

Effects of Tree Harvest on the Stable-State Dynamics of Savanna and Forest

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ABSTRACT: Contemporary theory on the maintenance and stability of the savanna biome has focused extensively on how climate and disturbances interact to affect tree growth and demography. In particular, the role of fire in reducing tree cover from climatic maxima is now well appreciated, and in certain cases, herbivory also strongly affects tree cover. However, in African savannas and forests, harvest of trees by humans for cooking and heating is an oft overlooked disturbance. Thus, we incorporate tree harvest into a population dynamic model of grasses, savanna saplings, savanna trees, and forest trees. We use assumptions about the differential demographic responses of savanna trees and forest trees to harvest to show how tree harvest influences tree cover, demography, and community composition. Tree harvest can erode the intrinsic basin of attraction for forest and make a state transition via fire to savanna more likely. The savanna state is generally resilient to all but high levels of tree harvest because of the resprouting abilities of savanna trees. In the absence of active fire suppression, our analysis suggests that we can expect to see large and potentially irreversible shifts from forest to savanna as demand increases for charcoal in sub-Saharan Africa. On the other hand, savanna tree species' traits promote savanna stability in the face of low to moderate harvest pressure.

Keywords: alternative stable states, savanna, forest, tree harvest, fire, fuelwood.

Introduction

Intuitively, tree harvest will impact savannas and forests by directly removing biomass. But does tree harvest affect the stability and demographic dynamics of savannas and forests? This is important to consider because contemporary theory suggests that the savanna biome is maintained by demographic bottlenecks that are (1) removed at low rainfall to promote seedling establishment and (2) imposed at intermediate and high rainfall to prevent canopy clo-

sure (Sankaran et al. 2004). In fact, where rainfall is high enough to support a closed-canopy forest, savanna often persists (Sankaran et al. 2005; Lehmann et al. 2011). Such observations imply a large role for disturbance. Thus far, tree harvest by humans has been overlooked as a disturbance in savannas, with most researchers focusing on fire and herbivory.

Disturbance by fire can maintain the savanna state by excluding forest trees and limiting savanna sapling recruitment to adult size classes. As a functional type, forest trees suffer increased mortality following fires relative to savanna trees and tend to resprout less vigorously (Hoffmann et al. 2003, 2012). Thus, under frequent fire, even if the climate favors forest trees, savanna trees will dominate. A shift to the savanna state results in a positive feedback wherein fire reduces tree densities and increases grass cover, which leads to more frequent fires (Higgins et al. 2000, 2010; Sankaran et al. 2004; Bond 2008; Hanan et al. 2008). At low and high rainfall, savanna and forest are climax biomes, respectively, but at intermediate rainfall, they represent alternative stable states (Beckage et al. 2009; Hirota et al. 2011; Staver et al. 2011b; Hoffmann et al. 2012).

Recent observational evidence also points toward savanna and grassland as alternative stable states at the arid end of the distribution (Hirota et al. 2011). However, compelling evidence for a mechanism that delineates savanna and grassland as alternative stable states is lacking, and the observational evidence provided by Hirota et al. (2011) may be subject to nonrandom errors that artificially impose discontinuities in continuous data (Hanan et al. 2014). In arid and semiarid savannas, occasional or frequent fire and/or persistent drought can completely eliminate trees if the death rate of savanna trees exceeds recruitment (Higgins et al. 2010), but whether the treeless state is continuous with savanna or represents a true alternative stable state requiring amplifying feedbacks—not simple density dependence—remains unknown (but see van Nes et al. 2014 for a proposed mechanism).

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Even within the stable savannas (i.e., savannas that exist as the climax state in lower rainfall regions [Sankaran et al. 2005]), tree cover and biomass can vary widely, depending on not only climate but also other disturbances. In addition to fire, herbivory has been invoked to explain tree cover in savannas (Scholes and Archer 1997; Bucini and Hanan 2007; Staver et al. 2009), but clear evidence is lacking for any consistent effect of herbivory in controlling the distribution of forest, savanna, and grassland at large spatial extents (Murphy and Bowman 2012). Grazing primarily influences tree cover indirectly by reducing fuel loads and fire frequency or intensity (Scholes and Archer 1997). Browsing—especially by large mammals, such as elephants or giraffes—can have impacts on tree cover (Asner et al. 2009; Staver et al. 2009; Staver and Bond 2014), but these effects are location dependent and tend not to generalize to all savannas.

Although tropical savannas represent some of the most densely populated biomes, most ecological research has focused on natural or intact savannas and forests, either implicitly or explicitly ignoring the role humans play in shaping vegetation structure and biome distributions. Recent work indicates how human manipulation of fire may have aided savanna expansion (Archibald et al. 2012), but most other human impacts have not been explicitly considered in models of savanna and forest vegetation (e.g., Murphy and Bowman 2012; Staver and Levin 2012).

In particular, there is a need to integrate human activities that directly affect tree abundance, biomass, and demography into theoretical models of grassland, savanna, and forest dynamics. Without such theoretical integration, we lack the ability to delineate the stability and dynamics of these states in reference to real world systems inhabited and influenced by humans. Fuelwood is the dominant source of energy in sub-Saharan Africa (Bailis et al. 2005; Arnold et al. 2006), so it is important to consider the mechanism by which tree harvest influences vegetation in savannas and forests, especially since recent advances in savanna ecology make clear the importance of demographic processes (Higgins et al. 2000, 2007; Sankaran et al. 2004; Hanan et al. 2008). Just as fire has differential effects on savanna and forest trees, we can expect similar dynamics in response to tree harvest.

To examine the effect of tree harvest on the stability of savanna and forest systems, we extend the population dynamic model of Staver and Levin (2012) by incorporating tree harvest on the basis of assumptions of the different resprouting abilities of forest and savanna trees after a harvest event. By including tree harvest, we can investigate how human activities may interact with other processes (fire, drought) to cause transitions from forest to savanna and from savanna to grassland. We use the model to address two questions: (1) Does tree harvest change the stable

state dynamics at the grassland-savanna ecotone and the savanna-forest ecotone? (2) Are climax savannas, which are highly populated, vulnerable to large reductions in tree cover under tree harvest? We find that (1) tree harvest can erode stability basins and make transitions to low tree abundance states via fire and drought more probable but that (2) the morphological and physiological adaptations of savanna tree species to fire increases the resilience of savannas to moderate wood harvest intensity.

Methods

Modeling Framework

We build on the modeling framework of Staver and Levin (2012) and add a tree harvest term (ρ ; fig. 1A). The model is not spatially explicit but assumes that all space is occu-

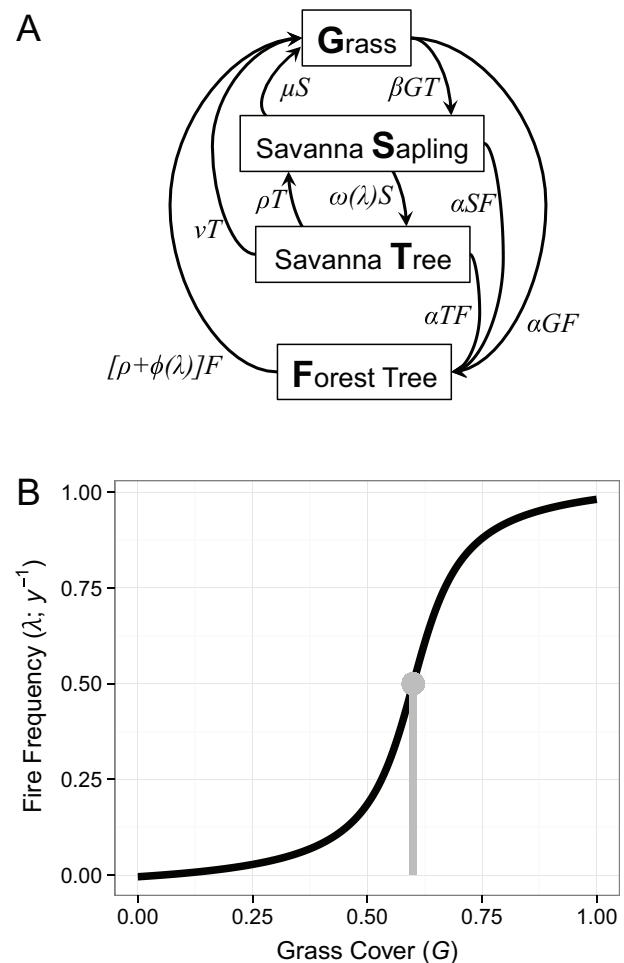


Figure 1: Conceptual diagram of the modified model (A) and functional form of fire probability (λ ; B). λ increases with grass cover (G) with a threshold response at 60% grass cover (i.e., 40% tree cover, shown by vertical gray line; see eq. [5]).

pied by some proportion of grass (G), savanna saplings (S), savanna trees (T), or forest trees (F), with grass being the default. The full model, following the notation of Staver and Levin (2012), is specified as four differential equations that sum to 0:

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

$$\frac{dS}{dt} = \beta GT + \rho T - \omega(\lambda)S - \mu S - \alpha SF, \quad (2)$$

$$\frac{dT}{dt} = \omega(\lambda)S - (\nu + \rho)T - \alpha TF, \quad (3)$$

$$\frac{dF}{dt} = \{\alpha(1 - F) - [\phi(\lambda) + \rho]\}F. \quad (4)$$

All terms are as in Staver and Levin's model (table 1), with two additions: wood harvest (ρ) and a modified fire frequency term (λ). Grass (G) is the default state: any space occupied by savanna saplings (S), savanna trees (T), or forest trees (F) reverts to grass upon mortality. This is true except for the special case of wood harvest, where adult savanna trees revert to the sapling state (empirical support for this assumption is described below). An implicit spatial competitive hierarchy is created by allowing only savanna saplings to establish in space occupied by grass, whereas forest trees can establish on areas occupied by grass or savanna saplings and trees. Savanna sapling establishment (β) and forest tree establishment (α) are constant rates relative to the propor-

tion of savanna adult trees and forest trees, respectively. Recruitment of savanna saplings to adult trees is mediated by fire frequency ($\omega(\lambda)$) and thus grass cover (fig. 1B), because fire limits sapling recruitment. Mortality of savanna trees (ν) is constant and proportional to occupied area. Mortality of forest trees is conditional upon fire frequency ($\phi(\lambda)$) and proportional to occupied area. Savanna sapling mortality (μ) is constant and proportional to occupied area.

We deviate slightly from Staver and Levin's model by conceiving of fire as a stochastic and annually discrete event driven by fire frequency (λ), which is a function of proportional grass cover. Probability of fire in a given year is a sigmoid function of grass cover, with an inflection point at 0.6 proportional grass cover, since—as discussed by Staver and Levin—above 40% tree cover fire tends not to spread (fig. 1B; also see Archibald et al. 2009, 2012). We incorporate fire as discrete events rather than implicitly through alterations in demographic rates to more closely match reality and to allow for a greater range of system variability than expected when using a step function for fire. Given the value of λ as determined by grass cover (G) at time t ,

$$\lambda_t = \max \left\{ 0, 0.5 + \left(\frac{1.1}{\pi} \right) \times \arctan [\pi 4(G_t - 0.6)] \right\}, \quad (5)$$

fire is a binomial stochastic event (i.e., a Bernoulli trial), with values 1 (fire) or 0 (no fire) that determine sapling recruitment rate (ω) and forest tree death rate (ϕ) at time t as

$$\begin{aligned} \omega_t &= \begin{cases} \omega_0 & \text{if Bernoulli}(\lambda) = 0 \text{ (no fire)} \\ \omega_1 & \text{if Bernoulli}(\lambda) = 1 \text{ (fire)} \end{cases}, \\ \phi_t &= \begin{cases} \phi_0 & \text{if Bernoulli}(\lambda) = 0 \text{ (no fire)} \\ \phi_1 & \text{if Bernoulli}(\lambda) = 1 \text{ (fire)} \end{cases}. \end{aligned} \quad (6)$$

Putting it all together, when the outcome of the Bernoulli trial with probability λ indicates a fire year, then $\omega(\lambda) = \omega_1$; otherwise, $\omega(\lambda) = \omega_0$, the intrinsic sapling recruitment rate that occurs during no-fire years. The same formulation applies for mapping $\phi(\lambda)$ to ϕ_0 or ϕ_1 . We now discuss these two vital rates in more detail.

Fire affects the demographic rates of forest and savanna trees differently. Adult savanna trees are rarely affected, and the main impact of fire in savannas is to reduce sapling recruitment to adult size classes, ω . In the absence of fire, ω approximates the time (t_s [years]) it takes for saplings to grow into the adult size class ($\omega_0 = 1/t_s$), while ω approaches 0 in the event of fire ($\omega_1 \rightarrow 0$; Higgins et al. 2000; Sankaran et al. 2004; Hanan et al. 2008; Staver et al. 2011a; Staver and Levin 2012). By contrast, both forest saplings and adult trees are typically killed by repeated fires. Forest trees can resprout, but slow accumulation of bark thickness makes them especially prone to fire-induced

Table 1: Definition of model terms following notation from Staver and Levin (2012), with addition of a wood harvest component

Model term	Definition
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_0	Savanna sapling-to-adult recruitment rate; no-fire year
ω_1	Savanna sapling-to-adult recruitment rate; fire year
ϕ_0	Forest tree death rate; no-fire year
ϕ_1	Forest tree death rate; fire year
μ	Savanna sapling death rate
ν	Adult savanna tree death rate
Disturbances:	
ρ	Tree harvest rate
λ	Fire frequency

death, meaning that forest saplings rarely survive under any scenario that includes stochastic fires with return times <14 years (Hoffmann et al. 2012). This precludes the need to consider life stages of forest trees, since fire occurrence increases overall forest tree mortality in this general model (Staver and Levin 2012). Thus, ϕ in the absence of fire is low, reflecting background mortality rates of adult forest trees ($\phi_0 \rightarrow 0$), but ϕ is much higher in fire years ($\phi_1 \rightarrow 1$).

We incorporate wood harvest (ρ) as a fixed proportion in the model (eqq. [1]–[4]) and on the basis of assumptions of forest and savanna tree response to being cut at the base. When a savanna tree is harvested, we assume that the state does not revert to the grass default but instead reverts to a savanna sapling (fig. 1A). This is based on empirical evidence from wood harvest experiments (Tiedeman and Johnson 1992; Shackleton 2001; Kaschula et al. 2005) and fire experiments (Hoffmann and Solbrig 2003; Hoffmann et al. 2003, 2004, 2012; Higgins et al. 2007) that show savanna trees resprout vigorously. Less is known about the response of forest trees to harvest, but limited evidence suggests that they can resprout (Mwau and Witkowski 2008). However, consistent with our assumptions related to forest tree response to fire, we assume that time-averaged resprout success after cutting is low for forest trees. Thus, in the model, forest trees die following harvest and revert to the grass state (fig. 1A). We assume that wood harvest impacts only adult trees, not saplings. After initial model analysis, we also explore the impact of a fixed-quota harvest rate.

Model Simulations

To simulate the model, we discretized equations (1)–(4) with an annual time step so that $dt = 1$ and for any state X ($X = G, S, T, F$), $X_{t+1} = X_t + (dX)/(dt)$ (see R code, available online). The discrete representation of equations (1)–(4) ensures that the demographic effects of stochastic and annually discrete fire events are realized at appropriate timescales within the model (i.e., demographic rates that vary according to fire/no-fire years). Throughout the rest of the article, we provide minimal analytical results and rely on numerical simulations to demonstrate the impact of tree harvest on forest and savanna vegetation state. All model simulations where average states (stochastic equilibria) are reported ran for 10,000 time steps (years), and average values of grass (G), savanna saplings (S), savanna trees (T), and forest trees (F) were computed after discarding the initial 5,000 time steps. Our focus is on forest-savanna-grassland transitions, so we begin with parameter values that provide stable simulation of those states and then vary tree harvest intensity and selected demographic parameters to explore impacts on vegetation structure. Parameter values for any given simulation are reported in figure legends. For harvest,

we simulate a continuum of harvest rates ranging from 0 to 0.1, representing chronic harvest rates between 0% and 10% per year. For most of sub-Saharan Africa, we consider this range of values reasonable, even if in populous regions local demand may be much higher. In preparatory simulations with $\rho > 0.1$, most systems show precipitous declines to zero tree cover, as often observed in reality near urban areas in Africa (Ahrends et al. 2010; Wessels et al. 2013).

We also present graphical analyses of the model to show how tree harvest can influence the existence and stability of equilibrium points. In these cases, we forego our use of stochastic fire and instead follow the step function approach of Staver and Levin (2012). Graphical analyses require a deterministic process so that equilibria can be inferred from unique intersections of model functions. Using the step function, ϕ (forest tree death rate) and ω (savanna sapling recruitment rate) are conditional only on grass abundance (G) so that ϕ_0 (low, intrinsic death) occurs when $G < 0.6$ and ϕ_1 (high, fire-related death) occurs when $G > 0.6$. Likewise, ω_0 (high, intrinsic recruitment) occurs when $G < 0.6$, and ω_1 (low, fire-limited recruitment) occurs when $G > 0.6$. Graphical analyses rely on plotting the left- and right-hand sides of stability conditions for equilibrium solutions. Since fire—and, in turn, relative grass cover—is the hypothesized driver of bifurcations in tree cover (fig. 1B), we differentiate equilibrium solutions with respect to grass cover to obtain stability conditions that can be plotted as a function of grass cover. To visualize equilibria, the right- and left-hand sides of the equilibrium solutions are each plotted as a function of grass cover, and equilibria are inferred where lines intersect. Stability of equilibria depends on the slopes of the two functions at intersections. Where we discuss equilibria and their stability mathematically, we note that $\omega(\lambda)$ and $\phi(\lambda)$ are equivalent to $\omega(G)$ and $\phi(G)$, respectively, because we ignore stochasticity when defining equilibria. We used the program MATLAB (ver. 7.9.0.529; MathWorks 2009) to calculate equilibria and stability conditions. We have provided all code (available online and at <http://github.com/atredennick/HarvestTheory>) to reproduce our analysis and figures.

Model Analysis and Results

Savanna Stability and the Savanna to Grassland Transition

If we consider a savanna system where forest trees are absent ($F = 0$), then at nonzero equilibrium (e.g., where $0 < S, T, G < 1$),

$$\omega(\lambda) = \frac{\mu(\nu + \rho)}{\beta G - \nu}. \quad (7)$$

Since fire frequency (λ) is a function of grass cover (fig. 1B), both sides of equation (7) can be plotted as functions of G ;

equilibria exist where the plotted functions intersect, and these equilibria are stable when the first derivative of the left-hand side of equation (7) with respect to grass cover (G) is greater than the first derivative of the right-hand side (fig. 2A); thus,

$$\omega'(\lambda) > \frac{-\beta\mu(\nu + \rho)}{(\beta G - \nu)^2}. \quad (8)$$

As can be seen, depending on harvest rate (ρ), between one and three equilibria exist, with stable points at high and low tree cover (fig. 2A). The equilibrium states are parameter dependent (for relationships between demographic parameters, harvest rate, and system stability, see app. A; apps. A and B available online), but in general, high harvest, low sapling recruitment, and high sapling death rate in combination yield a treeless state (fig. A1; figs. A1, A2, B1, B2 available online). Once achieved, the treeless (grassland) state is stable because it is tree limited. That is, the term βT in equation (B2) goes to 0, prohibiting sapling birth, establishment, and subsequent recruitment. However, this model does not take into account metapopulation seed-source dynamics that could prevent permanently stable treeless states.

Since we allow only tree harvest to impact adult savanna trees that can resprout, low to moderate levels of tree harvest have little effect on the stability of savanna (fig. 2B). High levels of tree harvest result in high mortality that cannot be compensated for by high sapling recruitment rates (fig. 2B). In that case, only a boundary equilibrium where $G = 1$ is possible (fig. 2A). Thus, the strength of fire limitation on sapling recruitment rates becomes important (eq. [7]): high fire limitation ($\omega_1 \ll \omega_0$) can result in savanna cover reducing to zero and a shift to the grassland state (fig. 2B, circles); low fire limitation ($\omega_1 \approx \omega_0$) results in the maintenance of the savanna state even under high rates of tree harvest but with reductions in tree cover (fig. 2B, crosses and circles). Within savanna, the effect of tree harvest is likely to vary with precipitation, which tends to positively influence recruitment rates.

Though savannas are resilient to tree harvest in general, total tree cover (saplings and adult trees) may belie underlying demographic dynamics. To demonstrate this, we plot the ratio of adult trees to savanna saplings at stochastic equilibrium ($T:S$; fig. 2C). Regardless of fire-year recruitment rate (ω_1), tree harvest drastically reduces the number of adult trees relative to saplings. While not important for the stability of savanna ecosystems as a biome defined broadly by a mix of tree (whether adult or sapling) and grass, savannas dominated by saplings rather than adult trees contain less biomass for human consumption and reduced shade, browse, and other goods and services provided by adult trees.

The stability of savannas as defined by equations (7) and (8) also depends on sapling death rate (μ) being rela-

tively low, since it appears in the numerator. Drought-prone, arid savanna systems under high harvest pressure will be more vulnerable to periodic droughts that impact saplings more heavily than adult trees (increasing μ). Thus, in combination, tree harvest and drought could—at least in theory—drive shifts from savanna to grassland (fig. 3A, 3B). Under drought conditions, sapling death rates will be higher and intrinsic recruitment rates lower. Thus, relative to nondrought (normal) conditions, a transition from stable savanna to grassland can occur at much lower harvest rates (fig. 3A, 3B). Graphical analysis of the system confirms our simulation results (fig. 3C).

Forest to Savanna Transition

If we consider a forest system where savanna trees (T) and saplings (S) are absent, at nonzero equilibrium (i.e., $F > 0$),

$$\alpha G = \rho + \phi(\lambda). \quad (9)$$

Ignoring stochasticity, we can plot both sides of equation (9) as functions of grass cover (G) to identify equilibria and their stability. This graphical analysis of a forest system without savanna trees or saplings shows how tree harvest easily makes grassland the only possible equilibrium (fig. 4A). At low harvest rate, high and low tree cover forest equilibria are possible. At any given harvest rate, assuming low forest tree death, it is forest tree birth rate (α) that will determine whether forest is a stable equilibrium state. For example, if forest tree birth rate is high, then the gray line representing αG in figure 4A would be more steeply positive, allowing for the possibility of one to two stable forest configurations even at high harvest (see also fig. A2). Thus, in forests, the balance between tree birth rates and harvest rates will be particularly important.

Introducing wood harvest to a stable forest equilibrium sequentially results in a shift from forest coverage to grass coverage (fig. 4B), at which point, given adequate rainfall and seed sources, savanna trees can invade (regions ii and iii of fig. 4C). This transition from forest to savanna is mediated by wood harvest and fire. The addition of wood harvest short-circuits system stability by removing forest trees and allowing grass establishment (regions i and ii of fig. 4C). At a certain level of tree harvest, there exists an amplifying feedback wherein fire levels increase dramatically (because of increases in grass cover and the nonlinear response of fire frequency to grass cover), and overall forest mortality ($\rho + \phi(\lambda)$) exceeds births (α). Grass cover continues to increase and, with it, fire. This amplifying feedback between tree harvest and fire in otherwise stable forest systems can cause dramatic and rapid increases in grass cover (regions i and ii of fig. 4C), allowing for invasion by

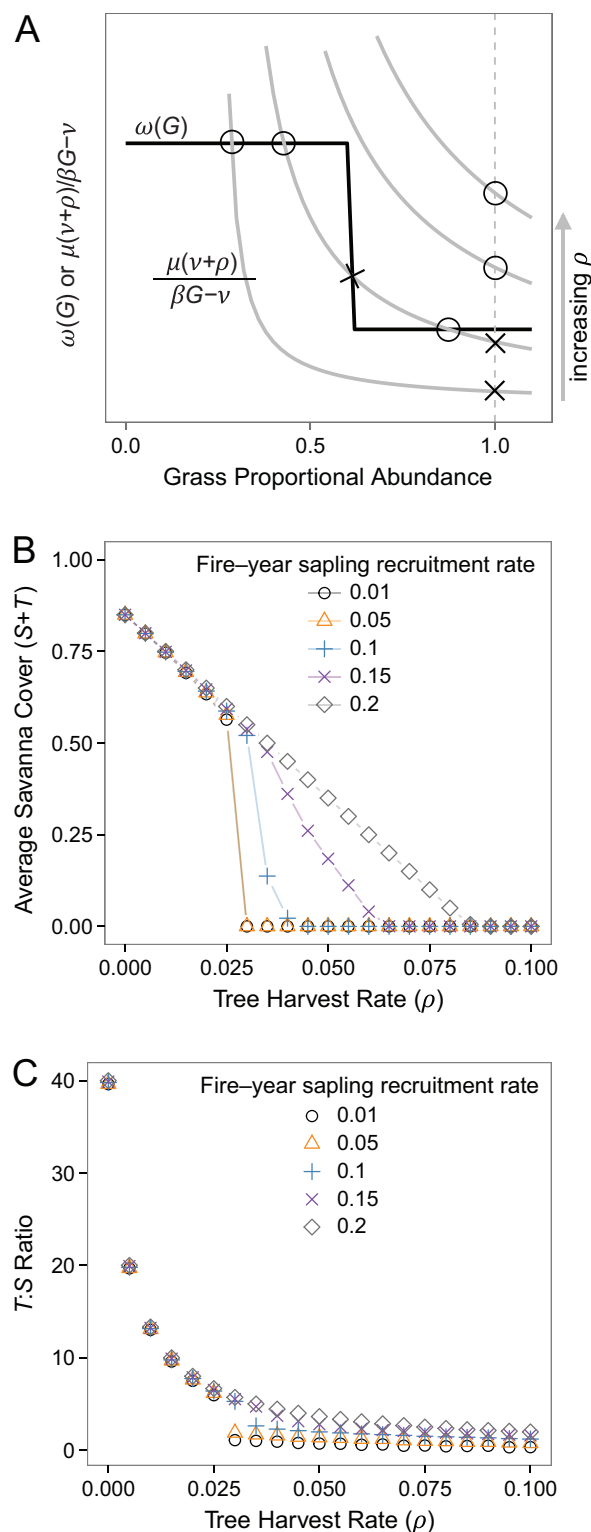


Figure 2: Graphical analysis of a savanna system (i.e., $F = 0$) at different harvest rates showing stability points where stable (circles) and unstable (crosses) equilibria occur at the intersection of terms describing sapling recruitment rate (ω , which varies with G because

savanna trees with functional traits capable of dealing with both harvest and fire (regions ii and iii of fig. 4C).

Tree harvest in a stable forest can result in complex behavior, such as cycling among states (fig. 4C). In these simulations, cycles occur when initially high forest cover declines under harvesting, allowing grass and fire into the system, followed by recruitment of savanna trees and recovery of fire-resistant tree cover that eventually suppresses grass production and fire (for savanna equilibria, see fig. 2A). This re-establishes the conditions under which forest trees can recruit and, over time, supplant the savanna tree functional group. Continued tree harvest, however, stimulates the cycle to begin again. When tree cover surpasses the 40% threshold required to reduce fire frequency, forest trees death rates are intrinsic (ϕ_0) rather than elevated by fire (ϕ_1). When this occurs, the invasion criteria for forest trees into stable configurations of savanna trees, saplings, and grass ($\alpha > [\phi(\lambda) + \rho]$) is satisfied, and forest trees can rebound (region iv of fig. 4C). However, tree harvest does eventually drive forest tree levels down again as forest trees replace savanna trees, and then forest trees are replaced by grass patches, which elevates fire frequency, and the cycles continue. Whether these cycles actually occur in nature and at what timescales remains an important question. At higher harvest rates (e.g., when $\rho = 0.15$), only a low tree cover savanna equilibrium is stable, and since forest tree death rate is higher when grass cover is higher, forest trees cannot invade, and the savanna state persists with no cycling.

Modeling Fixed-Quota Harvest

We have so far assumed that tree harvest is a constant rate proportional to area occupied by adult trees (T and F)—a fixed-proportion harvest. However, this approach may be unrealistic because harvest rates likely depend on local demand for fuelwood, which would often be independent of actual tree cover or biomass—a fixed-quota harvest. To study this possibility, we experimented with an alternative model for tree harvest represented in the model as a constant rate independent of tree cover (details in app. B). As expected, fixed-quota harvest amplifies the results we report above (fig. B1). Though we cannot compare the two

of fire) and net tree loss rate ($[\mu(v + \rho)]/(\beta G - v)$; A), the effect of tree harvest and sapling recruitment rate on total savanna cover (B), and the ratio of savanna trees to savanna saplings (T:S; C). In B and C, point values represent the average cover or ratio from a 10,000-year simulation after discarding initial 5,000 time steps. Symbols correspond to different values of sapling-to-tree recruitment during fire years (ω_1), as indicated in legends. Parameter combination represents a stable savanna when wood harvest (ρ) is absent ($\beta = 0.05$, $\mu = 0.1$, $v = 0.005$, $\omega_0 = 0.2$).

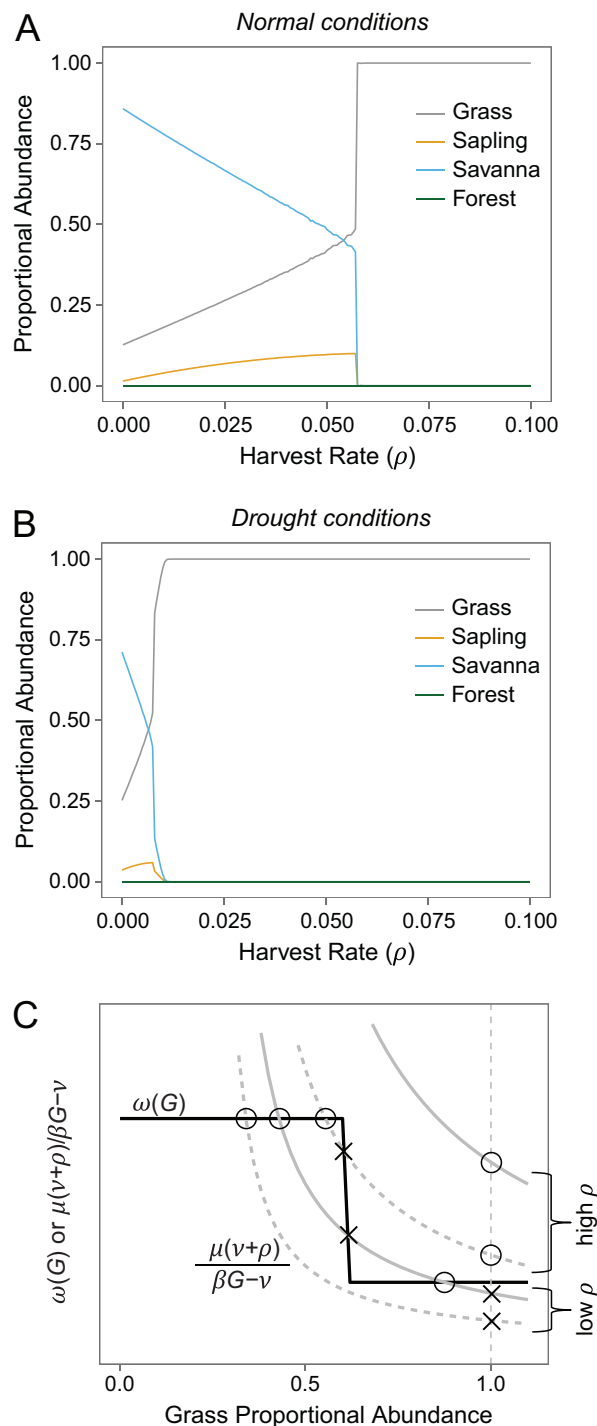


Figure 3: Effect of drought and tree harvest on savanna stability through interactions with fire. *A*, Relative abundance at stochastic equilibrium of grass, savanna saplings, and trees, with forest trees at different harvest rates under normal conditions. *B*, Same as in *A* but under drought conditions where, relative to *A*, sapling death rate (μ) is higher and sapling intrinsic recruitment (ω_0) is lower. *C*, Graphical analysis of a system where forest trees are absent ($F = 0$) at different harvest rates (high, low) and under normal conditions

harvest rates directly, transitions tend to occur at a fixed harvest rate of 2.5% (fig. B1), where a density-dependent harvest rate of 2.5% has only modest effects (figs. 3, 4). Thus, savannas and forests are less resilient to fixed-quota tree harvest. This result is in line with a long history of work comparing fixed-quota and fixed-proportion harvest (Beddington and May 1977).

The results of our analysis with fixed-quota harvest may apply most realistically in wetter, higher tree cover systems at the savanna-forest ecotone. In the more arid and low-tree-density savannas, there is evidence that people (on the basis of local customs or in response to government mandates) tend to conserve woody populations through harvest of deadwood rather than live trees (e.g., Shackleton 1998). Harvest of deadwood depends on the density and productivity of the woody community but has no direct demographic feedback. In Mali, West Africa, we have found a relationship between rainfall (and, implicitly, tree abundance) and the percentage of wood harvested from live trees (fig. B2). Data underlying figure B2 are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.vg121> (Tredennick et al. 2014). In so far as our data from Mali are representative of wood harvest practices elsewhere, they suggest that the dynamics of mesic savannas and forests where people tend to harvest live trees will be more strongly affected by fuelwood harvest than at intermediate and low rainfall and/or in situations where fuelwood harvest is confined to collection of deadwood. However, these general patterns can be confounded in highly populous regions where deadwood does not meet human demand. In such cases, people may be forced to rely on live wood, and rapid tree reductions—consistent with fixed-quota harvest—can occur (Wessels et al. 2013).

Discussion

Does tree harvest matter in savannas and forests? In forest systems, we find that tree harvest can act to reverse the dominance of forest trees over savanna trees (implemented in this model by a spatial hierarchy). Since savanna trees are both fire and harvest tolerant via resprouting, the savanna state becomes favored under conditions of moderate to high tree harvest, where forest tree death results in increased grass cover and, in turn, increased fire frequency (fig. 4). The model successfully reproduces empirical findings of frequent and self-amplifying fire events after forest

(dashed lines) and drought conditions (solid lines), on the basis of the simulations shown in *A* and *B*. Circles denote stable equilibria, crosses denote unstable equilibria. Parameter combinations: $\beta = 0.05$, $\mu = 0.08$, $\nu = 0.005$, $\omega_0 = 0.3$, $\omega_1 = 0.05$ (*A*); $\beta = 0.05$, $\mu = 0.15$, $\nu = 0.005$, $\omega_0 = 0.1$, $\omega_1 = 0.05$ (*B*).

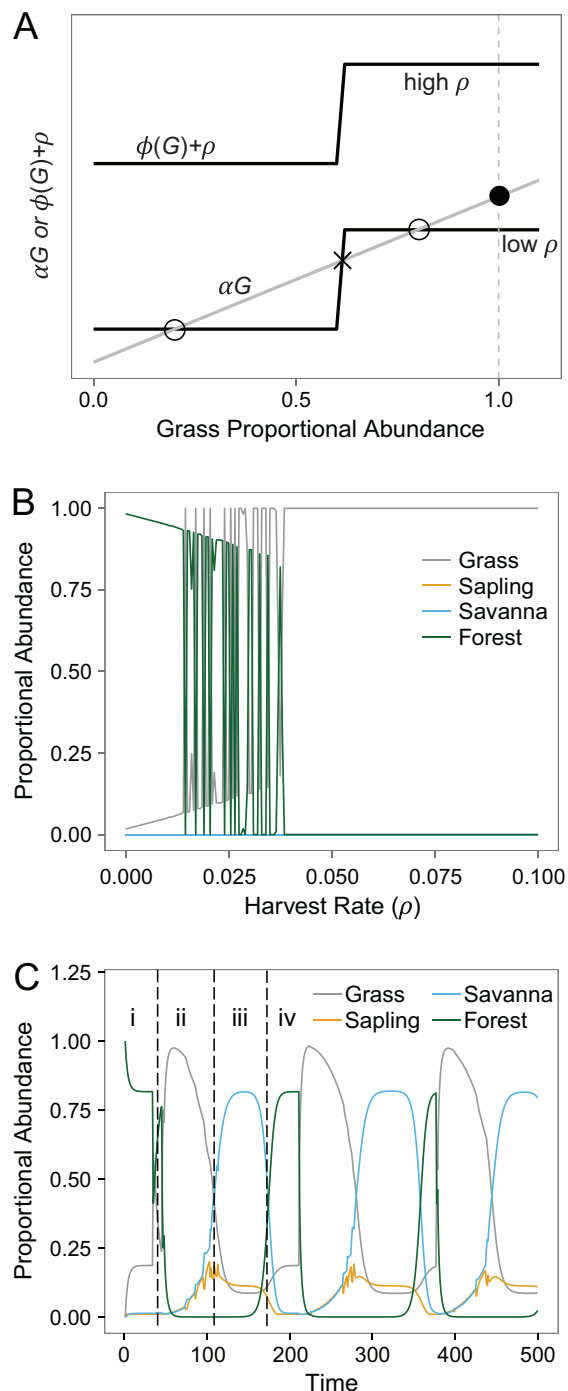


Figure 4: Response of a stable forest to tree harvest. A, Graphical analysis of a system with only forest trees (F) and grass (G). Equilibria exist wherever lines intersect, with conditionally stable equilibria denoted with open circles and unstable equilibria denoted with crosses. The filled circle represents an unstable boundary equilibrium when tree harvest (ρ) is low but a stable boundary equilibrium when harvest is high. Tree harvest rapidly results in grassland being the only possible equilibrium when $S + T = 0$. B, Relative abundance of grass and forest trees at stochastic equilibrium across a range of

tree removal in South American forests (Cochrane et al. 1999; Cochrane and Laurance 2002) due to increases in grass fuels (Silvério et al. 2013). This provides a pathway of savannization distinct from the view of human impacts resulting in a degraded forest that structurally resembles savanna but retains forest species (Scholes and Archer 1997; Ratnam et al. 2011). In contrast, since the functional traits of savanna and forest trees differ so greatly in response to fire and tree harvest, our results suggest that tree harvest can lead to a shift from forest species to savanna species. The final result is a shift from forest to savanna in both structure (lower tree cover) and function (savanna species) initiated by tree harvest and subsequently driven by fire. Depending on model parameters, post-tree harvest savannas can remain stable, or the system can cycle between savanna, forest, and grassland (fig. 4). Though our analysis has focused on African systems, our results also apply to the case of deforestation in South America, as exemplified by Silvério et al. (2013).

In arid regions, savanna is the climax state except under very dry conditions below about 150 mm of rainfall per year (Sankaran et al. 2005). In these arid savannas, seedling establishment is limited by moisture availability, and reproductive potential is stored in adult savanna trees with low intrinsic mortality (Higgins et al. 2000; Sankaran et al. 2004). Via this storage effect (Chesson 2000; Miller and Chesson 2009), trees can persist under arid conditions only if adult trees survive between highly variable rainfall events. Harvest of adult trees in arid savannas disrupts the storage potential of the system. This results in an overall reduction in adult individuals and makes the system more vulnerable to periodic or persistent drought (figs. 2C, 3). This has important implications for the more arid savannas of Africa, where climate change is already inducing changes in tree cover (Maranz 2009). Tree harvest has the potential to aggravate the effects of climate change on woody cover in grassland-savanna transition zones. It is important to note that in many arid regions, combinations of cultural and legal norms favor collection of deadwood as opposed to harvesting live wood (fig. B2; Shackleton 1998), reduc-

tree harvest rates. Because we use a stochastic fire term, the transition from forest tree to grass dominance is dynamic, but eventually at high harvest rates (greater than about 0.035), forest trees are excluded. C, When forest trees are excluded by a tree harvest–fire amplifying feedback, savanna trees can invade; for many parameter combinations, this results in going from an initial forest state (i) to cycles between low (ii) and high (iii) tree cover savannas and periods where all functional types are present (iv). For C, we allowed low levels of savanna saplings to be present each year to simulate a seed source in region i. Parameter combinations: $\alpha = 0.3$, $\phi_0 = 0.005$, $\phi_1 = 0.3$ (B); $\alpha = 0.3$, $\phi_0 = 0.005$, $\phi_1 = 0.5$, $\beta = 0.3$, $\omega_0 = 0.4$, $\omega_1 = 0.1$, $\nu = 0.005$, $\mu = 0.15$, $\rho = 0.05$ (C).

ing the impact of fuelwood harvest on woody populations. Rapid and severe reductions in woody cover are likely to occur in arid savannas in populous regions where deadwood supply does not meet human wood demand.

An interesting finding of our analysis is that savannas are generally resilient to low and moderate levels of tree harvest under environmental conditions representative of semi-arid to mesic savannas. The traits that many savanna trees have evolved to cope with frequent fire, resprouting, and rapid growth generally allow savanna trees to cope with tree harvest. Several studies report this result (Chidumayo 1990; Tiedeman and Johnson 1992; Okello et al. 2001; Shackleton 2001; Kaschula et al. 2005), but our analysis is the first to model the demographic consequences of tree harvest on savanna vegetation. While savanna as a biome can sustain tree harvest and maintain its general structure as a mix of woody and herbaceous species, our results suggest that the tree component will shift rapidly to smaller size classes (fig. 2C). This means that there will be less available biomass for human appropriation in savannas, even as the savanna biome persists.

Conceptually, our results indicate that tree harvest can erode intrinsic basins of attraction in forests and savannas and, in so doing, make transitions via fire or drought more likely (fig. 5). Where savanna and forest are alternatively stable, we find that tree harvest can erode the intrinsic basin of attraction for forest and make a state transition to savanna or cycles among states via fire more likely (fig. 5A). In South American forests, drought may also play a critical role in forests (Brando et al. 2014). Tree harvest could induce bistability in regions currently considered climatically deterministic forest (see Staver et al. 2011b), broadening the range of rainfall regimes where fire can maintain savanna. Where savanna is uniquely stable, the savanna state is resilient to all but high levels of tree harvest because of the resprouting abilities of savanna trees, and harvest of live trees mainly alters tree:grass ratios and the relative abundance of savanna saplings compared with savanna trees (fig. 5B). At the arid end of the savanna distribution, harvest can drive down tree populations and make a transition to grassland by drought more likely because tree harvest makes the savanna and grassland state equally probable (fig. 5C). However, tree harvest alone, especially if independent of tree cover, can also cause state shifts without an interaction with drought (figs. 3A, A1B). Once in a treeless state, the system can be tree limited, and the grassland state will remain stable so long as $\beta T = 0$, or, in ecological terms, so long as a seed source is absent. Thus, the relative stability of grassland and savanna under arid conditions is dependent on the rate of tree harvest and the availability of a seed source.

In contrast to our theoretical results, many empirical studies report woody encroachment into savannas. In Af-

rica, locally intense grazing can suppress fire frequency and result in woody encroachment into savanna (Archer et al. 1995; Roques et al. 2001; Goetze et al. 2006). There is also some evidence that increasing levels of atmospheric CO_2 concentration may facilitate a competitive advantage of C_3 trees and shrubs over C_4 grasses (Wigley et al. 2010; Bond and Midgley 2012; Higgins and Scheiter 2012; O'Connor et al. 2014). However, many of these studies have been conducted in areas where fuelwood and timber harvest is disallowed (Goetze et al. 2006) or occurs at low levels (Wigley et al. 2010; though in these studies tree harvest was not explicitly quantified). Consequently, our results and those of studies reporting woody encroachment should be considered context dependent, and in some cases, the interacting forces of climate change, fire management, and tree harvest will lead to dynamics not captured by the model presented here.

While the importance of increasing CO_2 remains uncertain, it is clear that active fire management will be important in regulating the effects of tree harvest on savanna and forest systems. For example, Holdo et al. (2009) used a simulation model to show how fire and tree removal by elephants, in the absence of heavy grazing, reduces woody cover over time via a similar feedback as the harvest-fire dynamic proposed here. In areas with high rates of tree harvest, active fire suppression may be necessary to avoid ecosystem transitions. If we were to include grazing in this theoretical model, the interaction between tree harvest and fire would be dampened because lower grass cover driven by grazing would reduce fire frequency. Likewise, there is potential for harvest to interact with the browse trap phenomenon (Staver and Bond 2014) in the same way harvest interacts with the fire trap, as proposed in our analysis.

The biome transitions predicted by this model are not merely of academic interest. Demand for wood fuels (firewood and charcoal) is high and projected to increase in most countries of sub-Saharan Africa (Bailis et al. 2005). Additionally, charcoal use and production is predicted to increase across all of sub-Saharan Africa (Bailis et al. 2005; Arnold et al. 2006). Charcoal production is an intensive form of land use that results in the widespread clearing of trees that is consistent with high levels of tree harvest (ρ) in our model. Our analysis suggests that moderate rates of wood harvest—by interacting with fire or drought—can drive persistent biome transitions from forest to savanna and from wooded savanna to open grassland. That high rates of wood harvest can reduce tree cover is an intuitive result. More surprising is our result that only moderate rates of tree harvest are required to drive state shifts because harvest interacts with extrinsic disturbances (fire) to amplify demographic consequences. In aggregate, our analysis suggests that as increases in charcoal demand and production are realized across the African continent, sudden

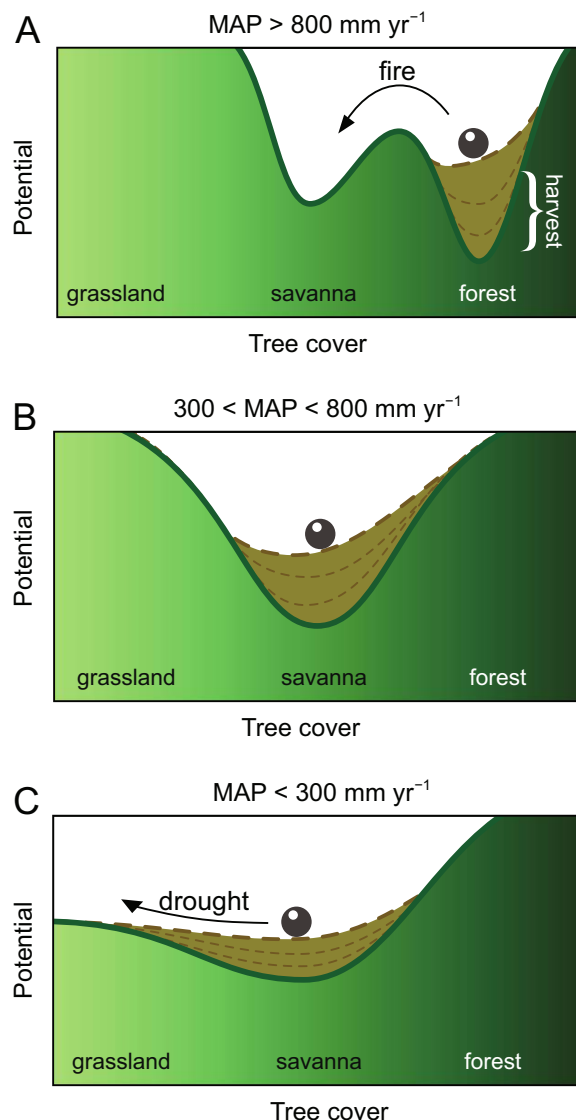


Figure 5: Conceptual representation of how tree harvest erodes stability basins and makes state transitions more probable. Dark green lines represent the intrinsic stability basins of the system, and dashed brown lines represent the erosion of basins by tree harvest. Tree cover increases along the X-axis, where we also show the broad distribution of grassland, savanna, and forest. Following the work of Livina et al. (2010), potential is on the Y-axis. A, Forest and savanna are alternate stable states at the mesic end of the savanna distribution (mean annual precipitation [MAP] $> 800 \text{ mm yr}^{-1}$ in Africa); harvest erodes the stability basin and makes a transition to savanna via fire more probable. This figure does not include the special case of a transition to savanna vegetation type while retaining high tree cover, but the concept of an easy transition to the savanna state via fire after harvest remains the same. B, Savanna is the climatically deterministic state at intermediate rainfall levels ($300 \text{ mm yr}^{-1} < \text{MAP} < 800 \text{ mm yr}^{-1}$ in Africa), but tree harvest can tip the basin toward lower tree cover. C, Savanna and grassland are continuous states at low rainfall levels ($\text{MAP} < 300 \text{ mm yr}^{-1}$ in Africa), but harvest reduces adult tree cover to low levels, and drought can more eas-

ily cause a transition to the grassland state. Once in a treeless state, the system is tree limited, and the grassland state can be stable boundary equilibrium when a seed source is absent. Note that in A and B, we do not include the trivial equilibrium of $G = 1$ because we assume that dispersal of seed and related recruitment occurs with high probability. MAP ranges for mesic, intermediate, and arid savannas from Sankaran et al. (2005).

Limitations of Our Approach and Empirical Implications

The model analysis presented here shows tree harvest as a potentially important process in savannas and forests. However, there are several limitations to our approach. First, a simple population dynamic model as presented here can help understand underlying dynamics but can rarely fully represent real systems. The model indicates the potential importance of tree harvest and provides insight into the magnitude of harvest required to drive state transitions. However, to estimate the effect of harvest on current biome distribution or to forecast future biome transitions likely requires a more detailed and mechanistic modeling approach.

Second, our results rely on differential demographic responses of savanna trees (they resprout) and forest trees (they do not resprout) to tree harvest. This assumption is well tested in terms of fire response for both tree types (but see Hoffmann et al. 2009 for counterevidence in South America) and postharvest resprouting of savanna trees (Shackleton 2001; Wessels et al. 2013), but to our knowledge, no data exist on the postharvest resprout rate of forest trees. However, we note that there is strong empirical support for a differential demographic response of forest and savanna trees to fire and for the coppicing ability of savanna trees after harvest.

Third, we assume that harvesting of a savanna tree results in reversion to the sapling state. This implies that newly established saplings have the same demographic rates as coppicing saplings from a harvested tree. It may well be the case that coppice regrowth grows faster than saplings growing from seed because they have larger root systems on which to draw. This would increase sapling-to-adult tree recruitment rates (ω_0 and ω_1) for postharvest saplings relative to regular saplings. Our qualitative interpretations of the model would not change if we included a separate rate for postharvest saplings, but our quantitative results would, of course, change. If our focus was on forecasting, this assumption would be important and require empirical tests.

These limitations, while constraining our inference, highlight opportunities for future empirical and theoretic-

cal work. First, our analysis clearly demonstrates the need to include tree harvest in mechanistic models of forest-savanna-grassland vegetation dynamics. Future theoretical work should aim toward explicitly modeling tree and grass biomass since harvest rates in the literature are most often reported in biomass per unit time. Our work here opens the door for more mechanistic and complex modeling approaches that combine vegetation models (e.g., Hanan et al. 2008; Beckage et al. 2009) with fuelwood demand models (e.g., Banks et al. 1996; Wessels et al. 2013) to forecast the impacts of tree harvest into the future. Second, experimental studies in the spirit of Hoffmann et al. (2003) investigating the harvest ecology of savanna and forest trees could test our fundamental assumption that savanna and forest trees respond differentially to tree harvest. In that same vein, our analysis highlights the need to compare growth rates of regular saplings and postharvest, coppicing saplings, similar to work undertaken by Wakeling et al. (2011).

Conclusions

In general, savannas are resilient to tree harvest as a result of traits that trees have evolved to cope with frequent fire. We can conclude that under low to moderate levels of tree harvest and in all but the most arid of savannas, harvesting of trees for fuel will act as a modifier of tree:grass ratios (*sensu* Sankaran et al. 2004) in savanna systems. However, at the arid and mesic ends of the grassland-savanna-forest continuum, tree harvest can have profound and potentially irreversible impacts. At the savanna-forest ecotone, an amplifying feedback between tree harvest and fire frequency can drive a biome transition from forest to savanna that will likely be persistent in the absence of active fire suppression. At the grassland-savanna ecotone, tree harvest can make a savanna more vulnerable to periodic droughts, which, in the best case, can result in a transition to a grassland or, in the worst case, can induce a pathway of desertification (Reynolds et al. 2007). Regardless, it is at these ecotones that tree harvest appears to have the greatest influence. As demand for wood fuel increases in sub-Saharan Africa in the coming decades, we should anticipate the boundaries of the savanna biome relative to forest to shift. Tree harvest will likely have small, localized impacts on the stability of the savanna biome, but the demographic shift toward low-biomass saplings predicted by our model analysis could have large impacts on the availability of wood for human appropriation.

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Stacked firewood harvested from the savanna surrounding Tiorola, Mali (West Africa). Photo credit: Andrew T. Tredennick.