# Herbivore–vegetation feedbacks can expand the range of savanna persistence: insights from a simple theoretical model

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Theoretical models of tree–grass coexistence in savannas have focused primarily on the role of resource availability and fire. It is clear that herbivores heavily impact vegetation structure in many savannas, but their role in driving tree–grass coexistence and the stability of the savanna state has received less attention. Theoretical models of tree–grass dynamics tend to treat herbivory as a constant rather than a dynamic variable, yet herbivores respond dynamically to changes in vegetation structure in addition to modifying it. In particular, many savannas host two distinct herbivore guilds, grazers and browsers, both of which have the potential to exert profound effects on tree/grass balance. For example, grazers may indirectly favor tree recruitment by suppressing the destructive effects of fire, and browsers may facilitate the expansion of grassland by reducing the competitive dominance of trees. We use a simple theoretical model to explore the role of grazer and browser dynamics on savanna vegetation structure and stability across fire and resource availability gradients. Our model suggests that herbivores may expand the range of conditions under which trees and grasses are able to stably coexist, as well as having positive reciprocal effects on their own niche spaces. In addition, we suggest that given reasonable assumptions, indirect mutualisms can arise in savannas between functional groups of herbivores because of the interplay of consumption and ecosystem feedbacks.

An old but persistent debate in ecology is the problem of tree-grass coexistence in savannas, or rather the lack of a general unified model that can explain the occurrence and persistence of the tree-grass mixtures that define savannas (Walter 1971, Sarmiento 1984, Bond 2008). A different way of framing this question is to ask: why do savannas have so few trees? In theory at least, the climatic and edaphic conditions that predominate in many savannas seem able to support closed canopy forests, but do not (Bond et al. 2005, Bond 2008), so savannas effectively comprise an 'uncertain ecosystem' (Bond 2008) that defies Whittaker's (1975) biome classification scheme. Many models, both conceptual and quantitative, have been proposed to explain the coexistence and relative balance of trees and grasses in savannas, with various degrees of success (Higgins et al. 2000, D'Odorico et al. 2006, Scheiter and Higgins 2007, Accatino et al. 2010, Calabrese et al. 2010, Beckage et al. 2011). These models vary in the degree to which they consider bottomup versus top-down forces to be important in determining tree-grass balance (Belsky 1990, Sankaran et al. 2004), but for the most part they coincide in paying relatively little attention to the role of consumers. Given that savannas represent one of the most widespread biomes in the tropics and subtropics (Frost 1996), and that they often support large biomasses of ungulate herbivores (Cumming 1982), it

is paradoxical that herbivory is often overlooked as an important process in the regulation of tree cover.

One of the earliest models proposed to explain the coexistence of trees and grasses in savannas was Walter's two-layer hypothesis (Walter 1971, Walker et al. 1981), which is based on the differential use of topsoil and subsoil moisture by each of these functional groups. Other models and empirical studies have similarly focused on water and nutrients as determinants of savanna vegetation structure (Eagleson and Segara 1985, Walker and Langridge 1997). A second class of models has emphasized the importance of top-down regulation in the form of fire and its role in suppressing tree growth and establishment (Hochberg et al. 1994, Menaut et al. 1990, Higgins et al. 2000, D'Odorico et al. 2006). These and other models, though often parameterized for particular locations, share the common implied goal of finding the simplest general mechanism able to explain savanna structure across a wide range of conditions. In an extensive review, however, Sankaran et al. (2004) have suggested that such mechanisms may vary among savannas, particularly as a function of rainfall. If this is the case, a more appropriate model may be the multi-factor conceptual model offered by Walker (1987), which proposed that a wide range of factors, including climate, edaphic factors, disturbance, herbivory, and

competition jointly play a role in determining tree–grass balance, with the relative strength of the various factors differing among geographic locations.

A common feature of most savanna models is the lack of a prominent role for herbivory as a general determinant of tree-grass balance. Herbivores are often mentioned as a factor affecting savanna structure (Walker 1987, Belsky 1990, Scholes and Walker 1993, Scholes and Archer 1997, Sankaran et al. 2004), but their importance is usually minimized relative to that of soil moisture availability and fire (Walker 1987), probably because large ungulate herbivore populations are not a general feature of savannas across the world (Cumming 1982). A wide range of studies, however, suggest that herbivores can dramatically modify vegetation structure in many savanna systems (Laws 1970, Caughley 1976, Sinclair 1979, Asner et al. 2009, Staver et al. 2009). Both conceptual (Belsky 1990) and quantitative models (van Langevelde et al. 2003, Baxter and Getz 2005, Holdo 2007) tailored to specific savanna systems in Africa have examined the role of vertebrate herbivores as key drivers of vegetation structure. A common feature of these models is that herbivores are treated as fixed parameters rather than dynamic variables, when in reality herbivore populations respond to changes in the relative proportion of trees and grasses, permitting feedback loops to occur between consumers and resources. Including these feedbacks in savanna models is important because this will allow us to understand not only the environmental conditions under which herbivores can alter tree-grass relationships, but also the conditions for persistence of herbivores in the system and the general importance of herbivory as a process regulating vegetation. In particular, the tree-grass coexistence debate revolves around the existence or possibility of a stable tree-grass state. Dynamic systems containing such states require a mixture of negative and positive feedbacks to maintain them, and these often emerge from trophic interactions.

In this paper, we examine the implications of introducing herbivores into a simple analytical model of trees and grasses in savannas, with the objective of answering the following questions: 1) how important are herbivores for tree-grass coexistence and the balance of tree and grass biomass in savannas? 2) how do the two main herbivore guilds (grazers and browsers) affect each other? Our approach consists of comparing the behavior of a simple tree-grass model with that of models containing either grazers or browsers alone, and both herbivore guilds together. This paper does not represent a novel theoretical attempt to explain tree-grass coexistence in savannas. Rather, we take existing ideas from the literature and analyze how trophic interactions alter the tree-grass balance. Our approach does not attempt to look for a minimalist model that produces coexistence, but is rather based on recent empirical work that demonstrates that coexistence is intrinsic to the system for some regions of parameter space, and not so for others (Sankaran et al. 2005). Our model integrates a number of factors that have been shown to be important in structuring savannas (tree-grass competition, moisture availability and fire) with herbivory within a dynamic framework.

# Material and methods

#### Background for the model

The framework we present here applies to savannas where both trees and grasses are consumed and may be regulated by herbivores. This is the case in many African savannas, but throughout the paper we will repeatedly draw on the Serengeti ecosystem of east Africa as a model system. This is an ecosystem we are familiar with, and the questions we pose here were originally inspired by the Serengeti. The vertebrate herbivores here are 'megaherbivores' (Owen-Smith 1988) that can largely escape regulation by predation either by virtue of large body size (e.g. elephants), or by aggregating in large herds (e.g. wildebeest). Figure 1 shows schematically how vegetationherbivore dynamics might be modeled in this and other similar savannas. Two herbivore guilds interact with their respective resources, with each guild specializing on one of two plant functional groups: browsers feed on trees or woody vegetation, and grazers feed on grasses or herbaceous vegetation (Fig. 1). Although within each of these guilds one may encounter mixed feeders (e.g. impala Aepyceros melampus), by and large it may be assumed that ungulate feeding habits can be divided into these two groups. The two resources, in turn, interact with each other. Tree-grass balance varies over space and time, and the proximate mechanisms (other than herbivory) that determine this balance and allow tree-grass coexistence may be numerous and complex (Sankaran et al. 2004). The consensus that emerges from a large body of research, however, is that in the absence of disturbance or herbivory, trees tend to be dominant over grasses, and the upper limit of tree cover is primarily dependent on rainfall (Sankaran et al. 2005), except when certain edaphic factors limit tree cover. This occurs for instance in the southeastern plains of the Serengeti, where a hardpan layer prevents root development and savanna gives way to an edaphic grassland, which we do not consider here (Belsky 1990). The dominance of trees over grasses is scale-dependent (Scholes and Archer 1997), but at the large scale that interest us here, grass biomass declines as a negative exponential function of tree cover (Holdo et al. 2009a). This intrinsic balance may shift when herbivory and/or fire are present. Fires tend to favor grasses, which can recover rapidly following burns



Figure 1. Schematic diagram showing the state variables of the system and their interactions.

since they do not need to develop large amounts of structural biomass during recovery like trees. The extent of fire damage to the tree layer may in turn be strongly influenced by the amount of grass present at the time of burning, given that in savannas, grasses are the primary fuel for fires (Starfield et al. 1993, Trollope 1996). Grass biomass may in turn be regulated by herbivores, with the result that grazers can indirectly influence tree biomass, as appears to occur in the Serengeti and other systems (McNaughton et al. 1988, van Langevelde et al. 2003). Conversely, the direct reduction in tree canopy cover by browsers can allow grass biomass to increase by relaxing competition for resource (Scholes and Archer 1997, van Langevelde et al. 2003). In theory, therefore, grazers and browsers can affect each other by exerting indirect effects on each other's resources.

#### **Model description**

The conceptual model depicted in Fig. 1 can be represented by a series of four differential equations, one for each of the state variables. It has been argued that, even in simple savanna models, the tree layer should be disaggregated into at least two size classes because fire usually does not consume wood and tends to disproportionately affect smaller trees (Hanan et al. 2008). Although this is true and important for reproducing realistic tree cover dynamics, our aim is to understand system equilibria rather than reproduce the transient dynamics of real systems, so we chose to use a simpler approach with a single variable for tree biomass. The equation for trees (denoted *W* for woody vegetation) is given by

$$\frac{dW}{dt} = \left(\frac{r_w}{W + \alpha_w} \frac{\Psi}{\Psi + \beta_w} - \delta_w - f\lambda H\mu_w - cB\right) W \tag{1}$$

Here it is assumed that tree growth follows Michaelis– Menten kinetics with respect to both light and water, a well-established functional form for resource uptake (Pacala and Kinzig 2002), with co-limitation by the two resources being expressed multiplicatively. In Eq. 1,  $r_w$  is a growth parameter,  $\alpha_w$  is the tree biomass at which self-shading slows growth to half of maximum, and  $\beta_w$  is the amount of rainfall  $\psi$  (used as a proxy for soil moisture in this simplified model) at which growth is half of maximum (for a given W). Tree biomass is assumed to decay at a constant rate  $\delta_w$ .

Losses to fire are given by the term  $f\lambda H\mu_w W$ , where f denotes the annual probability of an ignition event, the constant  $\lambda$  relates grass biomass H to the proportion of area burned, and  $\mu_w$  is the specific mortality term for W due to fire. We interpret this effect of fire as the instantaneous proportion of biomass burned (since our model is aspatial), but it can also be thought of as a measure of fire intensity, with higher fuel loads (H) giving rise to more intense fires (van Langevelde et al. 2003). In a spatially-implicit system with no size structure, the mathematical formulation for each of these cases will be equivalent. Following van Langevelde et al. (2003), we treat fire as a semi-dynamic process: fire is conditionally dependent on ignition events, which drive frequency, but fire extent is

also linearly dependent on fuel load, an effect captured by the positive feedback of H on fire in Fig. 1. The approximately linear relationship between the amount of area burned and grass biomass is supported by empirical data from the Serengeti (McNaughton et al. 1988, A. R. E. Sinclair unpubl.) and Kruger National Park in South Africa (D'Odorico et al. 2006).

Finally, we model the tree consumption term *cBW* by browsers as a simple Lotka–Volterra functional response, but more complex functional responses are possible and would be worth exploring in future studies.

The equation for grass biomass (H) is given by the expression:

$$\frac{dH}{dt} = \left(\frac{r_{h}}{H + \Theta W + \alpha_{h}}\frac{\Psi}{\Psi + \beta_{h}} - \delta_{h} - f\lambda H\mu_{h} - c'G\right)H$$
 (2)

Compared to Eq. 1, we include an additional term  $\theta W$ in the denominator of the growth equation for H, where  $\theta$  represents the competitive effect of trees on grasses. We thus assume that tree-grass competition is asymmetric, but more complex formulations are possible. The basic model for competition matches a form suggested by Schoener (1976) as a phenomenological descriptor of exploitative competition for systems where resources are partitioned among consumers. As mentioned above, the reasons for tree dominance over grasses may be complex. Here we simply assume that trees, by virtue of their large amount of structural biomass, are able to overtop and thus limit the light available to grasses. We assume that light competition is described by a simple weighted sum of the biomasses of the two functional groups; more complex functions (e.g. a negative exponential) might be more accurate, but would not affect the qualitative predictions we will draw from the model. Tree biomass saturates at a higher value than does grass biomass, and for a given value of  $\psi$ , we assume that tree biomass at equilibrium exceeds grass biomass. We therefore require that  $\beta_w > \beta_h$  and that  $\alpha_w > \alpha_h$  (see Table 1 for parameter values). This essentially means that, in terms of absolute biomass, grasses have a lower carrying capacity than trees. We also assume that  $r_h > r_w$  and  $\delta_h > \delta_w$ , i.e. grasses have faster growth and turnover than trees (Table 1); this is reasonable, due to the lack of slow-growing structural biomass in grasses. As in Eq. 1, there are terms for both losses to fire and consumption by grazers.

The equations for browser and grazer dynamics are given by

$$\frac{dB}{dt} = (bcW - m)B \tag{3}$$

and

$$\frac{dG}{dt} = (b'c'H - m')G \tag{4}$$

respectively, where b and b' are the conversion factors for food intake into browser and grazer biomass, respectively, and m and m' are browser and grazer mortality.

Table 1. List of model	variables and	parameters
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Variable or parameter	Definition	Value	Units
Variables			
В	Browser biomass		g m <sup>-2</sup>
G	Grazer biomass		g m <sup>-2</sup>
Н	Herbaceous biomass or grasses		g m <sup>-2</sup>
W	Woody biomass or trees		g m <sup>-2</sup>
Parameters			0
r <sub>w</sub>	Intrinsic growth of W	1350	g m <sup>-2</sup> y <sup>-1</sup>
$\alpha_{_W}$	Biomass at which growth of $W$ is $\frac{1}{2}$ max	1000	g m <sup>-2</sup>
$\beta_w$	Rainfall at which growth of W is ½ max	1000	mm y <sup>-1</sup>
$\delta_w$	Decay rate of W	0.2	y <sup>-1</sup>
$\mu_w$	Specific loss of W due to fire	0.5	,
r <sub>h</sub>	Intrinsic growth of H	1200	g m <sup>-2</sup> y <sup>-1</sup>
$\alpha_{b}$	Biomass at which growth of H is $\frac{1}{2}$ max	200	g m <sup>-2</sup>
θ	Reduction in growth of <i>H</i> due to <i>W</i>	0.25	-
$\beta_h$	Rainfall at which growth of <i>H</i> is ½ max	500	mm y <sup>-1</sup>
$\delta_h$	Decay rate of H	1.0	y <sup>-1</sup>
$\mu_{b}$	Specific loss of <i>H</i> due to fire	0.5	
Ψ	Rainfall	0-1500	$mm y^{-1}$
f	Fire frequency	0–1	y <sup>-1</sup>
λ	Effect of <i>H</i> on area burned	0.002	$m^2 g^{-1}$
С	Browser consumption	0.24	$m^2 g^{-1} y^{-1}$
b	Conversion coefficient for W into B	0.0006	σ,
т	Browser mortality	0.05	y <sup>-1</sup>
с′	Grazer consumption	0.05	$m^2 g^{-1} y^{-1}$
b'	Conversion coefficient for $H$ into $G$	0.023	<i>.</i> ,
m'	Grazer mortality	0.25	y <sup>-1</sup>

## **Model parameters**

To obtain reasonable values for the parameters in the model, we used a number of empirical relations from the Serengeti and elsewhere. We obtained initial estimates for the intrinsic decay rate of trees and grasses from van Langevelde et al. (2003). For most other parameters in Eq. 1 and 2, we chose parameter values that appeared reasonable based on our prior knowledge, and that provided good fits to empirical relationships between rainfall and biomass. In the case of trees, we fit Eq. 1 to the canopy cover versus annual rainfall relationship obtained by Sankaran et al. (2005), assuming no fire or herbivory. For grasses, we fit Eq. 2 to McNaughton's (1985) empirical relationship between annual rainfall and grass biomass. We had no suitable data for  $\theta$ , which controls the competitive effect of trees on grasses, so we chose a value that resulted in the competitive exclusion of grasses above an annual rainfall of about 1000 mm in the absence of fire. We treated wildebeest and elephants as representative model grazers and browsers, respectively, and derived plant consumption rates for each of these by using published allometric equations (Shipley et al. 1994, Wilmshurst et al. 2000). We obtained approximate demographic parameters from Fryxell et al. (2005) and Moss (2001). To estimate fire parameters, we used a time series relating area burned and wildebeest population density (Sinclair et al. 2009) to derive a relationship between grass biomass and area burned. First, we used annual rainfall records from Serengeti to estimate potential grass production from the McNaughton equations (McNaughton 1985), as described above, and then used our estimates of grass consumption and wildebeest population density to estimate the amount of grass available for burning after accounting for losses to herbivory. We used data in Pellew (1983) to estimate the effect of burning on loss of tree biomass. Table 1 gives a full list of model variables and parameter values.

#### Four model complexity types

To investigate the effects of grazers and browsers on treegrass coexistence and on each other's populations, we compared equilibrial solutions for four nested versions of the model. In the simplest case, we solved a two-equation model (model HW) consisting only of trees and grasses (Eq. 1 and 2), with no herbivores. We contrasted this with a model that incorporated only grazers (model HWG), or only browsers (model HWB), or the full model with both grazers and browsers (HWGB). We examined the equilibria as a function of two key parameters: fire frequency (f) and rainfall ( $\psi$ ). We analyzed the stability properties of model equilibria with a classic linearization approach (May 1973). In most model versions, we were able to derive equilibrium solutions algebraically by setting derivatives to zero and rearranging the equations, but in the case with no herbivores the solutions were too cumbersome to express analytically. In this case we solved the equations in Mathematica 4.1 using the parameter values in Table 1. To evaluate the local stability of the model equilibria, we conducted a linear stability analysis (May 1973). We also evaluated the global stability of model equilibria by solving the model numerically under a wide range of initial conditions. We were primarily interested in how coexistence and stability vary across two dominant savanna gradients: rainfall ( $\psi$ ) and fire frequency (*f*). The parameter  $\psi$ was given values between 100-1500 mm year<sup>-1</sup> (bracketing values for the Serengeti), and f ranged between 0 (no fire) and 1 (annual fires).

# **Results**

# Coexistence and relative biomass of trees and grasses as a function of abiotic factors (model *HW*)

In the absence of herbivores (model HW), there are two ways in which functional groups of plants interact - competition for resources (which favors trees), and indirect interference via fire (which favors grass). Woody plants suppress grass via a nonlinear competitive effect on grass growth. Grass sustains fires, which then increases tree mortality. This form of interference leads to the potential for alternative states along environmental gradients. Abstractly, the dynamics of the system play out in a phase space with axes of grass and woody plant biomass. In this space, model HW has two nonlinear isoclines, one for each plant functional group (not shown). These isoclines can either not intersect (corresponding to complete dominance by one of the functional groups), or intersect one to multiple times, corresponding to possible alternative stable states for the system. Which of these outcomes occurs depends upon where the system sits along a rainfall gradient.

Along a gradient of increasing rainfall, equilibrial vegetation structure ranges from a stable grassland state at one end (in which trees are excluded) to a stable woodland state at the other (where grasses are unable to persist) (Fig. 2A, 3A–B). Between these two states, trees and grasses can potentially stably coexist in a savanna phase. At the lower end of the rainfall gradient, fire always reduces tree cover (Fig. 3A-B) and causes a shift from savanna to a grassland for a given value of rainfall (Fig. 2A). At high rainfall, fire also leads to a decline in woody cover, but the system goes through a bifurcation (Fig. 3A-B): below a certain rainfall threshold, the savanna state is globally stable, and grasses can always invade, but above this threshold the ability of grasses to invade and coexist with trees depends on the initial tree biomass. At high rainfall and fire frequency, there are three steady state solutions: woodland, an unstable savanna state (not shown), and a locally stable savanna state (Fig. 2A, 3B). The system thus has two alternative stable states in this region - woodland and savanna. For a particular point in the parameter space for which these alternative states can occur, a decline in rainfall leads to a transition into a globally stable savanna state, and a decline in fire frequency leads to a transition to woodland. As discussed in Appendix 1, it is the addition of fire which leads to the potential emergence of alternative stable states along the gradient.

#### Effect of introducing grazers (model HWG)

The addition of herbivores to the tree–grass model (either singly or in combination) results in an increase in the extent of the savanna state across parameter space, a retreat of the grassland and woodland states, and the disappearance of alternative stable states (Fig. 2B–D). In the *HWG* model, grazers are predicted to persist in the system only at high fire frequency. Within their region of persistence, the savanna phase expands slightly at the expense of grassland



Figure 2. Vegetation phases at equilibrium as a function of annual rainfall  $\psi$  and fire frequency f(A) with no herbivores, (B) with grazers only, (C) with browsers only, and (D) with both grazers and browsers. The savanna and alternative stable state phases allow tree–grass coexistence, woody vegetation is excluded in the grassland phase, and herbaceous vegetation is excluded in the woodland phase. The dotted lines bound the regions of grazer ( $G^*$ ) and browser ( $B^*$ ) persistence at equilibrium (above the dotted line in (B) and to the right of it in (C) and (D)).



Figure 3. Grass (dashed lines, left axis) and tree (solid lines, right axis) biomass at equilibrium: (A) and (B) with no herbivores; (C) and (D) with grazers only; (E) and (F) with browsers only; and (G) and (H) with both browsers and grazers as a function of annual rainfall  $\psi$ . The left panels and right panels show the cases where fire is absent from the system (f=0) or occurring annually (f=1), respectively. Panels (B) and (F) show bifurcations where alternative stable states emerge along the rainfall axis (Fig. 2). Inflection points correspond to the points where the grazer and/or browser strategy becomes viable and herbivores can invade the system (the region of viability is shown as a grey box).

(Fig. 2B). At high fire frequency, the increase in grass biomass due to the reduction in tree biomass more than offsets the suppressive effect of fire on grasses, as suggested by model equilibria in the absence of herbivores (Fig. 3A). The grazer resource thus increases with fire frequency, and grazer persistence is possible when the rate of supply of grass biomass exceeds a minimum threshold (Fig. 2B). In the region of parameter space that allows grazer persistence, the savanna phase is stabilized (i.e. alternative equilibria disappear) because grass biomass is dictated only by the grazer life history parameters:

$$H^* = \frac{m'}{b'c'} \tag{5}$$

This only occurs when frequent fire occurs (contrast Fig. 3D with 3B) but not when fire is absent (a condition in which grazers cannot invade, leading to identical results for panels A and C in Fig. 3).

The consumption term -c'G in Eq. 2, which is not present in the case with no grazers, means that grass biomass at equilibrium is lower in the HWG model than in the HW model (Fig. 3D). The consequent reduction in the fire mortality term  $-f\lambda H\mu_m$  of Eq. 1 leads to a higher tree biomass when grazers are present (Fig. 3D, compared to the savanna state in 3B). Above the rainfall threshold, grazers can only invade if the system is already in the savanna state, since grazers can not invade if b'c'H < m', which is true in the woodland state because H=0 (Fig. 2B, 3A), and therefore the system continues to have alternative stable states above the threshold. The grazer equilibrium is globally stable below the threshold (within the parameter bounds that allow grazer persistence), and locally stable in the savanna phase above the threshold. At high rainfall therefore, a temporary reduction in fire frequency could lead to grazer extinction and the conversion of a savanna with grazers into a woodland.

#### Effect of introducing browsers (model HWB)

Unlike grazers, browsers (model HWB) are favored by a low fire frequency (Fig. 2C) because their food resource is maximized as f declines for a given value of rainfall. As is the case with grazers, browsers maintain their resource at a constant level given by:

$$W^* = \frac{m}{bc} \tag{6}$$

The suppression of tree biomass by browsers (Fig. 3E) limits the competitive effect of trees on grasses and causes an increase in grass biomass compared to the tree–grass model HW (Fig. 3A). Unlike the case of grazers, in the region of parameter space for which browser persistence is possible, there are no alternative stable states in the system.

#### Full model (model HWGB)

When grazers and browsers are both included in the model (model *HWGB*), only two vegetation phases remain: grassland and savanna (Fig. 2D), and within the region of

grazer-browser coexistence, the tree to grass ratio remains constant and the model equilibrium is globally stable (Fig. 3G-H). Along gradients within the zone of coexistence, vegetation composition should remain unchanged. The addition of browsers to a model which previously only had grazers has two effects on the grazers: first, it results in an expansion of the region in which grazers can persist, and second, it removes the alternative stable states in model HWG (Fig. 4A). The introduction of browsers reduces the competitive exclusion effect of trees on grasses (and thus on grazers) that previously occurred at low fire frequency. Similarly, the addition of grazers to the browser model HWB expands the zone of browser persistence along the rainfall-fire gradient. In this case, the reduction of fuel load caused by grazers at high fire frequency reduces tree mortality due to fire and increases the food resource of browsers (Fig. 4B).

#### Interactions between grazers and browsers

Within the region of parameter space for which grazerbrowser coexistence occurs, there is an emergent mutualistic interaction between grazers and browsers. The addition of browsers to model HWG results in an increase in the equilibrium grazer biomass  $G^*$  for any given fire frequency and rainfall value, and the converse is also true in most cases (Fig. 5). This occurs because each herbivore guild indirectly increases the food resource of the other by suppressing its own resource, freeing the other plant resource from either competition or fire. This effect is magnified by rainfall because the rate of resource input for plant growth increases as rainfall increases. The grazer-browser interaction shows opposite trends as a function of fire frequency, however (Fig. 5E-F). When there is no fire in the system, grasses (and thus grazers) exert no impact on trees, and the equilibrium solutions for  $B^*$  are the same in models with and without grazers (Appendix 1), independently of rainfall (Fig. 5F). As fire frequency increases, however, the suppressive effect of grazers on tree mortality due to fire becomes increasingly important. Thus, even though the equilibrium value of  $B^*$  declines slightly as a function of fire frequency



Figure 4. Regions of (A) grazer persistence when no browsers are present and (B) browser persistence when no grazers are present (shaded areas) as a function of annual rainfall  $\psi$  and fire frequency *f*. The area to the right of the dotted line represents the region of grazer–browser coexistence. The lightly shaded area in (A) is the region for which invasion by grazers is conditional on the system being in a savanna state when browsers are not present. If the system is in a woodland state, grazers cannot invade.



Figure 5. Herbivore biomass as a function of annual rainfall  $\psi$  and fire frequency f: (A) grazer biomass without (B-) and with (B+) browsers in the absence of fire (f=0) and (B) with annual fires (f=1); (C) browser biomass without (G-) and with (G+) grazers in the absence of fire (f=0) and (D) with annual fires (f=1).

in the full model (Appendix 1), browsers still do better at high than low fire frequency, compared to the case with no grazers (Fig. 5B, 5D). For grazers, browsers become increasingly important as a factor suppressing tree biomass (thus enhancing grass biomass) as fire frequency declines, which is why introducing browsers has a stronger effect on  $G^*$  at low than at high fire frequency (Fig. 5E).

# Discussion

# Herbivore effects on tree-grass ratios and coexistence

In a landmark paper, Hairston et al. (1960) proposed that, because herbivores are limited by predators in terrestrial ecosystems, vegetation tends to be regulated by bottomup (water and nutrients) rather than by top-down forces (herbivory). There are ecosystems, however, in which topdown factors appear to be of great importance in limiting vegetation biomass. For savannas in particular, there is ample evidence to suggest that such limitation, in particular due to fire and herbivory, can be fundamental in determining tree cover and the relative biomass of trees and grasses (Scholes and Archer 1997, van Langevelde et al. 2003, Sankaran et al. 2004), but it is not clear to what extent this is true in general for savannas. Here we show theoretically that herbivores can play a significant role in expanding the bounds of tree-grass coexistence across abiotic space. This may be a particularly important factor in systems like the Serengeti, where a number of vertebrate herbivores can escape regulation by predation, either due to large body size or to migratory and herding lifestyles (Fryxell and Sinclair 1988, Fryxell et al. 2007).

Our model provides a theoretical framework for predicting tree-grass balance in savannas as a function of three key drivers: water, fire and herbivores. The model fits the empirical relationship derived by Sankaran et al. (2005), who found that, independently of any other factors (grass biomass, fire or herbivory), tree cover reaches an upper limit determined only by rainfall below about 600 mm per annum (i.e. if trees are regulated by resources in dry savannas). Above this, trees and grasses can coexist if trees are suppressed by other factors (i.e. trees might be top-down regulated by megaherbivores in mesic savannas). Most studies of tree cover conducted over large (regional, continental or global) scales have found evidence for a rainfalldriven upper limit for tree cover (Sankaran et al. 2005, Bucini and Hanan 2007, Staver et al. 2011), but with significant variation in actual tree cover below this upper limit. We suggest that in a system characterized by intrinsically slow dynamics (given by the time to maturity and acquisition of fire resistance in trees), this variation is simply a reflection of systems that are, for the most part, in a transient phase.

The model suggests that herbivores can exert a considerable impact on the coexistence, stability properties, and relative proportion of tree and grass biomass. This finding is broadly consistent with the results of van Langevelde et al.'s (2003) model with fixed herbivore densities, with some important differences. As in their model, increasing fire frequency expands the parameter space for which alternative stable states can occur, specifically along a gradient of water availability (van Langevelde et al. 2003). This is because the difference between two stable attractors in the system (complete fire suppression due to tree shading when trees are dominant and uncontrolled burning when grasses dominate) is exacerbated by an increase in the probability of an ignition event. Put differently, the positive feedbacks in the system are enhanced as fire frequency goes up: an increase in grass biomass is facilitated by tree loss due to burning, allowing further grass expansion. A similar feedback mechanism can lead to tree dominance.

Our model also agrees with van Langevelde et al. (2003) in that an increase in herbivory can cause a reduction in the region for which alternative stable states can occur, although we show that this effect is far more striking when consumers are regulated by the vegetation. If predators or disease keep the herbivore populations in check, as occurred when rinderpest was endemic in the Serengeti (Holdo et al. 2009b), the herbivore impact on vegetation structure is obviously reduced. One less-apparent difference between the two models is that, although the stable savanna state is increased across rainfall and fire gradients by both browsing and grazing in our model, in van Langevelde et al.'s (2003) model the parameter space of savanna persistence declines as grazing increases. This is also a consequence of the non-dynamic nature of herbivores in their system. Simply increasing grazing as in the van Langevelde et al. (2003) model reduces the range of parameter values within which grass can persist, but if herbivores dynamically respond to a decline in grass biomass, as in our model, the effect is the opposite, and savanna increases. Both models could reasonably apply, depending on the extent to which herbivores are dynamically responsive to their resource base, at the spatial scale one is considering.

The results are consistent with the observations of Dublin et al. (1990) that alternative stable states can occur in savanna ecosystems such as the Serengeti, and more broadly, that such states are a pervasive feature of savannas globally (Hirota et al. 2011, Staver et al. 2011). The notion that bifurcations can occur in savannas and woodlands (Dublin et al. 1990, Starfield et al. 1993), particularly along precipitation gradients (Sankaran et al. 2005) is not new, but strong empirical evidence for alternative stable states has only emerged recently (Hirota et al. 2011, Staver et al. 2011). The model results are therefore not particularly surprising in this respect, except for one important aspect. Dublin et al. (1990) concluded, based on historical trends in animal population densities, that uncontrolled fires led to woodland decline in the 1960s in the Serengeti, and that browsers subsequently prevented woodland regeneration in the 1980s. They thus suggest that fire caused a shift between alternative stable states, and herbivory constituted the mechanism for the maintenance of the scrub state. Our model indicates that the opposite type of behavior is more likely in this system, with fire being responsible for the maintenance of alternative states (consistent with Staver et al. 2011), and herbivores leading to the disruption of such states. Even with frequent fires, relatively mesic savannas such as the northern Serengeti woodlands seem unlikely to revert to scrub or grassland without being 'nudged' into such an alternative stable state by the action of browsers. This of course depends on two key factors in our model. The first is the explicit dependence of fire spread on grass biomass. This assumption is strongly supported for the Serengeti for the period in question (A. R. E. Sinclair unpubl.), but may no longer be true at present, as managers increasingly control the amount of area burned, and burn early in the dry season when tree mortality is lowest (M. B. Coughenour pers. comm.). It is a critical assumption for many of the model conclusions: without it, there is no effect of grazers on tree biomass or on the browser population, as these effects are mediated exclusively by the grazer–fire interaction.

The second important factor is the magnitude of the competitive effect of trees on grasses via the parameter  $\theta$ , for which we do not yet have a reliable estimate. A lower value of  $\theta$  than that used in our model would expand the savanna state into regions of parameter space with higher rainfall, and increase the region of grazer coexistence into regions with lower fire frequency. The model behavior is therefore strongly dependent on the existence of asymmetric tree-grass competition in the form of the parameter  $\theta$  in Eq. 2, but we do not specify the nature of this effect (e.g. the depression in grass growth could reflect both competition for water and shading). We do not, for example, assume rooting niche separation between trees and grasses as a necessary condition for coexistence. We assume instead that trees and grasses are differentially limited (as inferred from the differences in their growth equations) by water and some other unspecified resource. This is a reasonable assumption given that it has been shown in the Serengeti that nutrient and light limitation can both be important for grass growth, and that the importance of these limiting factors vary with water availability (Belsky 1994). A second consequence of the strong asymmetry in tree-grass competition in the model is the perhaps counter-intuitive result that grazer abundance increases with fire frequency. This occurs because the reduction of the suppressive effect of trees on grasses by fire (i.e. the positive effect of fire on grass biomass) outweighs the negative effect of fire on grasses (because grasses have intrinsically fast growth rates compared to trees). Therefore, even though fire may 'compete' with grazers for a common resource, fire also displaces the strong competitive effect of trees.

An important assumption is the absence of top-down regulation on herbivores, either by predators or disease. These assumptions are reasonable for some of the key vertebrate herbivores in a system such as the Serengeti, at least under certain conditions. Through the first half of the twentieth century, the wildebeest population of the Serengeti was limited to low densities by rinderpest (Sinclair 1979), but a switch to bottom-up regulation through food limitation occurred in the 1970s (Fryxell and Sinclair 1988, Mduma et al. 1999, Fryxell et al. 2007). Wildebeest escape predator limitation by migrating in large herds (Fryxell et al. 1988). Elephants, in turn, are able to escape predation by virtue of their large size, and protection from humans can permit elephant populations to grow to where they drastically alter their resources in many parts of Africa (Laws 1970). Although the elephant population in Serengeti has not yet reached this stage, it has been increasing steadily over the past two decades. The system may thus be converging towards the type of equilibrium predicted by the model, provided that elephants eventually do become resource-limited, and that fires are allowed to burn in an uncontrolled fashion.

Related to the question of top-down regulation of herbivores is the issue of the intrinsic ability of herbivores to regulate their food sources. We have used a simple Lotka-Volterra framework for herbivore population dynamics, in which herbivores are able to perfectly track and limit their resources. The assumption of L-V dynamics, for example, gives rise to the counter-intuitive result that adding grazers (which compete with fire for resources) to the HW model eliminates the woodland state. More realistic formulations (e.g. assuming nonlinear functional and numerical responses) might restrict the ability of the herbivores to reduce vegetation biomass. For example, food quality declines with biomass as grasses accumulate fiber (Wilmshurst et al. 1999, Fryxell et al. 2004) and trees accumulate wood or secondary compounds. This could limit the ability of grazers to invade systems with high grass biomass (Fryxell et al. 2005) or of browsers to effectively exploit mature woodland (except in the case of elephants). As a result, we would expect that the expansion of the savanna state across parameter space would be somewhat less pervasive that predicted here.

Our model makes some additional simplifying assumptions. Modifications that would make the model more realistic might include a spatially-explicit approach (e.g. one that could include tree neighborhood effects on fire intensity or spatial variation in herbivore abundance due to herding behavior), seasonality and division of trees by age or size class. The latter is potentially of particular importance because other models have shown that variation in establishment ability and sensitivity to disturbance across tree size classes can be important factors allowing tree-grass coexistence (Menaut et al. 1990, Hochberg et al. 1994, Higgins et al. 2000) and generally affecting the dynamics of tree cover in response to fire (Hanan et al. 2008). Despite these potential limitations, the model serves as a baseline for examining the stability of the savanna biome (at equilibrium) as a function of trophic structure and the underlying abiotic template.

### Grazer-browser interactions

In addition to altering the balance of tree and grasses in the system, we show theoretically that herbivores can affect each other's populations. Our model focused on major functional groups of herbivores, which do not compete for food resources. The only realistic scenarios for examining this interaction are those in which the set of parameters in the model allow grazers and browsers to coexist. When coexistence occurs, the relationship is always mutualistic, with the exception of the case with no fire (in which case, grazers lack a mechanism that allows them to affect browsers, so the interaction is an asymmetric commensalism). In our investigations of model behavior, we find situations in which grazers can exert negative effects on browsers, and vice versa, but these only occur within regions of parameter space that do not result in coexistence. This suggests that fixing grazer numbers to explore effects on browsers (or the opposite) can lead to misleading conclusions being drawn about grazer-browser interactions, because of the possibility of indirect feedbacks occurring in the full system.

What are the consequences for the system under alternative scenarios? If a rinderpest epidemic were to cause a crash in the wildebeest population, as occurred at the turn of the 20th century (Sinclair 1979), the resulting increase in grass biomass, coupled with an increasing elephant population, could drive the system to grassland or scrub. At the opposite extreme, an increase in elephant poaching and stringent fire management coupled with continued high wildebeest numbers could lead to bush encroachment and eventual dominance by thickets and woodlands in areas previously characterized by savanna. At this point it should be noted that true extinction of either trees or grasses from a real savanna system is unlikely to occur. The logistic formulation we use in the model allows for the stable monodominance of one or the other functional group. In practice, however, the persistence of long-lived belowground storage organs provides a reserve pool of biomass that can recover when conditions change (Boaler and Sciwale 1966, Bond and Midgley 2001). Whole-tree mortality (as opposed to topkill), for example, is rare in these highly-disturbed systems, and trees can resprout almost indefinitely (Hoffmann 1998, Holdo 2006). In reality the 'grassland' state is therefore more likely to be a very sparsely wooded savanna rather than a true grassland, but in terms of tree to grass ratios this distinction may be unimportant. Perennial savanna grasses have been shown to exhibit a similar capacity for regrowth (McNaughton 1979, Fryxell et al. 2005). Still, historical data suggest that the Serengeti and many other savanna and woodland systems can exhibit large changes in tree to grass ratios as a result of the effects of fire and herbivores, particularly elephants (Caughley 1976, Leuthold 1996, Sinclair et al. 2007, Western 2007, Holdo et al. 2009a), even if complete displacement of either functional form is unlikely to occur (Holdo 2007). It is clear that the impact of herbivores on tree cover in particular is often underestimated (Asner et al. 2009), and we suggest that, in absence of topdown regulation, they have the potential to fundamentally alter the structure of tree-grass systems.

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# Appendix 1

Model equilibria. The full equilibria for model HW are not presented due to space considerations, given that the solutions contain third-order polynomials in  $H^*$  and  $W^*$ . Some insight, however, comes from considering partial equilibria.

When woody vegetation is present alone (i.e. H=0), then according to Eq. 1, one can neglect fire. In this case, equilibrial woody biomass equals

$$W^* = \left(\frac{r_w}{\delta_w}\right) \left(\frac{\Psi}{\Psi + \beta_w}\right) - \alpha_w \tag{A1}$$

Along a rainfall gradient, woody vegetation declines with decreasing  $\psi$ , and cannot persist if rainfall is too low. This threshold condition is

$$\Psi_{w} = \frac{\alpha_{w}\beta_{w}}{\left(\frac{r_{w}}{\delta_{w}} - \alpha_{w}\right)}$$
(A2)

When rainfall is below this amount, woody vegetation is predicted not to persist, even in the absence of fire. At the other end of the gradient, maximal woody plant biomass is

$$W_{\max}^* = \left(\frac{r_w}{\delta_w}\right) - \alpha_w \tag{A3}$$

If woody plants are absent, then the grass equilibrial biomass is

$$W^* = \left(\frac{r_h}{\delta_h}\right) \left(\frac{\Psi}{\Psi + \beta_h}\right) - \alpha_h \tag{A4}$$

and the maximal grass biomass expected if water is not limiting is

$$H_{\max}^* = \left(\frac{r_b}{\delta_b}\right) - \alpha_b \tag{A5}$$

The grass functional group can increase when rare and woody plants are at equilibrium, provided that

$$\frac{1}{H}\frac{dH}{dt} = \left(\frac{r_b}{\Theta W^* + \alpha_b}\right) \left(\frac{\Psi}{\Psi + \beta_b}\right) - \delta_b > 0$$

There is a minimum amount of rainfall needed to sustain the grassland, given by

$$\Psi_{b} = \frac{\alpha_{b}\beta_{b}}{\left(\frac{r_{b}}{\delta_{b}} - \alpha_{b}\right)}$$

If  $\psi_b < \psi_w$ , there is then a region of the gradient where grass can persist, but woodland cannot. Moreover, if this is true, and trees are present but scarce, grass can invade, so a savanna is guaranteed. So long as trees are scarce, an increase in rainfall increases grass biomass.

If fire were not present, then along a gradient in rainfall, from Eq. A1, woody vegetation would increase with increasing rainfall, up to the maximum given by Eq. A3. If  $W_{\text{max}}^* > H_{\text{max}}^*$ , and moreover,  $\theta > 1$ , then in this limit, grasses are excluded. Putting these pieces together, what one would see along a gradient in rainfall is a transition from grassland to savanna to woodland, with a hump-shaped relationship of grass biomass to rainfall.

When grass is present, however, one expects fire to also occur. This form of interference competition complicates the analysis, changes the slice of the gradient along which savanna is expected, and also leads to a richer array of potential outcomes. It is rather difficult to extract much transparent meaning from the third-order polynomials that describe the equilibrial conditions, but numerical analyses of the equilibria defined by these polynomials reveal clear patterns that might be expected.

What grazers and browsers do in the model is basically to constrain the biomass of one functional group, or both, which in turn also fixes the mortality due to fire, and also simplifies that analysis. For model HWG, the following steady-state solutions result in stable coexistence of H, W, and G:

$$H^* = \frac{m}{b'c'}$$
$$W^* = \frac{r_w \Psi}{(\Psi + \beta_w)(\delta_w + f\lambda\mu_w H^*)} - \alpha_w$$
$$G^* = \frac{r_b \Psi}{c'(H^* + \Theta W^* + \alpha_b)(\Psi + \beta_b)} - \frac{\delta_b + f\lambda\mu_b H^*}{c'}$$

For model *HWB*, the following steady-state solutions result in stable coexistence of *H*, *W*, and *B*:

$$H^{*} = \frac{-\left[\delta_{b} + \left(\frac{\theta m}{bc} + \alpha_{b}\right)f\lambda\mu_{b}\right] + \left[\delta_{b} + \left(\frac{\theta m}{bc} + \alpha_{b}\right)f\lambda\mu_{b}\right]^{2} - 4f\lambda\mu_{b}\left[\left(\frac{\theta m}{bc} + \alpha_{b}\right)\delta_{b} - \frac{r_{b}\Psi}{\Psi + \beta_{b}}\right]}{2f\lambda\mu_{b}}$$

$$W^{*} = \frac{m}{bc}$$

$$B^* = \frac{r_w \Psi}{c(W^* + \alpha_w)(\Psi + \beta_w)} + \frac{f \lambda \mu_w H^* - \delta_w}{c}$$

Finally, for the full model *HWGB*, the following stable equilibria result:

$$W^{*} = \frac{m}{bc}$$

$$H^{*} = \frac{m'}{b'c'}$$

$$B^{*} = \frac{r_{w}\Psi}{\left(\frac{m}{bc} + \alpha_{w}\right)(\Psi + \beta_{w})c} - \frac{\delta_{w}}{c} - \frac{f\lambda\mu_{w}m'}{b'c'c}$$

$$G^{*} = \frac{r_{b}\Psi}{\left(\frac{m'}{b'c'} + \frac{\Theta m}{bc} + \alpha_{b}\right)(\Psi + \beta_{b})c'} - \frac{\delta_{b}}{c'} - \frac{f\lambda\mu_{b}m'}{b'c'^{2}}$$