Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna

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Summary

1. Elephants and fire are individually well-known disturbance agents within savanna ecosystems, but their interactive role in governing tree-cover dynamics and savanna–forest biome boundaries remains unresolved. Of central importance are the mechanisms by which elephants vs. fire affect tree biomass and cover, and how – over long time periods – both factors interact with rainfall and soils to govern tree biomass and carbon dynamics.

2. Here, we evaluated the response of woody vegetation to 56 years of fire manipulation in South Africa's Kruger National Park, with three fire regimes (annual, triennial and unburned) replicated across a productivity gradient and subject to two periods of contrasting elephant abundances (generated by the cessation of culling in 1994).

3. Higher fire frequencies had a negative effect on woody biomass in the low-elephant period, but this effect was weak to negligible in the high-elephant period as the difference among fire treatments diminished. Moreover, elephants removed increasing amounts of woody biomass as productivity increased across study sites, but fire did not. We infer that elephant-induced tree mortality could overcome increases in woody-plant productivity, while fire-induced mortality alone could not.

4. Elephants caused woody-plant carbon to shift from a sink to a source; this effect was independent of fire treatment, with highest rates of net carbon removal in the wettest and most productive site.

5. *Synthesis.* Our results reveal a context-dependent interaction between fire and elephants as disturbance agents in savanna: the influence of fire on woody plants was sensitive to the abundance of elephants and diminished with increased plant productivity. In contrast, elephants were capable of shifting landscapes from relatively dense woodland to open savanna, even in unburned sites, and exerted strong impacts irrespective of site conditions and plant productivity.

Key-words: African savanna, carbon storage, elephants, fire, herbivory, Kruger National Park savanna ecology, tree biomass and cover

Introduction

At the scale of the African continent, tree cover and biomass are determined by the interplay of resources such as rainfall and nutrients, on the one hand, and disturbances such as fire and large-mammal herbivory on the other (Sankaran *et al.* 2005; Staver, Archibald & Levin 2011b). In regions receiving rainfall of 650–1000 mm year^{-1} or more, frequent burning is thought to shift landscapes towards open savanna and grassland, whereas fire suppression should lead to the development of closed-canopy woodland

(Bond, Woodward & Midgley 2005; Sankaran *et al.* 2005; Staver, Archibald & Levin 2011a). Similarly, large mammalian browsers and grazers can modify vegetation structure directly by consuming woody and herbaceous vegetation, respectively, and indirectly by altering fuel loads and fire regimes, which can collectively shift savanna landscapes towards either grassland or woodland (Dublin, Sinclair & McGlade 1990; Van Langevelde *et al.* 2003; Holdo 2007; Asner *et al.* 2009; Asner & Levick 2012). Elephants (*Loxodonta africana*), in particular, topple even large trees and thus can induce landscape-scale changes that favour grass over trees (Laws 1970; Asner & Levick 2012; Coverdale *et al.* 2016).

The effects of fire and herbivory may be important not only for the balance of grasses and trees in savannas, but

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also for the exchange of carbon between the landscape and the atmosphere. Woody plants can store substantial amounts of carbon, and fluctuations in woody vs. grass biomass and productivity can cause large changes in savanna carbon stocks (Holdo *et al.* 2009b; Pellegrini, Hoffmann & Franco 2014).

It has been challenging, however, to resolve both the independent *and* interactive effects of elephants and fire on African savanna landscapes (Van Langevelde *et al.* 2003; Furley *et al.* 2008; Guldemond & van Aarde 2008; Holdo, Holt & Fryxell 2009a; Midgley, Lawes & Chamaillé-Jammes 2010; Asner & Levick 2012) and carbon storage (Holdo *et al.* 2009b; Pellegrini *et al.* 2015). There are several reasons for this. First, experimental studies have not simultaneously manipulated elephants and fire (but see Pringle *et al.* (2015)), while observational studies are potentially confounded by covariation and feedbacks among plants, herbivores and fire (Dublin, Sinclair & McGlade 1990; Barnes 2001; Holdo 2007; Staver *et al.* 2009; Shannon *et al.* 2011; Daskin, Stalmans & Pringle 2016). Secondly, shifts in savanna vegetation generally occur over long time-scales of decades or more, which may not be captured in shorter term studies. Thirdly, the long-term influence of elephants and fire on savanna depends on the ability of vegetation to tolerate and/or recover from disturbance, which, in turn, hinges on resource availability (Higgins, Bond & Trollope 2000; Pringle *et al.* 2007; Staver, Archibald & Levin 2011a; Hoffmann *et al.* 2012); thus, there is a need not only to resolve elephant-fire interactions, but also elucidate their dependence on local environmental context.

We examined the interactive effects of elephants and fire in Kruger National Park (KNP), South Africa, drawing on data from a 56-year continuous experimental manipulation of fire regime at the landscape scale, which coincided with a dramatic increase in elephant abundance following a shift in management regime. Three experimental fire treatments (annual, triennial vs. unburned) began in 1954–1956 and were replicated in 7-ha plots across a large gradient in plant productivity (spanning a *c.* 50% increase in rainfall) across the KNP landscape (Biggs *et al.* 2003). This manipulative experiment was maintained over the course of a fortuitous 'natural experiment' initiated in 1994, when culling of elephant populations was suspended in KNP and elephant densities increased (Whyte, van Aarde & Pimm 2003; Hayward & Zawadzka 2010). These conditions provide a unique opportunity to examine the interactive effects of fire and elephant herbivory at realistic spatiotemporal scales across an ecologically meaningful gradient in rainfall and productivity.

We addressed three points. First, we evaluated the direction and magnitude of independent and interactive effects of elephants and fire on savanna vegetation structure. Secondly, we examined whether these effects differed among sites across a productivity gradient within KNP. Thirdly, we extrapolated from these results to quantify the impacts of elephants and fire on the long-term carbon balance of woody plant biomass, using established allometric relationships.

Materials and methods

STUDY SITE

Located in north-eastern South Africa, KNP encompasses gradients of increasing rainfall from north to south (*c.* 350–750 mm) and decreasing soil fertility from east to west reflecting the transition from basalt to granite soils (*e.g.* Asner *et al.* 2009). From 1954 to 1956, a replicated series of 7-ha experimental burn plots (EBPs) was established in each of four KNP regions distributed across these abiotic gradients (Mopani, Satara, Skukuza and Pretoriuskop), such that the data presented here come from plots with a range of environmental conditions and diverse savanna physiognomies.

Our EBP study sites span a gradient in plant productivity, caused by differences in mean annual precipitation (MAP; 496, 544, 650 and 737 mm, respectively) and soil types (fertile basalts in Mopani and Satara, infertile granites in Skukuza and Pretoriuskop) (Biggs *et al.* 2003). As a result (Fig. 1), the wettest site (Pretoriuskop) is most productive with greatest rate of woody biomass accumulation in absence of fire (see Results below) while the driest site (Mopani) is least productive with lowest biomass accumulation absent fire (Govender, Trollope & Van Wilgen 2006; Higgins *et al.* 2007). The sites at intermediate rainfall are more similar, with Satara possessing fertile soils despite lower rainfall and Skukuza less fertile soils but higher annual rainfall.

Within each region, the EBPs were replicated four times across an area of *c.* 20 km by *c.* 20 km, allowing us to evaluate three to four replicate treatments in each region, with the exact number depending on the survey period (Supporting Information). Within each EBP, we evaluated three treatments: (1) total fire exclusion; (2) triennial (i.e. every 3 years) burning, which approximates the historical KNP baseline (Govender, Trollope & Van Wilgen 2006); and (3) annual burning, which represents an increase in fire frequency relative to the baseline (Fig. S1 in Supporting Information). Both the triennial and annual burns are performed in August, at the end of the dry season, when fires occur naturally. Fuel loads and fire intensity have been measured since 1984, which allowed us to test for directional changes in either fuel load or fire intensity. We found no systematic changes in landscape fire intensity or fuel loads across the sites (Table S1), suggesting that fire behaviour has not shifted substantially between the low- and high-elephant periods.

In each region, we further compared the effect of fire on vegetation between periods of low- vs. high-elephant population density. During the first 40 years of this experiment, KNP elephant populations were systematically culled to maintain a total population of *c.* 7000 individuals (van Aarde, Whyte & Pimm 1999). In 1994, culling was suspended, leading to increased elephant densities throughout the park (Whyte, van Aarde & Pimm 2003; Hayward & Zawadzka 2010). We used a breakpoint analysis of changes in elephant population to define periods of low- vs. high-elephant abundance (see Inferring and validating elephant population regimes, below).

WOODY VEGETATION DATA

Vegetation data were available up to year 2012 for the Satara region, but only until 2004 for Mopani and Skukuza and 2000 for Pretoriuskop. We compiled historical woody-vegetation data (number of individuals, species identity and height) from four surveys of the EBPs in Satara (1956, 1971–1975, 1998, 2002–2003), and we conducted a fifth survey ourselves in 2012 (Table S2). For the other three regions (Mopani, Skukuza and Pretoriuskop), historical data were
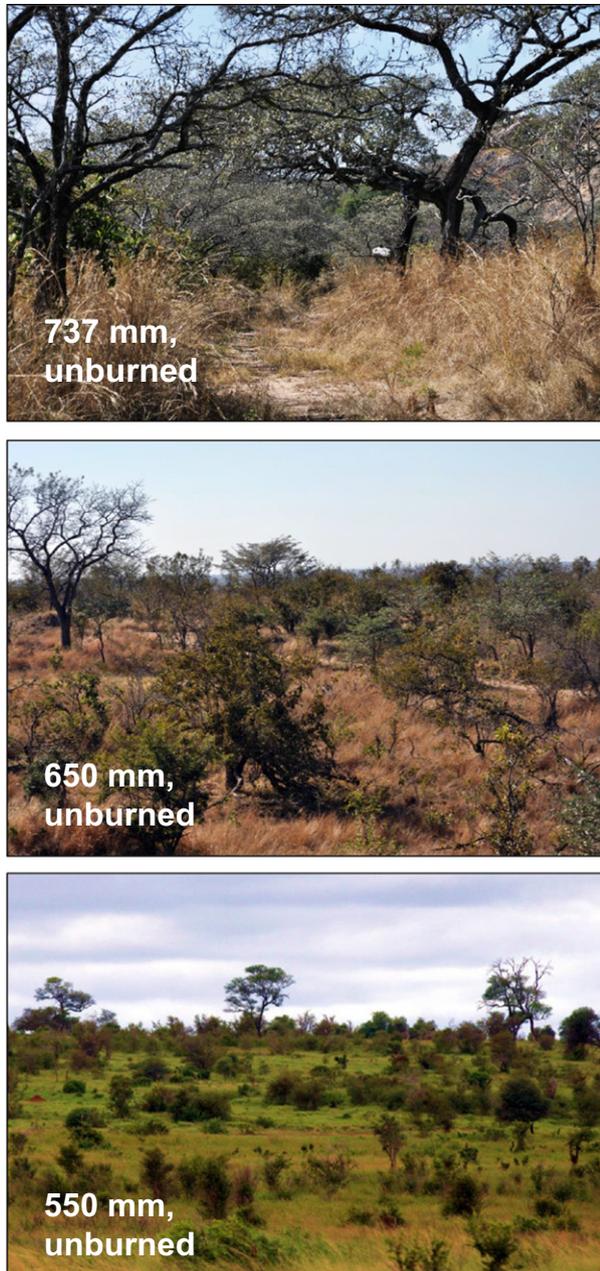
Fig. 1. Differences in vegetation structure in the unburned plots across three locations along the environmental gradient that differs markedly in precipitation. Upper photograph is from Pretoriuskop, receiving *c*. 737-mm mean annual precipitation (MAP) on granitic soils, middle photograph is from Skukuza, receiving *c*. 650-mm MAP on granitic soils, and lower photograph is from Satara, receiving *c*. 544-mm MAP on basalt soils. [Colour figure can be viewed at wileyonlinelibrary.com]

drawn from the same sources described above (1954–1956, 1970–1979, 1996–1998, 2000–2004). To our knowledge, no prior study has assimilated these historical data, which allow the evaluation of temporal dynamics across different EBP treatments.

We estimated above-ground woody biomass from height data using standard allometric calculations based on species-specific relationships derived from KNP (Nickless, Scholes & Archibald 2011); root biomass was estimated separately using published scaling relationships from a meta-analysis of tropical savannas and woodlands (Mokany,

Raison & Prokushkin 2006). We verified that our results were robust by calculating biomass using alternative equations that were based on different assumptions about these relationships, all of which yielded similar trends over time and were quantitatively similar [e.g. our allometric model used was on average 7.5% different from the multi-equation mean in the unburned plots (Figs S2 and S3)]. We then estimated carbon pools from biomass by assuming a per-mass carbon concentration of 490 mgC g^{-1} tissue dry weight (Pellegrini *et al.* 2015).

For evidence of the roles of elephants and fire in mediating transitions between the alternative ecosystem states of savanna and woodland, we examined Pretoriuskop – the only region where rainfall approached or exceeded a hypothesized threshold for woodland development in African savannas (Sankaran *et al.* 2005) and where woody cover could exceed 50% in the absence of fire. Because canopy cover inhibits grass, it is often used as an indicator of the woodland-to-savanna transition, with *c*. 50% thought to define the threshold in Africa (Staver, Archibald & Levin 2011a). We quantified canopy cover using a standard allometric approach relating stem height and crown area determined within KNP (Supporting Information).

INFERRING AND VALIDATING ELEPHANT POPULATION REGIMES

Beginning in 1966, annual aerial elephant counts were conducted throughout KNP, with the first census estimates and culling quotas produced in 1967 (Table S3). Prior studies have documented that the cessation of culling led to parkwide increases in elephant abundance (van Aarde, Whyte & Pimm 1999; Whyte, van Aarde & Pimm 2003). We fitted polynomial regressions to the trend in elephant numbers for KNP as a whole (third-order polynomial). The models yielded statistically significant fits explaining 95% of the variance for the KNP data ($F_{3,40} = 137$, $P < 0.0001$) and 68% for the Satara data ($F_{2,25} = 14$, $P < 0.0001$).

We used a breakpoint analysis [*breakpoints* function in *struchange* package in R; Zeileis *et al.* 2002) to quantitatively distinguish low- vs. high-elephant density periods (Young, Ferreira & Van Aarde 2009; Hayward & Zawadzka 2010) (see Appendix S1 for detailed explanation of survey methods). We found two breakpoints: first at 1996 (1992–1997, 2.5–97.5% CIs) reflecting rising elephant numbers following cessation of culling, and second at 2002 (2001–2003, 2.5–97.5% CIs) representing the acceleration of elephant population growth. Consequently, we defined the extended period prior to 1996–1998 as the 'low'-population regime with relatively constant numbers, and the period following 1996–1998 as the 'high'-population regime with rapidly increasing elephant numbers. We used vegetation data from between 1954–1956 and 1996–1998 as representing the 'low'-elephant period, and from 1996–1998 to 2012 (or 2000–2004 in Mopani, Pretoriuskop and Skukuza) as representing the 'high'-elephant period.

Next, we conducted a regionally explicit, but temporally more restricted (2000–2011), analysis of elephant populations, which confirmed that the increase in elephants was a parkwide phenomenon. First, a linear model including both time and region of the park (Far North, North, Central, South) illustrated that although elephant population size differed across regions ($F_{3,32} = 3.36$, $P = 0.03$) there was a strong rise in numbers independent of region ($F_{1,32} = 66$, $P < 0.0001$). Secondly, the elephant population size increased steadily through time within all regions (Far North: $r^2 = 0.71$, $P = 0.002$; North: $r^2 = 0.43$, $P = 0.038$; Central: $r^2 = 0.65$, $P = 0.005$; South: $r^2 = 0.83$, $P = 0.0002$; Figs S4 and S5). Thirdly, we found no

significant interaction between region and time ($F_{3,32} = 1.099$, $P = 0.36$), indicating that increases in population sizes followed quantitatively similar patterns across the park.

IDENTIFYING THE EFFECT OF ELEPHANTS ON WOODY VEGETATION

One way to isolate the role of elephants relative to other potential drivers of woody-biomass change is to take advantage of the known preferences of elephants for certain tree species and size classes of trees. First, elephant browsing should cause tree size distributions to become truncated, reflecting a disproportionate loss of large trees, which are vulnerable to elephants but relatively resistant to fire and other browsers (Shannon *et al.* 2008, 2011; Asner & Levick 2012). We assessed this by quantifying changes in the abundance of small (<3 m) vs. large (>3 m) trees in Satara unburned plots from 1998 to 2012.

Secondly, species preferred by elephants as forage should decrease in abundance, whereas non-preferred species should exhibit little change. The preference of elephants for certain tree species (e.g. Gandiwa *et al.* 2011; Ihwagi *et al.* 2012) is well documented. In Satara, *Acacia nigrescens* is a common tree and preferentially browsed by elephants (Whyte, van Aarde & Pimm 2003; Shannon *et al.* 2008, 2011), and we predicted that its abundance relative to non-preferred species should decrease as elephant abundances increased (from 1998 to 2012). We further analysed trends in the five most abundant woody-plant species (*Dichrostachys cinerea, Ehretia obtusum, Ormocarpum trichocarpum, Commiphora schimperi, Securinega virosa*), which are not preferentially browsed by elephants.

Thirdly, we quantified changes in disturbance characteristics of tree populations in the 1970s' and 2000s' surveys; both surveys recorded whether a tree had been snapped or fallen. We analysed the frequency of disturbed trees as well as their size distribution.

DATA ANALYSIS

We used repeated-measures ANOVAs to analyse whether there were significant temporal changes in woody biomass for each region. To further test the direction of such changes, we performed separate ANOVAs conducted in low- vs. high-elephant periods. Specifically, we tested whether the total woody biomass differed between the 1950s and 1990s and likewise between the 1990s and 2000s (or 2012, in the case of Satara). Similarly, we used ANOVAs to analyse how total biomass differed among treatments and/or landscapes.

Because relative rates of change are calculated from two time periods (e.g. 1950s–1990s), we used a slightly different approach. To test for the effect of elephant population regime, we used an ANOVA to test whether rates of change differed *between* elephant population regimes (i.e. relative rates of change in the low- vs. high-elephant periods). Comparisons among treatments and/or landscapes were performed using the same model structure that we used for total woody biomass.

To quantify elephants and fire effects on carbon dynamics across the productivity gradient, which we also analysed as rates of change, we performed an ANOVA comparing the rate of change in biomass carbon across sites in the low (1950s–1990s) and high (1990s–2000s) elephant periods. A Tukey's *post hoc* test with correction for multiple comparisons was used to compare among sites.

To test the impact of the high-elephant regime on tree communities, we used Welch's *t*-tests (to account for heterogeneous variances) to compare the densities of trees in large and small size classes in 1998 vs. 2012. To examine changes in relative tree species abundance

from 1998 to 2012, we calculated the change in density for each species from 1998 to 2012 and compared these differences using an ANOVA with a Tukey *post hoc* comparison. We analysed differences in woody canopy cover using Welch's *t*-test.

Results

### SHIFTS IN WOODY BIOMASS ACROSS SITES AND TREATMENTS

We first consider the Satara sites, which receive intermediate rainfall (544 mm MAP) and for which our long-term data set is most extensive. In fire-exclusion plots, the low-elephant regime was characterized by a steadily increasing woody biomass (Fig. 2a,b, Table 1). Woody biomass increased by 875%, from 3.7 to 36.1 Mg ha^{-1} between 1956 and 1998 ($F_{1,4} = 10.17$, $P = 0.033$; Table 1). This trajectory switched to one of biomass depletion in the high-elephant regime, however, with an 87% decrease in standing biomass between 1998 and 2012 (from 36 to 4.7 Mg ha^{-1}; $F_{1,4} = 9.72$, $P = 0.035$; Fig. 2a,b).

The decrease in standing biomass was rapid, with a rate of decline *c*. 2.6-fold greater than the rate of accumulation (-2.24 Mg ha^{-1} year^{-1} vs. 0.77 Mg ha^{-1} year^{-1} in high- vs. low-elephant regimes, respectively). The net result was a negligible change in woody biomass from start to end of the 56-year period of fire exclusion, but this net effect conceals large biomass changes that, over time, reversed in sign (Fig. 2c).

These results did not qualitatively differ when we expressed biomass on a relative (i.e. proportion of original) rather than absolute basis, which accounts for potential effects caused by initial biomass differences across plots (Supporting Information). The results also did not differ when we considered woody plant height rather than biomass, with mean height increasing significantly during the low-elephant period ($F_{1,243} = 74.6$, $P < 0.0001$) but decreasing during the high period ($F_{1,329} = 135$, $P < 0.0001$). We hereafter focus on woody plant biomass.

The response in woody biomass to elephant population differed markedly across the no-fire vs. fire treatments, consistent with an elephant-by-fire interaction. Biomass did not change significantly over time in the triennial or annual fire treatments, during either low- or high-elephant periods (Fig. 2a, Table 1) (low-elephant triennial: $F_{1,4} = 0.01$, $P > 0.5$ and annual: $F_{1,4} = 2.2$, $P = 0.21$; high-elephant triennial: $F_{1,4} = 0.95$, $P = 0.38$ and annual: $F_{1,4} = 0.77$, $P = 0.42$). This lack of trend differs qualitatively from the significant and directional changes observed in the unburned plots.

At the end of the high-elephant period, the annual fire treatment supported little woody biomass (0.72 Mg ha^{-1}) compared to the triennial (2.1 Mg ha^{-1}) or unburned (4.68 Mg ha^{-1}) treatments, indicating a strong overall fire effect across treatments ($F_{2,6} = 9.6$, $P = 0.013$) (Fig. 2a, Table 1). At the end of our study – 18 years after cessation of culling – the between-treatment differences in woody
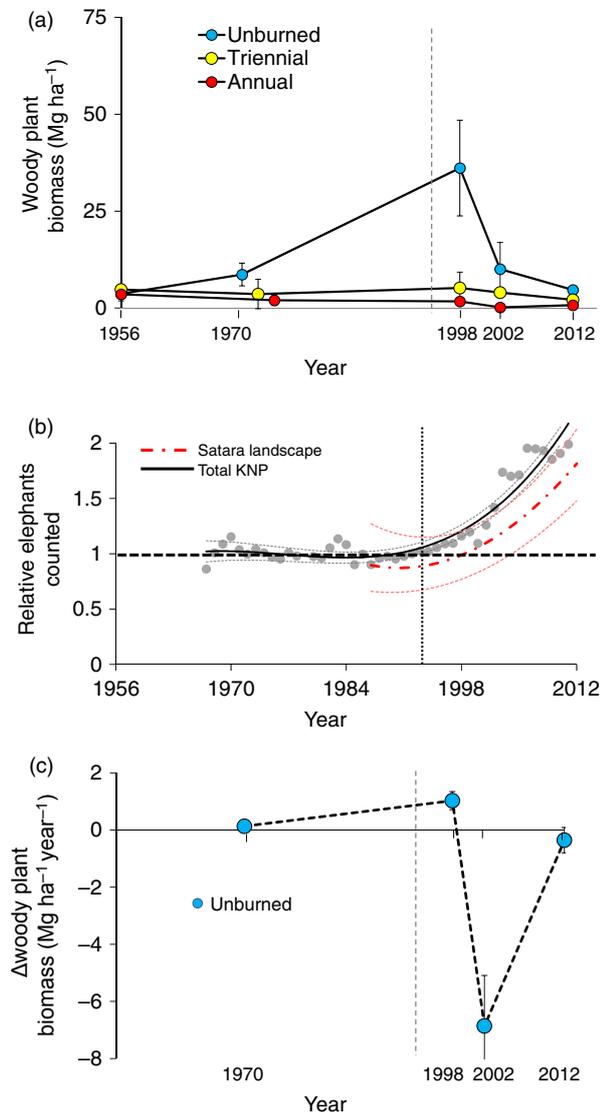
Fig. 2. Trends in relative elephant density and woody biomass. (a) Total woody-plant biomass (±SEM) across the three fire treatments in Satara. (b) Relative elephant density through time ± 95% CI. Filled circles and third-order polynomial regression for Kruger National Park (KNP) (1967–2011, $r = 0.95$); quadratic regression for Satara, no markers (1987–2012, $r = 0.68$). All values are relative to the average baseline elephant population during the culling period within each spatial scale (horizontal line at $Y = 1$). Dashed vertical line represents the cessation in culling in 1994. (c) Mean annual rate of change in woody biomass (±SEM) within the unburned plots in Satara. The points are centred on the time period of which they are integrated up to (e.g. the point at 1970 reflects the change in woody biomass from 1956 to 1970). [Colour figure can be viewed at wileyonlinelibrary.com]

biomass were somewhat muted, though there still existed a significant fire treatment effect ($F_{2,6} = 25.9$, $P = 0.001$): unburned plots went from having *c.* 31 Mg ha^{-1} more biomass than triennially burned plots in 1996 to only *c.* 2.5 Mg ha^{-1} more in 2012.

Taken together, these results show a large impact of elephants on standing woody biomass in plots protected from fire, but only a muted impact in plots that experienced frequent burning. This pattern results from differences in the

amount of woody biomass that accumulated across treatments over the low-elephant period, which was in turn subject to disturbance by elephants, with the result that woody biomass was determined by an elephant-fire interaction.

INFLUENCE OF ELEPHANTS ON WOODY VEGETATION

The co-occurrence of increasing elephant numbers with decreasing woody biomass in the unburned plots suggests a causal link, as do three additional lines of evidence. First, the density of large trees (>3 m tall) declined >90% during the high-elephant period (from 605 to 52 individuals ha^{-1}; Fig. 3a, Welch's $t_{2.12} = 5.2$, $P = 0.03$). Elephants are known to preferentially and uniquely topple large trees in KNP and elsewhere (e.g. Shannon *et al.* 2011). In contrast, the density of small trees remained stable over the same period (918–1113 individuals ha^{-1}, Welch's $t_{2.28} = -1.6$, $P = 0.23$).

Secondly, the density of the tree species most favoured by elephants, *A. nigrescens,* declined by 82% during the high-elephant period (Fig. 3b), but there were no significant changes in densities of the other five most common tree species (which collectively represent *c.* 85% of all individuals and *c.* 80% of biomass) (Fig. 3b, Table S5). The loss of *A. nigrescens* was especially marked among large trees, resulting in a truncated size-class distribution from 1998 to 2012. The contribution of *A. nigrescens* to total plot biomass declined from 78% in the 1990s to 25% in the 2000s (two-tailed *t*-test: $P = 0.03$) and accounted for *c.* 90% of the total woody biomass lost.

Thirdly, the frequency of snapped or fallen trees increased 5.5-fold over all the plots, and 10-fold in the unburned plots. The size-class distribution of these disturbed trees deviated from the size distribution of the general tree population, with disproportionately greater disturbance in large trees (Fig. S6). Taken together, each of the above patterns is consistent with the hypothesis that elephants acted as the major cause of the observed woody biomass decline from 1998 to 2012.

CONSISTENCY OF EFFECTS ACROSS SITES

Woody biomass in the other sites qualitatively followed the trends observed in Satara, but the magnitude of effects differed across sites and across the productivity gradient. Across all sites, stable or increasing woody biomass in unburned plots during the low-elephant regime was followed by a period of decreasing biomass starting in the 1990s at the start of the high-elephant regime (Fig. 4, Table S4, repeated-measures ANOVA, within-subjects effects of time: $F_{2,4} = 21.4$, $P = 0.007$ for Skukuza; $F_{2,4} = 209.7$, $P < 0.0001$ for Mopani; $F_{2,6} = 72.1$, $P < 0.0001$ for Pretoriuskop). As for Satara, these results did not qualitatively differ when analysed based on the relative rather than absolute change in biomass (Supporting Information).

The absolute change in woody biomass in both the low- and high-elephant regimes differed across sites (Fig. 5), reflecting differences in potential productivity across our sites. Under the low-elephant regime, the unburned treatment in the

Table 1. Mean plot woody biomass (Biomass, Mg ha^{-1}, ±SEM) across fire treatments in each landscape over time with corresponding underlying bedrock and mean annual precipitation (MAP) in mm. Exact replicate numbers differ across sites, years, and treatments and are presented in the Supporting Information

|		Unburned		Annual		Triennial	
		Biomass	±SEM	Biomass	±SEM	Biomass	±SEM
Pretoriuskop	1954	6.55	0.9	8.21	1.6	4.41	1.4
Granite	1970			13.79	4.5	17.39	5.4
737-mm MAP	1996	58.31	8.0	25.87	6.7	37.86	13.6
	2000	11.94	1.0	12.27	2.4	23.01	10.4
Skukuza	1954	9.51	1.0	8.12	0.3	8.12	0.5
Granite	1970	16.63	1.1	15.86	2.1	35.84	7.5
650-mm MAP	1997	26.61	4.9	11.77	2.6	22.72	2.5
	2004	19.34	2.6	4.81	3.4	10.43	0.0
Satara	1956	3.68	1.5	3.56	0.6	4.75	1.1
Basalt	1975	8.65	2.1	1.97	0.1	3.59	
544-mm MAP	1998	36.11	10.1	1.71	1.1	5.16	3.1
	2002	10.01	5.6	0.17	0.1	3.99	2.9
	2012	4.68	0.5	0.72	0.3	2.10	0.4
Mopani	1957	8.10	3.0	9.58	1.7	9.37	1.7
Basalt	1970	6.92	1.5	12.88	12.4	1.97	0.5
496-mm MAP	1999	11.54	2.6	3.54	0.7	8.00	1.1
	2004	4.14	0.5	1.30	0.1	1.56	0.2
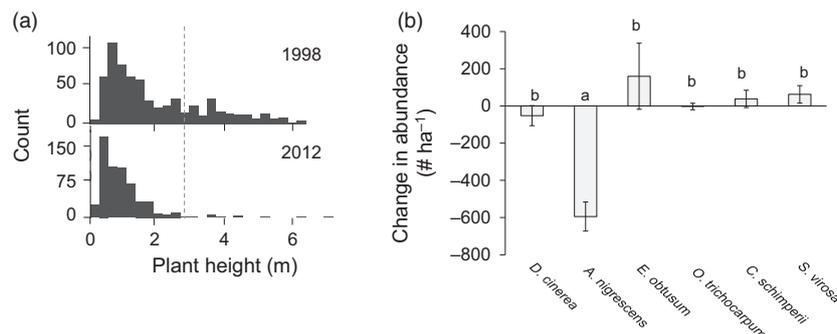
Fig. 3. Signatures of elephant activity in Satara. (a) Histogram of woody-plant height structure in unburned Satara plots in 1998, shortly after the suspension of culling, and in 2012. Dashed vertical line indicates the 3-m cut-off used to delineate large trees. (b) Change in absolute abundance from 1998 to 2012 for six of the most common woody species in unburned Satara plots (species arrayed from left to right in the order of relative abundance). *Acacia nigrescens* is preferentially consumed by elephants. Letters denote significance difference across species using Tukey's *post hoc* test (Table S3).

wettest site, Pretoriuskop, accumulated biomass at a 15-fold faster rate than the driest site, Mopani (1.23 vs. 0.08 Mg ha^{-1} year^{-1}). Under the high-elephant regime, these differences in magnitude were reversed in sign, with Pretoriuskop losing woody biomass at a *c.* 8-fold greater rate than Mopani (11.59 vs. 1.48 Mg ha^{-1} year^{-1}; Table S4).

A strong elephant-by-fire interaction was apparent in our analysis based on either absolute or relative (Supporting Information) biomass change. In all sites, unburned plots had greater woody biomass than both the fire treatments by the 1990s, but the absolute magnitude of the fire effect (i.e. the biomass difference between burned vs. unburned plots) differed across sites (Fig. 4). Moreover, only Skukuza showed a significant main effect of fire treatment ($F_{2,5} = 6.58$, $P = 0.05$), whereas elsewhere fire effects were contingent on

elephant regime (treatment × time interaction: Wilks' λ, $F_{4,8} = 4.93$, $P = 0.03$ for Mopani; $F_{4,12} = 4.41$, $P = 0.02$ for Pretoriuskop). The effect of fire treatment on woody biomass thus was dampened in the high-elephant period in three of the four experimental regions.

Across sites, the elephant effect on relative changes in woody biomass followed the same pattern as described above. Pretoriuskop, the most productive site, experienced the highest relative gains (+19% per year) during the low-elephant period, but also the most extreme losses (−20% per year) in biomass during the high-elephant period. In contrast, the least productive site of Mopani displayed substantially lower relative biomass gains (+1% per year) and also lower biomass losses (−13% per year) in the low-elephant period.
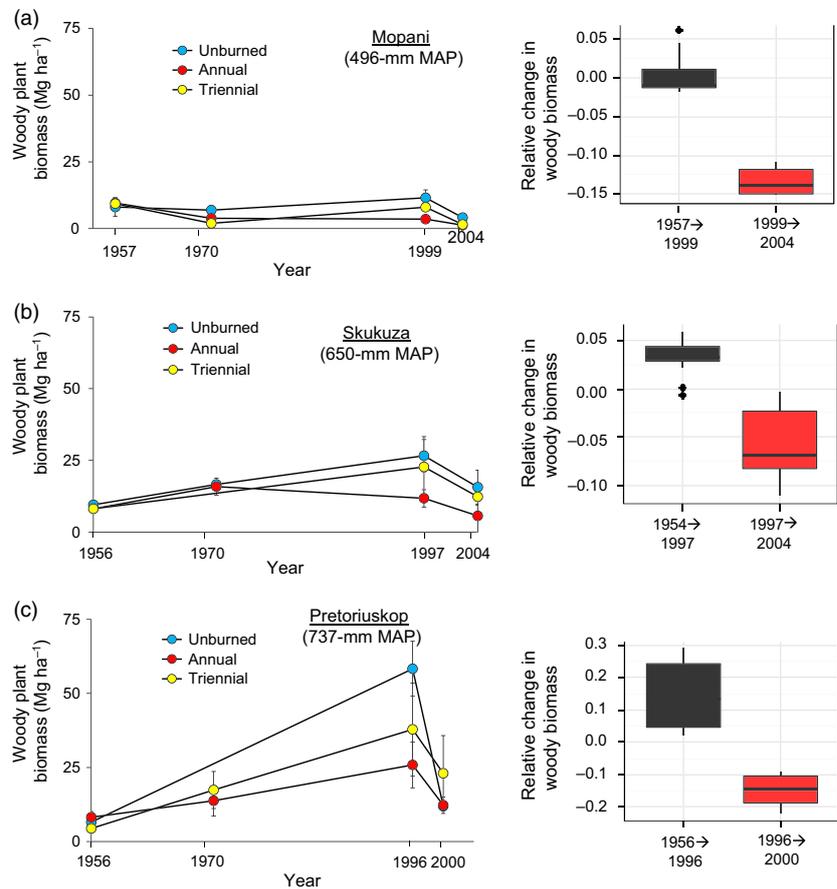
Fig. 4. Woody biomass (±SEM) through time in the experimental burn plots at (a) Mopani, (b) Skukuza and (c) Pretoriuskop. Triennially burned plots in Skukuza and unburned plots in Pretoriuskop were not sampled in the 1970s. Box-and-whisker plots adjacent to the longitudinal plots indicate the relative changes in woody biomass calculated during the low-elephant period (1954–1956 to 1996–1998) and high-elephant period (1996–1998 to 2000–2004). [Colour figure can be viewed at wileyonlinelibrary.com]

EFFECTS ON CANOPY COVER AND ON TRANSITIONS BETWEEN ECOSYSTEM STATES

Our site with the highest potential biomass production (Pretoriuskop) offers a unique opportunity to evaluate how the elephant-by-fire interaction can influence the transition between savanna and woodland, as rainfall at Pretoriuskop exceeds the 650-mm year^{-1} threshold considered necessary for woodland development (Sankaran *et al.* 2005).

In the low-elephant regime, when fire was excluded, the increase in canopy cover was especially large in Pretoriuskop, growing from 17% (±2% SEM) in 1954 to woodland with 83% cover (±14%) in 1996 (Welch's $t_{2.12}$ = 8.5, P = 0.01). Unexpectedly, however, canopy cover continued to increase in spite of being burned regularly (20–56% in triennial and 20–32% in annual). In contrast to the fire effect, canopy cover decreased across all plots during the high-elephant regime, with a decline from 83% (±14%) in 1996 to 16% (±1%) in 2000 (Welch's $t_{2.046}$ = 8.9, P = 0.01, Fig. 6; Table S6) in unburned plots, shifting the landscape from woodland back to open savanna.

IMPLICATIONS FOR CARBON STOCKS ACROSS SITES

The large changes in woody biomass have important implications for the carbon balance of the plots, but the net effects vary across sites. Plots protected from fire accumulated woody biomass C at substantial rates (40–604 kgC ha^{-1} year^{-1})
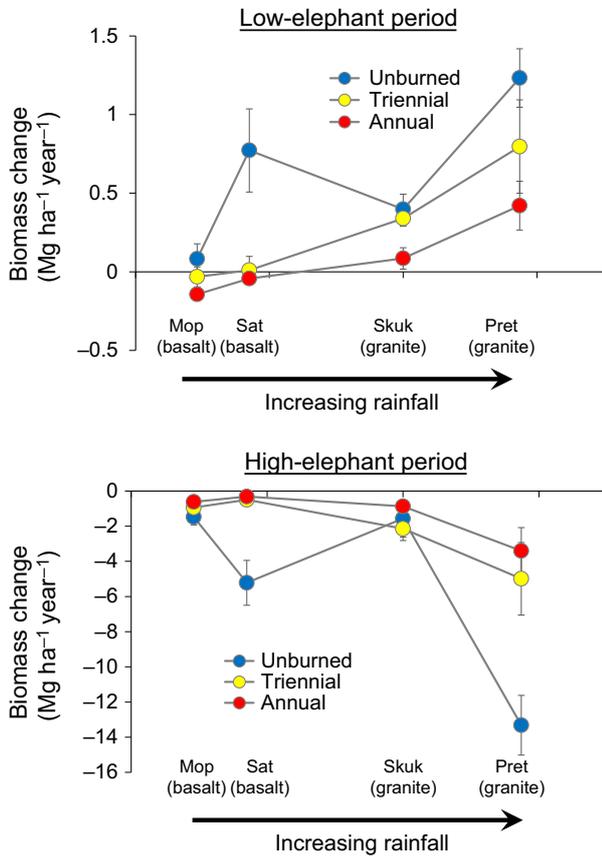
between the 1950s and 1990s, with rates generally greater in the site with the highest MAP. However, the wettest site also experienced the greatest carbon losses during the elephant population rise (−5680 kgC ha^{-1} year^{-1}; Tukey's *post hoc* comparing Pretoriuskop vs. Mopani P < 0.001, Skukuza P < 0.001, Satara P = 0.01). In contrast, plots in the wettest sites continued to accumulate woody biomass C despite being burned regularly (Table S7 and for total woody biomass see Fig. 5).

Discussion

Several previous studies have shown that both elephants and fire can independently influence savanna vegetation structure and dynamics (Higgins *et al.* 2007; Staver, Archibald & Levin 2011a; Asner & Levick 2012; Pellegrini *et al.* 2015). In this study, however, we sought to understand how these two factors interact to govern savanna vegetation structure, and, in turn, how this interaction depends on the ability of savanna vegetation to recover from disturbance.

Our results offer long-term confirmatory evidence of the independent influences of both elephants and fire on KNP vegetation. First, the dramatic park-wide increase in elephant population size coincided with large declines in woody biomass across the park. In addition, these vegetation changes were marked by several strong signatures of elephant activity. The decline in woody biomass was largely caused by removal of large trees, a size class that is preferentially browsed and damaged by elephants in particular (Shannon *et al.* 2011)

(Fig. 3a). Additionally, the tree decline was especially severe in *A. nigrescens*, a plant species that is preferentially browsed by elephants (Fig. 3b). Finally, in unburned plots, trees with evidence of disturbance (i.e. broken or fallen) increased 10-fold between the 1970s and 2000s, when elephant
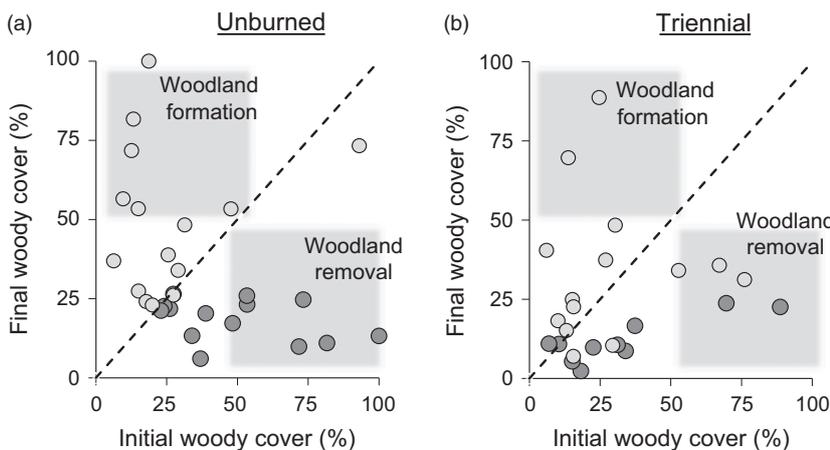
populations were increasing rapidly, and the size-class distribution of disturbed trees was skewed towards larger trees (Fig. S6). These independent lines of evidence, combined with the observed trends in the elephant population, implicate elephants as the factor that caused the large changes in vegetation and woody biomass across the park (Figs S4 and S5).

Secondly, frequent burning acted to reduce woody plant biomass growth across the study sites. The degree to which this occurred varied across sites and showed a strong interaction with the elephant effect as discussed below.

Our analysis of the interactive effects of elephants and fire on woody vegetation offers a nuanced picture that cannot be understood by analysing each factor independently (Figs 2 and 4). In the low-elephant period, woody biomass generally diverged across fire treatments, such that biomass was inversely related to fire frequency. During the high-elephant period, however, the effects of fire were muted, such that plots experiencing fire vs. protected from fire converged on similar levels of woody biomass. Moreover, the rates of relative change in woody biomass were no longer significantly different among fire treatments–indicating that elephants dampened or even negated the effects of fire on woody-biomass trajectories. However, a significant fire effect on standing woody biomass remained in some landscapes (Figs 2 and 4) even during the high-elephant period, indicating that elephants did not completely remove the effect of fire history on vegetation structure. We conclude that the effect of fire on savanna woody vegetation hinges critically upon the elephant population size, with diminishing absolute and relative influence of fire under high-elephant density.

Inclusion of site conditions in our analysis illustrated an additional interaction: the elephant-fire interaction itself depended on differences in site conditions, with evidence suggesting that differences in productivity driven by rainfall was a particularly important driver. The effect of fire alone differed across sites (Fig. 4), with woody-biomass accumulation being more sensitive to fire in dry sites (in spite of their high soil fertility) but accumulating in the wettest site even at annual or triennial burn intervals. We suggest that the higher productivity in the wettest site allowed the rate of woody biomass accumulation to reduce the consumptive effect of fire, but not of

Fig. 5. Rates of change in woody biomass (Mg ha^{-1} year^{-1}) during low-elephant periods (1950s–1990s) and high-elephant periods (1990s–2000s) displayed across sites ranked in the order of low to high precipitation (distance apart along the *x*-axis reflects differences in precipitation) with corresponding soil types of the landscapes (values averaged among strings, ±SEM). Landscape abbreviations are as follows: Mop, Mopani; Sat, Satara; Skuk, Skukuza; Pret, Pretoriuskop. [Colour figure can be viewed at wileyonlinelibrary.com]

Fig. 6. Changes in woody cover in the (a) unburned and (b) triennial fire treatments during the culling (1950s–1990s, white dots) and post-culling (1990s–2000s, black dots) periods across all regions. Dashed 1:1 line is shown for reference; points above the line represent net gain in tree cover during the relevant interval, whereas points below represent net loss. Shaded boxes indicate the regions corresponding to net formation of woodland and net loss of woodland.

elephants. Differences in fire intensity alone are unable to explain this trend, given that wetter sites actually have more intense burns (Govender, Trollope & Van Wilgen 2006) due to the greater accumulation of grass biomass and a sufficiently long dry season for this fuel to become combustible.

In contrast to fire, the negative effect of elephants differed little across our sites: regardless of plant productivity, high-elephant populations decreased woody biomass (Figs 4 and S7). This elephant effect was strong enough to cause the decline of woody biomass across all fire treatments at our wettest site (Pretoriuskop) (Figs 4 and S7). We conclude that the relative effect of fire vs. elephants on woody carbon pools is most different in the most productive site, in this case likely driven by higher rainfall.

Other differences across the sites such as soil fertility and community composition may also influence the response of savanna woody plants to fire and elephants (Pringle *et al.* 2016). In KNP, the more fertile soils of Mopani and Satara may also contribute to greater woody growth at those sites. For example, the Satara plots accumulated woody biomass at high rates (0.77 Mg year^{-1}), but frequent fire was able to control woody biomass accumulation. This may be due to the high grass biomass and intense fires in Satara, where fire intensities are similar to those in the wettest site, Pretoriuskop (Govender, Trollope & Van Wilgen 2006). However, we found that trends in elephant abundance were relatively consistent across these regions, suggesting little effect of soil type on changes in elephant density, and past studies have implicated rainfall over soils as being the primary driver of woody biomass in African savannas similar in rainfall to KNP (Sankaran *et al.* 2005; Staver, Archibald & Levin 2011a). Regardless of the exact mechanisms governing woody-biomass productivity, the higher productivity in the wettest site offsets the consumptive effects of fire, but not elephants.

We next asked whether our findings have further consequences for the individual and interactive roles of elephants and fire as stabilizing agents of the savanna biome. To do so, we examined changes in canopy cover at the wettest site, Pretoriuskop, interpreting 50% tree cover as signifying a potential switch from savanna to woodland conditions (Staver, Archibald & Levin 2011a). When elephant populations were low, tree growth in unburned plots was sufficient to allow a shift from savanna (17% tree canopy cover) to woodland (83% canopy cover) (Fig. 6), as expected given that rainfall is sufficient for woodland development (Sankaran *et al.* 2005). However, our results did not support the prediction that fire alone can maintain low tree cover in such mesic African savannas. To the contrary, woody cover during the low-elephant period increased sharply from 20–56% and 20–32% in the triennial and annual treatments, respectively, at Pretoriuskop. The subsequent increase in elephant numbers reverted woodland back to savanna in the unburned plots. Others have proposed that either fire alone or in combination with elephants or other herbivores can prevent woodland establishment and/or revert woodlands to open savanna (Laws 1970; Barnes 2001; Wigley *et al.* 2014; Dantas *et al.* 2016). Our results suggest that elephants can stabilize the savanna biome even where fire cannot: in contrast to

fire, elephants alone were able to reverse the accumulation of woody biomass in all of our sites across the entire range of MAP (496–737 mm year^{-1}).

These findings have important implications for the carbon balance in savannas. Fire suppression, low-elephant populations and high rainfall allowed woody biomass to act as large (up to 0.6 MgC ha^{-1} year^{-1}; Table S7) and persistent (over decades) net carbon sinks in the study plots. Exposure to annual burning shifted woody biomass into a net source of carbon over time at two sites, but total emissions differed across sites. In the two driest sites on fertile soils, we found a net loss of woody-biomass carbon with annual burning (−0.071 to −0.022 MgC ha^{-1} year^{-1}), while in the wettest sites on infertile soils the increased growth of trees resulted in a net gain of woody biomass carbon over time (0.39–0.21 MgC ha^{-1} year^{-1}).

Soils and herbaceous biomass are also important carbon storage pools in savannas (Jackson *et al.* 2002; Pellegrini *et al.* 2015). Large fire-driven losses of C from soil pools can be important in determining the ecosystem C balance, but these effects emerge over long time-scales and are linked to the turnover of plant biomass. Consequently, shifts in the woody biomass in savannas over time are likely to alter the carbon stored in soils in similar ways (e.g. Pellegrini, Hoffmann & Franco 2014). Grass biomass does indeed differ across the sites (Govender, Trollope & Van Wilgen 2006), and a better understanding of how grasses may have responded to fire and elephants would further illuminate the results of our study. Regardless, the size of the woody biomass C pool is critical, as it is dynamic on time-scales relevant for global climate change and can determine whether a landscape acts as a sink or source of carbon.

Despite annual fire, woody cover and biomass accumulated in Pretoriuskop, the site with highest rainfall and potential productivity. This was unexpected given the hypothesized role of fire in limiting tree cover in more mesic savannas with rainfall in the region of 650–1000 mm year^{-1} (Sankaran *et al.* 2005; Staver, Archibald & Levin 2011a). Multiple mechanisms may influence the accumulation of biomass in spite of frequent burning, including the growth of large (i.e. already fire resistant) trees and the possibility that rising atmospheric CO_2 concentrations stimulate woody biomass growth (Buitenwerf *et al.* 2011). Testing the consistency of these findings in savannas spanning an even wider range of precipitation regimes will help to further resolve the role of rainfall in modulating the effects of fire on tree cover.

Finally, consideration of grazing will contribute to a more comprehensive understanding of how different herbivore guilds interact with fire. Grazers have the potential to affect woody biomass dynamics through their manipulation of fire regimes, which can be caused by changes in herbaceous biomass and/or community composition. However, recent experimental and long-term observational studies suggest that the effects of release from browsing on woody cover may generally outweigh any accompanying grazer-driven shifts in fire regime (Staver & Bond 2014; Daskin, Stalmans & Pringle 2016). Future work is required to resolve this issue in the

context of the KNP EBP study: our experimental design allowed us to control for potential confounding effects of grazers on fire frequency, but understanding the combined interaction may ultimately provide even deeper insight into the interactive processes and feedbacks regulating savanna woody biomass.

Conclusions

Both elephants and fire can reduce tree biomass and cover in African savannas, but their combined effects are interdependent and contingent on environmental context. Most notably, the effect of fire declined as elephant populations increased, with elephants becoming the dominant agent of disturbance in the years following cessation of culling in 1994. At high productivity, elephants were able to reverse the trend of woodland formation in the most productive site, while fire had a more-limited effect. The elephant effect was stronger during this period because elephants (i) induced more rapid rates of tree loss than did fire and (ii) had a stronger effect on tree populations than did annual burning. We conclude that woody-plant biomass in KNP depends on the independent and interactive effects of elephants, fire, and productivity across sites. These interactions have substantial implications for carbon storage and emissions, and, over time, may even alter the sign of net carbon flux.

Author contributions

Acknowledgements

Data accessibility

Available data deposited in the Dryad Digital repository (Pellegrini *et al.* 2016) at http://dx.doi.org/10.5061/dryad.0gs71: and the rest can be requested via the SANParks website (www.sanparks.com).

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Supporting Information

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

Appendix S1. Description of methods and additional analyses.

Fig. S1. Maps illustrating the experimental design and plots utilized.

Fig. S2. Average ratio of plot level biomass calculated from diameter measurements $\ln(B_{d})$ or from diameter estimated from height measurements $\ln(B_{h})$ using the scaling relationship presented above.

Fig. S3. Comparing changes in woody biomass over time using the three different allometric equations in the Satara region.

Fig. S4. Distribution of regions in Kruger National Park with the Experimental Burn Plots (EBPs) outlined in black dots.

Fig. S5. Change in number of elephants counted from 2001 to 2011 across all four regions.

Fig. S6. Comparison of the size-distribution of trees surveyed in the 2000s with evidence of disturbance (evidence for stems being snapped/fallen) vs. no disturbance.

Fig. S7. Regression between plot woody biomass in the 1990s (initial woody biomass) and the total drop in woody biomass from 1990s to 2000s across landscapes (r^2 of 0.86).

Fig. S8. Comparison between the population census data (x-axis) and a modeled elephant density presented in van Aarde, Whyte & Pimm (1999).

Table S1. Analyses of changes in fuel load and fire intensity between the low vs. high elephant periods.

Table S2. Size-classes used in the survey in the 1950s.

Table S3. Elephant density (# counted per-km^2 surveyed) over time.

Table S4. Trajectories of woody biomass in the unburned treatments categorized into the two time periods based on elephant population trajectory.

Table S5. Results of Tukey HSD comparing the change in abundance (# per ha from 1998 to 2012) of the six most abundant species in the unburned Satara EBP.

Table S6. Percent woody cover from the 1950s–2000s across landscapes in the different fire treatments (mean and standard error).

Table S7. Rates of change in woody biomass carbon (kgC ha^{-1}) during low-elephant periods (1950s–1990s) and high-elephant periods (1990s–2000s) across landscapes (values averaged among strings, ±SEM).

Table S8. Equations for allometric relationships.