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The importance of history in understanding large tree mortality in African savannas

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Fire and elephant herbivory are major drivers of large tree mortality in savanna ecosystems. Although the spatial variation of these agents is well studied, less attention has been paid to how disturbance history influences tree mortality over time. In a long-term cohort study, we examined how the sequence of fire- and elephant-induced damage influences mortality of trees and determined whether risk of mortality is compounded over time. Data on over 2500 large trees were collected from 22 transects in Kruger National Park, South Africa, in 2006, and trees were resampled in 2008, 2011, 2015 and 2018. Over the 12-year period, we recorded a cumulative mortality of 47.6% with an estimated annual mortality of 3–5% from 2006 through 2015 and an increase to 8.8% in 2018. The main attributed agent of tree mortality was elephant damage, occurring either once or across multiple census periods. A classification tree analysis partitioned over different census periods showed that the probability of mortality of the 10 most common tree species depended not only on the type and intensity of elephant-induced damage and fire but also on the historical sequence of damage by these agents. Elephant damage to the main stem incurred up to 12 years earlier increased risk of mortality for large trees, especially in combination with fire damage. As expected, vulnerability to damage and risk of mortality varied among species, resulting in the potential for long-term changes in species composition over large areas. Overall, this study highlights how multiple interacting agents cause emergent and lagging patterns of mortality risk for large trees in savanna ecosystems, a result that only becomes apparent through fine resolution and long-term tracking of cohorts.

Keywords: cohort analysis, disturbance, elephant, fire, herbivory, savanna dynamics

Introduction

Savannas are dynamic habitats, consisting of a heterogeneous mix of trees and grass, that may vary in their dominance across time and space (Scholes and Archer 1997, Sankaran et al. 2005, Higgins et al. 2007). Large trees in these ecosystems play key

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structural and functional roles, from influencing nutrient cycling (Belsky et al. 1989, Treydte et al. 2007) and carbon sequestration (Coetsee et al. 2010) to providing resources for many taxa (Dean et al. 1999, Rushworth et al. 2018). The loss of large trees, therefore, is expected to have lasting and disproportionate impacts on savanna ecosystems. The regulation of woody vegetation dynamics in savannas has been attributed to multiple factors at various spatial and temporal scales. Among these, herbivory and fire are critical (Bond et al. 2005, Sankaran et al. 2008, Staver et al. 2011, Dantas et al. 2016, Staal et al. 2018).

Independently, fire and browsing exert direct effects on woody vegetation structure by reducing seed production (Goheen et al. 2018), suppressing the growth and establishment of saplings and young trees (Higgins et al. 2007, Asner et al. 2009, Hoffmann et al. 2009, Sankaran et al. 2013, Staver and Bond 2014, Werner and Prior 2016), and increasing the mortality of adult trees (Goheen et al. 2018). Top-kill and mortality of large trees are mostly attributed to the actions of megaherbivores, particularly African savanna elephants *Loxodonta africana* (Shannon et al. 2011, Asner et al. 2016, Morrison et al. 2016, Pellegrini et al. 2017). The effects of elephant browsing and damage on large trees can be compounded by fire (Shannon et al. 2011, Vanak et al. 2012). Despite strong independent effects of fire and herbivory, several studies found that neither of them acting alone is sufficient to produce a transition in state from woody dominated to grassland. Rather, the cumulative effects of fire and herbivory substantially reduce woody plant density and increase large tree mortality (van Langevelde et al. 2003, Midgley et al. 2010, Shannon et al. 2011, Vanak et al. 2012, Levick and Asner 2013, Pellegrini et al. 2017, Goheen et al. 2018), therefore allowing for the expansion of grasslands (Dublin et al. 1990, Trollope et al. 1998, Van De Vijver et al. 1999, Staver et al. 2009).

The relative importance of fire and herbivory in shaping dynamics of the woody component of savanna vegetation also depends on additional factors that vary at different spatial scales (Holdo 2007, Levick et al. 2009, Shannon et al. 2011). These include patterns of precipitation and geology (Asner et al. 2009, Wigley et al. 2014, Archibald and Hempson 2016). These abiotic features seem to explain treefall patterns in Kruger National Park (KNP) that are African savanna elephant induced and spatially clustered (Levick and Asner 2013). Although the importance of spatial context in determining patterns of large tree mortality is relatively well established (Levick et al. 2009, Vanak et al. 2012, Abraham et al. 2021), there are comparatively few long-term studies that explicitly examine dynamics of tree mortality over different temporal extents (Staver et al. 2007, Druce et al. 2008).

Above-ground dynamics of savanna trees unfold over multiple decades, and are marked by limited recruitment, generally slow progression to larger size classes, and frequent top-kill or size class reversions (Higgins et al. 2007, Midgley et al. 2010, Sankaran et al. 2013). Stochastic events that either suppress establishment and growth, such as large, intense fires or drought, or that lead to episodic release from disturbance, such as disease outbreaks among browsers, can strongly influence dynamics (Dublin et al. 1990, Prins and van der Jeugd 1993, Staver and Bond 2014). Variation in the intensity or frequency of these events over time results in complex spatial patterns in savanna woody vegetation (Levick et al. 2015, Pellegrini et al. 2017, Venter et al. 2017). Variation in the magnitude of drivers of savanna ecosystems over both space and time limits the ability to accurately predict vegetation dynamics (Touboul et al. 2018). It also presents challenges for the management and conservation of these systems, as stochastic drivers can trigger systemic shifts at the landscape level (Dublin et al. 1990, Touboul et al. 2018). The temporal extent of disturbance history is, therefore, of particular importance when trying to understand the survival of savanna trees (Shannon et al. 2011, Vanak et al. 2012, Morrison et al. 2016).

In earlier studies in Kruger National Park (KNP), we showed that disturbance history over a short period of time (2.5 years) was an important predictor of tree mortality (Shannon et al. 2011, Vanak et al. 2012). For example, trees that had been previously debarked by African savanna elephants and then experience a fire within two years were more likely to die (Shannon et al. 2011). In the KNP, fire occurrence is widespread and can be caused by both accidental and intentional ignition (prescribed burns for management); these fires range in intensity (e.g. heat per unit area) and frequency (Govender et al. 2006). The KNP elephant population is extensive with an average of 2.23 individuals km^{-2} on the granitic substrate zone and 2.71 individuals km^{-2} on the basalt zone (Abraham et al. 2021). Although the impacts of elephants on woody vegetation are pervasive throughout the park, the local severity depends on various factors including distance to water, geology, fire regime and tree densities, and these factors feed back again to whether damage is caused by bulls versus mixed herds (MacFadyen et al. 2019, Abraham et al. 2021). Elephants show preference for certain species, for example *Sclerocarya birrea*, over others (Shannon et al. 2008, Abraham et al. 2021). Given the stochastic variation in both fire and elephant damage across space and time, the predictive power of past events on subsequent mortality is likely to vary. Therefore, longer-term observations of the impacts of these drivers are necessary to better understand the emergence of lag effects and to determine if there are limits to the accumulation of damage before mortality.

Here we present the results of a 12-year study, on the effects of fire and African savanna elephants, on large tree (i.e. > 5 m) mortality in southern KNP. Using a cohort-based approach to study individual trees over a large spatial extent (2000 km^2), we asked how the sequence of disturbance events additively and synergistically influenced mortality risk and whether, and how, the risk of mortality was compounded over time. We first partitioned the entire study duration into time periods and examined how accrued damage over different periods of time influenced mortality risk for large trees. We then explicitly assessed the long-term effects of elephant- or

fire-induced damage to the main stem of a tree by examining the time frame over which past damage continued to influence large tree mortality.

Methods

The study was conducted in the southern part of Kruger National Park (25°28′–24°91′S, 31°95′–31°32′E), an area of approximately 2100 km^2 of mostly nutrient-poor granitic savanna. The study area, transect locations and sampling strategy are described in detail in Druce et al. (2008), Shannon et al. (2008) and Vanak et al. (2012). In brief, 2796 individual large trees (211 dead and 2585 living) that were ≥5 m height class were assessed in 2006 across 22 transects (10 m wide and 1.0–6.6 km long). Transects were re-surveyed in 2008 (all 22 transects), 2011 (all 22 transects), 2015 (14 transects) and 2018 (17 transects). To avoid the data gaps in survival due to transects that were not sampled in the 2015 and 2018 censuses, we estimated total mortality with the subsample of 1506 trees for which we had information on survival status in all five years. All results and discussion apply only to large trees (>5 m height).

To examine the effects of temporal variability in elephant and fire activity on mortality of trees, we used all available data for each census period (see the Supporting information for information on sample sizes for each census interval). We first examined the probability of mortality of the 10 most abundant tree species (as per the 2006 census data) in 2008, 2011, 2015 and 2018, separately, as a function of all predictors from 2006 onwards. These predictors included species identity, type of elephant or fire damage and the proportion of tree biomass damaged by elephants or fire in the previous and current sampling years (Table 1). Because fire and elephant damage are likely to have complex interactions, we used a classification tree (CT) approach based on conditional inference (Breiman et al. 1984, Hothorn et al. 2006) to explore their effects on tree mortality (response variable). CTs are an effective method for visualizing interactions between predictors. They recursively partition the data into increasingly homogenous subsets on the basis of predictors, while making no assumptions about the underlying response

Table 1. List of predictors and their description for the classification trees (CT) and GLMM analysis of the causes of large tree mortality in Kruger National Park between 2006 and 2018.

Predictor	Code	Description/range	Analytical method
Type of elephant damage (recorded at each census)	ele.type	Values: 0 – none, 1 – primary or secondary branches broken, 2 – main trunk debarked or tusk-gashed, 3 – main trunk pushed over or broken but re-sprouting, 4 – pushed over or main trunk broken, appears dead or roots exposed and eaten	CT
Type of fire damage (recorded at each census)	fire.type	Values: 1 – none, 2 – main/primary stem burned but alive, debarked area burnt or secondary stems burned; 3 – severe burning of main stem, appears dead	CT
Identity of ten most abundant species in 2006	species	Values: *Combretum apiculatum*, *C. hereroense*, *Lannea schweinfurthii*, *Philenoptera violacea*, *Sclerocarya birrea*, *Senegalia burkei*, *Senegalia nigrescens*, *Spirostachys africana*, *Terminalia sericea*, *Ziziphus mucronata*	CT
History of pushover or main stem or primary branches broken by elephants	ele.type4.hist	Values: 1 – none, 2 – occurred in 2015–2018, 3 – occurred in 2011–2015, 4 – occurred in 2008–2011, 5 – occurred in 2006–2008 or earlier	GLMM
History of fire damage to main stem or primary branches	fire.type3.hist	Values: 1 – no damage or unburned, 2 – occurred in 2015–2018, 3 – occurred in 2011–2015, 4 – occurred in 2008–2011, 5 – occurred in 2006–2008	GLMM
Proportion of tree biomass affected by elephant damage (recorded at each census)	ele.prp	Visually estimated as the proportion of canopy tree volume and/or stem bark circumference that was removed by elephant. Values for analyses are median of the following ranges estimated in the field: 0, 0.01–0.1, 0.11–0.25, 0.26–0.50, 0.51–0.75, 0.76–0.90, 0.91–1.0. Values: 0, 0.05, 0.18, 0.38, 0.63, 0.83, 0.96	CT and GLMM
Proportion of tree biomass affected by fire damage (recorded at each census)	fire.prp	Visually estimated as the proportion of canopy tree volume and/or stem bark circumference that was damaged by fire. Values for analyses are median of the following ranges estimated in the field: 0, 0.01–0.1, 0.11–0.25, 0.26–0.50, 0.51–0.75, 0.76–0.90, 0.91–1.0. Values: 0, 0.05, 0.18, 0.38, 0.63, 0.83, 0.96	CT and GLMM
Diameter of main stem in 2006	stem.diam	Measured 1 m above ground-level Values: 3–200 cm	GLMM
Height below lower crown in 2006	low.cr.ht	Visually estimated using a 1.8 m reference and binned to 1.5 m classes Values: 0–9.7 m	GLMM
Mean annual precipitation	rain	Derived from inverse distance interpolation of data from the South African weather service and Skukuza weather station in KNP. Values: 545–670 mm	GLMM
Slope position	slope.pos	C – crest, F – foot-slope, M – mid-slope	GLMM

Table 2. Mortality rate of large trees in a cohort from Kruger National Park sampled between 2006 and 2018.

Census year	Trees classified as alive in that year	Trees classified as dead in that year‡	% died[1]	% dead per annum	Cumulative % dead
2006	1506*				
2008	1350	156	10.36	5.18	10.36
2011	1211	139	10.30	3.43	19.59
2015	1073	138	11.40	3.80	28.75
2018	789	284	26.47	8.82	47.61

‡ Corrected for individuals that were found to actually be alive in a later census period.
* Includes only trees that were tracked across all census years.
[1] The number sampled dead in that year divided by the number that were alive in the previous sampling period.

functions (De'ath and Fabricius 2000). We chose conditional inference as a splitting criterion because it avoids bias towards predictors with multiple categories and predictors that cover a larger range of values (Strobl et al. 2009). Additionally, conditional inference trees have a statistical stopping criterion, which prevents over-fitting and eliminates the need for pruning (De'ath and Fabricius 2000). We constructed CTs in R (<www.r-project.org>) with the package 'party' (Hothorn et al. 2006).

We also used generalized linear mixed models (GLMMs) to explicitly assess the time-frame over which past, severe damage from elephant or fire to the main stem can continue to influence large tree mortality (in R with package 'lme4'; Bates et al. 2015). We included all species in this analysis, and we ran models for the 2015 and 2018 censuses separately, as these provided the longest observational windows for the tree cohort. The fixed effects included predictors related to history of severe elephant and fire damage to the main stem, abiotic factors (mean annual precipitation and slope position) and tree traits (lower crown height and stem diameter; Table 1). The random effects (intercept only) used in the models were species identity and transect ID stratified by Gertenbach landscape type (<www.thekruger.com/gertenbach/gertenbachintro.htm>; Gertenbach 1983), as several transects crossed more than one Gertenbach landscape type. We built three competing models for each time window (2006–2015 and 2006–2018) to explain tree mortality as a function of (a) only elephant or fire damage or the interaction between elephant and fire damage, (b) elephant and fire damage + tree traits and (c) elephant and fire damage + tree traits + abiotic factors (Supporting information). We used Akaike's information criterion corrected for small sample sizes (AICc) to select the best model (ΔAICc < 2; Burnham and Anderson 2002). We standardized continuous predictors (mean annual precipitation, lower crown height, stem diameter) by using z-scores and checked for multicollinearity using Pearson's r. None of the continuous predictors used in the models had Pearson's r > 0.7 We assessed goodness of fit with $R^2_{GLMM(m)}$ and $R^2_{GLMM(c)}$ (Nakagawa and Schielzeth 2013, Nakagawa et al. 2017). We conducted the analysis in R with the 'MuMIn' package. For both the CT and GLMM analyses, the response variable was whether the tree was alive or dead in the given census year, with trees that died prior to that census year removed from the data. Trees that were recorded dead in one census, but found alive in a subsequent census, were assigned status of alive for this analysis.

Results

A total of 1506 trees were tracked across all five censuses from 2006 through 2018. We found that 47.6% of this initial cohort did not survive to 2018 (n = 789 trees alive, 717 trees dead). Approximately 28.8% of the cohort had died by the 2015 census and an additional 18.8% had died by 2018 (Table 2). The percentage dead per annum between census periods varied from 3.4% to 5.2% from 2006 through 2015. There was a 2.3-fold increase in mortality between the 2015 and 2018 censuses (Table 2). From the set of 1506 trees, approximately 17% that were recorded as dead in 2008 had resprouted by 2011. Similarly, 18% of the trees recorded as dead in 2015 were alive in 2018.

Incidence of elephant and fire damage and their effects on mortality

Elephant browsing was the most frequently recorded source of damage across study trees, steadily increasing in percentage from 2008 to 2018 (maximum 59% of trees in a year; Fig. 1a). Fire damage alone affected a smaller percentage of the cohort and remained consistently low across census years (maximum 19.2% of trees; Fig. 1a). From 2008 to 2018, 1.6–4% of the trees surveyed were damaged by both elephants and fire (Fig. 1a). A maximum of 55% of trees with elephant damage alone died (Fig. 1b), whereas 4–9% of trees with only fire damage died (Fig. 1b). These mortality rates were relatively consistent across years. Mortality of trees with both elephant and fire damage was more variable (23–60% from 2008 to 2018) (Fig. 1b). The percentage of dead trees with no discernible elephant or fire damage was consistently low from 2008 through 2015 (0.5–7%), and then increased from 7 to 17% between the 2015 and 2018 censuses (Fig. 1b). Among all trees that survived until 2018, approximately 37% had no recorded signs of either elephant or fire damage (compared to 7.8% of dead trees; Fig. 2), and 85% were not damaged by both elephant and fire during the study.

Approximately 17% of 864 trees that died at some point in the 12 year study bore signs of elephant damage during a single census, whereas 22.5% and 6.5% of dead trees had some type of elephant damage during two and three census intervals, respectively (Fig. 2). By comparison, fire damage recorded in a single census was associated with 4% of all deaths and repeated fire damage with at most 1.4% of tree mortality (Fig. 2). Mortality among trees for which elephant damage was followed by fire damage in a subsequent census interval (7.8%) was greater than among trees for which fire damage was followed by elephant damage in a subsequent census interval (4.2%), suggesting that the order of occurrence of elephant and fire damage was an influential factor in explaining tree mortality (Fig. 2).

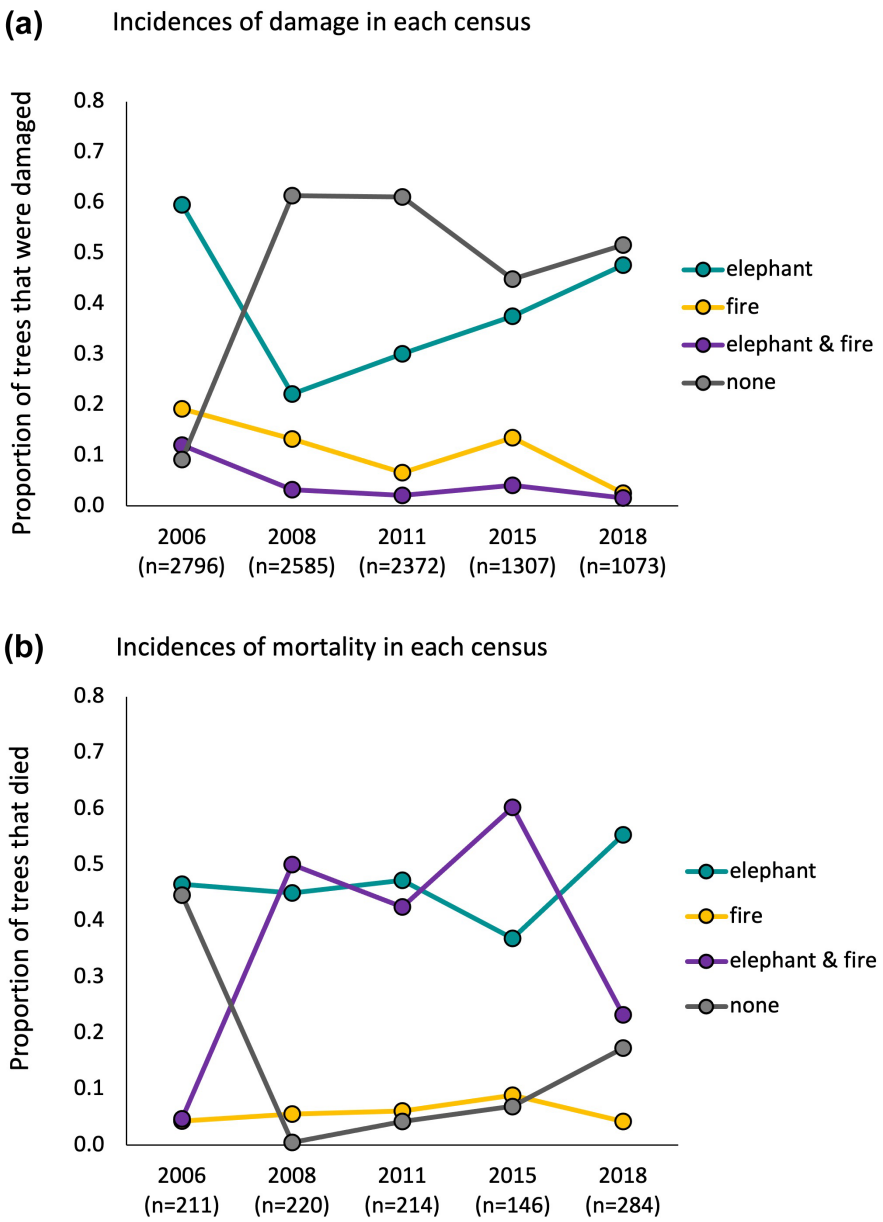

Figure 1. (a) Proportion of trees with recorded incidences of damage by elephant (green), fire (yellow), both elephant and fire (purple) and none (grey) in each census year. (b) Proportion of trees from each category of damage shown in (a) that were found dead in those census years. Number of trees sampled (a) and the number of trees that were recorded as dead (b) are reported below each census year.

Types of elephant and fire damage and their effects on mortality

Irrespective of survival status, the most frequently recorded types of elephant damage were breaking of secondary and smaller branches, followed by pushing over, debarking and then breaking of the main stem. Instances of pushing over were 2.5 times more common than breakage of the main stem. The most frequently recorded type of fire damage was burns on secondary and smaller branches, followed by burning of the main stem with absence of resprouting and then burning of debarked area on the main trunk.

The results of the CT analysis indicated that the type of elephant damage was strongly and significantly ($p < 0.05$) associated with mortality. Across all four census intervals, 76% of individuals that were pushed over or had a main stem broken (n = 311 trees) died within two to four years. (Fig. 3; Supporting information). Debarking or tusk-gashing of the main stem along with elephant damage to more than 80% of tree biomass (resulting from any type of elephant action including debarking or tusk gashing) also was significantly associated with mortality (Supporting information). The type of elephant damage was a stronger predictor of mortality than the proportion of tree biomass damaged by elephants.

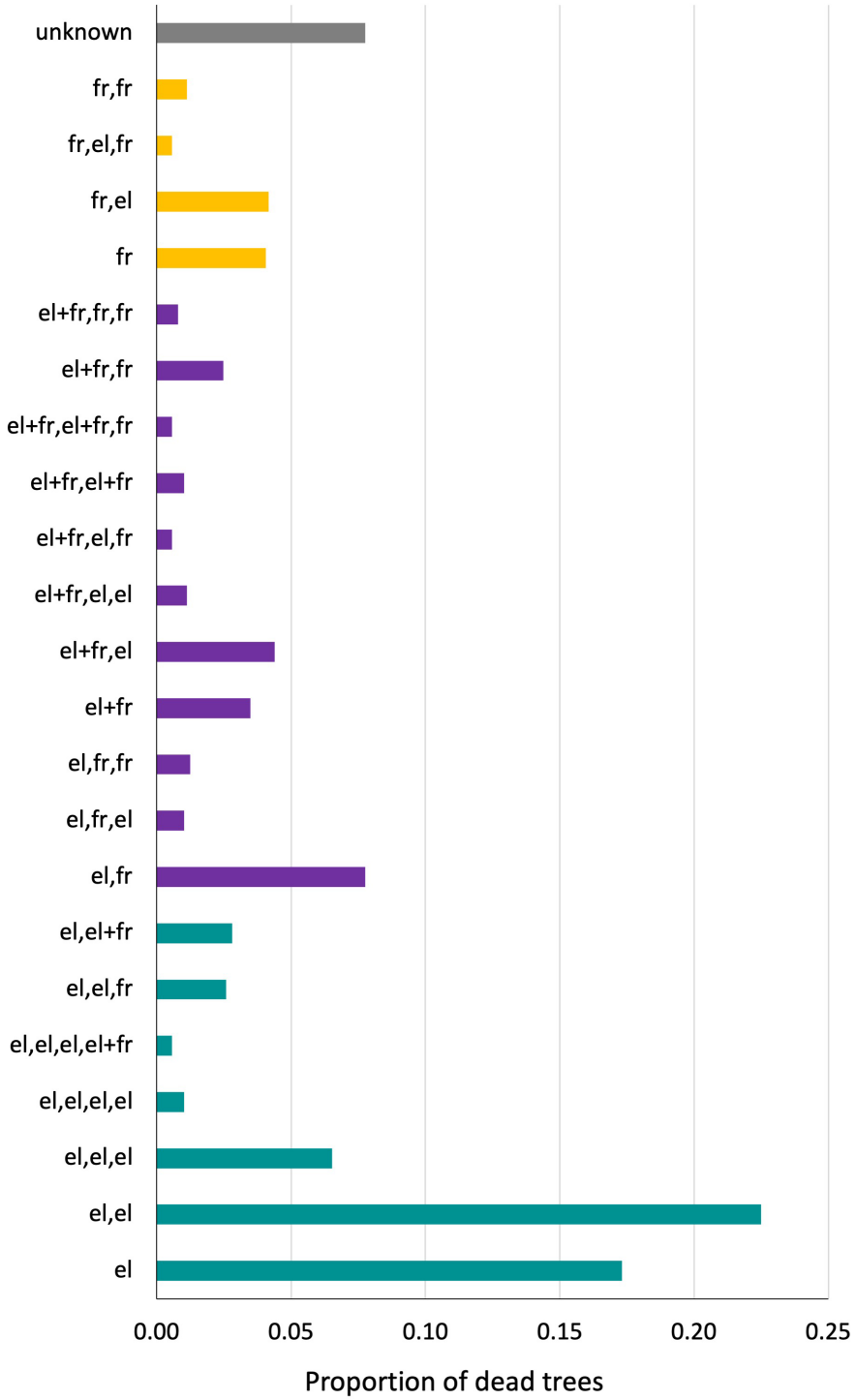

Figure 2. Proportion of mortality according to cause and sequence of damage for trees that died between 2006 and 2018. Comma separator indicates events recorded in different census intervals. 'el' – elephant damage, 'fr' – fire damage, 'el+fr' – both elephant and fire damage recorded within any given census interval. Trees with successive damage from elephants are in green, those with elephant and fire damage within or in successive census periods are in purple and those that first had fire damage followed by elephant damage are in yellow. Dead trees with no detectable damage from elephant or fire are in grey. Only proportions of mortality that are >0.01 are shown.

In 2015, recent fire damage that resulted in the severe damage of the main stem was the strongest predictor ($p < 0.05$) associated with tree mortality (Supporting information). This was the second-most important predictor for explaining mortality in 2011 as well (Supporting information). Overall, 75% of individuals with severe fire damage to the main stem and no elephant damage died within four years (Fig. 3). Therefore, irrespective of whether elephants or

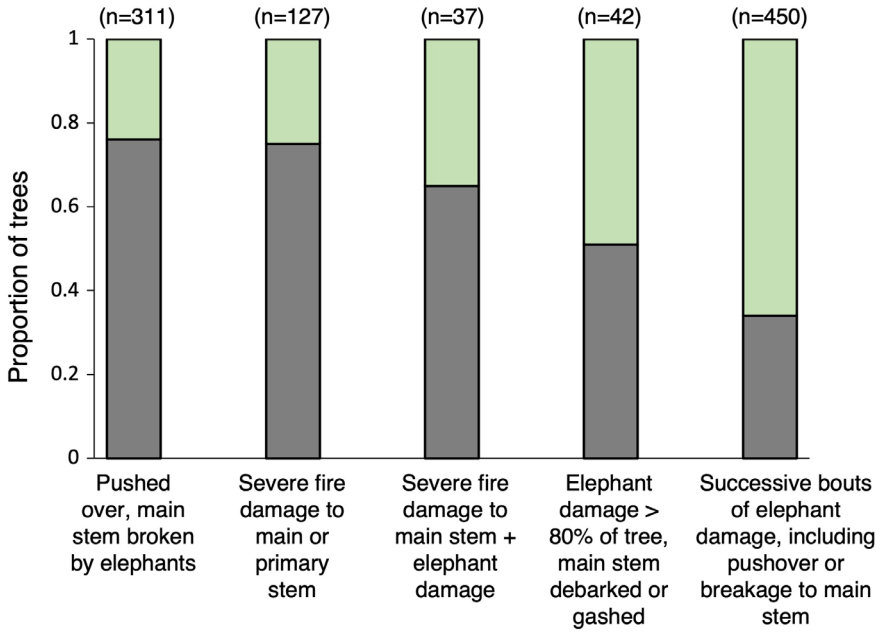

Figure 3. Overall summary of the proportion of trees that died (in grey) as a function of the types of damage. This graph is derived by calculating the average probability of mortality, weighted by the number of cases in the terminal nodes of the conditional classification trees corresponding to each 'pathway' of damage. Results are for the ten most abundant tree species across all classification trees (2008–2018). Sample sizes for the number of trees for each combination of damage are shown above each bar (Supporting information).

fire was the agent, 75% of trees with severe damage to the main stem died within four years.

The CTs indicated that interactions between fire and elephant damage, and lag effects of elephant damage, affected mortality. On average, 34% of individuals that survived being pushed over or having a main stem broken died in the subsequent census interval (Fig. 3, Supporting information). Sixty-five per cent of trees with severe fire damage to the main stem and elephant damage in the same census interval died by the next census (Fig. 3). Individuals that had been pushed over or broken, and then had fire damage in a later census interval, also had increased mortality compared to trees that did not experience fire after severe elephant damage (Supporting information).

Another combination of damage that increased mortality rates (on average by 22%) was debarking or tusk-gashing by elephants and burning of the main stem or primary stems – including the debarked area (Supporting information). In general, interactions between fire and elephant damage to the main stem significantly increased mortality (Fig. 1; Supporting information).

Species-specific impacts of elephant and fire damage

The frequency and impact of elephant and fire damage varied among species of trees (Supporting information). More than 90% of *Lannea schweinfurthii*, *Philenoptera violacea*, *Sclerocarya birrea* and *Ziziphus mucronata* individuals were affected by elephant browsing at some stage from 2006 through 2018. Conversely, the percentage of *Terminalia sericea* that were browsed at some stage from 2006 through 2018 (62.4%) was the lowest among species, followed by *Spirostachys africana* (63.7%) and *Combretum imberbe* (67.9%).

Species with the highest mortality among individuals with severe elephant damage were *Senegalia burkei* (38%), *S. nigrescens* (33%), *Z. mucronata* (31%), *S. birrea* (18%) and *L. schweinfurthii* (14%) (see also Fig. 4 separated for each census period, Supporting information). Although *S. nigrescens* ranked 9th of the 13 most abundant species with elephant damage (86% of trees damaged at some stage), it had the second highest mortality (33%). In contrast, although 90.5% of *P. violacea* were affected by elephants, 7% died. From 2006 through 2018, the species with the highest mortality rates among individuals with severe fire damage were *Z. mucronata* (43%), *S. nigrescens* (40%), *S. burkei* (31%), *S. africana* (29%), *S. birrea* (19%) and *Combretum apiculatum* (17%) (see also Fig. 4, separated for each census period).

Approximately 10% of *S. nigrescens* trees were burned and either pushed over or broken, and all died, whereas 18% of *C. apiculatum* individuals were damaged in a similar manner and 75% died (Supporting information). Among *S. nigrescens*, 61% of individuals that were debarked, and had fire damage to the main stem (including debarked area), died. The species with the greatest mortality following both elephant and fire damage were *Z. mucronata*, *S. birrea*, *S. nigrescens* and *C. apiculatum* (Fig. 4, Supporting information). Approximately 62% of *T. sericea* were affected by elephant browsing, yet only 4% died; relatively few trees were actually pushed over or pollarded. However, 14% (n = 64) with fire damage died.

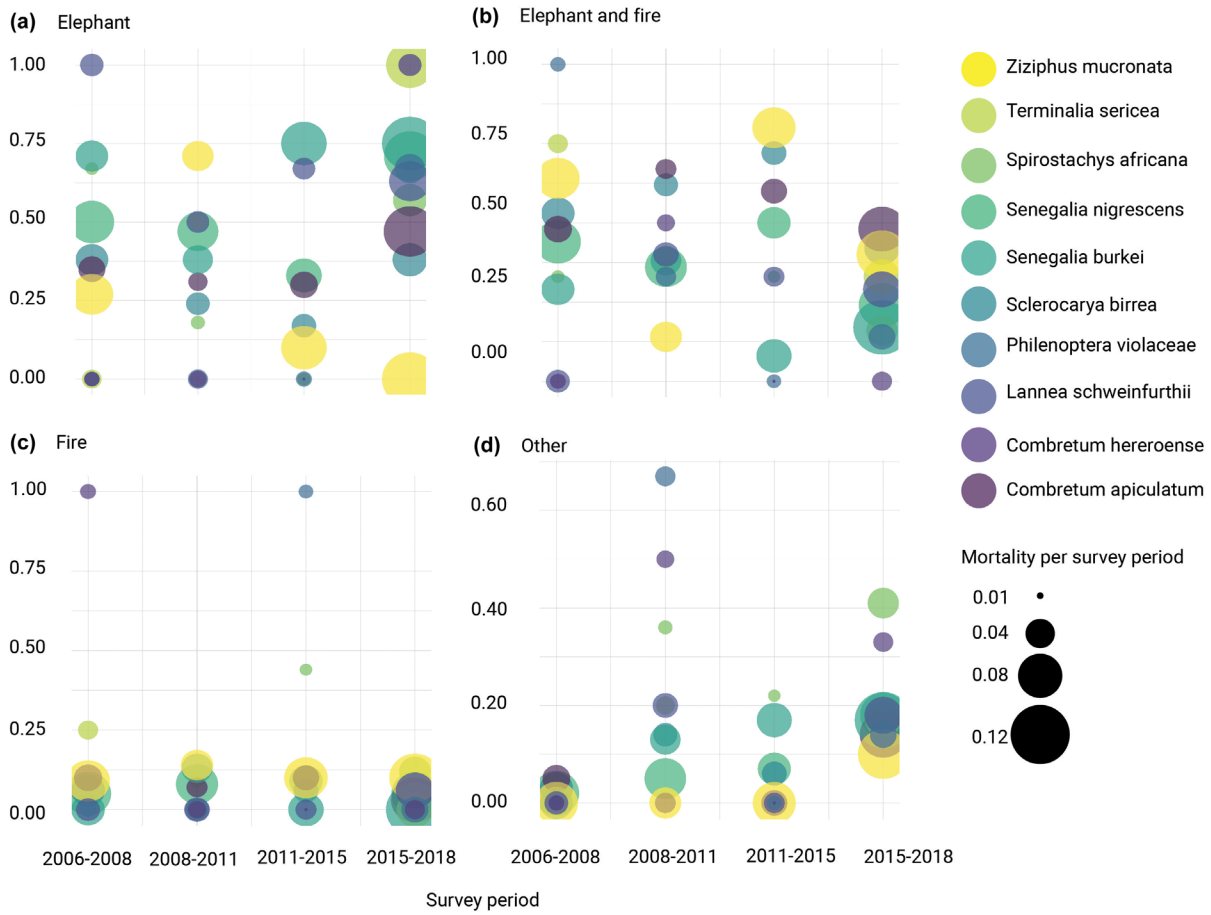

Figure 4. Species-specific trends in large tree mortality for the 10 most abundant species, separated by survey period and by cause of damage, in Kruger National Park. The y axis shows proportion of mortality that was attributed to a specific cause in a given census interval and the size of the circle reflects the mortality for that species per year per survey period (across all causes). The 2015–2018 census interval includes only trees that were sampled in both 2015 and 2018.

The lingering effects of past elephant- or fire-induced damage on tree mortality

Tree mortality in 2015 was best explained by elephant and fire damage, individual traits such as lower crown height and stem diameter of the trees in 2006 ($R^2_{GLMM(m)} = 0.29$ and $R^2_{GLMM(c)} = 0.54$). The model which included elephant and fire damage history, tree traits and abiotic factors such as slope position and rainfall performed equally well ($\Delta AICc < 2$; Supporting information). In 2018, tree mortality was best explained by predictors related to only elephant or fire damage that occurred from 2015 through 2018 and damage that occurred in previous census intervals ($R^2_{GLMM(m)} = 0.41$ and $R^2_{GLMM(c)} = 0.59$).

The results of the GLMMs were consistent with those of the CTs: type of elephant and fire damage were the strongest predictors of tree mortality. Severe elephant damage to the main stem, namely pushing over or breaking of the main trunk, was the most influential predictor of mortality in both 2015 and 2018. In both census periods, trees that were first recorded as pushed over or broken since the last census had much greater odds of mortality (as demonstrated by CT results). However, trees that were pushed over or broken from 2006 through 2008 had even greater odds of mortality in 2015 than those that were similarly damaged after the 2011 census (Table 3), indicating that mortality may have a long lag period. In the 2018 census, trees that were pushed or broken in 2006 had significantly increased odds of mortality (Table 3). In other words, trees that survived being pushed over or broken by elephants in the short term had a higher risk of mortality even 12 years later.

Severe fire damage to the main stem or primary branches was also a strong predictor of tree mortality in 2015 and 2018 (Table 3). In 2015, this type of fire damage significantly ($p < 0.05$) increased odds of mortality if it occurred after 2011 or in 2006. Severe fire damage recorded between 2008 and 2015 significantly increased the odds of mortality in 2018 (Table 3). Therefore, severe fire damage can also increase the odds of mortality over longer time periods. The interaction between proportion of tree biomass damaged by elephants and proportion damaged by fire (in the most recent census interval) was a significant ($p < 0.05$) predictor of mortality in 2015 (Table 3). It was not possible to test the effects of this interaction in 2018 due to the low incidence of both fire

Table 3. Best model and associated predictors of large tree mortality for 2015 and 2018 census data. Shown are odds ratios, and the lower (LCL) and upper (UCL) confidence limits for each parameter.

Census year in which mortality was modelled	Significant predictors from best model	Beta Ln (odds)[1]	LCL 2.5%	UCL 97.5%
2015 (n = 1307)	Main stem/primary branches pushed over or broken from 2011 to 2015	1.56**	0.53	2.58
	Main stem/primary branches pushed over or broken from 2008 to 2011	1.20**	0.36	2.04
	Main stem/primary branches pushed over or broken from 2006 to 2008	2.18***	1.00	3.36
	Main stem/primary branches burned from 2011 to 2015	1.83**	0.62	3.04
	Main stem/primary branches burned in or before 2006	2.17**	0.64	3.69
	Proportion tree biomass burned in 2015	2.23***	0.91	3.54
	Proportion tree biomass damaged by elephant: proportion biomass burned (2015)	−2.83*	−5.45	−0.22
	Lower crown height (in 2006)	0.48**	0.17	0.79
	Stem diameter (in 2006)	−0.38*	−0.71	−0.04
2018 (n = 1559)	Main stem/primary branches pushed over or broken from 2015 to 2018	3.88***	2.60	5.17
	Main stem/primary branches pushed over or broken from 2011 to 2015	1.57***	0.93	2.21
	Main stem/primary branches pushed over or broken from 2008 to 2011	2.21***	1.38	3.03
	Main stem/primary branches pushed over or broken from 2006 to 2008	1.57***	0.95	2.19
	Proportion tree biomass damaged by elephant in 2018	−5.45***	−6.43	−4.46
	Main stem/primary branches burned from 2011 to 2015	1.41*	0.19	2.63
	Proportion tree biomass burned in 2018	10.40*	0.81	19.98

[1] Significance level: *<0.05, **<0.01, ***<0.001.

and elephant damage. Other tree traits, such as small stem diameter and greater height of the lower crown, contributed significantly to increased mortality in 2015 (Table 3).

Discussion

Across 2100 km^2 in Kruger National Park, the annual mortality rate of trees remained fairly constant (3–5%) from 2006 through 2015 and then increased to 8.8% in 2018. Frequent and intense elephant browsing negatively affected the majority of sampled trees and was associated with seven times more deaths than fire damage alone. The probability of mortality as a result of elephant browsing or fire damage depended not only on the type and intensity of damage but also on the historical sequence or order of previous damage by these agents. Severe elephant damage to the main stem incurred up to 12 years earlier significantly increased the risk of mortality of trees, especially when subsequently exposed to fire.

The synergistic effects of elephant browsing and fire can reduce tree cover in savannas by killing mature canopy trees (Eckhardt et al. 2000, Shannon et al. 2011, Vanak et al. 2012). The primary mechanisms through which this happens include burning of the main stem that had survived being pushed over or broken by elephants but is now in a height class where fire is particularly damaging and burning of the main stem following debarking where the stem is no longer protected by bark (Moncrieff et al. 2008, Helm et al. 2011, Shannon et al. 2011). These patterns not only reflect the existence of an 'elephant trap' for trees in the KNP landscape (Asner and Levick 2012), wherein trees larger than 5 m have a high risk of elephant damage to the main stem potentially leading to mortality, but when pushed over or broken by elephants, these mature trees end up in the 'fire trap' which increases their risk of fire-induced mortality (Bond and Keeley 2005). Our work reinforces how the sequence and intensity of damage influences mortality of mature trees (Moncrieff et al. 2008, Midgley et al. 2010, Helm et al. 2011, Shannon et al. 2011); the effects of these combined drivers can be a prolonged process resulting in mortality over the course of several years.

Temporal context in tree mortality

The temporal order and pattern of disturbance affects decadal tree mortality. Fire has strong seasonal patterns but varies stochastically over days and years depending on rainfall and the associated availability of fuel (Archibald and Hempson 2016, Staver et al. 2017). Herbivory tends to be more consistent within and across seasons as well as years but can vary at decadal scales depending on herbivore population densities and movement (Archibald and Hempson 2016). Observational and experimental evidence indicate that elephant-induced treefall rates are higher, and, therefore, woody

biomass is lower, when fire frequency is high (Levick et al. 2015, Pellegrini et al. 2017). Our work indicates that in KNP, where fire return intervals are three to six years (van Wilgen et al. 2000), the likelihood of synergistic effects of a given fire event and recent and past elephant browsing poses a high risk of mortality of trees.

Annual rainfall varied considerably during the study period. There were two drought periods during the survey, below-average rainfall in 2006–2008 (Shannon et al. 2011, Asner et al. 2016) was followed in 2015–2016 by the most severe drought since the early 1990s (MacFadyen et al. 2018, Malherbe et al. 2020). These periods of below-average rainfall likely contributed to increased elephant damage in the early and latter part of the study (Fig. 1a, Shannon et al. 2011). It is also possible that drought stress, in combination with elephant damage, contributed to mortality in some of the census years (Birkett and Stevens-Wood 2005, O'Connor et al. 2007). The proportion of dead trees with no elephant or fire damage was particularly high in the first census of 2006 and again in 2018 (45% and 17%, respectively), compared to an average of 4% from 2008 through 2015, suggesting that drought may have influenced tree mortality in these years. The drought periods were interspersed with two wetter periods: above-average rainfall in 2010–2014 with an especially wet January in 2013 and average rainfall post-2016 (Malherbe et al. 2020). The area of the park that burned in any given year is very closely correlated with rainfall received, because this again relates to how much dry grass is available to burn (Wigley-Coetsee and Staver 2020). The interaction between elephants and fire was a lower cause of mortality between 2011 and 2015 (Fig. 1b, 4b–c), probably because fire was less prevalent in that period.

The mortality rates reported here are within the range of other studies in African savannas (Dublin et al. 1990, Eckhardt et al. 2000, Kerley et al. 2008, Helm et al. 2009, Mapaure and Moe 2009) and are higher than those reported from other parts of Africa where herbivory and fire are less important processes (Morrison et al. 2016). Recent estimates of treefall rate for the study region were about 5% per year (Levick and Asner 2013, Levick et al. 2015). Our results show that the actual mortality rate is lower due to the resprouting and coppicing abilities of some species (Helm et al. 2011). This regenerative ability is substantial, as up to 18% of individuals recorded as dead had resprouted within our study period (see also Morrison et al. 2016 for *Acacia* sp. in the Serengeti), thereby complicating the estimation of mortality in this system. However, previously large trees that are resprouting from the base after the main stem has died, and having effectively lost their canopy, are functionally lost from the large tree class. Large trees contribute in very specific ways to savanna ecosystems, for example, as perching and nesting sites for vultures and other large birds, as shelter for animals, as hydraulic pumps associated with nutrient pumps and enhancing local fertility and other resources and as nursing habitat for smaller species (Belsky 1994, Dean et al. 1999, Ludwig et al. 2004, 2008, Manning et al. 2006). As we are performing a cohort analysis, our reports on mortality rate do not include the progression of smaller trees into the large tree class over time and, therefore, do not necessarily reflect the overall population dynamics of trees.

Our findings indicate that sustained monitoring efforts over longer time periods will more accurately assess tree mortality patterns in this system. Noticeable from this long-term cohort study is the lag effects of predictors of mortality over time. Although recent and severe damage events caused by either elephants or fire will result in mortality within two to three years, major damage, even up to 12 years previously, can still render a tree vulnerable to risk of mortality.

Species-specific response to elephant and fire damage

The extent of elephant and fire damage varied considerably among dominant tree species, as did their ability to survive this damage. Bark stripping followed by burning of the debarked main stem did not seem to increase mortality of *S. birrea* trees (Helm et al. 2011), unlike what has been reported for *S. nigrescens* (Moncrieff et al. 2008). This may be due to the ability of this species to rapidly regrow bark and resprout epicormically as well as basally and the rapid growth of resprouting stems (Helm et al. 2011). *Combretum apiculatum* also shows a strong ability to resprout following damage (Shannon et al. 2008). This species accounted for almost 40% of the resprouts in 2011 of individuals that were recorded as dead in 2008. *Combretum apiculatum* is often a multi-stemmed species where any of the stems can become a future main stem when the tree is pushed over. Previous work has also shown *C. apiculatum* to be stimulated in terms of shoot length and stem circumference when browsed (Mamashela 2010) and to be very resilient to disturbance by browsers (Makhabu et al. 2006) and fire (Gandiwa and Kativu 2009). Furthermore, resprouting stems are capable of progressing to the 5 m height class within a few years (A. Vanak pers. obs.), minimizing the risk of top-kill by fire. Such differential mortality rates (between 18 and 38%), and ability to survive damage by elephants, can result in changes in composition of tree species over large areas (O'Connor et al. 2007), particularly in areas with high rates of elephant herbivory as well as intense fires.

Implications for monitoring and adaptive management

Understanding mortality risk of trees in African savannas is of interest both from an ecological perspective and from a conservation and management one (Dublin et al. 1990, Trollope et al. 1998, Lindenmayer et al. 2014). Accurate estimation of mortality rates requires sustained, long-term monitoring of individual trees and their responses to disturbance, especially given that the effects of elephant damage can persist and compound over many years. This is especially important when attributing the cause of death in regions as complex as KNP, where management interventions are routine (van Wilgen et al. 2004).

We suggest that monitoring over a decade or more may be required to detect temporal trends in demographic rates that could indicate potential shifts in savanna structure from woodland to open grasslands or thickets (Dublin et al. 1990, Trollope et al. 1998, Pellegrini et al. 2017). Although the mortality rate for the tree cohort remained relatively constant over the first 10 years, we recorded a considerable increase in mortality in the last census (2015–2018). This uneven rate of mortality would be undetected without long-term cohort sampling. We also saw that over the 12 years of this study, progression of trees into the 5 m height class was stochastic and intermittent and lower than mortality (Shannon et al. 2011; Vanak, A. unpubl.). It therefore appears that transitioning of trees into the 5 m class varies across years and may lag behind mortality rate, especially in the case of species such as *S. nigrescens* and *S. birrea* (Helm et al 2009). This can result in missing size-class cohorts (Helm and Witkowski 2012) or episodic recruitment events (Kraaij and Ward 2006, Staver et al. 2007) if disturbance pressure weakens. Given that elephant densities continue to increase in the study region, structural and compositional transformation of woodlands to open grasslands or thickets over time is possible (Trollope et al. 1998, Pellegrini et al. 2017). Management plans developed in a period of low browsing levels or browsing return rate may no longer apply, especially given the heightened risk of mortality with frequent fire. Similarly, planning for fire effects in isolation may not mitigate the combined and sequential effects, such as those we have identified.

An understanding of these patterns can help inform elephant and fire management policies (VanWilgen et al. 2014). For example, the active reduction of fire frequency or intensity in landscapes with higher densities of *S. nigrescens* and *S. birrea* may increase survival probability of individuals that have been pushed over or pollarded. Overall, this cohort study provides a better understanding of the synergy between fire damage and elephant browsing in causing the mortality of trees over time. Multi-decadal demographic studies on dominant savanna tree species improve the ability to predict mortality risk (Midgley et al. 2010, Staver and Bond 2014) and to detect and quantify the role of episodic recruitment events in the persistence of tree populations in savannas (Kraaij and Ward 2006, Staver et al. 2007).

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Author contributions

Arundhati Das and **Maria Thaker** share first authorship. **Arundhati Das**: Formal analysis (lead); Resources (supporting); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Maria Thaker**: Conceptualization (equal); Data curation (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Project administration (supporting); Resources (supporting); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Corli Coetsee**: Data curation (supporting); Investigation (supporting); Project administration (supporting); Resources (supporting); Visualization (supporting); Writing – review and editing (supporting). **Rob Slotow**: Conceptualization (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Writing – review and editing (supporting). **Abi T. Vanak**: Conceptualization (equal); Data curation (lead); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2280gb5sh> (Thaker et al. 2021).

References

Abraham, J. O. et al. 2021. Heterogeneity in African savanna elephant distributions and their impacts on trees in Kruger National Park, South Africa. – Ecol. Evol. 11: 5624–5634.

Archibald, S. and Hempson, G. P. 2016. Competing consumers : contrasting the patterns and impacts of fire and mammalian herbivory in Africa. – Phil. Trans. R. Soc. B 371: 20150309.

Asner, G. P. and Levick, S. R. 2012. Landscape-scale effects of herbivores on treefall in African savannas. – Ecol. Lett. 15: 1211–1217.

Asner, G. P. et al. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. – Proc. Natl Acad. Sci. USA 106: 4947–4952.

Asner, G. P. et al. 2016. Ecosystem-scale effects of megafauna in African savannas. – Ecography 39: 240–252.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients and tree–grass competition. – Ecology 75: 922–932.

Belsky, A. J. et al. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. – J. Appl. Ecol. 26: 1005–1024.

Birkett, A. and Stevens-Wood, B. 2005. Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. – Afr. J. Ecol. 43: 123–130.
Bond, W. J. and Keeley, J. E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. – Trends Ecol. Evol. 20: 387–394.
Bond, W. J. et al. 2005. The global distribution of ecosystems in a world without fire. – New Phytol. 165: 525–538.
Breiman, L. et al. 1984. Classification and regression trees. – Wadsworth and Brooks/Cole, Monterey, CA, USA.
Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. – Springer.
Coetsee, C. et al. 2010. Frequent fire affects soil nitrogen and carbon in an African savanna by changing woody cover. – Oecologia 162: 1027–1034.
Dantas, V. de L. et al. 2016. Disturbance maintains alternative biome states. – Ecography 19: 12–19.
Dean, W. R. J. et al. 1999. Large trees, fertile islands and birds in arid savanna. – J. Arid Environ. 41: 61–78.
De'ath, G. and Fabricius, K. E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. – Ecology 81: 3178–3192.
Druce, D. J. et al. 2008. Ecological thresholds in the savanna landscape: developing a protocol for monitoring the change in composition and utilisation of large trees. – PLoS One 3: e3979.
Dublin, H. T. et al. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. – J. Anim. Ecol. 59: 1147–1164.
Eckhardt, H. C. et al. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. – Afric. J. Ecol. 38: 108–115.
Gandiwa, E. and Kativu, S. 2009. Influence of fire frequency on *Colophospermum mopane* and *Combretum apiculatum* woodland structure and composition in northern Gonarezhou National Park, Zimbabwe. – Koedoe Afric. Protect. Area Conserv. Sci. 51: 36–48.
Gertenbach, W. 1983. Landscapes of the Kruger National Park. – Koedoe 26: 60–82.
Goheen, J. R. et al. 2018. Conservation lessons from large-mammal manipulations in East African savannas: the KLEE, UHURU and GLADE experiments. – Ann. N. Y. Acad. Sci. 1429: 31–49.
Govender, N. et al. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. – J. Appl. Ecol. 43: 748–758.
Helm, C. et al. 2011. Investigating the vulnerability of an African savanna tree (*Sclerocarya birrea* ssp. caffra) to fire and herbivory. – Austral Ecol. 36: 964–973.
Helm, C. V. and Witkowski, E. T. F. 2012. Characterising wide spatial variation in population size structure of a keystone African savanna tree. – For. Ecol. Manage. 263: 175–188.
Helm, C. V. et al. 2009. Mortality and utilisation of *Sclerocarya birrea* subsp. caffra between 2001 and 2008 in the Kruger National Park, South Africa. – S. Afr. J. Bot. 75: 475–484.
Higgins, S. I. et al. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. – Ecology 88: 1119–1125.
Hoffmann, W. et al. 2009. Tree topkill, not mortality, governs the dynamics of savanna – forest boundaries under frequent fire in central Brazil. – Ecology 90: 1326–1337.
Holdo, R. M. 2007. Elephants, fire and frost can determine community structure and composition in Kalahari woodlands. – Ecol. Appl. 17: 558–568.
Hothorn, T. et al. 2006. Unbiased recursive partitioning: a conditional inference framework. – J. Comput. Graph. Stat. 15: 651–674.
Kerley, G. I. et al. 2008. Effects of elephants on ecosystems and biodiversity. – In: Scholes, R. J. and Mennell, K. G. (eds), Elephant management: a scientific assessment for South Africa. Wits Univ. Press, pp. 146–205.
Kraaij, T. and Ward, D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. – Plant Ecol. 186: 235–246.
Levick, S. R. and Asner, G. P. 2013. The rate and spatial pattern of treefall in a savanna landscape. – Biol. Conserv. 157: 121–127.
Levick, S. R. et al. 2009. The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. – Biol. Conserv. 142: 1693–1700.
Levick, S. R. et al. 2015. Demographic legacies of fire history in an African savanna. – Funct. Ecol. 29: 131–139.
Lindenmayer, D. B. et al. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. – Conserv. Lett. 7: 61–69.
Ludwig, F. et al. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. – Plant Ecol. 170: 93–105.
Ludwig, F. et al. 2008. Impacts of savanna trees on forage quality for a large African herbivore. – Oecologia 155: 487–496.
MacFadyen, S. et al. 2018. Long-term rainfall regression surfaces for the Kruger National Park, South Africa: a spatio-temporal review of patterns from 1981 to 2015. – Int. J. Climatol. 38: 2506–2519.
MacFadyen, S. et al. 2019. Spatiotemporal distribution dynamics of elephants in response to density, rainfall, rivers and fire in Kruger National Park, South Africa. – Divers. Distrib. 25: 880–894.
Makhabu, S. W. et al. 2006. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. – Acta Oecol. 30: 136–146.
Malherbe, J. et al. 2020. Recent droughts in the Kruger National Park as reflected in the extreme climate index. – Afr. J. Range Forage Sci. 37: 1–17.
Mamashela, C. T. 2010. The effects of browsing on growth, structure and physiological aspects of *Acacia grandicornuta* and *Combretum apiculatum* – MSc thesis, Univ. of Zululand.
Manning, A. D. et al. 2006. Scattered trees are keystone structures–implications for conservation. – Biol. Conserv. 132: 311–321.
Mapaure, I. and Moe, S. R. 2009. Changes in the structure and composition of miombo woodlands mediated by elephants *Loxodonta africana* and fire over a 26-year period in northwestern Zimbabwe. – Afr. J. Ecol. 47: 175–183.
Midgley, J. J. et al. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. – Aust. J. Bot. 58: 1–11.
Moncrieff, G. R. et al. 2008. Stem mortality of *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. – J. Trop. Ecol. 24: 655–662.
Morrison, T. A. et al. 2016. Elephant damage, not fire or rainfall, explains mortality of overstorey trees in Serengeti. – J. Ecol. 104: 409–418.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.
Nakagawa, S. et al. 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. – J. R. Soc. Interface 14: 20170213.
O'Connor, T. G. et al. 2007. A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. – Biol. Conserv. 136: 329–345.
Pellegrini, A. F. A. et al. 2017. Woody plant biomass and carbon exchange depend on elephant – fire interactions across a productivity gradient in African savanna. – J. Ecol. 105: 111–121.
Prins, H. H. T. and van der Jeugd, H. P. 1993. Herbivore population crashes and woodland structure in East Africa. – J. Ecol. 81: 305–314.
Rushworth, I. et al. 2018. Vulnerability of vulture populations to elephant impacts in KwaZulu-Natal. – Bothalia 48: 1–10.
Sankaran, M. et al. 2005. Determinants of woody cover in African savannas. – Nature 438: 846–849.
Sankaran, M. et al. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. – Global Ecol. Biogeogr. 17: 236–245.
Sankaran, M. et al. 2013. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. – J. Ecol. 101: 1389–1399.
Scholes, R. J. and Archer, S. R. 1997. Tree–grass interactions in savannas. – Annu. Rev. Ecol. Syst. 28: 517–544.
Shannon, G. et al. 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. – J. Trop. Ecol. 24: 281–289.
Shannon, G. et al. 2011. Relative impacts of elephant and fire on large trees in a savanna ecosystem. – Ecosystems 14: 1372–1381.
Staal, A. et al. 2018. Resilience of tropical tree cover: the roles of climate, fire and herbivory. – Global Change Biol. 24: 5096–5109.
Staver, A. C. and Bond, W. J. 2014. Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. – J. Ecol. 102: 595–602.
Staver, A. C. et al. 2007. Continuous v. episodic recruitment in *Acacia* karroo in Hluhluwe-iMfolozi Park: implications for understanding savanna structure and dynamics. – S. Afr. J. Bot. 73: 314–314.
Staver, A. C. et al. 2009. Browsing and fire interact to suppress tree density in an African savanna. – Ecol. Appl. 19: 1909–1919.
Staver, A. C. et al. 2011. The global extent and determinants of savanna and forest as alternative biome states. – Science 334: 230–232.
Staver, A. C. et al. 2017. Soils and fire jointly determine vegetation structure in an African savanna. – New Phytol. 216: 1151–1160.
Strobl, C. et al. 2009. An introduction to recursive partitioning: rationale, application and characteristics of classification and regression trees, bagging and random forests. – Psychol. Methods 14: 323.
Thaker, M et al. 2021. Large tree mortality census KNP (2006-2018). – Dryad Digital Repository <https://doi.org/10.5061/dryad.2280gb5sh>.
Touboul, D. et al. 2018. On the complex dynamics of savanna landscapes. – Proc. Natl Acad. Sci. USA 115: E1336–E1345.
Treydte, A. C. et al. 2007. Trees improve grass quality for herbivores in African savannas. – Perspect. Plant Ecol. Evol. Syst. 8: 197–205.
Trollope, W. S. et al. 1998. Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. – Koedoe 41: 103–112.
Van De Vijver, C. A. et al. 1999. Changes in the woody component of an East African savanna during 25 years. – J. Trop. Ecol. 15: 545–564.
van Langevelde, F. et al. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. – – Ecology 84: 337–350.
van Wilgen, B. W. et al. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa between 1941 and 1996. – S. Afr. J. Sci. 96: 167e178.
van Wilgen, B. W. et al. 2004. Response of savanna fire regimes to changing fire-management policies in a large African National Park. – Conserv. Biol. 18: 1533–1540.
van Wilgen, B. W. et al. 2014. The ongoing development of a pragmatic and adaptive fire management policy in a large African savanna protected area. – J. Environ. Manage. 132: 358–368.
Vanak, A. T. et al. 2012. Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna. – Ecography 35: 315–321.
Venter, Z. S. et al. 2017. Implications of historical interactions between herbivory and fire for rangeland management in African savannas. – Ecosphere 8: 1–14.
Werner, P. A. and Prior, L. D. 2016. Demography and growth of subadult savanna trees: interactions of life history, size, fire season and grassy understory. – Ecol. Monogr. 83: 67–93.
Wigley, B. J. et al. 2014. Herbivores shape woody plant communities in the Kruger National Park: lessons from three long-term exclosures. – Koedoe 56: 1–12.
Wigley-Coetsee, C. and Staver, A. C. 2020. Grass community responses to drought in an African savanna. – Afr. J. Range Forage Sci. 37: 43–52.