Humans and elephants as treefall drivers in African savannas

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Abstract

Humans have played a major role in altering savanna structure and function, and growing land-use pressure will only increase their influence on woody cover. Yet humans are often overlooked as ecological components. Both humans and the African elephant, *Loxodonta africana*, alter woody vegetation in savannas through removal of large trees and activities that may increase shrub cover. Interactive effects of both humans and elephants with fire may also alter vegetation structure and composition. Here we capitalize on a macroscale experimental opportunity - brought about by the juxtaposition of an elephant-mediated landscape, human-utilized communal harvesting lands and a nature reserve fenced off from both humans and elephants - to investigate the influence of humans and elephants on height-specific treefall dynamics. We surveyed 6 812 ha using repeat, airborne high resolution Light Detection and Ranging (LiDAR) to track the fate of 453 685 tree canopies over two years. Human-mediated biennial treefall rates were 2-3.5 fold higher than the background treefall rate of 1.5% treefall ha^{-1} yr^{-2}, while elephant-mediated treefall rates were 5 times higher at 7.6% treefall ha^{-1} yr^{-2} than the control site. Model predictors of treefall revealed that human or elephant presence was the most important variable, followed by the interaction between geology and fire frequency. Treefall patterns were spatially heterogeneous with elephant-driven treefall associated with geology and surface water, while human patterns were related to perceived ease of access to wood harvesting areas and settlement expansion. Our results show humans and elephants utilize all height-classes of woody vegetation, and that large tree shortages in a heavily utilized communal land has transferred treefall occurrence to shorter vegetation. Elephant- and human-dominated landscapes are tied to interactive effects that may hinder tree seedling survival which, combined with tree loss in the landscape, may compromise woodland sustainability.

Keywords: communal land; disturbance; ecosystem engineer; human ecology; LiDAR; South Africa

Introduction

Humans have been an integral and ancient part of savanna structure and function (Bartlett 1956; Ellis 2011). Currently, savannas contain up to a third of the global human population and the majority of the world's agropastoralism (Safriel et al. 2005), and are under immense and growing land-use pressure (Sala et al. 2000; Ellis and Ramankutty 2008). Savanna woody cover determinants are frequently considered in terms of abiotic and herbivory factors (Sankaran et al. 2005), but human effects can also change the proportion of woody cover both directly, through land-use change (Belsky 1987; Higgins et al. 1999), and indirectly, by altering fire regimes (Bird and Cali 1998; Pyne 2001). Human impacts on savanna structure contribute to the emergent properties of tree cover (Bucini & Hanan 2007), highlighting the need to treat humans as ecosystem components (Worm et al. 2016).

Humans alter savanna vegetation structure and composition directly through wood removal (House and Hall 2001; Galvin and Reid 2011). In this context, human effects on vegetation can be contrasted to those of the iconic symbol of African savannas, the African elephant (*Loxodonta africana*), dominant in southern and eastern Africa since the late Pleistocene (Coppens et al. 1978). As the largest extant land herbivores, elephants are bulk feeders that alter ecosystem structure and composition (Laws 1970; Asner et al. 2015). This occurs directly through pollarding (Guy 1976) and uprooting (Shannon et al. 2008), or indirectly via debarking (Moncrieff et al. 2008). Although humans are comparatively smaller in mass to elephants, high human population densities substantially depress woody cover (Bucini & Hanan 2007). Humans and elephants have the potential to affect all vegetation height classes, with cascading effects on ecosystem function and biodiversity (humans: Janzen 1988; elephants: Cumming 1982). For example, humans and elephants facilitate the resprouting response of savanna species through continual harvesting (Luoga et al. 2004) and browsing (Jachmann and Bell 1985; Rutina et al. 2005) for fuelwood and forage respectively, potentially increasing the availability of a preferred stem size. Both agents are implicated in high rates of tree loss (humans: Ramankutty 2006; elephants: Laws 1970) and shrub layer increases (humans: Archer et al. 1988; elephants: Jachmann and Bell 1985).

Both elephant- and human-mediated effects on savannas are confounded by additional factors, including fire, heterogeneous resource distribution, the abiotic context, and land management and policy. Although associated with more fire ignitions, increased human population density results in greater landscape

fragmentation and lower grass fuel loads, with smaller burned areas as a consequence (Archibald et al. 2009). Humans intentionally burn savanna vegetation to encourage seasonal growth for livestock grazing or clear vegetation for croplands (Hall 1984). However, widespread fire suppression and overgrazing have been implicated in shrubland encroachment (Archer et al. 1995; Roques et al. 2001). In contrast, protected areas are the most burned land-use in southern African savannas (Archibald et al. 2010). Fire acts synergistically with elephant bark stripping to increase tree mortality (Moncrieff et al. 2008; Vanak et al. 2012). Elephant-fire contributions to large tree mortality, together with tree seedling suppression in the 'fire trap' (*sensu* Higgins et al. 2000) and cascading interactions with seedling herbivores (Rutina et al. 2005), have contributed to a reduction in large trees (Barnes 1983; Eckhardt et al. 2000).

Elephant foraging varies seasonally (Western and Lindsay 1984; Cerling et al. 2006), often centered around resource availability, particularly water (Western 1975; Chamaillé-Jammes et al. 2007), but is also mediated at different scales by soil nutrients (Asner et al. 2009). In contrast, human-associated wood harvesting patterns are affected by the perceived ease of access to wood resources, as well as the fine-scale socio-economic status of each household and "rural production system" context (Soussan 1988; Dovie et al. 2004). Nevertheless, despite different drivers of wood resource use, both elephant and human associated effects on woody vegetation are density dependent (humans: Vitousek et al. 1986; Bucini & Hanan 2007; elephants: Trollope et al. 1998; Skarpe et al. 2004).

Woody canopy structure and composition reflect the ecological context of multiple spatial and temporal processes (Watt 1947; Vanak et al. 2012; Scholtz et al. 2014), complex interactive effects with other species (Dean et al. 1999; Sankaran et al. 2005), humans (Turner et al. 2007; Ellis and Ramankutty 2008), and ecosystem processes (Belsky 1994; Treydte et al. 2007). Research on tree canopy dynamics has frequently focused on elephant impacts, but less so on humans as determinants of woody cover resulting from a paucity of data on rates and spatial patterns of human-mediated treefall. In most of African elephants' range, humans and elephants coexist (van Aarde et al. 2008), making inferences about treefall drivers unclear. However, in South Africa elephants only exist in fenced conservation areas, often bordered by rural, impoverished communities reliant on local natural resources. South Africa also contains nature reserves fenced off from both elephants and humans, creating a macroscale experimental opportunity for investigating the factors associated with savanna vegetation dynamics in the exclusive presence and absence of two major disturbance

agents. These results will augment valuable field-based research on elephant- (e.g. Shannon et al. 2008) and human-mediated treefall (e.g. Luoga et al. 2002) by providing a landscape scale geospatial context, especially when combined with detailed tree height specific information.

Here we use 'experimental' landscapes, utilized by either humans, elephants, or neither, combined with repeat high resolution, airborne Light Detection and Ranging (LiDAR) technology to quantify the relative impact of humans and elephants on height-specific treefall rates and to explore the following questions: 1) How do the rates and spatial patterns of treefall differ between human- and elephant-mediated landscapes, and what affects these differences? 2) What is the relative importance of other factors (e.g. fire, geology, hillslope, human-settlement specific differences) in influencing treefall within and between these sites? The insights provided by these questions will improve our understanding of anthropogenic contributions to savanna woody dynamics and have the potential to refocus questions on woodland sustainability.

Methods

Study area

The study sites were located in Mpumalanga province in the north-eastern portion of South Africa. This area is a multi-use conservation landscape with a graduated scale of land-use intensity across the subregion (Coetzer et al. 2014). Summer rainfall averages 750 mm p.a. in the northern study sites and 650 mm p.a in the south eastern extent, with mean daily maxima of 31 °C (minima 20 °C) and 26 °C (minima 8 °C) for summer and winter, respectively. The terrain is gently undulating and the geology is dominated by granite with local Timbavati gabbro intrusions. The vegetation is Granite Lowveld dominated by *Terminalia sericea, Combretum zeyheri* and *C. apiculatum* on the sandy, dystrophic uplands and *Acacia nigrescens, Dichrostachys cinerea* and *Grewia bicolor* on the deep, clayey, high sodium lowlands with dense stands of *T. sericea* delineating the seep zones (Rutherford et al. 2006). Localized Timbavati gabbro intrusions are characterized by Gabbro Grassy Bushveld, a more open savanna with fewer scattered trees on dark clay soils which swell and shrink (Rutherford et al. 2006).

Our LiDAR survey sites were two communal lands used by humans (hereafter referred to as Communal land$_A$ and Communal land$_B$), a private nature reserve containing elephants (Reserve$_e$), and a nature reserve fenced off from both humans and elephants which served as a "control site" (Reserve$_0$) (Fig. 1, Table 1). The two communal lands had approximately the same human population densities at the time of the surveys ('density' here defined as human population relative to available communal land area) (Table 1) and are state-owned, tribally-managed, former Apartheid 'homelands'. The human settlements that use Communal land$_A$ and Communal land$_B$ have the inherent socio-economic characteristics associated with their former 'homeland' status of extensive unemployment, low education levels, high population densities dependent on migrant labor and social grant remittances (Thornton 2002), coupled with a reliance on natural resources (Twine et al. 2003). Communal land$_A$ is communally utilized by the settlement of Justicia (2.0 humans per communal land ha) and Communal land$_B$ is used by Welverdiend (2.2 humans per communal land ha) (Table 1). Communal land$_A$ is adjacent to the privately-owned game reserve, Sabi Sand Wildtuin (SSW: Reserve$_e$) established in 1898 (Mabunda et al. 2003) with an elephant density of 2.55 elephants km^{-2} in 2011 (de Boer et al. 2015) (Fig. 1, Table 1). SSW is an association of separately managed farms with a joint focus on tourism-based conservation (http://www.sabisand.co.za). In 1961 a fence was erected between Kruger National Park (KNP) and SSW and removed in 1993, followed by a 17 fold increase (1992-2011) in elephant densities (de Boer et al. 2015), entering from KNP during winter (Hiscocks 1999). Communal land$_B$ neighbors state-owned Andover Nature Reserve (Reserve$_0$), a nature reserve with no elephants and fenced off from the adjacent communal land (Fig. 1). Giraffe are present in Reserve$_0$, but have not been implicated in treefall events (Scholes et al. 2003).

Airborne LiDAR mapping

Time series data from airborne LiDAR campaigns was collected in April 2010 and 2012 using the Carnegie Airborne Observatory systems (CAO) at 2000 m AGL with an effective laser point density of 4 laser shots m^{-2} (for technical details see: Asner et al. 2007; Asner et al. 2012). The CAO LiDAR systems have an integrated Global Positioning System-Inertial Measurement Unit (GPS-IMU) providing accurate locational data for each laser return in the point cloud. The surveys were conducted at the end of the wet, summer season before deciduous savanna trees lose their leaves to maximize vegetation height return accuracy. LiDAR returns were differentiated between those that reflected off the vegetation canopy or subcanopy and those that penetrated

through the vegetation and reflected off the ground surface. The last laser returns (ground returns) were interpolated to create a digital terrain model (DTM); the first returns (top-of-canopy returns) were used for producing a digital surface model (DSM). The difference between the DSM and the DTM provided a canopy height model (CHM) at 1m spatial resolution.

Individual tree identification

Although the LiDAR campaigns were conducted in the same month, variation in phenology between years could compound errors in a pixel-based analysis. In addition, the purpose of the research required monitoring individual trees over time. Thus, we delineated individual tree crowns from the CHM using an object-oriented approach. A crown segmentation method was used with Gaussian kernel smoothed data (to maximize whole-crown detection) and transformed to maximize object identification in multi-crown canopies (for details see: Asner et al. 2015). All crowns >1m in height were considered 'trees'. The centre point of each tree was geotagged with coordinates and the changes in the maximum height of each individual tree crown was monitored over time. Here, 'treefall' was said to have occurred if ≥75% of the original object-based crown height in 2010 was lost by 2012. This method does not detect partial canopy and branch loss (like that associated with pollarding and herbivory).

Treefall analysis

As this study was a 'comparative mensurative' experiment on a regional scale with no replicates per 'treatment' (e.g. reserve with/without elephants), the study is inherently pseudoreplicated (Hurlbert 1984). Thus, definitely identifying drivers of differences seen between sites would be irresponsible (Hurlbert 1984); we applied a holistic approach to this landscape study, explicitly acknowledging the underlying heterogeneity and made inductive conclusions, within the bounds of certain assumptions (Hargrove and Pickering 1992). Recognizing the pre-existing confounding variables between treatments (e.g. pre-existing differences in tree density), we reported both absolute and relative change and the combinative analysis of these patterns alludes to drivers of landscape-scale change, contributing hypotheses which can then be tested empirically in future studies. Treefall was reported as biennial loss in absolute numbers ha^{-1} and as a percentage ha^{-1} relative to the baseline number of standing trees in 2010. Treefall cannot be solely attributable to elephants and humans, but the relative contributions of other agents - such as wind (Spinage and Guinness 1971), frost (Childes and

Walker 1998[7]) and other herbivores (e.g. Yeaton 1988) - to treefall and subsequent coppice dynamics were unknown, but were assumed to be equal between sites.

Monthly fire data (2000-2012) were derived from remotely sensed MODIS burned area product (MCD45A1-V051) at 500 m resolution. This product was validated in South African savannas and accurately detected 85% of true burned area (Roy et al. 2005), although it is less efficient at identifying smaller burns (<50 ha) (Tsela et al. 2014). The data were binned into burned/unburned area and summed per year using the R (R Core Team 2013) packages: sp, rgdal and raster. For the purposes of this study, the data were divided into 'historical burns' (number of times burned p.a. from 2000 to 2010) and 'recent burns' (number of times burned p.a. from 2010 to 2012). Communal land extents were manually digitized using a series of aerial images (50 cm resolution; years: 2009, 2012; www.ngi.gov.za). Upland and lowland locations were generated from relative elevation models generated in SAGA GIS (SAGA User Group Association 2010) using the Terrain Analysis toolset. Ripley's multi-distance spatial cluster analysis was run in SAGA GIS using 100 m distance bands at 40 m intervals, with a boundary correction method to simulate outer values, measuring treefall clustering occurrences as the size of the neighborhood changes (Haase 1995). Ripley's cluster analysis tests the observed spatial homogeneity of fallen trees for departure from completely spatial randomness, expressed as regular or clustered distribution. All spatial analysis was performed in R v3.2.1 (R Core Team 2013). Absolute treefall rates were tested for significant differences using a non-parametric Kruskal-Wallis χ^2 test with a Tukey Kramer (Nemenyi) test (with Tukey distance approximation for independent samples) (R package: PMCMR). Kolmogorov-Smirnov (KS) tests were used to test for differences between sampled treefall height distributions. Treefall height classes were compared using ecologically relevant categories: 1-3m (e.g. Bond and Keeley 2005); 3-5m (e.g. Asner and Levick 2012); 5–10m (e.g. Dean et al. 1999); and >10m (e.g. Tews et al. 2004). A logistic regression model was used to identify significant variables associated with treefall. The model was run on a randomly selected sample of tree crowns with a distance constraint (40m) to avoid spatial autocorrelation (Legendre & Fortin 1989); the distance constraint was calculated from a semivariogram run in SAGA GIS. A fully-additive global model was generated from a binary response variable (treefall occurred = 1, treefall did not occur = 0) in sites containing elephants (Reserve$_e$), humans (Communal land$_A$ and Communal land$_B$), or neither (Reserve$_0$), in relation to various abiotic factors and ecologically-relevant interactions. Model selection was based on Akaike's information criteria (AIC) and

performed in R (package: MuMIn) using the 'dredge' tool and ranked in increasing values of ΔAIC (Δ_i) (Burnham & Anderson 2002). Tests for multicollinearity and overdispersion of the models (Logan 2010) raised no concerns. We used a model averaging approach to assess the strength of our best-fit model as models with $\Delta_i \leq 2$ can be considered not significantly different from each other (Burnham & Anderson 2002; Burnham & Anderson 2004). Model averaging calculates the relative importance of each variable by calculating each model's contribution in proportion to their Akaike weights (ω_i). Akaike weights can be treated as probabilities that model i is the best model for the dataset (Burnham & Anderson 2004). Model results were presented graphically (R package: biology) where odds ratios indicate the change in the odds of treefall occurrence (response variable) per unit increase in a predictor variable whilst holding the other predictor variables constant (Hosmer et al. 2013). Odds ratios for each categorical predictor variable were calculated relative to a reference level (see Supplementary material Appendix 1, Table A1).

Results

Treefall rates

Landscape-scale tree mapping identified 453 685 individual trees >1m in height across the entire area in 2010, of which 11 740 (2.59%) lost $\geq$75% of their original height, ranging across sites from 1.32% treefall in Reserve$_0$ to 4.18% treefall in Reserve$_e$. Human-mediated treefall rates were 2.29% in Communal land$_A$ and 4.74% in Communal land$_B$, exceeding the elephant-mediated treefall rate. Communal land$_B$ also contained the lowest total number of trees surveyed in 2010 (22 295 trees), compared to Communal land$_A$ (116 498 trees), Reserve$_e$ (135 402 trees), and Reserve$_0$ which had the highest number of trees (179 490). Proportional biennial treefall rates revealed greater disparities between sites than absolute rates as there was no significant difference between Reserve$_0$ and both Communal lands' treefall rates in absolute terms; when controlling for the amount of original standing trees there are significant differences between all sites (Table 2). Reporting proportional rates averaged per hectare revealed the spatial variability in treefall between sites. Accordingly, Reserve$_e$ had the fastest biennial treefall rate and highest variability at 7.6% $\pm$ 12.6 treefall ha^{-1}, followed by Communal land$_B$ with 5.3% $\pm$ 11.5 treefall ha^{-1} (Table 2).

In Communal land$_A$ treefall occurred relatively evenly (± 3%) across all height classes (Fig. 2). Communal land$_B$ shows high treefall occurrence (7.03%) in the 1-3 m height class. However, tree height classes >3m in Communal land$_B$ have very low sample numbers and low treefall occurrence (Fig. 2), an indication that this communal land has been heavily harvested in the past. Elephant-mediated treefall in Reserve$_e$ was concentrated in the >3m height classes (Fig. 2), peaking at >10% in the 5-10 m height class. However, the 1-3m height class in Reserve$_e$ also experienced considerable treefall of 4.6%.

Spatial variation in treefall rates

Treefall in Reserve$_e$ and Communal land$_B$ had the most clustered pattern (Fig. 3). Yet the treefall clusters were more spatially distributed in Reserve$_e$ (Fig. 4h) relative to the communal lands (Fig. 4d,f). High treefall rates in Reserve$_e$ were concentrated in 2 large clusters in the eastern portion of the study site (Fig. 4g), most of which occurred in vegetation <3m in height and were likely related to managed bush clearing. The two smaller red (>21 treefall ha^{-1}) patches of high treefall to the west of Reserve$_e$ were located over permanent water sources and the yellow (11-15 treefall ha^{-1}) patches dotted in the north east were along river courses (Fig. 4g). Relative treefall patterns revealed higher proportional rates in the western gabbro portion of Reserve$_e$ than in the eastern granite (Fig. 4h, D = 0.21, p <0.001; 13.44 ± 18.19% gabbro treefall ha^{-1}, n = 1029; 4.99 ± 8.34% granite treefall ha^{-1}, n = 1072). The communal lands had discrete clusters of treefall mostly within 1 km of the settlement (Fig. 4c-f). There were also high treefall rate hotspots on Communal land$_A$'s eastern boundary, adjacent to Reserve$_e$ (Fig. 4c-d). Treefall in Reserve$_0$ had the least clustered treefall of all sites (Fig. 3) and contained no visibly distinct high treefall hotspots (Fig. 3a-b).

Factors influencing treefall

Treefall was not significantly influenced by historical burns (>10 years), upslope or downslope location or the 2010 tree height (Supplementary material Appendix 1, Table A1). However, the odds of treefall occurring were increased (z = 1.93, p = 0.05) by recent burns between 2010 and 2012 (Fig. 5). Fires only occurred once in two years in Reserve$_e$ and Reserve$_0$, but occurred more frequently in the communal lands (Supplementary material Appendix 1, Fig. A1). The burned areas in the communal lands were furthest away from the settlements (Supplementary material Appendix 1, Fig. A1b-c). It is worth noting the location of the treefall clusters in Reserve$_e$ were spatially associated with the location of a contiguous burned area (Supplementary

material Appendix 1, Fig. A1d). Of all the sites, the odds of treefall increased most if the trees were in Communal land$_B$ (z = 4.57, p <0.001) or Reserve$_e$ (z = 5.65, p <0.001), relative to Reserve$_0$ (Fig. 5), thus treefall was best predicted by the presence of humans or elephants. Treefall occurrence odds decreased on granite geology (z = -2.62, p = 0.01); the corollary being that treefall odds increased on gabbro geology (Fig. 5). A synergistic interactive effect of geology and recent burns was also associated (z = 2.538, p = 0.01) with higher treefall occurrences (Fig. 5).

Discussion

Using large-scale, high-resolution LiDAR measurements we tracked the fate of over 450 000 individual trees across 6 812 ha of mixed-used landscapes, quantifying treefall rates and patterns between human- and elephant- mediated sites. Human-mediated treefall was 2.3 to 3.7 times higher than in the control site, Reserve$_0$ (Table 2). Thus, human-mediated relative treefall (3 - 5% ha^{-1} yr^{-2}) was a significant driver of savanna structural dynamics, approaching that of the elephant-mediated landscape (7% ha^{-1} yr^{-2}). Background treefall rates (1.45% treefall ha^{-1} yr^{-2}) in areas protected from both elephants and humans were comparable to herbivore exclosure experiments in Kruger National Park (KNP), South Africa, where a site with similar rainfall and geology to the control site, Reserve$_0$, had 1.9% background treefall ha^{-1} yr^{-2} (Asner and Levick 2012). Elephant-mediated treefall in Reserve$_e$ was on average 5 times higher than in the control site, Reserve$_0$ (Table 2). In comparison, elephants in KNP resulted in 6 times the background treefall rate outside the exclosures (Asner and Levick 2012), with estimated park-wide treefall rates of 12% ha^{-1} yr^{-2} (Asner et al. 2015). Although elephant-mediated large tree mortality varies from 1-2% yr^{-1} over multi-decadal cycles (e.g. van de Vijver et al. 1999), records of up to 20% yr^{-1} mortality have been recorded in some localities (e.g. Beuchner and Dawkins 1961; Pellew 1983). While there are field-based studies (e.g. Shannon et al. 2008) and landscape-scale studies (e.g. Asner and Levick 2012) that tracked elephant impacts on individual trees over time, analogous studies for human mediated treefall on a broad-scale are limited (Bucini & Hanan 2007). Here, we have quantified human-associated treefall in savannas.

Elephant- and human-related patterns of treefall differ spatially as they result from divergent functional processes (Watt 1947). We found that elephant-mediated treefall was spatially associated with landscape-

scale nutrient distribution. Treefall occurred predominantly on gabbro geology (Fig. 4-5), corresponding with other studies recording elephant use of vegetation on nutrient-rich soils (Eckhardt et al. 2000; Asner and Levick 2012), Shannon et al. (2008) also recorded higher rates of pushed over trees on gabbro geology, however Vanak et al. (2012) did not find higher levels of large tree mortality on these soils. Our research also shows elephant-associated treefall patterns were highly clustered, centering on surface water (Fig. 4g). Permanent surface water concentrates elephant effects on the landscape, leading to persistent use of vegetation resources in these areas, ranging from negligible vegetation structural change in wet years (e.g. Kalwij et al. 2010) to severe during droughts (e.g. Napier Bax and Sheldrick 1963). Although treefall in Reserve$_e$ in all height classes was markedly higher than background treefall, the 5-10 m height class was fivefold that in the control site (Fig. 2). While our results do not show an elephant utilization effect proportional with abundance like that in Shannon et al.'s (2008) transect study, we also do not have a clear 'elephant trap' in the 5-9 m height as per Asner and Levick's (2012) findings. Elephants were the main driver of treefall in all height classes in our study.

In contrast to elephant-mediated treefall associated with abiotic factors, the rate and pattern of treefall in communal lands was influenced by socio-economic factors and ease of access. Treefall in the communal lands was less clumped than elephant-mediated treefall patterns (Fig. 3), with high treefall rates (i.e. >15 treefall ha^{-1}) coalescing adjacent to settlements (Fig. 4c,e) – areas being clear-cut for settlement-associated expansion (Coetzer et al. 2013) – or on communal land boundaries to reinforce land ownership under perceived land claim threats. Communal land$_B$'s treefall occurred in the low height class (Fig. 2), an indication that shortages of trees >3 m are placing disproportionate harvesting pressure on the lower height classes. The high market-share of households purchasing wood in this area (Madubansi and Shackleton 2007) supports this finding. Despite both communal lands having similar human population densities (Table 1), Communal land$_B$ is a highly utilized area, accessible to other settlements as it borders a main road and neighbors the more urbanized sections of Bushbuckridge where communal lands have been subsumed by settlement expansion (Coetzer et al. 2013). Communal land$_A$ is a rare example of exclusive use by one settlement as it is fenced on two boundaries and the location is, relatively, remote. This is reflected in the height-specific treefall which is spread evenly across all height classes at relatively low levels compared to background rates in the control site, Reserve$_0$ (Fig. 2).

Fire frequency emerged as an important factor in treefall, but secondary to both elephant and human influence (Fig. 5). In recent work by Asner et al. (2015), fire frequency was also found to be a secondary factor to elephant and abiotic mediation on treefall. Although treefall may be positively associated with higher fire frequency, tree mortality is not necessarily higher under frequent fire conditions (Vanak et al. 2012), but large tree mortality is associated with high intensity fires (Bond & Keeley 2005; Smit et al. 2016). Savanna woody vegetation is largely fire-resilient: vegetation composition is largely unchanged by fire and individuals rarely suffer mortality, but vegetation structure is fire-responsive (Higgins et al. 2007; Pellegrini et al. 2015). Lower tree and greater grass biomass on gabbro geology drives more frequent fire returns in this landscape (Fig. 5), facilitating treefall in previously damaged trees, which substantially increases tree mortality (Shannon et al. 2011). This is particularly pertinent for tree species preferentially targeted by elephants, resulting in large areas with missing size classes of long-lived trees (Helm and Witkowski 2012). Indeed, the association of treefall with a gabbro-fire frequency-elephant nexus supports Vanak et al.'s (2012) findings on the strong association between the differential vulnerability of large trees to mortality and a three-way interaction between elephant, fire and landscape type. Though the magnitude of fire's effects is dependent on fire intensity (Smit et al. 2010), it is difficult to measure accurately over large scales (Archibald et al. 2013). Thus fire intensity's effects on vegetation structure and composition remains less certain.

Curiously, the presence of recent fires on communal lands was associated with increased treefall (Fig. 5). Although increased human population densities have been associated with more fire ignitions, but less intense fires over smaller extents (Archibald et al. 2009), we can only speculate on possible mechanisms for the association with more frequent burns and increased treefall in the communal lands. Tall trees with hard wood which are difficult to cut by hand are often burned for clearing agricultural fields, which can result in spreading fires and tree mortality (Luoga et al. 2000). In addition, patch burning to encourage grass regrowth for livestock grazing and cropland clearing is a common phenomenon in African rangeland systems (Hall 1984).

Elephant- and human-associated treefall rates (Table 2) represent the "mortality ceiling" of savanna vegetation as fallen trees frequently resprout. For example, in an extensive 30-month field survey in KNP, about 10% of trees in the 5-10m height class were pushed over by elephants, but of these, 60% survived (Shannon et al. 2008) through coppicing responses (Jachmann and Bell 1985; Owen-Smith 1998). Repeat

damage to large trees over 30 months was reported as 12.5% and 2.6% from elephant and fire, respectively, of which 36.6% died from the damage (Vanak et al. 2012), demonstrating substantial resilience of woody vegetation to disturbance. Coppicing responses to human-harvested trees have also been documented (Shackleton 1993; Luoga et al. 2004). Fuelwood and charcoal studies in savannas suggest woody vegetation communities shift under high use scenarios to ecosystems dominated by resilient species that coppice readily (Strømgaard 1986; Shackleton 1993). Although this research shows that both elephants and humans are substantial drivers of treefall in savannas and utilize all height classes of woody vegetation, tree loss *per se* does not result in woodland decline unless accompanied by lack of seedling recruitment (Augustine and McNaughton 1988). This occurs directly through loss of mature, seed-bearing trees and seedling herbivory by elephants or human livestock (e.g. elephants: Western and Maitumo 2004, goats: Hester et al. 2006), or indirectly, by rendering the trees 'functionally juvenile' through repeated hedging. Additionally, changes in woodland structure can trigger a cascade of interactions, such as that in Chobe riverfront, Botswana, where elephant-induced shrubland conversion facilitated increased seedling herbivory by expanding impala, *Aepyceros melampus,* habitat (Rutina et al 2005). Similarly, in human-associated woodlands, increased coppice regrowth and bush encroachment favors browsing goats over grazing cattle. To compound issues of tree seedling survival, human presence is associated with more frequent fires, trapping tree seedlings in the fire layer. Here we have shown that both elephants and humans, in combination with fire, can utilize all woody height classes. When large trees disappear from the landscape, more disturbance-related pressure is placed on the lower height classes, reducing structural complexity and compromising ecosystem resilience. Large-scale studies need to be combined with detailed height-class specific information to monitor woodlands to preclude woodland unsustainability.

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Table Legends

Table 1. Study site details with elephant and human densities.

Site Name	Site Name Abbreviation	Elephant density (individuals km^{-2})	Human density (humans ha^{-1} communal land	LiDAR survey coverage (ha)	Amount of site surveyed (%)
Sabi Sand Wildtuin	Reserve$_e$	2.55[a]	0	2101	61
Justicia communal land	Communal land$_A$	0	2.0 [b]	1699	61
Welverdiend communal land	Communal land$_B$	0	2.2 [b]	603	20
Andover Nature Reserve	Reserve$_0$	0	0	1674	27

[a] de Boer et al. 2015

[b] Population estimates based on the 2011 South African census and the ongoing MRC/WITS Rural Public Health and Health Transitions Research Unit demographic surveillance surveys (see Kahn et al. 2007).

Table 2. Average biennial rate of treefall ha^{-1} ± standard deviation. Reporting is in absolute and relative treefall rates.

Site	Absolute Rate ± SD (treefall ha^{-1} yr^{-2})	Relative Rate ± SD (% treefall ha^{-1} yr^{-2})	n (ha)
Reserve$_0$	1.32 ± 2.07^a	1.45 ± 2. 22^A	1674
Communal land$_A$	1.39 ± 2.72^a	3.33 ± 7.28^B	1699
Communal land$_B$	1.38 ± 3.16^a	5.34 ± 11.46^C	603
Reserve$_e$	2.33 ± 3.98^b	7.59 ± 12.60^D	2101

[a,b] Superscript letters mark significant differences for absolute rates between sites using Kruskal-Wallis χ2 test (χ2 = 158.85, p <0.001, df = 3) with a Tukey Kramer (Nemenyi) multiple comparisons test.

[A,B,C,D] Superscript letters mark significant differences for proportional rates between sites using pairwise Kolmogorov-Smirnov tests

Figure Legends

Fig. 1. Map of Bushbuckridge Municipality and surrounding conservation land showing the locations of the four airborne LiDAR survey areas, monitored in 2010 and 2012. Gabbro outcrop localities are delineated against a granite-dominated backdrop. The inset map shows the location of the Sabi Sand Wildtuin and Bushbuckridge Municipality in South Africa's northeast corner.
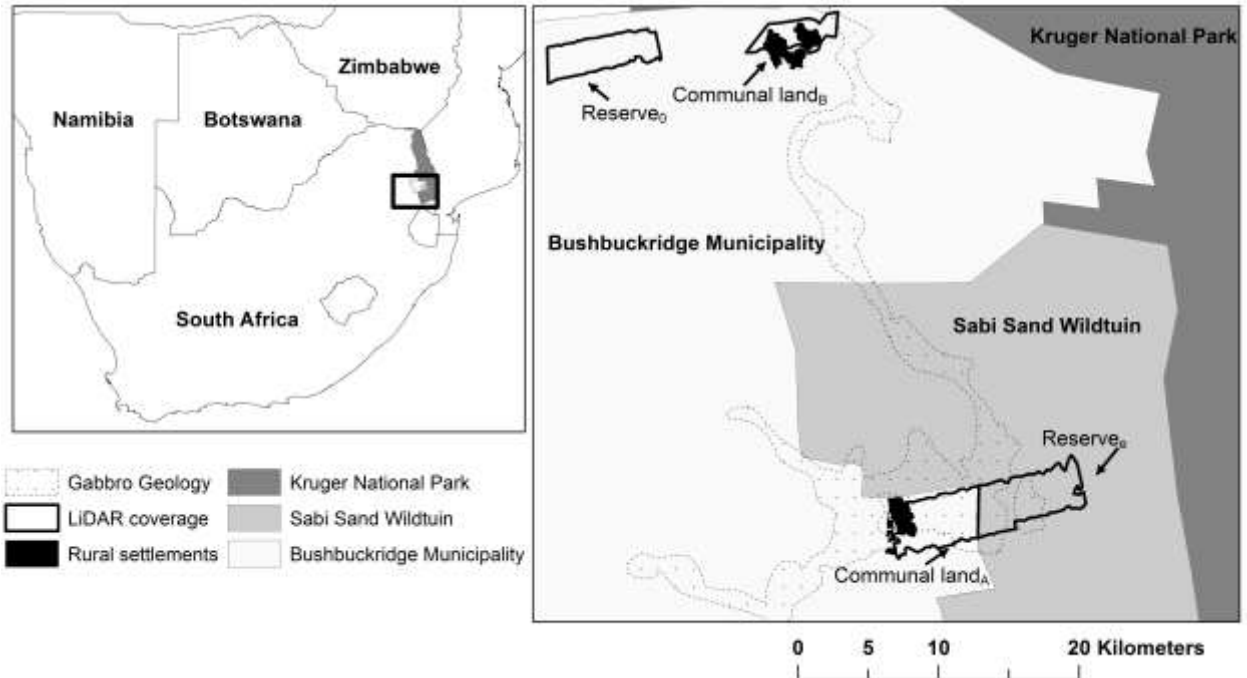
Fig. 2. Height class of felled trees, reported as a percentage of standing trees in each height class per site in 2010. Data are based on a random subsample of trees in each site. Sample numbers for each height class per site are shown above each bar. The legend denotes height classes of trees in 2010.
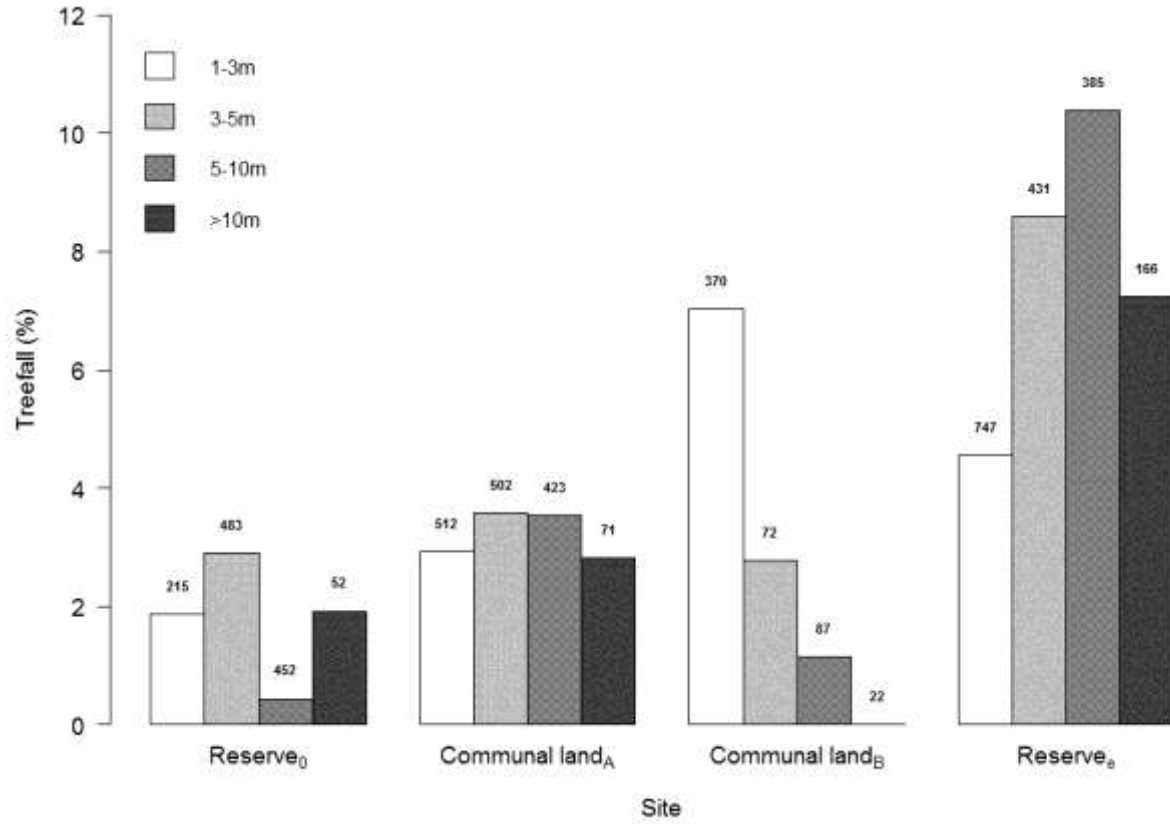
Fig. 3. Global cluster analysis of sites using Ripley's K statistic. The L-value is the difference between observed and expected differences of treefall locations. The L-value = 0 m reference line represents complete spatial randomness; L-values >0 m and <0 m represents more clustering or dispersal, respectively, than that expected from a random distribution. Elephant-mediated treefall (Reserve$_e$) shows clustering at a wide range of spatial scales, followed by human-mediated sites (Communal land$_B$ and Communal land$_A$). The site containing no humans or elephants (Reserve$_0$) shows the least clustered pattern of treefall.
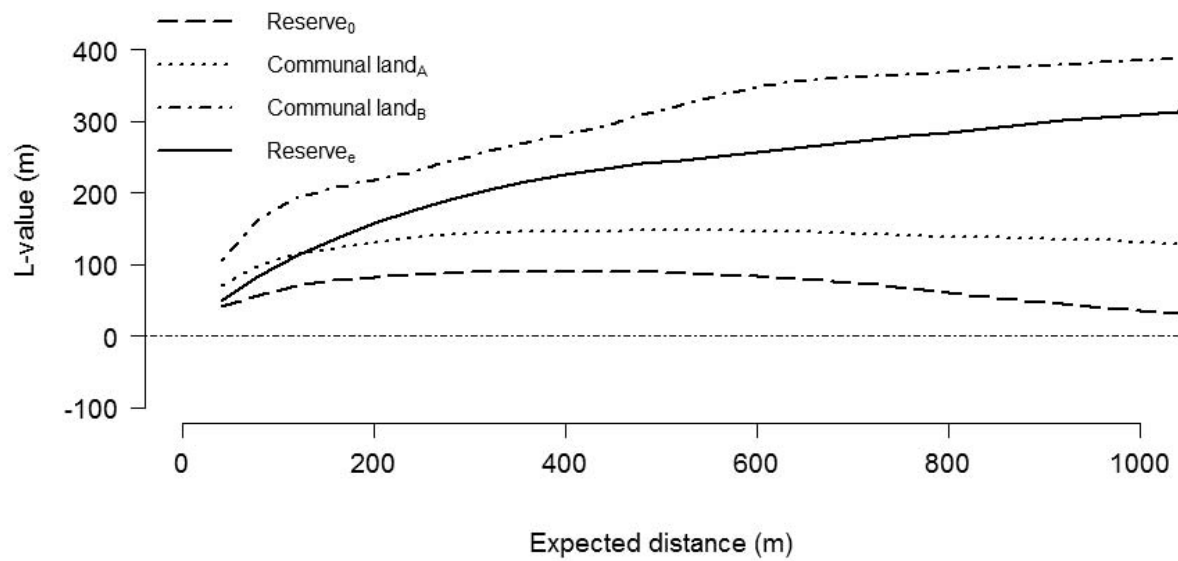
Fig. 4. Maps of biennial treefall rate expressed in absolute (left column) and relative (right column) treefall ha^{-1} for: a-b) Reserve$_0$; c-d) Communal land$_A$; e-f) Communal land$_B$; and g-h) Reserve$_e$. Communal land$_A$ and Reserve$_e$ are dominated by gabbro geology.

Treefall per hectare

0 - 3	
4 - 10	
11 - 15	
16 - 20	
>21	

Granite
Gabbro
Settlement

Relative treefall (%) per hectare

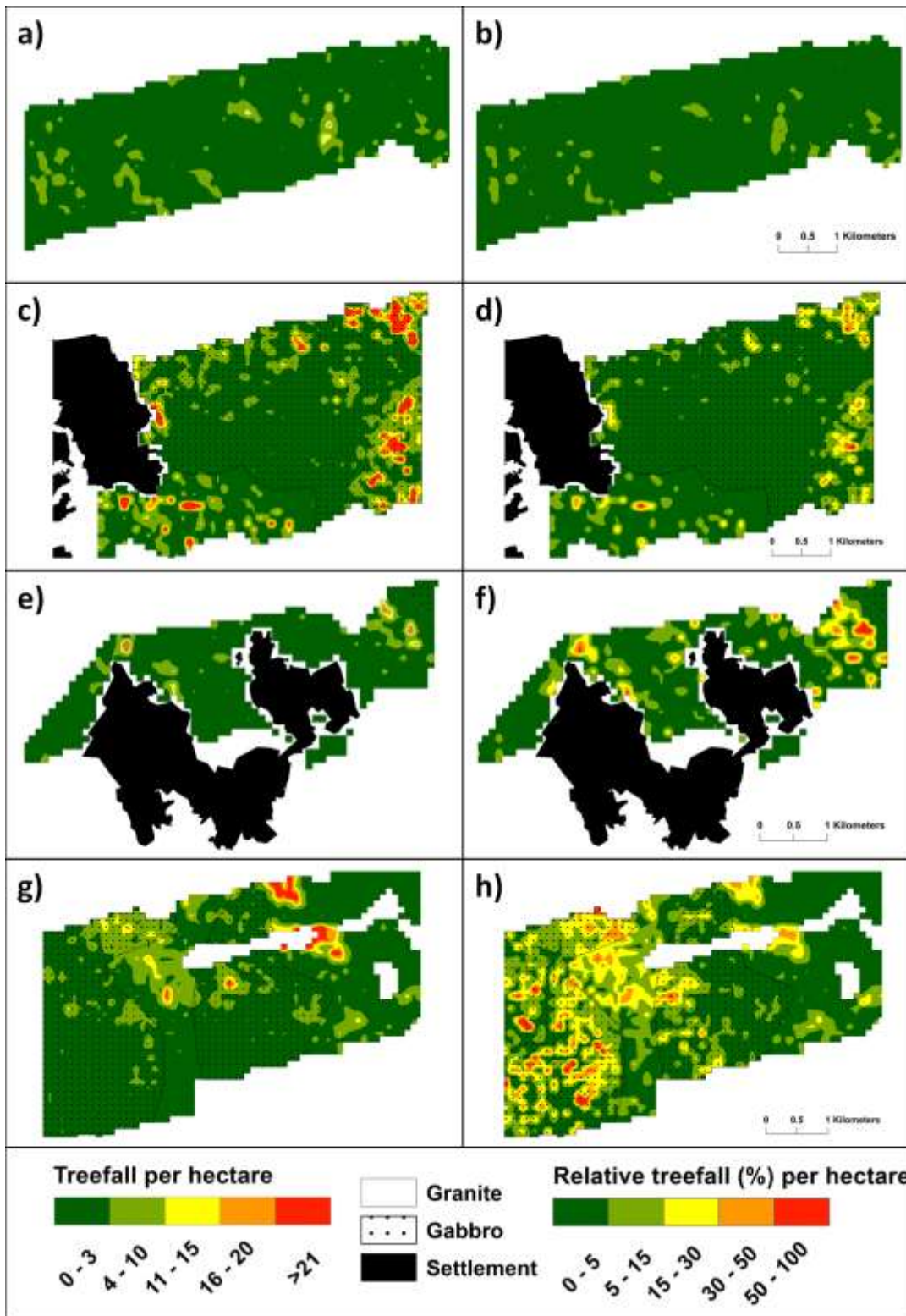|	
0 - 5	
5 - 15	
15 - 30	
30 - 50	
50 - 100	

Fig. 5. Odds-ratio coefficients of the best-fit logistic regression model (Model 1 in Supplementary material Appendix 1, Table A1) of treefall occurrence. Boxplot whiskers show 95% confidence intervals. Site predictor variables were relative to the reference site, $Reserve_0$. The odds of treefall occurrence increased with more recent burns between 2010 and 2012, as well as in sites containing humans or elephants, i.e. Communal $land_B$, and $Reserve_e$. Decreased treefall occurrence was also associated with geology (i.e. granite as the geology variable is relative to the reference geology, gabbro). Treefall occurrence increased with the synergistic effects of geology and recent burns.
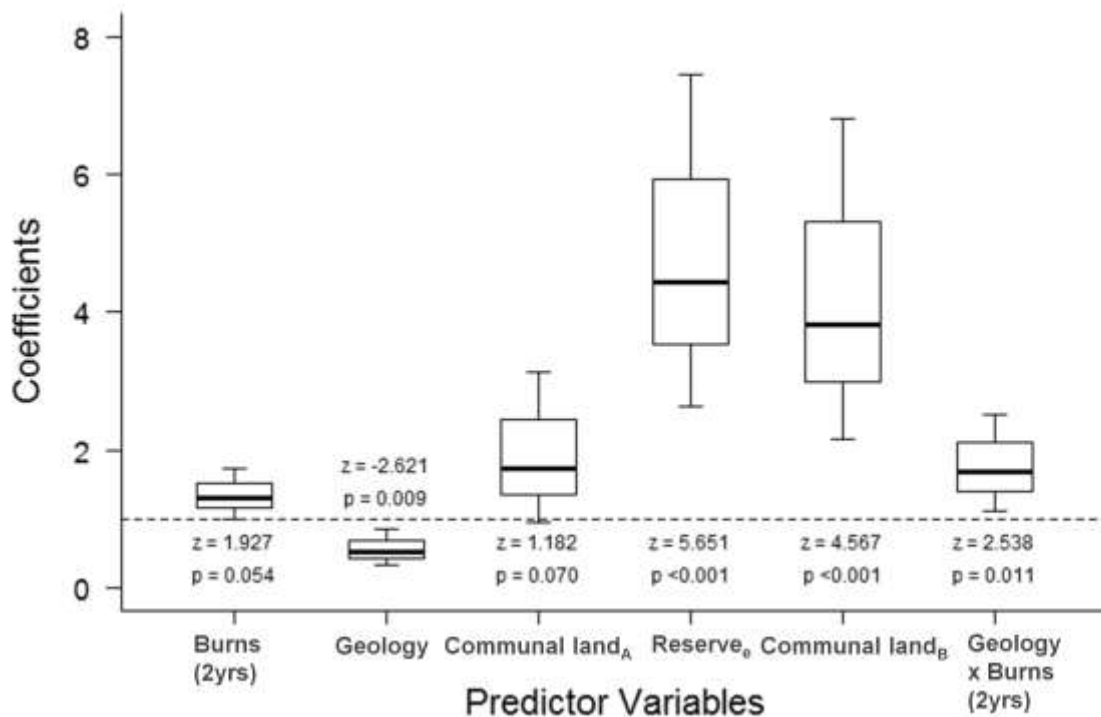
Supplementary Material

Appendix 1

Table A1. Model selection and averaging results of treefall occurrence in sites containing elephants (Reserve$_e$), humans (Communal land$_A$ and Communal land$_B$), or neither (Reserve$_0$), in relation to various abiotic factors. Models with AIC differences (Δ_i) ≤2 are ranked in order of increasing Δ_i with Model 1 as the best-fit logistic regression. Variables included in each model have their p-value recorded. Blank cells indicate those variables were not included in the model. Odds ratios of the categorical variables (Site, Geology, and Catena) are calculated relative to a base level (Reserve$_0$, Gabbro, and Lowlands, respectively).

	Logistic Regression Models				Model Averaging[**]	
Variables	**1**	**2**	**3**	**4**	p_{ip}	ω_{ip}
Site: Communal land$_A$	0.069	0.045	0.063	0.071	0.063	
Site: Reserve$_e$	<0.001	<0.001	<0.001	<0.001	<0.001	**1.00**
Site: Communal land$_B$	<0.001	<0.001	<0.001	<0.001	<0.001	
Burns 2yr	0.054	0.030	0.065	0.056	0.052	**1.00**
Geology: Granite	0.009	0.007	0.008	0.010	0.008	**1.00**
Burns 2yr x Geology	0.011	0.009	0.09	0.011	0.010	**1.00**
Old burns		0.285			0.286	**0.25**
2010 Height			0.362		0.362	**0.21**
Catena: Uplands				0.970	0.970	**0.14**
df	7	8	8	8		
Δ_i	0.00	0.84	1.18	2.00		
ω_i[*]	0.20	0.13	0.11	0.08		

** Model averaging relative p values (p_{ip}) and relative weights (ω_{ip}) are with respect to the global
model and indicate the relative importance of each variable. Variables are ranked in decreasing
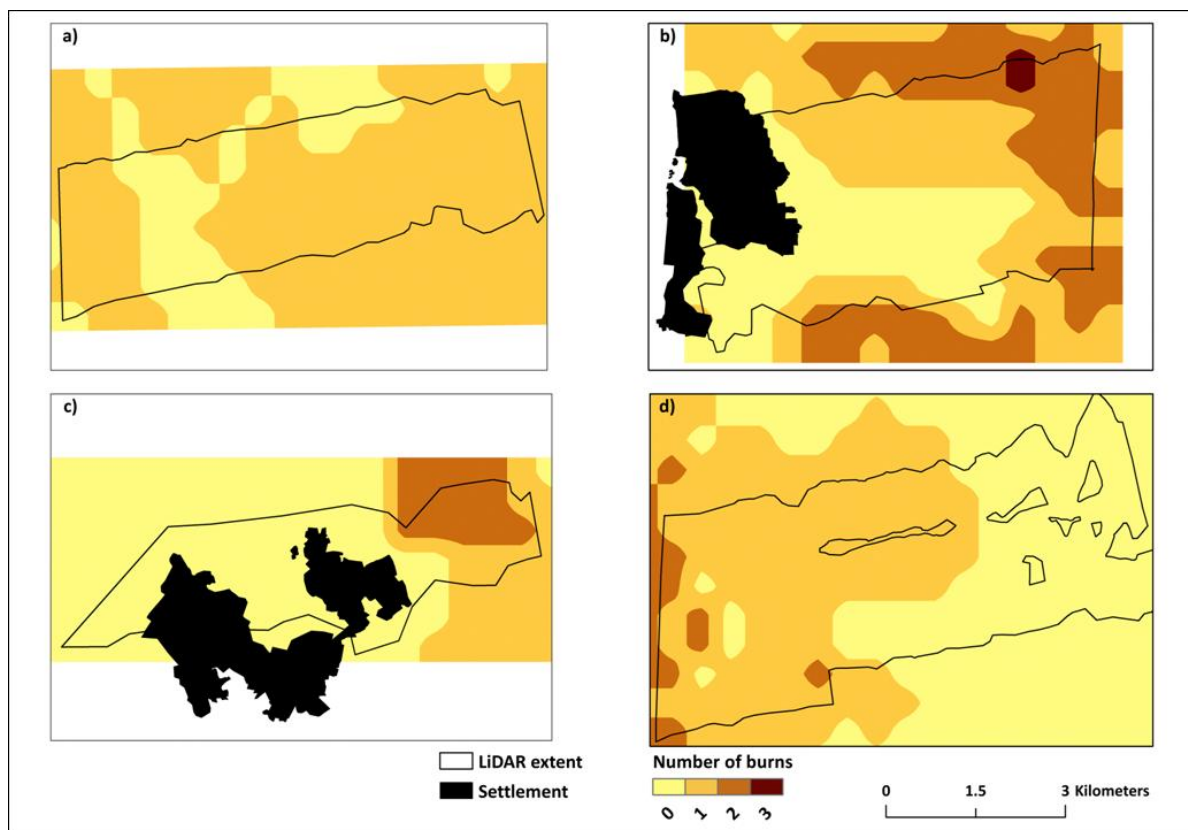ω_{ip}.

Figure A1. Number of burns between 2010 and 2012 for a) Reserve$_0$, b) Communal land$_A$,

c) Communal land$_B$, and d) Reserve$_e$.

Supplementary Material References

Burnham, K. P. and Anderson, R. P. 2004. Multimodel Inference: Understanding AIC and BIC

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