

Development and Parameterization of a Rain- and Fire-driven Model for Exploring Elephant Effects in African Savannas

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Abstract We describe the development and parameterization of a grid-based model of African savanna vegetation processes. The model was developed with the objective of exploring elephant effects on the diversity of savanna species and structure, and in this formulation concentrates on the relative cover of grass and woody plants, the vertical structure of the woody plant community, and the distribution of these over space. Grid cells are linked by seed dispersal and fire, and environmental variability is included in the form of stochastic rainfall and fire events. The model was parameterized from an extensive review of the African savanna literature; when available, parameter values varied widely. The most plausible set of parameters produced long-term coexistence between woody plants and grass, with the tree–grass balance being more sensitive to changes in parameters influencing demographic processes and drought incidence and response, while less sensitive to fire regime. There was considerable diversity in the woody structure of savanna systems within the range of uncertainty in tree growth rate parameters. Thus, given the paucity of

height growth data regarding woody plant species in southern African savannas, managers of natural areas should be cognizant of different tree species growth and damage response attributes when considering whether to act on perceived elephant threats to vegetation.

Keywords Elephants · Herbivory · *Loxodonta africana* · Plant demography · Spatial modeling · Tree–grass coexistence · Woody plants

1 Introduction

Savannas represent an important resource both in terms of their inherent biodiversity and for supporting human populations [84, 87, 89, 96]. They are characterized by the coexistence of woody plants and grasses, under the influence of water availability, fire, nutrients, and herbivory. As megaherbivores, elephants play a significant role in savanna vegetation dynamics, affecting nutrient cycling and vegetation turnover processes in particular [64, 79]. High local elephant populations—whether a result of the fencing of natural areas or human encroachment—may lead to intensified damage to woody plants, and subsequent change in the plant community [44, 62, 81]. There is some concern therefore on the influence of high elephant populations on diversity of savanna species, structure, and function [18, 24, 28].

High levels of browsing by elephant may compromise the viability of some woody plant populations [101], resulting in community changes coupled with a possible loss of species diversity [24] and structural diversity [111]. Concern has been expressed over further ramifications for other fauna. In the Zambezi Valley, Zimbabwe, lower species richness of birds, ants, and “total animals” (ants, bats, birds, and mantises) occurred in elephant-impacted

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sites than in nonimpacted sites [24]. In northern Botswana, habitat modification by elephants produced substantial changes in bird species composition, although bird species richness could be increased if elephant impacts remained patchy [41]. Rare antelope species such as bushbuck (*Tragelaphus scriptus*) are also adversely affected by the reduction in cover and quality browse [1].

It is not known how elephant populations historically coexisted with today's extant woody plant species, and the dynamic properties governing the elephant–woodland interaction are poorly understood. Traditionally, their coexistence was thought to be equilibrial [33, 61], but a predator–prey model of the elephant–tree interaction [20] suggested that the system could be cyclic, with an oscillatory period of approximately 200 years. The relationship of herbivory pressure with plant available moisture and plant available nutrients may allow for the possibility of limit cycles in low fertility soils where encroachment of high-quality grasses would be less likely to follow tree loss, thus permitting woodland recovery [7, 8]. Restriction of elephant movement could disrupt any natural cyclic behavior [59]; however, while a recent parameterization [30] of Caughley's [20] predator–prey model has reasserted the possibility of a fixed-point equilibrium, others have proposed the existence of multiple equilibria [27, 28], with fire and other herbivores acting as other major factors influencing vegetation state.

The reasons for tree–grass coexistence in savannas have been debated for decades. Trees may impede grass domination through rainfall interception, litter accumulation, shading, or rooting zone competition, and in turn grasses can prevent tree seedling recruitment and provide fuel for fire, thus inducing mortality or suppression of woody individuals [88]. Walter [119] formulated the first coexistence hypothesis based on moisture availability with reference to rooting depth, which proposed that as rainfall increases, grasslands undergo transition to woodlands because the availability of water in the lower soil horizons allows trees to establish deeper roots and survive drought conditions. This hypothesis was later incorporated in a simple model [118], which demonstrated a single stable equilibrium under those assumptions. Further conceptual models built in soil moisture and other physical properties of soil, as well as nutrient availability, fire, and herbivory (see [9] for a concise review). By emphasizing adult tree roots, however, the Walter hypothesis neglects the critical seedling establishment phase [85], and field studies have cast doubt on the existence of separate niches in the rhizosphere [10, 58, 89]. Others [121] have proposed moving away from equilibrium-based models to more event-driven “state-and-transition” models recognizing discrete vegetation states and the driving forces that may cause shifts between states. Savannas are now seen as inherently nonequilibrium but stable,

kept in a state of tree–grass coexistence by disturbances such as fire, drought, and herbivory [42, 55, 89], and thus not predictable by a simple model. For example, stochastic disturbances that enable opportunistic recruitment events may play a critical role in maintaining tree–grass coexistence [42]. However, realistic savanna behavior has also been produced by a deterministic model incorporating infiltration rates, fire, and herbivory [113]. A recent review [55] has urged a shift in focus to examine the mechanisms that may buffer coexistence at the boundaries of change into tropical forest or grassland, i.e., what mechanisms may prevent the *nonexistence* of savannas.

The role of space in modeling savanna dynamics is also important [21, 55]. For example, a patchy distribution of small, internally oscillatory subsystems of trees may be sufficient to secure the persistence of both trees and grasses [45]. While some spatial savanna models only achieved tree–grass coexistence within narrow or extreme parameter ranges [53, 69] (also see [85]), others have found that, for example, widespread seed availability assists tree persistence, and spatial attributes of reproduction (dispersal and clumping) can further enhance the likelihood of coexistence [45, 54].

On the other hand, most attempts at modeling elephant–savanna interactions have ignored spatial heterogeneity [12, 13, 20, 28–30, 82, 114]. Elephant–vegetation models have also tended to neglect woodland structure [20, 29, 30], the effects of climate, density-dependence, and competition with other vegetation [13, 28, 82] or variability in rainfall and fire [114].

We developed the model presented here as a tool to help assess the impacts that elephants have on savanna systems motivated by the fact that elephants have been controlled in the past through culling, which might again resume in the future. Given the serious ethical considerations of culling as a method of controlling elephant density, or the difficulties of translocating individual elephants, we endeavored to include as much realism into our model as possible while retaining sufficient flexibility and generality so that the model could be used as a management tool in a variety of ecological and logistical settings. Therefore, while we have included elements of spatial, structural, and environmental heterogeneity, we have focused on the population (rather than individual) level and avoided the complexity of larger models such as SAVANNA [17, 66]. An outline of the model and its usefulness in terms of examining elephant effects is presented elsewhere [5], but the details on the development of the model and a justification of the parameter values used to obtain a baseline set of values for running the model have yet to be published. Therefore, in this paper, we focus in detail on the model development and parameterization and explore some of its sensitivity to uncertainty in the key driving factors.

2 The Model

2.1 Model Structure

We chose a spatial extent for our model of 1 km² as a representation of a suitable scale for considering management issues, while we selected a grain of 1 ha as the suitable resolution for modeling ecological processes such as interplant competition. The time scale of models requires similar trade-offs: The time scale of vegetation changes usually exceeds management time horizons [120], and this is particularly the case when dealing with long-lived organisms such as trees and elephants. We simulated the vegetation-only component of our model for 500 years to investigate the effects of parameter combinations on long-term coexistence. When examining elephant effects [5], we reduced the time scale to 100 years after elephant introduction to better reflect the shorter time scale of management concerns. As annual wet and dry seasons are characteristic of savannas [96], we discretized time into half-year time steps (t). Initial conditions are given by $t=0$, and as the model starts in a wet season, the passage of any year can be represented by a wet season commencing at an even value of t followed by a dry season commencing at an odd value of t .

2.1.1 The Model Habitat

We generated a representative 1 km² patch of a model savanna ecosystem by linking together 100 1-ha cells, denoted below with the index $x=1, \dots, 100$. Within each cell, we modeled grass and woody vegetation, assuming uniform fire intensity and herbivory, and the cells were linked (by seed dispersal and fire spread) in a 10×10 grid, a spatial extent sufficient for producing consistent dynamics [45]. Moisture availability (as driven by rainfall in the model) and nutrient availability are both major influences on savanna dynamics [7, 9, 88]. We assume these factors are homogeneous across the grid and are implicitly incorporated in model parameter values. Other impacts not explicitly modeled include other (nonelephant) herbivores (which may act synergistically or antagonistically with elephant impact [11, 64, 82]); and other environmental factors such as frost [89], lightning, windthrow, disease [11, 23, 97], and insects [50, 89].

2.1.2 Vegetation

Structural diversity in savannas can be important for biodiversity. For example, decreased bird diversity has been attributed to structural homogeneity in elephant-affected woodlands [24, 41]. Therefore, it is appropriate to develop demographic models emphasizing changes and transitions in the vertical woody structure [85]. We modeled the tree population using nine stage classes based on height, the i th

of which (in cell x at time t) has number of individuals $w_{x,i}(t)$ ($i=1, 2, \dots, 9$). We delineated the stage classes by height to better examine vertical vegetation structure and because elephant use of woody plants is often measured with reference to tree height. To separate the classes, we define four broader “metaclasses” based on heights of <15 cm for seedlings ($i=1$), <1 m for saplings ($i=2, \dots, 5$), 1–2 m and 2–3 m for shrubs ($i=6$ and 7, respectively), and 3–5 m and >5 m for trees ($i=8$ and 9, respectively). The use of four sapling classes serves to prevent seedlings entering the shrub metaclass within 2 years, and so individuals advance automatically through those classes ($i=2, \dots, 5$) subject to adequate rainfall. We used a tenth vegetation class, $w_{x,10}(t)$, to denote the grass biomass (kg) in cell x at time t ; thus, we can write the vegetation state as a column vector:

$$\mathbf{w}_x(t) = (w_{x,1}(t), \dots, w_{x,10}(t))',$$

where the symbol ' indicates the transpose of a vector. An individual in each of the woody plant metaclasses is assumed to control a “resource area” of 0.01, 1, 9, and 25 m² (seedlings, saplings, shrubs, and trees, respectively [57]). Area covered by grass is also tracked, and the area of cell x controlled at time t by individuals in class i is given by $a_{x,i}(t)$, $i=1, \dots, 10$.

Plant growth depends on annual rainfall (adjusted for vegetation type) and competition between all woody plants and grass, which is modeled as a function of area [90, 94]. Plant survival is determined as functions of rain, fire, and elephant use. Due to belowground tissue storage, woody plants can resprout after the loss of aboveground tissue from fire or elephant browsing, and are modeled as reverting one or more stage classes.

2.1.3 Elephant Population

The model simulates only one representative square kilometer so that it does not make sense to couple the modeled vegetation to elephant population dynamics. Rather, we assess the impact of elephants visiting this square kilometer, i.e., elephants can be dealt with as a time-varying input into the model, and different scenarios may be analyzed. We consider this approach more realistic than limiting our analysis, as in some earlier studies [4, 5, 82, 99], to various constant elephant “stocking densities.” In addition, this approach naturally extends to a geographic information systems setting in which our model is used to evaluate the effects of elephants in each of many grid cells on top of which elephant movements are imposed (cf. [2]).

2.1.4 Elephant Herbivory

In southern Africa, elephants transfer the focus of their foraging from grass to browse during the dry season. The

timing of this shift depends largely on rainfall, which determines the amount of quality grazing remaining at the end of the wet season [32]; toppling and uprooting of trees improves food availability for elephants in the dry season [48]. Elephant dry season foraging in Lake Manyara National Park, Tanzania, consisted mainly of browsing, with grazing predominating at the lakeshore where woody plants are scarce [56]. Similarly, at Lake Kariba, Zimbabwe, elephant grazing, although generally low, was concentrated exclusively in the wet season [52]. In this model, we have assumed that elephants partition their foraging seasonally, grazing and browsing exclusively in the wet and dry season, respectively [40, 68].

2.2 Model Development and Parameterization

Figure 1 shows a flow chart depicting the model dynamics, described in detail below.

2.2.1 Rainfall

We incorporated rainfall seasonality [96] by iterating our model using 6-month time steps, assuming that each year's rainfall falls entirely in the wet season. Thus rainfall is modeled (for year $[t, t+2]$) as a sine wave plus noise, and normalized to take the value of 1 (i.e., changes in biological rates as a function of relative rainfall levels are scaled to long-term average rates). Using η as the amplitude (relative to the long-term mean) of wet-dry cycles of period ω years, the relative rainfall $r(t)$ is expressed as:

$$r(t) = \max\left(0, 1 + \eta \sin\left(\frac{\pi(t+1)}{2\omega} + z(t)\right)\right), \quad t \text{ even (start of wet season).}$$

$$r(t) = 0, \quad t \text{ odd (start of dry season).}$$

The stochastic variable $z(t)$, drawn from a normal distribution with zero mean and variance of σ_r^2 , accounts for interannual variation around the rainfall cycles. We assume that for each even t the value of $z(t)$ is drawn from the same

distribution (i.e., $z(t)$ is i.i.d.). Rainfall in southern Africa exhibits extended wet and dry periods of approximately 10 years each [36, 112]; thus, we use a period of $\omega=20$ years, i.e., a predominantly wet decade followed by a dry decade and so on. The amplitude of the cycles is set to $\eta=0.13$ (i.e., mean rainfall cycles between 87 and 113% of the overall mean [36]) and the variability around the resultant sinusoidal cycles is set to $\sigma_r=0.3$ [74]. We assumed that the rainfall is distributed evenly over the entire 1-km² grid [26].

2.2.2 Wet Season Dynamics

Wet Season Woody Plant Dynamics All growth and reproduction was assumed to occur in the rainy season. The woody plant dynamics for a wet season starting from time t were modeled as

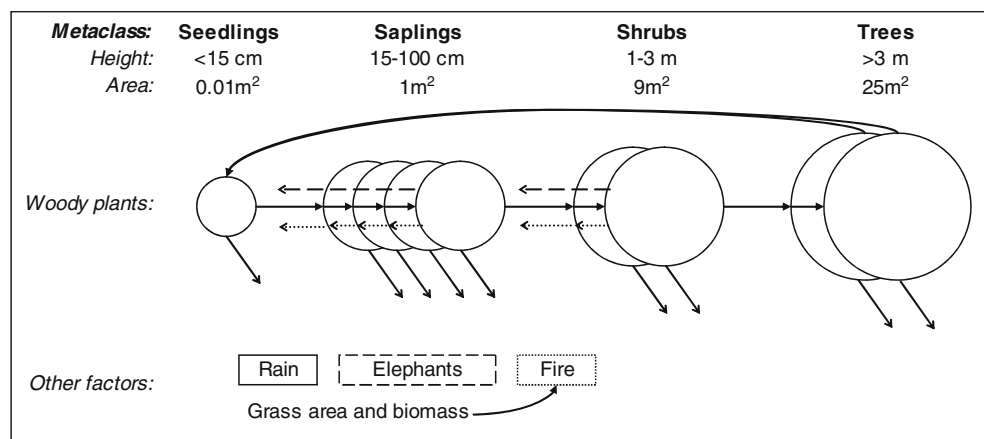
$$w_{x,i}(t+1) = (g_{x,i-1}w_{x,i-1}(t) + (1 - g_{x,i})w_{x,i}(t)) (1 - h_{x,i}(t)) \quad i = 2, 3, \dots, 9,$$

where $w_{x,i}(t)$ represents the number of individuals of woody class i (in cell x at time t), $h_{x,i}(t)$ is loss of individuals due to encroachment by larger individuals, and $g_{x,i}$ is the transition rate from class i to class $i+1$ for that cell and season. In general, $g_{x,i}$ will depend not only on t , but also on the current vegetation $\mathbf{w}_x(t)$ and on rainfall, i.e., $g_{x,i}=g_{x,i}(t, \mathbf{w}_x, r)$. Seedling dynamics ($i=1$) were modeled as

$$w_{x,1}(t+1) = (g_{x,0}c_x(t) + (1 - g_{x,1})w_{x,1}(t))(1 - h_{x,1}(t)),$$

where $c_x(t)$ is the expected number of germinants in cell x at time t , and $g_{x,0}$ is the proportion of these successfully recruiting (see below; the zero subscript refers to a notional class of presumptive seedlings). The seed bank is not explicitly modeled [69], rather the expected number of emerging seedlings depends on the adult tree population at

Fig. 1 Model dynamics emphasizing transitions between woody plant height classes. Woody plants progress to higher stage classes subject to sufficient rainfall and space (see also Fig. 2), and can be relegated to lower classes by elephant or fire impacts. Mortality can be increased by effects of elephants, (low) rainfall, and fire



the end of the previous wet season (i.e., which ran from $t-2$ to $t-1$) and is given by

$$c_x(t) = m \left[(1 - \delta)(w_{x,8}(t-1) + w_{x,9}(t-1)) + \frac{\delta}{4} \sum_{z=\text{neighbour of } x} (w_{z,8}(t-1) + w_{z,9}(t-1)) \right],$$

where m is the fecundity of mature trees (classes 8 and 9; individuals <3 m in height are assumed to be nonreproductive, and we make no distinction between seed production of the two adult classes $i=8$ and $i=9$). The parameter δ (dispersal) represents the proportion of seedlings originating from individual trees in the four neighboring cells. In this paper, we model fecundity as “viable seedlings produced per tree” rather than explicitly modeling seed production and survival. Values for seedling production vary widely in the literature. A mean establishment rate (including first year survival) of 0.064 (within a range of 0–0.222) has been reported for *Colophospermum mopane* seedlings in South Africa [93]. In Botswana, *C. mopane* establishment was measured as 1.13 and 1.73 seedlings per tree [13, 14], close to the value of 1.7 used to model *Acacia tortilis* dynamics in the Serengeti National Park, Tanzania [82]. Other models have used values of 4 viable seeds per plant per year [42], and 0.15–0.40 seedlings per tree per month [57]. A matrix population model of *Pterocarpus angolensis* used an establishment rate of 0.028 (including coppicing) [25]. Some fieldwork has yielded much higher estimates, however. Seedling production measured over 2 years in 6.25 m² quadrats was equivalent to 720 and 1,024 seedlings produced per hectare [90]. Combining counts of viable seedlings of *Acacia nilotica*, *A. tortilis*, and *Dichrostachys cinerea* [123] with an estimate of establishment for *Acacia karroo* seedlings [76] gives seedling production per tree as anywhere within the range of [232, 4,627]. We choose a value of $m=50$ for the number of potential seedlings per tree per year. Incorporating this value, and the model’s growth and survival rates, into a Lefkovich matrix gives a dominant eigenvalue of 1.5, i.e., potential annual population growth of 50%; however, this neglects the effects of competition (intraspecific and interspecific from grass) and environmental variability (fire and rainfall).

We modeled the transition rate from class i to $i+1$ as

$$g_{x,i}(t) = \min(\chi_{x,i}(t), \lambda_{x,i}(t)), \quad 0 \leq i \leq 8,$$

where $\chi_{x,i}(t)$ represents the underlying growth rate adjusted for competition and rainfall, and $\lambda_{x,i}(t)$ is the maximum growth of class i to $i+1$ in cell x without producing overcrowding. The growth algorithm is schematically depicted in Fig. 2. For seedling establishment, the proportion recruited is given by

$$\chi_{x,0}(t) = r(t)c_x(t),$$

and for plants already established ($i \geq 1$), the adjusted growth rate is given by

$$\chi_{x,i}(t) = r(t)\gamma_i\phi_{x,i}(\mathbf{w}_x(t)),$$

where γ_i is the underlying growth rate from class i to $i+1$ and $\phi_{x,i}(\mathbf{w}_x(t))$ is the proportion of those overcoming competition for space and resources.

Values for growth of savanna trees vary widely, and are measured in a variety of ways. A mean height increase of 4% was reported for unburned trees at Nylsvley Nature Reserve, South Africa [83]. Net annual shoot extensions of 15.3 and 31.2 cm (*A. tortilis* and *Acacia nigrescens*, respectively) in the Kruger National Park (KNP), South Africa, changed to 10.7 and 35.9 cm, respectively, close to waterholes [26]. In the Serengeti, mean annual growth of *A. tortilis* was found to be 16.5 and 44.2 cm, with and without giraffe browsing, respectively [82]; an earlier source had estimated annual growth of young *A. tortilis* as 30 cm [23]. Mean annual growth of coppiced *C. mopane* trees in Luangwa Valley, Zambia, was 13.4–19.2 cm [63]. In experimental conditions, *A. tortilis* seedlings grew 10–16 cm after 6 weeks under various light treatments [95]. Planted *C. mopane* seedlings achieved mean shoot heights of around 10 cm after 2 months of growth [71], and coppiced *C. mopane* had shoot growth of about 50 cm (dry season experiment) and 30 cm (wet season experiment), the results also depending on height of cutting and stump thickness [72]. Shoot growth measured at irregular intervals at Nylsvley fell in the range of 3–33 cm for *A. tortilis* and 3–15 cm for *A. nilotica*, over intervals of approximately 3–10 months [58], with this growth almost doubling where herbaceous vegetation had been removed.

Here we assume that woody plants grow by a vertical height of 30 cm year⁻¹ under mean conditions, and calculate the underlying transition rates γ_i by assuming equal size distribution within each height class. The transition rate from some height d_1 to height d_2 (in centimeters) is thus the proportion of the range (d_1, d_2) that lies within (d_1+30, d_2), or simply $1-30/(d_2-d_1)$. Recalling that individuals progress automatically between stages 2 and 5, this gives us values of $\gamma_i=1$ for $1 \leq i \leq 4$, and $\gamma_i=0.353, 0.3, 0.3, 0.15$ for $i=5, 6, 7, 8$, respectively.

Next we consider competition for light, nutrients, and water, and calculate $\phi_{x,i}(t)$, the “competition coefficient” (see also [38]). First, recall that we defined resource area (α_i) as that area controlled by an individual in class i . Then $a_{x,i}(t)$ is the total area in cell x controlled by all individuals in class i at time t , i.e.,

$$a_{x,i}(t) = \alpha_i w_{x,i}(t), \quad 1 \leq i \leq 9.$$

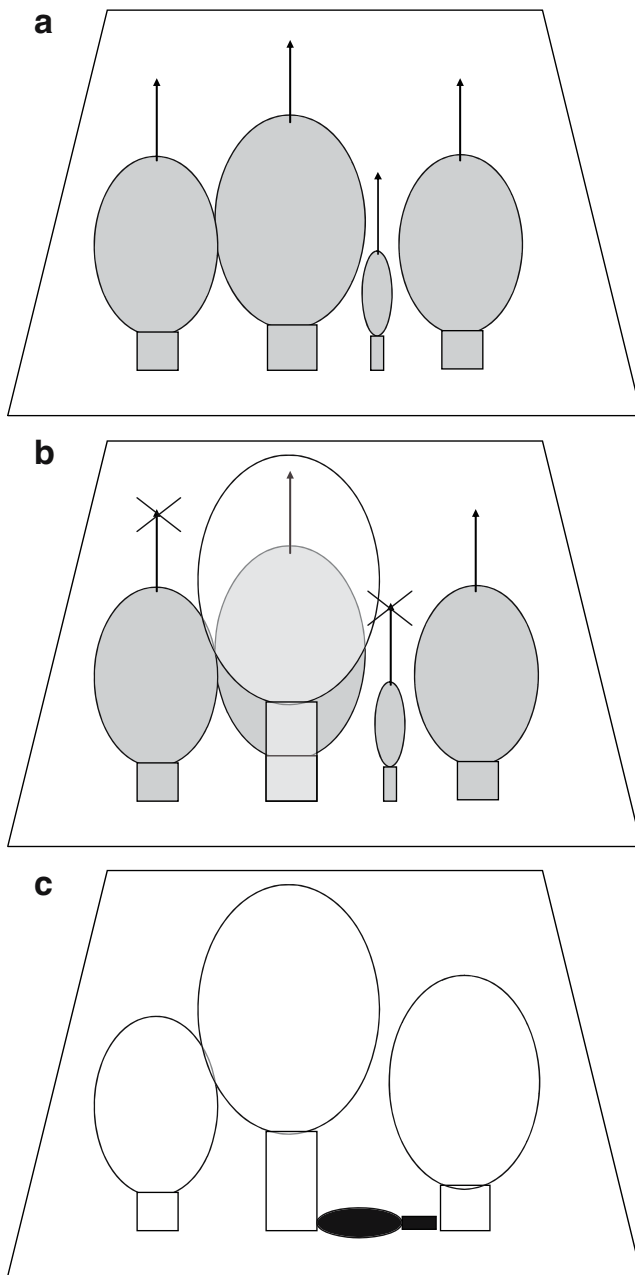


Fig. 2 Woody plant growth algorithm. **a** Schematic depiction of the woody component of a section of the savanna at the start of the wet season. From *left to right* we have classes $i=6, 7, 5$, and 6 , i.e., three shrubs and a sapling. These strive to advance to classes $7, 8, 6$, and 7 , respectively (i.e., one tree and three shrubs), and would do so at rate $g(i)$ if there was no crowding, and average rainfall. **b** The effect of the parameter λ : priority is given to the larger individuals and because the $i=7$ shrub grows into a tree ($i=8$), the growth of some other individuals is reduced. This is done on a per area basis. **c** The implementation of the parameter h : if the area is still overcrowded then self-thinning is induced. Priority is again given to the more mature individuals so that in this case the sapling dies

Calculation of $a_{x,10}(t)$, the area covered by grass, is elaborated in the subsection on wet season grass dynamics below. While little is known about interplant competition in savannas [42, 88], strong effects of nearest-neighbor distance have been demonstrated on canopy cover and growth of savanna trees [94]. Thus, we approximate competitive effects using the resource areas as follows:

$$\phi_{x,0}(t) = \phi_{x,1}(t) = 1 - \left(a_{x,10}(t) + \sum_{j=1}^7 a_{x,j}(t) \right).$$

Effectively, we assert that recruitment of seed (again employing the notional class $i=0$) into seedlings, and of seedlings into saplings, will be limited by competition from existing seedlings, saplings, shrubs, and grass. Within the sapling classes, growth is assumed to be automatic, so that $\phi_{x,i}(t)=1$ for $i=2, 3, 4$. Growth of individuals in classes $i=5, \dots, 8$ (i.e., growth of saplings to shrubs, and so on up to mature trees) is assumed to be limited by competition from individuals in equal or higher stage classes [69]:

$$\phi_{x,i}(t) = 1 - \sum_{j=i}^9 a_{x,j}(t), \quad i = 5, 6, 7, 8.$$

The expansion limiting coefficient, $\lambda_{x,i}$, comes into play in situations of strong woody dominance coupled with excellent growth conditions. Because we allow the more mature individuals to dominate, and thus grow in preference to smaller individuals, the coefficients $\lambda_{x,i}$ involve projecting total possible recruitment and then reducing that recruitment (in decreasing order of size) to prevent overflow (see Fig. 2). To derive the recruitment equations presented below, we have assumed that seedlings and saplings can grow under tree canopies but that shrubs cannot. Thus, to grow into seedlings, seeds can use bare ground or space under trees but not under existing seedlings, saplings, shrubs, or grass. Similarly, seedlings can only expand under trees or over bare ground to grow into saplings, saplings can only expand over seedlings or grass to grow into shrubs, and the expansion space available for the shrub class $i=7$ to grow into trees equals all but the existing trees. In the case of growth of shrubs to trees, $\lambda_{x,7}$ is simply the available area for new trees divided by $\alpha_8 w_{x,7}(t)$, the area which would be taken up by shrubs currently in class $i=7$, were they all to become trees (i.e., if the growth rate equaled 1). As we assume mature trees can dominate over all other classes, the available area for recruitment is given by total area, less area already occupied by adult trees, giving

$$\lambda_{x,7}(t) = \frac{1 - a_{x,8}(t) - a_{x,9}(t)}{\alpha_8 w_{x,7}(t)}.$$

This allows us to determine the actual rate of recruitment to the tree stage, $g_{x,7}(t)$ and then proceed to calculate the available space for sapling recruitment to shrubs and so on (dropping the x and t arguments for brevity):

$$\lambda_5 = \frac{1-a_6-a_7(1-g_7)w_7-a_8g_7w_7-a_8-a_9}{a_6w_5},$$

$$\lambda_1 = \frac{1-a_2-a_3-a_4-a_5(1-g_5)w_5-a_6g_5w_5-a_6-a_7(1-g_7)w_7}{a_2w_1},$$

$$\lambda_0 = \frac{1-a_1(1-g_1)w_1-a_2g_1w_1-a_2-a_3-a_4-a_5(1-g_5)w_5-a_6g_5w_5-a_6-a_7(1-g_7)w_7-a_{10}}{a_1c(t)}.$$

For those height classes deemed not to expand laterally upon growth to the next class (i.e. for transitions within metaclasses), we set $\lambda_i=1$ ($i=2, 3, 4, 6, 8$).

Any given level of growth, g_i , may also entail shading out other plants in the same or lower height class and so we introduce h_i as a ‘‘crowding coefficient’’, representing the proportion of plants overshadowed by the individuals growing from class i to $i+1$ (see Fig. 2). Again using per-area aggregation, we set h_i as the ratio of the extra area now occupied by the grown individuals (i.e., area encroached over) to the total area occupied by those plants, which can be crowded out by their growth, i.e., the area which had been available for the expansion of the growing individuals (the numerator of the λ_i above). Because we assume that crowding of shrubs is experienced equally by both shrub classes, and likewise for the sapling classes, this gives us (again space subscripts and time arguments are understood):

$$h_6 = h_7 = \frac{(a_8-a_7)g_7w_7}{1-a_8-a_9},$$

$$h_2 = h_3 = h_4 = h_5 = \frac{(a_6-a_5)g_5w_5}{1-a_6-a_7(1-g_7)w_7-a_8g_7w_7-a_8-a_9},$$

$$h_1 = \frac{(a_2-a_1)g_1w_1}{1-a_2-a_3-a_4-a_5(1-g_5)w_5-a_6g_5w_5-a_6-a_7(1-g_7)w_7}.$$

Note that we do not need any crowding coefficient for recruitment to the seedling class as this growth just ‘‘encroaches’’ over bare ground. Also note that h_1 and h_5 are applied to crowding out the grass layer too (see below).

Wet Season Grass Dynamics We also modeled wet season grass growth in terms of area covered and biomass. The area covered by grass is updated to account for changes in the woody vegetation cover (including woody growth during the wet season), reduced by the level of elephant grazing (it was assumed that elephants uproot whole grass tufts when grazing [56, 79]) and adjusted for rainfall amount:

$$a_{x,10}(t+1) = r(t) \left(1 - \sum_{i=1}^7 a_{x,i}(t) \right) (1 - u_{x,10}(t)) (1 - h_{x,1}(t) - h_{x,5}(t)), \quad t \text{ even},$$

where $u_{x,10}(t)$ represents the proportion of the grass in cell x that is grazed by elephants. As discussed above we reduce the grass area by the proportion of extra ground shaded out by individuals growing into the first sapling and shrub classes (i.e., entering classes $i=2, 6$). Although we allow grass to occupy the subcanopy space beneath adult trees in this model (without distinguishing between subcanopy and

extracanopy grass), others [70] have hypothesized that grass growing under adult acacias is more palatable, and is thus grazed down to such a level that its contribution to fuel for fires becomes insignificant. The area occupied by grass is rainfall-dependent as it is assumed that grass tufts expand or shrink in higher or lower rainfall conditions, which may be important in seedling recruitment dynamics.

The grass biomass is then updated to account for the productivity of the area $a_{x,10}(t+1)$, wet season senescence [47], and elephant grazing:

$$w_{x,10}(t+1) = s_{10}^w r(t) (1 - u_{x,10}(t))$$

$$(w_{x,10}(t) + \gamma_{10} a_{x,10}(t+1)),$$

where γ_{10} is the annual productivity of grass (kg/ha) and s_{10}^w is the wet season persistence (‘‘survival’’) of grass biomass. Grass production is highly dependent on soil and climatic properties and can vary between 500 and 4,000 kg ha⁻¹ for southern African savannas [80]. In KNP (mean rainfall=575 mm year⁻¹), annual biomass production is 2,600 kg ha⁻¹, with about 6.5% of this being grazed [80]. Here we use a figure of $\gamma_{10}=2,500$ kg ha⁻¹ to reflect the production level, net of grazing, at about 550–600 mm year⁻¹ mean rainfall. Grass mortality in a drought year was measured at 0.07–0.29, 0.74–0.97, and 0.82–0.86 (clay, sand/clay, and sandy soils, respectively) in Klaserie, South Africa [86]. Mortality of *Andropogon semiberbis* over 2 years in a neotropical savanna was 0.81–0.47 (dry seasons, successive years) and 0.22–0.24 (wet seasons) [91]. We use rates of $s_{10}^w = 0.8$ (wet season) and $s_{10}^D = 0.2$ (dry season) for grass biomass persistence (survival). Grass senescence has previously been modeled using a rate of 0.03 per day [47].

Elephant Grazing Elephants are assumed to visit each cell in proportion to the amount of grass biomass present in the cell, relative to the grid as a whole. Letting $l(t)$ be the elephant density (numbers per hectare) at time t and I_g the intake rate of grass by elephants (kg elephant⁻¹ wet season⁻¹), the elephant use of cell x is:

$$u_{x,10}(t) = l(t) I_g \frac{w_{x,10}(t) + \gamma_{10} r(t) \left(1 - \sum_{i=1}^7 a_{x,i}(t) \right)}{\sum_{z=1}^{100} \left(w_{z,10}(t) + \gamma_{10} r(t) \left(1 - \sum_{i=1}^7 a_{z,i}(t) \right) \right)}.$$

Note that we project grass biomass forward in time in the calculation of $u_{x,10}(t)$ to allow initial grass recovery from dry season burns, senescence, etc. For the grass intake rate, we use an estimate of 0.8–1.0% body mass intake per day [78] (after [60]), with a mean elephant body mass of 2,800 kg (see also [79] and references therein), giving $I_g=4,600$ kg elephant⁻¹ wet season⁻¹.

2.2.3 Dry Season Dynamics

We assumed for our model that fire, elephant browsing, and woody plant mortality occur only in the dry season (see Fig. 1), giving overall woody plant dynamics of

$$w_{x,i}(t + 1) = F_i(\mathbf{w}_x(t), s_i, r(t - 1), l(t)), \quad t \text{ odd,}$$

where s_i represents the mean survival rate of woody class i , and recalling that $r(t-1)$ is the rainfall from the previous wet season and $l(t)$ the elephant density at time t . Here F_i is a concatenation of functions incorporating the effects of mortality, elephant browsing and fire ($f_{\text{surv},i}$, $f_{\text{ele},i}$, and $f_{\text{fire},i}$ respectively), i.e.,

$$\begin{aligned} f_{\text{surv},i} &\equiv f_{\text{surv},i}(w_{x,i}(t), r(t - 1), s_i), \\ f_{\text{ele},i} &\equiv f_{\text{ele},i}(\mathbf{w}_x(t), l(t), f_{\text{surv},i}), \\ F_i &= f_{\text{fire},i} \equiv f_{\text{fire},i}(\mathbf{w}_x(t), f_{\text{ele},i}). \end{aligned}$$

We now consider each of the functions $f_{\text{surv},i}$, $f_{\text{ele},i}$, and $f_{\text{fire},i}$ in turn.

Woody Plant Survival The mortality of subadult woody plants depends on the rainfall for each year:

$$f_{\text{surv},i}(r(t - 1), s_i, w_{x,i}) = s_i r(t - 1) w_{x,i}, \quad i = 1, \dots, 7.$$

Savanna trees are generally well suited to harsh environments, with adaptations for disturbances and stresses from fire, herbivory, drought, and low soil fertility, thus, overall tree survival rates tend to be almost 100%, ranging from 94.4% (see [90] and references therein) to 99.5% [102] (also see [75, 83, 122]). Mortality tends to decrease with age, so that survival rates for seedlings are lower than those for mature individuals. Estimates for seedling survival range from close to zero for some sites [76] up to 0.99 [13, 27]. Seedling survival in two consecutive years has been measured as 0.981 and 0.873 for a mixture of species [90]. We use $s_1=0.95$ in this model. For sapling survival we use $s_i=0.99$, $2 \leq i \leq 5$, after an estimate based on 9-year *C. mopane* drought mortality [77]. The lowest published estimate of sapling survival, 0.78, is for *P. angolensis* [25]. The same authors give *P. angolensis* shrub survival as 0.948–0.969 [25], but again we adopt the value for *C. mopane* of $s_6, s_7=0.994$ [77].

For mature trees, we assumed greater tolerance of short-term fluctuations in rainfall, only experiencing increased mortality in droughts of greater than 2 years of duration [86]:

$$f_{\text{surv},i}(r(t - 1), s_i, w_{x,i}) = (s_i - \mu_{8-9}^r \xi(t)) w_{x,i}, \quad i = 8, 9,$$

where μ_8^r is the additional drought-related mortality experienced by mature trees, weighted for drought severity

(calculated from a 3-year running mean, i.e., through wet seasons at $t-5$, $t-3$, and $t-1$) according to the function $\xi(t)$:

$$\xi(t) = \frac{k^\zeta}{\left(\sum_{y=t-5}^t \frac{r(y)}{3}\right)^\zeta + k^\zeta}.$$

Given this form, the function ξ maps the 3-year mean relative rainfall to points on the interval $[0, 1]$, where ζ is a shape parameter describing the steepness of the drought response (cf. population density response [37]), and k is a half-saturation constant for drought-related mortality (i.e., the value of the 3-year mean causing 50% of the maximum drought-related mortality). Recall that $r(t)=0$ for odd values of t (dry seasons) so that in the above summations $r(y)=0$ for $y=t, t-2, t-4$. For adult trees, we use an underlying rate of 0.005 for age-related mortality, giving $s_8, s_9=0.995$. Nonelephant mortality to adult *Acacia* spp. in the Serengeti was estimated as roughly 1% [23]. *P. angolensis* adult survival has been measured as 0.944 and adult tree survival in Lamto, Cote d'Ivoire was modeled as 0.985 [45]. Survival estimates for *C. mopane* vary between 0.99 [13, 27] and zero observed adult mortality throughout a 9-year drought [77]. We set adult tree mortality in a full-scale drought ($\xi=1$) to $\mu_{8-9}^r = 0.05$ [86]. We use a drought mortality half-saturation value of $k=0.8$ (so that a 3-year average relative rainfall of 80% will result in drought-related mortality of $\mu_{8-9}^r/2$) and use quite a steep drought mortality onset curve by choosing a high value for the shape parameter, $\zeta=50$.

Elephant Browsing Using vector notation we express the effect of elephant browsing on the woody vegetation as:

$$\mathbf{f}_{\text{ele}}(l(t), \mathbf{w}_x) = (\mathbf{I} - \mathbf{E} \cdot \mathbf{U}_x(t)) \mathbf{w}_x,$$

where the vector $\mathbf{w}_x(t)$ denotes each cell's woody plant structure, \mathbf{f}_{ele} is the column vector $(f_{\text{ele},1}, f_{\text{ele},2}, \dots, f_{\text{ele},9})'$, \mathbf{I} is the (9×9) identity matrix, and \mathbf{E} is an elephant effect matrix (see below). $\mathbf{U}_x(t)$ is a 9×9 diagonal matrix with the elements of $\mathbf{u}_x(t)$, an elephant-use vector for cell x on the diagonal. The vector $\mathbf{u}_x(t)$ is composed of the elements $u_{x,i}(t)$ representing the proportion of each stage class browsed by elephants. This is calculated as a weighted sum of the woody vegetation, with the perceived "preference value" of each stage class (v_i) providing the weights. Elephant use of tree height classes in the Serengeti was in proportion to availability, except for the largely ignored <1 m range [23] (see also [82]). Some authors have noted that smaller *A. tortilis* individuals are less susceptible to elephant browsing [56, 73]. Other authors, however, recorded elephants predominantly foraging at lower heights, with, for example, 59.8 and 81.7% of feeding taking place at heights below 1.2

and 2 m, respectively [40]. In Venetia, South Africa, elephants preferentially chose *C. mopane* branches <1 m high while preferring trees <2 m high for return visits [92]. Studies in both the Luangwa Valley, Zambia [20], and Lake Kariba, Zimbabwe [67] recorded greater rates of elephant browsing of *C. mopane* occurring to thinner stems. In the Kasungu National Park, Malawi, the preferred elephant feeding height (of preferred species) was between 1 and 2 m (the height of impacted plants being thus somewhat higher), while for less preferred species, height classes were browsed in proportion to abundance—this would then result in maintenance of preferred species at the preferred feeding height [48]. A later study found a preferred feeding level of 2–3 m [49]; trees over this height (and below 7 m), however, were more likely to be toppled [48].

For adult trees of species that grow much higher than those modeled here, special consideration is required. For example, a study of marula (*Sclerocarya birrea*) adults in KNP found that the proportion of trees damaged by elephants tended to decrease with increasing height, and that the predominant damage type tended to switch from stem breakage to bark stripping as height increased [50]. Less elephant damage occurred to marula trees >8 m in height, with a greater occurrence of “extreme damage” in the 2- to 8-m individuals [50]. In the Serengeti, elephant browsing height may extend up to 6 m, with trees higher than 6 m tending to be uprooted [22]. Here we consider browsing of adult trees separately from that of the shrub and sapling metaclasses. We assume that plants <3 m high (and >15 cm, i.e., excluding seedlings) are selected in proportion to the abundance of each class ($2 \leq i \leq 7$), and similarly we assume that impact on adult trees is proportional to the abundance of each class ($i=8, 9$).

In the Kasungu National Park, Malawi, the number of trees used by elephants increased with tree density (up to densities of 300 trees ha⁻¹) [48]. We assume that within our square kilometer of interest, elephant browsing intensity is allocated across cells in proportion $\pi_x(t)$ to the cells’ perceived “attractiveness” (a preference-weighted sum of its woody plant availability) relative to the others’. Within each cell they forage on each stage class, with the exception of the tallest and shortest sizes, in proportion $\pi'_{x,i}(t)$ to each stage class’s preference-weighted availability [23] (see also [63]), where

$$\pi_x(t) = \frac{\sum_{k=1}^7 v_k w_{x,k}(t)}{\sum_{z=1}^n \sum_{k=1}^7 v_k w_{z,k}(t)},$$

$$\pi'_{x,i}(t) = \frac{v_i w_{x,i}(t)}{\sum_{k=1}^7 v_k w_{x,k}(t)}, \quad 1 \leq i \leq 7,$$

and n is the total number of cells in the grid ($n=100$ in this case). (Note that $v_1=0$ as we assume seedlings are not

browsed.) Thus the proportion of individuals browsed in each cell, of each stage class >3 m is:

$$u_{x,i}(t) = l(t) I_{1-7} \pi_x(t) \pi'_{x,i}(t) \frac{1}{w_{x,i}(t)}, \quad w_{x,i}(t) > 0,$$

$$1 \leq i \leq 7,$$

which simplifies to

$$u_{x,i}(t) = l(t) I_{1-7} \frac{nv_i}{\sum_{x=1}^n \sum_{k=1}^7 v_k w_{x,k}(t)}, \quad w_{x,i}(t) > 0,$$

$$1 \leq i \leq 7,$$

where I_{1-7} is the intake rate of subadult woody vegetation by elephants, in units of plants per elephant per dry season. Similarly, we calculate the proportion of adult trees browsed as:

$$u_{x,i}(t) = l(t) I_{8-9} \frac{nv_i}{\sum_{x=1}^n \sum_{k=8}^9 v_k w_{x,k}(t)}, \quad w_{x,i}(t) > 0, \quad i = 8, 9,$$

where I_{8-9} is the intake rate of adult trees by elephants (plants per elephant per dry season). (In the absence of some stage class i ($w_{x,i}(t)=0$) we set $u_{x,i}(t)=0$.) Tree uprooting rates of 1 per 25–40 h of observation in the Seronera woodlands, Tanzania [22], leads to a toppling rate of roughly 5.25 trees per elephant per week [23]. Elephant densities of approximately 0.4 per km² in the Chizarira Game Reserve, Zimbabwe, resulted in 22 trees per hectare killed [103], giving a much higher rate of 5,536 trees killed per elephant per year. In the Sengwa Research Area, Zimbabwe, toppling rates were 3 and 9 trees per day (by females and males, respectively) [40], with no toppling occurring in the wet season—for a 1:1 sex ratio this approximates to 1,095 adult trees toppled per elephant per year. Elephant-caused tree mortality has been modeled using 1,200 trees (elephants km² year⁻¹) as the maximum “predation” rate [30] (in a type II function [46] with a half-saturation density of 15 trees km⁻²; resulting in intake in the order of 1,200 over most of the range of tree density). We set $I_{8-9}=1,000$ adult trees toppled per elephant per dry season. Assuming this figure represents 15% of plant use [40, 100], then we set $I_{1-7}=5,667$ plants per elephant per dry season. For a 183-day dry season, we therefore have a rough visitation rate of $(1,000+5,667)/183=36.43$ plants per day (5.5 trees and 31 saplings/shrubs), which seems reasonable: Recorded handling times are 18 and 7.11 min for males and females, respectively, to complete browsing on two woody plants in immediate succession [100].

We then compose $\mathbf{u}_x(t)$ as the vector corresponding to the $u_{x,i}(t)$ ’s:

$$\mathbf{u}_x(t) = (u_{x,1}(t), u_{x,2}(t), \dots, u_{x,9}(t))'$$

The 9×9 elephant effect matrix \mathbf{E} maps the stage-specific effects of elephant browsing. Broken stems may either die or resprout. Resprouting saplings are assumed to reenter the seedling height class; similarly, shrubs are reduced to sapling height and trees may be reduced to sapling or shrub height. To reflect accelerated growth of coppiced individuals due to belowground stored tissue, plants reentering the sapling or shrub metaclasses are assigned to the highest cohort ($i=5$ or $i=7$) within those strata.

$$\mathbf{E} = \begin{pmatrix} \mu_1^e & -\rho_{21} & -\rho_{31} & -\rho_{41} & -\rho_{51} & 0 & 0 & 0 & 0 \\ 0 & \mu_2^e + \rho_{21} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \mu_3^e + \rho_{31} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \mu_4^e + \rho_{41} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mu_5^e + \rho_{51} & -\rho_{65} & -\rho_{75} & -\rho_{85} & 0 \\ 0 & 0 & 0 & 0 & 0 & \mu_6^e + \rho_{65} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mu_7^e + \rho_{75} & -\rho_{87} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mu_8^e + \rho_{85} + \rho_{87} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mu_9^e \end{pmatrix}$$

where μ_i^e is the proportion of class i plants killed by elephants, and ρ_{ik} is the proportion reduced in height from class i to k as a result of elephant browsing. Note that not all browsing needs result in death or stunting (if $\mu + \rho < 1$). Densities of *Adansonia digitata* (baobab), *Acacia albida*, and *Commiphora ugogensis* decreased by 45, 72, and up to 100%, respectively over 6 years in Ruaha National Park, Tanzania, with elephant densities of approximately 4.1 km^{-2} [3]. In KNP, adult marula (*S. birrea*) mortality of 7% was ascribed mainly to elephant damage [50]. The same rate has been used to model annual tree mortality under high elephant densities [28]. Nevertheless, elephant impact can be highly variable and opportunistic, e.g., within a single 24-h period, 6 bulls have killed 34% *Acacia gerrardii* and injured 22% in a 2-km² area [27]. Elephant effects can also be exacerbated by drought conditions, producing, for example, a 100% die-off of heavily browsed *C. mopane* (at a density of 6.7 elephants km⁻²) [65]. In the 2 years after the removal of a fence separating Sabi Sand Wildtuin from the adjacent KNP, of a total of 972 browsed trees >3 m tall, 285 (29.3%) had died [43]; similarly, for the shrub genus *Grewia* (<3 m tall), 119 had died out of 398 browsed (29.9%). A study of *A. nigrescens* in the north of KNP found 583 elephant-damaged trees out of a total of 951 trees, of which 264 trees (45%) were gored and ring-barked, ultimately resulting in their death [31]. Data from islands in Lake Kariba, Zimbabwe, shows that on average, 17.6% of elephant-damaged *C. mopane* individuals died, although this varied widely (3–67%) between islands [67]. In the Serengeti, 44% of elephant use of *Acacia* spp. resulted in removal of >75% of the canopy, which was likely to result in mortality in 55–80% of cases [23] (this damage class included toppled trees and 100% mortality was used in the subsequent analysis). We assume that toppled adult trees experience 80% mortality ($\mu_8^e = \mu_9^e = 0.8$), and set the mortality of browsed shrubs and saplings to 25% ($\mu_i^e = 0.25$, $2 \leq i \leq 7$).

Tree stunting (taken here to include both browsing down to a lower height class and browsing followed by resprouting) is determined as the proportion escaping death while being more than lightly browsed. Dry season elephant browsing in Luangwa Valley, Zambia, produced mean height reductions of 0.4–7.3 cm in coppiced mopane trees [63], depending on fire regime and extent of elephant use. Elephant damage to the woody plant community in Linyanti/Chobe, Botswana, was summarized in figures for frequency and intensity of damage [117]. For all species combined, approximately 25% experienced little or no damage, with 9.5 and 64.6% of impacted individuals experiencing medium and heavy damage, respectively. This pattern also occurs for the two most abundant nonriverine species in the sample, *C. mopane* (11.2 and 62.9% for medium and heavy damage, respectively) and *Combretum mossambicense* (3.0, 69.7%, respectively) [117]. If we assume that 25% of browsed individuals experience little damage, and 25% die (as discussed above), the remaining 50% will resprout into the next lowest metaclass, i.e., $\rho_{i1} = 0.5$ for $2 \leq i \leq 5$ and $\rho_{i5} = 0.5$ for $i = 6, 7$. For toppled trees, we divide the surviving 20% equally between the sapling and shrub metaclasses ($\rho_{i5} = \rho_{i7} = 0.1$, $i = 8, 9$).

Fire Grass biomass provides fuel for fires and in our model the probability of fire occurring is linearly related to grass biomass. Fire incidence is recorded by the binary variable $b_x(t)$ and the condition for cell x burning ($b_x(t) = 1$) is

$$b_x(t) = \begin{cases} 1 & \text{if } R_x < \psi w_{x,10}(t), \\ 0 & \text{if } R_x \geq \psi w_{x,10}(t), \end{cases}$$

where R_x is a uniform random variable drawn on $[0, 1]$ for each cell x , and the constant ψ scales biomass to a fire probability. Fire spread is modeled by identifying non-burning cells and repeating this procedure (drawing another random number for comparison) for each burning neighbor. For example, if a nonburning cell x has two burning neighbors, then two further values of R_x are drawn and compared with $\psi w_{x,10}(t)$. The procedure is further repeated until no additional cells burn. Logistic regression of KNP fire records related the probability of fire occurrence to grass biomass in kilograms per hectare (w_{10} in our model) for 1995 and 1996, with the latter year providing the better statistical fit [115]:

$$P(\text{fire}) = \frac{e^{0.0005w_{10}-2.7431}}{1 + e^{0.0005w_{10}-2.7431}}$$

This formula is almost linear over most of the biological range of biomass and here we use the approximation $P(\text{fire}) = w_{10}/10,000$ (i.e., $\psi = 10^{-4} \text{ kg}^{-1}$), which also ensures that no fire can occur in the absence of grass fuel ($w_{10} = 0$ gives $P(\text{fire}) = 0.0605$ in the above). Our value of $\psi = 10^{-4}$ gives

somewhat lower fire occurrence probabilities ($P(\text{fire})=1$ when $w_{10}=10,000 \text{ kg ha}^{-1}$) than those used to model grazing pressure on a Kalahari shrubland [120] ($P(\text{fire})=1$ when $w_{10}=3,000 \text{ kg ha}^{-1}$).

We modeled fire intensity assuming a linear relationship with grass biomass [42, 106], scaling to the biomass yielding maximum intensity:

$$\beta_x(t) = \frac{b_x(t)w_{x,10}(t)}{w_{\max}}$$

where a grass biomass of w_{\max} yields a fire intensity of $\beta_x(t)$. Other variables such as heat yield, rate of spread, relative humidity, fuel moisture, and wind speed [42, 106] can also affect fire intensity but we ignore these factors in this model. A grass fuel load of $4,000 \text{ kg ha}^{-1}$ is considered necessary to produce an “intense” fire [108]. We use $w_{\max}=5,000 \text{ kg ha}^{-1}$, which is twice the annual grass production under mean conditions, i.e., $\nu_{\max}=2\gamma_{10}$. This biomass, combined with other model equations and mean values for fuel moisture, wind speed, and relative humidity [42], yields an intensity of $3,686 \text{ kWm}^{-1}$.

Woody plants have their aboveground stems burned, which may cause death or resprouting. The proportion, $\tau_{x,i}(t)$, of those in class i experiencing top-kill is calculated as follows:

$$\begin{aligned} \tau_{x,1}(t) &= b_x(t) \\ \tau_{x,i}(t) &= \min\left(1, \frac{b_x(t)w_{x,10}(t)}{w^*}\right), \quad 2 \leq i \leq 5, \\ \tau_{x,i}(t) &= \mu_{6-7}^\beta \beta_x(t), \quad i = 6, 7, \\ \tau_{x,i}(t) &= \mu_{8-9}^\beta \beta_x(t), \quad i = 8, 9, \end{aligned}$$

where w^* is the grass fuel causing 100% sapling fire mortality, and μ_{6-7}^β and μ_{8-9}^β are the top-kill rates of shrubs and mature trees, respectively, in maximum intensity fires. These equations assume that all seedlings are killed by fire [53] and that aboveground tissue death is proportional to fire intensity for all other stage classes. A study of marula found individuals up to 1.5 m to be highly susceptible to fire, with the tallest tree affected by fire being 2.7 m and impact increasing with fire intensity [51]. In the Eastern Cape, woody plants up to 2 m high exhibited greater than 40% mortality in intense ($>2,500 \text{ kWm}^{-1}$) fires [110]. Medium-intensity fires can top-kill 100% of saplings ($<50 \text{ cm}$) [107]; this has been incorporated in a previous savanna model [69], with each fire completely burning the aboveground shoots, so that each individual reverted to the previous stage class after coppicing. We use a fuel load of $w^*=2,500 \text{ kg}$ as the grass biomass necessary to cause 100% sapling top-kill. Shrub top-kill rates have been reported as 30–97% (decreasing with increasing height for plants

between 1 and 3 m) [109] and 80.8% (comprised of 71.5% coppicing and 9.3% mortality, for trees and shrubs) [104, 105]. We use a shrub top-kill rate under maximum fire intensity of $\mu_{6-7}^\beta = 0.8$. Other models have used rates of 90% for top-kill of shrubs (i.e., rate of reversal to a sapling) [27] and 28–68% (depending on height and species) [75]. Although our tree class has been defined based on the fire escape height ($\geq 3 \text{ m}$ [82]), we also include a small level of fire-caused adult tree mortality ($\mu_{8-9}^\beta = 0.2$) to account for possible previous bark damage from porcupine [124] or elephants.

Savanna plants have evolved with fire and therefore show high levels of fire tolerance, a common strategy being high proportions of woody plants resprouting after top-kill by fires, although this ability of course varies by species [35, 39]. The net effect of fire on woody vegetation is therefore

$$f_{\text{fire},i}(w_{x,i}(t)) = (1 - \tau_{x,i}(t))w_{x,i}(t) + \kappa_{i+1}\tau_{x,i+1}(t)w_{x,i+1}(t),$$

where κ_i is the proportion of plants in stage class i that resprout after top-kill by fire; these are assumed to enter the next lowest stage class due to strong regrowth enabled by belowground biomass reserves. This change in height has been modeled as a net stunting effect, as well as top-kill followed by resprouting (this paper), for example, a model of the Masai Mara *A. tortilis* population used stunting rates of 90 and 95% for saplings and shrubs, respectively [27]. A similar model used maximum shrub stunting rates of 1% for *Acacia erioloba* and *C. mopane*, but 31% for *Baikiaea plurijuga* [13]; maximum stunting rates for the $<1\text{-m}$ class were 15, 50, and 70%, respectively. Other authors (see references in [34]) give fire-induced mortality rates typically in the order of 10%. Probabilistic height-dependent resprouting has been modeled using a maximum probability of 0.9 [42], with the resultant resprouting rates falling between 0.89 and 0.90 for all heights up to 3 m. Therefore, for simplicity we use the same value of $\kappa_i=0.9$ for all saplings and shrubs ($2 \leq i \leq 7$), with $\kappa_1=\kappa_8=\kappa_9=0$.

Dry Season Grass Dynamics Dry season grass dynamics are comparatively simple—we assume that grass is burned entirely in fires, and senesces (again depending on annual rainfall) in the absence of fire:

$$\begin{aligned} a_{x,10}(t+1) &= (1 - b_x(t))a_{x,10}(t), \quad t \text{ odd}, \\ w_{x,10}(t+1) &= r(t-1)s_{10}^D(1 - b_x(t))w_{x,10}(t), \end{aligned}$$

where s_{10}^D is the dry season persistence (survival) of grass biomass.

2.3 Model Implementation

The model was run 100 times for each parameter set, starting in the wet season of the first year of a wet cycle,

with every grid cell containing 50% cover each of grass and woody plants. The initial grass biomass is assumed to be 1,200 kg, roughly equivalent to one average year's production over half a hectare (i.e., $\gamma_{10}/2$). The initial woody structure is determined from the right eigenvector corresponding to the dominant eigenvalue of the Lefkovich matrix comprising the growth and survival rates [19], i.e., the stable class distribution that would result from a linear woody-only model ignoring competition, density dependence, fire, etc. We tested the model's sensitivity to parameter values, varying parameters individually by $\pm 50\%$ of their default value. We then focused on sensitivity to changes in the following variables, reflecting factors considered important in savanna dynamics, or processes for which data are scarce or imprecise: mean annual rainfall, probability of fire (ψ) for a given grass biomass, coppicing ability κ_i after top-kill by fire, and vertical growth of woody plants (affecting the transition rates γ_i). In each of these cases (except the fourth, demographic assertion) we allowed the model to run using the default parameter values for 100 years, allowing the initial transience to dissipate, before altering the test parameter. Each different parameter set used the same initial random seed.

3 Results

For the default parameter values, without elephants, woody plants and grass were found to coexist in each of the 100 stochastic runs. The composition of the savanna (based on mean of 100 cells) after 500 years under these conditions is shown in Fig. 3. For conciseness, we focus below on the state of the vegetation in terms of area covered by each meta-class at the end of a wet season, giving woody "juveniles" (seedlings and saplings combined), shrubs, trees, and grass.

Investigation of the sensitivity of the final (years 481–500) composition of the meta-classes to parameter changes of $\pm 50\%$ indicated that the model is most sensitive to changes in vegetation processes such as woody plant survival and grass production (Fig. 4). Without a concomitant increase in reproductive output, a decrease in woody plant survival results in grass dominance at the expense of the woody component, whereas increasing woody survival rates (but limiting to $s_i \leq 1$) has little effect due to the already high default values. High grass productivity acts together with increased fire intensity to suppress the woody component. Little sensitivity was detected to initial conditions or to the spatial extent of the grid. Rainfall-related parameters were also important, however, particularly variation in rainfall σ_r , drought mortality for trees μ_{8-9}^r , and its half-saturation constant, k .

Further investigating the influence of rainfall, Fig. 5 demonstrates the effect of changed rainfall regime on the mean vegetation trajectory. Rainfall regime was altered first

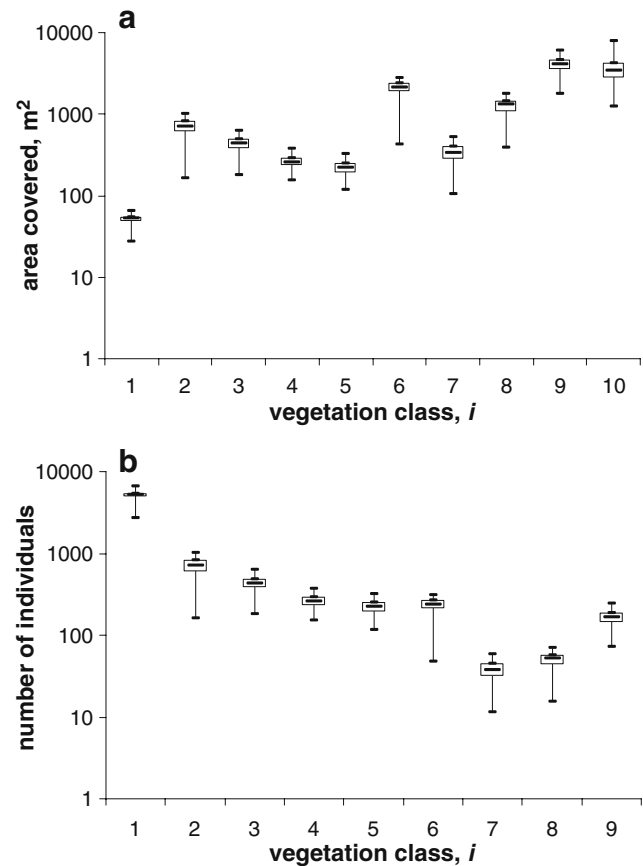


Fig. 3 Model results using the default parameter set showing the vegetation composition of the savanna after 500 years averaged across the grid. *Box plots* show minimum, maximum, interquartile range, and median of each vegetation class, i ($i=1$, seedlings; $2 \leq i \leq 5$, saplings; $i=6, 7$, shrubs; $i=8, 9$, trees; $i=10$, grass; see text for further details). **a** Final area covered by each vegetation class and **b** final number of individuals in each vegetation class. Elephant density is zero throughout

by simply multiplying $r(t)$ by 1.1 or 0.9 after 100 years to give a “wet” and a “dry” scenario (Fig. 5a and b, respectively). (Nominally we refer to these perturbations as a 10% increase or decrease in rainfall, although actual averages will be more of an increase and less of a decrease because $r(t)$ is constrained to be nonnegative.) The periodicity (ω) or amplitude (η) of long-term cycles were not altered with $r(t)$, nor was the standard deviation of annual rainfall (σ_r). Although tree–grass coexistence still occurs, the dominance shifts from trees to grass as conditions get drier. Figure 6a demonstrates this shift by plotting the vegetation end points (vegetation state 400 years after the rainfall change was instigated) for rainfall regimes between 80 and 120% of the default model.

Figure 6b–d presents results in the same fashion for sensitivity to fire probability, coppicing ability, and woody plant growth rate. As sensitivity to the probability of fire occurrence (ψ) for a given grass biomass was very slight near the default value of $\psi=10^{-4} \text{ kg}^{-1}$ (Fig. 6b), we also focused on the sensitivity of woody plant response to fire in

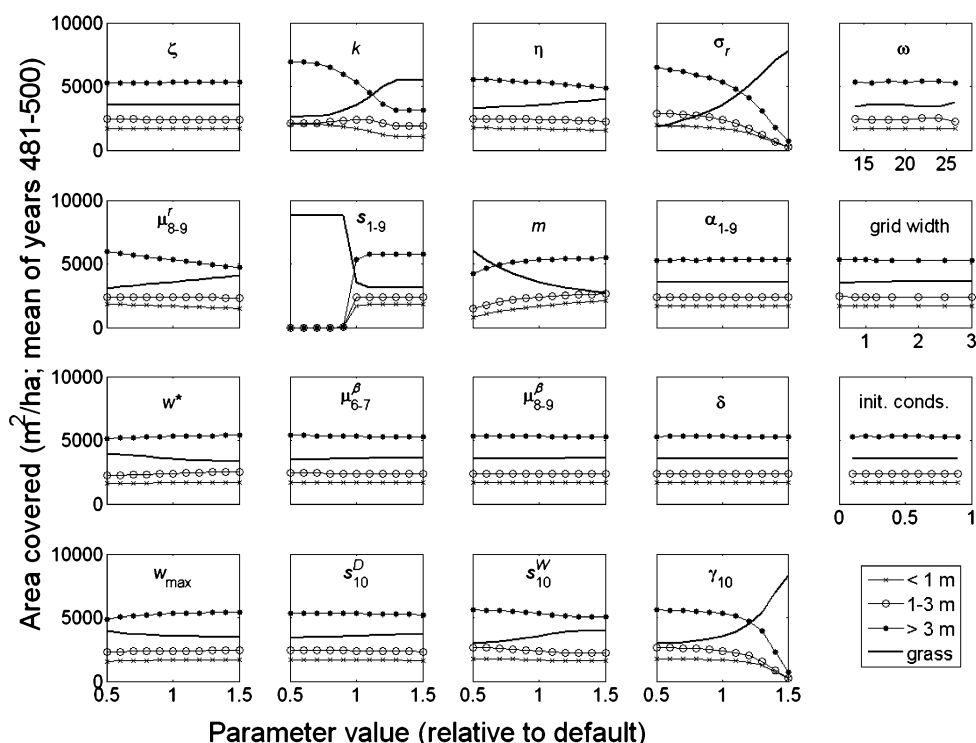


Fig. 4 Sensitivity of savanna model output (mean vegetation states over final 20 years and 100 iterations) to changes in model parameters. Parameters were varied individually by $\pm 50\%$ from their default values, except for wet-dry period length (ω , default value=20 years, varied over 14, 16, ..., 26 years); spatial extent of grid (“grid width,” default=1.0 km, varied from 0.5 to 3.0 km, i.e., 5 to 30 1-ha cells); and initial conditions (initial woody cover percentage, default=50%, varied from 10 to 90%). Other parameters and default values are drought severity shape parameter, $\zeta=50$; relative rainfall for $0.5\mu_{8-9}^r$ tree drought mortality, $k=0.8$; relative amplitude of wet-dry rainfall cycles, $\eta=0.13$; relative standard deviation in annual rainfall, $\sigma_r=0.3$; drought mortality for mature trees, $\mu_{8-9}^r=0.05$; survival of seedlings,

saplings, shrubs, and trees, $s_i=0.950, 0.990, 0.994,$ and 0.995 , respectively (all rates increased together by the same proportion to a maximum of 1); fecundity of mature trees, $m=50$ seedlings tree⁻¹ year⁻¹; resource area controlled by one seedling, sapling, shrub, and tree, $\alpha_i=0.01, 1, 9,$ and 25 m² respectively (all resource areas increased together by the same proportion); grass fuel required for a fire to kill all saplings, $w^*=2,500$ kg; shrub top-kill in maximum intensity fire, $\mu_{6-7}^r=0.8$; tree mortality in maximum intensity fire, $\mu_{8-9}^r=0.02$; seedling dispersal rate, $\delta=0.05$; grass fuel for maximum intensity fire, $w_{max}=5,000$ kg; dry season grass survival, $\mu_{8-9}^v=0.2$; wet season grass survival, $s_{10}^v=0.8$; and mean annual grass productivity, $\gamma_{10}=2,500$ kg/ha

terms of coppicing ability, κ_i (Fig. 6c), which has been found to vary widely in savanna plants [39]. We kept all κ_i values equal for the classes allowed to coppice ($2 \leq i \leq 7$) and altered all values together, again after the initial 100-year transitory period. Figure 6c shows the mean final state of vegetation as the proportion coppicing in each class $2 \leq i \leq 7$ was altered from 0 to 100%. Woody plant dominance increases as fire frequency or susceptibility to fire reduces. Sensitivity to the value used for woody plant growth (the default γ_i were based on a vertical height increase of 30 cm) is shown in Fig. 6d; as would be expected, faster woody plant growth leads to more tree dominance while slower growth leads to exclusion by grasses.

The spatial information generated by the model is summarized in Fig. 7, which examines spatial dominance patterns throughout the grid for some of the scenarios covered above. Output from the vegetation-only model for the default, 110% rainfall, and 90% rainfall scenarios is depicted in Fig. 7a–c (compare Fig. 3). In this case we describe a cell x as having low, medium, or high levels of

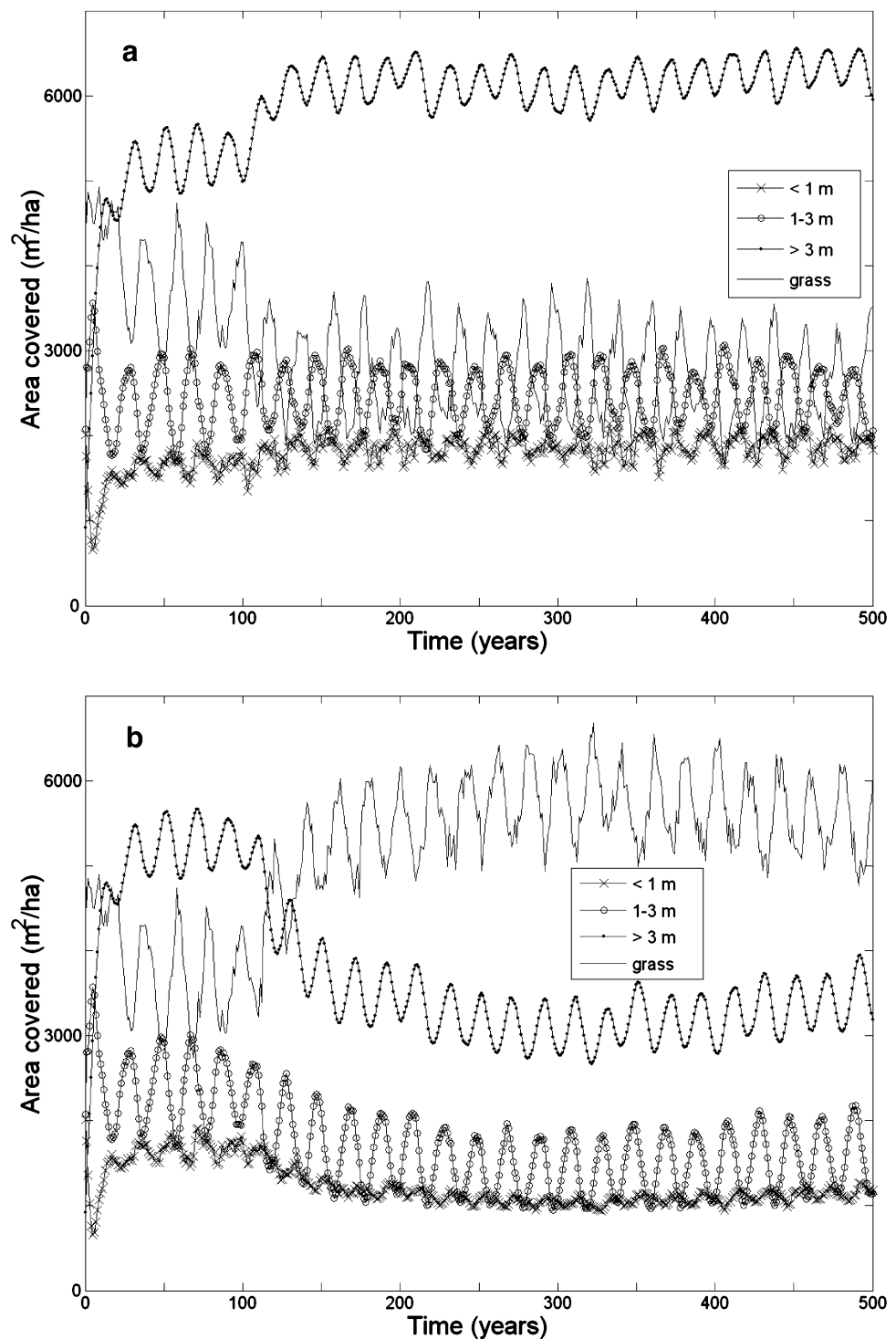
dominance by woody plants if the sum of woody cover ($a_{x,1} + \dots + a_{x,9}$) comes to more than 1/4, 1/2, or 3/4 of a hectare, respectively (these measures are somewhat arbitrary because as noted earlier the model allows seedlings, saplings, and grass to grow under adult tree canopies so that at any stage the vegetation cover may sum to more than one hectare).

We calculated the mean “fire return period” (FRP, the inverse of fire frequency) per cell for each simulation (Fig. 8). The default parameter set produced a FRP of 7.6 years, with other FRPs varying according to the effect of each scenario on the tree–grass ratio. Assumptions producing more grass-dominated results (less rainfall, increased fire probability, lower woody plant growth and coppicing ability, and introduction of elephants) yielded more fires and thus shorter FRPs.

4 Discussion

Our model produces long-term tree–grass coexistence and is useful for examining elephant effects on savannas [5].

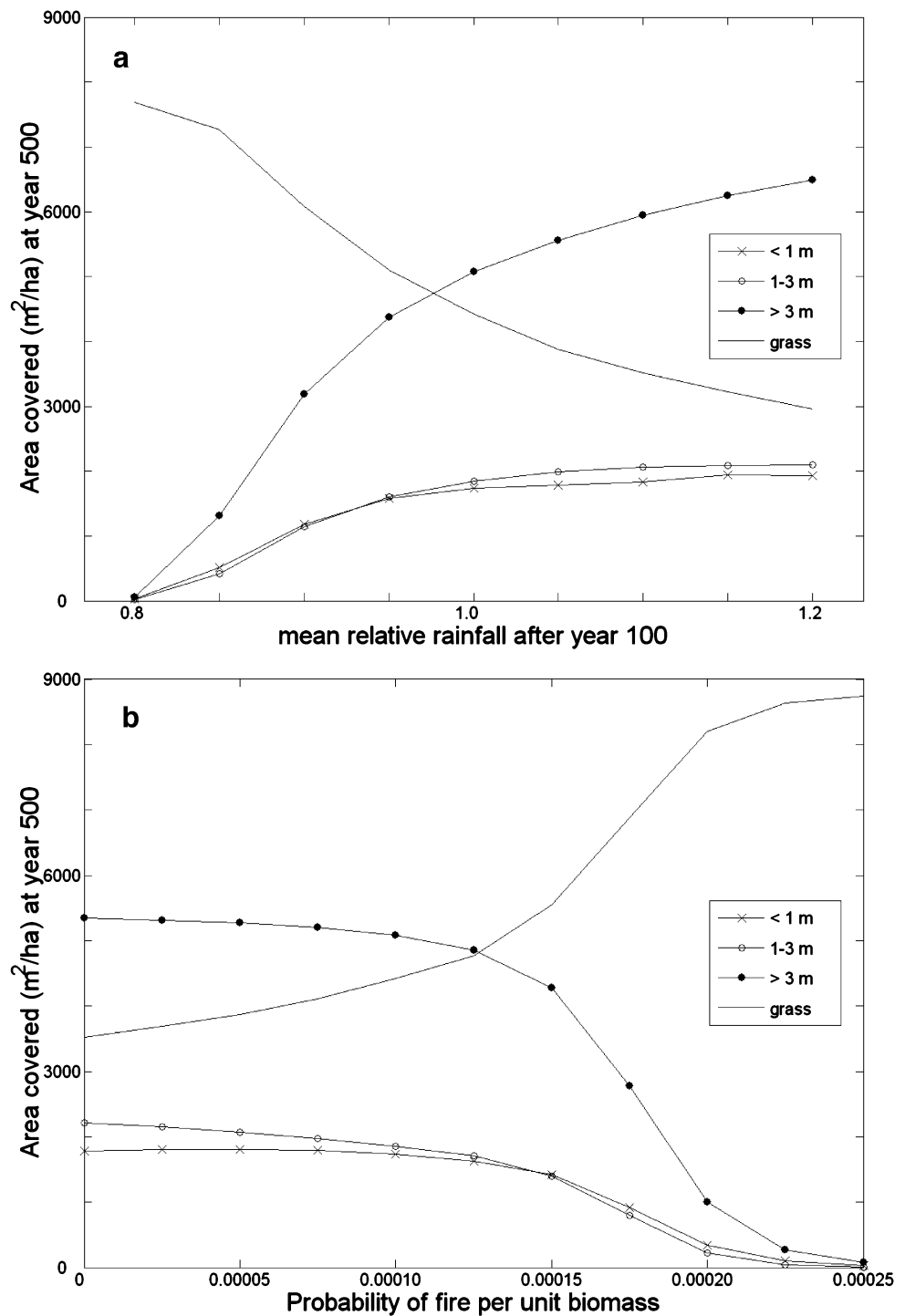
Fig. 5 Mean trajectories of 100 stochastic iterations for **a** wet (110% mean annual rainfall) and **b** dry (90% mean annual rainfall) scenarios, showing the mean area covered by woody plants in juvenile (<1 m high, i.e., seedlings and saplings), shrub (1–3 m), and tree (>3 m) classes, and by grass. Rainfall is adjusted after year 100 to allow initial transient dynamics to fade. Elephant density is zero throughout



The inclusion of realistic environmental stochasticity in the form of rain and fire variation allows further insights into savanna dynamics, which we now address. While we review our results in the context of these explicit environmental factors, we also bear in mind that other factors, such as soil type and nonelephant herbivory, may be allowed for by adjusting parameter values appropriately.

The important role of disturbance in maintaining tree–grass coexistence in savannas has been shown previously for an individual-based model [42]. The larger-scale demographic model we present here supports that view yet arrives at strikingly different dynamics. In our case the overriding disturbance factor comes from drought rather than fire (Fig. 4; cf. [42]). The incidence of extra tree

Fig. 6 Sensitivity of final vegetation composition to changes in **a** mean relative rainfall (default value 1.0), **b** ψ , the probability of fire occurrence relative to grass biomass (default value 0.0001), **c** resprouting rates (κ_i) of shrubs and saplings (default value 0.9), and **d** annual woody-plant vertical growth (default value 30 cm year⁻¹). All parameter adjustments take place at year 101, except for growth rates, which are fixed throughout. Mean area covered by each stratum after 500 years is plotted ($n=10,000$ for each point: 100 runs \times 100 cells)

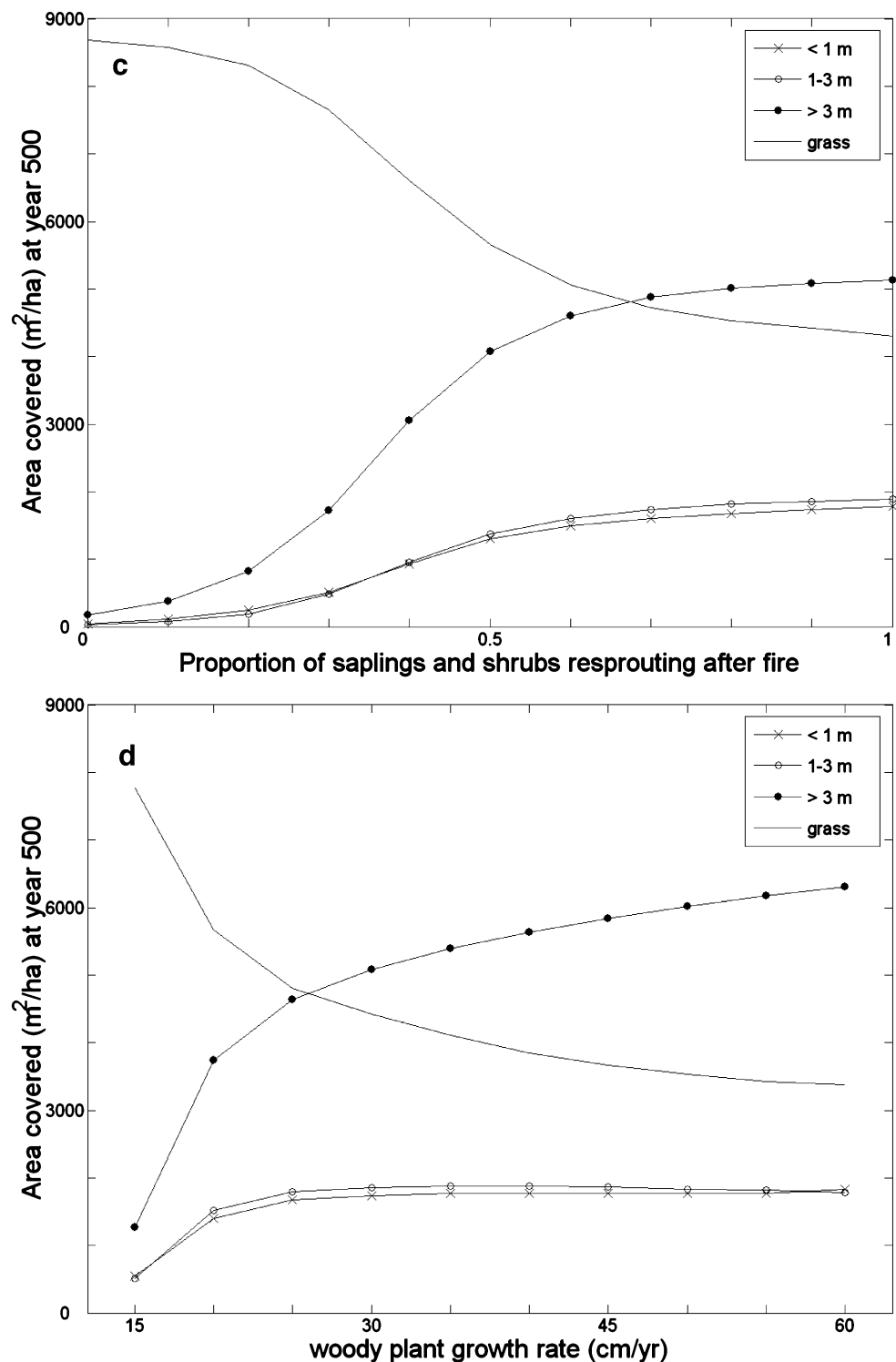


mortality in drought years ($\mu_{8-9}^r = 0.05$) rises sharply as rainfall declines, leading to a reduction in woody cover (Figs. 5b, 6a, and 7c; the proportions of 3-year rainfall averages falling below 80% mean annual rainfall in our simulations are 10, 15, and 25% for 110, 100, and 90% rainfall, respectively). This extra tree mortality is mitigated by strong recruitment of juveniles, in much the same way as variability in fire intensity can allow stems to opportu-

nistically recruit beyond the fire escape height [42], i.e., increased recruitment after disturbance allows tree persistence. The demographic bottleneck to allow this pulsed recruitment may be critical to savanna dynamics [15, 85].

A further difference in model predictions is the community shift under changes in rainfall regime: grass biomass has been predicted to increase with mean annual rainfall, producing fires of greater intensity and allowing grass

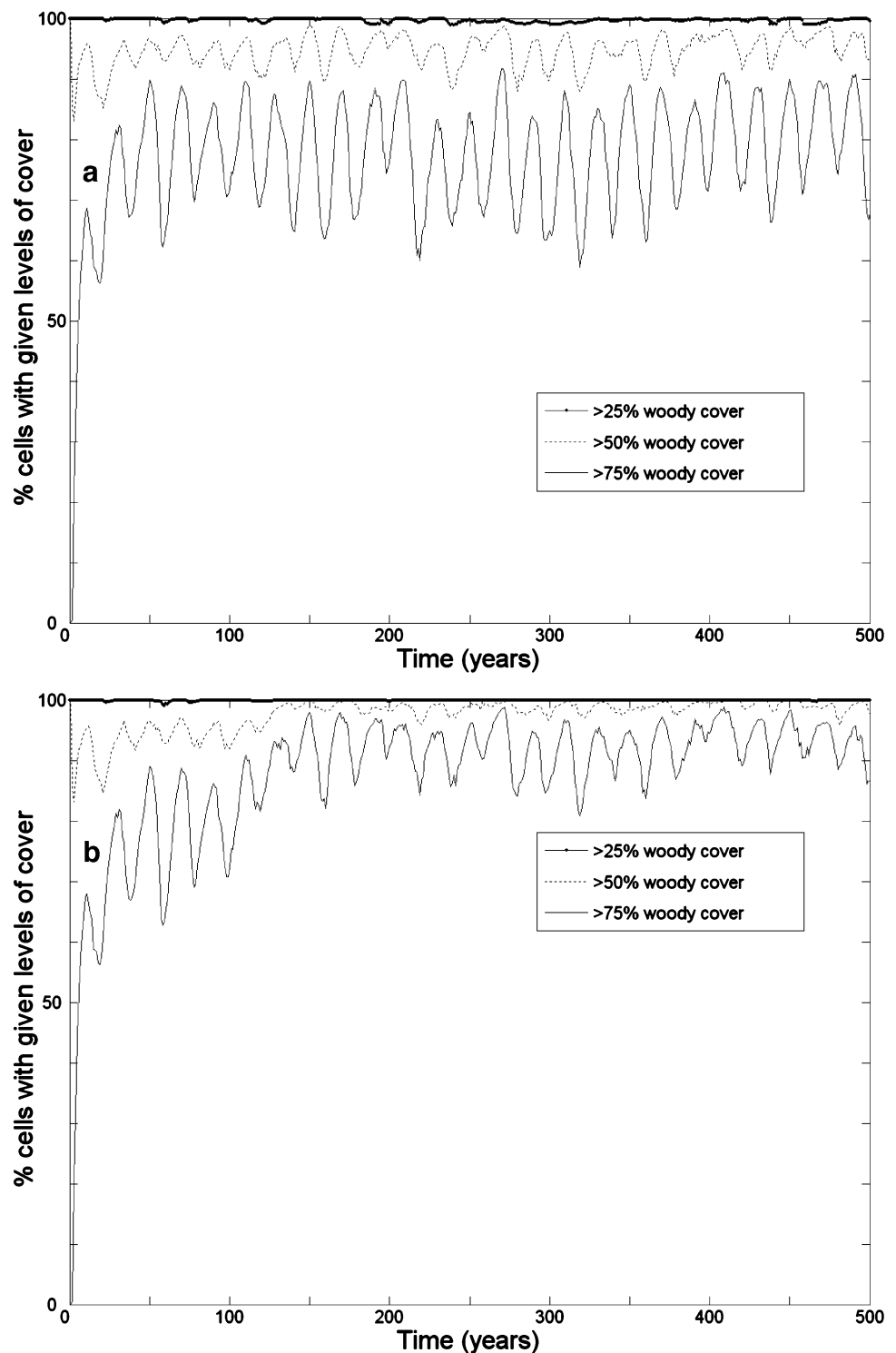
Fig. 6 (continued)



dominance [42], whereas our model shows increased woody dominance under wetter conditions (Figs. 5a, 6a, and 7b). Higher fire intensity in wet conditions (a result of higher grass biomass) has been invoked as a cause of woody decline [42]; although increased humidity may mitigate this effect. Our results suggest, however, that

reduced tree mortality in the concomitant absence of drought, and increased tree growth, can offset such fire intensities. In our model, fire intensity does indeed increase with rainfall (data not shown), but a protracted increase in mean rainfall allows the fire intensity effect (which should lead to grass dominance) to be counteracted by increased

Fig. 7 Mean percentage of cells with >25, 50, or 75% woody cover for **a** default, **b** 110% rainfall, and **c** 90% rainfall scenarios (corresponding to the mean trajectories shown in Figs. 3a, 5a and b)

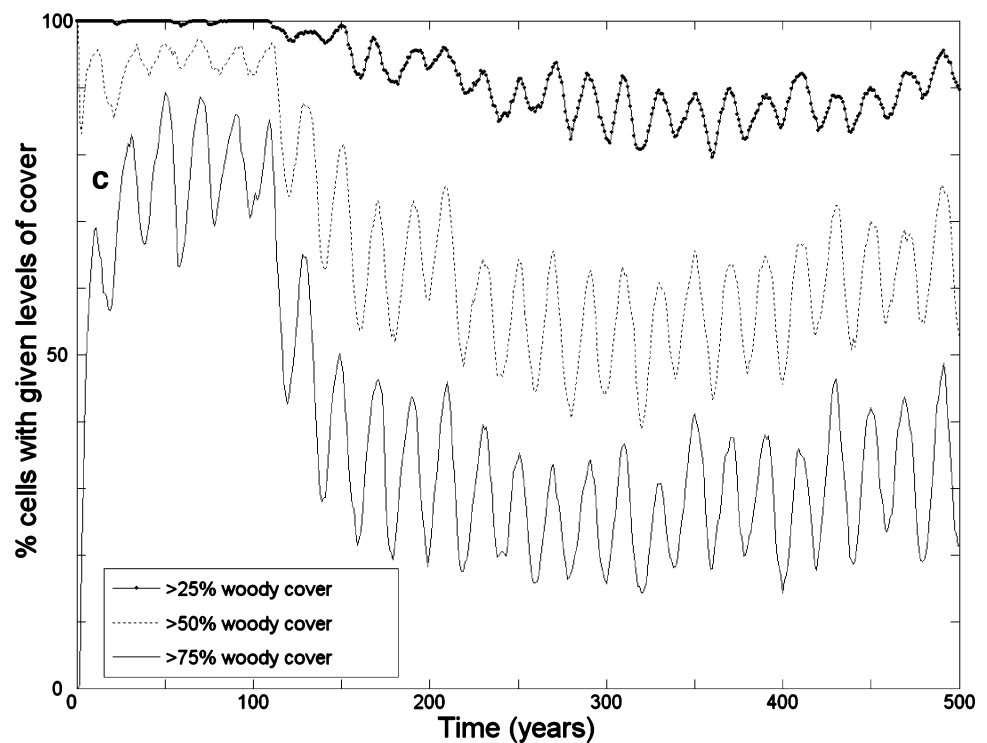


woody plant survival and recruitment. Other stochastic [53] and deterministic [113, 118] models also predicted a shift from grassland to savanna to woodland with increased rainfall or moisture availability.

This model and others [42, 113] are in agreement that reduced rainfall decreases woody plant dominance, via

recruitment limitation and extra incidence of drought-related mortality (this model). Reduction in the woody component of the KNP's marula-knobthorn (*S. birrea*–*A. nigrescens*) savanna between 1944 and 1981 was attributed mainly to an extended drought in the 1960s, interacting with elephant and fire effects [116]. Phase diagrams of

Fig. 7 (continued)



expected savanna composition with regional-scale rainfall and nutritional gradients suggest that a progression to either state (grassland or woodland) may be feasible [6, 8, 9, 118], depending on the region, species composition, and soil nutrient levels, which are not explicitly considered here.

By using a stochastic fire algorithm, fire occurrence in our model is integrated with the vegetation condition so that a 25% increase in ψ , the probability of fire per kilogram of grass biomass, does not necessarily translate to a 25% increase in fire frequency (Fig. 8). While yearly fires were not sufficient to exclude trees from an earlier savanna model [45], our model suggests that trees may be excluded by choosing very high values for ψ (Fig. 6b). Nevertheless the model is quite insensitive to reasonable changes in ψ (Fig. 6b: compare endpoints for 75 and 125% of the mean fire probability). Previous work also found the equilibrium level of trees to be insensitive to fire regime, unless fire mortality of seedlings was greater than 98% [45]. This insensitivity may arise because the result of reducing fire frequency is to allow grass fuel to build up, leading to increased fire intensity and woody plant mortality when the fire eventually occurs. The tree–grass balance is also quite robust to variation in the woody plants' response to fire, as demonstrated by the relative insensitivity to the proportion coppicing κ_i ($2 \leq i \leq 7$), shown in Fig. 6c (also see Fig. 8). Most savanna tree species have high rates of resprouting so that the rapid fall-off in woody plant cover as the κ_i decrease below 0.5 may indicate that $\kappa_i < 0.5$ is unlikely for savanna species, unless vulnerability to fire is reduced or

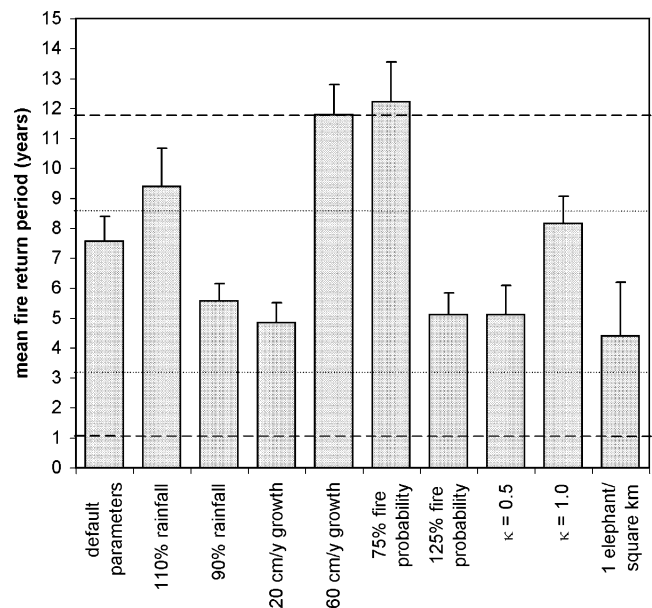


Fig. 8 FRPs (mean and standard deviation of 100 runs) for selected model scenarios, viz., default model parameters, 110% rain, 90% rain, annual woody growth of 20 cm, annual woody growth of 60 cm, 75% fire probability ($\psi = 0.75 \times 10^{-4}$), $\psi = 1.25 \times 10^{-4}$, coppicing ability reduced to $\kappa = 0.5$, $\kappa = 1.0$, and introduction of one elephant km^{-2} . All the parameter adjustments (including addition of elephants) take place at year 101, except for growth rates, which are set at year 0. FRPs indicate the mean interval between fires after parameters are adjusted. Horizontal lines represent typical (broken lines) and mean (dotted lines) ranges of FRPs reported for the KNP, South Africa [108]

compensated for by some extra feature such as higher seed production (ignored at this juncture) [16, 39]. Other modeling work has also suggested that coexistence is unlikely at coppicing rates below 0.6 [42].

As would be expected, enhanced woody plant growth leads to an increase in woody cover at the expense of grass (Fig. 6d), the higher growth rates allowing woody plants to compete more strongly with grass and to reach the fire escape height more quickly. This extra woody cover is manifested as an increase in adult trees at the expense of grass cover (even though grass is allowed to grow under tree canopies), with the subadult meta-classes being relatively unaffected as a result of their quicker turnover to reach the adult class. As knowledge of woody plant height growth rates for African savannas is sparse (see Section 2.2), this strong shift in the tree–grass balance within a reasonable range of growth estimates demonstrates the importance of obtaining pertinent demographic data. Of course, by modeling one generic tree species we have neglected the possible influence of interactions between fast- and slow-growing tree species, which may also differ in other life history strategies such as survival or fecundity (Fig. 4). Neither have we allowed for faster growth of coppiced individuals, due to stored reserves, which would favor the woody plant component [69].

With this model, we have attempted to capture essential savanna vegetation dynamics at temporal and spatial scales useful for making management decisions, rather than to investigate mechanisms for tree–grass coexistence. The model shows reasonable savanna dynamics; responds in reasonable fashion to variations in rainfall and fire; allows for a wide range of assumptions, parameters, and scenarios to be tested; and provides a panoply of results, which are merely summarized here. In striving for generality and flexibility in the model, many assumptions were necessary, which may affect the results to greater or lesser extents: for example, spatially homogeneous nutrient and water availability; seasonal partition of vegetation increase, decrease, and use by elephants; simplification of fire timing and of elephant population structure and dynamics, habitat use, and feeding patterns. Some of these assumptions can be addressed by judicious choice of parameters, for example, different edaphic conditions can be modeled by adjusting the values for grass productivity, woody growth rate, and drought response. The model is easily further extended by connecting the 1-km² blocks and allowing for environmental gradients across blocks, and including more detailed elephant demography and feeding patterns. Management discussions involving long-lived organisms must inevitably rely on models such as the one presented here to perform meaningful thought experiments and make informed decisions [98]. This research suggests that further work on woody plant demographics is essential before decisions are made based

on the putative impacts of elephants on savanna systems, particularly if those decisions involve culling elephants.

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