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Drought limits large trees in African savannas with and without elephants

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ABSTRACT

Consumers, including megaherbivores and fire, are considered important limiting forces for woody plants and canopy closure in African savannas. However, climatic events like drought can also play a significant role in limiting trees and maintaining tree-grass coexistence in savannas. The extent to which top-down control (e.g. megaherbivores) and bottom-up resource limitation through drought and competition interact to influence savanna tree mortality and woody structure is unclear. Here, we compared the change in the number of large trees before and after a severe drought in a savanna with elephants (*Loxodonta africana*) and one without elephants. Elephants and drought both limited the number of large trees at our sites, but contrary to our predictions, there was no interactive effect of these drivers on overall changes in tree densities. However, there was a synergistic effect on the dominant tree species, *Senegalia nigrescens*, such that tree loss post-drought was greater where elephants were present compared to where they were absent.

Hence, our results suggest that species-specific differences in drought resistance, as well as density-dependent factors, likely impact the severity of drought effects on savanna tree communities. In savannas, drought has the potential to exert strong control on tree survival and prevent canopy closure, thus partially filling the role of megaherbivores in limiting large trees when these consumers are absent. As drought severity and frequency are predicted to increase in the future, the influence of drought on savanna vegetation structure becomes increasingly important to consider.

Keywords: tree loss, *Loxodonta africana*, *Senegalia nigrescens*, climate, herbivory, density dependence

1. INTRODUCTION

The influence of consumers, climate and resources on structuring vegetation communities has been debated for decades (Bond, 2005; Hairston et al., 1960; Polis, 1999; Whittaker, 1975; Wilkinson & Sherratt, 2016). Despite this long-standing interest, there are still gaps in our comprehension of the relative importance of these drivers across ecosystems, with significant consequences for understanding the distribution of biomes across the planet (Archibald & Hempson, 2016; Bond, 2005; Wilkinson & Sherratt, 2016). Assessing the relative strength of climate and consumers on vegetation communities and the interactions between these drivers can improve our understanding of and ability to predict the consequences of a changing climate and the loss or replacement of consumers (Murphy & Bowman, 2012; O'Connor et al., 2014; Staver et al., 2011).

Tropical grassy savannas provide an excellent opportunity for studying interactions between climate and consumers because they are highly dynamic systems characterized by a discontinuous woody canopy that is maintained by both top-down processes like herbivory and fire and bottom-up ones like rainfall and soils (Bond, 2008; Higgins et al., 2000; Levick et al., 2009; Scholes & Archer, 1997). Importantly, these forces can limit large trees (≥ 5 m in height), which act as keystone structures in savannas, and maintain open canopies and the balance between trees and grasses (Dean et al., 1999; Milton & Dean, 1995; Tews et al., 2004). Herbivores play an important role in structuring savannas through control of woody growth, limiting tree establishment, survival and recruitment into larger size classes (Asner & Levick, 2012; Jacobs & Biggs, 2002; Shannon et al., 2008; Staver & Bond, 2014). Megaherbivores (>1000 kg; Owen-Smith, 1987), and African elephants (*Loxodonta africana*) in particular, can have a disproportionate impact on vegetation structure through their browsing, toppling and bark stripping of large trees (Asner & Levick, 2012; Bond et al., 2017; Helm & Witkowski, 2012; Moncrieff et al., 2008). Elephants, both alone (Asner et al., 2016; Hayward & Zawadzka, 2010; Morrison et al., 2016) and in combination with fire, are often considered the primary cause of mortality for large-sized trees (Das et al., 2022; Levick et al., 2009; Midgley et al., 2010; Moncrieff et al., 2008; Shannon et al., 2011). In contrast, fire by itself is generally not a significant cause of mortality for large trees that have escaped the fire trap, which is the vertical zone 2–3 m above ground within which fires have the strongest impact on trees (Asner et al., 2016; Davies et al., 2018; Morrison et al., 2016; Staver & Bond, 2014; Wakeling et al., 2011). Here we focus on elephants because of their disproportionate impact on large trees in savannas (Asner et al., 2016; Davies et al., 2018; Hayward & Zawadzka, 2010; Morrison et

al., 2016) and because their interaction with climate is still poorly understood (Case et al., 2019; Sankaran, 2019).

Increasingly common severe climatic events, like drought, may have marked effects on woody structure and maintaining open canopies in savannas (Case et al., 2020; Roques et al., 2001; Sankaran, 2019). Drought can cause substantial mortality in adult trees due to hydraulic failure, depletion of carbohydrate reserves and increased susceptibility to herbivores and pathogens (Anderegg et al., 2012; Choat et al., 2018; McDowell et al., 2011). However, the influence of drought on vegetation appears to be a function of its severity (Case et al., 2019; Fensham et al., 2009; Viljoen, 1995). Severe and extreme drought, defined as Palmer Drought Severity Index (PDSI) (a standardized measure of dryness using temperature and precipitation) values between -3 and -4 and <-4 , respectively (Dai et al., 2019; US National Drought Mitigation Center (<http://droughtmonitor.unl.edu>)), limits potential woody growth, shifting the limiting factors in savannas from consumers toward resource control (Bond, 2005; Fensham et al., 2009; Ruppert et al., 2015; Swemmer et al., 2018). With droughts likely becoming more frequent and intense (Engelbrecht et al., 2015), they have the potential to increase adult tree mortality and reduce woody cover (Case et al., 2019; Fensham et al., 2009).

The interaction between drought and herbivores is also likely to have important consequences for tree survival, hence affecting woody structure (Case et al., 2019; Sankaran, 2019). Specifically, effects of drought and megaherbivores may interact synergistically to increase tree mortality. Elephant-related damage can increase during periods of low rainfall when grass availability is limited and woody plants may make up a larger percentage of these mixed-feeders' diets (Abraham et al., 2019; Chafota & Owen-Smith, 2009; de Beer et al., 2006). Furthermore, the combined stress of drought and elephant damage may make large

trees more vulnerable to other causes of mortality such as carbon starvation, as droughts often trigger stomatal closure to avoid desiccation and canopy damage by elephants could further limit photosynthetic carbon uptake and disrupt trees' carbon balance (Bansal, 2015; McDowell et al., 2008; Sankaran, 2019). Alternatively, severe drought can have a significant direct effect on tree mortality regardless of top-down pressures, resulting in similar mortality with or without herbivory (Case et al., 2019). This bottom-up control may be amplified if density-dependent processes limit woody growth under drought conditions. For example, while density-dependent mortality has received relatively little attention, some evidence suggests competition among savanna trees can increase with reduced soil moisture, resulting in higher tree mortality in high density patches (Dwyer et al., 2010; Fensham & Fairfax, 2007; Macgregor & O'Connor, 2002).

Our goal was to investigate how drought and herbivory by megaherbivores (i.e. elephants) interact to influence large tree abundance in a southern African savanna system. We compared differences in the number of large trees before and after a severe drought in areas with high densities of elephants and areas with no elephants. We predicted that there would be a synergistic effect of elephants and drought on tree loss and damage due to elephants consuming more woody forage during drought and the increased vulnerability of drought-stressed trees to elephant damage (Chafota & Owen-Smith, 2009; Choat et al., 2018; de Beer et al., 2006).

2. METHODS

To understand the combined effects of drought and elephants, we sampled trees in two savanna landscapes, one with and the other without elephants, before, during and after a severe drought. Our study took place over 7 years (2013–2020), where the first two years captured pre-drought conditions characterized by normal rainfall, one year captured a severe drought (2015–2016),

and the four years post-drought were characterized by average or slightly below average rainfall at both sites. We sampled the elephant site in 2013, 2016, 2018 and 2020, while the elephant-free site was sampled in 2014, 2016 and 2020. We enumerated changes in the number of large trees (≥ 5 m tall) on plots from pre- to post-drought and compared those changes between the savannas with and without elephants to test for interactive effects of drought and herbivory.

2.1 Study sites

We collected data on two sites, one with elephants (Kruger National Park [KNP] in South Africa) and one 100 km to the south without elephants (Hlane Royal National Park, Eswatini), which are hereafter referred to as our elephant and elephant-free sites. In KNP (19,000 km²), our survey site was located in the Nhlowa Southern Basalt Supersite (25°14'32.74"S, 31°56'40.42"E), approximately 177 m above sea level, which is characterized by a sparse woody vegetation layer (around 6% shrub cover and 5% canopy cover) dominated by *Sclerocarya birrea*, *Senegalia nigrescens* (previously *Acacia nigrescens*) and *Dichrostachys cinerea* and a dense grass layer (approximately 2668 kg/ha) dominated by *Themeda triandra* (Loggins et al., 2019). This area had nutrient-rich basaltic soils, average temperatures ranging from 16°C in July to 27°C in January, an average annual rainfall around 600 mm that falls primarily during the wet season between November and March and a mean fire return interval of 4–5 years (McCleery et al., 2018). Our elephant-free site in Hlane (26°14'11.47"S, 31°54'12.36"E) (220 km²) was located in northeastern Eswatini at about 240 m above sea level. The site consisted primarily of *Senegalia nigrescens* and *Sclerocarya birrea* savanna averaging around 49% canopy cover on nutrient-rich basaltic soils with a relatively sparse grass layer averaging about 1621 kg/ha dominated by *Themeda triandra* and *Panicum maximum* and an increasing shrub layer

(approximately 36% shrub cover) dominated by *Dichrostachys cinerea* (Loggins et al., 2019; McCleery et al., 2018). The area experiences a warm wet season between October and March with a mean rainfall of 575 mm followed by a cool dry season with an average rainfall of 130 mm and average temperatures ranging from 18°C in July to 26°C in January (Monadjem, 2005; Monadjem & Bamford, 2009). From late 2015 to late 2016, a severe drought occurred across both sites (Case et al., 2019; Mlenga & Jordaan, 2019). In Kruger National Park, the average rainfall across the park was approximately 50% of the mean annual rainfall, and this drought was particularly severe in the southeastern section of the park where our site is located (Case et al., 2019). Rainfall returned to average or close to average totals between late 2016 and 2020 (Case et al., 2019). Eswatini also experienced a severe drought in 2015–2016 across the country (Mlenga & Jordaan, 2019). Similarly, the Palmer Drought Severity Index (PDSI) indicated that 2015–2016 was substantially drier across both sites compared to the preceding and following years (Figure 1, Abatzoglou et al., 2018; Dai et al., 2019).

These sites have slightly different fire regimes, with mean fire return intervals of 4-5 years in Kruger National Park and 5-7 years in Hlane Royal National Park (Smit et al. 2013, McCleery et al. 2018). Using MODIS burned-area data, we identified eight study plots at our site in Kruger that burned in June 2014 and nine plots that burned in June 2020, but there were no fires in Hlane over the course of this study (Giglio et al. 2021).

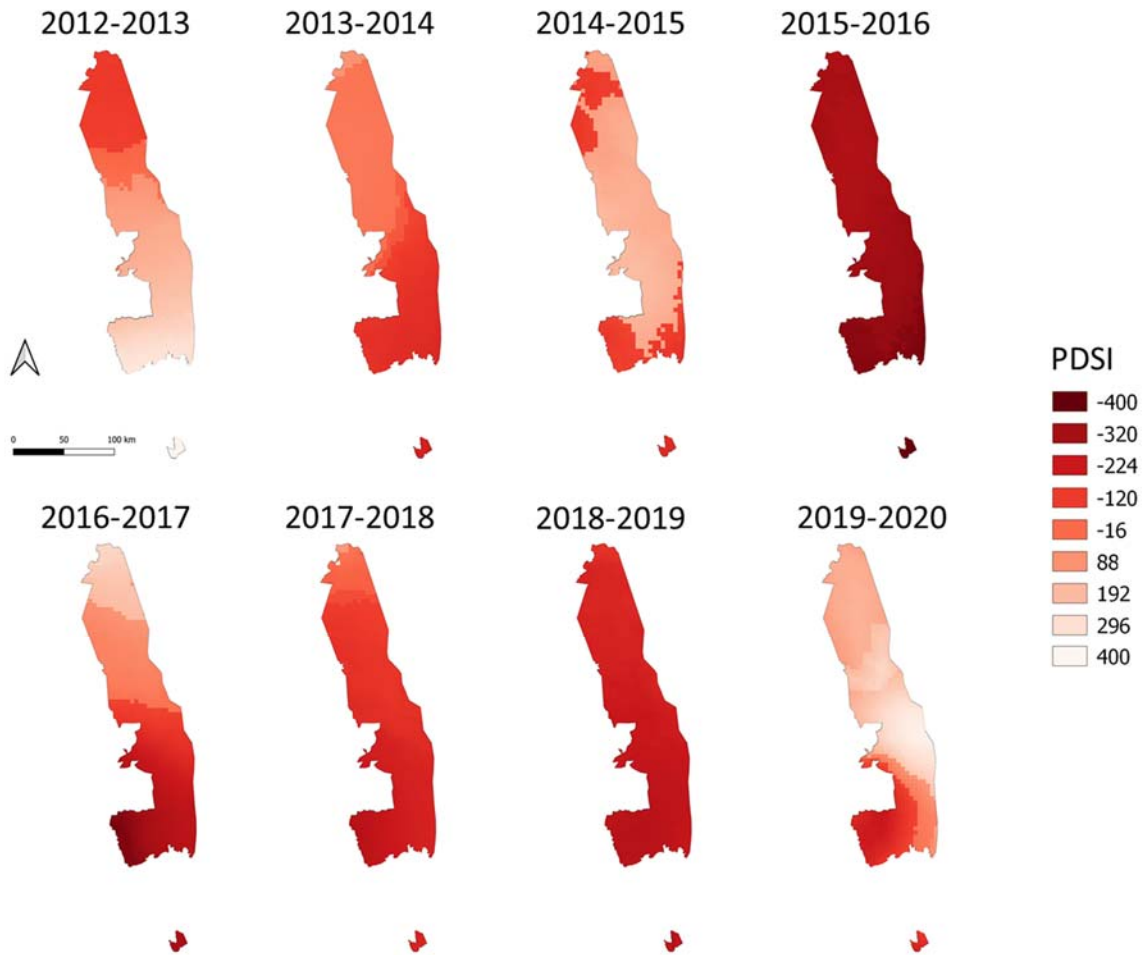


Figure 1. Average annual Palmer Drought Severity Index (PDSI) derived from the TerraClimate dataset using Google Earth Engine (Abatzoglou et al. 2018). Annual averages were calculated for the wet season (November to March) and mapped across both Kruger National Park, South Africa (elephant site, above) and Hlane Royal National Park, Eswatini (elephant-free site, below).

While both sites experience similar edaphic and climatic conditions, their megaherbivore communities differ. Importantly, there are high densities of elephants in KNP (estimated total population of > 17,000 as of 2015), whereas elephants have been absent from our plots in Hlane since the early 1900s (Blanc 2008, Ferreira et al. 2017). The composition of other herbivores is comparable across both sites and includes southern giraffes (*Giraffa camelopardalis*), as well as

smaller herbivores such as impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), and plains zebra (*Equus quagga burchellii*) (McCleery et al. 2018). *Senegalia nigrescens*, which is a long-lived species considered to be relatively drought tolerant, was the dominant tree species across both sites. However, at the elephant-free site, other large trees, including *Pterocarpus rotundifolius*, *Ziziphus mucronata*, and *Bolusanthus speciosus*, were more common compared to the elephant site.

2.2 Study design and data collection

We conducted this study on 50×50 m plots in both sites established as part of a long-term biodiversity monitoring effort in 2013 (McCleery et al. 2018). At the elephant site, these plots were arranged in four 30.25 ha grids separated by at least 1 km, with each grid consisting of nine plots each separated by 250 m. In late 2018, herbivore exclosure fences were erected on nine plots (three plots per grids), while the remaining plots ($n = ??$) were left unmanipulated; as a result we do not include information from any of these nine exclosure plots. At the elephant-free site, we sampled nine unmanipulated plots separated by 250 m. We collected data on 37 plots at the elephant site before the drought (2013 dry season), during the drought (2016 dry season), and after the drought in the 2018 dry season. We also collected post-drought data in the 2020 dry season, but due to the erection of exclosures at this site in 2018, we used data from only 11 control plots. At the elephant-free site, we collected pre-drought data in the 2014 dry season, during the drought (2016 dry season), and post-drought data in December 2020. On each plot, we counted all large, overstory trees > 5 m tall. We identified trees to species at both sites in all years except at the elephant-free site in 2020, when only the total number of large trees and number of the dominant species, *S. nigrescens*, were reported.

2.3 Analysis

We first determined if fire was associated with changes in the number of large trees. Based on our finding, we either pooled our data or included a variable for burned and unburned plots in subsequent analyses. Specifically, we tested for differences in the change in large tree density related to plots with and without fires in 2014 and 2020 compared to changes related to the 2016 drought. To accomplish this, we needed to quantify the change in the number of large trees over time (N_t/N_{t-1}), which here represents the net effect of large tree mortality and recruitment of smaller trees into this size class. To address this issue, we used a dynamic model, where the number of trees in the current year t was predicted by the number of trees in the previously sampled year. We fitted a Poisson mixed-effects model with the number of large trees on each plot at the elephant site in 2016, 2018 and 2020 as the response variable with fire and drought as binary fixed effects with an interactive effect between these variables. While the drought affected all plots at this site, only a subset of these plots burned in the 2014 and 2020 fires (8 and 9 plots, respectively), allowing us to test the effect of fire. The log of the number of trees in the previously sampled year was also included as a fixed effect. We included plot identity as a random effect and the log of the number of years between sampling occasions (two, three, or four years) as an offset term to account for differences in the lengths of sampling periods. Finding no significant effect of fire on large trees (estimate = -0.500 , $SE = 0.292$, $p = 0.088$), we pooled burned and unburned plots in all subsequent analyses.

To examine the effects of drought and elephants on large trees, we fitted a Poisson mixed-effects model as above with the number of large trees on each plot as the response variable and site, drought period in year t (i.e. pre = 2016, post = 2020), and the log of the number of trees in the previously sampled year as fixed effects. We included an interactive effect

between site and drought period to test for differences in drought impact between the elephant and elephant-free sites. We included plot identity as a random effect and the log of the number of years between sampling occasions as an offset. In addition to running these analyses for all large trees, we subsetted the data to include only *Senegalia nigrescens*, which was the dominant tree species at both sites. We fitted a similar Poisson mixed-effects model (described above) to test for differences in the number of *S. nigrescens* at the elephant and elephant-free sites before and after the drought.

To explore the potential for density-dependent factors to influence the change in the number of trees after the drought, we used the discrete-time Gompertz model ($N_{t+1} = \lambda N_t^{-b} N_t$), which becomes linear on the logarithmic scale:

$$x_{t+1} = r + (1 - b)x_t$$

where $x_t = \ln(N_t)$, $r = \ln(\lambda)$ or the intrinsic growth rate, and b is the strength of density dependence (Dennis et al. 2006, Lebreton and Gimenez 2013, Koons et al. 2015). In this model, $1 - b$ can be estimated as the slope of the linear regression of x_{t+1} on x_t (Lebreton and Gimenez 2013). However, this approach produces a biased estimate of b , such that density dependence tends to be overestimated (Lebreton and Gimenez 2013). Lebreton and Gimenez (2013) estimated this bias of b to be approximately 0.16 (95% CI: -0.20 – 0.35); therefore, values of b between 0 and 0.16 provide no, or weak, evidence of density dependence, while values greater than 0.16 provide strong evidence. Accordingly, to evaluate the potential for density-dependent effects during the drought, we fitted a linear model with the log of the number of trees on each plot post-drought (2020) as the response variable and the log of the number of trees in the previously sampled year and site as fixed effects. We conducted all of our analyses using the lmerTest package in R version 3.5.1 (Kuznetsova 2017, R Core Team 2018).

TABLE 1 Summary of all large trees (≥ 5 m) recorded on the sampled plots in the elephant and elephant-free sites before, during, and after a severe drought.

Species	Pre-drought (2013/2014)		Drought (2016)		Post-drought (2018)		Post-drought (2020)	
	Elephant	Elephant-free	Elephant	Elephant-free	Elephant	Elephant-free	Elephant	Elephant-free
<i>Senegalia nigrescens</i>	169	46	81	39	26	NA	7	40
<i>Vachellia gerrardii</i>	3	0	0	0	0	NA	0	NA
<i>Vachellia nilotica</i>	0	7	0	2	1	NA	0	NA
<i>Vachellia tortilis</i>	0	5	0	14	0	NA	0	NA
<i>Albizia forbesii</i>	1	0	0	0	0	NA	0	NA
<i>Bolusanthus speciosus</i>	0	31	1	31	0	NA	0	NA
<i>Ormocarpum trichocarpum</i>	0	0	0	5	0	NA	0	NA
<i>Philenoptera violacea</i>	4	0	5	0	1	NA	0	NA
<i>Pterocarpus rotundifolius</i>	0	25	0	10	0	NA	0	NA
<i>Lannea schweinfurthii</i>	2	0	1	0	2	NA	0	NA
<i>Ozoroa sphaerocarpa</i>	0	0	0	1	0	NA	0	NA
<i>Sclerocarya birrea</i>	13	2	7	4	1	NA	0	NA
<i>Combretum hereroense</i>	11	0	0	0	2	NA	0	NA
<i>Combretum imberbe</i>	4	8	6	2	0	NA	0	NA
<i>Spirostachys africana</i>	0	0	0	2	0	NA	0	NA
<i>Grewia hexamita</i>	0	8	0	6	0	NA	0	NA
<i>Berchemia zeyheri</i>	0	1	0	0	0	NA	0	NA
<i>Ziziphus mucronata</i>	0	18	0	10	0	NA	0	NA
<i>Balanites maughamii</i>	0	0	0	6	0	NA	0	NA
All species	207	157 ^a	101	132	33	NA	7	63

Note: The elephant-free site was not sampled in 2016, and only *S. nigrescens* were identified to species at this site in 2020.

^a6 individuals in the elephant-free site in 2014 were not identified to species.

3. RESULTS

3.1 All large trees

At the elephant site, before the drought in 2013, we observed an average of 5.59 large trees per plot (range: 0–35, $SD = 8.61$), 2.73 trees per plot (0–15, $SD = 3.87$) during the drought in 2016, 1.00 tree per plot (0–9, $SD = 1.73$) after the drought in 2018 and 0.64 trees per plot (0–3, $SD = 1.12$) in 2020 (Table 1). At the elephant-free site, there was an average of 17.44 trees per plot (6–39, $SD = 10.65$) pre-drought in 2014, 14.67 trees per plot (7–24, $SD = 5.05$) during the drought and 7.00 trees per plot (3–15, $SD = 3.97$) post-drought in 2020 (Table 1). In terms of species composition, before the drought, both sites were dominated by *S. nigrescens*, but the elephant-free site had a higher species richness than the elephant site (Table 1).

When assessing the impacts of fire and drought at the elephant site, we found no effect of fire on the number of large trees (estimate = -0.500 , $SE = 0.292$, $p = 0.088$). However, there was a significant negative effect of drought on the number of large trees (estimate = -1.027 , $SE = 0.289$, $p < 0.001$) and a positive relationship between the number of trees on a plot and the number of trees in the previous sampling year (estimate = 0.531 , $SE = 0.101$, $p < 0.001$).

Across both sites, the number of large trees (standardized by number of years between sampling periods) was four to seven times lower post-drought than pre-drought (Table 2, Figure 2a). Additionally, across all time periods, there were six to eleven times as many large trees at the elephant-free site compared to the site with elephants (Table 2, Figure 2a). There was no significant interaction between site and time period (Table 2), suggesting that elephants and drought did not have an interactive effect on large trees. Finally, there was a significant positive relationship between the number of trees in year t and the number of trees in the previously sampled year (Table 2), which suggests that the number of trees on a plot was predictive of the

number of trees in following years, as expected if there was temporal autocorrelation. Finally, we estimated the strength of density dependence, b , across both sites using the Gompertz growth model to be 0.603 ($1-b = 0.397$, $SE = 0.190$), providing substantial evidence for negative density-dependent processes (Figure 3).

TABLE 2 Fitted generalized linear mixed-effects models with a Poisson distribution for the effects of drought and elephants on the number of all large trees and the number of the dominant species, *Senegalia nigrescens*, on the study plots.

Response	Predictor	Estimate	SE	z value	p
All trees	Intercept	-0.839	0.177	-4.728	<0.001
	Drought	-1.582	0.410	-3.856	<0.001
	Site	1.307	0.211	6.182	<0.001
	Drought * site	0.207	0.436	0.476	0.634
	Number of trees at $t-1^a$	0.538	0.083	6.516	<0.001
<i>S. nigrescens</i>	Intercept	-0.822	0.180	-4.568	<0.001
	Drought	-1.538	0.417	-3.685	<0.001
	Site	0.943	0.290	3.251	0.001
	Drought * site	0.888	0.475	1.871	0.061
	Number of trees at $t-1^a$	0.383	0.088	4.365	<0.001

Note: Models included plot as a random effect and the log of the number of years between sampling occasions as an offset term.

^aThe number of trees at $t-1$ was included as a log transformed variable.

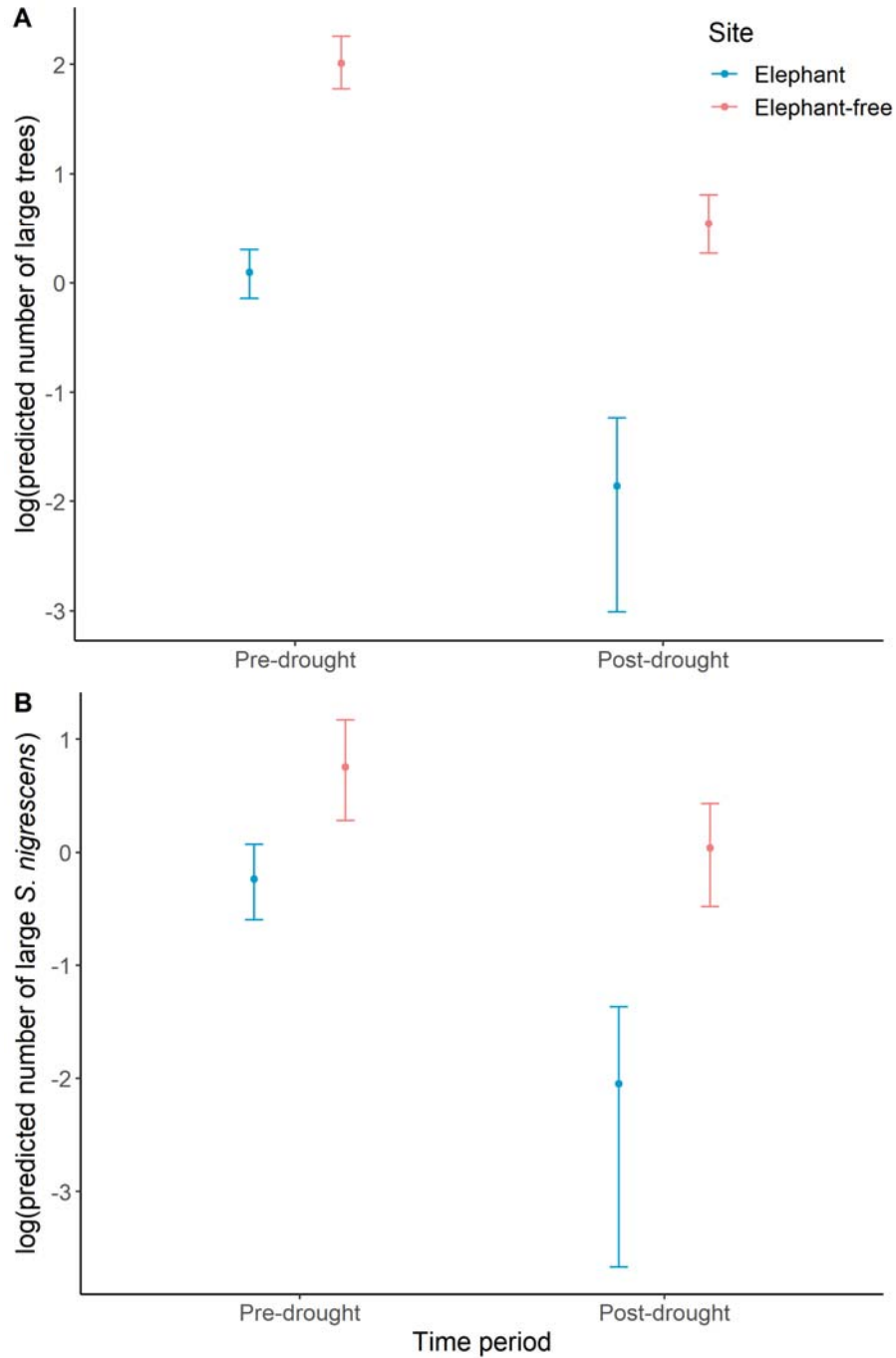


Figure 2. Log of the predicted number of trees over 5 m tall (standardized by number of years between sampling occasions) pre-drought (2016) and post-drought (2020) in the elephant site in Kruger National Park and the elephant-free site in Hlane Royal National Park for (A) all species and (B) *Senegalia nigrescens* only. Bars represent 95% confidence intervals.

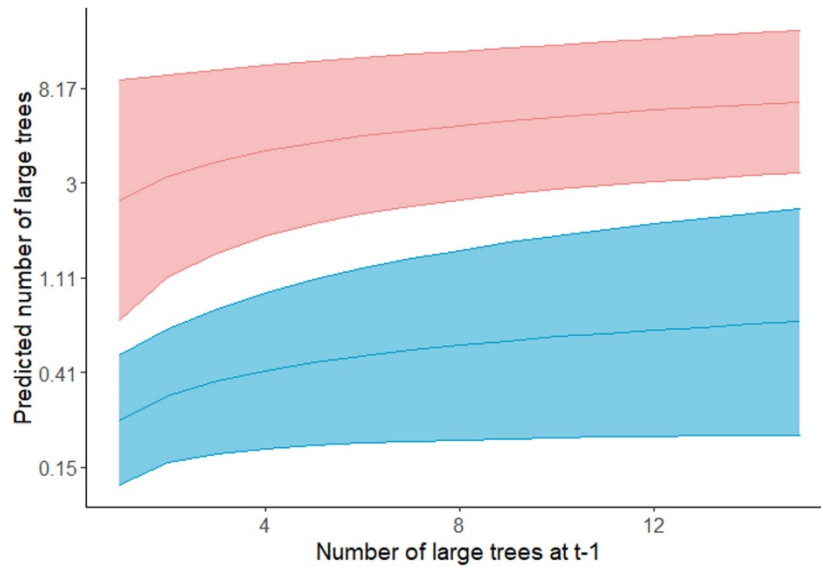


Figure 3. Predicted effect of the number of large trees per 50×50 m plot in 2016 on the log of the number of trees post-drought in 2020 (standardized by number of years between sampling occasions) (tick marks are spaced on the logarithmic scale but labelled with untransformed numbers) in the elephant site in Kruger National Park (blue) and the elephant-free site in Hlane Royal National Park (coral). Shaded bands represent 95% confidence intervals.

3.2 Dominant tree species

At the elephant site, *S. nigrescens* constituted 82% of the large trees before the drought, and this proportion remained similar both during the drought in 2016 (79%) and after the drought in 2018 (79%) but increased to 100% in 2020, when there were just seven large trees. At the elephant-free site, approximately 30% of the large trees before and during the drought were *S. nigrescens*, but this increased to 63% after the drought in 2020. Drought had a significant negative effect on the number of *S. nigrescens* at both sites (Table 2, Figure 2b). Additionally, the number of *S. nigrescens* was significantly greater at the elephant-free site than the site with elephants (Table 2, Figure 2b). There was not a significant interaction between drought period and site; however, results were suggestive of an effect such that at the elephant site, the number of *S. nigrescens* was about six times greater pre-drought than post-drought, whereas there were only

approximately twice as many *S. nigrescens* pre-drought than post-drought at the elephant-free site (Table 2, Figure 2b). This suggests that there were potentially synergistic negative effects of drought and elephants on the abundance of *S. nigrescens*; however, other species may have dampened this interactive effect, which was not observed for all large trees. Finally, there was a significant effect of the number of trees per plot in the previously sampled year on the number of trees at year t (Table 2).

4. DISCUSSION

Our results suggest, as expected, that both drought and elephants limit the number of large trees in savannas (Figure 2a), yet they did not act synergistically to reduce the total number of trees across all species (Figure 2a), providing no evidence of overall increased consumer control over vegetation during the drought (Abraham et al., 2019; Codron et al., 2006; McDowell et al., 2011; Sankaran, 2019). However, elephants and drought did have a synergistic negative effect on the number of *S. nigrescens*, the dominant tree species in this landscape, suggesting that other trees may have dampened this interactive effect and that interspecific differences in responses to drought and elephants are important to understanding community-level responses.

The strong negative effect of drought on all large trees suggests that drought may exert significant limitation on tree abundance in savannas, in addition to strong top-down control by consumers (Bond, 2005; Kruger et al., 2017; Lehmann et al., 2011). The observed drought effect and evidence of negative density dependence found here suggests that drought and competition for resources may help shape communities of mature savanna trees in ways that are comparable to the effect of elephants alone (Roques et al., 2001). As drought frequency and intensity are

predicted to increase across African savannas (Engelbrecht et al., 2015), they are likely to have a growing influence on the structure of vegetation communities (Bond, 2005; Sankaran, 2019).

Our findings concur with studies by Case et al. (2019), Swemmer (2020), and Trotter et al. (2022) on the same drought in Kruger National Park that observed increases in tree mortality, particularly for large trees, during the drought and limited recovery of these trees up to two years post-drought. However, results from Trotter et al. (2022) suggest there may be increased recruitment of juvenile trees post-drought, potentially aiding in the recovery of drought-adapted trees. Furthermore, in line with the lack of an interaction between drought and elephants as a disturbance agent in our study, Case et al. (2019) found that the effect of drought on tree mortality and growth tended to override the effects of herbivory and fire, and while Trotter et al. (2022) found an effect of fire on tree abundance and composition, this effect was additive rather than interactive. These studies also observed species-specific responses to drought, as species including woody encroachers like *Dichrostachys cinerea* suffered high rates of mortality during the drought, while others appeared to be more resilient (Case et al., 2019, 2020; Swemmer, 2020; Trotter et al., 2022). However, in contrast with our findings, *S. nigrescens* tended to be among the species experiencing the highest drought-related mortality rates (Swemmer, 2020, Trotter et al., 2022). Similarly, Swemmer (2020) found that tree mortality was not as high as observed in our study across all drought-affected landscapes, and suggested drought impacts were heterogeneous and linked to drought severity and tree composition. Taken together, the results from this and similar studies over a gradient of rainfall, soil and disturbance pressure across the park suggest that the effects of severe drought on savanna trees are often profound but can also vary substantially based on drought severity, abiotic factors and species composition (Case et al., 2019; Swemmer, 2020; Trotter et al., 2022).

While droughts have previously been reported as causing large tree mortality, the strength of this effect appears variable (Case et al., 2019; Fensham et al., 2009; Sankaran, 2019; Viljoen, 1995). One explanation for this variability may be the potential for density-dependent declines, particularly in the long-term absence of megaherbivores. In fact, at the same elephant-free site that we studied, Roques et al. (2001) found evidence for increasing negative density dependence among shrubs during droughts. Our data suggest that density dependence also had an influence on large trees in these savannas after the drought and is likely a limiting factor for savanna trees. Although our approach may have led to biased estimates of density dependence, the strength of density dependence estimated from our data exceeds any expected bias (Lebreton & Gimenez, 2013; Maelzer, 1970). The combined influence of negative density-dependent mechanisms and climatic events that limit resources on savanna trees deserves further investigation, particularly as droughts have the potential to exacerbate density-dependent factors like competition for soil moisture, and tree mortality during droughts is often greater in high density patches (Dwyer et al., 2010; Fensham & Fairfax, 2007; Macgregor & O'Connor, 2002; Sankaran, 2019). Here, we observed the impact of drought after four years, suggesting that smaller trees did not recruit into larger size classes quickly enough to replace the large trees lost to drought. The loss of large savanna trees to elephants and drought and their slow replacement may help create open canopies but may also deprive savannas of the resources provided by these keystone structures (Engelbrecht et al., 2015; Sankaran, 2019; Tews et al., 2004).

In contrast with the patterns observed for all large trees, there was a trend for a greater loss of the dominant species, *S. nigrescens*, post-drought when elephants were present, suggesting a synergistic effect of drought and elephants on this species (Figure 2b). *Senegalia nigrescens* made up a greater proportion of all large trees pre-drought at the elephant site (82%)

compared to the elephant-free site (30%); however, the proportion of *S. nigrescens* increased substantially post-drought at the elephant-free site (63%). *Senegalia nigrescens* and other species (including *P. rotundifolius*, *Z. mucronata* and *B. speciosus*) found on the elephant-free site may vary in their vulnerability to droughts due to differences in functional traits related to their ability to tolerate or avoid droughts (Fensham et al., 2017; Fensham & Fairfax, 2007; Rice et al., 2004; Sankaran, 2019). Given the increased proportion of *S. nigrescens* after the drought at the elephant-free site, it appears to be relatively more drought-resistant than other species. For example, *Z. mucronata* has comparatively shallow roots that may make it more sensitive to drought (Zhou et al., 2020). However, in the elephant site, drought-stress may have reduced large *S. nigrescens*' carbon uptake, making it more difficult to resprout and recover after elephant damage, or these combined stressors may have led to tree death through carbon starvation (Bansal, 2015; McDowell et al., 2011; Sankaran, 2019). Alternatively, elephant browsing and toppling of *S. nigrescens*, which are often utilized by elephants, may have increased during the drought when grass availability was limited (Abraham et al., 2019; Shannon et al., 2008). Improved characterization of species-specific drought resistance for savanna trees will be important for understanding and predicting changes across savannas with varying communities (Case et al., 2020; Sankaran, 2019).

While we found strong effects of elephants and drought on savanna trees, there are some caveats that limit the conclusions we can make. Like most field-based studies of drought, our study was opportunistic and using two unreplicated savanna landscapes constrained our ability to generalize the influence of drought and elephant on trees. Nonetheless, data from extreme climatic events across such broad spatial scales are rare and can provide significant advancement of our understanding of these disturbances (Smith, 2011; Swemmer, 2020). Furthermore, while

we found no evidence to suggest that fire influenced large trees, this study was not designed to explicitly address the role of fire alone or in combination with other drivers (Kruger et al., 2017; Midgley et al., 2010; Sankaran, 2019; Staver et al., 2012). However, elephants appear to outweigh other potential drivers of tree mortality, including fire (Hayward & Zawadzka, 2010; Asner et al., 2016; Morrison et al., 2016; Davies et al., 2018; but see Smit et al., 2016), and evidence suggests that the direct effect of severe drought tends to overwhelm effects of fire on tree mortality (Case et al., 2019; Fensham et al., 2017). Most compellingly, fire did not have a significant effect on the number of large trees at the elephant site, which is expected because fire alone is generally not a significant cause of mortality for large trees that have escaped the fire trap (Asner et al., 2016; Davies et al., 2018; Morrison et al., 2016; Trollope, 1984). Additionally, our test of density-dependent declines in large trees could be strengthened by including the densities of shrubs and smaller trees that could influence density-dependent mortality of large trees. While we did not have the data required for these analyses, future studies should examine this issue in more detail.

As droughts are predicted to become more frequent and intense in African savannas under future climate change (Engelbrecht et al., 2015), they may play an increasingly large role in limiting tree cover (Case et al., 2019; Engelbrecht et al., 2015; Fensham et al., 2009; Viljoen, 1995). Simultaneously, the loss of megaherbivores, which is a concern across much of the continent, could accelerate a shift in the relative strength of consumer and climate control in African savannas (Bond, 2005; Chase et al., 2016; Wittemyer et al., 2014). Alternatively, in savannas where megaherbivore populations are increasing, including protected areas like Kruger National Park, the combination of high densities of megaherbivores and increasingly frequent droughts could result in a long-term loss of large trees (Asner & Levick, 2012; Eckhardt et

al., 2000; Shannon et al., 2008). Consideration of these bottom-up and top-down forces and their interactions is essential to gain a clear understanding of how vegetation patterns are determined in these complex and dynamic systems and predict future changes in savanna vegetation structure and composition.

ACKNOWLEDGMENTS

This project was funded by NSF IRES Grants (No. 1459882 and 1952393), NSF Graduate Research Fellowship Program Grant No. 1744592, and U.S. National Institute of Food and Agriculture, Hatch project FLA-WEC-005125.

We thank Mduduzi Ngwenya, Imanuel Lindokuhle Zwane, Phillip Mhlaba, Alison Bijl, Jack Hartfelder, Muzi Sibya, and all the members of the IRES program for their efforts in the field. We thank Corli Wigley-Coetsee for her input and comments on early drafts of this manuscript. We also thank South African National Parks, Tal Fineberg, and the staff at the Savannah Research Center and the Mbuluzi Game Reserve for their support.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at [http://doi.org/\[doi\]](http://doi.org/[doi]), reference number [reference number]. Data will be archived in Dryad upon article acceptance.

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