

# Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti

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**Abstract.** Vertebrate herbivores and fire are known to be important drivers of vegetation dynamics in African savannas. It is of particular importance to understand how changes in herbivore population density, especially of elephants, and fire frequency will affect the amount of tree cover in savanna ecosystems, given the critical importance of tree cover for biodiversity, ecosystem function, and human welfare. We developed a spatially realistic simulation model of vegetation, fire, and dominant herbivore dynamics, tailored to the Serengeti ecosystem of east Africa. The model includes key processes such as tree–grass competition, fire, and resource-based density dependence and adaptive movement by herbivores. We used the model to project the ecosystem 100 years into the future from its present state under different fire, browsing (determined by elephant population density), and grazing (with and without wildebeest present) regimes. The model produced the following key results: (1) elephants and fire exert synergistic negative effects on woody cover; when grazers are excluded, the impact of fire and the strength of the elephant–fire interaction increase; (2) at present population densities of 0.15 elephants/km<sup>2</sup>, the total amount of woody cover is predicted to remain stable in the absence of fire, but the mature tree population is predicted to decline regardless of the fire regime; without grazers present to mitigate the effects of fire, the size structure of the tree population will become dominated by seedlings and mature trees; (3) spatial heterogeneity in tree cover varies unimodally with elephant population density; fire increases heterogeneity in the presence of grazers and decreases it in their absence; (4) the marked rainfall gradient in the Serengeti directly affects the pattern of tree cover in the absence of fire; with fire, the woody cover is determined by the grazing patterns of the migratory wildebeest, which are partly rainfall driven. Our results show that, in open migratory ecosystems such as the Serengeti, grazers can modulate the impact of fire and the strength of the interaction between fire and browsers by altering fuel loads and responding to the distribution of grass across the landscape, and thus exert strong effects on spatial patterns of tree cover.

**Key words:** *Acacia*; *elephants* (*Loxodonta africana*); *GIS*; *migration*; *savanna dynamics*; *SD model*; *spatial coupling*; *spatial heterogeneity*; *Tanzania*; *tree–grass interactions*; *wildebeest* (*Connochaetes taurinus*).

## INTRODUCTION

Shifts in the amount of woody cover as a result of climate change, fire, herbivory, and human agency have the potential to exert strong impacts on ecosystem function in savannas (Ringrose et al. 1998, Hoffmann et al. 2002, Jackson et al. 2002, Scanlon et al. 2005, Pringle et al. 2007). Savannas comprise 40% of the terrestrial land mass and sustain a significant fraction of the population of many developing countries (Scholes and Walker 1993), so these changes may have deep impacts on human welfare globally. It is thus critical that we obtain a better quantitative understanding of how the multiple factors that influence savanna woody cover interact with each other, both for the management of particular ecosystems and to assess the regional and global implications of shifts in shrub and tree cover.

A long-standing challenge in ecology is the formulation of a general theory of tree–grass regulation in savannas (Belsky 1990, Scholes and Archer 1997, Higgins et al. 2000, Sankaran et al. 2004). Savannas can exhibit marked spatiotemporal variation in tree biomass, but it is still not well understood how this variation emerges from climate, edaphic factors, herbivores, fire, or interactions among these variables (Scholes and Walker 1993, Sankaran et al. 2004, 2005, Bond 2005, Bond et al. 2005, White 2006). In African savannas, it is clear that three main factors can strongly affect the relative biomass of woody and herbaceous vegetation: soil moisture, fire, and mammalian herbivory (Walker 1987, Scholes and Walker 1993, Bond 2005). What is less clear is how these factors interact dynamically, both locally and across productivity gradients, to structure vegetation, given that strong feedbacks can occur among plants, herbivores, and fire (Frost and Robertson 1987). Such feedbacks have the potential to greatly influence system behavior, and it is important to understand such feedbacks to develop long-term management strategies

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and to project the impacts of climate change and pressure from a rising human population.

Further complexity is added by the fact that African savannas are often characterized by the presence of two distinct major vertebrate herbivore guilds: grazers, which feed primarily on grasses and forbs, and browsers, which feed primarily on woody vegetation. Few studies (e.g., van Langevelde et al. 2003) have so far explored the relative importance of grazers and browsers (or for that matter, mixed feeders) as determinants of tree-to-grass ratios in savannas, and to the best of our knowledge, none have so far explicitly investigated how grazing, browsing, and fire interact to determine savanna tree cover. Grazers and browsers can both modulate the effects of fire on tree dynamics by affecting fuel biomass, either directly through grass consumption, or indirectly by reducing the competitive effect of trees on grasses (Norton-Griffiths 1979, Frost and Robertson 1987, Holdo 2007). In a dynamic system, grazers and browsers may also potentially interact with each other by exerting reciprocal effects on their own food resources. This three-way browser-grazer-fire interaction may be particularly important in African savannas because these systems are often dominated by megafaunal assemblages that fill both the grazing and browsing niches (Owen-Smith 1988).

Understanding the interactions and feedbacks among grazers, browsers, and fire may be critically important for the management of woody cover in many savanna ecosystems. Managers have long been concerned both by unwanted increases (bush encroachment in rangelands) and losses (declines in woody canopy cover in protected areas) in woody cover (Laws 1970, Martin et al. 1992, Prins and Vanderjeugd 1993, Smit and Rethman 2000, Western 2006), so the development of predictive models of woody biomass dynamics is an important goal for these systems. Given the importance of tree cover for climate, ecosystem processes, biodiversity, and human livelihoods within the savanna biome (Scholes and Walker 1993, Hoffmann et al. 2002, Jackson et al. 2002), it is important to understand how the management of fire and herbivore abundance might impact tree dynamics, since they are to some extent under human control.

We are here primarily concerned with the potential for losses in tree cover in savanna systems that are both fire-prone and dominated by elephants. Elephants stand apart from most other browsers because of their ability not only to slow the recruitment of trees from small to large size classes, but to rapidly reduce tree cover over short periods of time by toppling and ringbarking mature trees (Laws 1970, Guy 1989, Ruess and Halter 1990, Holdo 2006). Across Africa, elephants have often been implicated as the key drivers of large changes in tree abundance (Buechner and Dawkins 1961, Laws 1970, Dublin et al. 1990, Ben-Shahar 1993, Van de Vijver et al. 1999, Western and Maitumo 2004). We address the question of tree cover regulation in savannas by developing a semimechanistic simulation model (dubbed SD, for Savanna Dynamics) to investigate the

role of browsers, grazers, and fire in determining the amount of tree cover in savannas. We focus on a few key drivers and system components within a framework that allows herbivores to move adaptively across the landscape in response to changes in food availability (McNaughton 1985, Fryxell et al. 2004) brought about by fire, consumption levels, and rainfall. This model thus enables us to explore the combined effects of fire, browsing, and grazing on vegetation structure.

SD differs from previous simulations of fire and/or herbivore effects in savannas (e.g., Starfield et al. 1993, Baxter and Getz 2005, Holdo 2007, Liedloff and Cook 2007) in a number of key respects: (1) unlike previous models, we use a spatially realistic framework to simulate vegetation dynamics at the landscape scale, using a GIS-based lattice that incorporates realistic spatial variation in edaphic factors, as well as nutrient and climatic gradients; (2) we take into account the effects of herbivory on both grasses and trees; and (3) we incorporate feedbacks of the vegetation on herbivores and fire. Thus our model treats herbivory and fire as dynamic processes rather than only as fixed drivers. We believe that our model can thus be potentially applied across a wide range of conditions, permitting assessment of a wide range of management and conservation scenarios in African savannas. SD is a model of intermediate complexity, with less mechanistic detail than models such as SAVANNA (Boone et al. 2002) and FLAMES (Liedloff and Cook 2007), but with sufficient complexity to generate realistic landscape-level simulations of vegetation, fire, and herbivore dynamics, unlike the case for simpler models (van Langevelde et al. 2003, D'Odorico et al. 2006).

We use the Serengeti ecosystem of East Africa as a case study for the investigation of vegetation-herbivore-fire dynamics in the present paper, for a number of reasons: first, it is an open, fire-prone ecosystem characterized by strong abiotic (both climatic and edaphic) gradients and by the presence of both grazing and browsing ungulate herbivore guilds that can profoundly affect vegetation structure (Sinclair 1975, Pellow 1983, McNaughton 1985). The heterogeneity in abiotic and biotic factors across the landscape means that the Serengeti essentially incorporates the range of variables that determine vegetation structure across most African savannas, and thus this system represents an excellent laboratory for the study of vegetation dynamics in savannas. Second, historic records reveal strong shifts in tree-to-grass ratios in the Serengeti as a result of changes in the fire regime and herbivore populations (Norton-Griffiths 1979, Sinclair 1979), and such records provide a rich source of data for parameterizing and validating models. Finally, the Serengeti is itself of great importance for the conservation of biodiversity and ecological processes in the savanna biome (Sinclair et al. 2007), and we hope to provide a useful management tool for this and other savanna ecosystems.

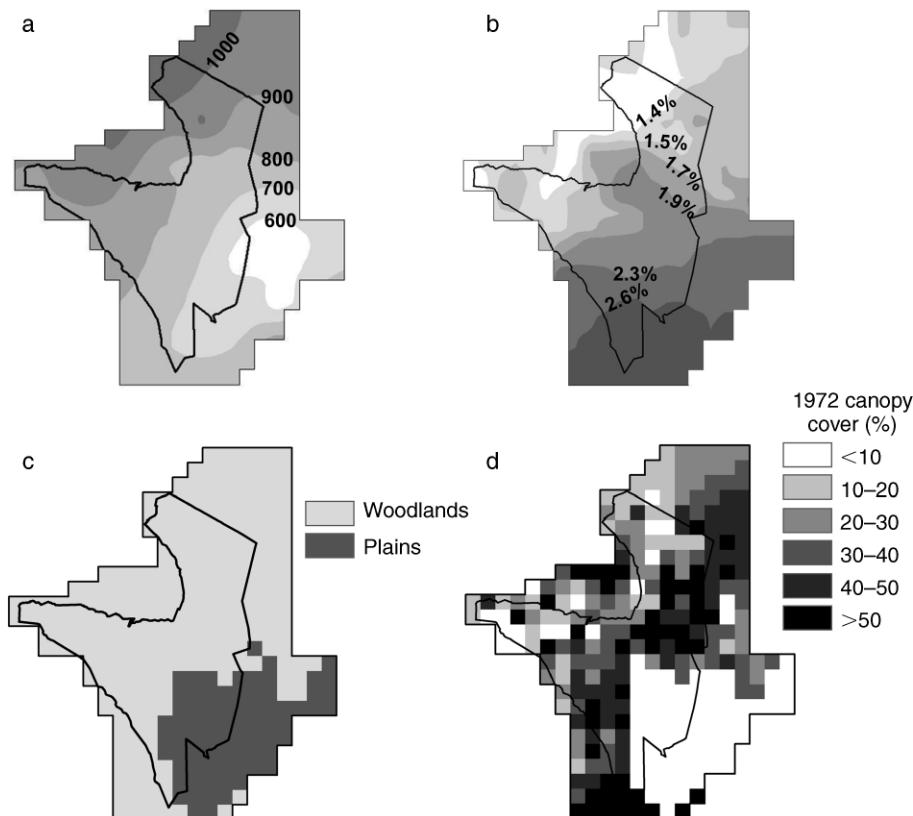


FIG. 1. (a) Isohyets (mean mm per annum between 1960 and 2001); (b) grass N concentration (%); (c) plains and woodland habitats; and (d) 1972 percent canopy cover in the greater Serengeti ecosystem (GSE). The Serengeti National Park boundary is shown in outline.

After introducing the model structure, we show that the model provides good fits to the long-term dynamics of key variables in the Serengeti. We then conduct simulations to explore the future trajectory of the system and the sensitivity of the model to uncertainty in the parameters. Our primary objective in this paper is to examine how interactions between fire, browsing, and grazing determine vegetation structure across rainfall and fertility gradients. We first address the question of how contrasting fire frequencies and elephant population densities are predicted to determine the average future trajectory of tree cover in the Serengeti-Mara ecosystem, and how the elephant–fire interaction is in turn affected by the presence of grazers. We then investigate how these factors are predicted to affect patterns of tree cover across space. Finally, we examine the effects of elephant population density and fire on the wildebeest population and the effect of the grazer–browser interaction on fire.

#### MATERIAL AND METHODS

##### *Study system*

The greater Serengeti ecosystem (GSE hereafter) comprises  $>30\,000\text{ km}^2$  of savannas and grasslands in Tanzania and Kenya. The GSE includes two national

parks, several game reserves and game management areas, and unprotected land along its periphery, and is thus subject to a range of anthropogenic resource utilization regimes. Following well-established precedent, we define the GSE as the area that approximately bounds the resident and migratory wildebeest populations of the Serengeti-Mara complex (Maddock 1979, Sinclair 1979). We presently ignore the effects of human activity both within the protected areas and in the small fraction of the western GSE that is settled. We will address these effects and socio-ecological interactions in an upcoming paper.

A marked southeast to northwest rainfall gradient characterizes the system (Fig. 1a), as well as a fertility gradient that runs approximately opposite to the rainfall gradient (Fig. 1b). The ecosystem is predominantly woodland savanna, but significant areas of pure grassland occur, notably in the southeastern plains and the Mara in the northern sector (Fig. 1c). Throughout much of these grassland areas, trees are almost entirely absent due to the presence of a hardpan layer close to the soil surface (Belsky 1990). In the woodland habitat, on the other hand, the amount of tree cover can vary considerably (Fig. 1d). The rainfall gradient is the engine that drives the seasonal migration of the wildebeest and

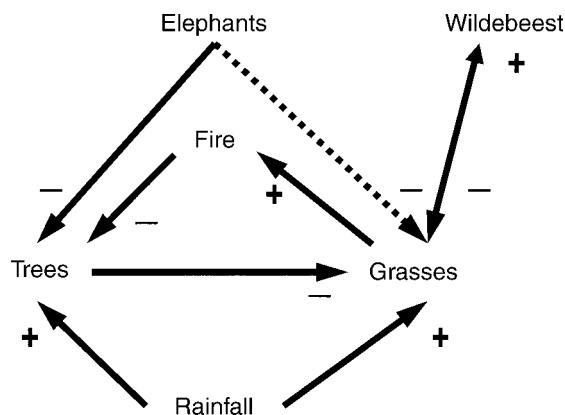


FIG. 2. Schematic representation of the key players in the Serengeti plant-herbivore dynamics (SD) model and their interactions. The dashed line indicates a weak effect of elephants on grasses.

other ungulates (Sinclair 1979, Boone et al. 2006). During the wet season, when grass production in the Serengeti plains is high, the wildebeest migrate south, returning to the northern woodlands as green grass becomes increasingly restricted to areas with dry-season rainfall (McNaughton 1979).

#### Model description

The savanna dynamics (SD) model focuses on a number of key processes in the ecosystem (see Fig. 2): grass and tree growth, mortality, and consumption; herbivore population dynamics and movement; and fire dynamics; all of which are influenced by rainfall. The model is implemented on a spatially explicit, GIS-based framework, which facilitates comparison of the model with empirical data sets for particular systems (in this case the Serengeti, but SD may easily be modified and applied to other ecosystems). The state variables in the model are tracked within cells embedded in a lattice. The lattice represents the GSE, and covers 30 700 km<sup>2</sup>, divided into 307 10 × 10 km cells. The choice of boundaries for the GSE and cell size follows Maddock (1979). The agents represented by the model (Fig. 2) include “keystone” species (two dominant herbivores, wildebeest *Connochaetes taurinus*, which as noted above “define” the Serengeti by their migratory behavior, and elephants *Loxodonta africana*), as well as the two major plant physiognomic categories, trees and grasses. The model distinguishes green from dry-grass biomass, but does not track separate grass species. Furthermore, because fire-driven mortality is strongly dependent on tree size (Pellew 1983), the model tracks the size structure of trees. We model single generic grass and tree species. (For the latter we use *Acacia tortilis*, because data are readily available for this species and it is the most abundant and widely distributed tree species in the ecosystem.)

Wildebeest are the dominant grazers in the Serengeti (Sinclair 2003), accounting (by our estimate) for over

half the herbaceous biomass consumed by large herbivores in this ecosystem. Elephants are mixed feeders whose impact is most readily apparent on the tree community (Croze 1974a, b, Pellew 1983, Dublin et al. 1990). Although giraffe may affect tree growth in the Serengeti (Pellew 1983), our primary concern in this paper is with the role of the elephant population, which has been expanding rapidly over the past decade. In the present version of the model, we do incorporate giraffe browsing indirectly (in the tree growth coefficients) but treat it as a constant. Future extensions of the model will include other species (e.g., resident herbivores such as buffalo, giraffe, and carnivores) as explicit dynamical variables.

The model is time discrete and uses different time steps for different compartments, to reflect a balance between crucial biological detail and computational efficiency. Potentially rapid changes in grass biomass over short time periods (McNaughton 1985) dictate that grass growth, consumption, and decay occur on a daily time scale. Wildebeest herbivory and local population dynamics are also modeled with a daily interval to match the rapid dynamics of their resource. Wildebeest movement among cells occurs on a weekly scale (for faster computational execution; using this longer time scale for movement does not affect model results). Tree dynamics, by contrast, follow an annual time step. Rainfall varies monthly. During simulations, a year's worth of rainfall data (12 months from November of the previous year to October, assuming that the wet season begins in early November) is randomly selected from the 1960–2006 historical record and used to drive grass and tree growth for one annual cycle. This process is repeated for each year of the simulation. This climatic driver and the fire submodel are the only stochastic components in an otherwise deterministic model.

*The model landscape.*—The model uses three types of raster data sets or maps generated through a GIS analysis: rainfall, habitat type, and plant nitrogen content (Fig. 1). These GIS layers play a dual role. In addition to being used to fit free parameters in the model, they are also used to generate model inputs for simulations. We created monthly rainfall layers for the GSE for the period 1960–2006 using monthly rainfall data from 204 gauges distributed throughout the Serengeti ecosystem (TAWIRI records). We generated the rainfall raster files with an inverse distance-weighted technique in ArcGIS 9.1 (ESRI, Redlands, California, USA) using 12 nearest neighbors and power 2 (Legendre and Legendre 1998:747–748). We produced the habitat type map by joining shapefile and raster vegetation layers from multiple sources into a composite layer for the entire GSE (Oindo et al. 2003; M. Coughenour, unpublished data; D. Herlocker, unpublished data; K. L. Metzger, unpublished data). We used multiple sources because no single map currently available covers the entire GSE. The rationale for developing the habitat map was to identify treeless areas of the landscape to

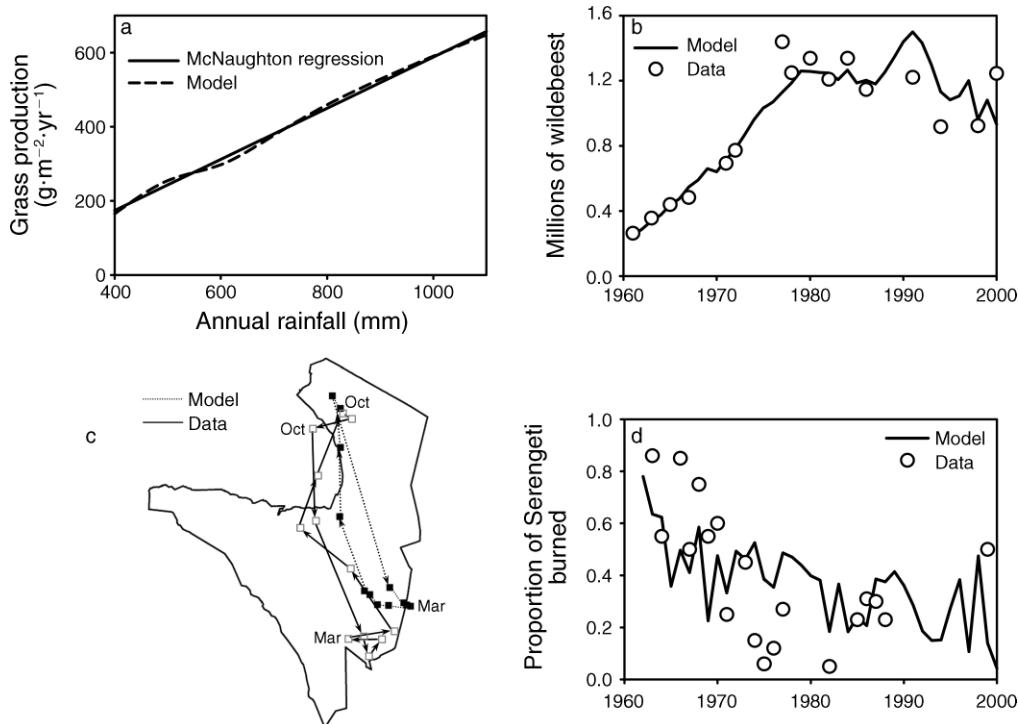


FIG. 3. (a) Grass production as a function of annual rainfall predicted by McNaughton's (1985) empirical function and the corresponding savanna dynamics (SD) model fit; (b) model fit to wildebeest census data; (c) model fit to actual and simulated monthly locations of "center of mass" of Serengeti wildebeest population averaged over the 1969–1972 time period; (d) model fit to fire extent data over a 40-year period in the Serengeti.

prevent the model from allowing tree growth in habitats where woody vegetation is excluded due to edaphic constraints (Sinclair 1979, Belsky 1990). In addition, for the woodland habitat, where trees do occur, we were able to infer past patterns of tree canopy cover from maps developed by M. Norton-Griffiths (*unpublished data*) based on aerial photography. We used these maps to initialize our model runs and as a data layer for the fitting of our wildebeest movement submodel (R. M. Holdo, R. D. Holt, and J. M. Fryxell, *unpublished manuscript*) (Appendix A). We used ordinary kriging (Cressie 1993) to estimate canopy cover for missing cells of the GSE.

We produced the plant nitrogen layer (Fig. 1b) by combining field data from 114 sampling sites surveyed by S. J. McNaughton (*unpublished data*) throughout Serengeti National Park (NP) (site values being calculated as unweighted means for all grass species sampled at a given site) with a map of soil types (Jager 1982) to estimate plant N in undersampled areas. To arrive at this plant N map, we first assigned plant N values to each polygon from the soil type layer that contained a plant survey site. Because an analysis of variance showed significant differences in plant N among soil types (R. Holdo, *unpublished data*), we assumed that soil type can to some extent predict plant N. We assigned mean plant N values for each represented soil type to polygons in the soil type layer that did not overlap with

the set of available plant N survey sites. We then used the resulting population of originally sampled sites, plus extrapolated sites (placed at the centroids of polygons), to generate a plant N raster layer with ArcGIS, using ordinary kriging with an exponential semivariogram model (Legendre and Legendre 1998:749–750).

*Parameter estimation and model fitting.*—We obtained most model parameters from the literature (Table A1). When parameter estimates were not available, we obtained them by fitting subsets of the model to relevant data sets using generalized least squares and a simulated annealing algorithm (Hilborn and Mangel 1997, Hurtt and Armstrong 1999, Holdo et al. 2007; see Appendix B). Data sources used for model fitting included an empirical function relating grass production and rainfall in the Serengeti (McNaughton 1985), fire history data (Sinclair et al. 2007; M. Norton-Griffiths, *unpublished data*), wildebeest census data (obtained from TAWIRI, the Tanzania Wildlife Research Institute, Arusha, Tanzania), and detailed monthly distribution maps of wildebeest collected over the three-year period 1969–1972 (Norton-Griffiths 1973, Maddock 1979). The fits of these components are shown in Fig. 3. The fitting of the wildebeest movement component of the model is described in detail elsewhere (R. M. Holdo, R. D. Holt, and J. M. Fryxell, *unpublished manuscript*).

*Model equations.*—Appendix A lists the equations (and their derivation) used in the model to simulate the

following processes: grass dynamics, herbivore movement and population dynamics, fire, and tree dynamics. A full list of state variables and model parameters is given in Appendix A: Table A1. Additional parameters (matrix coefficients) corresponding to the tree dynamics submodel are listed in Appendix C.

#### *Model simulations*

*Tree cover as a function of fire, elephant population density, and wildebeest.*—In the current model implementation, we assumed that the size of the wildebeest population is determined by the amount and protein content of its food supply (green grass), but that the size of the elephant population is entirely determined by extrinsic factors (immigration due to habitat loss external to the GSE and poaching, for example) and fixed over time. The occurrence of fire within each cell is the product of two variables: the occurrence of ignition events and the amount of fuel available (dry grass), which determines the amount of area burned (Sinclair et al. 2007). This allowed us to evaluate model output as a function of two external drivers: elephant population density, and the presence of fire. For most of our simulations, we assumed that elephants are evenly distributed throughout the woodland habitat of the GSE. This assumption makes our model results easier to compare with other systems, because population density is defined by a single, spatially invariant value. We also ran some simulations in which we assumed that elephant spatial distributions, though fixed over time, varied across space in accordance with census data (the 1969–1972 recce data; Appendix D). This enabled us to make more specific predictions for the Serengeti. In a future version of the model, we will relax the assumption that the elephant population is fixed in time and space; at present (unlike the case for wildebeest) we lack data that would allow us to simulate adaptive movement patterns by elephants.

We projected the model 100 years into the future with mean population densities ranging between 0 and 1 elephants/km<sup>2</sup>, and fire present or absent (and for some simulations, fire on alternate years), assuming an initial wildebeest population of 10<sup>6</sup>, and an initial mean canopy cover of 37% (Fig. 1d). These conditions represent those found in the Seronera area of the park in the 1970s (Norton-Griffiths 1979, Pellew 1983). To evaluate the impact of grazing on tree cover, we ran simulations with and without wildebeest present in the model. We simulated precipitation by drawing randomly from GIS layers created from rain gauge data spanning the period 1960–2006. Our results represent mean values for 25 runs for each combination of factors. The output variables presented here are: woody cover (the summed crown cover across all tree size classes), wildebeest population density, and area burned. Most of our results present the output variables aggregated across the entire landscape, but we also show spatial variation in model output for woody cover and fire. To evaluate the amount of spatial heterogeneity in tree cover across

the landscape, we computed the standard deviation in woody cover across all the cells in the lattice.

*Sensitivity analysis.*—To examine the robustness of model predictions as a function of parameter values, and to identify the components of the system that are most likely to affect its dynamics, we conducted a sensitivity analysis on 19 model parameters (Table A1). We conducted 25 100-year runs of the model (assuming the presence of fire and 0.1 elephants/km<sup>2</sup>) for each combination of parameter values, and used relative changes in the mean woody cover (across the woodland habitat) as our response variable. We ran the model with each target parameter set at either 80% or 120% of its “best” value, while keeping all other parameters at their default values. We calculated the difference in woody cover predicted from using the extreme values of each parameter and expressed the model sensitivity as this difference, presented as a percentage of the woody cover predicted with the default value.

## RESULTS

### *Woody cover as a function of herbivory and fire*

The model predicted that elephant browsing and fire will have strong effects on total woody cover (Fig. 4a, b) and the size structure (Fig. 4c, d) of the Serengeti tree population over the next century. In the default scenario (with wildebeest present, at equilibrium with their food supply), the 100-year woody cover declined as a function of elephant population density within the values tested, and declined strongly in the presence of fire, even when fire was a semiannual occurrence (Fig. 4a, b). When fire was added to the system, small increases in elephant population density (starting from zero) led to faster initial declines in woody cover than occurred when fire was absent, suggesting a synergistic interaction between elephants and fire (Fig. 4a). When wildebeest were removed from the system, the effects of fire were magnified, and even small increases in elephant population density were predicted to lead to strong declines in woody cover and conversion from woodland to grassland (Fig. 4b).

Whereas fire alone (i.e., with no elephants present) was not predicted to cause a decline in woody cover over the next century (we assumed an initial tree canopy cover of 37%), the exclusion of wildebeest resulted in a severe loss in tree cover, and this loss was predicted to become almost complete with even a small elephant presence (Fig. 4a, b). If the current average density of 0.15 elephants/km<sup>2</sup> (estimated for the entire savanna habitat of the ecosystem) is maintained over the next 100 years, the model predicted that the amount of woody cover would be largely controlled by the presence of fire. Without fire, the present-day elephant population did not change mean woody cover, but with fire (even as a semiannual occurrence), the system became much less woody, a change that would be exacerbated by any factor (e.g., a disease outbreak) that might cause a crash in the wildebeest population (Fig. 4b).

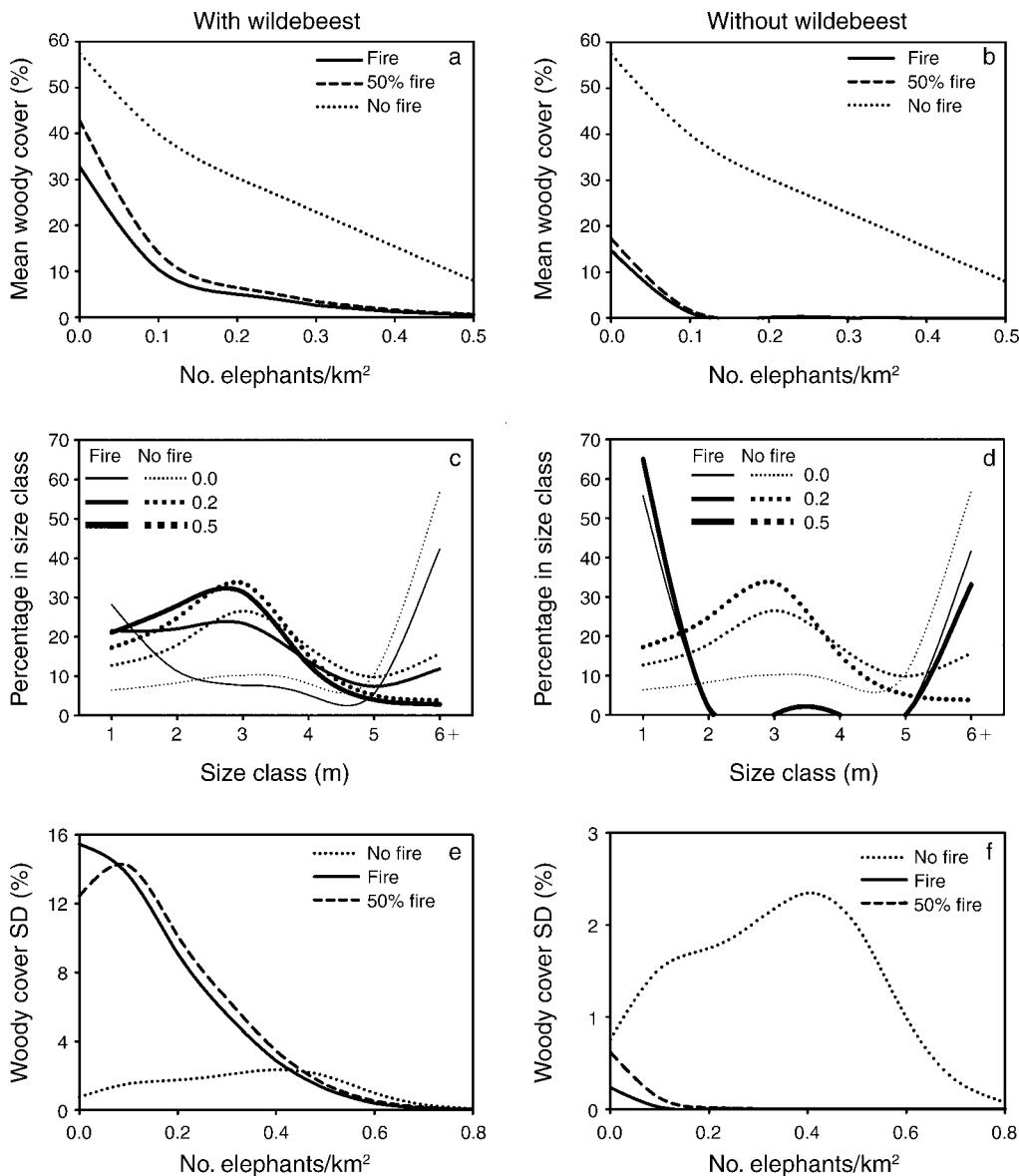


FIG. 4. Model predictions for the greater Serengeti ecosystem from 100-year simulations: (a, b) mean percent woody cover; (c, d) relative tree size class distributions; and (e, f) spatial heterogeneity in woody cover (as measured by the standard deviation in percent woody cover across the woodland habitat) as a function of elephant population density (no. elephants/km<sup>2</sup>) and fire, either with (a, c, and e) or without (b, d, and f) wildebeest present in the model. Values shown represent means for 25 runs.

The results suggest that focusing on total woody cover can be misleading, however, as indicated by the results for the tree size class distribution (Fig. 4c, d). The model predicted that increases from 0 to 0.5 elephants/km<sup>2</sup> would lead to profound changes in the size structure of the tree community (Fig. 4c). Increasing population density shifted the size distribution of trees from mature to small height classes (Fig. 4c), showing that the woody cover that remained in the system would largely shift from woodland to scrub under these conditions. These conclusions are relatively independent of the presence of fire when wildebeest are present in the system, and thus

able to regulate the amount of fuel (grass) available for burning (Fig. 4c), but when wildebeest were “removed,” the system shifted from being dominated by intermediate and large trees (depending on elephant population density) in the absence of fire (Fig. 4c), to being dominated almost entirely in the presence of fire by new recruits <1 m in height and mature trees that are tall enough to escape the effects of fire (Fig. 4d).

*Spatial variation in tree cover*

Herbivory and fire were predicted to affect not only the average tree cover across the landscape, but also its

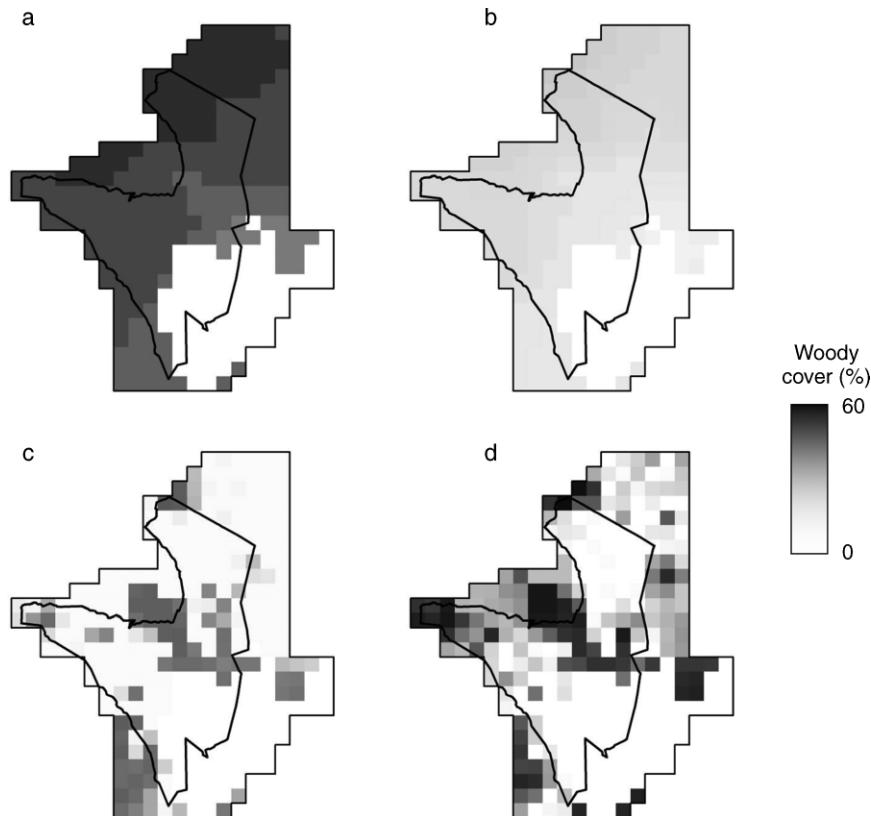


FIG. 5. Predicted woody cover values after 100 years for the woodland habitat of the greater Serengeti ecosystem under four scenarios: (a) no elephants or fire; (b) 0.5 elephants/km<sup>2</sup> and fire; (c) 0.1 elephants/km<sup>2</sup> (i.e., a total population of 3070 elephants) and fire, assuming an even distribution of elephants throughout the ecosystem; and (d) a population of 3070 elephants distributed according to 1970s census data and fire. Values shown represent means for 25 runs.

spatial heterogeneity (Fig. 4e, f). Without fire, at low and high values of elephant population density the landscape was predicted to be relatively homogeneous (as indicated by the low variance in woody cover across lattice cells, Fig. 4e, f), being uniformly dominated by trees and grasses, respectively (Fig. 5a, b). At intermediate values of elephant population density, the amount of tree cover was predicted to be highly variable across the landscape (Fig. 5c, d). The unimodal relationship between elephant population density and habitat heterogeneity shifted toward the left (lower population density) or disappeared completely when fire was added to the model (Fig. 4e). At low elephant population density, the effect of fire was to increase the amount of heterogeneity in the landscape, but this effect was neutralized or reversed at high population density (Fig. 4e). In contrast, removing wildebeest from the system caused fire to lower rather than increase the amount of heterogeneity (Fig. 4e, f).

Fire suppression was predicted to result in a gradient of increasing woody cover following the southeast to northwest rainfall gradient (Fig. 5a). The introduction of fire substantially changed this pattern (Fig. 5c), resulting in a landscape characterized by a mosaic of habitats that contrasted widely in terms of woody cover

(Fig. 5c). This pattern followed no apparent relationship with rainfall (compare with Fig. 1a), but was matched by the distribution of the fuel layer and the spatial distribution of fire (Fig. 6b). When wildebeest were present in the model, fire frequency was lower than when they were excluded, but fire was also more variable across space (Fig. 6a, b). The patchiness in woody cover was caused by the spatial distribution of fire frequency in the landscape, which in turn was driven by wildebeest grazing patterns. This conclusion is supported by the fact that when wildebeest were removed from the model, the spatial distribution of fire frequency (Fig. 6a) changed dramatically, and appeared to be driven by increasing rainfall towards the northwestern boundary of the ecosystem, as was the case for the distribution of woody cover in the absence of fire (Fig. 5b).

In the absence of the moderating influence of grazers on fire, the range of conditions that generated spatial patchiness in tree cover was restricted to elephant population densities that were at or below those encountered at present (Fig. 5b). Even at moderate elephant population densities, strong elephant–fire interactions tended to drive the system into an open grassland state (Fig. 5b). This is because, all else being equal, herbivore exclusion causes a decline in the

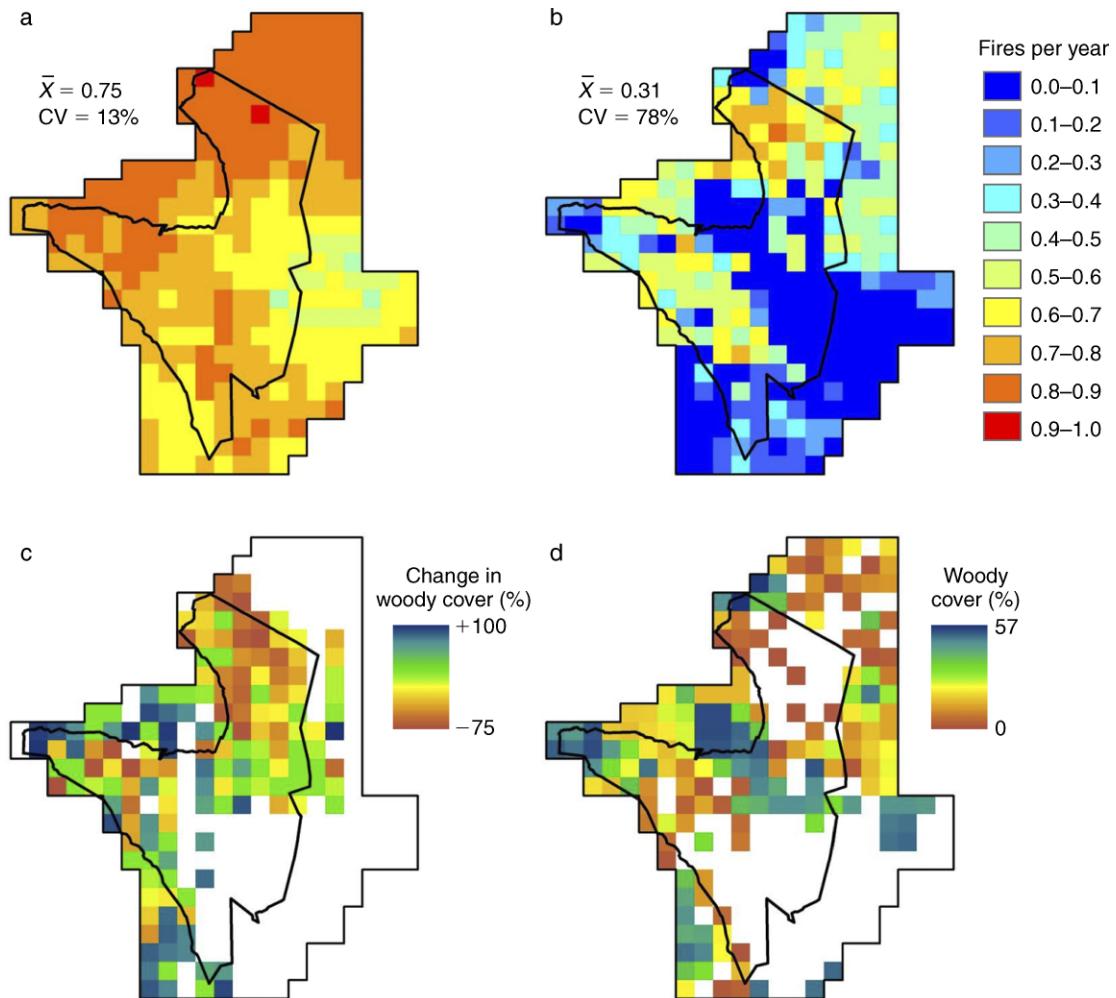


FIG. 6. Predicted fire frequency (100-year mean) across the GSE (a) without wildebeest and (b) with wildebeest present, assuming a uniform population density of 0.1 elephant/km<sup>2</sup>, as in Fig. 7c; (c) observed change in woody cover over a 10-year period between 1962 and 1972, and (d) predicted long-term (100-year) woody cover distribution across the GSE assuming a 1960s population density (~0.1 elephant/km<sup>2</sup>). The means and coefficients of variation in panels (a) and (b) were calculated across the entire landscape.

patchiness and an increase in the frequency of fire across the landscape (Fig. 6).

#### *Response of wildebeest and fire extent*

The wildebeest population, as a dynamic variable in the model, was also predicted to respond to elephant population density and fire (Fig. 7a). In the absence of fire, elephant population density had only a slight effect on the size of the wildebeest herd. At low population density, increases in elephant population open the tree canopy and lead to a reduction in the suppressive effect of trees on grass biomass, thus promoting grassland area and wildebeest carrying capacity. At higher population density, on the other hand, elephants, as mixed feeders, begin to compete with wildebeest for grass, and therefore have a slightly negative effect on wildebeest carrying capacity (Fig. 7a). When fire was introduced into the system, the reduction in canopy cover became

even more widespread, and the wildebeest population was predicted to increase as a result of the reduction in woody cover. The synergistic nature of the elephant–fire interaction on woody cover (Fig. 4a) was also manifested in the response of the wildebeest population (Fig. 7a). The spatial extent of fire was strongly influenced by wildebeest, which regulate the amount of fuel in the landscape, and to a lesser extent by elephants, which promote grassland expansion (and thus fire spread) by reducing woody cover (Fig. 7b).

#### *Observed and predicted changes in woody cover*

The dominant pattern of change in woody cover predicted by the model for the Serengeti, namely the persistence of woodland in the central, southwestern, and extreme western portions of the ecosystem, vs. grassland and scrub in much of the remainder of the GSE, especially the north of Serengeti NP (Figs. 5c and

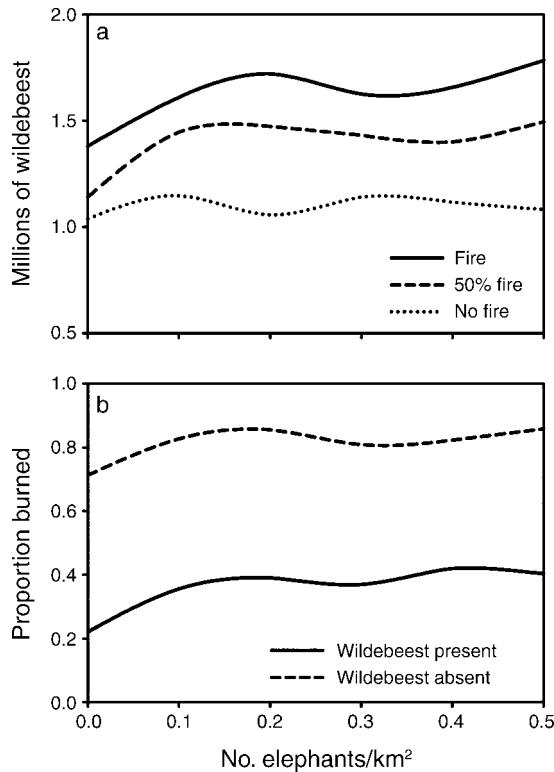


FIG. 7. Predicted effects from 100-year simulations of (a) elephant population density and fire on the size of the wildebeest population; and (b) elephant population density and the presence of wildebeest on the amount of area burned in the greater Serengeti ecosystem. Values shown represent means for 25 runs.

6d), was consistent with trends in woody cover change observed by M. Norton-Griffiths (1979) over a 10-year period in the 1960s (Fig. 6c). These changes can largely be ascribed to the effects of fire (Fig. 6c), which are in turn partly controlled by spatial patterns of wildebeest herbivory as a result of the migration. Most notably, the spatial pattern of woody cover predicted for the system is largely independent of the elephant population, given the similarity between simulations assuming uniform or census-based patterns of elephant population distribution across the landscape (Fig. 5c, d). This result is bound, however, to be largely dependent on future trends in the size of the elephant population, with large increases in the latter leading to a more uniform distribution of scrub and grassland habitat across the GSE (Fig. 5b).

#### Sensitivity analysis

The sensitivity analysis suggested that the amount of tree cover predicted by the model was most sensitive to parameters affecting (1) the amount of area that burns each year, and (2) tree growth (Appendix E). The parameters affecting burning can be grouped into those with direct effects (the constant  $\kappa_2$  in Eq. A.9, Appendix A) or indirect effects on the amount of grass available

for burning:  $\delta_G$  and  $f$  in Eqs. A.1 and A.2 of Appendix A, which determine the rate of conversion of green to dry grass,  $a_w$ , which in turn controls the wildebeest numerical response and thus subsequent grass consumption, and  $q$ , which influences wildebeest movement, and thus grazing patterns. The parameters that affect tree growth include  $d_0$  and  $a$  in Eq. A.17 in Appendix A.

#### DISCUSSION

##### *Effects of herbivory and fire on woody cover*

Our model accounts more fully than has previous work for the effects of browsers, grazers, and fire on spatial patterns of tree cover in savannas across abiotic gradients. To the best of our knowledge, this is the first study to show the importance of grazer–browser interactions for the regulation of tree dynamics via the effects of fire, and how the interplay of these factors influences spatial patterning in the landscape. Our results suggest that grazers can have strong secondary effects on tree cover, in particular its patchiness, by moderating the influence of fire. When wildebeest are excluded from the model, there is a strong elephant–fire interaction, driven by the positive feedback among trees, grasses, and fire. In our model, as elephants open up the tree canopy, grass suppression declines and fire becomes more widespread, leading to a further reduction in tree cover, accounting for the synergistic elephant–fire interaction that we observe. With wildebeest present, however, this effect is diluted because as grass consumption increases, the extent to which grass biomass is determined by tree–grass competition is reduced, and therefore so is the strength of the tree–grass–fire feedback.

Three key conclusions can be drawn from the spatial patterns that emerge from the simulation results. First, the model suggests that, under certain conditions (intermediate elephant population density and no fire), tree dominance is positively related to the amount of rainfall within the Serengeti. This results from the positive effect of rainfall on tree growth. Grass production also increases with rainfall, but since we assume that trees are competitively dominant over grasses, the net result is a positive correlation between tree cover and precipitation. When fire is present in the model, however, the direct correlation between tree dominance and rainfall disappears: since grass production is positively correlated with rainfall, fire frequency also increases with rainfall, and thus also tree damage and mortality. These results follow from the model's built-in assumption that tree–grass competition is asymmetrical, and trees eventually displace grasses in the absence of fire. This is a potentially significant result, because it shows that highly mobile grazers can lead to vegetation patterns that are difficult to predict from underlying environmental gradients, which might otherwise exert dominant effects on tree cover. Further empirical work is required to understand how the strength and outcome of tree–grass competition vary as a function of rainfall. In particular, it should be noted

that although the predicted spatial pattern of tree cover does not follow a simple monotonic relationship as a function of rainfall when fire and wildebeest are both present in the model, it seems likely that rainfall (and possibly also plant nitrogen content) plays an important indirect role in determining tree spatial patterns by influencing the wildebeest–grass–fire relationship. This is because the woody cover patterns that emerge in Fig. 5c occur consistently across many model runs. The results indicate that the patterns are in large measure the outcome of deterministic forces; in our model in particular, these are mean rainfall spatial patterns and plant nitrogen distributions, which influence the wildebeest distribution patterns, and thus indirectly spatial patterns in the vegetation.

A second important point is the difference in the relationship between the amount of spatial heterogeneity and elephant browsing intensity on the one hand, and heterogeneity and fire frequency, on the other. In the case of elephant browsing, at the two extremes of the range of values simulated, the system is controlled either by plant competition (at low elephant population density) and so becomes dominated by trees, or by disturbance (at high elephant density), and becomes dominated by grasses. The homogeneous spatial patterns that emerge at these two extremes are the result of a dynamic equilibrium between the rate of tree growth and recruitment and the intensity of elephant browsing. At intermediate elephant population densities, the system tends towards neither woodland nor grassland; the relative proportion of trees and grasses across the landscape is largely determined by the amount of rainfall, which, though varying systematically on average along a gradient, also has a stochastic component, and is therefore conducive to generating variation across space, amplified by spatial variation in herbivory.

Finally, we show that herbivore mobility can act as a key agent of spatial coupling in savannas. The amount of area burned locally is a function of fuel load, which varies spatially. Since fire is a stochastic process, fuel loads that lead to an expected fire probability that is neither 0 nor 1 (i.e., when  $p(t) \sim 0.5$  [Appendix A: Eq. A.9]) will produce the greatest amount of spatial variation in fire frequency. Grazers increase this variation in two ways. First, by simply lowering the average amount of grass throughout the landscape, grazers tend to make fires less widespread and more variable for any given ignition frequency (Fig. 5). Second, by responding numerically and by movement to the distribution of grass cover throughout the landscape, the model predicts that grazers increase the patchiness of fuel loads throughout the landscape. A knock-on effect of such patchiness is increased heterogeneity in the amount of tree cover, provided that the suppressive effects of browsing and fire are not strong enough to convert the entire landscape to grassland. Although it may appear surprising that introducing grazers to the system could increase the variance in grass

abundance across the landscape, this result is consistent with prior work in the Serengeti, in which it has been found that grazers seek out areas that maximize their energy intake rather than their total intake (Wilmshurst et al. 1999; R. M. Holdo, R. D. Holt, and J. M. Fryxell, *unpublished manuscript*). Since energy intake does not increase monotonically with grass biomass, due to the accumulation of low-quality senescent tissues, grazers often prefer areas with a small standing biomass of green grass over areas with a larger biomass of dry grass (Fryxell et al. 2004, 2005), and this effect can magnify differences in biomass across the landscape.

#### *Implications for elephant and fire management*

If fire is kept in check, the model suggests a decline in woody biomass above a population density of  $\sim 0.2$  elephants/km<sup>2</sup>; if the elephant population does not deviate significantly from its current level, the amount of tree cover is likely to remain relatively stable. In reaching these conclusions, we assumed that elephants are evenly distributed throughout the landscape, which is not the case (Dublin and Douglas-Hamilton 1987, Campbell and Borner 1995; Appendix D). The present elephant population of  $\sim 3000$  individuals translates into  $\sim 0.15$  elephants/km<sup>2</sup> within the savanna portion of the GSE. In reality, elephants tend to aggregate in certain areas within the Serengeti National Park and Mara Game Reserve (Campbell and Borner 1995), so that densities within portions of these areas may exceed those necessary for eventually tipping the system into a scrub or grassland state (Appendix D). Conversely, other areas may experience increases in canopy cover. The model predictions are broadly consistent with the observation that at population densities below  $\sim 0.2$  elephants/km<sup>2</sup>, the amount of tree cover (particularly in the short term) is likely to be driven more by fire and giraffe browsing (which strongly affects tree growth and recruitment) than by elephant damage (Pellew 1983, Dublin et al. 1990, Ruess and Halter 1990). A question of some concern, however, is how the amount of tree cover will change in the system as the elephant population continues to increase. At present, the number of elephants in the Serengeti equals or surpasses its historic maximum (Serengeti parks records, *unpublished data*), and continues to grow. The elephant population has grown by  $>10\%$  per annum since the early 1990s, and may thus soon approach a point where elephant browsing begins to have a significant impact on tree cover. The model suggests a strong relationship between elephant population density and tree cover, a finding supported by previous research conducted elsewhere (Holdo 2007). A doubling or tripling of the current population past a threshold of  $\sim 0.4$ – $0.5$  elephants/km<sup>2</sup> could thus have serious implications for the vegetation of the Serengeti.

Equally or more important is fire management policy. At present, the fire regime in the Serengeti appears to have diverged from the historical model proposed here

(hot fires late in the dry season) toward a regime of early prescribed burns that probably have a far lower impact on tree cover than predicted by the model. Reducing the chance that uncontrolled hot fires will occur late in the dry season is likely to mitigate the impact of elephants in this ecosystem, even though these fires cover extensive areas throughout the western sector of the GSE (S. Eby, *unpublished data*). So alteration in prescribed fire management may be able to compensate in part for changes in elephant numbers.

Our predictions assume that the wildebeest population is largely food limited, and that the amount of fuel in the landscape will therefore be kept in check. There has been increasing concern, however, that a new outbreak of rinderpest and/or a population crash following a severe drought could lead to a rapid decline in the wildebeest population (A. Dobson, *personal communication*). Fig. 4 shows some of the predicted changes that would emerge following such a collapse. Our model results suggest that further increases in the elephant population, when coupled with a severe reduction in the wildebeest herd and late dry season burning, could lead to a rapid decline in the amount of tree cover in the Serengeti, and hence to a drastic shift in the entire landscape, with the potential for cascading effects on biodiversity.

#### *Model uncertainty*

Further work is required to better understand the role of movement of both browsers and grazers in determining vegetation structure. In a future paper, we will relax the assumptions that elephant numbers are fixed in space and time. We expect that relaxing these assumptions will affect the amount of spatial variation in vegetation structure. This is because of the potential for positive feedbacks between elephants and fire: when trees are toppled or burned in a particular patch, resprouts increase food availability within the preferred feeding height of elephants (Frost and Robertson 1987), increasing the incentive for elephants to return to that patch. This localized disturbance also facilitates the spread of fire, which causes further resprouting and loss of mature trees. In our current model implementation, grazers rather than browsers are the primary drivers of spatial heterogeneity in tree–grass distributions. It is not clear at present how well this result matches reality, since our model allows grazers (but not browsers) to move adaptively across the landscape in search of high-quality food patches. This assumption is somewhat warranted, however, by the fact that the most highly mobile herbivores in the Serengeti are all grazers, namely wildebeest, Thomson's gazelles (*Gazella thomsoni*), and zebras (*Equus burchelli*), whereas the remaining grazers and all browsers are nonmigratory. One hypothesis for the origin of the wildebeest migration is that it is a mechanism for escaping resident predators on a seasonal basis (Fryxell et al. 1988). If that is the case, it is possible

that predation pressure plays an important indirect role in the distribution of tree cover across the landscape.

The results of the sensitivity analysis suggested that model outcome is quite strongly influenced by uncertainty in parameters associated with the competitive relationship between trees and grasses, tree growth rate, and the effect of fuel load on fire prevalence. Much of the uncertainty in the model is centered on the tree–grass–fire relationship, rather than on herbivore functional and numerical responses or grass production. This indicates that gaps in our understanding of how tree growth and recruitment vary as a function of rainfall, and of how trees and grasses compete with each other, should be prime areas for future empirical research. In particular, more research is required in the following areas. (1) The spatial pattern of grass suppression by trees: since isolated trees may actually promote grass growth under the canopy (Belsky et al. 1993, Belsky 1994, Belsky and Canham 1994), how does the switch from facilitation to competition depend on the density and size distribution of trees within a particular neighborhood, and does this pattern vary across rainfall gradients? (2) Do grasses suppress the growth and survivorship of trees in the smallest size classes through competition for resources? (3) How does tree mortality (rather than fire occurrence) vary as a function of fuel load?

#### *Future directions*

Because our model is driven by spatially realistic data layers and allows for dynamic responses of vegetation, herbivores, and fire, it provides a suitable framework for the exploration of a wide range of questions for this and other savanna systems. Although the model is tailored to the Serengeti, which is exceptional in some respects, e.g., in terms of primary productivity (Sinclair 1977), it may be easily modified for other savannas through a recalibration of a number of parameters. This is because the savanna dynamics (SD) model has been designed for intermediate complexity, with sufficient biological detail to simulate realistic scenarios, but with enough simplicity to require the estimation of a relatively small number of parameters.

Among some additional future questions that the model can explore we include: (1) How are changes in the rainfall regime as a result of global climate change likely to affect vegetation structure, fire patterns, and herbivore populations in the Serengeti? (2) How are wildebeest migration patterns impacted by changes in rainfall, the fire regime, and tree cover? We will address these questions in upcoming papers. In addition, we presently ignore the effects of human impacts such as poaching and agriculture on the behavior of the system, and will address these effects in the context of a socio-ecological model based on SD. Of key importance here is the role of humans in setting fires. The system-wide extent of burning in the Serengeti is strongly related to the size of the wildebeest population (Sinclair et al. 2007), and has (counterintuitively) declined even as

human populations have expanded (Campbell and Hofer 1995). Yet the spatial pattern of fire occurrence is strongly biased toward the populated western areas of the GSE (Dempewolf et al. 2007), suggesting an important role of humans in determining spatial patterns of fire occurrence. We propose to address this issue in the future by validating our model results against spatial fire data.

### Conclusions

Previous studies, both empirical and theoretical, have shown that elephants and fire can exert strong effects, either independently and in combination, on vegetation structure across a range of savanna and woodland ecosystems (Laws 1970, Caughley 1976, Pellew 1983, Dublin et al. 1990, Baxter and Getz 2005, Holdo 2007). Few studies have investigated the simultaneous effects of grazers and browsers on tree-to-grass ratios and tree cover. Van Langevelde et al. (2003) used a simple mathematical model to show that in fire-prone savannas, both browsers and grazers can independently affect the equilibrium and stability of tree-to-grass ratios. Our study expands on that model by incorporating spatial structure, grazer–browser interactions, and feedbacks of the vegetation on herbivores. This broader context is critical because it demonstrates that: (1) the synergistic interactions between browsers and fire are magnified in the absence of grazers; (2) grazers, via their effects on fire, can greatly affect the spatial pattern of tree cover when they respond numerically and spatially to resource availability across the landscape. Such mobile consumers can strongly modify the local structure of vegetation in ways that are not reflected by the mean results produced by low-dimensional models and spatially circumscribed empirical studies. An understanding of the spatial structure of ecosystems both as determinants of ecological processes, and as emergent properties that feed back on those very processes, is essential for developing quantitative models that can be used by managers. Such managers are concerned with understanding the factors governing resilience and sustainability in coupled socio-ecological systems (Holling et al. 2002). This is particularly the case in systems such as the Serengeti, where key players can respond adaptively in their movement behaviors to shifts in landscape structure.

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#### APPENDIX A

Savanna dynamics model equations and their derivation, including a table of state variables and model parameters (*Ecological Archives* A019-005-A1).

#### APPENDIX B

A table showing the hierarchical procedure used to estimate model parameters by fitting model output to data (*Ecological Archives* A019-005-A2).

#### APPENDIX C

A list of matrices representing the effects of elephant damage, fire damage, and growth across tree height classes in the savanna dynamics model (*Ecological Archives* A019-005-A3).

#### APPENDIX D

A figure showing the distribution of elephants across the greater Serengeti ecosystem (*Ecological Archives* A019-005-A4).

#### APPENDIX E

A figure showing the results of a sensitivity analysis conducted on key model parameters (*Ecological Archives* A019-005-A5).