

Soils and fire jointly determine vegetation structure in an African savanna

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Summary

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- Savanna vegetation is variable, and predicting how water, nutrients, and chronic disturbances interact to determine vegetation structure in savannas represents a challenge.
- Here, we examined *in situ* interactions among rainfall, soils, grasses, fire, and elephants that determine tree layer responses to resource gradients in Kruger National Park in South Africa, using 363 long-term monitoring sites throughout the park.
- Grass biomass increased with rainfall and on nutrient-rich clay soils. Fire frequency, too, increased with rainfall. Conversely, tree density was greater on sandier soils, where water infiltrates more readily, and in areas where the maximum interval between fires was longer, irrespective of average fire frequency. Elephant density responded positively to tree density, but did not contribute significantly to decreasing tree density.
- Savanna vegetation structure was reasonably predictable, via a combination of rainfall (favoring grasses), soil (sandy soils favoring trees), and fire (limiting trees until a longer interval between fires allows them to establish). Explicit consideration of bottom-up and top-down interactions may thus contribute to a predictive understanding of savanna vegetation heterogeneity.

Introduction

Savanna, a biome defined by the co-dominance of trees and grasses, is characterized by its large variability in tree cover (Sankaran *et al.*, 2005; Bucini & Hanan, 2007; Bond, 2008) and grass biomass (Balfour & Howison, 2002; Govender *et al.*, 2006). A predictive understanding of the processes that give rise to such variability is an ongoing challenge that depends on resolving the fundamental roles of resource availability but also chronic disturbances by fire and herbivory in determining the distribution of the biome and vegetation structure within it (Scholes & Archer, 1997; Bond, 2008). Historically, savanna ecology has focused on resolving whether bottom-up (water, soils and nutrients) or top-down processes (fire and herbivory) are primarily responsible for extant variation in vegetation structure (Scholes & Archer, 1997; Bond, 2008). However, recognition that these processes interact is growing, and a predictive understanding of savanna variation will depend on integrating bottom-up and top-down perspectives in savanna ecology (Sankaran *et al.*, 2004, 2005, 2008; Bucini & Hanan, 2007).

On the one hand, trees and grasses may coexist because they source soil resources from different soil layers. Resource limitation certainly is responsible for limiting tree cover in many, if not all, savannas (Sankaran *et al.*, 2005). In theory, grasses root in shallow soil layers and use surface water and nutrients, while trees root deeper and use deeper water (Walter, 1971); these predictions are borne out in some recent empirical work in savannas

(Seghieri, 1995; Bhattachan *et al.*, 2012; Kulmatiski & Beard, 2012). However, trees do not always root more deeply than grasses (Seghieri, 1995; February & Higgins, 2010; O'Donnell *et al.*, 2015), such that root-niche separation does not provide a ubiquitous mechanism to maintain tree–grass coexistence. Moreover, models have suggested that, even when trees and grasses root separately, they may still compete, because water in deep soil layers first passes through shallow layers where grasses have access (Holdo, 2013). Experiments show that grasses often out-compete trees for water (Riginos, 2009; February *et al.*, 2013) and nutrients (Cech *et al.*, 2008; Cramer *et al.*, 2010) under average ecological conditions.

Temporal responses to water and nutrient availability provide another possible axis of differentiation between trees and grasses. In some systems, trees seem to respond more slowly than grasses to rainfall arrival within a season (Rodríguez-Iturbe, 2000; Laio *et al.*, 2001; Scanlon *et al.*, 2005). However, in others, trees green up in advance of rainfall arrival and thus respond more quickly to rainfall arrival than grasses do (Archibald & Scholes, 2007; Ryan *et al.*, 2016). Soil texture may also mediate this process, by influencing the availability of water at different times of year (Fensham *et al.*, 2015). Thus, in theory, temporal niche differentiation may also contribute to determining tree–grass coexistence (Scanlon *et al.*, 2005).

An alternative dominant perspective suggests that tree–grass coexistence is maintained not by resources but by chronic disturbances, especially from fire (Higgins *et al.*, 2000; Bond *et al.*,

2005) and herbivory (Baxter & Getz, 2005; Staver *et al.*, 2009; Staver & Bond, 2014). Controlled fire experiments have demonstrated repeatedly that, by suppressing the maturation of saplings into adult trees, fire strongly impacts vegetation structure in savanna (Brookman-Amisshah *et al.*, 1980; Moreira & Klink, 2000; Higgins *et al.*, 2007), and global-scale analyses have suggested that fire is largely responsible for the extensive distribution especially of mesic savannas (Bond *et al.*, 2005; Staver *et al.*, 2011a,b). Modeling work has shown that fire – especially variability in fire through time – does provide a plausible mechanism to maintain the coexistence of trees and grasses (Higgins *et al.*, 2000). Moreover, although periodic fire experiments have shown that fire frequency can affect tree density and cover (Higgins *et al.*, 2007), long periods between fires, even where fires are frequent on average, may allow trees to emerge in variable savanna landscapes (Higgins *et al.*, 2000; Wakeling *et al.*, 2011).

Meanwhile, herbivore exclusion experiments generally show a qualitatively similar effect to that of fire (Staver & Bond, 2014): wherever grazers and browsers are excluded from savanna, trees respond with increased growth (Staver *et al.*, 2009; Sankaran *et al.*, 2013; but see Holdo *et al.*, 2009). Elephants in particular can have dramatic effects on vegetation by toppling large trees (Asner *et al.*, 2009). Formal theoretical evaluations and large-scale syntheses of the role of herbivory in maintaining tree–grass coexistence are mostly lacking, however.

Understanding how these processes combine and interact in real savanna landscapes presents the major challenge moving forward in savanna ecology. Continental-scale analyses suggest that tree cover generally increases with rainfall (Sankaran *et al.*, 2005; Bucini & Hanan, 2007; Good & Caylor, 2011; Staver *et al.*, 2011a,b; Lehmann *et al.*, 2014), and varies to some extent with fire frequency even within savanna (Sankaran *et al.*, 2008; Lehmann *et al.*, 2014). But grass biomass and fire frequency also appear to increase with increasing rainfall (Higgins *et al.*, 2000; Govender *et al.*, 2006; Archibald *et al.*, 2009), with concomitant effects on the tree layer (Bhattachan *et al.*, 2012; Tomlinson *et al.*, 2012). These large-scale analyses have documented broad patterns, but have been unable to constrain the variation in vegetation structure within and across savannas to a satisfying degree. Savannas may simply experience more unexplainable variation than other systems, especially at small scales (Scanlon *et al.*, 2007). Alternatively, we may hitherto have lacked the type and quality of data necessary to disentangle the interactive effects of rainfall, fire, herbivory, and especially soils on savanna vegetation.

Here, we have directly addressed the combination of these factors to examine how they determine vegetation structure in Kruger National Park in South Africa (Kruger). The geography of Kruger represents a natural experiment: it spans significant gradients in rainfall on soils from two contrasting geologic parent materials. Together with its unparalleled spatially extensive data sets of grass biomass, fire history, herbivore populations, and tree density, this natural experiment makes Kruger an ideal setting to ask how system-level interactions produce emergent patterns of vegetation responses to climatic and edaphic variability. One of the great strengths of Kruger's monitoring effort is that data sets

include information on size-structured tree density, not just on ecosystem-level metrics such as tree cover or biomass, which are usually the focus of large-scale analysis (Bucini & Lambin, 2002; Sankaran *et al.*, 2005, 2008; Staver *et al.*, 2011a,b; Lehmann *et al.*, 2014). Another strength is a long record of herbaceous layer monitoring, which is also lacking from all existing large-scale analysis. These elements may provide additional insights into constraints from fire and herbivory, both of which are principally demographic and vary by tree size (Trollope & Tainton, 1986; Hanan *et al.*, 2008; Moncrieff *et al.*, 2011; Staver & Bond, 2014). Thus, we examined interactions between all components of the savanna system for insights into how bottom-up and top-down processes interact to determine vegetation heterogeneity in savannas.

Materials and Methods

Study area

Kruger covers nearly 20 000 km² (22°20' to 25°30'S; 31°10' to 32°00'E) in low-elevation areas (260–839 m; the 'lowveld') of northeastern South Africa. It is dominated by two underlying parent materials, a granite and a basalt, broadly characterized as nutrient poor and nutrient rich, respectively (Venter, 1990). Mean annual rainfall ranges from 450 mm in the north to 750 mm in the south, although inter-annual variation is significant. The flora of Kruger includes > 400 species of tree and shrub and > 200 species of grass (Venter, 1990). Dominant tree families include the Fabaceae (including *Colophospermum mopane* and species of *Acacia*; Kirk ex J.Léonard) and the Combretaceae (including species of *Combretum* and *Terminalia*).

Fire is a major ecological feature of the park; the average fire return interval is *c.* 3.5 yr, but fire regimes vary locally, ranging from one fire per year to one every 34 yr (Van Wilgen *et al.*, 2004; Govender *et al.*, 2006). The time-scale of fire observation in the park has spanned conspicuous shifts in fire management policy in the park, but direct evaluations have found that policy-level interventions have been largely ineffective in changing fire regimes, at least at relatively large spatial and temporal scales, which instead have responded more directly to variation in grass biomass, arising from variation in rainfall (Van Wilgen *et al.*, 2004, 2008; Govender *et al.*, 2006).

The park is host to a diverse assemblage of African mammals. Impala (*Aepyceros melampus*) are by far the most numerous herbivore in the park (6.4 km⁻² or 380 kg km⁻²), while elephant (*Loxodonta africana*) make up the largest biomass (0.7 km⁻² or 1900 kg km⁻²). Herbivore biomass totals *c.* 6080 kg km⁻². Spatially explicit herbivore population data are not available for anything besides elephants, but anecdotal evidence suggests that herbivore impacts on vegetation vary substantially.

Data on grass biomass, tree populations, rainfall, fire, and soils

Kruger management established 533 Veld Condition Assessment (VCA) sites throughout the park in 1989 to monitor grass

biomass to inform fire management. Of these, grass was consistently monitored on 363 sites (see Supporting Information Fig. S1a). Because informing fire management was the primary goal, sites were located mostly in areas where herbivore impacts are relatively mild (i.e. sites were not located in areas dominated by grazing lawns, such as sodic sites and areas near rivers, where fires are rare). Grass biomass was measured every year in April from 1989 to 2008 in plots of 50 m × 60 m with a calibrated disc pasture meter. Measurements to derive plot-level grass biomass estimates were taken every 2 m along four 50-m transects, running at 0, 20, 40 and 60 m along the length of the plot.

A one-time tree census was added to monitoring efforts in 2008 at 222 sites. Tree data were collected at selected points along the same transects where grass data were collected: 30 m and 50 m along the first and third transects (which were located at 0 m and 40 m along the length of the plot), and 20 m and 40 m along the second and fourth transects (located at 20 m and 60 m along the length of the plot). Trees were recorded by size structure: the species and height of each tree were recorded (1) within 1 m of the sampling point for woody plants with a height of ≤ 1 m, (2) within 2 m of the sampling point for woody plants with a height > 1 m and ≤ 3 m, and (3) within 5 m of the sampling point for woody plants with a height > 3 m. Canopy size was also recorded for trees with height > 3 m. This plot design corrects for rarity of larger trees in savanna systems but still provides a quantifiable estimate of tree density and tree population structure. Densities were calculated using two size classes – saplings with height ≤ 3 m and trees with height > 3 m – but for direct comparison with remote-sensing-based tree cover estimates (from the MODIS satellite), tree cover was calculated as the per cent aerial canopy cover only of trees larger than 5 m tall.

Rainfall data were collected by Kruger management at a separate network of 22 sites throughout the park since 1989 and were interpolated to produce rainfall distribution maps (Fig. S1b). Kruger also keeps records of the spatial distribution of fires throughout the park, whether set by management or accidental (Fig. S1c); older records were kept by hand and have been digitized, while more recent ones were based on fire-scar mapping from MODIS satellite-derived data (accurate to 250 m). Thus, a continuous record is available dating from 1945 until 2008, although for this study only data that overlapped with the temporal extent of grass biomass monitoring (i.e. 1989–2008) were used. Spatially explicit elephant population data are available from annual fixed-wing aerial population censuses maintained by the park from 1985 to 2012, which were used to estimate time-averaged elephant density estimates (Fig. S1d). Average annual rainfall, fire, elephant density, and parent material data for each site were extracted from spatially explicit records in R v.2.8.1 (R Core Team, 2015).

Soil samples were collected to a depth of 20 cm at a subset of 58 of the most easily accessible sites (37 on granitic parent material and 21 on basaltic; Fig. S1b) during the rainy seasons of 2010 and 2011. Samples were collected at each of the corners and in the middle of the 50 × 60 m plots for a total of five samples per site, then homogenized and subsampled. Samples were dried at

60°C for 4 d, sieved at 2 mm, and then ground. Total soil carbon (C) and nitrogen (N) were analyzed via combustion on an NC 2500 Elemental Analyzer at Princeton University (detection limit *c.* 0.02% by weight; Carlo Erba Elantech, Lakewood, NJ, USA). Total soil phosphorus (P) was analyzed via nitric acid/hydrogen peroxide closed vessel microwave digestion at the University of California at Davis Soils Analytical Lab (ICP-AES; detection limit *c.* 0.001% by weight) (Sah & Miller, 1992; Kulmatiski & Beard, 2012). Soil texture was estimated by dispersion of soil aggregates using a 50 g l⁻¹ sodium hexametaphosphate (SHMP) solution and subsequent measurement based on changes in suspension density via a hydrometer (ASTM 152H (H-B Instruments, Trappe, PA, USA); detection limit of *c.* 1% sand, silt and clay) (Sheldrick & Wang, 1993). Soil sand, clay and silt content add up to 100%; sand content was therefore perfectly anti-correlated with clay + silt, and we have used only the former in statistical analysis.

Comparison with remote sensing data

To evaluate the scope of Kruger's rainfall gradient with continental variation in rainfall, we compared Kruger tree cover directly with tree cover estimates from the Landsat satellite (30 m resolution in the year 2000) (Hansen *et al.*, 2013) and from MODIS Vegetation Continuous Fields Collection 5 (500 m resolution in the year 2000) (Hansen *et al.*, 2002, 2003). Mean annual rainfall estimates were derived from the Tropical Rainfall Measuring Mission (TRMM) 3B42 Daily gridded rainfall product, available at a 0.25° resolution (Nicholson *et al.*, 2003). Tree cover layers were re-projected to a Lambert equal area projection with a 25 × 25 km resolution using bilinear interpolation to match the resolution of the TRMM rainfall data. We restricted our analysis to savannas in continental sub-Saharan Africa, and masked areas with winter rainfall (where vegetation would have a qualitatively different relationship with rainfall) and areas with > 10% cropland, swampland, water bodies, or urban areas using Global Land Cover 2000 (Bartholomé & Belward, 2005).

Data analysis

All statistical analyses were performed in R v.2.8.1. We modeled interactions between rainfall, geologic substrate, soil properties, grass, fire regimes, and the tree layer via structural equation modeling using the 'sem', 'lavaan', and 'semsem' packages. We defined plausible candidate models via local estimation (Grace *et al.*, 2007, 2010); variables were always included when they were significant at *P* < 0.05. Alternative candidate models were constructed to compare covarying independent variables (see Table S1) and to evaluate variables that were locally significant at the level of *P* < 0.1, to liberally include potential drivers. We then selected the best model at each scale by selecting the model with $\Delta\text{AIC} \geq 2$ compared with the next best model (where ΔAIC is the change in the Akaike Information Criterion) (Table 1) (Bolker, 2008). Where no single model was considered the best model, we selected the simplest model with $\Delta\text{AIC} < 2$ more than the model with the minimum AIC. We compared spatial SEM

Table 1 Results of nonspatial structural equation modeling examining relationships among savanna components in Kruger National Park, South Africa

| Model structure | | | Δ AIC | P from χ^2 |
|-----------------------------------------------------------|--------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------|--------------|-----------------|
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>rain</u> Max ~ <u>fire</u> Elephants ~ tree dens | Saplings ~ <u>rain</u> + <u>max</u> Tree density ~ sand + max + <u>elephants</u> Tree cover ~ tree density | 6.8 | 0.04 |
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>grass</u> Max ~ <u>fire</u> Elephants ~ tree dens | Saplings ~ <u>rain</u> + <u>max</u> Tree density ~ sand + max + <u>elephants</u> Tree cover ~ tree density | 35.3 | < 0.01 |
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>rain</u> Max ~ <u>fire</u> Elephants ~ tree dens | Saplings ~ <u>rain</u> + <u>max</u> Tree density ~ sand + max Tree cover ~ tree density | 0.8 | 0.03 |
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>rain</u> Max ~ <u>fire</u> Elephants ~ tree density | Saplings ~ <u>rain</u> Tree density ~ sand + max Tree cover ~ tree density | 4.7 | 0.01 |
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>rain</u> Max ~ <u>fire</u> Elephants ~ tree dens | Saplings ~ <u>max</u> Tree density ~ sand + max Tree cover ~ tree density | 0.0 | 0.03 |
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>rain</u> Max ~ <u>fire</u> Elephants ~ tree dens | Saplings ~ <u>1</u> Tree density ~ sand + max Tree cover ~ tree density | 17.8 | 0.02 |
| Sand ~ geology P ~ sand + rain C ~ sand N ~ sand | Grass ~ rain + sand Fire ~ <u>rain</u> Max ~ <u>1</u> Elephants ~ tree density | Saplings ~ <u>rain</u> + <u>max</u> Tree density ~ sand + max Tree cover ~ tree density | 32.0 | 0.07 |

Candidate models were constructed via a combination of linear modeling of each component separately. In each case, differences from previous models are underlined for emphasis. Geology, geologic substrate; rain, annual rainfall; sand, soil per cent sand; P, soil per cent phosphorus; C, soil per cent carbon; N, soil per cent nitrogen; grass, grass biomass; fire, fire frequency; max, maximum inter-fire interval; elephants, elephant density; sapling, sapling density; tree cover, per cent tree cover. We selected the model with Δ AIC < 2 more than the 'best' model; in this case, the simplest model was the best model.

results in the package 'sesem' (Lamb *et al.*, 2014) with traditional nonspatial models to determine whether accounting for spatial autocorrelation was important (Figs S2, S3).

Results

Spatially explicit structural equation modeling revealed that nonspatial models were preferred to models that explicitly accounted for spatial distributions (Fig. S2). Moreover, few variables showed any improvement in the strength of predictive relationships with increasing distance lag (Fig. S3). Analyses are thus presented hereafter for nonspatial structural equation models.

Soils

Granitic and basaltic parent materials were characterized by distinct soil texture; soil sand content ($= 1 - (\text{clay} + \text{silt content})$) was significantly higher on granite than on basalt parent materials (Table 1; Figs 1, 2a). Higher sand content was in turn linearly associated with lower soil C, N, and P (Table 1; Figs 1, 2b–d), probably in direct response to nutrient retention by clay and silt.

Grass biomass

Grass biomass increased with mean annual rainfall and decreased with soil sand content (Table 1; Figs 1, 3a). Increasing rainfall clearly favored grass biomass accumulation; responses to soil texture indicate a grass biomass response either to water availability (if clay-rich soils retain moisture in surface layers; Holdo, 2013) or to nutrient availability (as clay-rich soils retain soil nutrients), although structural equation modeling indicates a more direct relationship between soil texture and grass biomass than with soil nutrients.

Fire

Fire increased in frequency most directly with increasing rainfall (Table 1; Figs 1, 3b), presumably reflecting a response to increased grass biomass accumulation rates, although the response of fire frequency to rainfall was more direct. An interaction with grazing by herbivores other than elephants (usually considered to be more intense on nutrient- and clay-rich basaltic soils; Redfern *et al.*, 2006) may prevent fire frequency from increasing in response to grass biomass on nutrient-rich basalts.

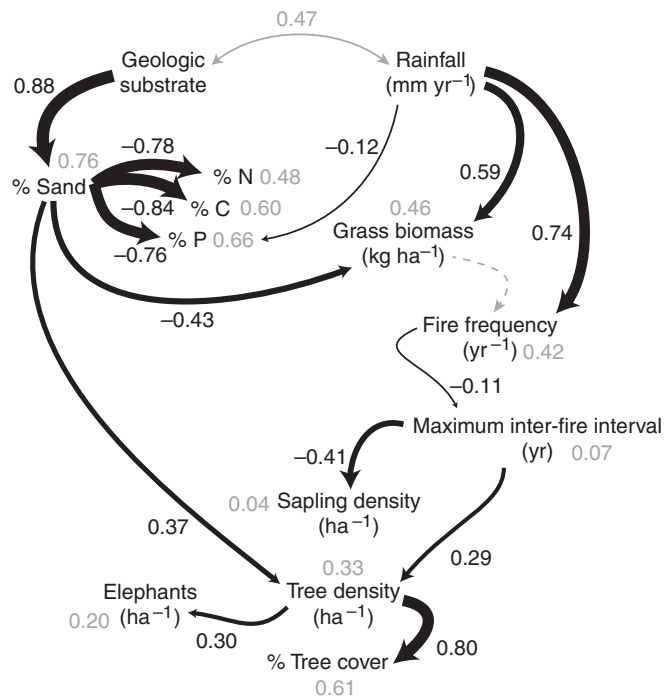


Fig. 1 Structural equation modeling results showing probable interactions among soil, rainfall, grass, fire, and tree savanna components. Black lines show statistically supported effects; line widths scale with the strength of the effect (given in black text). Gray text attached to each variable shows its total R^2 . The gray dotted line denotes a link between grass biomass and fire frequency that has been widely reported but was not supported here. See Table 1 for model selection results.

By contrast, the maximum interval between successive fires was much less predictable, although fire frequency did weakly constrain the maximum time between fires (Table 1; Fig. 1). Unexplained variability in the maximum inter-fire interval suggests a role for stochasticity in fire spread and possibly even fire management (although Kruger management attempted to implement a regular 3-yr fire return interval throughout the park for most of its documented history; Van Wilgen *et al.*, 2004) in shaping fire regimes.

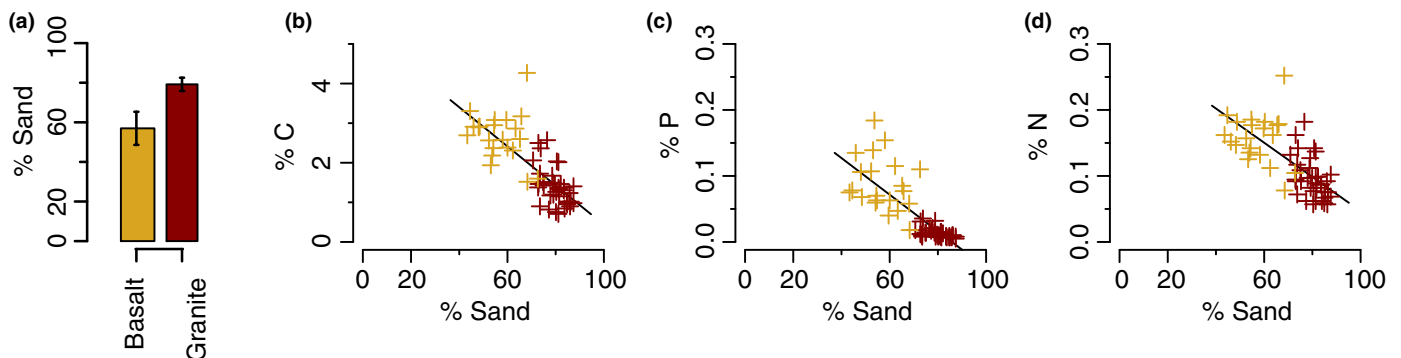


Fig. 2 Soil texture variation by (a) parent geology, (b) soil per cent carbon (C), (c) soil per cent phosphorus (P), and (d) soil per cent nitrogen (N), to soil per cent sand. Yellow and red represent plots on basaltic and granitic parent materials, respectively. Error bars, \pm SD; black lines represent lines of best fit, shown only when relationships were statistically supported. See Table 1 and Fig. 1 for model results.

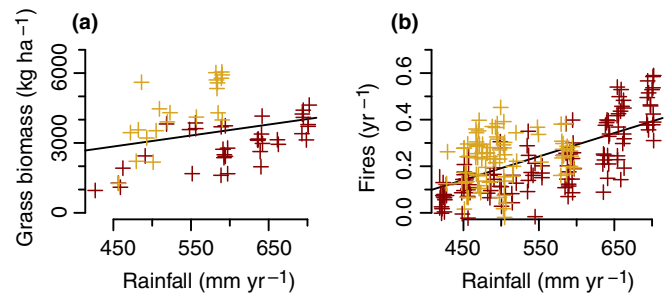


Fig. 3 Mean grass biomass (a) and fire frequency (b) response to rainfall and geologic substrate. Yellow and red represent plots on basaltic and granitic parent materials, respectively. Black lines represent lines of best fit, shown only when relationships were statistically supported. See Table 1 and Fig. 1 for model results.

Tree density

Sapling density (of trees with height ≤ 3 m) was not very predictable (Table 1; Fig. 1). Maximum inter-fire interval was the preferred predictor of variation in sapling density, and sapling density decreased with more time between fires (Fig. 4). However, sapling density was not predictable compared with other components of the Kruger savanna system.

Large-tree density (of trees with height > 3 m) was quite predictable, however (Table 1; Fig. 1). The idea that elephant density and large-tree (height > 3 m) density were linked was well supported. Higher elephant densities were associated with higher tree density (Table 1; Figs 1, 5). However, once we had accounted for that interaction and other determinants of tree density, elephants had relatively minor effects on local variation in tree density (Fig. 1).

Tree density also strongly increased with increasing soil sand content and increasing maximum inter-fire interval (Table 1; Figs 1, 6). The combination of soil sand fraction, maximum inter-fire interval, and elephant density explained a substantial degree of variation in large-tree density – 33% at the plot level. Tree cover varied closely with large-tree density.

Meanwhile, rainfall was not a significant determinant of large-tree density (Table 1; Figs 1, 6). This runs counter to studies at the scale of all savannas, which have noted a strong role for

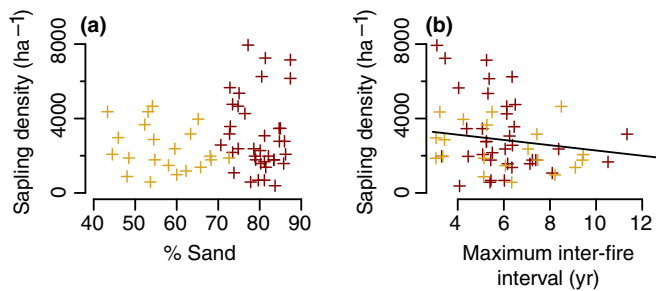


Fig. 4 Sapling (height ≤ 3 m) density response to soil per cent sand (a) and maximum interfire interval (b). Yellow and red represent sections on basaltic and granitic parent materials, respectively. The trend line is shown only for maximum inter-fire interval, as it was the significant predictor of sapling density. Black lines represent lines of best fit, shown only when relationships were statistically supported. See Table 1 and Fig. 1 for model results.

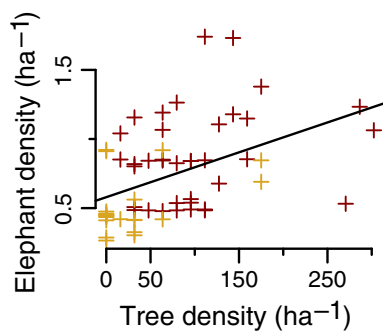


Fig. 5 Tree (height > 3 m) density relationship with elephant density. Structural equation modeling suggested that elephant density responded to tree density, but that elephant effects on trees were not a prominent determinant of tree density. Yellow and red represent sections on basaltic and granitic parent materials, respectively. Black lines represent lines of best fit, shown only when relationships were statistically supported. See Table 1 and Fig. 1 for model results.

rainfall in determining maximum potential tree cover (but with significant residual variation; Sankaran *et al.*, 2005, 2008; Staver *et al.*, 2011a,b). This is probably not particularly noteworthy, however, as Kruger's rainfall gradient (~ 400 – 700 mm mean annual rainfall) is sizeable but nonetheless minor compared with the total range in rainfall over which savannas occur (see Fig. S4 for a comparison with the relationship between rainfall and tree cover over sub-Saharan Africa, showing that Kruger has tree cover and variability consistent with other savannas, but a relatively narrow range of rainfall).

Discussion

Our results indicate: (1) that grass biomass increased directly with rainfall and decreased with soil sand content, (2) that higher rainfall also resulted in higher fire frequency (probably mediated by grass biomass; Govender *et al.*, 2006; Archibald *et al.*, 2009), but that the maximum interval between successive fires was less predictable, (3) that, unlike grass biomass, large-tree density increased with soil sandiness, probably reflecting soil moisture water dynamics, and (4) that long periods

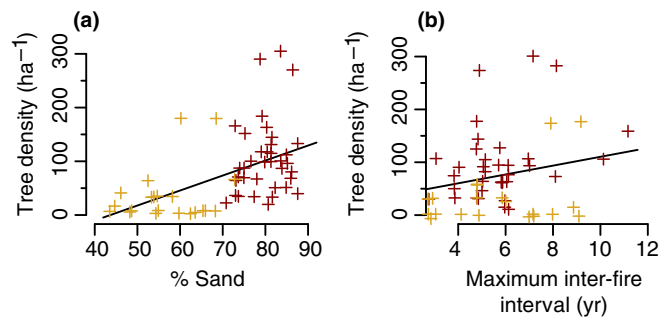


Fig. 6 Tree (height > 3 m) density response to soil per cent sand (a) and maximum interval between fires (b) at the landscape level. Yellow and red represent sections on basaltic and granitic parent materials, respectively. Black lines represent lines of best fit, shown only when relationships were statistically supported. See Table 1 and Fig. 1 for model results.

between fires decreased small tree density and increased large-tree density.

Bottom-up constraints on grasses vs trees

Here, we observed a ready response of grass biomass to rainfall and soil texture. This appears consistent with experiments showing that, locally, grasses have direct access to water (Riginos, 2009; February *et al.*, 2013; Holdo & Brocato, 2015) and nutrients (Cech *et al.*, 2008; Craine *et al.*, 2009; Cramer *et al.*, 2010) because they compete more effectively for resources than trees do. Statistical results indicate that grass biomass increases more directly with increasing rainfall and soil clay/silt content than it does in response to increasing soil nutrient availability. This may simply mean that total soil N and P do not reflect available nutrient concentrations, which can be difficult to define and measure. Alternatively, soil moisture, resulting from an interaction between rainfall and soil texture, may truly be more limiting of grass biomass than nutrients.

However, this may be an oversimplification – tree density was highest (and grass biomass lowest) on sandy soils, where potential infiltration of water to deeper soil layers is greatest (see also Williams *et al.*, 1996; Sankaran *et al.*, 2008; Case & Staver, 2017), which suggests that hydrology may substantially modify the dynamics of tree–grass competition. Tree vs grass access to water may in fact depend on rates of water infiltration to deeper soil layers, where only trees have roots (February & Higgins, 2010; Kulmatiski & Beard, 2012; Holdo & Nippert, 2015; Nippert & Holdo, 2015). Although recent evidence suggests that trees do not exclusively use deeper water than grasses (see e.g. Seghieri, 1995; February & Higgins, 2010; O'Donnell *et al.*, 2015 for examples of shallow-rooting trees), trees sometimes can have deeper roots and can access deeper water than grasses (Seghieri, 1995; Bhattachan *et al.*, 2012; Kulmatiski & Beard, 2012; Mazzacavallo & Kulmatiski, 2015). Infiltration might therefore alleviate water/nutrient limitation in the soil subsurface, thereby promoting faster growth rates of deeper rooted trees in sandy soils than clayey ones.

Recent work has suggested another mechanism by which soil texture could impact tree occurrence; instead of sandy soils

benefiting trees, it has been suggested that clay soils may induce water stress (Colgan *et al.*, 2012; Colgan & Asner, 2014; Fensham *et al.*, 2015). Because they are subject to much lower water potentials under dry conditions, clay soils may prevent the accumulation of large trees in savanna landscapes by inducing higher levels of large-tree mortality compared with sandy soils (Fensham *et al.*, 2015). This mechanism cannot explain the much higher grass biomass associated with clay soils, but may nonetheless contribute to decreasing tree density and cover.

Positive large-tree responses to soil sand indicate that access to water availability probably does benefit trees. However, this did not directly translate into a positive tree density response to rainfall. The rainfall gradient in Kruger may simply be too short to reflect large-scale patterns (Sankaran *et al.*, 2005, 2008). Grass competition may also play a role, or higher fire frequency at higher rainfall (Govender *et al.*, 2006; Archibald *et al.*, 2009) may mask the direct impacts of rainfall on trees. Thus, even if water does directly benefit trees, this may only be apparent locally when rainfall does not more directly benefit grasses and result in increasing fire frequency.

Fire and tree density

The structure of the tree layer in this savanna was also limited by the fire regime, although less by fire frequency than by consistently short intervals between fires. Large-tree density (height > 3 m) increased as the longest period between fires increased, while sapling density (height ≤ 3 m) decreased. This is a novel result and makes sense – growth rates being equal, trees probably recruit from saplings to trees during the longer periods without fire. Trees are more vulnerable to fires when they are small (Hoffmann, 1999); while they resprout readily from below-ground root reserves (Hoffmann *et al.*, 2009; Schutz *et al.*, 2009), fires prevent saplings from growing into large trees. Saplings that grow faster become fire-resistant more quickly (Wakeling *et al.*, 2011), but a longer interval between fires may also promote tree establishment even by slower growing trees (Higgins *et al.*, 2000).

Empirical evidence demonstrating that the maximum inter-fire interval determines fire effects on trees suggests the key question: what drives variation in time between fires in savanna? Intuitively, the maximum interval between fires was loosely constrained here by the total fire frequency, which in turn increased with rainfall (probably mediated by increasing grass biomass (Govender *et al.*, 2006; Archibald *et al.*, 2009), although local variability, data quality or sampling season obscured this well-established relationship here). However, the relationship between average frequency and the maximum interval between fires was not tightly predictive, and fire regimes were relatively variable even though partially determined by bottom-up processes.

One possibility is that fire frequency decreases during and after droughts, when grass biomass accumulates more slowly (Van Wilgen *et al.*, 2004). While trees probably do not recruit during droughts (Fichtler *et al.*, 2003; Brienens & Zuidema, 2006; Therrell *et al.*, 2006), they may escape the effects of fire in the years following drought, when a lagged grass recovery (Sala *et al.*,

2012) prevents intense fires even though water is available. Trees could thus potentially recruit during long fire-free intervals associated with droughts. Alternatively, temporal variation in fire frequency may be related to variations in grazer pressure, especially related to major collapses in grazer populations resulting from disease (Holdo *et al.*, 2009); explosions in fire frequency with herbivore population collapse have been observed only in the Serengeti, however, where grazers are strongly dominant. Most savanna herbivore communities include browsers and mixed feeders, and thus tree establishment – rather than tree suppression – is usually associated with reductions in herbivore populations (Prins & van der Jeugd, 1993; Staver & Bond, 2014), so this mechanism is probably less important in Kruger. A final possibility is that fire is stochastic. The distribution of inter-fire intervals may be predictable, either over very long time-scales or across sites (Schertzer *et al.*, 2015), but the length of time between any two fires may not be.

Unfortunately, fire experiments have uniformly been established to examine the effects of periodic, not stochastic, fire regimes (Brookman-Amisshah *et al.*, 1980; Moreira & Klink, 2000; Russell-Smith *et al.*, 2003; Higgins *et al.*, 2007), and few areas have a reliable fire record sufficiently old to give reasonable estimates of the maximum historical interval between successive fires. Here, we show that, although fire frequency varied predictably with rainfall, the maximum time between fires was less predictable. The most prominent fire effects on tree emergence were thus uncoupled from the tight bottom-up relationship between rainfall, grass biomass, and fire frequency.

Herbivores and tree density

Curiously, elephant and tree density were positively related at the level of landscape spatial pattern, which obscured the negative effects of elephants on trees that have been documented elsewhere (Moncrieff *et al.*, 2008; Asner *et al.*, 2009). This probably reflects a preference by elephants for woodier environments (Loarie *et al.*, 2009; Young *et al.*, 2009). Having accounted for all other sources of variation in tree density, elephants were a minor determinant of tree density. This may be partially attributable to scales of observation, however, given a long history of previous results demonstrating impacts of elephants on trees (Pellew, 1983; Baxter & Getz, 2005; Guldmond & Van Aarde, 2008); elephants can move around substantially, such that using large-scale aerial counts may not be helpful for evaluating their effects on plot-scale tree heterogeneity.

Unfortunately, data were not available to consider the impacts of smaller herbivores on the spatial heterogeneity of savanna vegetation, which can be substantial (Staver *et al.*, 2009; Sankaran *et al.*, 2013; Staver & Bond, 2014). Nonetheless, herbivores do represent a potential alternative (or supplementary) pathway that may reduce tree growth, density, and cover on clay- and nutrient-rich soils, where herbivory, especially by the diverse meso-herbivore community found in Kruger, can be intense (Redfern *et al.*, 2003, 2006). Intense browsing by meso-herbivores may thus account for some unexplained variation in tree cover, or alternatively may be responsible for some of the reported negative

response of large-tree density and cover to clay- and nutrient-rich basaltic soils. This merits further direct evaluation.

Conclusions

Patterns of spatial heterogeneity in savanna suggest that vegetation structure responds to joint constraints from bottom-up and top-down processes. On the one hand, grasses and trees responded to rainfall and soil texture differently, consistent with a conceptual model in which water infiltration into deeper soils on sands promotes tree growth, while surface soil moisture, which is higher on clay soils and in higher rainfall areas, generally favors grasses. Water stress or more intensive herbivory on clay soils may also contribute to decreasing tree density and cover.

Meanwhile, fire had strong effects on large-tree (height > 3 m) density and cover; trees were denser where a long period without fires had released suppressed saplings. Although average fire frequency was tightly constrained by rainfall (probably via its effects on grass biomass), fire was variable through time (perhaps stochastically) such that some areas experienced a longer lull between fires than others. Fire limitations on tree emergence were thus partially orthogonal to the tight coupling between rainfall, grass biomass, and fire frequency. Together, these joint constraints emphasize that explicit consideration of both bottom-up and top-down processes in savannas promises a predictive understanding of spatial variability in savanna vegetation structure and tree–grass interactions.

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Author contributions

A.C.S. designed the analysis, collected soil data, and wrote the paper. J.B. synthesized and curated climate, vegetation, fire, and herbivory data. L.H. provided conceptual and manuscript feedback.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Maps of Kruger National Park, South Africa, showing geologic substrate, mean annual rainfall, mean fire frequency, and elephant density.

Fig. S2 Model AIC by lag distance for spatial structural equation modeling results.

Fig. S3 Strength of path by lag distance for spatial structural equation modeling.

Fig. S4 Savanna tree cover in Africa from Landsat and MODIS remote-sensing products plotted in comparison with tree cover from Kruger.

Table S1 Correlation matrix for all variables included in structural equation models

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