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Variability in fire-induced change to vegetation physiognomy and biomass in semi-arid savanna

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Abstract. Fire plays an intrinsic role in shaping the biophysical attributes of savanna ecosystems. Savanna fires limit vegetation biomass below their climatically determined potential, but the magnitude of this effect and how it varies across heterogeneous landscapes are poorly understood. In this study, we explore woody tree structure and canopy characteristics across a fire manipulation experiment that has been maintained for 63 yr in South Africa's Kruger National Park. Our study design assessed three late dry-season fire regimes (biennial, triennial, and unburnt) across a precipitation gradient (737–496 mm/yr) spanning four different landscapes with a mixture of sandy and clay soils. We used terrestrial laser scanning (TLS) to quantify tree height, canopy cover, and aboveground carbon storage across the experimental treatments. Vegetation physiognomy was influenced by the interaction between landscape and fire frequency. In the absence of fire, woody height, cover, and biomass increased with increasing rainfall. The presence of fire acted to reduce structure and biomass as expected, but the magnitude of this effect increased with increasing rainfall. We found minimal difference between the effects of biennial or triennial burning—except at the wettest site where the triennial fire plots had half the biomass of those burnt biennially. The rainfall dependent fire–vegetation relationships shown here provide empirical quantification of top-down constraint by fire and highlight the challenges of predicting responses to disturbances in these inherently heterogeneous ecosystems. Robust quantification of 3D structure and dynamics through TLS will be useful for constraining carbon stock models and predicting trajectories of change under future climate and land-use conditions.

Key words: fire frequency; Kruger National Park; savanna; terrestrial laser scanning; vegetation structure.

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Introduction

Savannas cover roughly 20% of the world's dry tropical landscapes (Scholes and Archer 1997, Murphy et al. 2015). They are critical to the regulation of the terrestrial carbon cycle and contribute 30% of global net primary production (Grace et al. 2006). Savanna ecosystems are characterized by a mixed physiognomy that includes a continuous grass layer mixed with variable amounts of woody cover (Sankaran et al. 2008). Because of the contrasting response of the two coexisting plant guilds (trees and grasses) to environmental and climatic variables such as water and light availability, and rising CO_2 concentration and temperature, it is challenging to isolate the effects influencing the relative abundance of these co-occurring life forms. Classical ecological theory, such as Walter two-layer hypothesis, predicts the equilibrium coexistence of trees and grasses due to spatial niche separation and assumes that grasses use subsurface water, while trees have access to deeper water reserves (Walter 1971, Ward et al. 2013). In addition to water availability, tree–grass coexistence has been ascribed to the stochastic interactions between edaphic conditions and consumer control (herbivores and fires) (Coughenour and Ellis 1993, Scholes and Archer 1997, Bond and Keeley 2005, Levick and Rogers 2011); however, an ecological explanation for the observed savanna structural intricacy that unites the characteristics of these factors in space and time is still not available.

Fire exerts strong control on savanna structure, and modification of fire regimes influences the functioning of savanna vegetation communities (Moreira 2000, Bond et al. 2005, Govender et al. 2006, Higgins et al. 2007, Smit et al. 2010, Levick et al. 2012). Fire-driven structural changes occur at multiple scales, altering vertical canopy height distributions and plant basal area at the local scale, and changing the tree–grass balance at landscape scales. These hierarchically nested structural variations have important implications for ecological processes, including changes in carbon stocks (Bond et al. 2005, Higgins et al. 2007), nutrient cycling (Pellegrini et al. 2015), hydrology, (Asner et al. 2004, Savadogo et al. 2007), and wildlife habitat availability (Parr and Andersen 2006). Therefore, studying the effects of prevailing fire regimes on vegetation structure is integral to understanding the current changes occurring in these ecosystems, such as loss of large trees and increased shrub thickening (Levick and Asner 2013), and for forecasting ecosystem response under changing climate and land-use scenarios.

Natural and anthropogenic fires in savanna ecosystem account for the vast majority of global burned areas, with 20% burnt annually (Dwyer et al. 2000, Lehmann et al. 2014), thus reducing the substantial dry matter (Scholes et al. 1996). Numerous studies corroborate that fire mostly reduces woody biomass and the absence of fire could potentially transform these landscapes into closed woodlands (Van Wyk 1971, Bond et al. 2005). A four decade fire manipulation study across the savannas of Kruger National Park, South Africa, showed that total fire suppression allowed significant increases in woody biomass; lower fire frequency regime caused smaller increases, but more frequent fires resulted in greater losses of woody biomass (Higgins et al. 2007). Similarly, Australian estimates suggest that while the net ecosystem productivity in savannas without fire is 3 $\mathrm{Mg{\cdot}Cha^{-1}{\cdot}yr^{-1}}$, it is only 1 $\mathrm{Mg{\cdot}Cha^{-1}{\cdot}yr^{-1}}$ with fire (Williams et al. 2004), as well as tree diversity of mesic savannas in Australia increases where fire is excluded (Lawes et al. 2011), with few species typically associated with rainforest (Williams et al. 2003). Significant changes in fire regimes could therefore potentially lead to a biome switch.

Fire limits woody plant demography through its impact on seedling recruitment, growth, and topkill (Higgins et al. 2000, Bond and Keeley 2005, Hanan et al. 2008). Topkill in tree saplings prevents them from escaping the zone of influence of grass fueled fires, thus causing multi-stemmed morphology and reducing the number of larger size classed individuals (Enslin et al. 2000, Jacobs and Biggs 2001). Similarly, even with some large individuals topkill can cause considerable loss of biomass, which cannot be quickly regained (Hoffmann and Solbrig 2003). The capacity to resprout depends on the interactive effect of characteristics of the fire regime, that is, frequency, season and intensity (Gill 1975), bud availability and their level of protection, and availability of resources (nutrients and water) (Clarke et al. 2013). Resprouting increases with increasing soil fertility and moisture gradient which causes canopy and understorey closure rapidly after fire events (Clarke et al. 2005). In wet (high-rainfall) savannas, where tree–grass competition is reduced due to water availability, trees can potentially escape the flame zone and gain taller canopies despite high fire frequency (Lawes et al. 2011, Levick et al. 2012). On the other hand, lower fire frequencies can result in more intense, destructive burns due to greater accumulation of fuel load (Govender et al. 2006).

Burn intensity can be experimentally manipulated by selecting the season of the fire, as well as the return frequency. Early dry-season fires are of low intensity and less extensive, while late dry-season burns often produce high-intensity fires (van Wilgen 2009). High-intensity fires can be very effective at reducing encroachment by woody shrubs in the wet savannas, which opens up the landscape but at the same time such practices result in the loss of large trees (Smit et al.

2016). Further, the effects of fire regimes on vegetation structure can vary with geological substrates, through the differential soil and vegetation patterns that they give rise to (Smit et al. 2010, Levick et al. 2012). In addition, the vegetation–fire dynamics can be regulated by herbivory which alters the fuel loads, thereby collectively shifting savanna landscapes toward either grassland or woodland (Asner and Levick 2012, Pellegrini et al. 2017). However, it is often difficult to characterize the relative effects of herbivory from other ecological processes, leading to uncertainty about its relative importance as a driver of vegetation structure across landscapes (Levick and Rogers 2008, Asner et al. 2015, Davies et al. 2018).

Monitoring with traditional field-based techniques has provided insights into the role of fire regimes in shaping woody vegetation structure (Enslin et al. 2000, O'Regan 2005, Higgins et al. 2007, Devine et al. 2015). However, field inventory studies are restricted to specific plots and rely on sampling strategies such as belt transects or quadrats, which may not adequately describe the spatial variability of vegetation structure within a landscape. In recent years, airborne light-detection and ranging (LiDAR) techniques have emerged as a key remote sensing technology for advancing the knowledge of vegetation structural changes in savannas due to fire (Smit et al. 2010, 2016, Levick et al. 2012). These approaches have enabled the characterization of vegetation organization in space and time, including canopy position, extent, and connectivity (Lefsky et al. 2002). Nevertheless, in a mixed tree–grass system significant proportion of the vegetation occurs in short size-classes and resides beneath the overstory canopy. Airborne instruments often fail to detect the shrub stratum canopy and stem architecture. The effect of the arrangement of fine-scale vegetation elements becomes more critical when examining the effect of fires on vegetation communities at small and local scales. As such, there is a need to capture and describe these complex vegetation structures in greater detail.

Terrestrial LiDAR, also referred to as terrestrial laser scanning (TLS), characterizes the three-dimensional (3D) distribution of vegetation structure at high resolution and accuracy (Dassot et al. 2011). In doing so, it enables measurement of conventional woody biophysical parameters with less uncertainties (Calders et al. 2015) and allows for the creation of new metrics such as canopy density and base height which capture additional aspects of woody vegetation structure (Newnham et al. 2015). Cuni-Sanchez et al. (2016) demonstrated the potential of one such new metric, that is, vertical plant profiles across a Central African savanna forest mosaic for assessing long-term structural differences among the vegetation types. These new metrics have provided fresh insights into the distribution, abundance, and diversity of vegetation species. Terrestrial laser scanning data can therefore be used to inform conservation managers as to the impacts of fire policies on fine-scale changes in savanna structure.

In this study, we employ advances in TLS technology to capture the 3D structure of woody vegetation across a long-term fire experiment in Kruger National Park, South Africa. Our specific aims are to explore: (1) How vegetation structure (average and maximum height, canopy cover) and aboveground carbon storage respond to varying fire frequencies; (2) does the effect of fire regimes vary across plot and landscape scale; and (3) how differences in rainfall across the landscapes interact with fire frequency in altering vegetation structure.

Methods

Study site and experimental design

Our study focused on the experimental burn plots (EBPs) of Kruger National Park (KNP), a national reserve covering 1.9 million ha in north-eastern South Africa (Fig. 1). Kruger National Park is comprised primarily of sub-tropical wooded savannas and consists of mopane (*Colophospermum mopane*), knobthorn (*Acacia nigrescens*), marula (*Sclerocarya bierra*), *Combretum* species, sicklebush (*Dichrostachys cinerra*), and silver cluster-leaf (*Terminalia sericea*) (Gertenbach 1983).

The park encompasses a gradient of increasing rainfall from the semi-arid north (400 mm mean annual rainfall) to the mesic south (750 mm mean annual rainfall) (MacFadyen et al. 2018). Soils are heterogeneous and are related to the geomorphological division between granites in the west, weathering to sandy soils, and clay soils derived from basalt erosion in the east. The

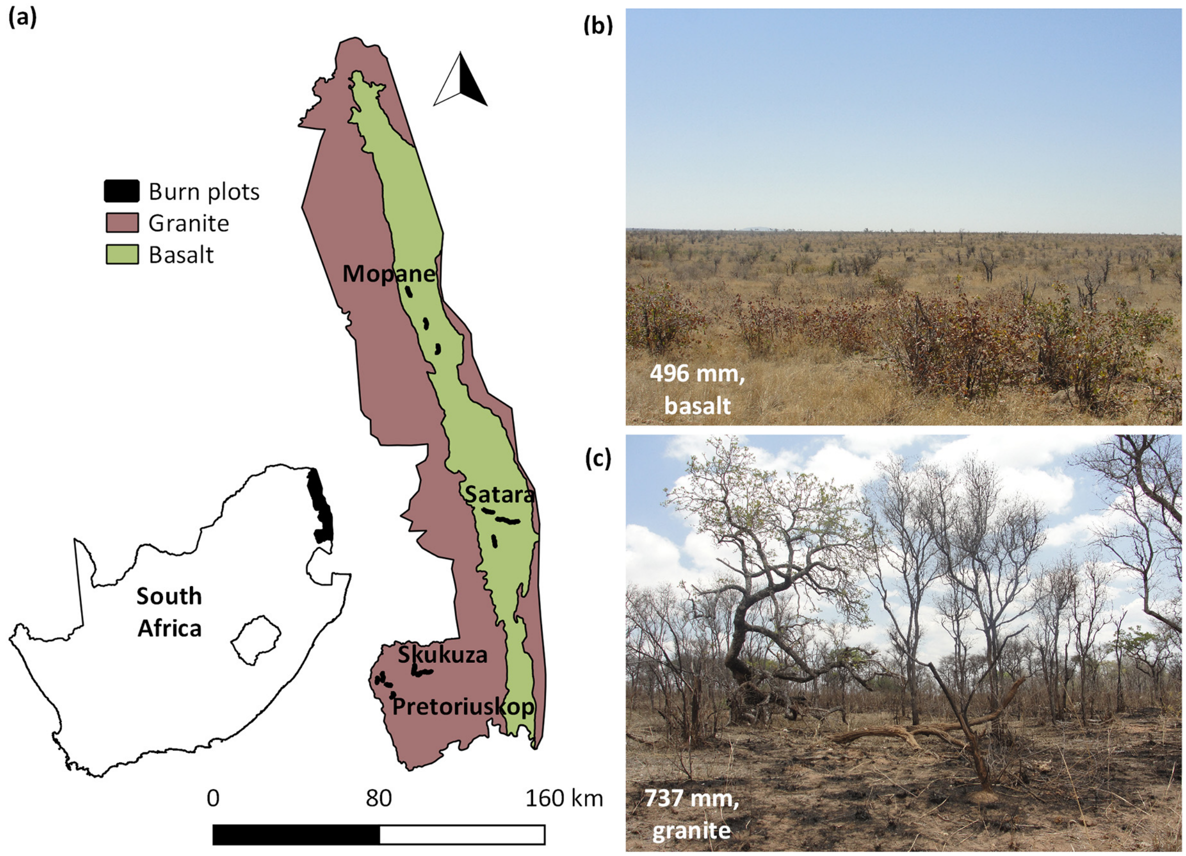

Fig. 1. (a) Location of the four experimental burn plots within Kruger National Park, South Africa. Differences in vegetation structure along the precipitation gradient. (b) Upper photograph is from Mopane EBP receiving 496-mm mean annual precipitation (MAP) on basaltic soils. (c) Lower photograph is from Pretoriuskop EBP receiving 737-mm MAP on granitic soils.

EBPs were set up in the KNP in 1954 to study the effects of fire on vegetation under grazing pressure from herbivores (van Wilgen et al. 2007). The experiment consists of application of controlled fires at varying frequencies (annual, biennial, and triennial) and seasons (Dry: August and October; Wet: February, April, and December), on a set of 7-ha plots with four replicates across the four major vegetation landscapes (Mopane, Satara, Skukuza, and Pretoriuskop) of the KNP.

Our study focused on all four EBP regions, stretching from Mopane and Satara in the north to Skukuza and Pretoriuskop in the south. We investigated two burn strings at each site, and the selected EBPs spanned 168 ha with differing plant productivity and physiognomies, caused by the gradients in mean annual precipitation (MAP) (Mopane: 496 mm, Satara: 544 mm, Skukuza: 650 mm, and Pretoriuskop: 737 mm), geology, and soil types (fertile in Mopani and Satara, infertile in Skukuza and Pretoriuskop) (Biggs et al. 2003). Within each EBP, we evaluated three late dry-season treatments: (1) fire exclusion (unburnt), (2) October triennial burn, and (3) October biennial burn. The late dry-season fires were considered due to their effect on demographic legacies of current tree populations (Levick et al. 2015), since between 1941 and 1996, most management fires in KNP and surrounding savanna landscapes were concentrated in the late dry season (Govender et al. 2006).

Woody vegetation data

We mapped EBPs across four landscapes in October 2016 using the RIEGL VZ-2000 terrestrial laser scanner (RIEGL Laser Measurement

Systems GmbH). The RIEGL VZ-2000 is a multiple return LiDAR scanner which operates in the near-infrared spectrum (wavelength 1500 nm) with a beam divergence of 0.30 mrad. The laser ranging data were combined with an external differential global positioning system (GPS) (accuracy 3 cm), to determine the 3D location of each laser return. Inertial measurements (roll, yaw, and pitch) of the scanner were collected through an internal compass and inclination sensors. We used a systematic scanning design, by placing the scanner at 50-m intervals along each EBP, giving a minimum of 15 scans per EBP (Fig. 2). These multiple single scans ensured complete coverage of the vegetation structure within the EBP. However, to reduce the time and effort required for multi-scan approach (see Liang et al. 2016), we utilized a vehicle rooftop mount for operating the scanner, with a scanner height of 2.5 m. The LiDAR data for all the scan positions were collected at 1010-kHz pulse repetition rate and an angular sampling of 0.02° in both azimuth and zenith direction, ensuring sufficient point density to enable fine-scale description of even smaller woody vegetation.

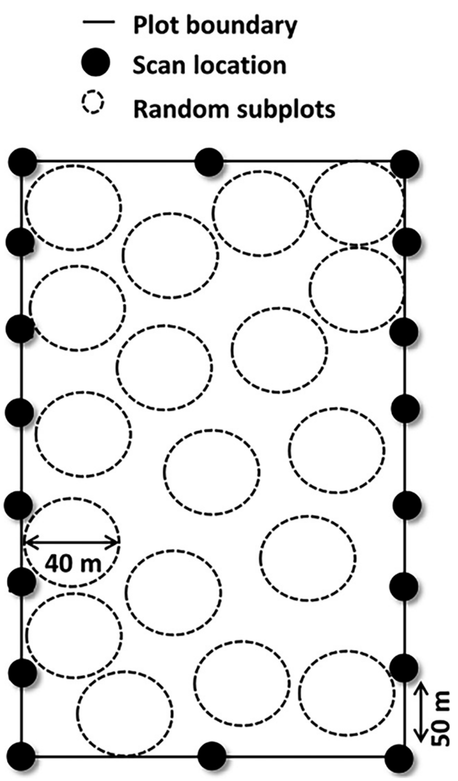

Fig. 2. The TLS scanning setup of the EBPs with solid black dots indicating the scan locations. Sampling of the EBPs was achieved by placing random circles of 40 m radii depicted with dotted circles.

Point cloud processing

Multiple LiDAR scans of each EBP were first co-registered using the RiSCAN PRO package (RIEGL GmbH). A coarse registration between the scans was achieved using large woody trees (branch tips and nodes) as tie points, which were present in all the scans. Since the LiDAR survey took place in the leaf-off stage at the end of the dry season, the occlusion of woody trees by bushes and understory from different scan positions was minimized. The coarsely merged scans were fine tuned by eliminating the translation and rotation errors with a multi-station adjustment (MSA) approach. MSA iteratively adjusts the position and orientation of each point cloud by least square error optimization. Once the best fit between the scans is completed, the calculated transformation matrix is applied to all the raw point clouds, to associate them into a common coordinate system. The standard deviation of the registered scans for all EBPs ranged from 0.01 to 0.02 m. Registered point clouds were then filtered to remove noisy isolated points or those with low reflectance using the default reflectance filters in RiSCAN PRO. The presence of noise was often attributed to dust in the atmosphere, wind, or edges of the bushes close to the scanner. Point clouds were then trimmed to include only 3D data within the EBP region.

The preprocessed LiDAR data were used to derive height normalized point clouds (Fig. 3), which were subsequently used to produce count frequency rasters by batch scripting several modules of LAStools (rapidlasso GmbH, 2014; Isenburg 2014). We computed height count rasters from 0 m, at every 0.5-m interval of the LiDAR data, and scaled them to percentage canopy profiles. Woody canopy height was estimated at a step size of 0.05 m to create approximately 8000 × 9000 pixel rasters using the highest 'z' coordinate among all the LiDAR returns in the corresponding pixel area. The resulting canopy height grids were hard classified in SAGA GIS (SAGA GIS, 2016; www.saga-gis.org), assuming the LiDAR data between 0.0 and 0.5 m as

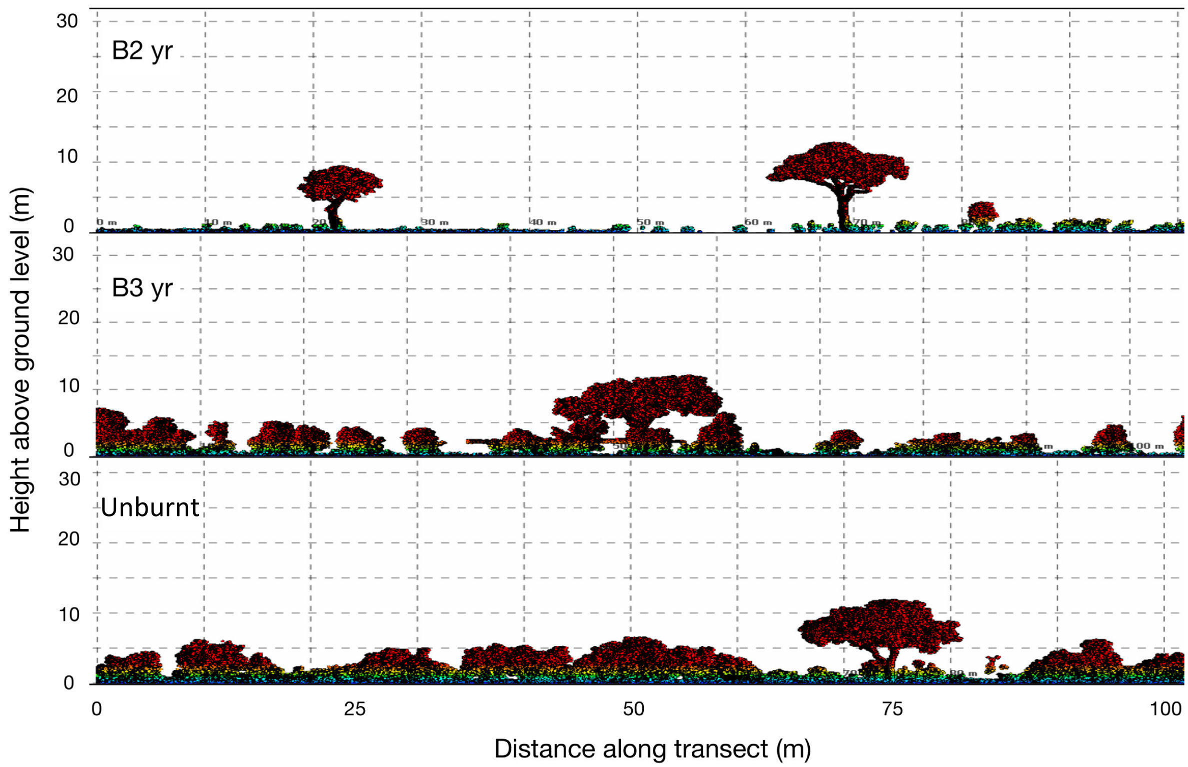

Fig. 3. Normalized height distribution of vegetation within a 100 × 30 m transect of the laser footprint, represented at 5 m height increments. The color scale from green through red indicates increasing vegetation height. The panel shows data from biennially (B2-yr) and triennially (B3-yr) burnt plots, and fire exclusion (unburnt) from the Satara site, with maximum height of 12 m.

ground points, while the points between 0.5 and 30 m were categorized as woody vegetation. The reclassified grids were then expressed as the percentage canopy cover.

Statistical analyses

We distributed eighteen 0.12-ha plots (20 m radius) randomly within the TLS 3D data of each EBP treatment, totaling 432 sample plots (Fig. 2), to assess differences in vertical canopy profiles, cover, and height comparisons. The "20 m" radius size of the subplots enabled us to sample large area of the plots and subsequently minimizing the edge effect. Percentage canopy cover and mean height of each sample plot were computed for all pixels higher than 0.5 m. We used a one-way ANOVA and Tukey's post hoc ($P < 0.05$) test to compare the differences in mean canopy cover and mean canopy height between areas of fire and fire exclusion (unburnt) in different landscapes. The relationship between fire frequency and landscape and their effect on woody cover, average, and maximum height were analyzed using linear mixed effects models in R (Team-RCore, 2016), with the package NLME (Pinheiro et al. 2014). Explanatory variables in the model were fire frequency and landscape (Mopane, Satara, Skukuza, and Pretoriuskop), while the subplots nested within each treatment replication and landscape were specified as the random variable. Models with all possible combinations were fitted using maximum likelihood (ML) method and were evaluated using Akaike's information criterion (AIC), a model selection index, which favors both model fit and simplicity (Burnham and Anderson 2002). From the AICs, the ΔAIC score for each model was calculated by comparing them to the least AIC score model, for assessing the probability of the best-fitting model, where for the best model ΔAIC = 0. For each model, we calculated Akaike weights (w_I), a normalized relative likelihoods of the models (Wagenmakers and Farrell 2004). Next, Akaike weights were used to calculate the weight of evidence (w_+) for each of the explanatory variable by adding the Akaike weights for all the models in which the explanatory variable was present (Burnham and Anderson 2002).

Aboveground biomass at the plot level was estimated from the TLS data-derived single predictor variable 'HXCC' (Colgan et al. 2013) (Eq. 1), where H is the mean top-of-canopy height of a plot and CC is the mean canopy cover of a plot. This equation was preferred as it is derived from actual weighing of the harvested tree samples and considers the specific wood density. Furthermore, many of the tree species sampled in this study are commonly found in KNP.

$$AGB_{plot} = -11.5 + 25.8\, H_{plot}\, XCC_{plot} \quad (1)$$

Results

Shifts in vegetation structure across fire frequencies and landscapes

At the regional scale, fire frequency did not significantly influence the average height of woody plants ($F_{2,\ 432} = 0.154$, $P = 0.85$). Analysis of change in maximum height over all landscapes also revealed a non-significant effect of fire frequency ($F_{2,\ 432} = 0.72$, $P = 0.48$). However, the response of woody cover to fire treatments differed markedly across the no-fire (unburnt) vs. fire treatments ($F_{2,\ 432} = 45.75$, $P < 0.001$), with the highest woody cover observed in the unburnt plots. At the regional scale, the effect of triennial fire treatments was more pronounced in reducing woody cover (11.18%, $P < 0.001$) than the biennial fires, which led to a decrease of canopy cover by 8.5% per 0.12 ha ($P < 0.001$).

Landscapes varied in average vegetation height from 1.5 m in northern dry Mopani EBPs to 4.5 m in southern wet Pretoriuskop EBPs. At the landscape scale, fire frequency had a divergent effect on average vegetation height. In the southern wet savanna sites, average height was higher in the biennially burnt plots, whereas in the northern dry savanna unburnt plots had taller vegetation. Triennial and biennial fire treatments in Mopani EBP strings led to a significant decrease in average height by 0.34 m and 0.32 m, respectively ($F_{2,\ 105} = 9.53$, $P < 0.001$) (Fig. 4). In contrast, fire regimes did not significantly influence the average height in Satara and Pretoriuskop burn plots (Satara: $F_{2,\ 105} = 0.419$, $P = 0.65$; Pretoriuskop: $F_{2,\ 105} = 0.917$, $P = 0.40$). However, for Skukuza, the unburnt plots had 0.40 m less average height than the biennially and triennially burnt plots ($F_{2,\ 105} = 3.298$, $P = 0.040$) (Fig. 4). The variation in average height across the burn plots was best explained by the linear mixed model when only landscape variable ($w_I = 0.7$, $w_+ = 0.71$) was taken into account (Tables 1 and 2).

Maximum vegetation height exhibited a varied response to differences in fire frequency regimes, with taller canopies present in the annually burnt plots of the wetter southern EBPs of Pretoriuskop and Skukuza (Fig. 4). However, the maximum

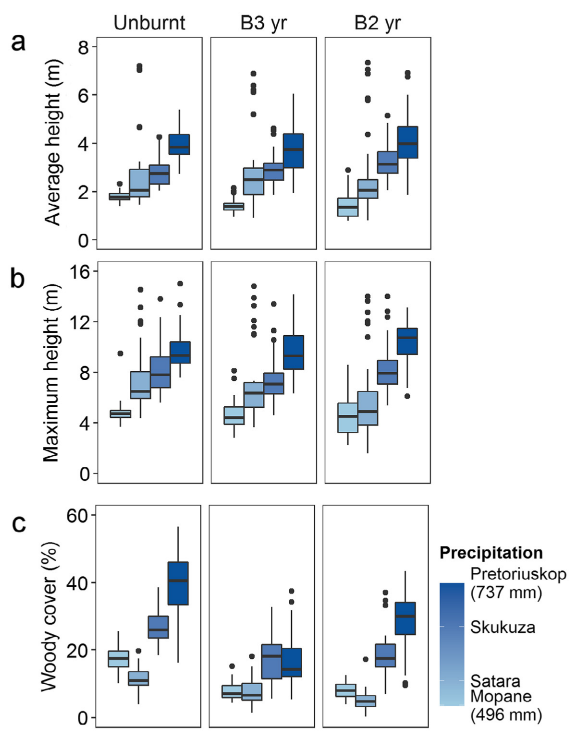

Fig. 4. Average height (a), maximum height (b), and canopy cover (c) in plots subjected to different burn treatments. B2 = biennial, B3 = triennial, and Unburnt = fire exclusion. Color shading indicates the increasing MAP from Pretoriuskop to Mopane.

Table 1. Results from an analysis of the effects of fire frequency and landscape upon three-dimensional vegetation characteristics at the EBPs in Kruger National Park, South Africa.

Structural parameters Model terms	Average height			Maximum height			Woody cover		
	AIC	ΔAIC	w_I	AIC	ΔAIC	w_I	AIC	ΔAIC	w_I
Fire frequency × landscape	314.08	29.22	0	174.23	30.25	0	421.86	6.43	0.02
Fire frequency + landscape	297.21	12.34	0.01	156.68	12.71	0.001	415.43	*	0.54
Fire frequency	295.43	10.56	0.003	153.95	9.97	0.005	416.30	0.87	0.35
Landscape	248.86	*	0.7	143.97	*	0.7	419.31	3.87	0.07
Null model	286.65	1.78	0.2	146.71	2.73	0.2	420.18	4.75	0.04

Note: Results are the Akaike's information criterion for linear mixed effect models, with * referring to the most parsimonious model.

Table 2. The importance of two variables (landscape and fire frequency) examined as predictors of average and maximum vegetation height, and woody cover, with * referring to the variables with reasonable level of support as predictors.

Variable	w_+
Average vegetation height	
Fire frequency	0.004
Landscape	0.71*
Maximum vegetation height	
Fire frequency	0.006
Landscape	0.70*
Woody cover	
Fire frequency	0.91*
Landscape	0.63

heights observed in the northern Mopane EBPs were similar across the fire treatments and unburnt plots (Fig. 4b). In common with the linear mixed models for average height, landscape rather than fire frequency had its most considerable effect on the maximum height of the woody vegetation (w_I = 0.7, w_+ = 0.71) (Tables 1 and 2). In the Pretoriuskop and Skukuza wet savannas, the maximum height was 13.89 m and 8.61 m higher than the drier Mopani EBP strings.

The magnitude of effects of fire frequency on woody canopy cover differed across the sites and across the productivity gradient. In all the EBPs across the park, woody cover was at a maximum in the unburnt plots compared to the burnt plots (Fig. 4). Although both the northern EBPs lie in the same geological substrate and have similar fire treatments, woody canopy cover response to different fire frequency varied significantly across the two regions (Fig. 4). A Tukey post hoc test revealed that triennial fires were more effective in reducing the woody cover by 10% in Mopani EBPs, whereas triennial fires in Satara EBPs reduced the woody cover only by 3.5% as compared to the biennial fires, which had the effect of decreasing the Satara canopy cover by 6.3%. In southern EBPs, triennial fire was associated with less canopy, which reduced the canopy cover by 9.29% and 21.9% for Skukuza and Pretoriuskop, respectively. The best model explaining the woody cover heterogeneity was obtained by fitting the fire frequency and landscape (w_I = 0.54) (Table 1). Fire frequency (w_+ = 0.91) proves to be an important predictor in determining the woody cover across the different landscapes (Table 2). The woody cover in Pretoriuskop and Skukuza was 13.6% and 7.12% higher than the woody cover observed in northern dry EBP strings. A contrasting feature observed is that Satara has 6.45% lower woody cover than Mopani strings. High woody cover is reduced by the triennial fire than the biennial fire at wet sites (Pretoriuskop), whereas fire frequency has a relatively lower effect at dry sites (Satara) (Fig. 4).

Vertical vegetation profiles

The structural height distinction between burnt and unburnt plots is demonstrated by their vertical height distribution profiles (Fig. 5). In the unburnt treatments, all the plots except for Satara contained higher frequencies of LiDAR returns from the shrub layer (0.5–2 m) (Mopani: 10.83%, Satara: 5.535%, Skukuza: 7.49%, and Pretoriuskop: 6.43%). In contrast, plots subjected to fire treatments exhibited a different pattern, with a reduced percentage of LiDAR returns from the shrub layer.

The response of the vegetation to different fire frequencies was heterogeneous across the

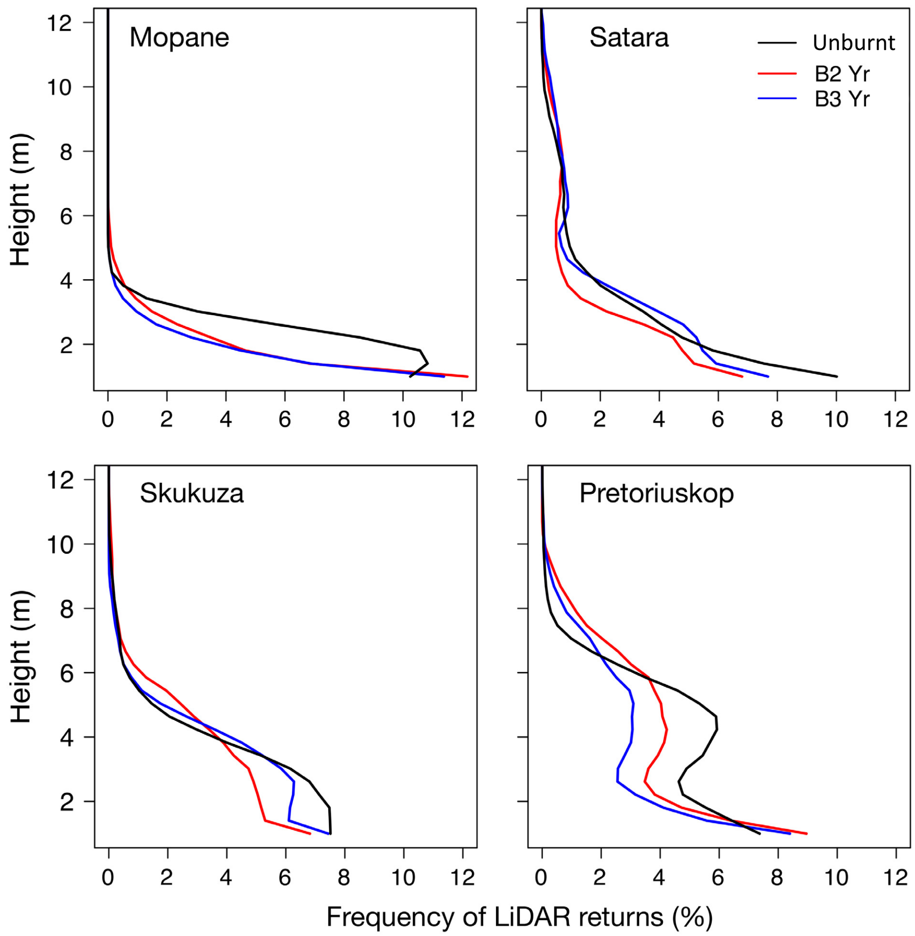

Fig. 5. Structural responses of woody vegetation height to different fire frequencies as a function of landscape type.

landscapes with higher fire frequencies associated with lower canopy height in the drier northern EBPs (0.057% LiDAR returns at 5 m canopy height in unburnt plot), but with taller canopies in the wetter southern EBPs (5.8% LiDAR returns at 5 m in unburnt plot) (Fig. 5). Finer scale exploration of the vegetation canopy height distributions at the four landscapes revealed contrasting physiognomies, with northern EBPs (Mopani and Satara) displaying an inverse J distribution, while that of the southern EBP (Pretoriuskop) exhibiting a bi-modal height class structure. In all landscapes, the slope of the vertical distribution profiles decreased with increasing fire frequencies and the shift in the slope was stronger in the triennial fire regimes than the biennial fires. The two southern EBP sites (Skukuza and Pretoriuskop) have the same underlying granite geology and geographic proximity, but the 3D vertical canopy profiles for the two sites were entirely different due to difference in MAP (>100 mm) and vegetation species composition. A greater proportion of the LiDAR returns from the 4–6 m height class were observed in the triennial fire regime of Skukuza site, while at Pretoriuskop triennial fires were associated with less LiDAR returns from the taller canopies. The transition from overstorey height class to reduced canopy (shrubs) due to fire varied across the landscapes. The natural break (inflection) occurred at heights of 1.5 m (Mopani), 1 m (Satara), 1 m (Skukuza), and 2.8 m (Pretoriuskop). The changes in the shape of the canopy height profiles reflect a complex dynamic relationship between woody vegetation structure and fire frequency under different climatic and edaphic conditions.

Aboveground biomass across the sites

The importance of fire regimes vs. resources (climate and soil) in shaping the vegetation was evaluated with woody plant biomass. Fire suppression allowed woody biomass to accumulate at substantial rates (7–33 tC/ha), which increased along the MAP gradient from north to south (Fig. 6). The difference between the potential biomass (unburnt plots) and actual biomass (burnt plots) for the rainfall deficit landscapes was very small. At the two dry sites on basalt geology, annual burning resulted in a loss of woody biomass carbon (0.5 tC/ha). In contrast, the wettest sites on granite substrate continued to accumulate woody biomass up to 20 tC/ha under the increased fire frequency regime. However, the wettest sites experienced the greatest aboveground biomass losses during less frequent fire events. Also, for the Skukuza landscape, which receives 100 mm less MAP than Pretoriuskop, the difference between the woody plant biomass generated by the biennial and triennial fires is much less, while at Pretoriuskop the woody plant biomass in the fire treatments differs by 15 t/ha.

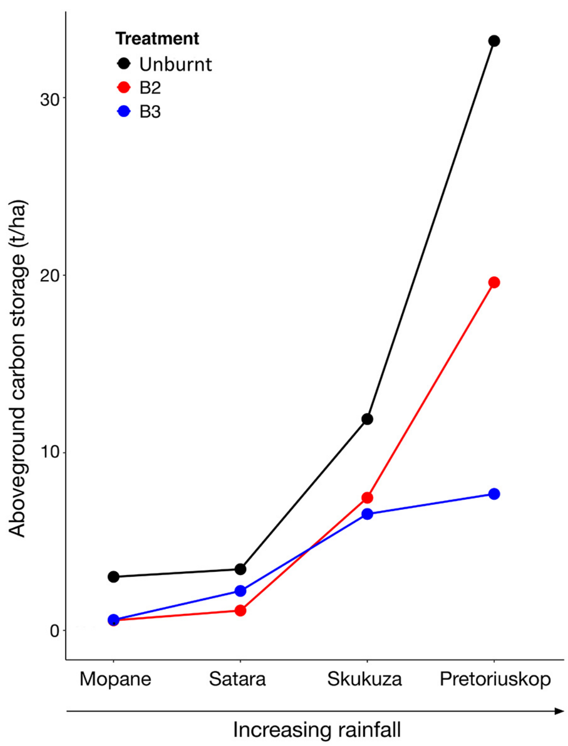

Fig. 6. Woody biomass in plots subjected to different burn treatments estimated from the terrestrial LiDAR point cloud data. Results are shown for the long-term experimental burn plots at Mopani and Satara, the dry savanna, and Skukuza and Pretoriuskop, the wet savanna subjected to a burn frequency of B2 = biennial, B3 = triennial, and Unburnt = fire exclusion.

Discussion

Regional variation in vegetation structure in the absence of fire

At a regional scale, the spatial pattern of woody vegetation structure appears to be driven by the interplay of multiple environmental gradients. In KNP, the east–west geological and north–south rainfall gradient have been hypothesized to be largely responsible for variation in woody vegetation structure. While this assumption was true for all 3D vegetation structure metrics, the differences in their magnitudes were distinct. When we consider the fire excluded plots of our study, we observe that the northern basaltic regions have shorter and sparser canopies than the woody canopies of the southern granite substrate (Fig. 4). The basalt landscapes are characterized by clay soil, which tightly binds moisture during dry season, resulting in a low water availability (Colgan et al. 2012). Low water availability has the potential to increase competition between grasses and juvenile trees, thereby keeping the woody vegetation short. Conversely, granite substrates support taller woody vegetation because of the competitive edge of trees over grass in terms of deeper rooting systems with access to more stable moisture reserves (Alizai and Hulbert 1970, Walter 1971). Consistent with this observation, the southern granite plots, which receive 737 mm/yr MAP, have 23% more woody cover (Fig. 4) than the dry basaltic control plots. The woody cover in savannas increases linearly with MAP, and a MAP of 650 mm/yr and above is sufficient for canopy closure; thus, local disturbance such as fire regimes becomes a key factor in constraining the spatial expansion of the woody vegetation (Sankaran et al. 2005).

Top-down control by fire in savanna system

The 63 yr of prescribed burning across the EBPs of the KNP have led to marked differences in woody vegetation structure, and our results indicate that the patterns and processes of vegetation structural change vary at different spatial scales. When averaged across the four experimental sites (Mopane, Satara, Skukuza, and Pretoriuskop), fire frequency had no significant effect on average height. At the landscape scale, however, average canopy height declined in the northern Mopane plots and increased in the Skukuza plots, with increasing fire frequency. Differences in average canopy height across the northern low MAP regions of the park may be due to the confounding effects of water stress, arising from the increased tree–grass competition, whereby trees produce shorter multiple stems rather than a single taller stem. It is also possible that different species respond differently to the fire regimes. For instance, in the Skukuza landscape, fire-treated plots were associated with a greater proportion of LiDAR returns in the 4–8 m height classes, and a lower LiDAR returns above 4 m in the fire excluded plots (Figs. 4b and 5). Similar findings are reported by Levick et al. (2015), who showed that the Skukuza fire exclusion regions were associated with shorter vegetation, while a greater proportion of the taller vegetation was observed in the higher fire frequency. The vegetation communities in the Skukuza are dominated by *Combretum apiculatum*, which Higgins et al. (2007) hypothesized regenerates poorly under low fire frequencies and that saplings are shade intolerant.

Our study has shown that the effect of fire frequency on woody vegetation structure differs by region, in relation to rainfall and soil type. For the EBPs in the drier regions (MAP = 544 mm/yr) of the park, the maximum height of the woody vegetation was usually reduced under higher fire frequency conditions, while the wetter southern region of the park supported taller vegetation canopy under high fire frequency (Fig. 4b). Moreover, the wetter sites of KNP possessed much higher canopy cover under a high frequency burning regime. In the regions of high fire occurrence, fire stimulates the growth of the plant, in an effort to exceed the flame zone (Archibald and Bond 2003, Bond and Keeley 2005). Also, the highest fire frequency considered in our study is burning every two years, which is a sufficient time frame in a wet region to stabilize competition among the trees and grasses, leading to greater growth and survival of trees (Archibald and Bond 2003). However, deriving an understanding from this explanation is not simple as fire intensity is a linear function of fuel load which increases with increasing MAP (Govender et al. 2006). For instance, frequent fires lead to a reduction in fire intensity by preventing the buildup of grass fuel load, thereby facilitating more individuals into the upper height classes and more canopy expansion. However, an additional year in between the successive fires at a wet site will cause large reductions in the woody canopy cover due to high-intensity fires arising from greater accumulation of the fuel load between the fire events (Fig. 4c).

As the rainfall increases from north to south across the reserve, there is a gradual transition of distribution of vegetation communities. The response of vegetation communities to fire regimes differs with their adaptation capabilities, in relation to environmental stresses and herbivory. The complex interactions associated with the plant species and environmental stresses are evident from the vertical vegetation profiles (Fig. 5). The vegetation structure in the northern basalt region is depicted by a flat height class distributions. The flattened height class distribution or inverse J shaped indicates a strong top-down control on vegetation structure in the basalts. Basalts weather to nutrient-rich soil and support high herbivory density, which keeps the juvenile trees within the firetrap and weakens the larger trees by girdling, increasing their vulnerability to future fire events (Helm et al. 2011, Moncrieff et al. 2011). Presence of inflection points at 0.5 m and 2 m in the EBPs distributed across Satara landscape indicates a feedback from the selective foraging activities of the herbivores, resulting in a patchy distribution of vegetation damage by fire (Fig. 5). As such the influence of fire on vegetation structure is sensitive to the herbivory density (Pellegrini et al. 2017). However, the high nutrient concentration in basalts leads to increased grass production, high fire intensity, and reduced vegetation height (Bond and Keeley 2005).

Empirical evidence of "consumer control"

Our exploration of woody biomass across the experimental treatments contributes to a more comprehensive understanding of consumer control by fire, which was conceptualized previously by Bond and Keeley (2005). Our results provide the first quantitative test of this conceptual model (Fig. 6). At dry sites, woody biomass was found to be less sensitive to fire frequency, instead presence of fire alone was more influential in lowering the biomass. The effect of fire frequency on woody biomass is greater in the wetter sites, where woody biomass in biennial and triennial burnt plots differed by 10 t/ha. Notable here is the mesic site Pretoriuskop on granites, where unburnt plots supported up to 33 tC/ha of the woody biomass and those burned every two years retained more woody biomass than those burned every three years. This was unexpected given the role of fire in limiting woody vegetation in more mesic savannas. Multiple mechanisms may influence the increase in woody biomass in spite of frequent burning, including growth of fire-resistant trees, and the plausible increase in atmospheric CO_2 concentrations could increase the chances of trees escaping fires (Bond et al. 2003, Buitenwerf et al. 2012). Still the large differences between potential (unburnt plot) and actual (burnt plots) woody biomass at wet sites suggest significant consumer control on savanna ecosystems.

Limitations and future directions

Recently, there have been many vegetation structure models derived from airborne LiDAR and spaceborne datasets, to explain the role of fire in shaping savanna systems and tree–grass balance (Bucini et al. 2010, Smit et al. 2010, Levick et al. 2012, 2015). Given the KNP's low to medium woody cover, present remote sensing models cannot account for impacts of fire on the structure and dynamics of dual layering or sub-canopy woody vegetation. In turn, TLS measurements provided dense 3D point clouds, capturing the high degree of heterogeneity inherent across the EBPs, and enabled us to quantify the structural features accurately. Savannas exhibit complex vegetation structure with substantial seasonal variations between trees and grasses (Archibald and Scholes 2007), so TLS mapping should ideally be conducted in leaf-off periods to prevent occlusion by grasses and shrubs. Our use of TLS point cloud data and high-resolution canopy height profiles has provided some useful insight into savanna woody vegetation spatial patterns emerging from fire regimes and landscape interaction at the plot scale. However, there is much more to be learned from the 3D metrics in terms of woody canopy architecture and biomass allometry.

We have focused heavily on the effect of fire frequency at small and site-specific scales and acknowledged the interaction of fire with a single determinant landscape as a function of rainfall. It is likely that the interactive effects of fire regimes and herbivory abundance may vary the woody biomass significantly. Also, despite the large spatial extent of each burn treatment, plot-based experiments fail to depict the stochastic relationship between disturbance regimes, and environmental and topographic processes (Levick et al. 2012, Staver 2017). Therefore, we recommend the integration of 3D inventory metrics with broader-scale remote sensing analyses to achieve a comprehensive model that accounts for the productivity of savanna systems under a wide range of topographic and bio-climatic conditions. However, a single regional model cannot adequately represent savanna woody vegetation characteristics at a global scale. In our study, relationship between moisture, fire regimes, and woody vegetation structure vary across the four landscapes of KNP (Fig. 5). Differences in these relationships reflect the greater role of region-specific climate, phenology, growth rates, canopy architecture, and biomass allometry of woody taxa in determining the structure of savanna vegetation. Similarly, Lehmann et al. (2014) predicted net decrease in African woody biomass from a single global model, whereas the regional model predicted a net increase. Thus, any such extrapolation to a global scale must incorporate the evolutionary and environmental differences of each regional ecological setting, to underpin the trajectories of change in vegetation to future climate, with implications for global carbon stocks.

Implications for management

The fire-induced changes reported here in both the vertical and horizontal components of the woody layer highlight the large influence that land managers can exert on savanna vegetation through alteration of fire frequency. Our findings show that through long-term biennial and triennial burning in the Mopane landscape, diverse woody structures are being transformed to short homogenized communities together with significant changes in canopy cover and aboveground carbon storage (Fig. 5). Frequent fires in combination with browsing will lead to higher abundance of short height class individuals by preventing woody tree recruitment. Longer fire return intervals could be beneficial to woody recruitment, but at the same time may serve to suppress canopy height because of high-intensity fires.

A broad spectrum of fixed fire treatments are applied across KNP as a whole, but deeper investigation is needed to ensure that there is enough variability for trees to escape the flame zone and attain the upper height class and canopy expansion. Presence of large trees substantially influences the carbon sequestration potential (Levick and Asner 2013), and faunal diversity (Cumming et al. 1997) of the system. Fire managers have been encouraged to introduce spatio-temporal variability in the fire regime through landscape scale patch mosaic burning (Parr and Andersen 2006), but managers have less control over the total area of the park burnt annually due to the occurrence of unplanned fires (van Wilgen et al. 2014). Increased woody cover of the mesic Pretoriuskop sections of the southern granitic substrate is of growing concern, yet it is an area with one of the highest fire frequencies in the park. Importantly, it is not just variation in frequency that is needed, but variation in fire intensity, with infrequent hot fires needed to combat thickening (Smit et al. 2016). Stratifying ignition locations by catchment and hillslope position could result in a more diverse spatial pattern of fires over time (Levick et al. 2012).

Lastly, our findings here provide useful quantification of the degree to which different fire regimes can suppress aboveground carbon storage, and how this changes with spatial context. These trends are of global significance, at a time when many countries hosting the savanna biome are contemplating carbon sequestration initiatives (Bradshaw et al. 2013, Russell-Smith et al. 2013, Lipsett-Moore et al. 2018).

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