



Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an African savanna

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The vegetation dynamics of the savanna ecosystem are driven by complex interactions between biotic and abiotic factors, and thus are expected to exhibit emergent properties of biocomplexity. We explore the relative importance of static and dynamic drivers in explaining the patterns of mortality of large trees in the Kruger National Park, South Africa. Data on large trees were collected from 22 transects in April 2006, and these transects were re-sampled in November 2008. Of the 2546 individually-identified trees that were re-sampled, 290 (11.4%) died in the interim. We tested several competing hypotheses with varying levels of complexity, and found that mortality of large trees was affected mainly by both static (geophysical and landscape characteristics) and dynamic (elephant damage and fire) factors that were either additive or interactive in their effects. Elephant damage was the main predictor of tree mortality, but fire also played an important role depending on the landscape type. Other static variables such as position-on-slope, height below canopy, and altitude had weak effects in explaining tree mortality. These results indicate that keystone features such as large trees, show differential vulnerability to mortality that is landscape-specific. For conservation managers, this implies that the dynamic drivers (elephant and fire) of tree mortality have to be managed at the specific landscape-level. We suggest that this emergent biocomplexity in the spatial and temporal patterns of large tree mortality is not unique to the African savannas, but is likely widespread across heterogeneous landscapes.

Interest in the field of biocomplexity has increased in recent years, as growing evidence points to the importance of complex interactions between living organisms and the abiotic components of the environment (Michener et al. 2001, Anand and Tucker 2003). The emergent properties from these interactions are not always obvious and can depend on a range of behavioural, biological, chemical, physical and social effects (Michener et al. 2001). The vegetation dynamics of the African savanna are an excellent example where biocomplexity in the interaction between static and dynamic factors can be expected. The African savanna is a heterogeneous and highly productive system that is defined by a continuous grass layer interspersed with trees (Scholes and Archer 1997). At the regional and landscape scales, resource availability (water and nutrients) and disturbance regimes (fire and herbivory) drive savanna vegetation dynamics (Van Wilgen et al. 2004, Sankaran et al. 2007). Water availability is considered the primary resource driver (Kerckhoff et al. 2004, Sankaran et al. 2005), but the top-down effects of fire (Van Langevelde et al. 2003, Van Wilgen et al. 2004, Higgins et al. 2007) and herbivory (Van Langevelde et al. 2003, Augustine and McNaughton 2004, Shannon et al. 2008) play key modifying roles in both the physiognomic structure and species composition of woody vegetation.

Fire directly affects the composition of woody vegetation by causing differential mortality of some species; but fire can also change the physiognomic structure of woody vegetation through the removal of biomass (top-kill; Holdo 2007). In fact, fire frequency has marked effects on both biomass and size structure of trees but does not directly reduce tree density (Higgins et al. 2007). Savanna ecosystems also support an abundance of large herbivores, which utilize woody vegetation for both forage and refuge. African elephant *Loxodonta africana* are considered to be one of the main drivers behind changes in woody vegetation structure and composition due to their large body size, potentially high population densities, and generalist foraging behaviour, which involves the removal of mature trees from the ecosystem (Guldemand and van Aarde 2008).

There is increasing concern that the loss of large mature trees in landscapes frequented by elephant and where fires are intense may result in the transformation of woodland savanna into scrub or grassland (Owen-Smith et al. 2006, Druce et al. 2008). Large trees (≥ 5 m in height) are a major component of the savanna biome, playing a key role in ecosystem function through the provisioning of forage, shade, and refuge (Dean et al. 1999), whilst also functioning as nutrient pumps (Belsky et al. 1989, Treydte et al. 2008). Large trees also

generate pronounced habitat heterogeneity at multiple spatial scales (Manning et al. 2006). Thus, the persistence of, and potential threats to, large trees are important considerations when assessing the viability of savanna ecosystems.

It is now readily accepted that key ecological drivers such as rainfall, fire and herbivory operate in a complex interactive manner (Holdo 2007, Sankaran et al. 2007). For example, as elephant remove woody vegetation, grass production is stimulated, which can fuel fire frequency and intensity (Dublin et al. 1990, Holdo et al. 2009). Debarking by elephant may also render large trees susceptible to mortality by subsequent fire damage (Moncrieff et al. 2008). Geology, topography, soil and water are key environmental variables that directly influence vegetation structure and composition across a range of scales, from the plant to the landscape (Venter et al. 2003, Sankaran et al. 2005). As a result, the impacts of fire and herbivory on large trees are also expected to change with landscape structure (Higgins et al. 2007). Yet, despite the growing evidence of interactive effects on savanna vegetation, the combination of the dynamic fire and elephant drivers with static landscape-level geophysical drivers have rarely been robustly analysed (Mapaure 2001).

Here, we used a detailed approach of studying individually-identified trees in the Kruger National Park (KNP), South Africa, to examine the drivers of large tree mortality in

the savanna ecosystem, with the expectation that biotic and abiotic factors are non-additive in their effects. We specifically examined the relative contribution of static factors, such as geology, soil type, altitude, slope, aspect, surface water, tree characteristics and Gertenbach landscape type (Gertenbach 1983), with dynamic factors of elephant utilisation and fire damage. Because of the biocomplexity of the system, we expected that no single driver would best explain large tree mortality across the landscape, and that the contributions of the most important drivers of large tree mortality, elephant damage and fire, will be landscape-specific (Table 1).

Methods

We conducted this study in the southern section of the KNP (25°28′–24°91′S; 31°95′–31°32′E) in an area of approximately 2100 km². The study site and the transect locations are described in detail in Druce et al. (2008) and Shannon et al. (2008).

Large tree sampling

During April 2006, we surveyed large trees across 22 strip-transects that were 10 m wide and varied in length from

Table 1. List of parameters that explain the patterns of mortality of large trees in the Kruger National Park, South Africa. Shown are predicted and observed effects for each parameter estimate (β_i) with $\beta_i > 0$ indicating a positive effect on tree mortality, $\beta_i < 0$ indicating a negative effect, and $\beta_i = 0$ indicating no effect. $>>$ and $<<$ indicate strong effects based on the odds-ratios.

Models	Parameters in the model	Effect on tree mortality		
		Predicted	Observed	
Fire damage	previous fire (2006), recent fire (2008), frequency	$\beta_{\text{fire2006}} > 0, \beta_{\text{fire2008}} > 0, \beta_{\text{firefreq}} > 0$	$\beta_{\text{fire2006}} > 0, \beta_{\text{fire2008}} >> 0, \beta_{\text{firefreq}} = 0$	
Elephant damage	previous damage (2006), recent damage (2008)	$\beta_{\text{elephant2006}} > 0, \beta_{\text{elephant2008}} \geq 0$	$\beta_{\text{elephant2006}} > 0, \beta_{\text{elephant2008}} >> 0$	
Landscape type ^a in interaction with elephant utilization and fire damage	ATK = <i>Acacia welwitschii</i> on Karoo sediments	$\beta_{\text{ATK} \times \text{Elephant}} >> 0, \beta_{\text{ATK} \times \text{Fire}} > 0$	$\beta_{\text{ATK} \times \text{Elephant}} >> 0, \beta_{\text{ATK} \times \text{Fire}} = 0$	
	CCW = <i>C. collinum</i> / <i>C. zeyheri</i> woodland	$\beta_{\text{CCW} \times \text{Elephant}} > 0, \beta_{\text{CCW} \times \text{Fire}} = 0$	$\beta_{\text{CCW} \times \text{Elephant}} >> 0, \beta_{\text{CCW} \times \text{Fire}} = 0$	
	MCW = mixed <i>Combretum</i> / <i>Terminalia sericea</i> woodland	$\beta_{\text{MCW} \times \text{Elephant}} > 0, \beta_{\text{MCW} \times \text{Fire}} = 0$	$\beta_{\text{MCW} \times \text{Elephant}} = 0, \beta_{\text{MCW} \times \text{Fire}} = 0$	
	LSP = Lowveld Sour Bushveld of Pretoriuskop	$\beta_{\text{LSP} \times \text{Elephant}} \geq 0, \beta_{\text{LSP} \times \text{Fire}} >> 0$	$\beta_{\text{LSP} \times \text{Elephant}} > 0, \beta_{\text{LSP} \times \text{Fire}} >> 0$	
	ToG = Thornveld on Gabbros TSC = thickets of the Sabie and Crocodile Rivers	$\beta_{\text{ToG} \times \text{Elephant}} >> 0, \beta_{\text{ToG} \times \text{Fire}} >> 0$ $\beta_{\text{TSC} \times \text{Elephant}} > 0, \beta_{\text{TSC} \times \text{Fire}} \geq 0$	$\beta_{\text{ToG} \times \text{Elephant}} >> 0, \beta_{\text{ToG} \times \text{Fire}} = 0$ $\beta_{\text{TSC} \times \text{Elephant}} >> 0, \beta_{\text{TSC} \times \text{Fire}} > 0$	
Tree characteristics	species ^b , crown diameter (CrD), height below canopy (HbC), stem diameter (StD), tree height (TH)	$\beta_{\text{spp}} \neq 0$ (varies by species), $\beta_{\text{CrD}} > 0, \beta_{\text{HbC}} > 0,$ $\beta_{\text{StD}} < 0, \beta_{\text{TH}} > 0,$	$\beta_{\text{spp}} = 0,$ $\beta_{\text{CrD}} = 0, \beta_{\text{LcrH}} > 0,$ $\beta_{\text{StD}} = 0, \beta_{\text{TH}} = 0,$	
	Physical factors	distance to river and water, geology: basalt, granite, gabbro soil: shallow sand (ShSand), moderately deep sand (MDSand), shallow clay (ShClay), moderately shallow clay (MDClay), deep clay (DClay)	$\beta_{\text{water}} > 0, \beta_{\text{river}} > 0,$ $\beta_{\text{basalt}} < 0, \beta_{\text{granite}} > \beta_{\text{gabbro}} > 0,$ $\beta_{\text{ShSand}} > \beta_{\text{MDSand}} > \beta_{\text{ShClay}} > 0,$ $\beta_{\text{DClay}} < \beta_{\text{MDClay}} < 0$	$\beta_{\text{water}} = 0, \beta_{\text{river}} = 0,$ $\beta_{\text{basalt}} = \beta_{\text{granite}} = \beta_{\text{gabbro}} = 0$ $\beta_{\text{ShSand}} = \beta_{\text{MDSand}} = \beta_{\text{ShClay}} = \beta_{\text{MDClay}} =$ $\beta_{\text{DClay}} = 0$
		Topographical factors	altitude, position-on-slope: crest, middle, foot	$\beta_{\text{Alt}} < 0, \beta_{\text{Foot}} > \beta_{\text{Crest}} > 0, \beta_{\text{Middle}} < 0$

^afrom Gertenbach (1983), ^b39 species of large trees were identified.

1.0 to 6.6 km (total length = 67 km; described in Shannon et al. 2008). Large trees were defined by height (≥ 5 m) and we focussed on mature, established trees and not on saplings and shrubs. We recorded the location and species of all large trees on the transect, and for each of these trees, recorded the following characteristics: total height, height below the canopy, widest canopy diameter, stem diameter (measured 1 m above the ground) and the number of stems. We estimated the extent of canopy volume removed by elephant and/or giraffe *Giraffa camelopardalis*, as well as the proportion reduced by dieback from drought (modified from Walker 1976). We also estimated the proportion of bark removed and all agents of bark removal (e.g. elephant, porcupine *Hystrix africaeaustralis* and baboon *Papio ursinus*). Elephant contributed to $> 90\%$ of canopy volume removed and $> 99\%$ of occurrences of bark removal. Damage to trees was classified into percentage of tree removed using six broad categories: 1) 1–10%, 2) 11–25%, 3) 26–50%, 4) 51–75%, 5) 76–90%, and 6) 91–100% (Shannon et al. 2008). We also recorded if trees had suffered from recent fire damage (< 6 months) based on physical evidence. Hereafter, elephant damage and fire damage that were identified in 2006 will be referred to as ‘previous elephant damage’ and ‘previous fire damage’ respectively. Note that these measures do not indicate that damage occurred in 2006 alone, but that the damage was quantified in 2006.

In November 2008, we resurveyed 21 out of the 22 transects (2636 trees) and 2546 individual trees were re-located based on their geographic coordinates (97% success in relocation). Once located, each tree was re-assessed by the same observer to determine whether additional damage or death occurred during the preceding 30 months. As before, we estimated the extent of canopy volume removed assuming an intact/undamaged tree. We then subtracted this cumulative estimate in 2008 from damage estimated in 2006 to obtain an estimate of additional damage since the previous survey. This ‘recent elephant damage’ was an additive and not cumulative measure of damage to the tree and was classified into 6 categories as above. New occurrence of fire damage (‘recent fire damage’) was also recorded. We omitted 24 trees from analysis because of incomplete data.

In ARCGIS 9.3 (ESRI Inc) we overlaid the locations of resurveyed trees with GIS layers (www.sanparks.org/parks/kruger/conservation/scientific/gis/), and for every tree, we determined landscape type (www.thekruger.com/gertenbach/gertenbachintro.htm; Gertenbach 1983), soil type, geology, position on slope (foot, mid, or crest), fire frequency, and distance to nearest river and waterhole.

Statistical analysis

A generalized linear model with a binary response (live tree = 0, dead tree = 1) and a logit-link function was used to determine the parameters that best explain tree mortality at the time of the resurvey. We created a global model consisting of all the explanatory parameters derived from the GIS layers, as well as the characteristics of the tree (species, height, crown diameter, etc.), the extent of previous and recent elephant damage, and whether the tree suffered previous or recent fire damage. All parameters were included in

the global model after testing for multicollinearity (tolerance values = 0.32–0.98).

We created 28 sub-models to test specific a priori hypotheses explaining tree mortality. Models comprising single-factors and additive factors fell under six broad categories: 1) fire frequency and damage, 2) elephant damage, 3) landscape type, 4) tree characteristics, such as species, height, and crown diameter, 5) physical factors, such as geology, soil, and distance from water sources, and 6) topographical factors, such as slope, position-on-slope, and altitude (Table 1). Models comprising interactive factors and additive + interactive factors included combinations of parameters from multiple single-factor hypotheses with interaction terms between the three key parameters: elephant damage, fire damage and landscape type. Single-factor and additive models were based on the assumption that drivers were sufficient to either independently or additively explain patterns of large tree mortality. Interactive and additive + interactive models assume that drivers act synergistically, as would be expected under the assumptions of biocomplexity. The hypothesised effects of these parameters and predicted outcomes (Table 1) were derived from the literature and from the authors’ observations. The fit of candidate models were assessed using Akaike weights (ω_i) based on Akaike’s information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002).

We also conducted a second-stage model selection procedure to create a minimized or refined AIC_c model with parameters drawn from several a priori hypotheses. Deriving a minimized AIC_c model is a useful post-hoc method to detect models that were not previously hypothesized, especially in the context of identifying emergent additive and interactive parameters. We tested the influence of each parameter in the global model with all major interactions, by individually removing them and recording changes to AIC_c until a minimized AIC_c model was obtained.

We determined the magnitude of effect of each single factor parameter on the probability of mortality in the top-ranked model(s) with the odds-ratio (Hosmer and Lemeshow 2000). Odds-ratios indicate the change in the odds of the response variable (i.e. probability of mortality) with every unit increase in the predictor variable, when all other predictor variables are held constant. The effects of the interactive terms on the probability of mortality were explored graphically (Hosmer and Lemeshow 2000).

Results

A total of 2546 trees were surveyed in both 2006 and 2008, of which 290 trees (11.4%) suffered mortality within the 30-month interval. Of the models tested to explain patterns of mortality, the minimized AIC_c model ($\omega_i = 0.99$) consisting of both static and dynamic additive and interactive factors was a better fit to the data than our best a priori model (Table 2). Among the dynamic factors, previous elephant utilisation ($\beta = 1.89 \pm 0.25$ SE) and previous fire damage ($\beta = 0.64 \pm 0.23$ SE) were strong additive predictors of tree mortality on all landscapes types (Fig. 1). The effects of previous elephant damage and previous fire damage may, however, be confounded by more recent damage,

Table 2. Top four a priori hypothesized models and the model with minimised Akaike's information criterion adjusted for small sample size (AIC_c) that explain the mortality of large trees in the Kruger National Park, South Africa. Note that the minimised AIC_c model best explained mortality of trees. Columns include AIC_c score, difference from the lowest AIC_c (Δ AIC_c), and Akaike's model weight (ω_i).

	AIC _c	Δ AIC _c	ω_i
A priori hypothesized models			
elephant06 + fire06 + elephant08 + fire08 + elephant08 \times fire08 + elephant08 \times landscape + fire08 \times landscape + elephant08 \times fire08 \times landscape + soil type + altitude + height below canopy + position-on-slope	841.80	0.00	0.73
elephant06 + fire06 + elephant08 + fire08 + landscape + elephant08 \times fire08 + elephant08 \times landscape + fire08 \times landscape + elephant06 \times fire06 \times landscape + soil type + altitude	844.68	2.79	0.17
elephant06 + fire06 + elephant08 + fire08 + landscape + elephant08 \times fire08 + elephant08 \times landscape + all physical factors	845.81	4.00	0.10
Global model	886.60	44.79	0.00
Minimised AIC _c model			
elephant06 + fire06 + elephant08 + fire08 + landscape + elephant08 \times fire08 + elephant08 \times landscape + fire08 \times landscape + elephant08 \times fire08 \times landscape + height below canopy + position-on-slope + altitude	834.13	-7.67	0.99

as 12.5% (n = 317) of all surveyed trees suffered repeated elephant damage and 2.6% (n = 66) suffered repeated fire damage. Of these repeatedly impacted trees, 36.6% died between the surveys (n = 107 of repeated elephant damage, 33 of repeated fire damage).

Among the static factors in the model with best fit, position-on-slope was the strongest predictor of mortality as trees on mid-slopes ($\beta = 0.63 \pm 0.24$ SE) were more likely to suffer mortality than trees on crests (Fig. 1). Mortality of trees on foot-slopes was similar to those on crests. Although included in this model, height below canopy ($\beta = 0.12 \pm 0.07$ SE) and altitude ($\beta = 0.01 \pm 0.002$ SE) were weaker predictors of tree mortality (Fig. 1).

The three-way interaction between recent elephant damage, recent fire damage, and landscape was a stronger predictor of mortality in the best model than the two-way interactions or the additive effects of these parameters. Thus, the effects of elephant and fire damage on tree mortality were landscape-specific. On the Thickets of the Sabie and Crocodile rivers (TSC) landscape (Fig. 2a), the *Combretum collinum*/*C. zeyheri* Woodland (CCW) landscape (Fig. 2b) and the Lowveld Sour Bushveld of Pretoriuskop (LSP) landscape (Fig. 2d), mortality of unburned trees was determined predominantly by recent damage by elephant. However, for trees that suffered recent fire damage on the TSC landscape, lower levels of recent elephant damage was sufficient to cause mortality (Fig. 2a). On the CCW landscape, both dead and live trees suffering from recent fire damage had similarly low levels of recent elephant damage (Fig. 2b). There was a

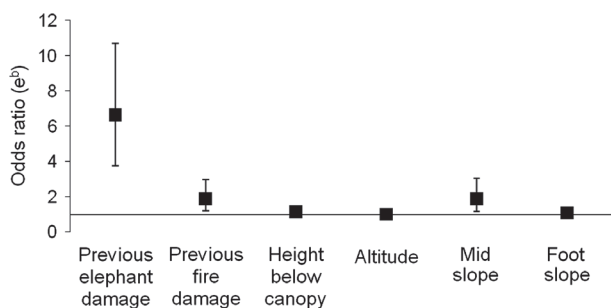


Figure 1. Odds-ratios (\pm 95% confidence interval) of additive parameters in the model that best explains the mortality of large trees in the Kruger National Park, South Africa.

similar pattern for burned trees on the Thornveld on Gabbro (ToG) landscape, but for unburned trees, elephant utilisation was only marginally higher for dead compared to live trees (Fig. 2c). Fire had the strongest effect on the mortality of trees on the LSP landscape, as no trees survived recent fire (Fig. 2d). Finally, there were no fires in the period between surveys on the *Acacia welwitschii* Thickets on Karoo Sediments (ATK) landscape and on the Mixed *Combretum Terminalia sericea* Woodlands (MCW) landscape (Fig. 2e, f). High recent elephant damage explained large tree mortality on the ATK landscape (Fig. 2e), but elephant damage was low on the MCW landscape and accounted for mortality of only one tree (Fig. 2f).

Discussion

The effects of elephant and fire damage on woody vegetation structure have been relatively well studied in the savanna landscape (Van Langevelde et al. 2003, Holdo et al. 2009). We found that these dynamic drivers not only have additive effects, but also interact with static geophysical factors, creating heterogeneity in mortality patterns of large trees across the landscape. Consistent with the expectation of emergent patterns of biocomplexity, the effects of elephant and fire damage on mortality were specific to the landscape types of KNP.

Specific properties of these landscape types, such as geology, soil type, soil depth, slope and perennial water sources not only influence the type of vegetation that the landscape supports, but how the impacts of elephant and fire manifest. On most landscapes, elephant damage was a major contributor to the mortality of trees that did not suffer from fire damage (Fig. 2), a pattern that is consistent with other studies on the effects of elephant damage on large trees in general (reviewed by Kerley et al. 2008). Several studies have shown that elephant preferentially browse in open woodland habitats at intermediate distances from permanent water (Owen-Smith 1992, Shannon et al. 2006). Tree usage by elephants is further influenced by the ruggedness of the terrain, which improves forage quality and creates nutrient hotspots (Nellemann et al. 2002). The likelihood of tree-pushing by elephant also is facilitated by shallow soils associated with open woodlands compared to deeper clay

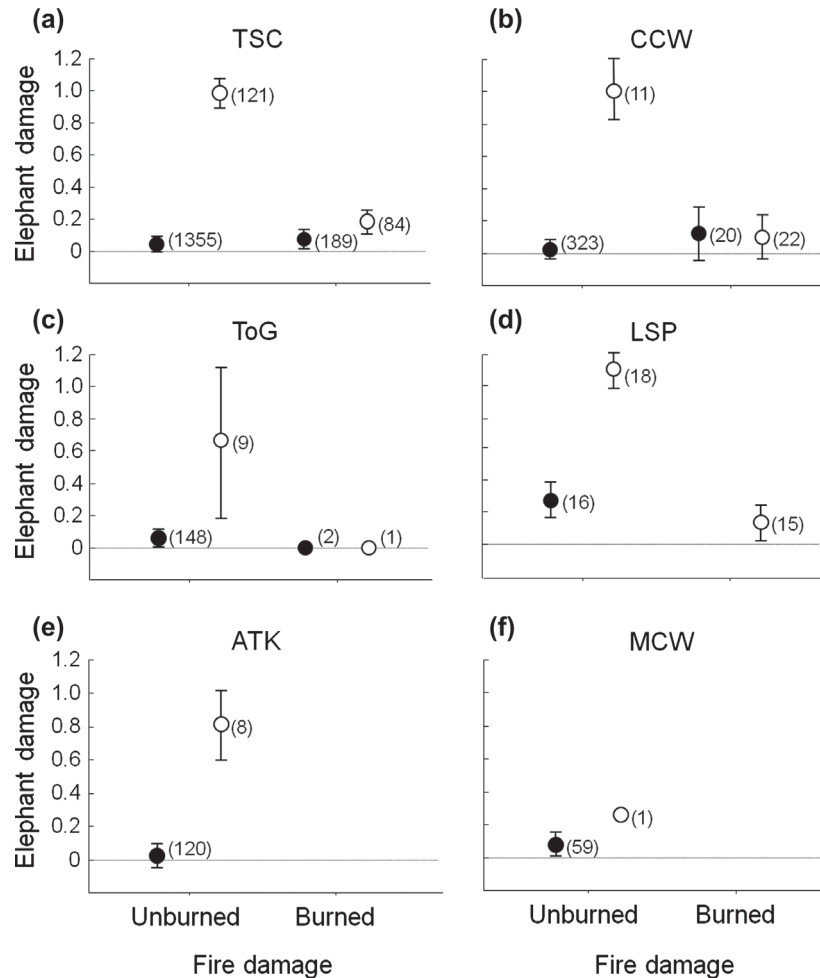


Figure 2. Landscape-specific interaction between recent fire damage (unburned, burned) and recent elephant damage (proportion of tree volume removed, arcsin transformed) in explaining mortality of large trees in the Kruger National Park, South Africa. Filled circles denote live trees and open circles denote dead trees. Error bars indicate 95% confidence intervals from the mean and numbers in parentheses are the sample sizes of trees. Landscape types are a) TSC = Thickets of the Sabie and Crocodile Rivers, b) CCW = *C. collinum/C. zeyheri* Woodland, c) ToG = Thornveld on Gabbros, d) LSP = Lowveld Sour Bushveld of Pretoriuskop, e) ATK = *Acacia welwitschii* thickets on Karoo Sediments, and f) MCW = Mixed *Combretum/Terminalia sericea* Woodland.

soils that predominate close to rivers (Shannon et al. 2006, O'Connor et al. 2007). These foraging preferences of elephant and the location of trees may explain why some trees were repeatedly impacted by elephant, further exacerbating their probability of mortality.

Our results also demonstrate that fire plays an important role in driving the mortality of mature trees, despite the predictions of some studies which suggest that this is unlikely to be the case (Bond and Keeley 2005, Higgins et al. 2007). For example, on the LSP landscape, all large trees within burned areas were killed, likely due to the higher intensity fires that are common on this landscape (Gertenbach 1983). Despite the fact that some trees experienced repeated fires, we found no support for the importance of fire frequency in explaining large tree mortality in any of the landscape types. Heterogeneity in the intensity of fires may play a larger role in tree mortality, as hotter fires are more likely to kill trees than frequent cooler fires.

In some landscape types, the interaction between recent elephant damage and recent fire better explained the pattern of mortality of trees. In the TSC landscape, fire damage

alone was not sufficient to cause tree mortality. Instead, the combination of recent fire damage with low levels of recent elephant damage killed trees. This may have resulted from the increased susceptibility of debarked trees to 'top kill' by subsequent fire (Moncrieff et al. 2008, Chafota and Owen-Smith 2009). The combination of fire and elephant damage, however, was not sufficient to explain tree mortality on the CCW and ToG landscapes, as there were small differences in elephant damage between live and dead trees that also suffered fire damage (Fig. 2b, c). The sample size of trees that were recently burned was low on the ToG landscape (Fig. 2c), and thus we are cautious in interpreting this interaction. The pattern of tree mortality on the CCW landscape does suggest that, in addition to elephant and fire damage, other drivers such as drought, frost or disease, may also have contributed to the mortality of trees (Holdo 2007, Chafota and Owen-Smith 2009).

Contrary to our expectations, several factors were poor predictors of large tree mortality (Table 1). Certain species, such as *Sclerocarya birrea*, *A. nigrescens* and *C. apiculatum*, are more likely to be heavily foraged by elephant (Shannon et al.

2008). Yet, we found few differences in mortality between species, suggesting that elephant may be targeting these species in proportion to their availability on the landscape (Shannon et al. 2008). Furthermore, although taller trees were expected to suffer greater mortality due to pushing over by elephant (Shannon et al. 2008), we found that height below canopy was a better predictor of mortality than tree height (Table 1). Other studies have shown that elephant utilize and push over trees on the gabbro substrate more than trees on the granite or basalt substrates (Eckhardt et al. 2000, Shannon et al. 2008). Yet we found no effect of substrate on the mortality of trees, suggesting that the levels of elephant utilisation on these substrates were not distinct enough to result in differences in mortality.

The mortality of large trees in KNP was clearly affected by complex dependencies and feedback loops between dynamic (elephant and fire) and static (geophysical and landscape characteristics) factors. Approximately 11% of trees in the > 5 m height class suffered mortality within the 30-month inter-survey period, but only 5% were recruited into this height class (Shannon et al. unpubl.). This imbalance in mortality and recruitment rates would seem to suggest that the extinction of trees from this ecosystem is imminent. However, although this rate of recruitment appears too low to prevent decline, recruitment rates were species specific (Shannon et al. in press) and may go through pulses, with episodic events playing a key role (Staver et al. 2007). Given the current rates of recruitment and the landscape-specific vulnerability of individual trees to mortality, we expect that density and composition of tree species are likely to change unevenly across the different landscape types. While this short-term study gives us an accurate measure of some of the major drivers of mortality, this period may be too short to effectively and simultaneously understand long-term dynamics of the tree population as well as drivers of recruitment, and hence we caution against the conclusion that overall tree populations are in imminent decline.

The management of heterogeneity itself, and the processes that create heterogeneity, are explicit in KNP's management plans (Biggs and Rogers 2003, Rogers 2003). The strategic adaptive management programme of KNP (Biggs and Rogers 2003, Rogers 2003) includes a structure-specific threshold of potential concern (TPC; <www.sanparks.org/conservation/park_man/kruger.pdf>, accessed 3 May 2010) for woody vegetation, which addresses both the abundance and diversity of large trees. TPCs are upper and lower thresholds in a predefined indicator which, when breached, prompt an assessment or management action to address the cause of change (Biggs and Rogers 2003). So far, management actions for maintaining woody vegetation structure are still at a park-wide scale, through the control of single drivers (for example: culling of elephant; Carruthers et al. 2008), which is inadequate as it oversimplifies the dynamics of such complex and heterogeneous ecological systems. We propose that TPCs for large trees need to be developed and monitored at the level of specific landscape types, and should incorporate change over time, rather than just using snap-shot data sets (Druce et al. 2008). This continuous monitoring approach will also prove valuable for detecting pulsed mortality and recruitment events, as well as the effects of stochastic events such as droughts, which may only be captured at larger temporal scales.

We show geophysical- and landscape-level effects on mortality of large trees, but the processes and mechanisms underlying this heterogeneous pattern of vulnerability remain to be robustly explored across KNP. The interactions between abiotic and biotic drivers point to an emergent biocomplexity in the patterns of large tree mortality in African savannas. Indeed, we expect biocomplexity to emerge around keystone features, such as large trees, given their prominent role in the ecosystem. Such biocomplexity is likely not unique to KNP, or even to African savannas, and is probably widespread across heterogeneous landscapes.

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