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Abstract

Questions: How is woody vegetation patchiness affected by rainfall, fire and large herbivore biomass? Can we predict woody patchiness and cover over large-scale environmental gradients?

Location: Hluhluwe-iMfolozi Park, South Africa.

Methods: We quantified variation in local patchiness as the lacunarity of woody cover on satellite-derived images. Using Random Forest regression we analysed how both average woody cover and its patchiness depend on annual rainfall, fire frequency and grazer and browser metabolic biomass densities.

Results: Fire frequency and rainfall were the clearest predictors, whereas effects of large herbivores on woody vegetation were smaller and more complex. Under low rainfall conditions (500 $\mathrm{mm \cdot yr^{-1}}$) trees had less total cover and were more regularly spaced across the landscape (lower patchiness). Woody cover and vegetation patchiness increased with rainfall whereas fire frequency decreased woody cover and further increased patchiness.

Conclusion: These results suggest a switch from competition between neighbouring trees under low rainfall conditions towards benefits among neighbours with increasing fire frequencies. Whereas overall woody cover and its patchiness are two independent aspects of savanna woody vegetation patterns, both need to be investigated to obtain a good understanding of the functioning and diversity of savanna ecosystems.

Introduction

Problems of pattern and scale are central for the understanding of ecosystems (Levin 1992; Ritchie 2009). Savannas are broadly characterized as tree–grass mixtures at the landscape scale, but at finer scales they are heterogeneous landscapes characterized by a continuous grass layer interspersed with discontinuous patches of woody canopy (Frost et al. 1986; Scholes & Archer 1997). This woody cover can range from sparse but widespread trees or shrubs to larger stretches of closed-canopy woodlands alternating with pure grassland. The nature of spatial patchiness (dispersed or aggregated) of woody canopy across the landscape strongly affects many community and ecosystem processes, including nutrient cycling (Sitters et al. 2013, 2015), herbivore distributions (WallisDeVries et al. 1999; Kie et al. 2002), fire percolation (Archibald et al. 2009; Beckage et al. 2009; Schertzer et al. 2015), fire–herbivore interactions (Kerby et al. 2007), predator–prey interactions (Riginos & Grace 2008; Riginos 2015), soil erosion (Reid et al. 1999) and evapotranspiration (Joffre & Rambal 1993). In turn, ecological processes shape the spatial patterning of woody vegetation across the landscape. Given the geographic extent and socio-economic importance of

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savannas (Frost et al. 1986; Scholes & Archer 1997), combined with their anticipated sensitivity to climate and land-use change (Scheiter & Higgins 2009; Hirota et al. 2010; Anadon et al. 2014; Midgley & Bond 2015), a thorough understanding of the drivers of the main aspects of spatial patterns of woody vegetation is urgently needed.

Spatial patterns in woody vegetation can be described by two independent parameters: the coverage or amount of woody species biomass per surface area at coarse spatial scales (i.e. the tree–grass ratio) and the degree of local patchiness or clustering of woody species across the landscape, given a particular total cover at the landscape scale. Most research so far has investigated the determinants of the landscape-level percentage woody cover, yielding important insights into the functioning of savanna ecosystems (Sankaran et al. 2005, 2008; Bucini & Hanan 2007; Staver et al. 2011; Lehmann et al. 2014). Generally, woody cover increases along regional rainfall gradients, whereas fire negatively affects woody cover. Interestingly, this negative effect of fire on woody cover becomes stronger at higher rainfall (Bucini & Hanan 2007; Bond 2008; Lehmann et al. 2014), due to increased fire frequency and intensity as a result of increased fuel loads (more dead grass left standing at the start of the dry season). Therefore, grasslands and forests can form two alternative stable states at higher amounts of annual rainfall (1000–2500 $\mathrm{mm \cdot yr^{-1}}$; Staver et al. 2011). Soil nutrients, soil texture and large grazer and browser biomass have also been found to significantly affect woody cover, but effect sizes are generally much smaller (Sankaran et al. 2005, 2008).

In contrast to understanding of the determinants of overall woody cover, insight into the determinants of its local patchiness remains limited. Nevertheless, this patchiness, especially patch size, is an important landscape characteristic, as the strength of local feedback mechanisms generally increase non-linearly with woody patch size (Ludwig et al. 2000). For example, as woody patch size increases, important resources, like nutrients and water, become increasingly concentrated inside those patches (Ludwig et al. 2000). Similarly, woody species inside larger patches are better protected against fire as trees jointly outshade grasses (Hochberg et al. 1994). Therefore, better understanding of the determinants of woody patchiness is now needed to complement insights on the drivers of total woody cover.

Spatial investigations of ecological phenomena, such as woody cover distributions, can be dependent on the spatial scale (or measurement resolution) and extent of the observations (Turner 1989) or can be independent of this, e.g. in case of fractal patterns (Ritchie & Olff 1999). Spatial variance generally decreases with scale, resulting in higher predictability of observed patterns at coarse resolution (Wiens 1989). Furthermore, mechanisms and pattern types can be scale-dependent (Saab 1999; Kie et al. 2002), and predictor variables might operate at different spatial scales (Levin 1992). Herbivore effects on trees and shrubs can be very localized, whereas fire and rainfall generally perform at much coarser spatial scales (Frost et al. 1986). Therefore, testing the robustness of conclusions on drivers of spatial patterns across different spatial scales is critical (Wiens 1989).

Here, we investigate how patchiness of woody vegetation is affected by annual rainfall, fire and large grazer and browser metabolic biomass densities in Hluhluwe-iMfolozi Park, South Africa. In addition, we study how these factors affect overall woody cover. We used park-wide maps of woody vegetation distributions (resolution 0.5 m), derived from satellite imagery, and investigated the spatial patterns in woody vegetation at four spatial resolutions (100, 250, 500 and 1000 m) to examine pattern robustness across spatial scales. Besides identifying the determinants of woody vegetation patchiness, the main objective of this study, we also analysed determinants of percentage woody cover to enable a comparison with previous studies. Last, we used obtained model results to predict woody patchiness and cover for the whole park, and compared those with observed patterns of woody vegetation.

Methods

Study site

This study was conducted in Hluhluwe-iMfolozi Park (HiP), South Africa. This 900 $\mathrm{km^2}$ game reserve hosts a variety of large herbivores that are present in high numbers (Waldram et al. 2008). Mean annual rainfall is correlated with altitude and ranges from ca. 500 mm in iMfolozi to 900 mm in Hluhluwe (Balfour & Howison 2002). Vegetation structure varies from open grasslands and thickets to closed, fine-leaved and broad-leaved woodlands (Whateley & Porter 1983). On average, 26% of the park is burned annually, and the mean fire return period is 3.8 yr (Balfour & Howison 2002).

Woody cover

Woody cover distribution for HiP was estimated using satellite-derived colour images (26 Mar 2014 for iMfolozi and 8 May 2014 for Hluhluwe, ca. 0.5-m resolution) from Google Earth using Google Earth Pro (Google 2015. Hluhluwe-iMfolozi Park, South Africa. 280 13′ 20.74”S, 310 57′ 02.45”E, Eye alt 78.06 km. Digital Globe 2015. Available at https://www.earth.google.com. Accessed 26 March 2014 and 8 May 2014). We used the green band to distinguish between woody and non-woody vegetation; trees and shrubs generally show higher greenness than herbaceous vegetation. We visually investigated different cut-off values for high greenness, and found that a threshold of 95 [out of the relative colour scale of 0–255 (RGB)] best represented the observed woody patterns when compared with the satellite-derived colour image. This threshold is somewhat arbitrary, and the percentage woody cover observed would increase with a higher threshold value. Nevertheless, patterns of woody cover distributions for different cut-off values are highly correlated and only differ slightly quantitatively, whereas observed levels of patchiness are qualitatively similar (see Fig. 1). Therefore, the actual choice of threshold value does not affect our conclusions.

Rainfall

A 180-m resolution rainfall map (range: 504–862 mm·yr^{-1}) for the park was used based on ground stations and regression kriging, with methods described in Veldhuis et al. (2014).

Fire frequency and return interval

Annual recordings by park rangers (ground-based hand-drawn maps) of areas burned between 1955 and 2011 were digitized and rasterized into 1-ha (0.01 km^2) pixels (Balfour & Howison 2002). Subsequently, these layers of annual fire extent were used to determine fire return interval (in years) and fire frequencies (number of burns between 1955–2011) for the whole park (100-m resolution).

Dung counts

Dung counts were used to estimate large herbivore abundance (Cromsigt et al. 2009a,b). We used 24 fixed line transects from min. 3.9 to max. 10.4 km length that are used biannually by observation teams to monitor the abundance of all large herbivore species within the park (Fig. 2; see Cromsigt et al. 2009a for more details on transect methods). Dung counts were conducted by observation teams between Oct and Nov 2014, recording the number of all dung pellet groups for all herbivore species larger than hare on and within 1 m on each side of the transect. Pellet groups were summed per species for every 5 m of transect length and their position was georeferenced. For white rhinoceros, that mostly defecate in middens, all middens visible from the transect were counted.

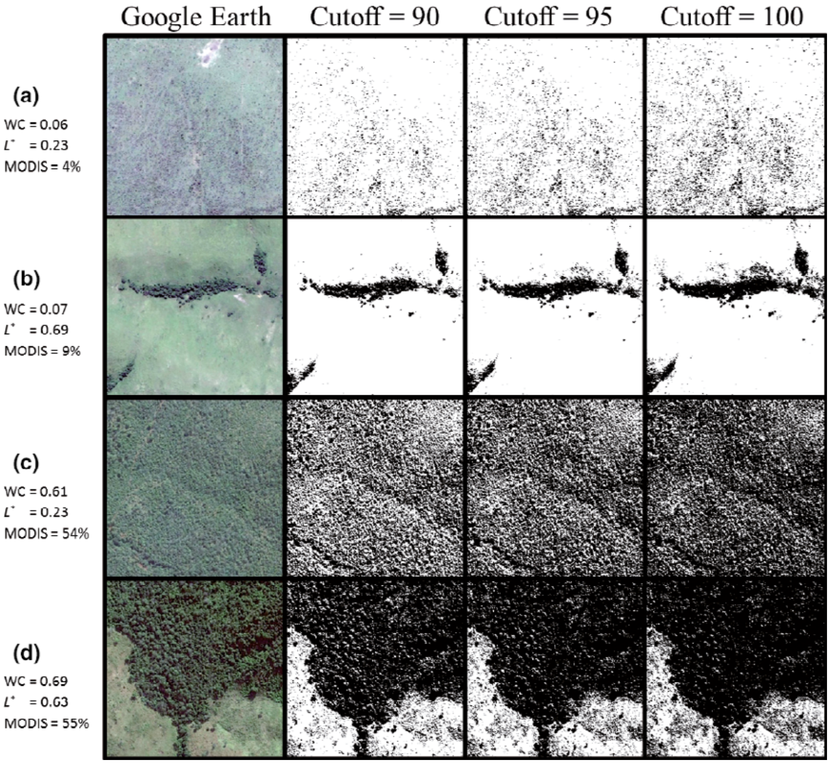

Fig. 1. Google Earth satellite images (provided by DigitalGlobe, 26-3-2014 and 8-5-2014) and three woody cover classifications based on different threshold cut-off values for the green band (90, 95, 100), where a cut-off values of 90 means that all values <90 are classified as woody. Four landscapes, characterizing the extremes found in terms of landscape structure are shown. (**a**) Low woody cover and low normalized lacunarity. (**b**) Low woody cover and high normalized lacunarity. (**c**) High woody cover and low normalized lacunarity. (**d**) High woody cover and high normalized lacunarity. Woody cover estimates from MODIS are given for comparison. WC = woody cover, $L*$ = normalized lacunarity.

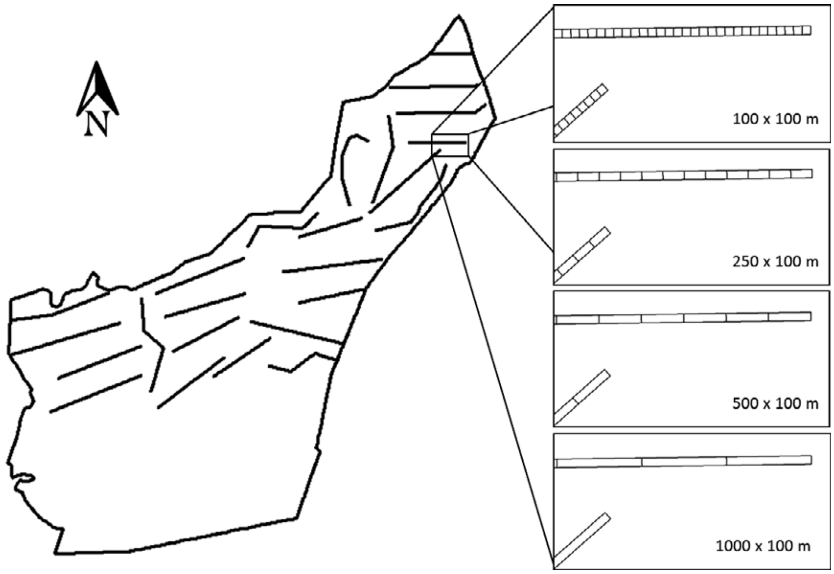

Fig. 2. Outline of Hluluwe-iMfolozi park showing the positioning of the 24 transects and enlargements of a small area to display the study design of the four different spatial scales.

Spatial scale and variables

We created rectangular polygons covering 50 m on both sides of each transect (100 m total width) and with different lengths (100, 250, 500 and 1000 m) to investigate the effect of spatial scale on patchiness estimates (Fig. 2) using ArcGIS Desktop 10.2, ESRI, Redlands, CA, US. Within each polygon we extracted mean rainfall, fire frequencies and fire return interval from the obtained maps (see above). To obtain an estimate of herbivore use for each polygon we summed all dung counts per herbivore species per polygon and combined this value (used as a relative measure of herbivore density) with the total number of individuals of that species within HiP (absolute herbivore densities; Census data 2014, Ezemvelo KZN Wildlife, unpubl), assuming that the average number of dung counts reflected average species densities across the park, and that the transects are a representative sample of the different habitats of the park (Fig. 2). We divided the total number of each herbivore species (N_t) by the total area of the park (A_t = 90 000 ha) × the area covered by the polygons (A_p) for each spatial scale, representing the number of animals that would occupy the area covered by the polygons. For each species, that number of animals was then divided by the total number of dung counts (D_t) (representing the number of animals per dung count) × the dung counts for each polygon (D_p) (representing the number of animals per polygon). This gave us the number of individuals (N_p) for each species for each polygon following: $N_p = (N_t/A_t) \times A_p \times (D_p/D_t)$. The obtained values of animals per polygon were then expressed as metabolic biomass density MDB (in $kg^{0.75}{\cdot}ha^{-1}$) for each species as $MBD = (N_p \times B^{0.75})/A_p$, where N_p is the count of a species in a specific polygon, B is the body mass per individual of that species (kg), and A_p is the polygon area (ha). The body masses for different species (average over sexes and life stages) were taken from Smith et al. (2003). We then summed the MDBs of grazers and browsers to obtain an estimate of area usage by both herbivore functional groups. African buffalo (*Syncerus caffer*), warthog (*Phacochoerus africanus*), blue wildebeest (*Connochaetes taurinus*), white rhinoceros (*Ceratotherium simum*) and Burchell's zebra (*Equus quagga*) were treated as obligate grazers, while grey duiker (*Sylvicapra grimmia*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*) and black rhinoceros (*Diceros bicornis*) were identified as obligate browsers (Codron & Codron 2009). African elephant (*Loxodonta africana*) was assumed to be a mixed feeder [50% grazer, 50% browser; Codron et al. 2011)]. Impala (*Aepyceros melampus*) was considered a mixed feeder, but as a preferential grazer (75% grazer, 25% browser) and nyala (*Tragelaphus angasii*) a mixed feeder, as a preferred browser (25% grazer, 75% browser) based on stable isotope analyses (Botha & Stock 2005; Codron & Codron 2009).

The average woody cover (%) was calculated as the mean of all pixel values of the woody cover map within each polygon using ArcGIS Desktop (ESRI), ranging between 0 and 1, where 1 denotes 100% woody cover. Patchiness of woody vegetation was calculated as the lacunarity of the spatial pattern (Mandelbrot 1983; Allain & Cloitre 1991; Plotnick et al. 1996). Lacunarity is a measure for how a pattern fills space, where patterns with more and larger gaps generally have a larger lacunarity. Stemming from the Latin *lacuna* (gap), a forest with more or larger gaps would have a higher lacunarity. For this we used a gliding box algorithm, with box sizes of $r = 1, 3, 5, 9, 17, 33$ and 65 ($1r$ is approximately 0.5 m). Lacunarity can be expressed as $L(r) = (s_s^2(r)/s(r)^2) + 1$ in which $s(r)$ and $s_s^2(r)$ represent the mean and variance of the pixel values for box size r, respectively (Plotnick et al. 1996). Therefore, lacunarity is dependent on, in our case, the percentage woody cover. The lacunarity parameter therefore needs to be normalized, to acquire two independent measures of woody vegetation patterns. We therefore follow the approach of Roy et al. (2010), normalizing the lacunarity parameter as $L^*(r) = (L(r) - 1)/(1/\varphi - 1)$ where $L^*(r)$ is the normalized lacunarity at box size r, φ is the percentage woody cover (01) and thus $1/\varphi$ is the lacunarity at box size 1. We then plot the normalized lacunarity curves as a function of box size (see Appendix S1 for the curves of the four examples in Fig. 1). To obtain a single value for normalized lacunarity for each polygon we took the average of box sizes 3, 5, 9, 17, 33 and 65, resulting in values ranging between 0 and 1, with higher values representing a higher degree of woody patchiness (i.e. clustered) and lower values representing regularly spaced woody vegetation (see Fig. 1). Intermediate values suggest random patterns in woody distributions. Woody cover and normalized lacunarity were not related to each other (LM: $P = 0.31$, $R^2 = 0.0005$; Appendix S2).

Data analysis

We analysed the dependence of the normalized lacunarity and average woody cover on rainfall, fire, large grazer and browser metabolic biomass at all four spatial scales (100, 250, 500 and 1000 m). We started the analysis with fitting variograms using standard routines in the 'geoR' package (Appendix S3; Ribeiro & Diggle 2001) to determine the extent of spatial autocorrelation of the dependent variables.

We then analysed relationships between our response variables (normalized lacunarity and woody cover) and the four predictors of woody cover (i.e. rain, fire, grazer MBD and browser MBD) using Random Forest regression (Regression forests), package 'randomForest' (Liaw & Wiener 2002). Random forest (RF) regression is a machine learning method that operates through construction of a large number of regression trees by randomly taking subsets of the data and predictor variables (Breiman 2001). The large benefit over conventional techniques such as standard linear model multiple regression is that regression trees accommodate non-linear relationships between predictor and response variables and are invariant to monotonic changes in, and correlations between, the explanatory variables. We calculated 2000 trees for each spatial scale using 90% of the data and tested their goodness of fit on the remaining 10%. RF models are less easily visualized and interpreted than standard Regression Trees but do provide the opportunity to determine the importance of each predictor variable and partial dependence. The importance of each variable calculated using permutation tests, in which the values of a variable is randomly rearranged, followed by calculation of the increase in mean squared error; the larger this increase, the more important the variable. Partial dependence plots (PDP) show the response to a predictor variable averaged over the distribution of the other predictors. These PDPs show the change in the average predicted value over the range of a specific explanatory variable. Therefore, PDPs are especially valuable when multiple explanatory variables are correlated, as their partial nature describes the effects of the independent variables.

As RF is a relative new technique (especially in ecology), its sensitivity to spatial autocorrelation has not been rigorously tested. Therefore, we also analysed our data using LMM, for which techniques to incorporate spatial autocorrelation have been reliably demonstrated, to increase the robustness of our statistical analysis. Location was therefore included as random variable, correcting for the spatial autocorrelation structure using the 'corRatio' (normalized lacunarity) and the 'corExp' (woody cover) functions, from the 'nlme' package in R (Zuur et al. 2009; R Foundation for Statistical Computing, Vienna, AT). These correlation structures were chosen based on AIC criteria. We started with full models with all four explanatory variables and their two-way interactions. Backward step-wise model selection procedures were used based on the BIC criteria (Schwarz 1978). We chose BIC over AIC criteria because of the large sample sizes ($n = 1784$ for 100-m resolution), and BIC tends to be more conservative against over-fitting.

Last, we used these RF models based on the transect data to make park-wide predictions (500-m resolution) of normalized lacunarity and woody cover based on our park-wide maps of rainfall and fire frequencies. Subsequently, these maps were validated with the observed normalized lacunarity (Google Earth) and woody cover (based on Google Earth and MODIS). Moderate resolution imaging spectroradiometer (MODIS) satellite measurements of canopy reflectance were obtained from the MOD44B Collection 5 product (Townshend et al. 2011). Prediction accuracy was determined by intersecting 1000 randomly generated points with all maps and subsequently linear regression models were constructed between predicted and observed values. All statistical analyses were executed in R v 3.2.2.

Results

Patchiness of woody vegetation

Relative importance values for normalized lacunarity (i.e. degree of patchiness) identified fire return interval as the most important predictor variable for all spatial scales (Table 1). Rainfall was also an important predictor, almost as important as fire at finer spatial scales. Grazer MBD was also significant but its importance was much smaller, whereas browsers MBD did not affect normalized lacunarity at all but the finest scale (100 m). The overall variance explained by the RF model increased towards coarser resolutions from 10% (100 m) to 31% (1000 m) based on cross-validation. Linear models generally gave similar results to RF models, with the exception of rainfall at finer scales, where it became non-significant (Table 2). An explanation for this discrepancy can be found in the partial dependence of normalized lacunarity on the different predictor variables. For coarser spatial scales (500 and 1000 m) there was a more or less linear positive dependence on rainfall, indicating that woody vegetation became more patchy towards higher rainfall (Fig. 3). However, at the two finer scales (100 and 250 m) this trend became non-linear, with no apparent effect between 500 and 650 mm, then a steep increase towards 700 mm, followed again by no effect between 700 and 850 mm rainfall yr^{-1}. The linear models used likely had problems capturing these non-linear effects. Furthermore, normalized lacunarity decreased with fire return interval between 2 and 5 yr, after which it had no apparent effect. Grazers had a positive effect on normalized lacunarity and browsers showed a complex non-linear relationship, which matches their low importance in explaining normalized lacunarity.

Percentage woody cover

Rainfall was the most important predictor of percentage woody cover, followed by fire return interval, browser MBD and grazer MBD at smaller spatial scales (100 and 250 m; Table 1). In general, the patterns were similar when analysed at different spatial scales. The proportion of variation explained was higher than for normalized lacunarity and similar across spatial scales (ca. 40%), following

Table 1. Relative importance values of the different predictor variables for explaining normalized lacunarity and woody cover. Importance values represent the percentage increase in mean squared error when values for the particular predictor are randomly assigned throughout the data set. To obtain relative importance values, the most important predictor was assigned a value of 100 and the others were scaled appropriately. Models represent 2000 random trees based on 90% of the data set and were validated on the remaining 10% of the data set to obtain a measure of goodness of fit (% Var Exp).

	Normalized Lacunarity				Woody Cover			
	100 m	250 m	500 m	1000 m	100 m	250 m	500 m	1000 m
Annual Rainfall	96	98	76	75	100	100	100	100
Fire Return Interval	100	100	100	100	91	87	63	53
Grazer MBD	40	9	39	34	18	14	16	15
Browser MBD	28	−4	4	−9	51	65	74	100
%Var Exp	10	13	24	31	42	35	44	39

Table 2. Results of linear models with spatial autocorrelation structure for woody cover and normalized lacunarity for the four spatial scales of the study. Standardized coefficients are given for all significant predictors obtained by backwards steps-wise procedure and comparison of BIC values. Marginal and conditional R^2 were estimated following Johnson (2014).

	Normalized Lacunarity				Woody Cover			
	100 m	250 m	500 m	1000 m	100 m	250 m	500 m	1000 m
Annual Rainfall	n.s.	n.s.	0.027	0.042	0.079	0.094	0.118	0.019
Fire Frequency	0.019	0.036	0.033	0.030	−0.088	−0.088	−0.097	−0.092
Grazer MBD	0.006	0.009	0.017	0.021	n.s.	n.s.	n.s.	n.s.
Browser MBD	n.s.	n.s.	n.s.	n.s.	0.013	0.039	0.055	0.127
Rainfall × Fire	n.s.	n.s.	n.s.	n.s.	−0.030	−0.023	n.s.	n.s.
Rainfall × Grazer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Rainfall × Browser	n.s.	n.s.	n.s.	n.s.	0.011	0.017	0.023	0.058
Fire × Grazer	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Fire × Browser	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Grazer × Browser	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Marginal R^2	0.04	0.13	0.26	0.37	0.23	0.33	0.45	0.51
Conditional R^2	0.05	0.14	0.28	0.40	0.23	0.34	0.46	0.53
BIC	−4077	−1341	−607	−272	−2202	−658	−323	−146

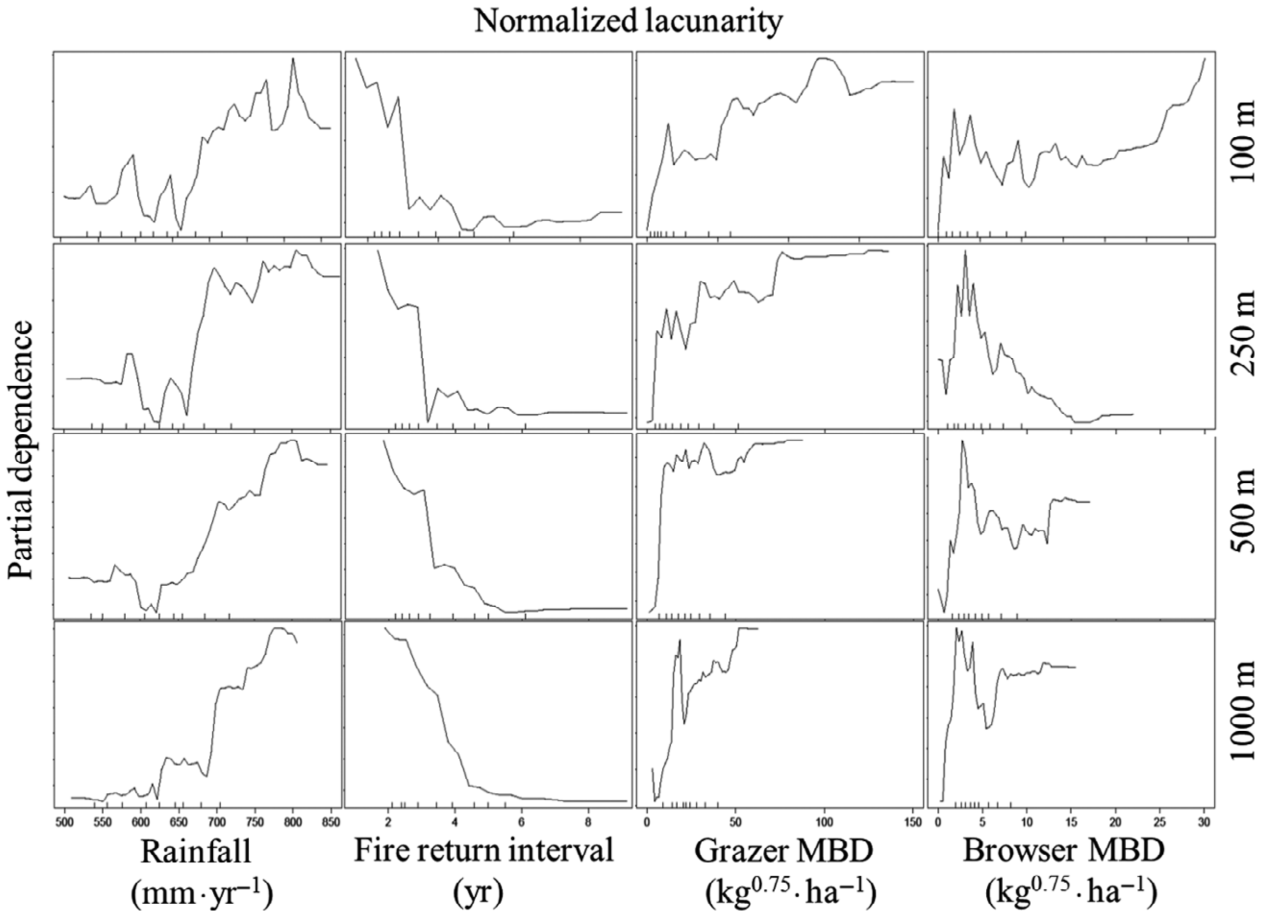

Fig. 3. Partial dependence of normalized lacunarity on rainfall (mm·yr^{-1}), fire return interval (years), grazer and browser metabolic biomass densities (kg$^{0.75}$·ha^{-1}) at four different resolutions (100, 250, 500 and 1000 m). The plots show the relationship between the response and each of the explanatory variables, corrected for the other predictors. Deciles of the data are presented as small black tick marks on the *x*-axis. Normalized lacunarity increased with rainfall between 600 and 750 mm·yr^{-1}, while it decreased with fire return interval between 2 and 4 yr, with no effect for higher return intervals. Normalized lacunarity appears to be positively related to grazer MBD, whereas it showed a complex non-linear relationship with browsers MBD.

cross-validation. Linear models also revealed rainfall, fire return interval and browser MBD as significant predictor variables for woody cover (Table 2). However, the presence of significant interaction terms made it hard to determine their relative importance. The significant negative interaction between rainfall and fire indicates a stronger negative effect of fire on woody cover under increased rainfall conditions (at 100 m and 252 m resolution). Similarly, browser MBD showed a stronger positive relationship with woody cover under high rainfall conditions. Grazer MBD was identified as non-significant, in contrast to the RF models. Partial dependence plots showed clear patterns between woody cover and the four predictor variables that were similar at all spatial scales (Fig. 4). Woody cover increased linearly with rainfall. Fire return interval had a positive effect on woody cover between 2 and 5 yr, whereas it was no longer affected by a further increase in years between fires. Grazer MBD negatively influenced woody cover at low to intermediate densities, after which woody cover again increased. Browser MBD was positively related to woody cover, suggesting an opposite causal direction, i.e. woody cover determined the distribution of browsers instead of vice versa.

Park-wide predictions and observations

Fire and rainfall were thus identified as the most important predictors of both normalized lacunarity and percentage woody cover. Therefore, we were able to use the park-wide maps of annual rainfall and fire frequency as input for the obtained RF models created using the transect data to extrapolate the observed patchiness outside the transects, enabling a verification of the predictions outside the study region. We used Google Earth and MODIS (only woody cover percentage) for this (Fig. 5). Landscapes with high normalized lacunarity (green areas upper panel, high

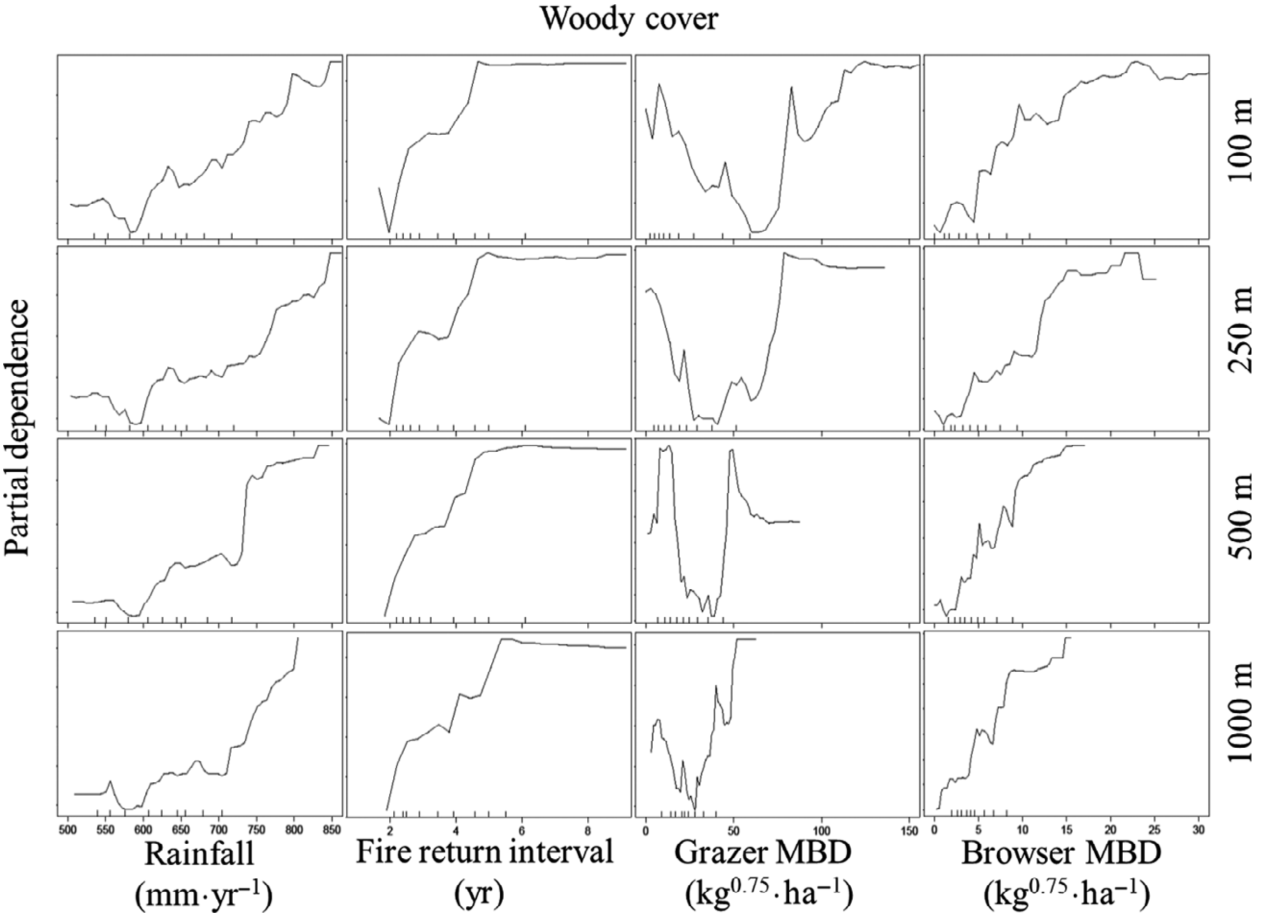

Fig. 4. Partial dependence of woody cover on rainfall (mm·yr^{-1}), fire return interval (years), grazer and browser metabolic biomass densities (kg$^{0.75}$·ha^{-1}) at four different resolutions (100, 250, 500 and 1000 m). Woody cover increases with rainfall between 500 and 800 mm·yr^{-1}. Woody cover also increases with fire return intervals between 2 and 5 yr, but has no effect above the threshold of 5 yr. Woody cover decreased between low and intermediate grazer MBD but increased again with higher grazer MBDs. Browser MBD was positively associated with woody cover up to about 15 kg$^{0.75}$·ha^{-1}, above which there was no longer apparent effect. Patterns were similar for all resolutions.

amount of clustering) are found in the parts of the park that exhibit a combination of high rainfall and high fire frequency. High percentage woody cover is found under the high rainfall conditions with low fire frequencies in the north of the park and intermediate woody cover is found in the Hluhluwe basin. These predictions correspond well to the observations from Google Earth and MODIS. It is important to note that the maps of normalized lacunarity and percentage woody cover are not equal, indicating that both variables are independent from each other and all four possible combinations of high/low rainfall and high/low fire frequency can be found within the park and represent very different landscapes (Fig. 1).

Discussion

The main objective of this study was to investigate the determinants of patchiness of woody vegetation, in addition to drivers of average woody cover. Fire and rainfall were identified as the most important predictors, both increasing woody vegetation patchiness. Grazers also significantly increased patchiness, although their effect size was much smaller. Furthermore, percentage woody cover increased with rainfall, whereas fire negatively affected woody cover. Browsers showed a strong positive relationship with woody cover. Patterns were generally robust across spatial scales (between 100 and 1000 m). Furthermore, results from linear models (including spatial autocorrelation) were overall similar to RF models, although they failed to identify non-linear relationships.

Shifts in woody vegetation patterns across the rainfall gradient

Under low rainfall conditions, we found decreased woody cover that was more regularly spaced across the landscape.

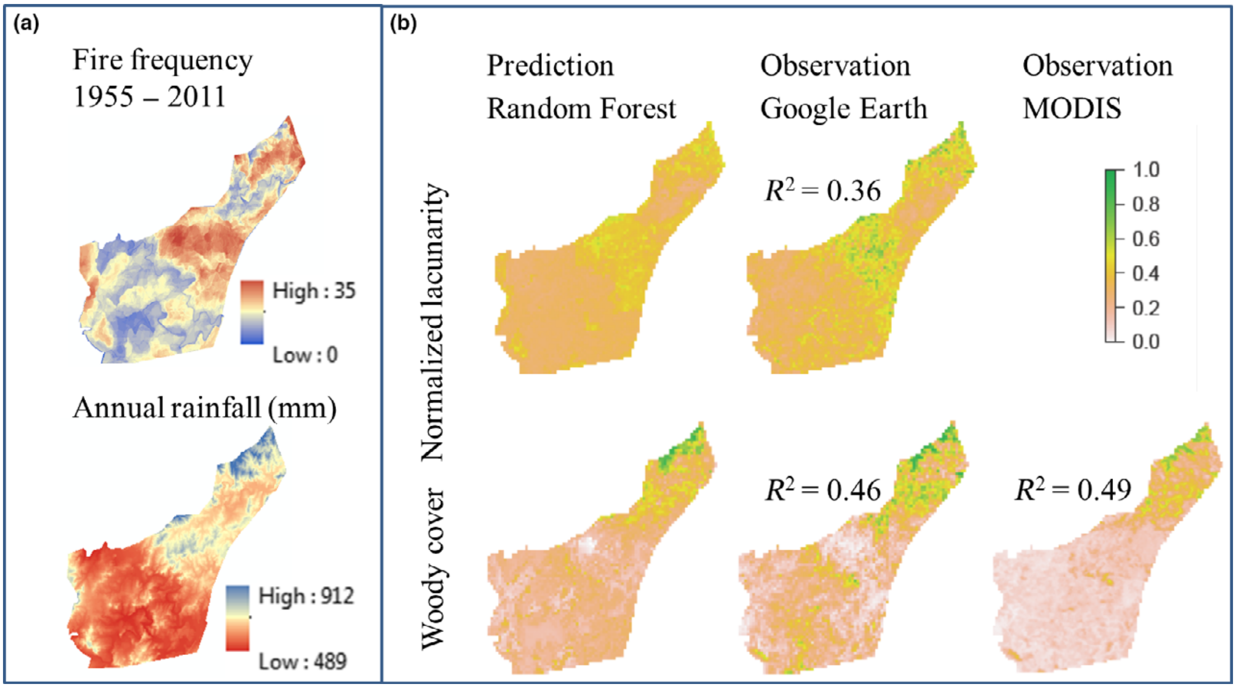

Fig. 5. (**a**) Maps of fire frequency and annual rainfall for Hluhluwe-iMfolozi Park. (**b**) Predicted and observed normalized lacunarity (top row) and woody cover (bottom row) for Hluhluwe-iMfolozi Park. Predictions were modelled by Random Forest regression based on data from 24 transects across the park, followed by regression-kriging based on rainfall and fire frequency maps for the park. Observed maps were constructed using Google Earth and MODIS. R^2 denotes the explained variance of the observed map with our predicted values.

This regular spacing, or over-dispersion, of trees and bushes can be interpreted as an outcome of competitive interactions (Pielou 1962; Greig-Smith 1983). Belowground competition for water under these water-limited conditions is not unlikely where savanna trees often have root systems that extend laterally well beyond their crowns (Belsky 1994; Scholes & Archer 1997; Schenk & Jackson 2002), and plants in arid environments tend to have increased lateral root spread (Casper et al. 2003). Indeed, empirical evidence for tree–tree competition generally comes from more arid savannas (<650 mm MPA; e.g. Smith & Goodman 1986; Meyer et al. 2008; Moustakas et al. 2008). Furthermore, not surprisingly, percentage average woody cover increased with rainfall (Sankaran et al. 2005, 2008) and woody vegetation patchiness increased, probably as a result of reduced competition for water between trees. Additionally, fire decreased woody cover (Bond et al. 2003; Bond 2008) and further increased patchiness of woody vegetation, which is consistent with previous findings (Barot et al. 1999; Kennedy & Potgieter 2003; Moustakas 2015). This clustering of trees with increased fire frequency suggests tree–tree facilitation in protection against fire (Bacelar et al. 2014; Moustakas 2015). The resulting landscape under high rainfall conditions hosts two well-known alternative stable states, self-stabilizing through positive feedback mechanisms (Van Langevelde et al. 2003; D'Odorico et al. 2006; Hanan et al. 2008; Staver et al. 2011): (1) large patches of closed-canopy woodlands that protect themselves from fire; and (2) large open grassland areas where frequent burning prevents woody establishment.

Large herbivores and the need for experimental testing

We found a clear positive relationship between browser MBD and woody cover. However, three recent studies investigated the effect of herbivore exclusion on woody biomass, and all conclude strong negative effects of browsers on woody biomass (Sankaran et al. 2013; Staver & Bond 2014) and seed production (Goheen et al. 2010). This suggests that the positive relationship found in this study is merely a result of woody cover increasing browser MBD instead of vice versa. Grazer MBD showed a humped-shaped relationship with woody cover (in agreement with Sankaran et al. 2005), possibly as a result of an interaction effect not accounted for in our data set. For example, grazers might avoid patches with high woody cover due to reduced food and increased predation risk (Riginos & Grace 2008; Riginos 2015), but at the same time increase woody cover at high biomass densities due to reduced tree–grass competition and reduced fire effects (Cramer et al. 2010; February et al. 2013).

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Grazer MBD showed a positive linear relationship with normalized lacunarity, indicating increased clustering of woody species with high grazer densities. Few studies have experimentally tested the effect of grazers on woody patchiness, but large grazers seem to decrease the clustering of woody individuals (Seifan & Kadmon 2006; Browning et al. 2014). This is the opposite of our findings, suggesting it is more likely that grazers avoided patches with regularly spaced woody vegetation instead of instigating clustered woody vegetation patterns. Furthermore, normalized lacunarity first increased with browser MBD and subsequently decreased; it is not clear what caused this hump-shaped pattern.

An alternative explanation (apart from interaction effects) for the humped-shaped relationships found in this study (both grazer MBD with woody cover and browser MBD with normalized lacunarity) might be found in the intermediate disturbance hypothesis (IDH) or the stress gradient hypothesis (SGH). Both IDH (Grime 1973; Wilkinson 1999) and SGH (Michalet et al. 2006; Kawai & Tokeshi 2007) identify hump-backed patterns along gradients of disturbance and stress, respectively. Changes in interaction strength and sign across gradients of abiotic conditions, herbivore densities and fire frequencies, which are the causal mechanisms behind these patterns, are poorly studied in African savanna ecosystems and deserve further investigation.

Conclusion

Overall, our study identified fire frequency and annual rainfall as the most important determinants of woody vegetation patchiness across multiple spatial scales (100–1000 m). Under low rainfall (500 mm·yr^{-1}) woody species were more regularly distributed across the landscape. With increasing rainfall (900 mm·yr^{-1}), not only percentage woody cover increased, but also the patchiness of woody vegetation, which was further increased by more frequent fires. Large herbivores only had a limited effect on woody patchiness (and cover) and showed mixed relationships with both cover and patchiness. Woody cover and patchiness are two separate aspects and should both be taken into account to describe the patterns in woody vegetation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Normalized lacunarity curves of the four landscapes displayed in Fig. 1.

Appendix S2. Relationship between woody cover and normalized lacunarity.

Appendix S3. Empirical variograms of normalized lacunarity and woody cover.

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