LETTERS

Determinants of woody cover in African savannas

Mahesh Sankaran[1], Niall P. Hanan[1], Robert J. Scholes[2], Jayashree Ratnam[1], David J. Augustine[3], Brian S. Cade[4], Jacques Gignoux[5], Steven I. Higgins[6], Xavier Le Roux[7], Fulco Ludwig[8], Jonas Ardo[9], Feetham Banyikwa[10], Andries Bronn[11], Gabriela Bucini[1], Kelly K. Caylor[12], Michael B. Coughenour[1], Alioune Diouf[13], Wellington Ekaya[14], Christie J. Feral[15], Edmund C. February[16], Peter G. H. Frost[17], Pierre Hiernaux[18], Halszka Hrabar[19], Kristine L. Metzger[20], Herbert H. T. Prins[21], Susan Ringrose[22], William Sea[1], Jörg Tews[23], Jeff Worden[1] & Nick Zambatis[24]

Savannas are globally important ecosystems of great significance to human economies. In these biomes, which are characterized by the co-dominance of trees and grasses, woody cover is a chief determinant of ecosystem properties[1–3]. The availability of resources (water, nutrients) and disturbance regimes (fire, herbivory) are thought to be important in regulating woody cover[1,2,4,5], but perceptions differ on which of these are the primary drivers of savanna structure. Here we show, using data from 854 sites across Africa, that maximum woody cover in savannas receiving a mean annual precipitation (MAP) of less than ~650 mm is constrained by, and increases linearly with, MAP. These arid and semi-arid savannas may be considered 'stable' systems in which water constrains woody cover and permits grasses to coexist, while fire, herbivory and soil properties interact to reduce woody cover below the MAP-controlled upper bound. Above a MAP of ~650 mm, savannas are 'unstable' systems in which MAP is sufficient for woody canopy closure, and disturbances (fire, herbivory) are required for the coexistence of trees and grass. These results provide insights into the nature of African savannas and suggest that future changes in precipitation[6] may considerably affect their distribution and dynamics.

Savannas occupy a fifth of the earth's land surface and support a large proportion of the world's human population and most of its rangeland, livestock and wild herbivore biomass[1]. A defining feature of savanna ecosystems is the coexistence of trees and grasses in the landscape[1]. The balance between these two life forms influences both plant and livestock production, and has profound impacts on several aspects of ecosystem function, including carbon, nutrient and hydrological cycles[1–3,7]. The mechanisms that promote tree–grass coexistence and the factors that determine the relative proportions of these two life forms across different savanna types remain, however, unclear[1,2,4,5]. Because savannas are anticipated to be among the ecosystems that are most sensitive to future changes in land use and climate[8–10], a thorough understanding of factors that structure savanna communities is urgently required to guide management efforts[2,4].

Explanations for the persistence of tree–grass mixtures in savannas are varied and invoke such different mechanisms as competition for water and nutrients[11–13], demographic bottlenecks to tree recruitment[5,14], and disturbances including fire[1,5,14–17] and large mammal herbivory[15,16,18]. Empirical studies provide support both for and against each alternative mechanism and, consequently, perceptions differ on the relative importance of resource limitation versus disturbances in controlling savanna structure[1,2,4,5]. The lack of consensus arises, in part, because most studies have been small-scale and site-specific, and have often focused on a single determinant[2]. But savanna systems are diverse and occur under a wide range of bioclimatic conditions[2], and it is likely that the importance of different processes in regulating woody cover may vary in different savanna regions. Thus, a comprehensive model that explains both coexistence and the relative productivity of tree and grass components across diverse types of savanna is unlikely to arise from studying individual systems in isolation: it requires a synthesis of data from savannas across broad environmental gradients[2,4].

Here we use a continental scale analysis of African savannas to investigate how the relative importance of resource availability (water, nutrients) and disturbance regimes (fire, herbivory) in regulating woody cover varies across broad environmental gradients. In particular, we are interested in determining whether broad-scale trends in savanna structure are indicative of 'stable' or 'unstable' dynamics[1], or whether savannas show elements of both across their geographic range of occurrence. We use 'stable' in a limited sense to mean that coexistence of trees and grasses in savannas is not dependent on disturbances such as fire and mammalian herbivory, while recognizing that woody community biomass and cover are dynamic, not static, properties of the system.

Specifically, we considered that if water availability is the primary determinant of woody cover in savannas[11–13], then precipitation

[1]Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA. [2]Division of Forest Science and Technology, CSIR, PO Box 395, Pretoria 001, South Africa. [3]USDA Forest Service, Commanche National Grassland, PO Box 12, Springfield, Colorado 81073, USA. [4]US Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80526-8818, USA. [5]Ecole Normale Superieure, Laboratoire d'ecologie, UMR 7625 CNRS, Université de Paris 6 ENS, 46 Rue d'Ulm, 75230 Paris Cedex 05, France. [6]Umweltforschungszentrum Leipzig Halle, Sekt Okosyst Anal, Permoserstrasse 15, D-04318 Leipzig, Germany. [7]Microbial Ecology Laboratory, UMR 5557 CNRS, Université Lyon 1 USC INRA 1193, Bâtiment G. Mendel, 43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne, France. [8]CSIRO Centre for Environment and Life Sciences, CSIRO Plant Industry, Private Bag 5, Wembley, Western Australia 6913, Australia. [9]Department of Physical Geography and Ecosystems Analysis, Lund University, Sölvegatan 12, 223 62 Lund, Sweden. [10]Department of Botany, University of Dar es Salaam, PO Box 35060, Dar es Salaam, Tanzania. [11]Department of Agriculture and Game Management, Private Bag X6011, Port Elizabeth Technikon, Port Elizabeth 6000, South Africa. [12]Department of Civil & Environmental Engineering, Princeton University, Princeton, New Jersey 08544, USA. [13]Centre de Suivi Ecologique, BP 15532, Dakar, Senegal. [14]University of Nairobi, Department of Range Management, PO Box 29053, Nairobi, Kenya. [15]Environmental Sciences Department, University of Virginia, PO Box 400123, 291 McCormick Road, Charlottesville, Virginia 22904-4123, USA. [16]Department of Botany, University of Cape Town, University Private Bag, Rondebosch 7700, South Africa. [17]Institute of Environmental Studies, University of Zimbabwe, PO Box MP 167, Mount Pleasant, Harare, Zimbabwe. [18]CESBIO, 18 Avenue E. Belin, 31401 Toulouse Cedex 9, France. [19]Mammal Research Institute, University of Pretoria, Pretoria 002, South Africa. [20]Department of Zoology, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin 53706, USA. [21]Resource Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands. [22]Harry Oppenheimer Okavango Research Centre, University of Botswana, Private Bag 285, Maun, Botswana. [23]University of Potsdam, Institute of Biochemistry & Biology, Plant Ecology & Nature Conservation, Maulbeerallee 2, D-14469 Potsdam, Germany. [24]Scientific Services, Kruger National Park, Private Bag X402, Skukuza 1350, South Africa.
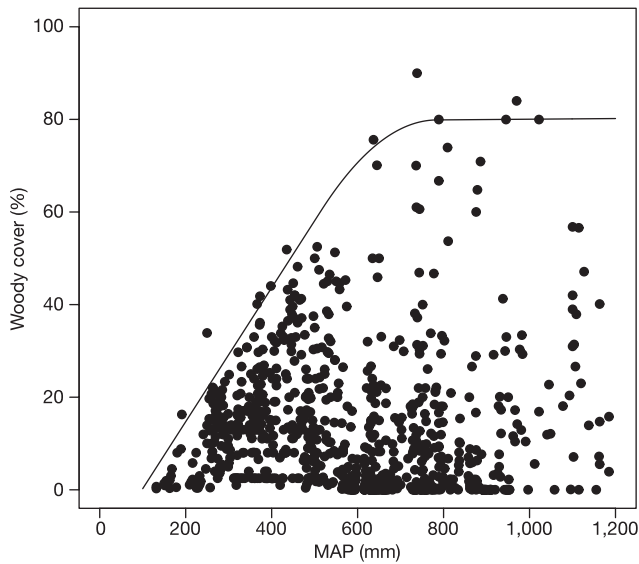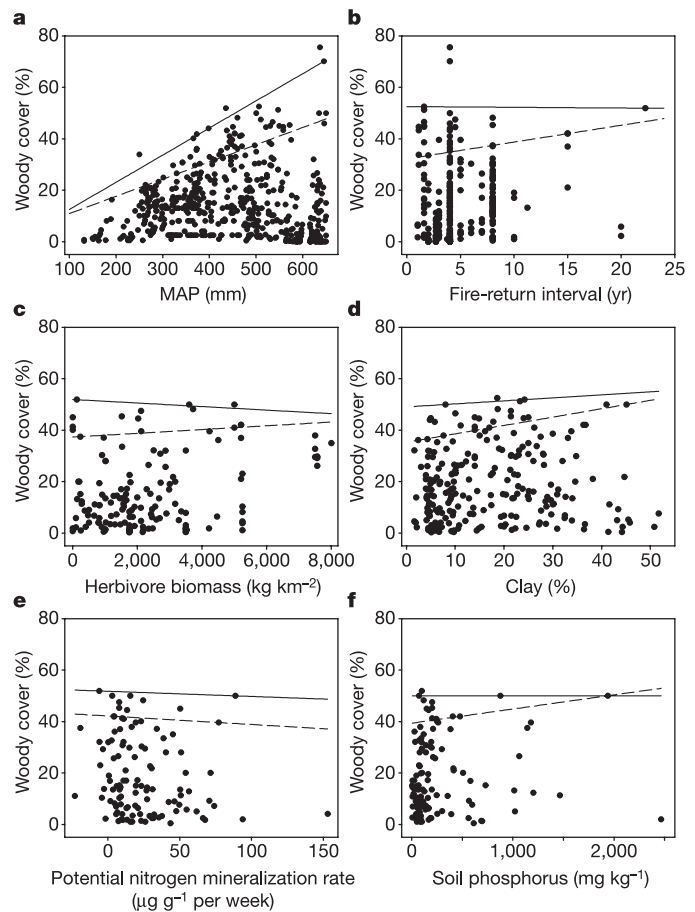
Figure 1 | Change in woody cover of African savannas as a function of MAP. Maximum tree cover is represented by using a 99th quantile piece-wise linear regression. The regression analysis identifies the breakpoint (the rainfall at which maximum tree cover is attained) in the interval 650 ± 134 mm MAP (between 516 and 784 mm; see Methods). Trees are typically absent below 101 mm MAP. The equation for the line quantifying the upper bound on tree cover between 101 and 650 mm MAP is $Cover(\%) = 0.14(MAP) - 14.2$. Data are from 854 sites across Africa.


Figure 2 | Woody cover as a function of MAP, soil properties and disturbance regimes in arid and semi-arid savannas. Relationships between woody cover and MAP (**a**; $n = 529$), fire-return intervals (**b**; $n = 302$), herbivore biomass (**c**; $n = 145$), percentage of clay (**d**; $n = 234$), nitrogen mineralization potential (**e**; $n = 109$) and soil total phosphorus (**f**; $n = 118$) for savannas receiving <650 mm MAP. Unbroken and broken lines represent the 99th and 90th linear quantiles, respectively. Maximum woody cover increased with MAP, but showed no consistent relationship with other variables. For MAP, both quantile slopes were significantly different from zero. For fire-return intervals, herbivore biomass, clay and nitrogen mineralization rates, neither regression line had a significant non-zero slope. For total phosphorus, the 90th but not the 99th quantile slope differed from zero.

should limit the potential tree cover that can be supported at any given site, and maximum realizable woody cover should gradually increase with MAP[4,12]. By contrast, if disturbances such as fire and herbivory primarily maintain savannas[4,5,15], then we expect an abrupt, rather than gradual, increase in maximum realizable woody cover with increasing MAP[4]: below a critical threshold of rainfall sufficient to permit tree growth outside riparian areas or depressions, grasslands should dominate; above this threshold, the maximum woody cover should correspond to a closed-canopy woodland state[4]. Depending on the level of disturbance, a particular location might have reduced woody cover, but the upper bound would not depend on MAP.

We evaluated relationships between woody cover and MAP, soil characteristics (texture, percentage nitrogen, nitrogen mineralization, total phosphorus) and disturbance regimes (fire-return intervals, mammalian herbivore biomass) from 854 sites across Africa (Supplementary Fig. S1 and Methods). Woody cover ranges from 0 to 90% across sites and tends to increase with MAP (Fig. 1). More particularly, within a narrow range of MAP from ~100 to 650 mm, an upper bound exists on the maximum realizable woody cover (Fig. 1). In these arid to semi-arid sites ($<650 \pm 134$ mm MAP; see Fig. 1), maximum realized woody cover increases with MAP (Fig. 2a), but shows no relationship with fire-return intervals, herbivore biomass or soil characteristics (Fig. 2b–f), suggesting that the observed upper limit on woody cover in arid and semi-arid African savannas is primarily a consequence of moisture limitation. The presence of an upper bound on woody cover in these savannas that is linked primarily to MAP is not consistent with the view that savannas are inherently unstable systems maintained by disturbances.

Within this MAP range ($<650 \pm 134$ mm MAP), our analysis suggests that tree–grass coexistence is stable to the extent that disturbances such as fire and herbivory, although capable of modifying tree to grass ratios, are not necessary for coexistence. In these "climatically determined savannas"[17] ($<650 \pm 134$ mm MAP), restrictions on maximum woody cover as a result of water limitation permit grasses to persist in the system. By contrast, in areas that

receive a MAP in excess of 650 ± 134 mm, water availability seems to be sufficient to allow trees to approach canopy closure such that grasses may be effectively excluded. These "disturbance-driven savannas"[17] represent unstable systems in which disturbances such as fire, grazing and browsing are required to maintain both trees and grasses in the system by buffering against transitions to a closed-canopy state[5,17].

Whereas MAP drives the upper bound on woody cover in arid and semi-arid savannas, disturbance regimes and soil characteristics impose significant controls on savanna structure by influencing woody cover below the bound. A regression tree analysis of mean woody cover for a restricted subset of sites for which all data were available (Fig. 3 and Methods) further highlights the importance of MAP as a principal driver of savanna structure and suggests that MAP also mediates the relative importance of other savanna drivers such as fire and soil characteristics.

Below a MAP of ~350 mm, woody cover is typically low (Fig. 3). In these sites, soil properties and disturbances such as fire and herbivory rarely regulate woody cover. As MAP increases above this threshold, fire in particular becomes a common factor that reduces woody cover
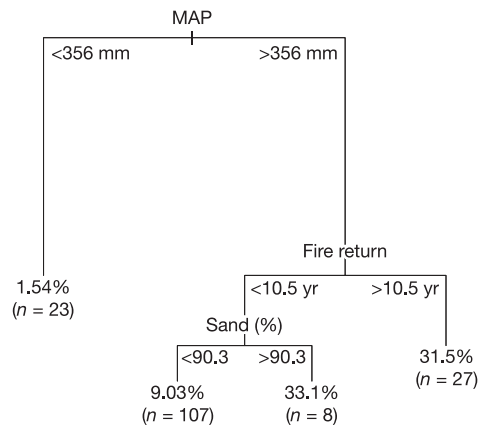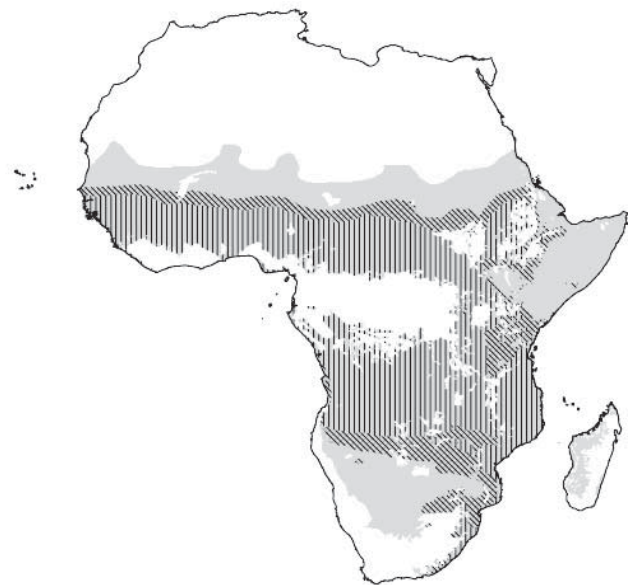
Figure 3 | **Regression tree showing generalized relationships between woody cover and MAP, fire-return interval and percentage of sand.** The tree is pruned to four terminal nodes and is based on 161 sites for which all data were available. No consistent herbivore effects were detected. Branches are labelled with criteria used to segregate data. Values in terminal nodes represent mean woody cover of sites grouped within the cluster. The pruned tree explained ~45.2% of the variance in woody cover, which is significantly more than a random tree ($P < 0.001$). Of this, 31% was accounted for by the first split; the second split explained an additional 10% of the variance in woody cover.

Figure 4 | **The distributions of MAP-determined ('stable') and disturbance-determined ('unstable') savannas in Africa.** Grey areas represent the existing distribution of savannas in Africa according to ref. 30. Vertically hatched areas show the unstable savannas (>784 mm MAP); cross-hatched areas show the transition between stable and unstable savannas (516–784 mm MAP); grey areas that are not hatched show the stable savannas (<516 mm MAP).

below the MAP-controlled upper bound (Fig. 3). Woody cover is higher, on average, where fires are infrequent (fire-return interval >10.5 yr). In sites with more frequent fires, woody cover is typically low, except on very sandy soils (mostly concentrated on the Kalahari sand sheets), which tend to support higher woody cover (Fig. 3). The dependence of fire frequency on MAP presumably arises because increased grass production in mesic sites leads to greater fuel loads that can support more frequent fires[14] (Supplementary Fig. S2). Very high sand content, which correlates with low nutrient availability (Supplementary Table S1), may promote higher woody cover if the positive effects of coarse-textured soils, such as lower wilting points[19] and greater water percolation to soil layers below grass rooting depths[1,11,12], override the negative effects associated with lower nutrient availability in these soils[19].

Herbivore effects on woody cover are, however, less apparent. Although we found a tendency for grazers to enhance woody cover and browsers and mixed feeders to depress it, such effects were weak and could not be generalized beyond our data set (see Methods; measures of herbivore biomass were retained in the complete, but not pruned, regression tree). The lack of consistent herbivore effects across sites most probably reflects differences in herbivore guilds, seasonality of herbivory, and variation in herbivore body-size distributions across sites, features for which data were not available. Larger, more detailed data sets will undoubtedly provide greater resolution of how different driver variables interact to influence mean woody cover.

These results have the power to inform savanna management strategies because they bear directly on our ability to predict savanna responses to changing environmental drivers. In particular, our data indicate that woody encroachment, a phenomenon in which many savannas across the world show a directional trend of increasing woody cover[1], may be a bounded process in savannas receiving a MAP of <650 ± 134 mm, ultimately limited by water availability. For sites close to or at the MAP-controlled bound (Fig. 1), changes in precipitation regimes that lead to increased water availability[6] therefore may be a cause for concern with respect to woody encroachment. However, the enormous variation in woody cover, with most sites far from the climatic bound (Fig. 1), suggests that processes other than MAP regulate actual tree cover in many savannas of Africa. In particular, our results suggest that if disturbances by fire, browsers

and humans were absent, then large sections of the African continent would switch to a wooded state (hatched regions in Fig. 4).

The patterns described here for African savannas suggest that the dominant ecological theories for tree–grass coexistence in these systems need to be combined: it is clear that most savannas are strongly affected by disturbances that maintain woody cover well below the resource-limited upper bound. Disturbance-based models do not consider and are unable to explain, however, the upper bound to tree cover. The results emerging from this continental scale analysis strongly indicate that water limits the maximum cover of woody species in many African savanna systems, but that disturbance dynamics control savanna structure below the maximum. These results have important implications both for our understanding of the fundamental nature of African savanna systems and for our ability to predict their responses to changing environmental drivers. It remains to be established whether the patterns observed here for African savannas also hold in other tropical savanna regions or in temperate savannas where the effects of winter precipitation and temperature on moisture distribution through the soil profile can markedly alter water partitioning between woody and herbaceous plants, and thus can influence maximum woody cover.

METHODS
Data collection. Data on projected woody cover (the percentage of ground surface covered when crowns are projected vertically), MAP, soil characteristics (texture, total nitrogen and phosphorus, and nitrogen mineralization), fire and herbivory regimes were gathered from several sources for a range of sites across Africa. We included only sites for which vegetation was sampled over sufficiently large spatial scales (>0.25 ha for plot measurements and >100 m for transect sampling). Sites located in riparian or seasonally flooded areas, or in net water run-on areas such as depressions, and sites in which trees were known to access ground water resources (that is, sources of water not dependent on rainfall in the immediate vicinity or in recent years) were excluded from the analysis because MAP is not a relevant descriptor of water availability in these sites. We also excluded sites that had been cultivated or harvested by humans <10 yr before sampling from the analysis.

Rainfall data included estimates from field measurements and regional rainfall maps ($n = 469$) and from fitted climatic grids (0.05° resolution,

$n = 383$) of monthly mean rainfall for Africa from the ANU-CRES (ref. 20; http://www.ncgia.ucsb.edu/conf/SANTA_FE_CD-ROM/santa_fe.html and http://cres.anu.edu.au/outputs/africa.php). Fire-return periods were obtained from field records ($n = 182$) and from burnt-area maps of Africa at 5-km resolution ($n = 670$) derived from AVHRR (advanced very high resolution radiometer) images based on 8 yr of data (1981–1983 and 1985–1991; ref. 21). Herbivore density estimates were available for 180 sites. Soils were obtained from 166 sites and analysed under standardized laboratory conditions for texture, total nitrogen and phosphorus, and nitrogen mineralization potential (see Supplementary Information). Our data set included sites encompassing a wide range of rainfall (132–1,185 mm MAP), fire-return intervals (1 to >50 yr), herbivore biomass (0–8,000 kg km^{-2}), soil texture (sand, 6.7–98%; clay, 0.6–62.8%), soil percentage nitrogen (0.013–0.31%), soil total phosphorus (5–1,465 µg g^{-1}) and potential nitrogen mineralization rates (−22.8 to 153 µg g^{-1} per week; see Supplementary Fig. S3).

Data analyses. To characterize the effects of MAP on the upper limit to woody cover across sites, we analysed data using a bent-cable form of a piece-wise linear model[22] estimated with nonlinear quantile regression[23], as implemented in the 'quantreg' library in the statistical package R (http://www.r-project.org/). We used 0.90 to 0.99 conditional quantiles to obtain estimates near the upper boundary of the percentage of woody cover as it changes with MAP, which better reflects the process of MAP limiting maximum woody cover than does mean regression[24] (see Supplementary Information for details of this and additional analyses). We conducted additional analyses on the subset of sites that received <650 mm rainfall annually to investigate further how fire regimes, herbivory and soil properties influenced the upper bound on woody cover that was evident in these sites. We analysed these data by linear quantile regression[25], as implemented in the 'quantreg' library, which permits computation of confidence intervals for estimated parameters[26] and enabled us to test whether the regression slopes were different from zero.

In addition to analysing patterns in maximum woody cover, we used regression tree analysis[27], as implemented in the 'rpart' library in R, to determine how resource availability and disturbance regimes influenced mean realized woody cover in sites (see Supplementary Information). After tree construction, cross-validation procedures were used to prune trees to a size that best represented relationships that could be generalized outside the sample to the rest of the continent[28]. Woody cover values were log-transformed to stabilize variances[28]. To avoid problems arising from collinearity among soil variables, only sand content was retained for the analysis as it was the variable that was most strongly correlated to other soil variables (Supplementary Table S1). The results of the analysis were unchanged if grazer biomass and mixed feeder plus browser biomass were retained as two separate variables, or if total herbivore biomass was used as the predictor variable. The analysis was based on 161 sites for which data on MAP, fire-return intervals, herbivore biomass density and soil sand content were available. To determine whether the pruned tree explained more variance than a random tree of equal complexity, the square of the correlation coefficient (r^2) of the pruned tree was compared with r^2 values of similar sized trees generated from 2,000 random associations between predictor variables and woody cover[29]. Further details on the methodology and results from additional analyses are provided in the Supplementary Information.

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