
Deciphering the distribution of the savanna biome

Author(s): Caroline E. R. Lehmann, Sally A. Archibald, William A. Hoffmann and William J. Bond

Source: *The New Phytologist*, July 2011, Vol. 191, No. 1 (July 2011), pp. 197-209

Published by: Wiley on behalf of the New Phytologist Trust

Stable URL: <https://www.jstor.org/stable/20869154>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/20869154?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

New Phytologist Trust and Wiley are collaborating with JSTOR to digitize, preserve and extend access to *The New Phytologist*

Deciphering the distribution of the savanna biome

Caroline E. R. Lehmann^{1,5}, Sally A. Archibald², William A. Hoffmann³ and William J. Bond⁴

¹School for Environmental Research, Charles Darwin University, Darwin, NT 0909, Australia; ²Natural Resources and the Environment, CSIR, PO Box 395, Pretoria, South Africa; ³Department of Plant Science, North Carolina State University, Raleigh, NC, 27695, USA; ⁴Department of Botany, University of Cape Town, Rondebosch, 7701, South Africa; ⁵Present address: Department of Biological Sciences, Macquarie University, NSW 2109, Australia

Summary

Author for correspondence:

Caroline Lehmann

Tel: +61 2 9850 6270

Email: caroline.lehmann@mq.edu.au

Received: 16 December 2010

Accepted: 28 January 2011

New Phytologist (2011) **191**: 197–209

doi: 10.1111/j.1469-8137.2011.03689.x

Key words: alternate stable states, C₄ grasses, fire, flammability, forest, herbivory.

- We aimed to identify the limits of savanna across Africa, Australia and South America. We based our investigation on the rich history of hypotheses previously examined: that the limits of savanna are variously determined by rainfall, rainfall seasonality, soil fertility and disturbance.
- We categorized vegetation on all continents as 'savanna' (open habitats with a C₄ grass layer) or 'not-savanna' (closed habitats with no C₄ grass layer) and used a combination of statistical approaches to examine how the presence of savanna varied as a function of five environmental correlates.
- The presence of savanna is constrained by effective rainfall and rainfall seasonality. Soil fertility is regionally important, although the direction of its effect changes relative to rainfall. We identified three continental divergences in the limits of savanna that could not be explained by environment.
- Climate and soils do not have a deterministic effect on the distribution of savanna. Over the range of savanna, some proportion of the land is always 'not-savanna'. We reconciled previous contradictory views of savanna limits by developing a new conceptual framework for understanding these limits by categorizing environmental factors into whether they had a positive or negative effect on woody growth and the frequency of disturbance.

Introduction

Understanding the factors that govern the distributions of biomes is a fundamental challenge for plant ecology. In the case of tropical savannas, the task is particularly difficult because of multiple interacting factors. Climate, hydrology, herbivory, fire and soil characteristics can all influence the distribution of savanna (Tinley, 1982; Furley, 1992; Hopkins, 1992; Ruggiero *et al.*, 2002; Bond, 2008). However, we lack a conceptual framework for understanding how these interact to determine the limits of the savanna biome.

Tropical savannas are mixed tree–C₄ grass systems that occur across *c.* 20% of the terrestrial surface (Scholes & Hall, 1996). Savannas and C₄ grasslands became prominent features of tropical landscapes *c.* 6–8 Mya as a result of a rapid global increase in the dominance of C₄ grasses (Cerling *et al.*, 1997). In some regions, C₄ grasses replaced pre-existing C₃ grasslands (Strömberg, 2004). However, C₄ grasslands also displaced forests, thickets and shrublands, biomes that coexist with savanna in modern landscapes, and define the modern limits of savannas (Keeley & Rundel,

2005). Interconversion between savanna and these other vegetation types occurs today, often in response to human activity (Bond & Parr, 2010). Large areas of tropical savanna and grasslands have been encroached by trees or shrubs (Asner *et al.*, 2004; Wigley *et al.*, 2009), whereas elsewhere forests have been invaded by grasses as a result of fire (Barlow & Peres, 2008).

In this article, we consider savanna to include any system with a continuous layer of C₄ grasses, regardless of whether trees are present. Shrublands, thickets and forests are referred to collectively as 'closed-canopy ecosystems', even if they do not possess a truly closed canopy. The defining characteristic of these systems is that the cover of woody plants is sufficiently dense to shade out C₄ grasses.

In distinguishing between savanna and closed-canopy ecosystems, we emphasize the presence or absence of C₄ grasses because of their unique biology, which has important consequences for vegetation dynamics (Bond & Midgley, 2000; Sage & Kubien, 2003; Keeley & Rundel, 2005; Bond, 2008; Leakey, 2009). C₄ grasses dominate in areas of high growing season temperatures (Sage, 2004). In

such climates, C_4 grasses are extremely productive if ample light is available, permitting the rapid accumulation of highly flammable fuels. However, C_4 grasses are physiologically incapable of dominating the low-light environment of closed-canopy ecosystems because of the metabolic costs of C_4 photosynthesis (Sage & Kubien, 2003). The combination of high productivity, high flammability and shade intolerance causes C_4 grasses to play a critical role in mediating the transition between savanna and closed-canopy ecosystems.

In savanna, the likelihood of fire is influenced by the traits of the vegetation. A high density of grasses permits frequent fire, which, in turn, maintains an open canopy, thereby promoting C_4 grasses, and initiating a positive feedback between savanna and fire (Beckage *et al.*, 2009). By contrast, a closed-canopy state, in which C_4 grasses are excluded, creates a humid microclimate, and thus also greatly reduces the flammability of the vegetation (Ray *et al.*, 2005). These closed-canopy habitats therefore resist burning, allowing them to persist in close proximity to frequently burned savanna (Bowman, 2000). The absence of grasses is critical for the low flammability of these systems, so that the canopy density at which grasses are excluded represents a critical threshold in the transition from one state to another. Although we understand the physical constraints to C_4 grass growth, we lack a theoretical framework of why mixed tree– C_4 grass systems dominate across the tropical zone, and where and why they are replaced by closed-canopy formations across the range of savanna.

There have been numerous attempts to identify the environmental limits of savanna. Nix (1983), drawing on information from South America, identified a range of 1000–1500 mm mean annual rainfall within which savannas dominate. Stott (1988) identified a range of 800–2000 mm mean annual rainfall and a dry season of 5–7 months within which savanna dominates in South-East Asia. Scholes & Walker (1993) moved away from precise rainfall limits and identified a monthly mean temperature of $> 10^\circ\text{C}$ throughout the year, a wet season warmer than the dry season, at least 60 d where there is enough moisture for plant growth and at least 60 d where there is not enough moisture for plant growth. Schimper (1903) and Sarmiento (1984) considered that rainfall seasonality, via water limitations to forest plant growth, prevented closed-canopy formations from occurring. Lloyd *et al.* (2008) suggested that rainfall seasonality is important in extending grass dominance into arid systems. Low soil fertility has been considered by many as promoting savanna (Cole, 1960; Goodland & Pollard, 1973; Nix, 1983; Stott, 1988; Haridasan, 1992; Lloyd *et al.*, 2008). However, over much, if not all, of the current extent of tropical savannas, the environmental conditions can also support forest, thickets and shrublands as evidenced by landscape patterns (Bowman, 2000; Russell-Smith *et al.*, 2004), manipulation experi-

ments (Woinarski *et al.*, 2004; Higgins *et al.*, 2007), model experiments (Bond *et al.*, 2005) and palaeoclimate data. Similarly, large areas occupied by these ecosystems have the potential to persist as savanna or closed-canopy formations once the shift has occurred (Laws, 1970; Johnson, 2009). Most authors consider fire to be an important characteristic of the savanna biome, but differ in the extent to which fire is perceived as a passive response (Lloyd *et al.*, 2008) to the presence of flammable C_4 grasses and savannas, or a major factor accounting for the existence of savannas (Bond, 2008).

As a result of the largely stochastic nature of fire regimes, local correlative studies have limited use in inferring environmental controls on the distribution of savanna and closed-canopy vegetation. However, at sufficiently large scales, patterns should be governed by the mean behaviour of the dynamics between savanna and closed-canopy systems. It should then be possible to identify the environmental limits in which grass-dominated savanna vegetation gives way to either mesic closed-canopy forest on the one hand, or arid and semi-arid thicket or shrubland on the other.

This study aims to identify the environmental limits of C_4 -dominated savannas across tropical Africa, Australia and South America. On all three continents, C_4 grass-dominated savannas are widespread, but the history and compositional makeup of the savannas are vastly different. We used best available vegetation maps to classify each continent into savanna and not-savanna vegetation. We assessed the probability of a location being savanna along a productivity gradient. We then determined where along this productivity gradient the savanna–closed-canopy boundary existed on each continent, explored reasons for this and developed our conceptual model of how these transitions occur. Although the concepts discussed here are relevant to alternate stable states, and grass- and woody-dominated ecosystems worldwide, we focus on tropical savanna systems dominated by C_4 grasses.

Materials and Methods

The extent of savanna vegetation was determined via a composite of vegetation maps covering Africa, Australia and South America. We primarily used maps developed from ground observations. Satellite-based products are subject to the influence of recent land-use change and generally use arbitrary cut-offs for what constitutes 'forest' based on tree cover estimates (Fairhead & Leach 1998). The distinctions used to assess whether a vegetation type was classified as savanna were the presence of a dominant C_4 grass layer and discontinuous tree cover. Hence, vegetation units classified as 'closed-canopy' (not-savanna) comprised shrubland, thicket, heath, forest, dry forest, rainforest, evergreen tropical forest, moist tropical forest and closed forest. We omitted from our analysis any vegetation units described as azonal vegetation, sand, desert, waterlogged, seasonally

inundated, riverine forest, alluvial or floodplain grasslands, montane, submontane, alto-montane, afro-montane, Highveld, agriculture, salt flat or water. High-altitude tropical grasslands were not sampled, as these systems represent a temperature constraint to woody growth, and are generally dominated by C_3 grass species and therefore do not fit within the limits of our definition of savanna. Classification was based on the metadata accompanying each vegetation map and consultation with regional experts.

Vegetation maps

Africa The vegetation map developed by White (1983) was used to define the limits of savanna in Africa. This map remains the only continent-wide vegetation classification system. The major vegetation types are grassland, grassy shrubland, secondary wooded grassland, edaphic grassland mosaics, forest transitions and mosaics, woodland, woodland mosaics and transitions, bushland and thicket, bushland and thicket mosaics, Cape shrubland, forest, semi-desert vegetation, desert and transitional scrubland. Areas not classified and excluded from the analysis were alto-montane vegetation, anthropic landscapes, azonal vegetation and Highveld grassland formations.

Australia A composite of four vegetation maps were used. These were: (1) Northern Territory Government 1 : 1 000 000 map (<http://www.nt.gov.au/nreta/natres/natveg/vegmapping/>); (2) Australian Tropical Savannas 1 : 1 000 000 map (Fox *et al.*, 2001); (3) Queensland Regional Ecosystems (Queensland Herbarium, 2011); and where there were gaps in the coverage of these maps to 30°S the (4) Geosciences Australia 1 : 5 000 000 map was used that covers the Australian continent. We classified the biomass-accumulating *Triodia* spp.-dominated grasslands of Australia as 'not-savanna'. Unlike other C_4 grasses, perennial *Triodia* spp. act functionally as shrubs, accumulating above-ground biomass gradually over many years and with long-lived evergreen leaves, and may carry fire when they are green (i.e. not cured). This is unlike other C_4 grasses, which only carry fire once they have senesced and cured. Australia is unique in that large tracts of the arid and semi-arid zones are covered by these hummock-forming grass species. Co-occurring woody species have life history traits characteristic of crown fire regimes, such as fire-stimulated recruitment and nonsprouting (= obligate seeder), fire responses which are absent from the surface fire regimes of savannas (Allan & Southgate, 2002).

South America As a result of a lack of detailed vegetation maps for the entire continent, and because the vast majority of South American savannas are contained within Brazil and Venezuela, we used two vegetation maps representing these countries. For Brazil, we used the 1 : 5 000 000 Vegetation Map of the Instituto Brasileiro de Geografia e Estatística

(IBGE), digitized by the USGS EROS Data Center. Based on the descriptions of the vegetation classes by the IBGE (1992), we considered as savanna any vegetation classified as Cerrado, Campos or tree-grass Caatinga. For Venezuela, we used the map developed by Huber & Alarcón (1988), where savanna was considered as open savanna and savanna with trees. Seasonally inundated savannas described as open savanna prone to flooding, savanna with trees prone to flooding and swamp herblands were excluded.

Dataset

We examined the vegetation maps 30° north and south of the equator on each continent, which is the latitudinal band in which C_4 grass species dominate. A major aim of our study was to quantify the environmental constraints of C_4 grassy systems, and as such we did not use environmental limits to define our study area; rather, we chose a uniform latitudinal cut-off. We generated a random set of points across each continent with the minimum enforceable distance between points of 0.25°, and each point was classified as savanna or not-savanna.

We collated information on four factors, a priori, that were considered to be important regional and local determinants of the presence of savanna – effective rainfall, rainfall seasonality, soil fertility and topographic complexity. These factors are known to affect both ecosystem productivity and fire return period.

We calculated effective rainfall as MAP – PET, where MAP is the mean annual precipitation from the 0.5° resolution WorldClim data (<http://www.worldclim.org/>) and PET is the potential evapotranspiration from the 0.5° resolution dataset from the University of Delaware (www.climate.geog.udel.edu/~climate/).

Soil fertility has been inferred by a number of studies as a determinant of the presence of savanna (Goodland & Pollard, 1973; Cole, 1986; Stott, 1988; Haridasan, 1992; Lloyd *et al.*, 2008). Soil fertility affects both the productivity of trees and grasses and, where there are mega-herbivores, the extent of grazing and browsing. Soil fertility was determined as a product of total exchangeable bases (TEB) extracted from the International Geosphere–Biosphere Programme (IGBP) Harmonized World Soils Database (<http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/>), which nominally has a resolution of 1 km and where high values of TEB correspond to high soil fertility. TEB is considered to be a particularly appropriate measure of fertility for savanna systems (Nix, 1983).

Rainfall seasonality was first mooted as important for the determination of the distribution of savannas by Schimper (1903), but this correlation has never been quantified. Tropical Rainfall Measurement Mission (TRMM) monthly rainfall data (Huffman *et al.*, 2007) provided at a 0.25° resolution were used to calculate rainfall seasonality, and

were defined using an index which gives an indication of how evenly dispersed rainfall is throughout the year. A value of zero represents equal rain in all months, a value of 100 indicates that all rain fell in 1 month and a value of 50 approximates a 5-month dry season. Markham (1970) provides a definition of this index.

Topographic complexity affects fire spread, and thus also fire return times and the probability of disturbance (Stambaugh & Guyette, 2008; Archibald *et al.*, 2009). If frequent fires are important for the presence of savanna, topographic complexity is likely to be an important indicator of the likelihood of fire spread. Shuttle Radar Topographic Mission (SRTM) global topographic data were used to calculate topographic complexity, which is defined as the standard deviation of 90-m resolution elevation values within a 1-km cell (*c.* 100 values in each cell).

'Continent' was included as a fixed effect in our analyses. Millions of years of plant and landscape evolution separate Africa, Australia and South America, and it has been suggested that there is divergence in the limits of savannas amongst continents (Knapp *et al.*, 2004; Bond, 2008; Lloyd *et al.*, 2008).

We were interested in understanding whether the distribution of fire is a driver of the distribution of savanna, rather than a passive response. Fire occurrence and savanna presence are closely related because of the flammability of *C₄* grasses. Hence, the direct inclusion of information on fire in our analyses would have produced circularity in any arguments of a dynamic relationship between climate, vegetation and fire. The area burned can be used as an index of fire return period through space-for-time substitution, although it presents problems in systems that do not burn uniformly. As an example, a 9-yr dataset is insufficient to describe systems such as the *Triodia*-dominated hummock grasslands (not-savanna) of central Australia, and other semi-arid and arid systems known to have long fire return periods (Greenville *et al.*, 2009). However, rainfall seasonality and topographic complexity are two important correlates of fire (Archibald *et al.*, 2009). We used the monthly MCD45A1 burnt area product to determine whether or not individual point locations had burned in the last 9 yr (9 yr was the length of the Moderate Resolution Imaging Spectroradiometer (MODIS) data product).

Analyses

Mapping the probability of savanna and fire occurrence

The dataset generated for each continent was ordered in terms of MAP and binned (ranging from 100 to 4000 mm) in 80-mm intervals. Within each interval, the probability of the presence of savanna was calculated as the mean of all points within that rainfall interval (0, not-savanna; 1, savanna; thus the mean value is the probability of the presence of savanna). If a pixel burned within the time period

of the satellite data (9 yr), fire occurrence was classified as one, and, if it did not burn, it was classified as zero. The probability of fire was calculated as the mean of all points within that rainfall interval. These two metrics were plotted against MAP to compare the limits of savanna and fire (Fig. 1).

The arid and mesic transitions Processes driving the transition from savanna to forest on the mesic end of the continuum, and from savanna to arid shrubland/thicket/spinifex on the arid end of the continuum, are unlikely to be similar. For the statistical analyses, the datasets were therefore split into 'arid' and 'mesic', with the divider being the rainfall at which savanna occurrence is maximized for each continent. The environmental drivers were explored and explained separately for each transition.

Statistical modelling of the presence of savanna We examined the ability of five environmental correlates to predict the distribution of savanna (Table 1: MAP – PET, soil fertility, rainfall seasonality, topographic complexity and 'Continent'), and used these to develop 32 models, with a binomial response variable (savanna presence/absence). The 32 models were contrasted in an information theoretical framework described below.

For the statistical models, the presence/absence point data and environmental information were area averaged at a 0.5° resolution. This means that all points within a given 0.5° cell (up to five points) were summed and averaged to create a gridded dataset with values of savanna presence ranging from zero to unity. Spatial analyses in R are limited by the inability to construct a distance matrix for > 4000 points. Hence, the dataset was randomly subsampled for 4000 gridded values from each transition (4000 of 4247 arid transitions; 4000 of 4125 mesic transitions).

We used a method developed by Murphy *et al.* (2010) to construct autoregressive error (ARerr) models that account for inherent and induced spatial autocorrelation in non-normal data. The ARerr models were constructed as generalized nonlinear models using the packages gnm and ncf in the free-ware program R version 2.11.0. Particular to ARerr models is that the spatial weights of the distance matrix are assigned according to the correlation structure of the residuals for the model in question. The spatial correlation structure was determined by constructing a nonspatial version of the global model. Using the residuals from the nonspatial model, a correlogram based on Moran's *I* was plotted and spatial autocorrelation was modelled as a function of distance. The modelled correlation between two points was then used to estimate the spatial weights for the model in question.

Models were evaluated using ΔQAIC_c ($\Delta\text{QAIC}_c = \text{QAIC}_{c_i} - \text{QAIC}_{c_{\min}}$), a robust form of Akaike's Information Criterion, a model selection index favouring model parsimony that accounts for overdispersion in data (Burnham & Andersen, 2002). Values of $\Delta\text{QAIC}_c < 2$

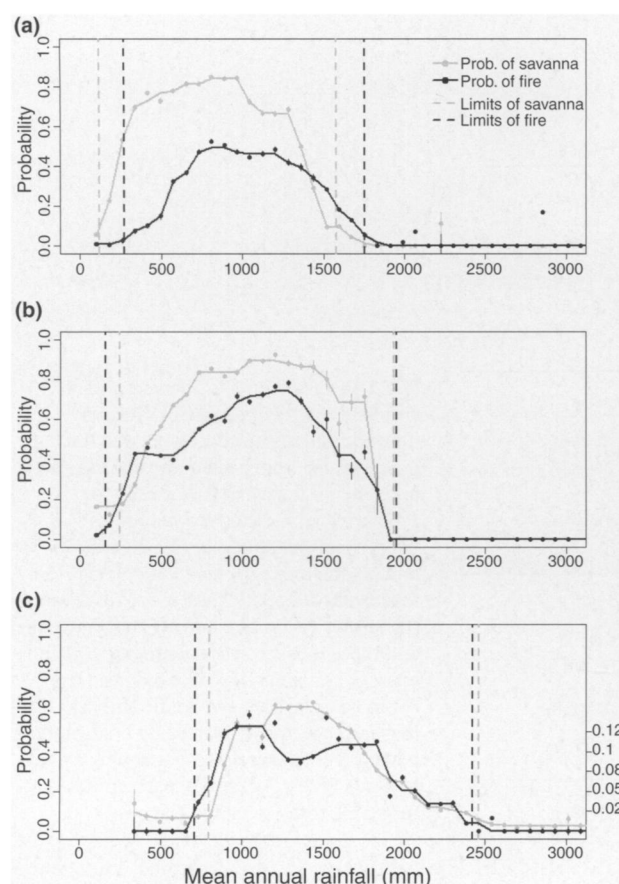


Fig. 1 The probability of savanna occurrence and the annual probability of fire occurrence as derived from our analyses of vegetation maps and MODIS fire data across continental rainfall gradients of Africa (a), Australia (b) and South America (c). In (c) the right-hand y-axis represents the probability of fire. The dashed lines represent the limits of both savanna and fire. These were calculated as the difference between the minimum and maximum values, and the limit occurs when the value drops below or increases above 5% of this difference. This was performed on the arid and mesic transitions separately (i.e. the threshold is calculated independently each time).

indicate that an alternative model performs almost as well as the best model ($DQAIC_{c_{min}}$), and $\Delta QAIC_c > 10$ suggests it is highly unlikely that the alternative model is appropriate. Based on $QAIC_c$, Akaike weights (w_i) were calculated for each of the 32 models in the analysis. w_i is equivalent to the probability of a given model being the most parsimonious in the candidate set. From each model set representing each of the arid and mesic transitions, the global model was used to estimate the predicted effects of each correlate on the probability of savanna presence.

Regression tree modelling We also used a nonparametric approach to explore how the environmental data were explicitly correlated with the distribution of savanna. A regression tree is a classification method that predicts class membership by recursively partitioning data into more homogeneous subsets, referred to as nodes (Breiman *et al.*, 1984). Regression trees provide a set of rules for the classification of data into categories (savanna or not-savanna) by identifying split conditions which decrease the deviance at each node in the tree. Split conditions are explicit, and accommodate nonlinear relationships. The importance of different explanatory variables was assessed by randomly permuting each variable in turn, running the model, and assessing the increase in root-mean-square error (RMSE) that occurred; variables that are important for the final prediction would result in a greater increase in RMSE when randomly permuted. Currently, there is no good method of accounting for spatial autocorrelation with regression tree modelling, which means that the results from this analysis need to be interpreted in the light of the statistical models described above.

Results

Distribution of savanna and fire

An initial assessment of the distribution of fire and savanna across a rainfall gradient indicated marked differences

Table 1 Model rankings from the gnm analyses of the arid and mesic transitions showing the top ranked ($QAIC_c < 10$ and highlighted in bold), univariate and null (italics) models

| Arid transition | | | | | Mesic transition | | | | |
|--|----------|----------------|-----------------|--------------|--|----------|----------------|-----------------|--------------|
| Model | Rank | $QAIC_c$ | $\Delta QAIC_c$ | %DE | Model | Rank | $QAIC_c$ | $\Delta QAIC_c$ | %DE |
| <i>RPET + SF + RS + TC + CONT</i> | 1 | 4986.71 | 0.00 | 26.99 | <i>RPET + RS + TC + CONT</i> | 1 | 4526.78 | 0.00 | 22.60 |
| <i>RPET + SF + RS + CONT</i> | 2 | 5019.38 | 32.67 | 26.36 | <i>RPET + SF + RS + TC + CONT</i> | 2 | 4527.48 | 0.71 | 22.63 |
| <i>CONT</i> | 18 | 5477.52 | 490.81 | 17.87 | <i>RPET</i> | 22 | 4832.28 | 305.50 | 16.53 |
| <i>RS</i> | 23 | 5600.38 | 613.67 | 15.58 | <i>RS</i> | 24 | 4875.19 | 348.41 | 15.70 |
| <i>RPET</i> | 28 | 6132.52 | 1145.81 | 5.85 | <i>CONT</i> | 28 | 5142.49 | 615.71 | 10.55 |
| <i>TC</i> | 29 | 6384.10 | 1397.39 | 1.25 | <i>SF</i> | 30 | 5414.30 | 887.52 | 5.25 |
| <i>Null</i> | 31 | 6450.53 | 1463.82 | 0.00 | <i>TC</i> | 31 | 5626.55 | 1099.77 | 1.13 |
| <i>SF</i> | 32 | 6451.17 | 1464.45 | 0.02 | <i>Null</i> | 32 | 5683.04 | 1156.26 | 0.00 |

CONT, continent; %DE, percent deviance explained; RPET, effective rainfall calculated as mean annual precipitation – potential evapotranspiration (MAP – PET); RS, rainfall seasonality; SF, soil fertility; TC, topographic complexity.

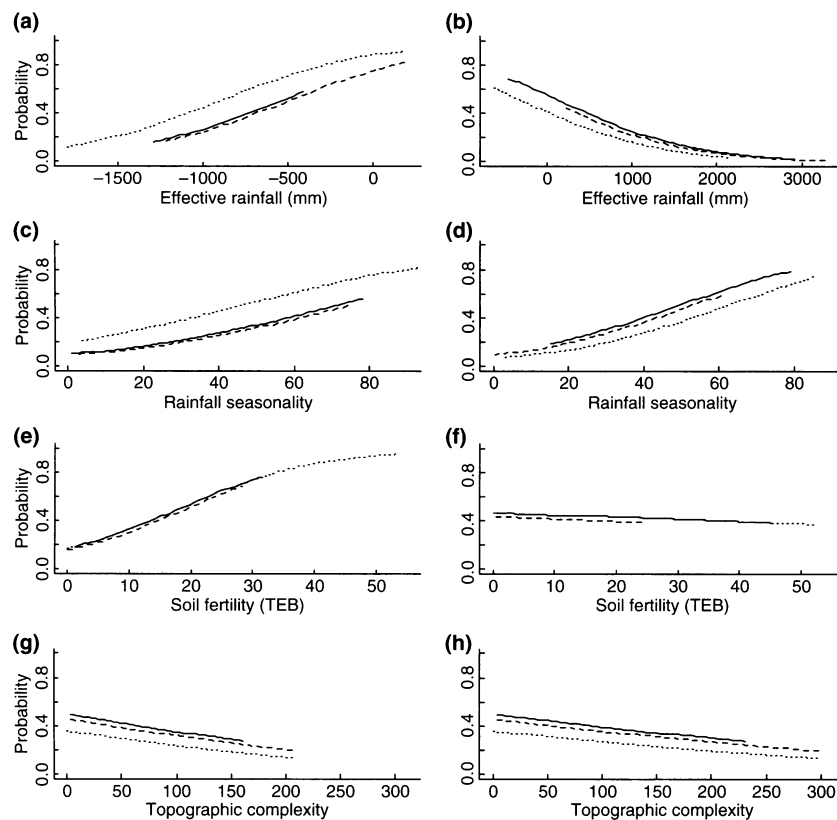


Fig. 2 Predicted effects of environmental correlates on the presence of savanna derived from our statistical models. The global model from each of the analyses of arid and mesic savannas was used to estimate the predicted magnitude and direction of the effects of effective rainfall for arid (a) and mesic (b) savanna, rainfall seasonality for arid (c) and mesic (d) savanna, soil fertility for arid (e) and mesic (f) savanna and topographic complexity for arid (g) and mesic (h) savanna. For Africa (dotted line), Australia (solid line) and South America (dashed line), the median value of all other environmental correlates was kept constant to predict the effect size of each correlate in turn. TEB, total exchangeable bases.

between continents (Fig. 1). Savannas in South America occurred at up to 2500 mm MAP, which is 500 mm above the limit of savanna in Australia, and 750 mm above Africa's wettest savannas. Similarly, a substantial proportion of the savannas of Australia and Africa occurred at rainfall amounts well below 1000 mm MAP, which was not the

case in South America (Fig. 1). In Australia and South America, fire occurrence was closely associated with the presence of savanna along this rainfall gradient (Fig. 1). In Africa, however, savanna extended far into areas of low rainfall where burning was infrequent (Fig. 1a).

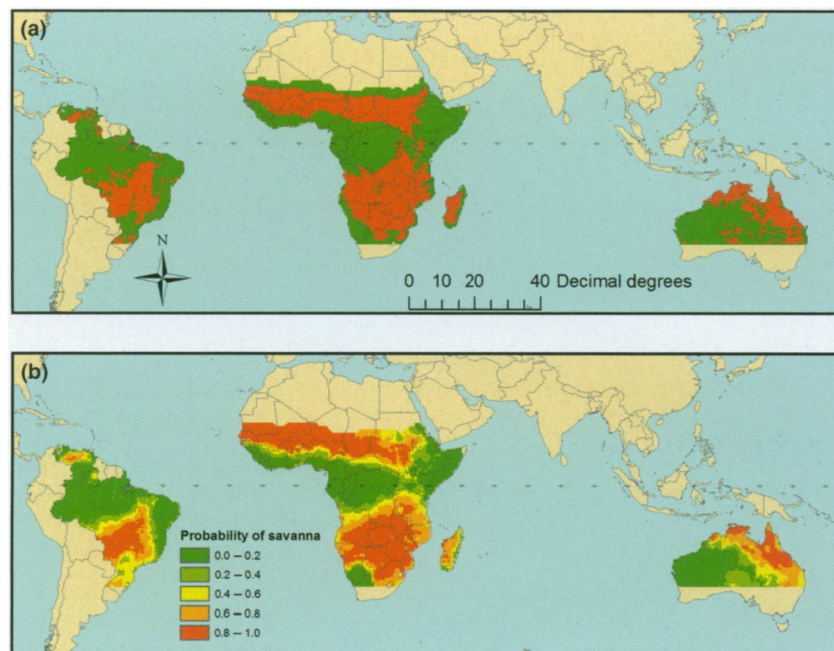
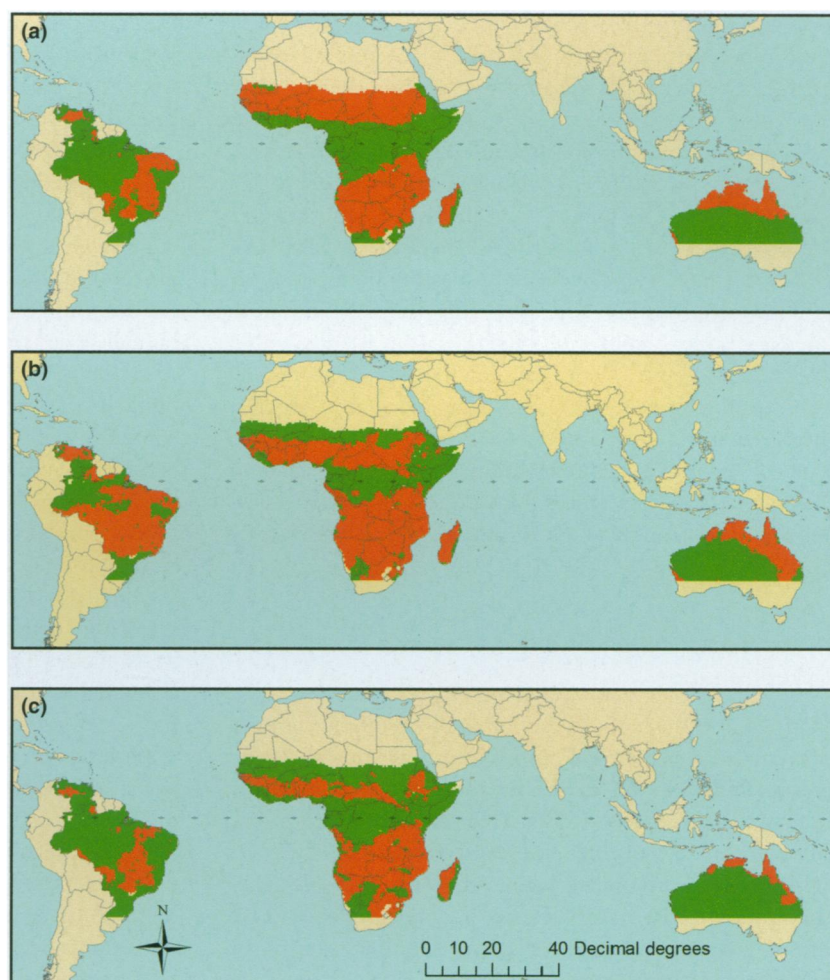


Fig. 3 Observed and predicted extent of C₄ savannas across Africa, Australia and South America. (a) The observed extent of savanna was mapped as a product of the classification process outlined in the Materials and Methods section. (b) The predicted extent of C₄ savannas ranges from 0% to 100% with increments of 20% as shown in the figure key. The predicted extent was calculated from the statistical models as outlined in the Results section.

Fig. 4 Predicted distribution of C_4 savanna from best-fit models for each continent. Vegetation was predicted from a statistical model run for a single continent containing the variables – effective rainfall, rainfall seasonality, soil fertility and topographic complexity – and mapped onto this and the other two continents. Panels show model fits for African savannas (a), Australian savannas (b) and South American savannas (c). Brown represents a > 50% chance of savanna occurring, and green corresponds to a > 50% chance of closed-canopy formations, regardless of whether these are tropical forest, tropical dry forest or semi-arid thickets and shrublands.



Environmental drivers of the mesic savanna–forest transition

The statistical models of the mesic savanna–forest transition showed that all covariates had relevance in determining the probability of savanna (Table 1). When the effect of each variable was examined in isolation, effective rainfall and rainfall seasonality had the greatest influences (16.5% and 15.7% of the deviance explained (DE), respectively), followed by ‘Continent’ (10.6% DE), soil fertility (5.3% DE) and topographic complexity (1.1% DE).

When all variables were included in the model, the spatial global model explained 22.63% of the deviance in the data, and the nonspatial global model explained 34.36% of the deviance; hence, *c.* 12% of the deviance could be attributed to the spatial structure of the data. The response to MAP – PET was remarkably consistent across continents after accounting for all other variables (Fig. 2). On all continents, the probability of savanna occurrence was < 20% where MAP – PET exceeded 1200 mm (Fig. 2). Rainfall seasonality had a strong positive effect on the presence of savanna,

indicating that savanna is most extensive where rainfall is most seasonal. Africa required more seasonally concentrated annual rainfall than either Australia or South America to achieve the same probability of savanna occurrence (62 vs 49 and 52, respectively, for a 50% probability). Soil fertility explained 5% of the deviance in the data when examined in isolation; however, this effect disappeared when all other variables were taken into account (Fig. 2). Topographic complexity had a weak negative effect on the presence of savanna.

We found good agreement between our observed and predicted distributions (Fig. 3). Overall, Australia had a higher probability of savanna occurrence, albeit a small difference, relative to Africa and South America (Fig. 2). However, when the envelope of Australian savannas was plotted onto the environmental space of Africa and South America, the extent of mesic closed-canopy formations was much reduced (Fig. 4).

Regression tree results confirmed the importance of rainfall seasonality in the mesic savanna–forest transition. Here, rainfall seasonality was the most important correlate of

savanna, reducing the RMSE by 50% more than the next most important variable (MAP – PET). Across all continents, areas with rainfall seasonality < 52 (equivalent to a dry season of < 5 months) were highly unlikely to be classified as not-savanna. The regression tree identified all continents as having a high probability of savanna occurring where MAP – PET < 570 mm – as long as they are also seasonal systems (Table 2, split #4). It also highlighted the existence of savanna on rare, but biogeographically important, sites of very low soil fertility and very high rainfall in South America (Table 2, split #3), which occur as islands within the Amazon forest. These very low-fertility, high-rainfall sites do not exist in Australia or Africa, and so it is not clear whether this is a true continental distinction, or simply a result of a lack of representation on other continents. Continental-scale differences found across the mesic transition were not strong enough to justify splitting the data by continent (Table 2).

Environmental drivers of the arid savanna–shrubland/thicket transition

Continental differences in the limits of savanna were most apparent across the arid continuum, where we found considerable variation in the breadth of the productivity gradient occupied by savanna (Fig. 2). Results from the statistical models of the arid savanna–shrubland/thicket transition found that all covariates had relevance in determining the probability of savanna. When the effect of each variable was examined in isolation, ‘Continent’ had the greatest explanatory power, explaining 17.5% of the deviance in the data. Rainfall concentration explained 15.6% of the deviance in the data, followed by MAP – PET (5.85%

DE) and topographic roughness (1.25% DE). On its own, soil fertility explained virtually none of the deviance in the data: 0.02% DE. The global model explained 27% of the deviance (Table 1), and the nonspatial global model explained 38% of the deviance in the data; hence, 11% of the deviance in the data could be accounted for by the spatial structure of the data.

For a given effective rainfall, there was a 23–46% higher probability of savanna occurring in Africa relative to Australia and South America (Fig. 2). Similarly, for a given rainfall seasonality, there was a 26–49% higher probability of savanna occurring in Africa, and a 34–44% higher probability of the presence of savanna for a given topographic complexity. From Fig. 3, a 50% probability of savanna occurrence in Africa corresponds to a rainfall seasonality of 45, whereas, in Australia and South America, the rainfall seasonality must exceed 71 and 74, respectively. Importantly, the environmental conditions of low rainfall and high seasonality do not occur in arid South America, where seasonality does not exceed this value. In isolation, soil fertility explained little of the deviance in the data but, when examined in combination with all environmental correlates, showed high relevance (Table 1, Fig. 2). This suggests the importance of a possible interaction between soil fertility and other factors as, across all continents, our analysis predicts that increasing soil fertility is correlated with an increased probability of arid savanna occurrence (Fig. 2).

When we delved further into the role of ‘Continent’ via regression trees, there was strong agreement between the statistical models and regression tree of divergence amongst continents in the arid limits of savanna (Table 2). In contrast with the mesic transition, there seemed to be continental-level differences in savanna occurrence that

Table 2 Split conditions identified by a regression tree run on data representing the mesic and arid transitions (with ‘Continent’ included as a factor)

| | | | | | % correctly classified | | | | | |
|---|-------------------------|-------------------------|----------|--|------------------------|--------------|-------------|-----|-----|------|
| | | | | | Split | Total points | Veg class | AFR | AUS | S.AM |
| MESIC TRANSITION: overall accuracy = 0.34, Cohen's kappa = 0.62 ($P < 0.001$) | | | | | | | | | | |
| Rain concentration < 52 | | | | | #1 | 1760 | Not-savanna | 82 | 78 | 80 |
| Rain concentration ≥ 52 | MAP – PET ≥ 570 | TEB ≥ 1.1 | | | #2 | 66 | Not-savanna | 69 | 100 | 78 |
| | | TEB < 1.1 | | | #3 | 67 | Savanna | – | – | 76 |
| Rain concentration ≥ 52 | MAP – PET < 570 | | | | #4 | 509 | Savanna | 85 | 92 | 76 |
| ARID TRANSITION: overall accuracy = 0.61, Cohen's kappa = 0.32 ($P < 0.001$) | | | | | | | | | | |
| MAP – PET < –760 | Continent = S.AM | | | | #5 | 52 | Not-savanna | – | – | 98 |
| | Continent = AFR or AUS | Rain concentration < 72 | TEB < 30 | | #6 | 2087 | Not-savanna | 92 | 85 | – |
| | | | TEB ≥ 30 | | #7 | 47 | Savanna | 50 | 74 | – |
| | | Rain concentration ≥ 72 | | | #8 | 1484 | Savanna | 79 | 66 | – |
| MAP – PET ≥ –760 | Rain concentration < 38 | | | | #9 | 1727 | Not-savanna | 94 | 52 | 78 |
| | Rain concentration ≥ 38 | | | | #10 | 4483 | Savanna | 76 | 85 | 58 |

‘Total points’ represents the total number of points in each split category. Also given is the percentage of points on each continent that were correctly classified by each split. Some sets of environmental conditions were not represented on all continents.

AFR, Africa; AUS, Australia; PET, potential evapotranspiration; S.AM, South America; TEB, total exchangeable bases.

could not be explained by variation in environmental drivers. In Africa and Australia, sites with low effective rainfall could be savanna if they had very high rainfall seasonality or high soil fertility (Table 2, splits #7,#8), but savanna was never present in South America for values of effective rainfall < -760 mm (Table 2, split #1). This was demonstrated by plotting the limits of South American savannas onto Africa and Australia, which resulted in a substantial reduction in the extent of savanna in semi-arid regions (Fig. 4).

Discussion

We found that, across the tropics, the balance between savanna and closed-canopy ecosystems is fundamentally similar because effective rainfall and rainfall seasonality constrain their distribution (Figs 1–3 and Tables 1–2). Savannas are commonly perceived to occupy an intermediate position in the continuum between grassland and forest. However, many tropical landscapes contain mosaics of savanna and closed-canopy systems, and these mosaics have persisted over millennia. That such strikingly different vegetation occurs as a mosaic hints that the limit of savanna is not simply, and deterministically, defined by climate and soils. Our analysis confirms this: over the entire range of environmental conditions in which savannas occur, some fraction of the land surface is 'not-savanna' (Fig. 1).

We present evidence of globally applicable environmental limits to mesic savanna, as there is consensus across regions in the direction and magnitude of the effects of effective rainfall, rainfall seasonality, soil fertility and, to a lesser extent, the topographic complexity of landscapes. Our results corroborate previous studies showing that the presence of savanna correlates with edaphic conditions and moisture availability (Cole, 1960; Stott, 1988; Furley, 1992; Haridasan, 1992; Ruggiero *et al.*, 2002; Lloyd *et al.*, 2008), although we provide an alternative interpretation for how these soil and climate constraints operate in a causal manner to limit savanna. Lastly, 'Continent' was an important correlate of savanna extent, primarily at the arid limit of savanna, and we discuss divergences amongst continents in the limits of savanna and present hypotheses and evidence for why these might exist.

Can the counteraction between woody plant growth and disturbance govern the limits of savanna?

While quantifying the limits to savanna is useful, it fails to untangle the ecological mechanisms that actually limit savanna. However, savanna-limiting mechanisms are not intuitive, primarily because woody plants and C₄ grasses respond differently to the same climatic parameters. Total effective rainfall, rainfall seasonality and soil fertility affect the growth rates of both woody plants and C₄ grasses. Further, frequent fire reduces woody growth rates and tree

density, but engenders an environment more suitable for C₄ grasses (i.e. reduced competition from trees). If the disturbance interval exceeds the time required for canopy closure, savanna will be replaced by closed-canopy (not-savanna) vegetation (Fig. 5). Thus, understanding the rate of canopy closure, which is governed by woody growth rates relative to fire frequency, is vital to understanding the limits and persistence of savannas, particularly across the mesic transition.

We consider that the extent of savanna is determined by the counteraction between rates of canopy closure, caused by the colonization and growth of trees, and the frequency of disturbance, promoted by C₄ grass abundance, which results in canopy opening. If the environmental conditions in which savannas dominate are determined by this counteraction, then when factors affecting these processes have been accounted for we should find convergence in the distribution of savanna across the globe. However, if savannas in different parts of the world have different environmental limits, we need to search for alternative ecological explanations or turn to historical differences to explain these divergences.

Using the above framework, we believe that it is possible to integrate previous and seemingly contradictory observations of the environmental limits of savanna. Importantly, the relevance of local correlations between the presence of savanna, soil fertility and/or water-holding capacity can be incorporated into our framework if they are understood as factors that increase woody growth rates – thereby reducing the efficacy of fire in maintaining an open canopy (Fig. 5a). From Fig. 5(a), we see that the exact boundary between savanna and closed-canopy vegetation should depend on the shapes of relationships of potential tree and grass productivity to climate and disturbance – for which there are few data available; the form of these relationships may well be influenced by phylogeny and the architectural and functional traits of tree and grass species.

Concepts of climate–disturbance–vegetation interactions constraining the limits of savanna can be contrasted with the hypothesis that the modern and palaeo-extent of savanna vegetation is attributable to the efficiencies of the C₄ photosynthetic system, as C₄ grasses are superior competitors to woody plants under low but seasonal rainfall because of lower whole-plant construction costs and high water-use efficiency (Orians & Solbrig, 1977; Edwards *et al.*, 2010). Hence, C₄ grasses colonize open habitats. However, decade-old fire exclusion and model experiments show that, across many savanna systems, the competitive effect of C₄ grasses is not strong enough to prevent tree recruitment in the absence of disturbance (Russell-Smith *et al.*, 2003; Higgins *et al.*, 2007; Asner *et al.*, 2009; Lehmann *et al.*, 2009; Staver *et al.*, 2009), and an increase in the density of woody stems often leads to coincident reductions in grass biomass (Belsky, 1994; Menaut *et al.*, 1995; Mordelet & Menaut, 1995; Scholes & Archer, 1997; Ludwig *et al.*, 2004). Our results, together with a recent study examining distribution of fire

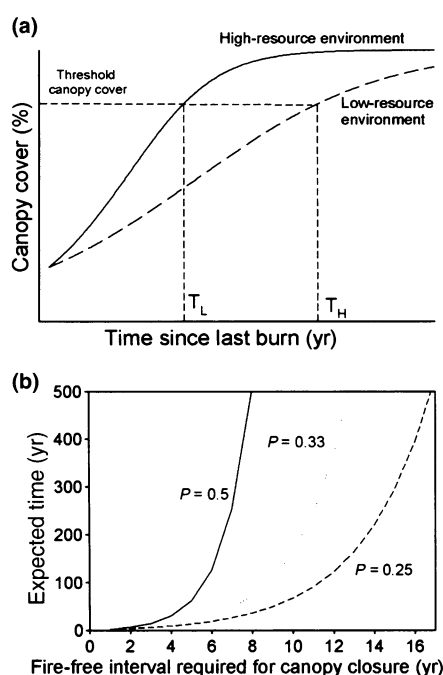


Fig. 5 (a) Graphical representation of the effect of soil resources on the time required to reach the nonflammability threshold. Resource availability determines the rate of canopy closure, so that the time required to reach an alternative stable state is considerably shorter for the high-resource environment than for the low-resource environment. (b) Examples of the time required to reach canopy closure where different probabilities of fire operate. For example, 0.5 corresponds to the probability of a fire event occurring once in 2 yr.

across Africa (Archibald *et al.*, 2009), suggest that the limits of C_4 -dominated systems are caused by the dynamic roles of succession and disturbance as described in Fig. 5. Here, effective rainfall and rainfall seasonality are proximate drivers, and soil fertility locally modifies resource availability, and topographic complexity locally modifies the probability of fire. However, the remarkable divergence between continents in the arid limits of savanna is intriguing.

Why is rainfall seasonality important in limiting savanna?

Rainfall seasonality was the most important predictor of the presence of savanna. Across the mesic transition, any area with a rainfall seasonality of < 52 (equivalent to a dry season of < 5 months) had $< 20\%$ probability of being savanna across all continents. Across the arid transition, seasonality in combination with adequate effective rainfall was necessary for the presence of savanna. Rainfall seasonality may be particularly important because it acts both to *reduce* the rates of canopy closure (Sarmiento, 1984) and to *increase* fire frequency (Archibald *et al.*, 2009). Pronounced rainfall seasonality promotes fuel curing, affecting both the spatial connectivity of fuels and the period over which fuels are available to burn (Bradstock, 2010). Rainfall seasonality is also

related to interannual rainfall variability, and hence the probability of drought, which promotes both sapling tree death (Fensham *et al.*, 2009) and reduces adult woody growth rates. Rainfall seasonality therefore has a strongly countervailing influence on woody growth and the probability of disturbance. By referring to Fig. 5(b), this alone might prove its importance in explaining the limits of savanna.

Why does the role of soil fertility differ between the arid and mesic transitions?

We found a contrasting effect of soil fertility across the mesic and arid transitions (Fig. 2; Table 2). In very wet areas, low-fertility sites were more likely to be savanna (Fig. 2; Table 2, split #3). These results conform to the notion that increased soil fertility lessens growth constraints on woody plants, thereby increasing woody growth rates and productivity. Hence, in sites of very low fertility, the time required for a site to achieve a closed canopy that excludes C_4 grasses is increased, simultaneously providing a greater opportunity for disturbance to occur (Fig. 5b).

In arid areas, high-fertility sites were more likely to be savannas (Fig. 2; Table 2, split #7). Across the African arid transition, browsing and large mammal disturbance are important mechanisms maintaining open formations (Laws, 1970; Holdo *et al.*, 2009a; Staver *et al.*, 2009); this is likely to be important in more fertile systems (Coe *et al.*, 1976; Fritz & Duncan, 1994; Asner *et al.*, 2009), and low-rainfall systems (Staver *et al.*, 2009), which would explain why low-rainfall, high-fertility systems are more likely to persist as savanna (Fig. 3). In Australia, the distribution of biomass-accumulating *Triodia* sp. ecosystems (that we consider to be 'not-savanna') is correlated with sandy infertile soils (Nano & Clarke, 2008). Land systems with soils that have higher clay contents and a low water-holding capacity, relative to the well-sorted sands of semi-arid Australia, tend to support savanna (Fox *et al.*, 2001), as they favour shallow-rooted grasses, akin to the Walter hypothesis of tree-grass coexistence (Walter, 1971). In our analyses, arid sites of extreme fertility represent a tiny percentage of combined landmasses. However, these cases provide information to explore processes promoting savanna.

What is the role of 'Continent'?

Some of the different patterns, with regard to precipitation, that we have observed (i.e. Fig. 1) can be explained by differing combinations of other factors. Very low-fertility, high-rainfall savannas are only found in Brazil and Venezuela (our South American region of study) – but so, too, are the very low-fertility and high-rainfall environments which promote these savannas. Similarly, savannas occur in the very low-rainfall (MAP < 500 mm) areas of Africa and Australia because they are fertile, and these highly fertile soils are not

widespread in Brazil and Venezuela. It is important to note, however, that deciduous forests are typically associated with fertile soils in South America, but these were not sufficiently abundant in our dataset to counter the prevailing trend.

Here we discuss three important examples in which differences between continents cannot be explained by modern-day environmental constraints. Africa has a much higher probability of savanna presence across the arid transition than either Australia or South America (Figs 2, 4a). Consequently, African savannas occupy a greater land area than would otherwise be anticipated were continent not factored into our analyses (Fig. 4). Mega-herbivores and large predators were eradicated from South America and Australia over 20 000 yr ago, but not from Africa. Browse disturbance is critical in determining rates of woody plant growth in arid regions, and large-mammal grazing and trampling reduce fuel loads and can prevent fire (Lehmann *et al.*, 2008; Asner *et al.*, 2009; Holdo *et al.*, 2009b). This is supported by the large discrepancy between the probability of savanna and fire occurrence where MAP < 1400 mm across Africa (Fig. 1). There are historical accounts and palaeo-ecological studies from Africa and elsewhere which demonstrate that the addition or removal of large mammals induced radical changes to vegetation (Laws, 1970; Holdo *et al.*, 2009b; Johnson, 2009). Hence, according to our framework (Fig. 5), a disturbance other than fire (i.e. mammalian herbivory) that reduces woody plant growth and prevents closed-canopy formations would need to operate in these regions. From our analysis, the continent-level differences in rainfall seasonality required to promote savanna across arid Africa and, similarly, the correlation between soil fertility and the arid savanna-shrubland/thicket transition point to the role of herbivores in extending the dominance of savanna across the African continent.

In Australia, savanna extends into wet habitats where rainfall is not as seasonally concentrated as in either Africa or South America. Applying these Australian limits to Africa and South America results in a reduction in the extent of the Amazon and Congo Basin forests (Fig. 4b). The Australian mesic transition is almost entirely confined to a small portion of the north-east of the continent (Fox *et al.*, 2001). As a result of the small dataset pertaining to the Australian mesic transition, the power of this result is diminished and, to an extent, an artefact of the differences in range of rainfall seasonality found across the three continents. However, Australian mesic savannas are dominated by tree species from the *Eucalyptus* genus (Fox *et al.*, 2001), and there is much evidence to suggest that *Eucalyptus* and fire are co-dependent (Gill *et al.*, 1981; Bradstock *et al.*, 2002), with species from the genus having adaptations to tolerate fire (bark thickness and substantial resprouting potential) and, in some species, adaptations that promote fire (elevated fuels and highly flammable leaf litter).

Beckage *et al.* (2009) showed how these characteristics can promote fire and savanna in mesic environments. The phylogenetic peculiarities of eucalypts might therefore be the explanation for the mesic limit of savanna in Australia.

Finally, there is a lack of savanna at sites of low rainfall in South America (Fig. 4c; Table 2, split #1), although very similar environmental conditions correlate with a high probability of savanna in Africa and Australia (Figs 2, 4 and Table 2). Across the Neotropics, savanna and adjacent fire-sensitive biomes are recognized as occupying similar environmental envelopes (Pennington *et al.*, 2000, 2009). Simon *et al.* (2009) demonstrated that the fire-sensitive arid thickets, semi-arid dry forests and forests of Brazil are the ancestral biomes for the lineages of tree species that dominate the Brazilian savanna. Further, of the diverse array of tree species that dominate the Cerrado, many have congeners specific to either the gallery forests of the Cerrado or the Amazon (Hoffmann *et al.*, 2009). Anecdotal reports suggest that differences in the soils between the Caatinga and Cerrado, not captured in this analysis, are highly important in understanding the transition between Caatinga and Cerrado vegetation (Lloyd *et al.*, 2008). Thicket vegetation similar to Caatinga does occur in Africa under similar environmental conditions, but is not the dominant landscape type, as it appears to be over an extensive area in Brazil.

Conclusion

The relationship between vegetation and climate is dynamic and so, too, is the relationship between vegetation and disturbance. We provide a conceptual framework in which to consider the limits of savannas, and suggest that, at global scales, interactions between climate, disturbance and vegetation underpin the limits of savannas as a result of the counteraction between factors promoting woody plant growth and disturbance intervals. Of these drivers, rainfall seasonality has a strongly contrasting effect on both. The mosaics of savanna and closed-canopy systems are compelling evidence that across mesic environments these are distinct, alternative ecosystem states, as has been suggested (Sternberg, 2001; Warman & Moles, 2009). By contrast, the mechanisms maintaining the arid limits are less clear, although, across Africa, it appears that disturbance-centred feedbacks involving mega-herbivores are crucial.

Acknowledgements

The ARC-NZ Vegetation Function Network via WG49 provided the opportunity to develop the ideas presented here. Many thanks to the participants of WG49 for providing a stimulating and collaborative environment. David Roy and Luigi Boschetti provided access to the MODIS fire data. Brett Murphy provided statistical advice on dealing with spatial autocorrelation. Rod Fensham and Nick Cuff

provided access to the NT and QLD vegetation mapping and helped with the classification of Australian vegetation. Don Butler, Colin Prentice and Mahesh Sankaran provided helpful feedback on a draft manuscript.

References

- Allan GE, Southgate RI. 2002. Fire regimes in the spinifex landscapes of Australia. In: Bradstock RA, Williams JE, Gill AM, eds. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge, UK: Cambridge University Press, 145–176.
- Archibald S, Roy DP, van Wilgen BW, Scholes RJ. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology* 15: 613–630.
- Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29: 261.
- Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences, USA* 106: 4947–4952.
- Barlow J, Peres CA. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 363: 1787–1794.
- Beckage B, Platt WJ, Gross LJ. 2009. Vegetation, fire, and feedbacks: a disturbance mediated model of savannas. *The American Naturalist* 174: 805–818.
- Belsky AJ. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree–grass competition. *Ecology* 75: 922–932.
- Bond WJ. 2008. What limits trees in C₄ grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39: 641–659.
- Bond WJ, Midgley GF. 2000. A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* 6: 865–869.
- Bond WJ, Parr CL. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biological Conservation* 143: 2395–2404.
- Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525–538.
- Bowman DMJS. 2000. *Australian rainforests: islands of green in a land of fire*. Cambridge, UK: Cambridge University Press.
- Bradstock RA. 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography* 19: 145–158.
- Bradstock RA, Williams JE, Gill AM. 2002. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge, UK: Cambridge University Press.
- Breiman L, Friedman J, Olshen R, Stone C. 1984. *Classification and regression trees*. Belmont, California, USA: Wadsworth & Brooks/Cole.
- Burnham KP, Andersen DR. 2002. *Model selection and multimodel inference*. New York, NY, USA: Springer.
- Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158.
- Coe MJ, Cumming DH, Phillipson J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22: 341–354.
- Cole M. 1960. Cerrado, caatinga and pantanal: the distribution and origin of the savanna vegetation of Brazil. *Geographical Journal, The Royal Geographical Society* 126: 168–179.
- Cole M. 1986. *Savannas: biogeography and geobotany*. London, UK: Academic Press.
- Edwards EJ, Osborne CP, Stromberg CAE, Smith SA, C₄ Grasses Consortium. 2010. The origins of C₄ grasslands: integrating evolutionary and ecosystem science. *Science* 328: 587–591.
- Fairhead J, Leach M. 1998. *Reframing deforestation: Global analyses and local realities; studies in west Africa*. Routledge.
- Fensham RJ, Fairfax RJ, Ward DP. 2009. Drought-induced tree death in savanna. *Global Change Biology* 15: 380–387.
- Fox ID, Neldner VJ, Wilson GW, Bannink PJ. 2001. *The vegetation of the Australian tropical savannas*. Brisbane, Australia: Environment Protection Agency.
- Fritz H, Duncan P. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society of London B* 256: 77–82.
- Furley PA. 1992. Edaphic changes at the forest–savanna boundary with particular reference to the neotropics. In: Furley PA, Proctor J, Ratter JA, eds. *Nature and dynamics of forest–savanna boundaries*. London, UK: Chapman and Hall, 91–117.
- Gill AM, Groves RH, Noble IR. 1981. *Fire and the Australian biota*. Canberra, Australia: Australian Academy of Science.
- Goodland R, Pollard R. 1973. The Brazilian cerrado vegetation: a fertility gradient. *Journal of Ecology* 61: 219–224.
- Greenville AC, Dickman CR, Wardle GM, Letnic M. 2009. The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *International Journal of Wildland Fire* 18: 631–639.
- Haridasan M. 1992. Observations on soils, foliar nutrient concentrations and floristic composition of cerrado *sensu stricto* and *cerradão* communities in central Brazil. In: Furley PA, Proctor J, Ratter JA, eds. *Nature and dynamics of forest–savanna boundaries*. London, UK: Chapman & Hall, 171–184.
- Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DIW, Enslin B, Govender N, Rademan L, O'Regan S, Potgieter ALF *et al.* 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88: 1119–1125.
- Hoffmann WA, Adasme R, Haridasan MT, de Carvalho M, Geiger EL, Pereira MAB, Gotsch SG, Franco AC. 2009. Tree topkill, not mortality, governs the dynamics of savanna forest boundaries under frequent fire in central Brazil. *Ecology* 90: 1326–1337.
- Holdo RM, Holt RD, Fryxell JM. 2009a. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications* 19: 95–109.
- Holdo RM, Sinclair ARE, Dobson AP, Metzger KL, Bolker BM, Ritchie ME, Holt RD. 2009b. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. *PLoS Biology* 7: e1000210.
- Hopkins B. 1992. Ecological processes at the forest–savanna boundary. In: Furley PA, Proctor J, Ratter JA, eds. *Nature and dynamics of the forest–savanna boundaries*. London, UK: Chapman and Hall, 21–33.
- Huber O, Alarcón C. 1988. *Mapa de vegetación de Venezuela. 1 : 2,000,000*. Caracas, Venezuela: Ministerio del Ambiente y de los Recursos Naturales Renovables and Fundación BIOMA.
- Huffman G, Adler R, Bolvin D, Gu G, Nelkin E, Bowman K, Hong Y, Stocker E, Wolff D. 2007. The TRMM multi-satellite precipitation analysis: quasi-global, multi-year combined-sensor precipitation estimates at fine scale. *Journal of Hydrometeorology* 8: 38–55.
- IBGE. 1993. *Mapa de Vegetação do Brasil (Vegetation Map of Brazil)*. Rio de Janeiro, Brazil: Instituto Brasileiro de Geografia e Estatística.
- Johnson CN. 2009. Ecological consequences of late Quaternary extinctions of megafauna. *Proceedings of the Royal Society B: Biological Sciences* 276: 2509–2519.
- Keeley JE, Rundel PW. 2005. Fire and the Miocene expansion of C₄ grasslands. *Ecology Letters* 8: 683–690.
- Knapp AK, Smith MD, Collins SL, Zambatis N, Peel M, Emery S, Wojdak J, Horner-Devine MC, Biggs H, Kruger J *et al.* 2004.

- Generality in ecology: testing North American grassland rules in South African savannas. *Frontiers in Ecology and the Environment* 2: 483–491.
- Laws R. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos* 21: 1–15.
- Leakey ADB. 2009. Rising atmospheric carbon dioxide concentration and the future of C₄ crops for food and fuel. *Proceedings of the Royal Society B: Biological Sciences* 276: 2333–2343.
- Lehmann CER, Prior LD, Bowman DMJS. 2009. Fire controls population structure in four dominant tree species in a tropical savanna. *Oecologia* 161: 505–515.
- Lehmann CER, Prior LD, Williams RJ, Bowman DMJS. 2008. Spatio-temporal trends in tree cover of a tropical mesic savanna are driven by landscape disturbance. *Journal of Applied Ecology* 45: 1304–1311.
- Lloyd J, Bird MI, Vellen L, Miranda AC, Veenendaal EM, Djagbletey G, Miranda HS, Cook G, Farquhar GD. 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree Physiology* 28: 451–468.
- Ludwig F, de Kroon H, Berendse F, Prins HHT. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology* 170: 93–105.
- Markham C. 1970. Seasonality of precipitation in the United States. *Annals of the Association of American Geographers, Routledge* 60: 593–597.
- Menaut J, Lepage M, Abbadie L. 1995. Savannas, woodlands and dry forests in Africa. In: Bullock SH, Mooney HA, Medina E, eds. *Seasonally dry tropical forests*. Cambridge, UK: Cambridge University Press, 64–92.
- Mordelet P, Menaut J-C. 1995. Influence of trees on above-ground production dynamics of grasses in a humid savanna. *Journal of Vegetation Science* 6: 223–228.
- Murphy BP, Paron P, Prior LD, Boggs GS, Franklin DC, Bowman DMJS. 2010. Using generalized autoregressive error models to understand fire–vegetation–soil feedbacks in a mulga–spinifex landscape mosaic. *Journal of Biogeography* 37: 2169–2182.
- Nano CEM, Clarke PJ. 2008. Variegated desert vegetation: covariation of edaphic and fire variables provides a framework for understanding mulga–spinifex coexistence. *Austral Ecology* 33: 848–862.
- Nix H. 1983. *Climate of tropical savannas*. *Proceedings: Biological Sciences*.
- Orians GH, Solbrig OT. 1977. A cost–income model of leaves and roots with special reference to arid and semi-arid areas. *The American Naturalist* 111: 677–690.
- Pennington RT, Lavin M, Oliveira-Filho A. 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics* 40: 437–457.
- Pennington TR, Prado DE, Pendry CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27: 261–273.
- Queensland Herbarium. 2011. *Regional Ecosystem Description Database (REDD)*. Version 6.0b–January 2011, (January 2011). Brisbane, Australia: Department of Environment and Resource Management.
- R Development Core Team. 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. URL: <http://www.r-project.org/foundation>.
- Ray D, Nepstad D, Moutinho P. 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecological Applications* 15: 1664–1678.
- Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST. 2002. Soil–vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, southeastern Brazil. *Plant Ecology* 160: 1–16.
- Russell-Smith J, Stanton PJ, Whitehead PJ, Edwards A. 2004. Rain forest invasion of eucalypt-dominated woodland savanna, Iron Range, north-eastern Australia: I. Successional processes. *Journal of Biogeography* 31: 1293–1303.
- Russell-Smith J, Whitehead PJ, Cook GD, Hoare JL. 2003. Response of eucalyptus-dominated savanna to frequent fires: lessons from Munmarlary, 1973–1996. *Ecological Monographs* 73: 349–375.
- Sage RF. 2004. The evolution of C₄ photosynthesis. *New Phytologist* 161: 341–370.
- Sage R, Kubien D. 2003. Quo vadis C₄? An ecophysiological perspective on global change and the future of C₄ plants. *Photosynthesis Research* 77: 209–225.
- Sarmiento G. 1984. *The ecology of neotropical savannas*. Cambridge, MA, USA: Harvard University Press.
- Schimper AFW. 1903. *Plant geography on a physiological basis*. Oxford, UK: Clarendon Press.
- Scholes RJ, Archer SR. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517–544.
- Scholes RJ, Hall DO. 1996. The carbon budget of tropical savannas, woodlands and grasslands. In: Breyer AI, Hall DO, Melillo JM, Agren GI, eds. *Global change: effects on coniferous forests and grasslands*. Chichester, UK: Wiley, 69–100.
- Scholes RJ, Walker BH. 1993. *An African savanna*. Cambridge, UK: Cambridge University Press.
- Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009. Recent assembly of the cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences* 106: 20359–20364.
- Stambaugh M, Guyette R. 2008. Predicting spatio-temporal variability in fire return intervals using a topographic roughness index. *Forest Ecology and Management* 254: 463–473.
- Staver AC, Bond WJ, Stock WD, van Rensburg SJ, Waldram MS. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* 19: 1909–1919.
- Sternberg LDL. 2001. Savanna–forest hysteresis in the tropics. *Global Ecology and Biogeography* 10: 369–378.
- Stott P. 1988. The forest as phoenix: towards a biogeography of fire in mainland South East Asia. *The Geographical Journal* 154: 337–350.
- Strömberg CAE. 2004. Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the Great Plains of North America during the late Eocene to early Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 207: 239–275.
- Tinley KL. 1982. The influence of soil moisture balance on ecosystem patterns in southern Africa. In: Huntley BJ, Walker BH, eds. *Ecology of tropical savannas*. Berlin, Germany: Springer-Verlag, 175–192.
- Walter H. 1971. *Ecology of tropical and subtropical vegetation*. Edinburgh, UK: Oliver and Boyd.
- Warman L, Moles A. 2009. Alternative stable states in Australia's wet tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology* 24: 1–13.
- White F. 1983. The vegetation of Africa: a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa. ((Natural Resources Research: 20)-). Paris: United Nations Educational, Scientific and Cultural Organization.
- Wigley BJ, Bond WJ, Hoffman MT. 2009. Bush encroachment under three contrasting land-use practices in a mesic South African savanna. *African Journal of Ecology* 47: 62–70.
- Woinarski JCZ, Risler J, Kean L. 2004. Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* 29: 156–176.