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RESEARCH PAPER

A continental-scale analysis of tree cover in African savannas

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ABSTRACT

Aim We present a continental-scale analysis that explores the processes controlling woody community structure in tropical savannas. We analyse how biotic and abiotic factors interact to promote and modify tree cover, examine alternative ecological hypotheses and quantify disturbance effects using satellite estimates of tree cover.

Location African savannas.

Methods Tree cover is represented as a resource-driven potential cover related to rainfall and soil characteristics perturbed by natural and human factors such as fire, cattle grazing, human population and cultivation. Within this framework our approach combines semi-empirical modelling and information theory to identify the best models.

Results Woody community structure across African savannas is best represented by a sigmoidal response of tree cover to mean annual precipitation (MAP), with a dependency on soil texture, which is modified by the separate effects of fire, domestic livestock, human population density and cultivation intensity. This model explains *c.* 66% of the variance in tree cover and appears consistent across the savanna regions of Africa.

Main conclusions The analysis provides a new understanding of the importance and interaction of environmental and disturbance factors that create the broad spatial patterns of tree cover observed in African savannas. Woody cover increases with rainfall, but is modified by disturbances. These 'perturbation' effects depend on MAP regimes: in arid savannas (MAP < 400 mm) they are generally small (< 1% decrease in cover), while in semi-arid and mesic savannas (400–1600 mm), perturbations result in an average 2% (400 mm) to 23% (1600 mm) decrease in cover; fire frequency and human population have more influence than cattle, and cultivation appears, on average, to lead to small increases in woody cover. Wet savannas (1600–2200 mm) are controlled by perturbations that inhibit canopy closure and reduce tree cover by, on average, 24–34%. Full understanding of the processes determining savanna structure requires consideration of resource limitation and disturbance dynamics.

Keywords
Africa, disturbance, fire, savanna, tree cover, tree–grass interactions.

INTRODUCTION

The vegetation of climatically similar regions of the world often presents similar structural and functional attributes, independent of the evolutionary history of the flora and fauna. Such ecological convergence implies that global patterns of vegetation are broadly predictable from environmental variables, primarily precipitation and temperature. In addition to climate, however, other factors such as soil characteristics, fire, herbivory and human activities are important forces in the development and control of vegetation structure and function.

Savannas are defined on the basis of both ecological characteristics and climatic attributes. The common characteristic of all savannas is the coexistence of woody and herbaceous vegetation

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in regions where seasonality is controlled by distinct dry seasons, rather than by cold (Scholes & Archer, 1997). Ecologists have long been interested in the mechanisms that create and maintain the coexistence of trees and grasses in savanna systems. The factors responsible for the coexistence of these two very different forms of vegetation are varied: early hypotheses centred on interspecific competition and vertical niche separation between the roots of woody and herbaceous species in the soil (Walker & Noymeir, 1982; Scholes & Archer, 1997). More recent work has highlighted the importance of disturbances such as fire, herbivory and human activities (Higgins *et al.*, 2000; van Langevelde *et al.*, 2003; Sankaran *et al.*, 2004, 2005).

The critical importance of water is well recognized for savanna vegetation (Scholes & Archer, 1997; Walker & Langridge, 1997; Sankaran *et al.*, 2004). Mean tree cover among sites and maximum observed tree cover increase with mean annual rainfall, but substantial variation in tree cover occurs with disturbance and climate variability (Fernandez-Illescas & Rodriguez-Iturbe, 2004; Wiegand *et al.*, 2006). The role of soil substrate is inseparable from the role of water because it acts as a temporary store for precipitation inputs and as a regulator for the major outflows through evapotranspiration and deep percolation (Noy-Meir, 1973). The inverse texture hypothesis (Noy-Meir, 1973) has generally been interpreted with respect to primary productivity, with fine-textured soils able to support more net primary production (NPP) than coarse soils at higher rainfall (above MAP *c.* 400 mm) and coarse soils supporting higher NPP at low rainfall (Sala *et al.*, 1988). However, in his 1973 paper, Noy-Meir also relates the inverse texture hypothesis to the prominence of perennial vegetation, stating that in wetter climates fine-textured soils will support 'taller and denser perennial vegetation' than coarse-textured soils, and vice versa for dry climates. This prediction with respect to the impact of soil texture and rainfall on the success of perennial versus annual plants, or indeed woody versus herbaceous plants, has not, to our knowledge, been tested with observational or experimental data.

Woody community structure in savannas is also strongly affected by fire (Hochberg *et al.*, 1994; Gignoux *et al.*, 1997; Higgins *et al.*, 2000; Bond & Keeley, 2005), herbivory (Ellis & Swift, 1988; Skarpe, 1991; Van de Koppel & Prins, 1998), and other perturbations linked to human land use (Belsky, 1987; Ellis & Galvin, 1994; Higgins *et al.*, 1999; Laris, 2002). Fire and herbivory alter the mix of plant growth-forms, and competitive interactions between them, through direct consumption of living and dead plant material. Savannas are the most frequently burnt ecosystems (Barbosa *et al.*, 1999; Dwyer *et al.*, 2000) and fire is considered to have a large regulatory influence on emergent vegetation structure (Scholes & Archer, 1997; Jeltsch *et al.*, 2000; House *et al.*, 2003; Sankaran *et al.*, 2004). In particular, fire frequency can control the probability of escape of tree seedlings from the flame zone and survival to mature size classes. Fires can thereby suppress woody cover and contribute to the coexistence of trees and grass in mesic and wet savannas (Higgins *et al.*, 2000). Browsers can have analogous effects, suppressing seedlings by browsing (Prins & Van der Jeugd, 1993; Van de Koppel & Prins, 1998), whereas grazers (particularly domestic cattle) are generally considered to suppress grass biomass and thereby release woody plants from competition and reduce the frequency or intensity of fires, leading to increased woody cover (Bond *et al.*, 2005; Metzger *et al.*, 2005). Humans also interact directly with the system using land for pasture, agriculture, fuel and timber, and causing alterations in proportions of tree cover (Sinclair & Fryxell, 1985; Homewood *et al.*, 2001; Shackleton *et al.*, 2005).

Sankaran *et al.* (2004) suggest that the integration of resource-based and disturbance-based models is required to explain the coexistence of trees and grass and their relative abundance in savannas. A landscape-scale study conducted in an arid savanna of Namibia by Wiegand *et al.* (2006) concluded that the tree–grass ratio is influenced both by primary (rain and nutrients) and secondary (fire and herbivory) determinants. Significant advances in understanding savanna ecology have been made over many years of research, but published studies often base ecological conclusions, and mathematical models, on data from a small number of sites with particular climatic, edaphic and disturbance characteristics, thus limiting the broad relevance of the conclusions. Comprehensive analyses aimed at separating the role of resources and competition from the role of disturbances across broad-scale climatic and environmental gradients are relatively few and far between. In this paper we develop and test a series of empirical, but functionally meaningful, models to investigate variability in tree cover across all African savannas. Our aim is to identify the processes that create and modify tree cover at these large continental scales where climate, soil type and disturbances by fire, herbivores and humans vary substantially. We examine the extent to which variations in annual precipitation, soil nitrogen and texture, fire frequency, cultivation intensity, cattle density and human population may contribute to observed emergent properties of tree cover across Africa.

In the following sections we develop a conceptual model for the ways in which climate and other factors interact to control woody community structure in savanna systems. We translate these concepts into quantitative models and test the alternative hypotheses using satellite-derived tree-cover data. Achieving a broad understanding of resource use and the influences of perturbation requires describing the processes that drive variation in the dynamics of the development and persistence of tree cover. A general model predicting tree cover must discriminate the action of different factors and evaluate their effects in relation to their intensity. We use our models to illuminate possible dynamics that are common among African savannas and to quantify the importance and role of climate, soil and disturbance in controlling observed tree cover across the savannas of Africa.

METHODS

Conceptual framework

We postulate that the coexistence of trees and grasses in savannas results from competition between the two vegetation forms as well as their complex interactions with climate, soil biochemistry, fire, herbivory and human activities. These factors can lead to direct mortality of trees or grasses, or change the competitive

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Table 1 Data sets used in analysis of African savanna tree-cover dynamics. The data set consists of 10 layers. The last column relates each variable to eqns 1 and 3. The lower case letter defines the variable symbol. The letter *U* stands for the 'undisturbed tree cover' term and *M* for the 'modifications by perturbation' term. Summary statistics, mean and range are reported.

Data layer	Symbol and summary statistics	Origin	Description
Tree cover	*tc* (response variable) mean (*tc*) = 16% min = 0%, max = 89%	500 m MODIS Vegetation Continuous Fields (Hansen *et al.*, 2003)	Proportional estimates of tree cover derived from monthly composites of MODIS satellite data of 2002. Resolution: 500 m; units: per cent
Mean annual precipitation (MAP)	MAP; *U* mean (*r*) = 769 mm min = 11 mm, max = 2192 mm	ANU-CRES fitted climatic grids (Hutchinson *et al.*, 1996)	Total monthly rainfall values averaged over period 1951–95. Resolution: 0.05 ; units: mm
Growing season length (GSL)	GSL; *U* avg (*g*) = 127.5 days min = 2 days, max = 337 days	ANU-CRES fitted climatic grids (Hutchinson *et al.*, 1996) Potential evapotranspiration (Allen *et al.*, 1998)	GSL = (average monthly rainfall/PET) × (days per month) (Sankaran unpublished data) Resolution: 0.05 ; units: days
Soil texture	*s*; *U* Classes: fine, medium and coarse	Zobler soil data sets (texture layer) Source: UNEP/GRID (Zobler, 1986)	Global distribution of soil texture classes Resolution: 1
Soil nitrogen	*n*; *U* mean (*n*) = 832 g/m^2 min = 0 g/m^2, max = 4875 g/m^2	Global gridded surfaces of selected soil characteristics Source: IGBP-DIS (Global Soil Data Task Group, 2000).	Total nitrogen density. Resolution: 0.08 ; units: g/m^2
Fire frequency	*f*; *M* mean (*f*) = 2 years min = 0 years, max = 1 year	GVM, Joint Research Center, Italy (Barbosa *et al.*, 1999)	Burned areas in 1981–91 derived from NOAA-AVHRR GAC data over the period 1981–91. Resolution: 8 km; units: fire return over 8 years
Cultivation intensity	*c*; *M* mean(c) = 16% min = 0%, max = 100%	International Livestock Research Institute (ILRI); UNEP-GRID & GISS (Matthews, 1983)	Percentage that is under cultivation, versus the percentage of natural vegetation, including five classes. Resolution: 1 ; units: %
Human population density for 2002	*p*; *M* mean (*p*) =19 km^{-2} min = 0 km^{-2}, max = 8906 km^{-2}	Oak Ridge National Laboratory (ORNL) LandScan Global Population Database 2002: http://www.ornl.gov/sci/landscan/	Census counts (at sub-national level). Resolution: 0.01 ; units: number of people per cell
Cattle density	*l*; *M* mean (*l*) = 7 km^{-2} min = 0 km^{-2}, max = 242 km^{-2}	World Resources Institute – PAGE, 2000 http://earthtrends.wri.org/text/economics-business/map-246.html	Density of cattle in Africa compiled by the International Livestock Research Institute (ILRI). Resolution: 0.09 ; units: cattle per km^2
Biome		IUCN, as digitized by UNEP/GRID in 1986. Created by Udvardy (1975).	Biogeographical provinces of the world, Africo-tropical realm: biogeographical provinces are defined as ecosystematic or biotic subdivisions of the realms (floral 'regions' and faunal 'provinces')

interactions between them (Sankaran *et al.*, 2004). To explain the fraction of tree cover in African savannas, we propose to partition the variation of tree cover into two primary constituents: the potential cover configuration in undisturbed systems (*U*) and a modification of *U* dependent on perturbation interactions (*M*). We relate each constituent to a different set of explanatory variables: the first consisting of climatological and soil descriptors, and the second consisting of natural and human-related perturbations. In this approach, we build models using separate multiplicative terms *U* and *M*:

$$tc = UM \quad (1)$$

where *tc* is percentage tree cover, *U* is composed of functions *u* that depend on variables related to undisturbed tree growth and *M* is composed of functions *m* that depend on variables related to perturbation. By partitioning, we seek to resolve the relative importance of: (1) environmental components that determine the structure of the vegetation in the absence of perturbations; and (2) the perturbation components that create a departure from the 'potential' (i.e. undisturbed) state.

Models

Given the conceptual framework, we now choose explanatory variables and structure alternative models. Each model comprises a set of predictors and functions that describe ecological or heuristic relationships of tree cover with the predictors. Table 1 shows the variables used for the analysis, their relation to the potential–perturbation framework and their notation. The response variable is percentage tree cover (*tc*) estimated using the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor onboard NASA's Terra satellite (Hansen *et al.*, 2003).

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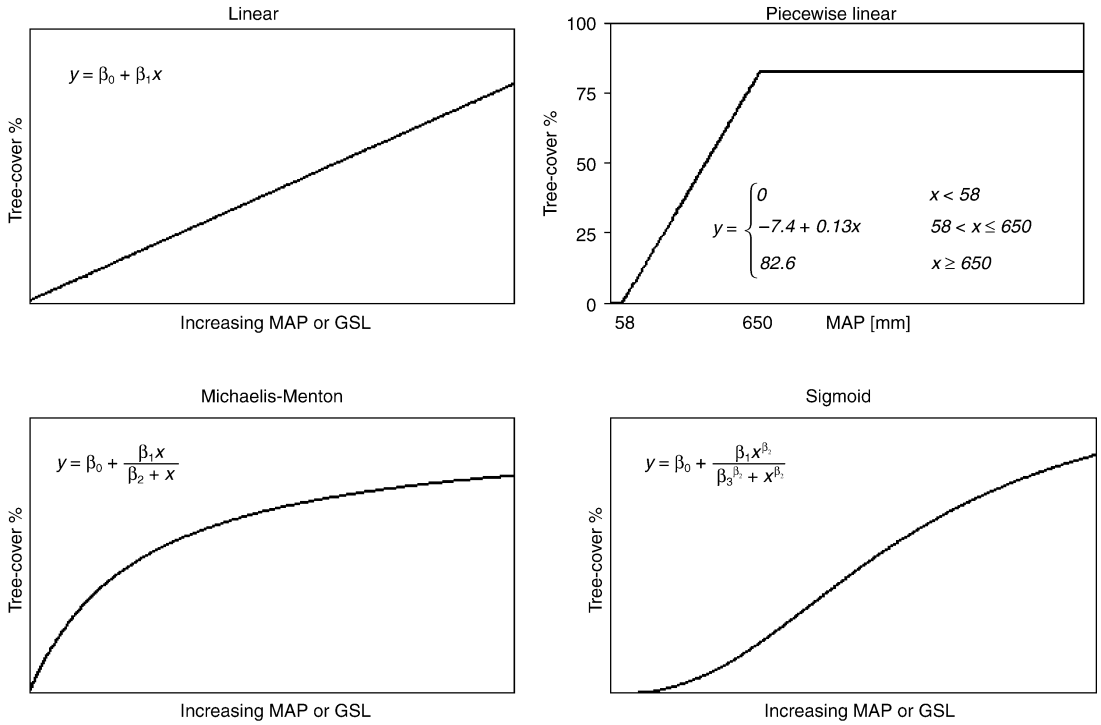

Figure 1 Hypothesized functional responses of tree cover to moisture. The independent variable could be either mean annual precipitation (MAP, mm) or growing season length (GSL, days).

The independent variables for U (eqn 1) are mean annual precipitation (MAP) or, alternatively, growing season length (GSL). GSL was computed from rainfall and potential evapotranspiration estimates (Allen *et al.*, 1998) to explore whether other aspects of climate (that take into account both rainfall and evaporative demand) need to be considered in addition to rainfall. Soil texture and soil nitrogen effects were also included in U to represent the possible impacts of these on water and nutrient relationships that might alter the climate-driven woody community structure. The term M depends on the perturbation variables fire frequency, cattle density, human population density and cultivation intensity. Pearson correlation coefficients between predictor variables are less than 0.5, indicating that the variables are not strongly correlated.

In structuring the models, we consider four alternative functions u (Fig. 1) representative of hypotheses concerning the response of tree cover to moisture (using either MAP or GSL). (1) *Linear*: the linear response represents the case in which tree cover increases proportionally with water across the rainfall gradient. This can be considered as the null model and the following alternative functions are attempts to account for more complex responses of tree cover to moisture regimes. (2) *Michaelis–Menton*: the shape of this function reflects a saturation hypothesis where at relatively high moisture the response levels out as canopy closure approaches and other factors become limiting. (3) *Sigmoid*: this curve corresponds to the hypothesis that a minimum amount of moisture is required for woody plants to establish and survive and that tree cover then increases to an asymptote as canopy closure approaches. (4) *Piece-wise linear*: this line results from quantile regression of tree cover on rainfall determined by Sankaran *et al.* (2005) using independent field measurements. We used the piece-wise linear equation with fixed parameters as reported by Sankaran *et al.* (2005) to provide an estimate of the moisture-driven potential tree cover from which we attempted to fit the perturbation effects.

The full term U relates tree cover to MAP or GSL using one of these four curves with an adjustment for different soil texture classes, multiplied by a linear function of soil nitrogen. Conceptually, U represents tree cover in undisturbed systems but it is recognized that such conditions rarely occur in reality because most savannas are perturbed to a greater or lesser degree. The relationships described by U will be referred to as climate-driven tree cover and can be considered to be the mean climate response around which low-perturbation points lie.

The term M (eqn 1) is based on parametric functions with a rational form:

$$m(v) = 1 - \alpha v^{\beta} \tag{2}$$

where v is a perturbation variable in the interval [0,1] and α and β are parameters ($\beta > 0$). Each function m depends on one perturbation variable and decreases or increases the value of tree cover predicted by the term U by the fraction αv^{β} depending on the nature of the interactions and the patterns embedded in the observations. This mathematical structure permits both suppression and facilitation of moisture-driven tree cover by perturbations, with convex, quasi-linear and concave forms possible depending on fitted parameter values.

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In composing different models of tree cover, a moisture function was always selected, with or without soil nitrogen and texture functions, to form *U*. The *U* term was then tested with all possible combinations of the perturbation functions *m* (including models with, and without, perturbations), making a total of 512 candidate models.

Statistical framework

A critical aspect of inference in environmental science involves the search for an appropriate approximating model supported by empirical data. Information theory approaches allow evaluation of the weight of evidence for multiple hypotheses represented by a set of possible models, and selection of a single model or a subset of models (where there is ambiguity) that provide the 'best', and most parsimonious, representation of the data (Burnham & Anderson, 2002). Models that are poor at explaining the information in the data, which have errors in their structure and/or predictor choice, receive high model-selection uncertainty.

The Bayesian information criterion (BIC) (Schwarz, 1978) offers a way to provide balance between accuracy and parsimony. The expression of the BIC entails terms representing lack of fit based on the maximized likelihood associated with the model parameters, a bias correction factor related to model complexity and a penalty term dependent on sample size. This criterion was developed within the Bayesian framework (Hoeting *et al.*, 1999; Hobbs & Hilborn, 2006) and provides a method for approximating model posterior probabilities that is accurate when the sample size is large, i.e. more than 20 times the number of predictors (Kass & Raftery, 1995). The application of the BIC assumes that all models and parameters are initially equally likely (Hoeting *et al.*, 1999; Wintle *et al.*, 2003); this is the 'default' approach when there is insufficient information to define prior distributions.

In traditional (frequentist) statistics there is an absence of formal methods for deriving and incorporating model uncertainty conditional to the data. Frequentist approaches and the Akaike information criterion (AIC) (Akaike, 1973) do not account for sample size and, when a data set is large, they would favour complex models that better fit variance but may fail to identify the factors of importance (Kass & Raftery, 1995; Zucchini, 2000; Johnson & Omland, 2004).

In this paper, we were interested in finding one or more models that describe tree-cover patterns in order to better understand which factors and processes give rise to it. We used the BIC to evaluate objectively and rank models of differing complexity by extracting a sample of data points from the continental data set that was large compared with the model dimensions. Relative differences among model BIC values enable the derivation of posterior probabilities called 'weights' (*w*) that allow the candidate models to be ranked and quantify model selection uncertainty (Burnham & Anderson, 2002; Hobbs & Hilborn, 2006).

Implementation

We defined the savanna regions of Africa using a bioregion map (Table 1) and, within these, we selected areas with MAP less than 2200 mm. We randomly sampled 0.02% from the 500-m tree-cover data set obtaining 13,416 points for the subsequent analysis. This sample size represents a trade-off between a sample that is representative of the variability in tree cover across the continent while also being manageable for statistical analyses. The difference between the population mean (15.96 ± 0.09%) and sample mean (15.86 ± 0.31%) was not statistically significant.

We extracted data for all the other variables (Table 1) at the sample locations. In many cases the data available with continental coverage for Africa are at much coarser spatial resolution than the tree-cover data set (see, for example, soil texture and cultivation intensity in Table 1). This scale mismatch means that some fine-scale responses of tree cover to potential drivers cannot be represented in the following analysis. However, we decided against degrading the response variable (*tc*) to the coarsest resolution since there is real information in *tc* at these scales, and we are interested in the extent to which fine-grain patterns respond to the fine-scale drivers that are available. In this situation, the coarse resolution data sets provide our 'best estimate' of conditions at the *tc* locations, with an expectation that the resulting relationships will be weaker than would be expected if all data were available at high resolution.

The values of the perturbation variables and soil nitrogen were rescaled in the interval [0,1] between minimum and maximum to make their effects comparable and to enhance the numerical stability of the statistical models. Log and square-root transformations were applied to soil nitrogen and human population variables, respectively, adjusting for skewness. We implemented the models using SAS software (SAS, 2000) and fitted them using PROC NLMIXED with the optimization technique based on a dual quasi-Newton algorithm. The SAS procedure provides BIC values from which we calculated the weights *w*.

RESULTS

Among the 512 competing models, 96% satisfied convergence criteria but only 35% of the fitted solutions had both high likelihood ranking and, when examined more closely, fitted parameter values that were physically and biologically meaningful. Table 2 lists the four models with the highest BIC weights. Note that the summed BIC weights of the first four models are 0.999, indicating almost no empirical support in the data for the 508 models not shown in Table 2. The model for African savanna woody cover with best support ($w = 0.88$) from this analysis is:

$$tc = \left(t_0 + \frac{\alpha_s MAP^{\beta_s}}{\gamma^{\beta_s} + MAP^{\beta_s}}\right)(1 + \alpha_n n)(1 - \alpha_f f^{\beta f}) \\ (1 - \alpha_p p^{\beta p})(1 - \alpha_c c^{\beta c})(1 - \alpha_t l^{\beta t}). \quad (3)$$

This model accounts for 66% of the variability in the sample data set and includes all the predictors and 18 parameters. Table 3 reports the parameter estimates and their 95% confidence intervals. The parameters t_0, α_s, β_s, and γ define the shape of the sigmoidal rainfall-driven tree-cover response. The parameter t_0 represents the minimum percentage tree cover, α_s gives the

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Table 2 Four models with highest posterior model probabilities based on the Bayesian information criterion (BIC). All these models are structured with the sigmoid function. The presence of a predictor in a model is marked by a dot (MAP = mean annual precipitation, GSL = growing season length, s = soil texture, n =soil nitrogen, f = fire frequency, c = cultivation intensity, p = human population and l = cattle density). K is the number of free parameters; for each model i, $\Delta_i = \mathrm{BIC}_i - \mathrm{BIC}_{\min}$ and w_i is the derived BIC weight (model posterior probability).

	Climate potential		Soil		Perturbations				Statistics		Weights
Model	MAP	GSL	s	n	f	c	p	l	K	Δ_i	w_i
1	•		•	•	•	•	•	•	18	0	0.8786
2	•		•	•	•		•	•	16	4	0.1189
3	•		•		•	•	•	•	17	12	0.0022
4	•		•		•		•	•	15	16	0.0003

Table 3 Summary statistics for the parameters of the best model. The second column reports the parameter symbols as in eqn 3. The indices sf, sc and sm are for fine, coarse and medium soil texture classes. Parameters for the effects of soil nitrogen, fire frequency, cultivation, human population and cattle density are also shown.

Variable	Parameters	Estimate	SE	95% CI	
MAP	t_0	−0.9	0.2	−1.4	−0.4
	α_{sf}	117.9	6.9	104.3	131.5
	α_{sc}	110.6	7.1	96.7	124.5
	α_{sm}	110.9	5.9	99.2	122.7
	β_{sf}	2.2	0.1	2.1	2.4
	β_{sc}	2.6	0.1	2.4	2.8
	β_{sm}	1.96	0.06	1.84	2.08
	γ	1435.8	65.7	1306.9	1564.6
Soil nitrogen	α_n	0.27	0.07	0.14	0.40
Fire frequency	α_f	0.38	0.01	0.36	0.40
	β_f	0.54	0.04	0.46	0.61
Cultivation intensity	α_c	−0.4	0.1	−0.6	−0.2
	β_c	3.6	0.6	2.3	4.8
Human population	α_p	1.01	0.05	0.91	1.10
	β	1.24	0.06	1.12	1.36
Cattle density	α_l	0.45	0.05	0.36	0.54
	β_l	0.33	0.04	0.26	0.40

SE, standard error; MAP, mean annual precipitation; CI, confidence interval.

tree-cover range, β_s determines the curvature and γ is the MAP value at $tc = \alpha_s/2$. The parameters α_s and β_s showed a dependence on soil texture categories (s). The parameter α_n defines a linear effect of soil nitrogen, and the parameters α_j and β_j control the perturbation effects, with $j = f$, c, p and l being indices for fire frequency, cultivation intensity, human population and cattle density, respectively.

The sigmoid function was selected in all the top-ranked models and hence has the greatest support in the data. There is effectively no support for models structured with linear, piecewise linear or Michaelis–Menten functions. Associated with the sigmoid shape, MAP is a better predictor than GSL. The soil texture variable, soil nitrogen and all the perturbation variables, fire frequency, human population, cultivation and cattle density, appear in the best model with virtually no uncertainty as to the significance of their effects.

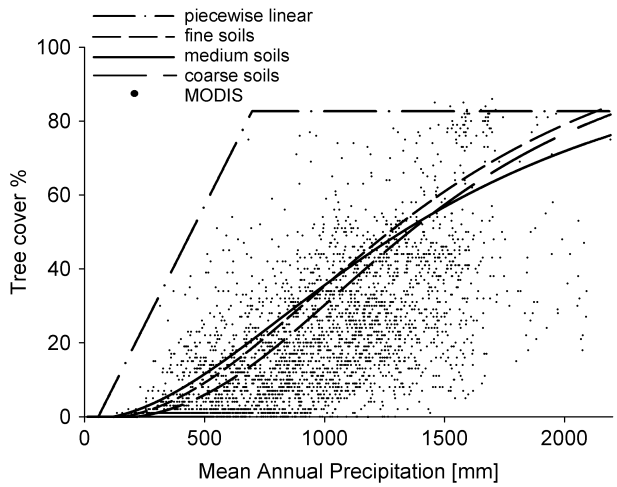

Figure 2 Tree cover % versus mean annual precipitation (MAP): MODIS-based tree cover % (dots), predicted rainfall-driven tree cover on three class of soil texture (solid and dashed lines), and piecewise linear relationship (dash-dotted line) marking the upper bound on tree cover found by Sankaran *et al.* (2005).

The fitted sigmoid lines represent predicted tree cover on fine, medium and coarse soils for locations with little or no perturbation and low soil nitrogen (Fig. 2). Fine-textured soils appear to have slightly higher tree cover than coarse soils across all rainfall zones with MAP > 300 mm. The medium soil texture class is similar to the fine-textured soils at low rainfall, but at high rainfall it appears to have lower cover than even the coarse soils (perhaps related to the relatively small number of savanna points in the very high rainfall zones above 1700 mm MAP).

The perturbation effects are shown in Table 3 and Figure 3. The relationships are plotted with larger symbols to represent the interquartile range to give an idea of the distribution of the perturbation variables across the intensity range. The contribution of soil nitrogen to rainfall-driven tree cover appears to be positive, but for 75% of the points this effect is relatively weak ($\alpha_n n < 0.13$ in eqn 3). More frequent fires, higher cattle density and larger human population densities all tend to depress rainfall-driven tree cover. Cattle-normalized values do not exceed 0.04 (10 cattle per km^2) for 75% of the locations and rainfall-driven tree cover is reduced at the maximum by a factor −0.16 (term $-\alpha_l l^{\beta l}$ in eqn 3). The interquartile ranges show that suppression of tree cover by fire and human population is often important (*c.* −0.24 at their 75th percentiles). At the highest extremes, fire and cattle appear to reduce potential tree cover by a factor of −0.4. However, these are less strong modifiers than human population, which at its highest levels in urban areas (8900 people per km^2) can effectively eliminate tree cover. An unexpected result concerns the positive effect of cultivation: for most of the pixels cultivation appears to have

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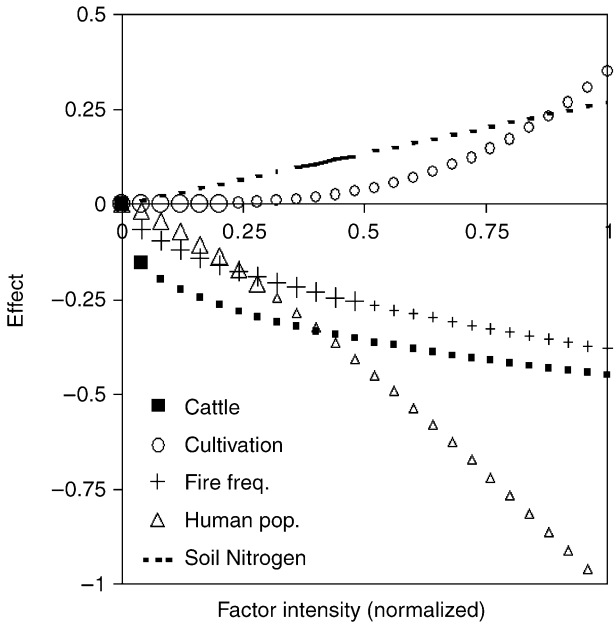

Figure 3 Effects of perturbation ($-\alpha v^{\beta}$) and soil nitrogen ($\alpha_n n$) on unperturbed tree cover (eqns 2 and 3). Larger symbols mark the response interval for the interquartile range (i.e. data within the 25th and 75th percentiles) of each factor.

relatively minimal effect on woody cover (< 0.002), but the fitted response curve suggests that where cultivation intensity is > 0.75 (more than 75% cultivated land) this can result in an increase from rainfall-driven woody cover by a factor of 0.1–0.3.

To validate our results, we used the best model (eqn 3 and Table 3) to predict tree cover on a new random sample that was 10 times larger than the pilot sample. The model predictions fit the MODIS observations with a slope of 0.98 (P value = 0.002) and an intercept of –0.03 (P value = 0.5; R^2 = 0.65), and show moderate dispersion [root mean square error (RMSE) = 10.9] (Fig. 4). The residuals from all predictions were normally distributed with homoscedastic variance, though with some tendency to overestimate tree cover in dry systems and underestimate it at the wetter end of the rainfall gradient (Fig. 4).

Impacts of perturbation across rainfall zones

At the continental scale, MAP defines the functional base line for tree cover, while the perturbations increase or, more generally, decrease that tree cover depending on the intensity of the various perturbation factors. We analysed the average effect of the perturbations at different MAP levels. For this purpose, we divided the MAP range (0–2200 mm) into classes of 100 mm and, for each one, calculated the average values of the perturbations and their modifying effects with respect to the rainfall-driven tree cover U. Figure 5 shows the trends for each perturbation and their summed effects. Maximum fire frequencies occur in the semi-arid and mesic savannas (800–1500 mm; Fig. 5a) and lead, on average, to 20–25% (–0.2 to –0.25) suppression of the rainfall-driven tree cover. Human population (Fig. 5c) in savannas does not exceed an average density (averaged within each rainfall interval) of more than about 30 people per km^2 and its largest negative effect (–0.17 to –0.23) on tree cover occurs in areas with MAP higher than 600 mm. Cattle density (Fig. 5d) reaches its highest averaged value of 16 cattle per km^2 at 800 mm MAP, where it decreases the rainfall-driven tree cover by about –0.15. For MAP < 700 mm, cattle density appears to have a stronger negative effect than fire, but both effects are relatively limited in the drier savannas. The suppressive action of fire increases

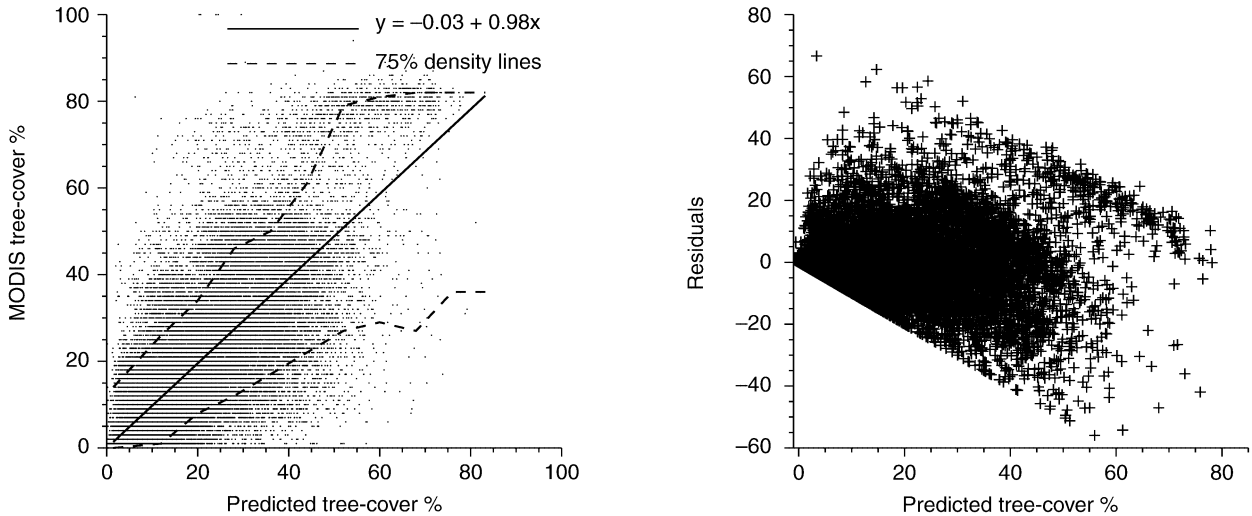

Figure 4 Left panel: percentage tree cover predicted by the best-selected model for an independent data set versus MODIS-based percentage tree cover. The solid line represents the linear fit (R^2 = 0.65, RMSE = 10.9%). The dashed lines enclose 75% of points, indicating the degree of spread around the linear fit. Right panel: residuals versus predicted tree cover for the pilot sample based on the best model equation. The sharp line cutting the lower portion of the distribution corresponds to the large subset of points classified with zero percentage tree cover in the MODIS-based map, but predicted with values > 0 by the best selected model. We verified the normality of the residuals by examining quantile–quantile plots and histograms.

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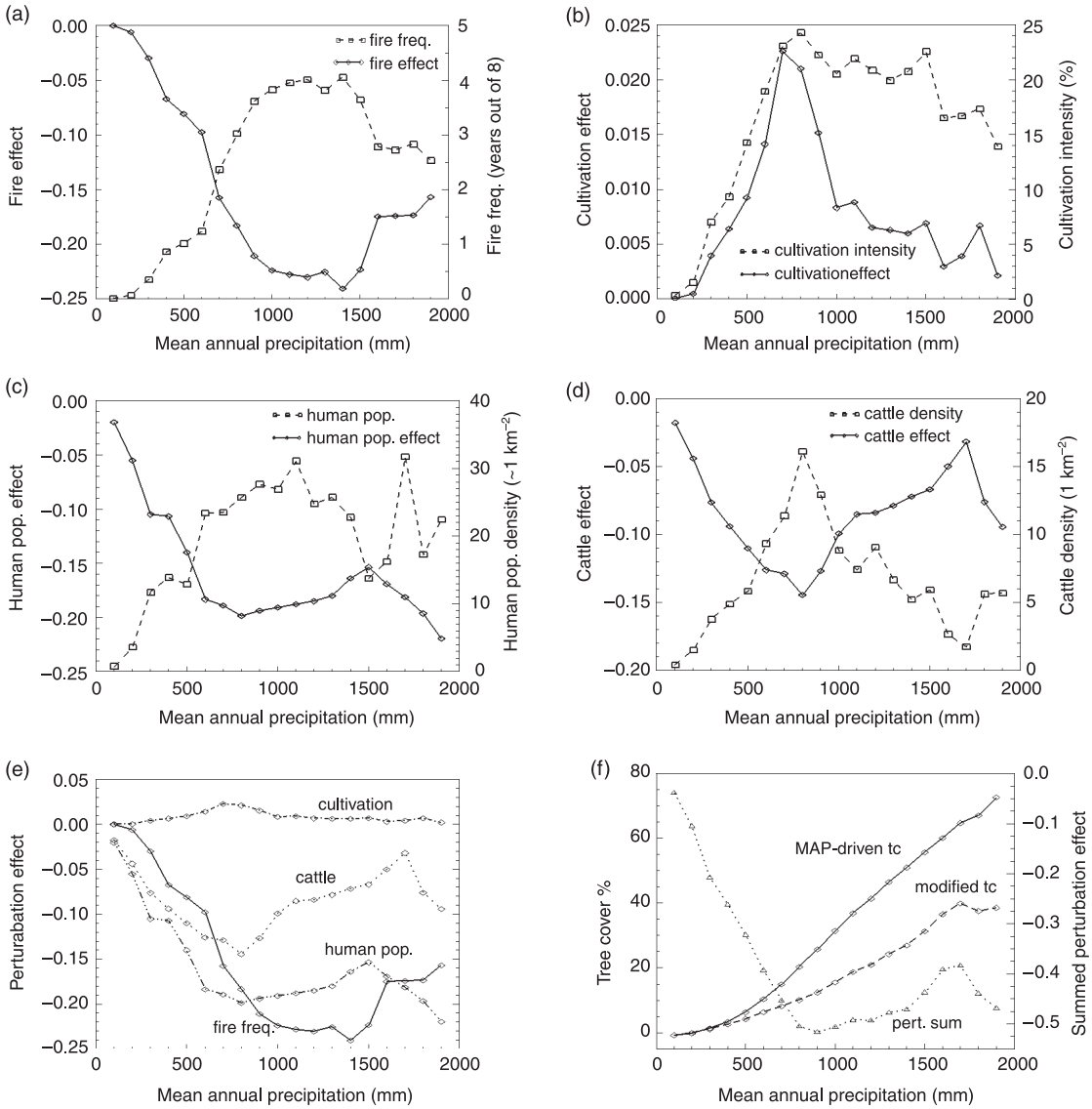

Figure 5 Perturbations in relation to mean annual precipitation (MAP). The top four panels (a), (b), (c) and (d) report the averages of the perturbation intensities (v, eqn 2) and the averages of the nonlinear perturbation effects ($-\alpha v^{\beta}$, eqns 2 and 3) for each rainfall zone. The perturbation effects are hence given as fraction of loss (fire frequency, human population and cattle density) or gain (cultivation) with respect to the rainfall-driven tree cover. Panel (e) shows the averaged perturbation effects and (f) shows the averaged rainfall-driven tree cover for each rainfall zone and the modified tree cover resulting from the zonally averaged summed effects of the perturbations.

between 800 and 1500 mm MAP where fire becomes a more important factor in reducing zone-averaged tree cover than human population (Fig. 5e). The positive effect of cultivation (Fig. 5b) is generally small, never surpassing a proportion of 0.024 of the rainfall-driven tree cover, which corresponds to a 0.4% increase in actual tree cover at 700 mm. Figure 5(f) compares the rainfall-driven tree cover to the modified tree cover and highlights the fact that the perturbing agents have a relatively minor influence when MAP < 400 mm, but they become increasingly important in determining actual tree cover as MAP increases above 600 mm in both relative (reduction with respect to the climate-driven tree cover) and absolute (percentage reduction in tree cover) terms.

Model robustness

Statistical analysis and model fitting should be relatively insensitive to the sample data used for the analysis and model parametrization. We performed the model selection analysis on 10 independent random samples of 13,416 points (the same number of points as the pilot sample) from the continental data set. We tallied the proportion π_i of samples for which model i was selected as the best model among the 10 data sets. The first four models selected using the pilot sample (Table 2) were also the top-ranked models across all 10 independent data sets. The same model (eqn 3) was ranked first with a frequency $\pi_1 = 0.5$ and weights $w > 0.76$. Models 2 and 3 were each selected twice as

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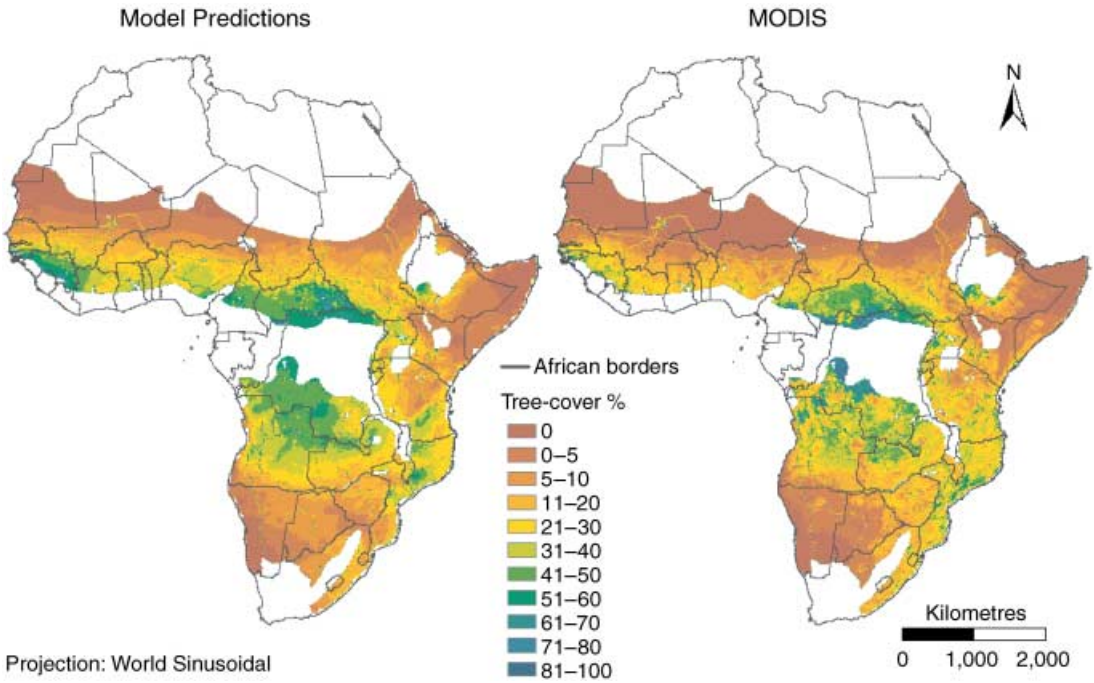

Figure 6 Percentage tree cover in African savannas. Left: model-averaged predictions. Right: values retrieved from the MODIS tree-cover data set (Hansen *et al.*, 2003). The white areas of the maps fall outside the study area [the savanna regions selected according to the biome map (Udvardy, 1975) and a maximum mean annual precipitation threshold of 2200 mm] and were not part of the analysis.

'best' and model 4 was selected once. The parameter estimates of the best models were in general not significantly different from the estimates obtained for the pilot sample. On two occasions the cattle-density effect indicated a weaker grazing effect than in the pilot data set. These results suggest that while there is some sensitivity to the sample data set in the model selection procedure, the balance of evidence supports a model containing all the perturbations, while indicating lower relative importance of the soil nitrogen and cattle-density predictors.

We studied the residuals from the predictions with respect to the savanna bioregions to assess whether model performance varied among the different savanna types. The comparison of residuals suggests that the model performs very well across biomes, with little bias among regions, suggesting that the processes controlling tree cover in these diverse savanna types are similar.

Figure 6 shows predictions of woody cover for the whole of the African savanna region based on the best model parameters obtained using the pilot sample alongside the MODIS tree-cover map. These maps demonstrate the ability of the fitted model to reproduce the broad-scale patterns of tree cover in Africa, but also show that the fine-scale variability is often missed in the model, reflecting in large part the lack of fine spatial resolution information on the long-term intensity and impact of many of the important drivers.

DISCUSSION

Savannas are highly dynamic systems, where stochastic events (e.g. wet or dry years, more or less frequent fires) can have a considerable impact on woody community demographics, from seed production to seedling emergence, seedling and sapling survival, and adult recruitment. Thus woody cover in any single savanna location is strongly contingent on prior conditions, over 1 or 2 years for seedlings and small trees, but over decades for adult trees. Such historical contingency could be used to support the non-equilibrium view of savannas (Ellis & Swift, 1988). That is, savanna structure fluctuates widely, and with no preferred directionality, based on a multi-year history of rainfall and disturbance variability. On the other hand, the analysis of Sankaran *et al.* (2005) showed that maximum woody cover is rainfall-limited in arid and semi-arid areas (< 650 mm MAP) but not in wetter savannas (> 650 mm; Fig. 2). These results were interpreted to suggest that the drier savannas of Africa are climatically 'stable' (canopy closure is prevented by insufficient mean rainfall), while the wetter savannas are 'unstable' (canopy closure and grass exclusion are possible). However, in almost all cases, woody cover is well below the mean climate potential woody cover because of climate variability and disturbance events. Thus, most savanna locations are in a 'disequilibrium' state. During periods of near average climate and low disturbance, such savanna systems presumably relax, with directional preference, towards the climatic potential cover. However, since climatic variability and disturbance are so prevalent in savannas, the probability of a savanna location actually achieving the woody canopy cover corresponding to the mean climate is low.

In this analysis we asked the question: 'what are the processes determining tree cover in African savannas?'. We concentrated on mean rainfall and disturbance statistics across the continent as primary drivers of actual tree cover. We recognize, however, that

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temporal variability (the historical contingency discussed above) in both rainfall and disturbance can have strong effects on local woody community dynamics. The 500-m tree-cover data product based on MODIS observations (Hansen *et al.*, 2003) provided data at an appropriate scale and resolution for discriminating the main features of tree cover in the African savannas. We tested and applied empirical curves that: (1) reflect hypotheses relating the nature of tree–grass interactions in drought-limited systems, and the impact of disturbances such as fire, herbivory and humans, on tree community structure; and (2) were flexible enough to allow the relationships inherent in the data to determine the shape, direction and magnitude of the response functions. Inherent in our approach is the idea that the disequilibrium dynamics and variability discussed above, and the complexity of the driving factors, are such that the processes are difficult to discern using data from a small number of sites. However, by extracting a very large data set from the whole of Africa, representing the full range of climatic, soil and disturbance conditions, we hope to identify and quantify both the mean resource (i.e. rainfall) response and the more stochastic and highly variable disturbance-based responses.

The model with the highest support in the data included a sigmoidal increase in tree cover with MAP and strongly supported all the predictor variables. Thus, at the continental scale, rainfall is a primary driver, but it is not sufficient to explain the observations without accounting for the effect of other factors. The selected model supports a complex behaviour of woody vegetation from which some important general behaviours for the ensemble of African savannas can be extracted.

Three major types of savannas can be defined based on the sigmoidal response to MAP: arid savannas (MAP < 400 mm), where tree cover is low and is relatively insensitive to increasing rainfall; semi-arid/mesic savannas (400 < MAP < 1600 mm), where potential and average tree cover increase rapidly with MAP; and finally mesic/wet savannas (MAP > 1600 mm), where tree cover is high on average, relatively insensitive to MAP and limited by other agents. We obtained a weak response of tree cover to rainfall when MAP < 400 mm. Previous research has shown that the pulse-reserve hypothesis may be particularly relevant for arid systems: woody establishment is driven by non-mean-field precipitation characteristics, such as amounts of rainfall in particularly wet years, or the seasonal distribution or size of individual rain events (Higgins *et al.*, 2000; Fernandez-Illescas & Rodriguez-Iturbe, 2004; Reynolds *et al.*, 2004). In semi-arid areas, MAP sets a tree-cover line around which a large variability is created by perturbations (Fig. 2). In mesic/wet savannas, we observed a weakening of MAP control on tree cover, where the systems would tend to converge to a wooded state and disturbances are essential for the coexistence of trees and grass (Sankaran *et al.*, 2005).

The influence on the climatic relationship of environmental factors such as soil nitrogen and soil texture, while statistically significant, is relatively small. Fine soils appear to support higher tree cover across the rainfall gradient but we were not able to detect the differential benefit of soil texture on woody cover postulated by the 'inverse texture hypothesis' (Noy-Meir, 1973). Furthermore, Sankaran *et al.* (2005) found a weak positive relationship between soil sand content and tree cover in semi-arid and mesic savannas (> 350 mm MAP), which appears to contradict the inverse texture hypothesis and our results. Thus, while the soil water availability considerations of the inverse texture hypothesis may have direct impacts on vegetation productivity (Sala *et al.*, 1988), they appear less directly linked to the competitive interactions, demographic and disturbance dynamics that control woody cover in African savannas. Soil nitrogen appears to have a positive but relatively weak effect on tree cover, increasing it by a few per cent above the moisture-driven level.

The model analysis revealed several relationships between tree cover and the disturbance factors that change with the MAP regime (Fig. 5). Given the nature of the data set and our analyses, we cannot assess causality, but the results provide (correlative) support for hypotheses regarding the role of different processes in controlling vegetation structure. In arid systems, perturbations have little impact on tree cover. In semi-arid and mesic savannas, MAP controls maximum tree cover and perturbations act as modifiers. The cattle density effect is negative and generally less strong than the effects of fire and human population. A small positive contribution to tree cover comes in association with cultivation, but overall the combination of perturbation factors causes a decrease from the rainfall-driven tree cover. In mesic and wet savannas (MAP > 1600 mm), precipitation no longer strongly limits tree cover and thus the combined effects of disturbance factors are most important in determining tree cover, with fire being more effective than humans and cattle in the emergent tree-cover fraction.

The effect of cattle reducing rainfall-driven tree cover was not expected, since grazing is commonly considered to be a major cause of woody encroachment (Jeltsch *et al.*, 1997; Roques *et al.*, 2001). This is mostly observed in areas affected by over grazing (Scholes & Archer, 1997), but the coarse spatial resolution of the cattle data available at continental scales for Africa tends to spatially homogenize density, with only 0.2% of the points having cattle density higher than 50 km^{-2}. Hence the statistical relationship is mainly driven by low-density values (Figs 3 & 5). Moreover, the absence of shrubs in MODIS tree-cover product (Hansen *et al.*, 2003) is likely to make it somewhat insensitive to shrub encroachment *per se*. The important role of wild herbivores in structuring savanna vegetation (Cumming *et al.*, 1997; Scholes & Archer, 1997) could not be analysed in this study because comprehensive data on wild herbivore biomass outside of the major parks are not available. The increase in woody cover with agricultural intensification (Fig. 3) is also counter-intuitive but may correspond to the cultivation and protection of shade and fruit trees on the margins of arable fields. Equally important, particularly in the semi-arid regions where cereal crops (millet, sorghum and maize) and fallow rotations are prevalent, is the possibility that rapid resprouting and recolonization of woody species adapted to cultivated areas (e.g. *Guiera senegalensis* in west Africa) may lead to overall small increases in the woody cover of the agricultural areas. Direct cultivation of economically important tree crops such as karite (*Butyrospermum parkii*) and gum Arabic (*Acacia senegal*) in the drier (e.g. Sahelian and

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Sudanian) regions, or fruit and beverage plantations in the wetter regions (> 1800 mm MAP), may also play a role in this relationship.

The MODIS tree-cover data set was created using a supervised regression tree approach (Hansen *et al.*, 2002) and therefore contains spatial and numerical noise and error. The reported standard error of estimates varies from 8 to 18%, which is similar to the residuals of our best models. A particular limitation of the MODIS tree-cover data set, however, is that woody plants less than 5 m in height were not included in the ground calibration data sets and hence the product tends to underestimate woody cover in savannas where shrubs are common. This may explain the presence of zero or near-zero tree cover in the MODIS data set in areas where we might expect woody plants to be present in greater abundance (e.g. the southern Kalahari and eastern Namibia). This omission may explain why our predicted tree-cover values have a tendency to overestimation at the low range of MAP. We also tend to underestimate tree cover, relative to the satellite observations, in high-rainfall areas surrounding the moist tropical forests of the Congo Basin (MAP *c.* 2000 mm; Figs 4 & 6). It appears that our model is less effective in these forest–savanna transition zones, possibly because of changing relationships with the various biotic and abiotic factors.

This work relates to the recent study by Sankaran *et al.* (2005), who used data from 850 field sites (*c.* 0.25–0.5 ha) across the African continent. We included their quantile regression line as one of the candidate models for this analysis, but it provided overall model fits that were far less efficient in representing the data than the sigmoid curves. As discussed above, the selected sigmoid curves do not predict a maximum, but rather predict the MAP-dependent cover. In fine-scale data sets, such as the Sankaran *et al.* (2005) study, local heterogeneity (dense or sparse locations) is likely to be more important than in the relatively coarse scale (500 m = 25-ha pixels) of the MODIS data used here. Nevertheless, the MODIS data do show a small number of locations with tree cover matching the maximum MAP line of the Sankaran *et al.* (2005) study (Fig. 2), suggesting underlying agreement between the data sets despite the scale mismatch.

This study confirms the need to look at savannas as systems with multiple dynamic behaviours that only a combination of the resource- and perturbation-based theories can interpret. However, due to the statistical nature of this analysis, we cannot resolve specific mechanisms behind the data trends. The unexplained 44% variability in the data is probably related to data quality issues, and our failure to include certain processes and mechanisms that occur at very fine (patch-landscape) scales. As noted by other authors (Gillson, 2004; Wiegand *et al.*, 2006), research at multiple scales may provide a better understanding of the roles of rainfall (amount and variability), landscape-scale processes and both local and broad-scale perturbations in determining tree cover. It seems very likely that the complexity of tree-cover patterns observable at different scales is an emergent property of different factors, processes and interactions in the progression from plant and patch scales, through landscape to regional and continental scales.

CONCLUSION

Savanna ecosystems comprise coexisting herbaceous and woody vegetation forming a continuum between grassland with few scattered shrubs and trees to closed canopy woodland with few grasses. Recognition of the determinants, interactions and dynamics creating and maintaining tree–grass mixtures has been a challenge for ecologists who have developed varied theories. The conceptual framework and the character of the models developed here (intermediate between mechanistic and phenomenological) offer an integrative attempt to build our understanding of vegetation structure in savanna at very coarse (continental) scales.

The selected model was able to identify some of the controls and the processes that create coarse-scale patterns of tree cover in African savannas and explained 66% of observed variance. Given relatively coarse spatial resolution of some data sets, the predictions were not able to capture all of the tree-cover heterogeneity at finer scales seen in the MODIS tree cover (Fig. 6). Furthermore, our analysis inherits any errors or biases inherent in the tree-cover data. We cannot improve on that data set with our models but we can use the MODIS data to provide a very large sample of data from across the continent and examine relationships and patterns that are difficult, if not impossible, to discern within one region or across a small number of sites.

Our work confirms the need for a synthetic approach to explain the coexistence of trees and grass based on both resource limitation and disturbance dynamics. Together with the large literature on savanna dynamics and tree–grass interactions at the site scale, this research provides some new understanding of the relative importance and interaction of environmental and disturbance factors that create the broad spatial patterns of tree cover observed in savannas across Africa. Whether these patterns will hold for other tropical savannas, or the mixed tree–grass systems of temperate latitudes, remains open to further research.

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