5*A*, 5*C*, 5*E*). The addition of a negative forest tree feedback on fire frequency still allows for the stable equilibrium in a savanna state but shifts the region of parameter space supporting a savanna (fig. 5*B*, 5*D*), and it completely eliminates the potential for a savanna in some regions of parameter space (fig. 5*F*). The savanna tree component of the savanna equilibrium increases and the grass component declines with decreasing fire frequency until a threshold is reached where the community abruptly transitions to a forest (fig. 6). The location of the threshold again depends on both initial conditions (fig. 6*A*, 6*C*, 6*E*) and the presence of a negative feedback of forest trees on fire frequencies (fig. 6*B*, 6*D*, 6*F*), creating the potential for a hysteresis and alternative stable states. The threshold exhibits larger shifts in location in response to initial conditions and the presence of a negative forest tree feedback (e.g., fig. 6*F*) than it does with the grass-fire (i.e., fig. 3) or savanna tree–fire feedbacks (i.e., fig. 4).

Discussion

We used an analytical three-state demographic model of savanna dynamics to explore the hypothesis that vegetation-fire feedbacks could lead to stable, persistent savannas. Previous studies that have examined grass-fire feedbacks in two-state model systems have concluded that these feedbacks are destabilizing to savannas (D'Odorico et al. 2006) but that they can lead to sudden shifts in states even where models involve soil water niche partitioning (van Langevelde et al. 2003). We also find that grass-fire feedbacks do not lead to a stable savanna in our model (although they do stabilize grasslands). A broader suite of vegetation feedbacks in a more complex system (e.g., three rather than two state variables), however, can potentially generate stable savannas. We show that feedbacks between

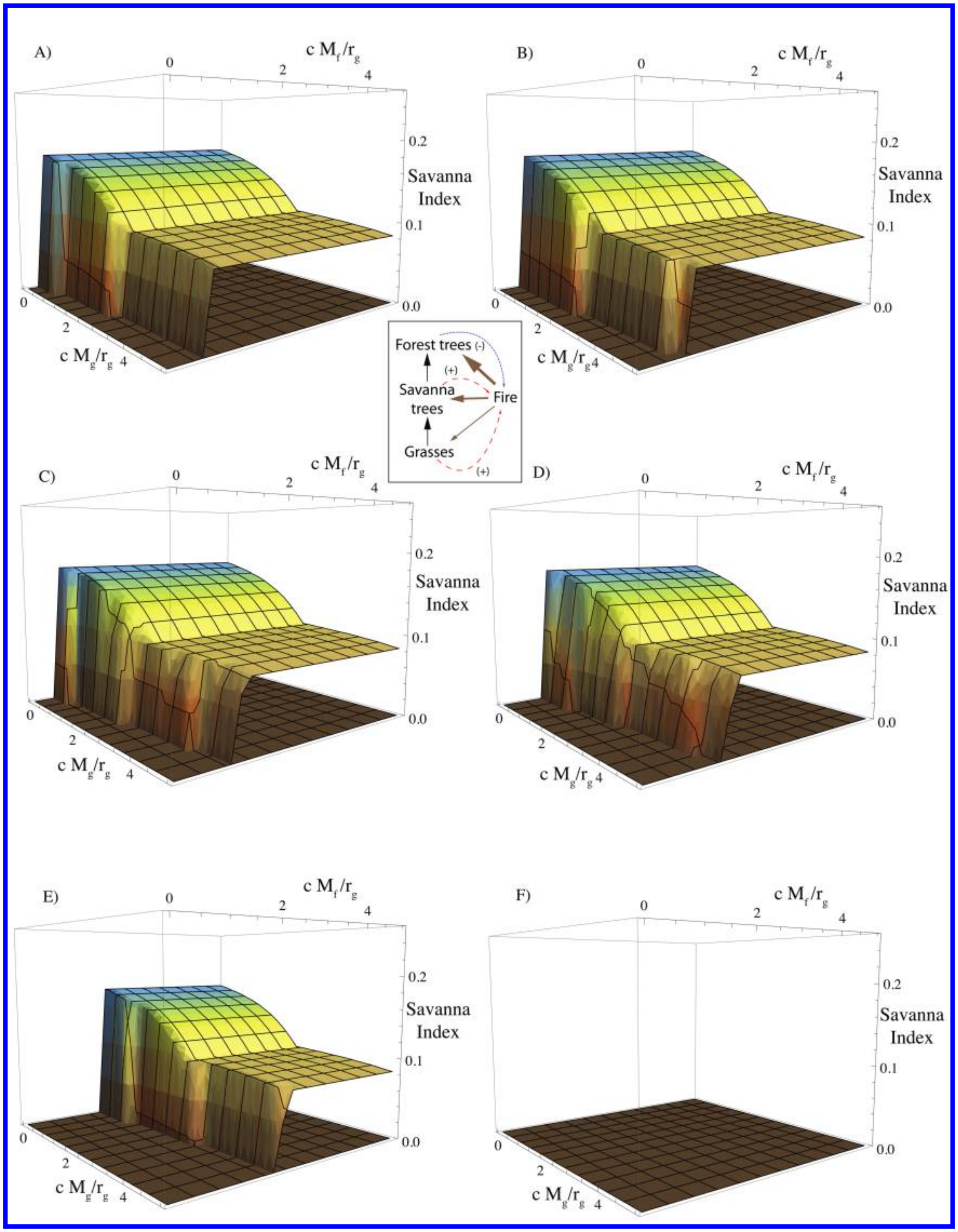

Figure 5: The range of parameter space that supports a savanna is shown for the case of a positive grass–savanna tree feedback on fire frequency alone (*A*, *C*, *E*) or with an additional negative forest tree feedback on fire frequency (*B*, *D*, *F*). The *X*- and *Y*-axes of the figure panels represent the variables K_A (i.e., cM_f/r_g) and K_C (i.e., cM_g/r_g) from the nondimensionalized equations (4)–(6). The *Z*-axis indicates the range of a "savanna index," given by $gs(1 - f)$ across the third variable, K_B (i.e., cM_s/r_g). The final two variables in the nondimensionalized equations, R_b (i.e., r_s/r_g) and R_c (i.e., r_f/r_g), are determined by the intrinsic growth rates, which were set to the values $r_g = 1.5$, $r_s = 0.07$, and $r_f = 0.09$, as in previous figures. The simulated communities were initially in a grassland (*A*, *B*), mixed (*C*, *D*), or forest (*E*, *F*) state, as described in figure 3. The region of parameter space that supports savannas declines as the initial forest tree fraction increases (from top to bottom row), and this pattern is more pronounced in the presence of a negative feedback of forest trees on fire frequency (*B*, *D*, *F*). In *F*, in fact, no region of parameter space supports a savanna. The inset corresponds to the appropriate conceptual model from figure 1 that describes fire frequency.

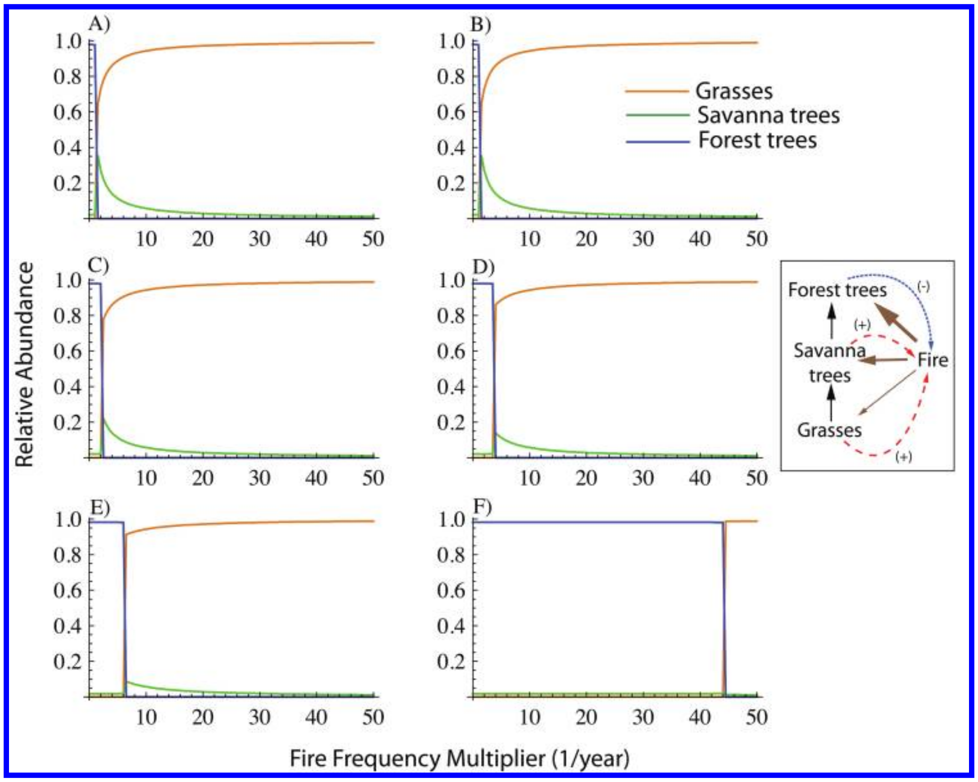

Figure 6: Relative biomass of grass, savanna trees, and forest trees when fire frequency is determined by a feedback with grass and savanna trees only (*A*, *C*, *E*) or with an additional negative feedback of forest trees (*B*, *D*, *F*). The initial condition of the simulated community was grassland (*A*, *B*), mixed (*C*, *D*), or forest (*E*, *F*), as described in figure 3. A grass–savanna tree feedback on fire frequency can maintain the system as a savanna, but the transition to forest occurs at higher fire frequencies than in a system with a solely savanna tree feedback on fire frequency. The location of the threshold is sensitive to both a negative feedback of forest trees on fire (*B*, *D*, *F*) and the initial community state (grassland, mixed, or forests, from the top to bottom). A savanna state was absent from panel *F*: the system transitioned directly from a grassland to forest. The inset corresponds to the appropriate conceptual model from figure 1 that describes fire frequency.

fire and savanna trees or between fire and grasses and savanna trees together can result in persistent savannas. Previous savanna models generated only disequilibrium communities, suggesting that niche-partitioning models were required to produce stable savannas (van Langevelde et al. 2003; Sankaran et al. 2004). Although fire has long been recognized as an important determinant of savanna communities (e.g., Chapman 1932*a*, 1932*b*) and it is influenced by some savanna tree species (e.g., Platt 1999; Bond et al. 2005), fire regimes have largely been modeled as environmental characteristics that are external to savanna systems (e.g., Brenner 1991; Jeltsch et al. 2000; Beckage and Platt 2003; Beckage et al. 2005*b*). We designate these as "climatic equilibria" in the sense that the presence of savannas is determined by strict climatic control of fire regimes (Beckage et al. 2003, 2006). In the absence of a vegetation-fire feedback, the savanna state is stable as long as fire frequency is maintained within specified bounds by climatic conditions.

We identified two potential fire-vegetation feedbacks that can stabilize savannas: fire and savanna trees alone and fire with savanna trees and grasses together. In both cases, the magnitude of the loss term for the savanna overstory in our model is driven by savanna tree abundance, at least in part, so that the savanna trees indirectly limit their own populations through a positive feedback with fire frequency. More savanna trees result in a higher fire frequency that, in turn, results in greater mortality of savanna trees (primarily of juveniles; e.g., Rebertus et al. 1993; Grace and Platt 1995; Brockway et al. 2006), limiting the abundance of savanna trees in a "density-vague" manner similar to that proposed by Strong (1984, 1986).

These vegetation-fire feedbacks combine with three other aspects of our model to stabilize savannas. (1) Hierarchical competition favors the overstory at the expense of the grass layer. This results in gradual displacement of grasses by trees in the absence of disturbance. (2) Trees, but not grasses, are negatively affected by fire: increasing/

decreasing fire frequency should decrease/increase tree densities, but it should not directly affect grasses (e.g., Setterfield 2002). (3) The competitive relationship between fire-resistant savanna trees and fire-sensitive forest trees is structured by a trade-off between traits that confer resistance to fire at the expense of competitive ability in the absence of fire. Savanna trees have a host of adaptations that confer resistance to fire, including thicker bark (that offers protection from high temperatures in fire), greater allocation of biomass to roots (to facilitate resprouting after fire damage), and seedling characteristics that protect against fire. Savanna trees are therefore more resistant to fire than are forest trees, which suffer relatively high rates of mortality in fires (e.g., Platt 1999; Hoffman 2000; Hoffman and Franco 2003; Hoffman et al. 2003). Forests trees, in contrast, have characteristics that result in competitive advantages in low-light environments (e.g, forests), such as greater allocation to leaves and greater height (Hoffman and Franco 2003; Hoffman et al. 2003). The facilitation of fire by savanna trees in our model limits their populations, but it also prevents their extirpation by less fire-tolerant but competitively superior forest trees. The feedback of savanna trees (with or without grasses) on fire frequency also allows the grass layer to persist with the savanna trees by limiting overstory density and maintaining the community as a savanna.

Our model results suggest a scenario for development of savannas. Populations of graminoids benefit from traits that facilitate fire; a feedback between fire and grasses promotes a grassland state without fire-intolerant trees (Platt and Gottschalk 2001; Keeley and Rundel 2005). In this case, our model indicates that the landscape can be in one of two states: fire-facilitating grassland or closed forest. Savanna trees with traits that enhance fire tolerance at the expense of competitive ability in the absence of fire but do not promote fire should not persist in the presence of fire-intolerant, competitively superior hardwoods. Such a hypothetical tree species would be predicted to displace the grass component, reducing the frequency of fire and then eliminating fire completely, before being extirpated by competitively superior fire-intolerant forest tree species. The community would eventually become a forest. This is the replacement sequence observed in the southeastern United States for fire-tolerant trees (e.g., some oaks) that do not facilitate fire (e.g., Veno 1976; Landers 1991). If a hypothetical tree species instead promoted fire, in addition to being resistant to fire damage (sensu Platt 1999), then the outcome based on our model would be a stable savanna. The savanna tree would initially invade a grassland, but it would facilitate frequent fires, preventing the conversion to a forest and concurrently limiting its own density, thus maintaining an open canopy in which a grass groundcover would be persistent. The result would be the co-occurrence of savanna trees and grasses that each promote fire to form a stable savanna.

We suggest that fire-facilitating savanna tree species are ecosystem engineers (sensu Jones et al. 1994) that modify characteristics of fire regimes in their environment. Empirical studies support the concept that savanna trees contribute to frequent low-intensity fires. For example, savanna species that facilitate fire in savannas in the southeastern U.S. include the longleaf pine (*Pinus palustris*), the south Florida slash pine (*Pinus elliottii* var. *densa*), some oaks (e.g., *Quercus laevis*), and warm-season grasses (Williamson and Black 1981; Platt et al. 1988; Rebertus et al. 1989; Platt 1999; Kane et al. 2008). Similar species occur in other ecosystems (e.g., Bond and van Wilgen 1995; Garder 2006). Savanna trees such as longleaf and south Florida slash pines shed their needles more frequently than do nonsavanna pines (Mirov 1967; Landers 1991), adding substantially to fire fuel loads (Herndon and Taylor 1985), which results in increased fire temperatures and fire spread that is more uniform (Rebertus et al. 1989; Glitzenstein et al. 1995; Grace and Platt 1995). Savanna trees may also be more likely to convert lightning strikes into fires because of resin-rich boles (Platt et al. 1988). Savanna trees are also more resistant to fire damage than are forest trees (Hoffman 2000; Hoffman et al. 2003; Gilliam et al. 2006). The implication is that savanna trees may facilitate frequent low-intensity fires by shedding large amounts of pyrogenic litter, creating continuous fuels that promote fire spread (Platt et al. 1988; Glitzenstein et al. 1995; Slocum et al. 2003; Kane et al. 2008), particularly when they are combined with grasses and herbaceous groundcover that provide a matrix of well-aerated fine fuels (Thaxton and Platt 2006). The likelihood of fire spread across the landscape increases as these fuels accumulate (Higgins et al. 2000; Platt and Gottschalk 2001), and the resultant high frequencies of fire favor savanna trees that are resistant to fire damage over less fire-tolerant species (Williamson and Black 1981; Rebertus et al. 1989; Glitzenstein et al. 1995). The evolution of fire-facilitating traits in savanna trees, while controversial, has empirical support (Mutch 1970; Williamson and Black 1981; Platt et al. 1991; Kane et al. 2008), and it does not require group selection arguments (Bond and Midgley 1995). The resin content, the bark thickness, and the frequency of fires experienced by some savanna trees all covary, for example, suggesting adaptations for facilitating and resisting frequent fires (Mutch 1970; Landers 1991; Richardson 2000). Thus, savanna species could act as ecosystem engineers that facilitate fire, resulting in savannas in landscapes that would otherwise become closed forests.

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