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Spatiotemporal distribution dynamics of elephants in response to density, rainfall, rivers and fire in Kruger National Park, South Africa

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Abstract

Aim: African elephants are ecosystem engineers. As such, their long-term patterns of distribution and abundance (i.e., space-use intensity) will influence ecosystem structure and function. We elucidate these patterns for bull versus herd groups, by analysing the spatiotemporal dynamics of an increasing elephant population in relation to key ecological drivers: rainfall, distance to major rivers and time since last fire. Significant changes to the long-term patterns of elephant density and group-type probabilities are identified and explained.

Location: Kruger National Park, South Africa.

Methods: Using almost three decades of census records (1985–2012), we applied Multiple Point Process Models to assess the influence of rainfall, rivers and fire in shaping elephant space-use. Significant changes to the long-term patterns of elephant density and group type were also identified using kernel density estimates and the spatially varying probability of encountering either bull or herd group.

Results: Bull and herd groups are no longer clearly segregated as available empty space becomes more limited. Bull and herd groups have dichotomous resource selection functions, in that bulls concentrate in areas receiving lower rainfall but more frequent fires while herds concentrate in higher rainfall areas experiencing less frequent fires. Both bull and herd groups concentrate closer to major rivers, emphasizing rivers as important spatial drivers. Overall, densities increased most significantly closer to rivers and in areas experiencing fewer fires. Fire was also a strong agent of group-type change, as the probability of finding bulls, contrary to herds, significantly increased as fire return periods shortened.

Main conclusions: Elephant distribution and abundance patterns have homogenized in response to increased space limitations, with group-specific, fire-driven distribution patterns emerging overtime. Results herein should be used to help manage elephant space-use through the establishment of possible refuge areas and the development of more empirical research into elephant impacts in future.

KEYWORDS
African elephant, distribution and abundance, dynamics, Kruger National Park, protected area, space-use intensity, spatiotemporal, spatstat

1 | INTRODUCTION

African Elephants (*Loxodonta africana*) are ecosystem engineers that alter and create habitats as they select for preferred resources in the landscape (Pringle, 2008; Ripple et al., 2015). Their role in shaping the structure and function of habitats is therefore a central research theme for southern African countries where elephant populations are thriving (IUCN, 2015; Kerley et al., 2008). The disparity between countries in terms of elephant conservation management is however very broad, even in the face of heightened concerns over increased elephant poaching and illegal trade (IUCN, 2015, 2016; MIKE, 2016; Wittemyer et al., 2014). For example, as Central Africa fights to protect elephants from extinction, protected areas in southern Africa struggle to balance the conservation of this iconic species against their potentially damaging effects to the environment and by extension other species (Kerley et al., 2008). The Kruger National Park (Kruger) in South Africa is one such protected area, with elephant numbers rising from ~10 animals in 1905 to over 17,000 in 2015 (Ferreira, Greaver, & Simms, 2017). As these numbers continue to grow, questions persist about the effects of high elephant densities on integrated biodiversity outcomes (Ferreira, Freitag-Ronaldson, Pienaar, & Hendriks, 2012; Ferreira et al., 2017). Key concerns include changes to vegetation structure, associated species diversity and distribution patterns, system processes such as fire regimes, and the exacerbation of human–animal conflicts (Ferreira et al., 2012; Kerley et al., 2008; Rutina & Moe, 2014; SANParks, 2008; Scholes & Mennell, 2008). Understanding the long-term distribution dynamics of elephants is a fundamental component for elephant conservation management strategies that aim to address these concerns.

Over the years, studies conducted on Kruger's elephants have helped develop much of the current understanding of elephant distribution dynamics and their role in the ecosystem (e.g., van Aarde, Whyte, & Pimm, 1999; Grainger, van Aarde, & Whyte, 2005; Codron et al., 2006; de Knegt et al., 2011; Asner & Levick, 2012). Despite this cache of knowledge, Kruger's new elephant management plan (Ferreira et al., 2012) highlights gaps in our understanding of the population-level drivers of elephant distribution and abundance patterns. Ferreira et al. (2012) strongly emphasize the complexity of elephant conservation and call for biogeographical research into possible mechanisms and drivers of elephant distribution and abundance in Kruger. Dubbed space-use intensity, the patterns of elephant distribution and abundance are described as an expression of an elephant's response to key resources, as well as anthropogenic and natural disturbance events (de Knegt et al., 2011). However, elephant foraging behaviour and associated distribution patterns are also known to be sexually segregated (de Knegt et al., 2011; Ruckstuhl, 2007; Smit, Grant, & Whyte, 2007; Stokke & du Toit, 2002). That is, bull and herd groups will use space differently as a result of different social or habitat cues and are thus expected to have varied responses to the spatial arrangement of key resources, disturbances in the landscape and the relative positions of other elephant groups. Group type (bull or herd) therefore needs to be taken into account when trying to understand how the space-use intensity of a growing elephant population may respond to key environmental covariates (Ferreira et al., 2012; MacFadyen et al., 2013). In Kruger, key environmental covariates include rainfall variability (Birkett, Vanak, Muggeo, Ferreira, & Slotow, 2012), surface water availability (Chamaillé-Jammes, Valeix, & Fritz, 2007; Loarie, van Aarde, & Pimm, 2009), vegetation phenology (Young, Ferreira, & Aarde, 2009), topography and landscape heterogeneity (Grainger et al., 2005; Murwira & Skidmore, 2005). Significant disturbance events may include elephant culling operations between 1966 and 1994 (Whyte, 2001), the erection of more than 400 artificial water points from 1946 until 1995 (Smit, 2013) and fire (Smit, Smit, Govender, van der Linde, & MacFadyen, 2013; van Wilgen, Govender, Smit, & MacFadyen, 2014). Using a biogeographical approach, we study broad-scale distribution and abundance patterns of elephants in Kruger from 1985–2012, in relation to the patterns of selected covariates. We posit that in distinguishing significant changes to these long-term patterns, we may determine where elephant impacts may potentially be most significant (Grainger et al., 2005; Valeix et al., 2011). Ultimately, this should help focus research into the more empirical effects of high elephant densities in confined areas. Our overall aims are therefore to examine the long-term changes to sexually segregated gradients of elephant space-use and identify the underlying resource selection functions. Using almost three decades of elephant population data, we investigate how the densities of bull versus herd groups respond to changes in various environmental conditions, namely rainfall, distance to major rivers and fire frequency. These specific covariates were selected because (a) rainfall has a well-established relationship with vegetation productivity and habitat condition (Chamaille-Jammes, Fritz, & Murindagomo, 2006; Richard & Poccard, 1998) that actuate ungulate dynamics in Africa (Ogutu, Piepho, Dublin, Bhola, & Reid, 2008); (b) distance to major rivers is an indicator of available surface water as well as landscape position and associated habitat gradient; (c) while fire frequency provides insight into the synergistic relationship between elephants and fire (Dublin, Sinclair, & McGlade, 1990; Shannon et al., 2011); (d) moreover, all data sets overlap with the census period, 1985–2012.

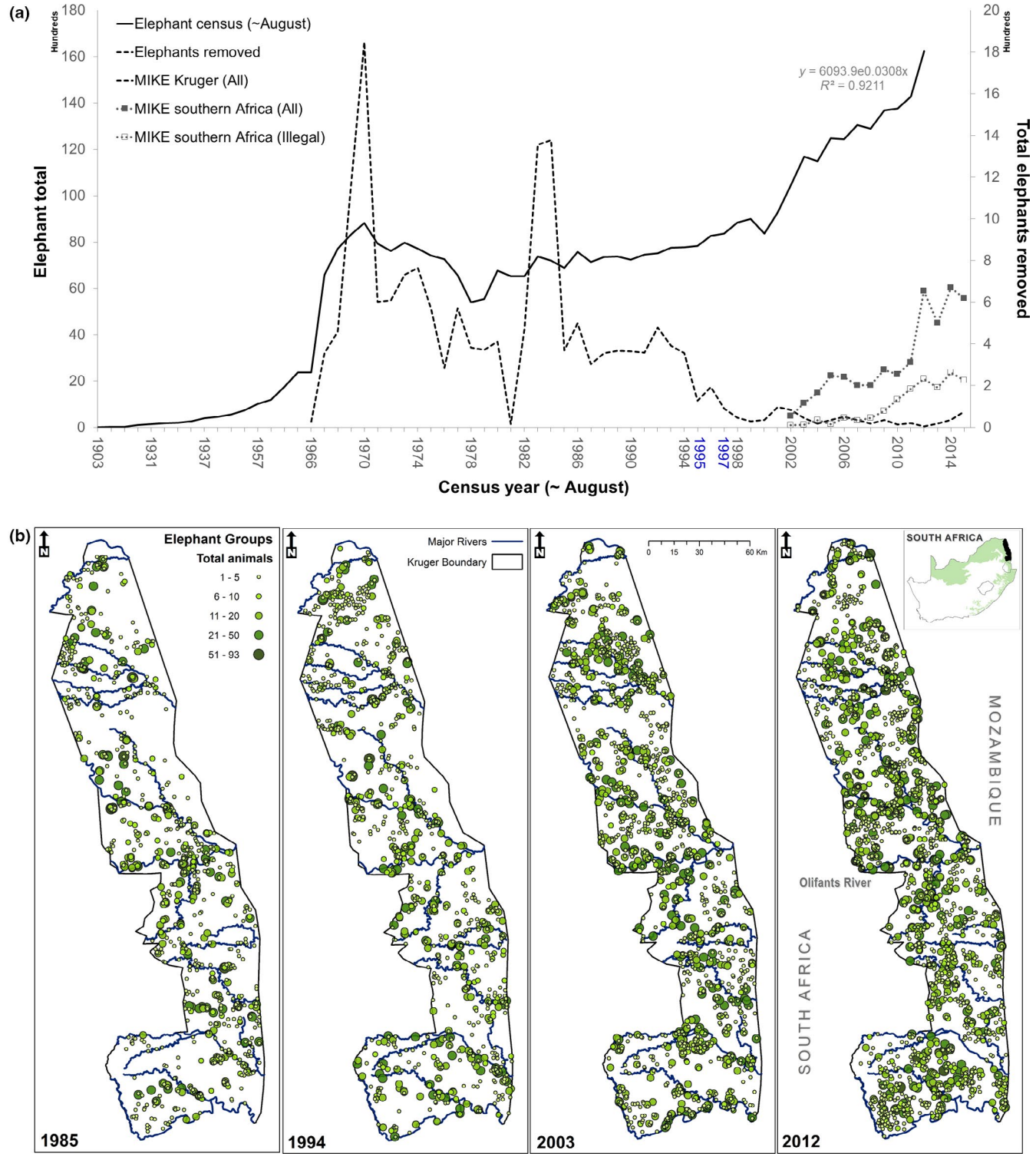

FIGURE 1 Elephant populations in the Kruger National Park (KNP) from 1985 to 2012. (a) Elephant population growth from 1905 to 2012 (solid line), with numbers of animals culled or translocated from 1966 to 2003, and carcasses recorded by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) programme for Monitoring the Illegal Killing of Elephants (MIKE) from 2002 to 2015 (dashed lines; CITES, 2016). Grey dotted lines with [▪] markers represent MIKE records of all elephant carcasses for southern Africa, while those marked with [□] represent MIKE records of illegally killed elephants in southern Africa (MIKE, 2016). The equation in grey text on the top right shows the exponential trend for increasing elephant numbers from 1977 to 2015 ($y = 6{,}093.9e^{0.0308x}$; $R^2 = 0.9211$). Years marked in blue on the y-axis, represent the moratorium on large-scale culling operations (1995), and the start of KNP's artificial water point closure programme (1997; Whyte, 2001; SANParks, 2016). (b) Elephant population maps for selected years in KNP: 1985, 1994, 2003 and 2012 (see Supporting Information Video S1 for all years)

The influence of rainfall, rivers and fire in shaping elephant space-use is assessed using a Multiple Point Process Model (MPPM; Baddeley, Rubak, & Turner, 2015). Together with MPPM, we also diagnose significant changes to long-term total elephant and group-type distribution and abundance patterns using kernel density estimates and the spatially varying probabilities of encountering bull versus herd groups. Specifically, we investigated (a) the spatial processes (resource selection function) that govern the distribution of elephants, accounting for group-type differences, while controlling for density increase over time; (b) significant changes to long-term total elephant distribution and abundance patterns (regardless of group type) and; (c) significant changes to long-term elephant group-type distribution patterns (spatial probabilities of encountering bull vs. herd elephants in the landscape).

2 | MATERIAL AND METHODS

2.1 | Study area

Kruger is South Africa's largest protected area (~20 000 km^2), located in the north-east of the country, bordering Zimbabwe and Mozambique. Falling within the savanna biome, Kruger is bounded by the Limpopo River in the north and the Crocodile River in the south. The area receives summer rainfall (long-term mean of 542 mm) which generally decreases from south to north and slightly increases from east to west (Gertenbach, 1980). The climate is subtropical with temperatures ranging from 26.4°C in summer (December–March) to 17.8°C in winter (June–August) (Zambatis, 2006). Historical elephant records begin with a population of approximately 10 animals recorded in 1905 (de Pienaar & V., van Wyk, P., & Fairall, N., 1966), followed by an exponential increase in numbers from 1977 to 2015 (Figure 1a) culminating in over 17 000 animals (Ferreira et al., 2017).

2.2 | Data collation

2.2.1 | Elephant records

Elephant population data have been collected annually in Kruger since 1962 (Pienaar et al.., 1966), using aerial census techniques described in full by Whyte (2001) and later by Ferreira et al., (2017). In summary, helicopter counts were conducted annually between July and August for the whole park. Coordinates of each group sighting were captured along with total number of animals and a group-class code (OB: bull only group; O[c]: mixed herd group [calves indicated in brackets]). Importantly, all results reported here are therefore representative of the winter (July–August) distribution and abundance patterns of elephants in Kruger. We recognize that these patterns will vary seasonally (van Aarde, Ferreira, Jackson, & Page, 2008; Codron et al., 2006), but since elephants utilize woody plants more heavily in these drier winter months (Codron et al., 2006; Thomas, Holland, & Minot, 2008) data from this time period may be more relevant to understanding elephant impacts. We collated these census records from 1985 to 2012 (SANParks, 2016) as point localities (x, y) georeferenced to Universal Transverse Mercator (UTM) zone 36 South, World Geodetic System 1984 (WGS84). Each point is characterized by the census year, elephant group type (bulls or herd) and total number of elephants in each group (Figure 1b and Supporting Information Video S2). The resulting data set represents mark-weighted localities of bull and herd groups from 1985 to 2012 (group points n = 35,117, individual animals n = 276,306, years n = 28). From these, we created a hierarchical data frame (hyperframe) containing 28 separate point pattern data frames for each year marked by group type and weighted by the total number of animals in each group (functions 1–3 in Supporting Information Table S1; Baddeley et al., 2015). All point patterns and subsequent covariates were rescaled from UTM metres to kilometres to avoid singularity errors and simplify graphics (function 4 in Supporting Information Table S1). While our aim was to explain the natural variability in winter distribution and abundance patterns of elephants, we accept that some variability may in part be due to measurement error or sampling variation (Baddeley et al., 2015). However, we assume these effects to be negligible as the census methodology has remained unchanged since 1985 and since elephants are highly mobile animals any small locational errors will be of little consequence to the intrinsic long-term patterns of elephant space-use.

2.2.2 | Rainfall and distance to rivers

Rivers and rainfall are known to influence elephant movement and distribution response at different scales (Grainger et al., 2005; Chamaillé-Jammes et al., 2007; de Knegt et al., 2011). Both are indirect indicators of water availability as well as habitat structure, composition and function in the landscape (Shen et al., 2017). For example, riparian vegetation closer to rivers or valley bottoms, has larger trees with wider crown diameters compared with the crests or uplands (Fu & Burgher, 2015). Areas with higher rainfall are also generally more productive and would therefore show a greater Normalized Difference Vegetation Index (NDVI) response for example (Birtwistle, Laituri, Bledsoe, & Friedman, 2016; Martiny, Camberlin, Richard, & Philippon, 2006). We therefore selected distance to all major rivers and annual rainfall as key spatial covariates of Kruger's elephant distribution and abundance patterns (Figure 2a). Annual precipitation data (CHIRPS) were collated from the Climate Hazards Group data portal for the period 1983–2012 (Funk et al., 2015); these data were processed and stored as array entries in the hyperframe already containing the individual marked point patterns (functions 17, 19, 18 and 23 in Supporting Information Table S1). A three-year moving mean was then calculated for each year to capture the influence of not only the current but the preceding three years rainfall on vegetation resources and ultimately elephant distribution patterns (Birkett et al., 2012; Garstang et al., 2014). We used a three-year moving

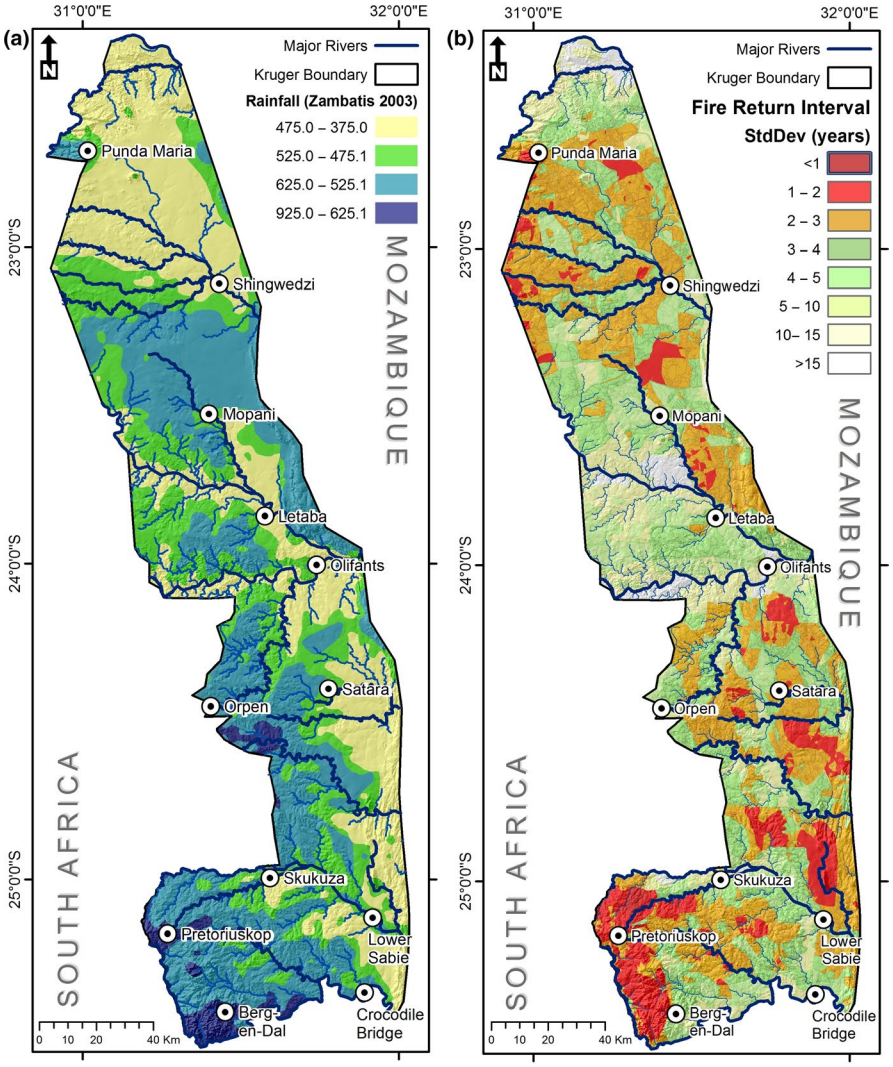

FIGURE 2 Long-term mean annual rainfall and fire return intervals with major rivers in the Kruger National Park. (a) Mean annual rainfall after Zambatis (2003) and (b) Fire return intervals after Smit et al. (2013) displayed in increments of standard deviation in the number of years since the last fire

average to represent potentially longer term rainfall effects since we did not expect the winter distribution and abundance patterns of elephants to respond strongly to rainfall received in only a single preceding summer season. Our distance to rivers covariate was created using all major rivers (i.e., third order and higher), which are more likely to hold permanent water and provide riparian vegetation favoured by elephants (Cullum & Rogers, 2011). The layer representing these rivers was imported as a data frame of spatial lines and converted into line segment patterns, ultimately forming a distance to major rivers surface which was added as a function class to our hyperframe (functions 24, 10 and 11 in Supporting Information Table S1).

2.2.3 | Fire return interval

Fire return interval is included here as a more ecologically relevant measure of fire frequency, in that fire return period is reset after each fire (i.e., current year burnt =0 years since fire) and is not a cumulative 72-year measure of fire "impacts" (Smit et al., 2013). Areas with longer return intervals will therefore experience fewer fires compared with those with shorter return intervals. Fire is included here because the synergistic relationship between elephants and fire is well documented, that is fire stimulates elephant foraging activities while intensive browsing by elephants followed by fires can increase tree mortality rates (Dublin et al., 1990; Shannon et al., 2011). In African savannas, the separate and compound effects of elephants and fire can therefore alter habitat composition and structure to the point where an ecosystem state may change, for example from a woodland to a grassland state (Asner, Vaughn, Smit, & Levick, 2015; Dublin et al., 1990; Levick, Baldeck, & Asner, 2015). Thus, fire return interval was added to test whether longer or shorter fire return intervals had any effect on the point patterns of elephants in Kruger. Return intervals were calculated from Kruger's burn scar geodatabase, which has polygon records of known fires from 1941 until the present (see Smit et al., 2013 and Govender, Mutanga, & Ntsala, 2012). We overlaid all burn scar polygons from 1941 to 2012 and converted the resulting polygon attributes to a binary rasterstack (1 = no burn; 0 = burn) (functions 20 and 17 in Supporting Information Table S1). A moving fire return table was computed by iteratively

TABLE 1 Results of the mixed-effects multiple point process model. Linking herd and bull group intensity of space-use to environmental variables. The intercept value represents the linear predictor or the estimated logarithmic intensity of elephants per km^2 excluding covariate effects (i.e., if covariate values were zero). The standard deviation (*SD*) represents the deviation of the linear predictor caused by annual random effects. The coefficient values represent the logarithmic factor by which this linear predictor would increase/decrease should the covariate value increase/decrease by 1.0

Random effects [Formula: ~1 | year]					
SD: 0.022					
Relative *SD*: 7.76					
Fixed effects					
	Value	***SE***	***t*-value**	***p*-Value**	**Effect (%)**
(Intercept)	−1.264	0.050	−25.16	<0.001	
3 years moving rainfall—Bulls	−0.003	0.000	−25.81	<0.001	-26^{+100}
Distance to rivers—Bulls	−0.119	0.015	−7.73	<0.001	-11^{+1}
Moving fire intervals—Bulls	−0.006	0.002	−2.71	0.007	-3^{+5}
No. of years since 1985—Bulls	0.007	0.003	2.58	0.016	$+7^{+10}$
3 years moving rainfall—Herd	0.003	0.000	39.40	<0.001	0^{+100}
Distance to rivers—Herd	−0.281	0.018	−15.76	<0.001	-33^{+1}
Moving fire intervals—Herd	0.025	0.002	10.59	<0.001	$+10^{+5}$
No. of years since 1985—Herd	0.026	0.002	12.44	<0.001	$+39^{+10}$
ANOVA					

Note. Effect: +100 mm rainfall | +1 km from major river | +5 years to fire return interval | +10 years from record start 1985.

counting the intervals between fires for each pixel from 1941 to 2012 (Figure 2b; Smit et al., 2013). If you imagine a spatiotemporal matrix, with rows representing pixel IDs (grid locality) and columns years (1985–2012), filled with 1's (unburnt) and 0's (burnt). The moving fire return table/matrix is calculated for pixel 1, moving across years, counting the 1's until a 0 is encountered, and the fire return interval is reset to 0 (i.e., it burnt that year). These fire return intervals were added to the hyperframe of elephant point patterns as annual pixel image objects (functions 3 and 23 in Supporting Information Table S1).

2.3 | Analysis

2.3.1 | Elephant point patterns

Prior to running any regression analyses, we tested whether the data violated standard statistical assumptions of homogeneity and stationarity. Furthermore, a Monte Carlo test of spatial segregation, an inhomogeneous empty space function and a standardized form of the inhomogeneous cross-type L function, with border correction and a random labelling simulation expression was used to determine whether bulls and herd groups should be treated differently in proceeding models (functions 8 and 9 in Supporting Information Table S1). The cross-type L function was specifically used here to measure group-type independence by comparing the expected number of bull points lying within a distance *r* of a typical herd point to a randomized group-type assignment (Baddeley et al., 2015).

2.3.2 | Elephant winter resource selection

We first investigated the spatial processes that may govern the distribution of elephants, accounting for group type (bull vs. herd), in winter using the aforementioned spatial covariates: rainfall, distances to major rivers and fire return interval). To evaluate the influence of key resources, while still accounting for unknown random variability, we used a mixed-effects point process model for multiple point patterns (MPPM). MPPMs are similar in structure and output to generalized linear models. The key difference being that the response variable is a series of point patterns of which the intensity is a function of different covariates (Baddeley et al., 2015). This means our response variable is essentially the spatial distribution of elephant densities, marked by group type, from 1985 to 2012. Time since 1985 was included to control for the confounding effects that increased densities would have on detecting general elephant resource selection functions. Distance to rivers, rainfall and fire return interval were included as fixed effects representing observable spatial covariates that may account for known variability in our point patterns (Baddeley et al., 2015). We do however also acknowledge the possibility of unobserved random effects that will likely produce random or unknown variability in our point pattern processes (Baddeley et al., 2015). To account for this, we included census year as a random variable to represent those unknown annual effects not accounted for by our covariates. Our mixed-effects point process model (function 12 in Supporting Information Table S1) was then fitted simultaneously to all point patterns using the following formula:

$$\lambda(u)_n = \exp(\beta_0 + m_{bh}\beta_1 S(u)_n + m_{bh}\beta_2 R(u)_n + m_{bh}\beta_3 F(u)_n + m_{bh}\beta_4 Y(u)_n + \alpha_n) \quad (1)$$

where $\lambda(u)_n$ is the elephant point pattern (or space-use) intensity function for each year n (1985–2012), β_0 is the intercept, β_1; β_2; β_3 and β_4 are coefficients to be estimated, and $S(u)$; $R(u)$; $F(u)$ and $Y(u)$ are the effects of surface rainfall as a three-year moving average, distance to rivers, fire return interval and number of years from the start of the data record (1985) at location u and year n respectively. These fixed effects were conditioned upon elephant group type, that is points classified as bull m_b or herd m_h groups. Random effects α_n were included to account for unknown variability amongst years within each group type. With the above model specifications, the intensity of elephant space-use $[\lambda(u)_n]$ was thus allowed to vary as a function of the average amount of rainfall received in the preceding three years (i.e., the three-year moving average), distance to major rivers, fire return interval and number of years since 1985, for each year. The response was also allowed to vary annually by group type (bull vs. herd).

Due to the large sample size (n = 35,117 group points, df =276,306 total animals and dendf = 1,596,369 residual degrees of freedom that is the denominator estimated during MPPM using standard kernel density estimation techniques), it is important to consider the potential for the "p-value problem" to affect our MPPM results (Lin, Lucas, & Shmueli, 2013). Results are therefore interpreted in the context of the magnitude of the effect size rather than significance alone (Lin et al., 2013). Consequently, effect size was calculated using the above Formula 1, where the intercept value β_0 represents the estimated logarithmic intensity of elephants per km^2 $[\lambda(u)_n]$ excluding all covariate effects (i.e., if covariate values were zero). The standard deviation is the deviation of $\lambda(u)_n$ caused by annual random effects $[\alpha_n]$. The coefficient values β_{1-4} are thus the logarithmic factor by which $\lambda(u)_n$ would increase or decrease should the covariate value increase or decrease by one unit. Model validation was performed using an analysis of deviance (ANOVA) for MPPM and a residual K-function (i.e., goodness-of-fit test) to access model accuracy according to Baddeley et al., (2015) (functions 13 and 14 in Supporting Information Table S1).

2.3.3 | Elephant space-use intensity change

Changes to long-term elephant distribution and abundance patterns in Kruger from 1985 to 2012 were estimated as follows: (a) Elephant density was first calculated using a kernel smoothed intensity function for each point pattern (n = 28) with a 5 km bandwidth (σ) and Diggle's edge correction (function 16 in Supporting Information Table S1). We chose 5 km as a bandwidth as this represents half the distance an elephant would be expected to travel in a day (de Knegt et al., 2011). Diggle's edge correction was used to minimize the bias of the park boundary edge effect in our analysis (Baddeley et al., 2015). (b) Significant changes to these long-term density patterns were then identified using the kernel density estimates, which were stacked and indexed by time to detect significant Breaks in the Seasonality and Trend (BFAST) of elephant density (functions 17, 21, 22 and 24 in Supporting Information Table S1; Verbesselt, Hyndman, Newnham, & Culvenor, 2010; DeVries, Verbesselt, Kooistra, & Herold, 2015). BFAST is a time series change detection method originally developed for remotely sensed time series products (Verbesselt, Zeileis, & Herold, 2012). Changes to Kruger's elephant density patterns were thus assessed by comparing historical (1985–1997) and current patterns (1998–2012) using the function bfmSpatial (function 25 Supporting Information Table S1; Dutrieux, DeVries, & Verbesselt, 2014). Changes detected were then mapped to illustrate areas experiencing significantly higher or lower densities of elephants in the past 14 years (1998–2012) compared with the previous 14 years (1985–1997). (c) The areal proportions of grouped distance to rivers (11 discrete distance classes) and fire return period classes (9 discrete classes) were then calculated for different magnitude categories of density change from (b) and the relative proportions of these significant changes analysed (function 20 in Supporting Information Table S1). The effects of distance to major rivers and fire frequency on the magnitude of change in overall elephant density were then assessed using a Pearson's chi-squared test of independence (function 26 in Supporting Information Table S1).

2.3.4 | Elephant group-type distribution change

Changes in distribution patterns of elephant bull groups versus elephant herd groups were estimated in a similar three-step process described above. However, instead of elephant density (2.3.3 [a]), group-type probabilities were calculated for each year as the (a) spatially varying probabilities of encountering bull versus herd groups, which were mapped using a relative risk function (function 15 in Supporting Information Table S1; De Lucca et al., 2013; Baddeley et al., 2015). In this way, the probability of encountering a specific group type (i.e., bull or herd) was computed using a smoothing bandwidth (σ^2) of 5 km and Diggle's edge correction function as described above (Baddeley et al., 2015).

All analyses were carried out in R version 3.3.1 (R Core Team, 2016) with all R packages and functions used, and references thereof, described in Supporting Information Table S1. Larger computations were performed using the Rhasatsha High Performance Computing system at Stellenbosch University (Rhasatsha HPC, 2016).

3 | RESULTS

3.1 | Elephant point patterns

A Monte Carlo test confirmed our initial hypothesis of significant sexual segregation: point clustering (Ripley's Inhomogeneous K-function) differed each year by group type (T = 0.3354, p < 0.05; Baddeley et al., 2015; function 5 and 6 in Supporting Information Table S1). Results of the border-corrected inhomogeneous empty space function similarly showed highly variable clustering distances across years (function 7 in Supporting Information Table S1; Supporting Information Figure S1). That is, elephants were significantly clustered (p < 0.05) in earlier years with observed empty space distances below

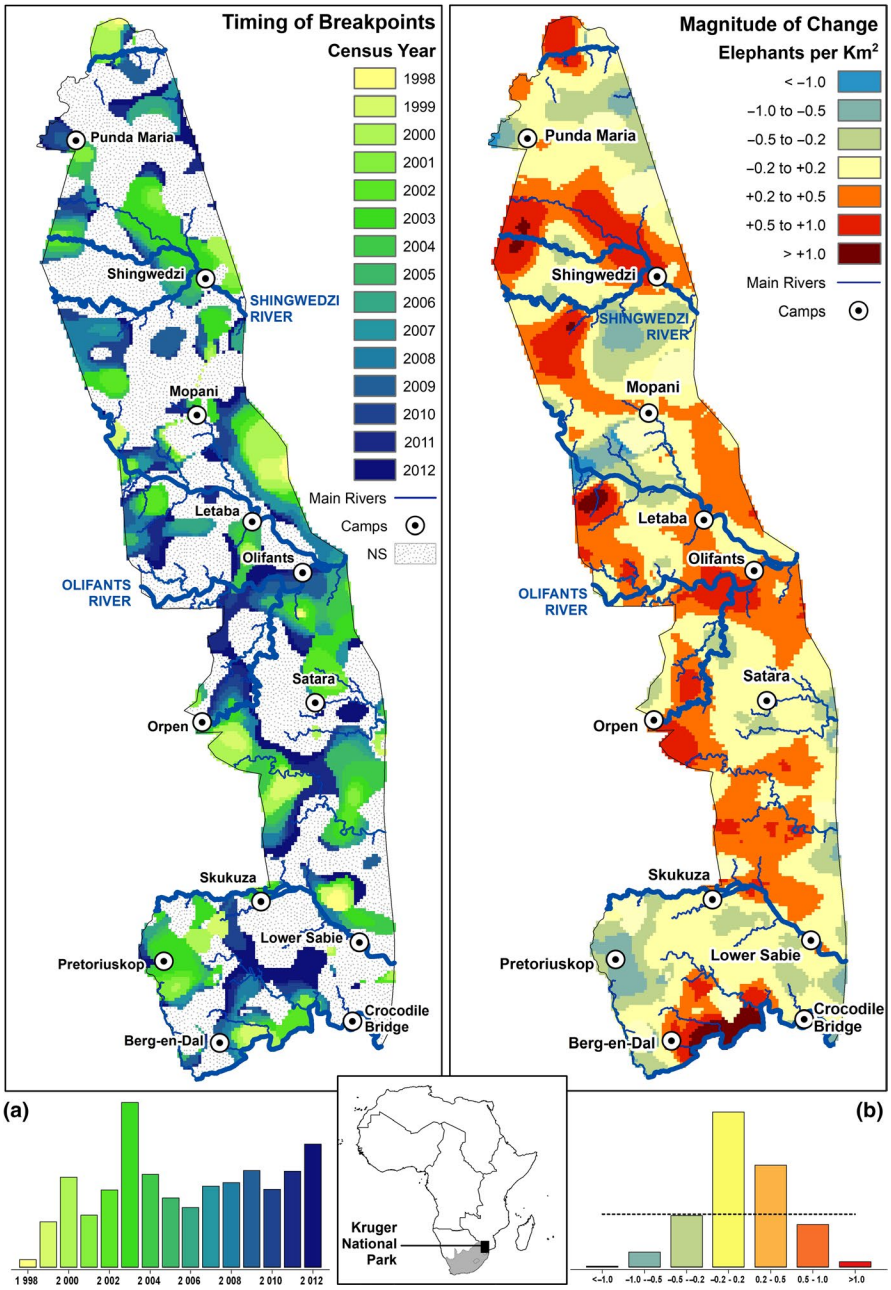

FIGURE 3 Results of Breaks for Additive Seasonal and Trend (BFAST) (Verbesselt et al., 2010) analysis, showing the location and timing of significant change to elephant density patterns across Kruger from 1985 to 2012 (BFAST, $p < 0.05$). (a) shows the timing of the most significant changes (breakpoints) with NS representing no significant change. (b) shows the magnitude and direction of (positive-darker red or negative-lighter blue) change

the theoretical curve of random distribution. More recent years (e.g., 2009–2012) however, showed no significant evidence of clustering (Supporting Information Figure S1). The cross-type L function further illustrates how the level of association between bull and herd groups has changed amongst years (Supporting Information Figure S2), leading us to differentiate sexes in the proceeding models.

3.2 | Elephant resource selection

As expected the densities of both groups increased significantly over time, with the difference of 10 years resulting in 7% more bulls and 39% more herd elephants (Table 1). Controlling for this density increase over time, bull and herd elephant groups differed in their response to rainfall and fire but responded similarly to the effects of increased distance to rivers (Table 1). Both bull and herds concentrated closer to major rivers, although this effect was stronger in herd groups (33% fewer animals 1 km further from rivers) compared with bulls (11% fewer animals 1 km further from rivers). Bull densities were significantly lower in areas receiving higher rainfall (26% fewer bulls in areas with 100 mm more rain) while herd densities in such areas did not change from the mean (Table 1). Bull densities were also lower in areas experiencing longer fire return intervals (3% fewer bulls with a 5-year fire return interval) while herd densities were significantly higher in areas experiencing fewer fires (10% more herds with a 5-year fire return interval). Random annual effects accounted for 7.8% of the remaining variability in elephant herd and bull densities from 1985 to 2012. Although model fit did fluctuate from year to year, these differences were not significant indicating

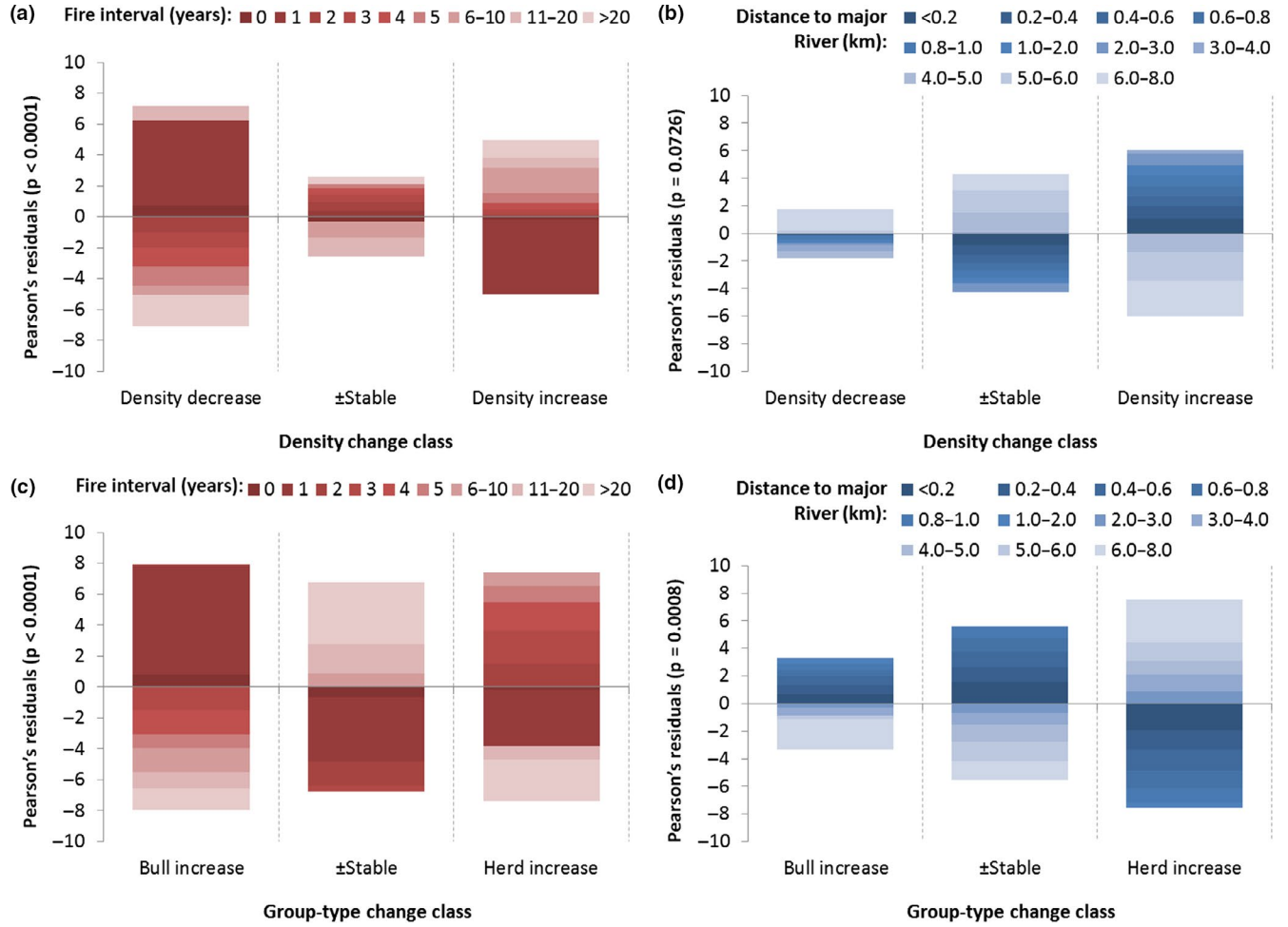

FIGURE 4 Pearson's residuals plots from chi-squared test of independence showing the relation between fire return periods, distance to major rivers and significant changes to elephant density and group-type probability during the period 1998–2012 compared with the period 1985–1997. The y-axis represents the standardized difference between the observed and expected values of elephant densities. Negative and positive values therefore depict greater decreases or increases than would be expected by chance. The different panels show (a) the significant effect of fire as an agent of density change; (b) the marginally significant effect distance to major rivers have on density change. Although, areas undergoing significant increases were overwhelmingly closer to rivers (darker blues); (c) the significant effect of fire as an agent of group-type probability change, with shorter fire return intervals (darker reds) dominating those areas showing an increase in the probability of encountering bull elephants; (d) the significant effect distance to major rivers has on group-type probability change with bull elephants increasing closer to rivers (darker blues) and herd elephants generally increasing further from major rivers (lighter blues)

good model fit for bulls, $\chi^2 = 24{,}830$, $df = 24{,}775$, $p = 0.401$ and herds, $\chi^2 = 23{,}673$, $df = 23{,}618$, $p = 0.399$ overall.

3.3 | Elephant space-use intensity change

The increasing trend in elephant densities is spatially variable (Supporting Information Video S2). The location and timing of significant changes ($p < 0.05$) to elephant density from 1998 to 2012 compared with 1985–1997 is likewise spatiotemporally dynamic (Figure 3). Interesting, the strongest increase in density occurred in 2003 (Figure 3a), which was a below average rainfall year that consequently also experienced relatively few fires (i.e., 1,000 km^2 burned vs. long-term average of ~3,000 km^2; Supporting Information Figure S3). The overall magnitude and direction of these changes, shown in Figure 3b, illustrate those areas experiencing significant decreases to long-term elephant density patterns in lighter shades of blue; and those experiencing significant increases in darker shades of red. Areal proportions of the above density changes, classified within zones of different fire frequencies and distances to river classes, revealed varied relationships (Figure 4; Supporting Information Figure S4). Nonetheless, fire was identified as a significant agent of density change, $\chi^2(16, 27) = 73.501$, $p < 0.0001$ (Figure 4a). More specifically, areas experiencing higher fire frequencies (intervals of ≤2 years between fires depicted by darker shades of red in Figure 4a) were generally associated with decreased elephant densities, more so than would be expected by chance (Figure 4a; Supporting Information Figure S4a). In contrast, areas experiencing intermediate to low fire frequencies (intervals of ≥5 years between fires depicted by lighter shades of red in Figure 4a) were associated with increased

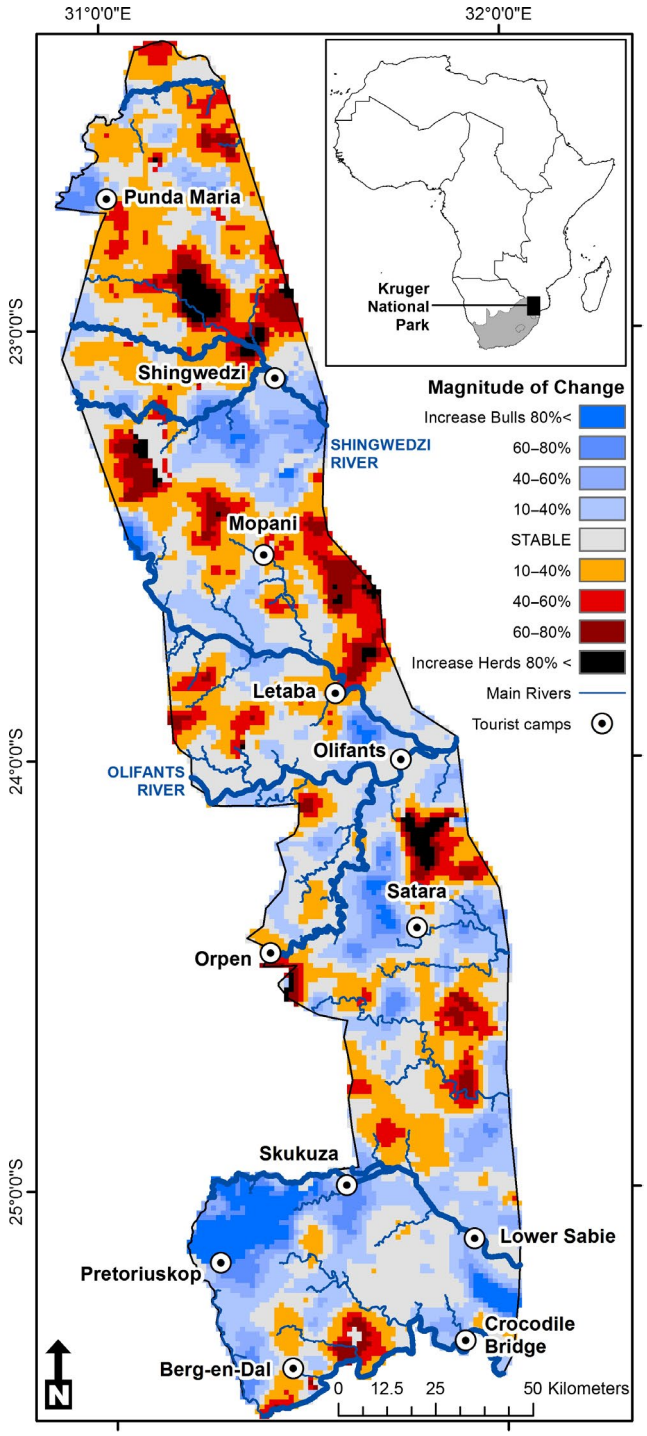

FIGURE 5 Significant change in spatially varying probabilities of bulls versus herd elephant groups in the period 1985–2012 (BFAST, $p < 0.05$). Darker blue areas on the map represent those areas that are becoming increasing bull dominated. Darker red areas represent those areas that are becoming increasingly dominated by herd groups

densities (Figure 4a; Supporting Information Figure S4a). Areas significantly increasing in elephant densities were generally closer to rivers (<2 km), $\chi^2(20, 33) = 29.834$, $p = 0.073$ (Figure 4b; darker shades of blue), while the largest decreases were further away from major rivers (>5 km) (Supporting Information Figure S4b).

3.4 | Elephant group-type distribution change

Both bull and herd groups showed clear changes to their long-term patterns of distribution over time (Supporting Information Supporting Information Video S3). In general, herd-dominated areas have expanded in comparison with bull-dominated areas (Figure 5). More specifically, the probability of encountering herd elephants has generally increased north of the Olifants River, except for small pockets south of the Shingwedzi River and into the Punda Maria sandveld where the probability of encountering a bull group has instead increased significantly ($p < 0.05$) (Figure 5). In contrast, bull elephants showed a significant increase ($p < 0.05$) in the Pretoriuskop area (Figure 5). Similarly, the areal proportions of the above significant changes to long-term group-type probabilities showed that fire was a significant agent of change, $\chi^2(16, 27) = 134.52$, $p < 0.0001$ (Figure 4c). That is, the probability of encountering bull elephants increased in areas with higher fire frequencies (darker shades of red in Figure 4c; Supporting Information Figure S4c). While herd elephants appeared to do the same but at intermediate frequencies of fires (lighter shades of red in Figure 4c; Supporting Information Figure S4c). Group-type probabilities also shifted significantly in relation to major river systems, $\chi^2(20, 33) = 46.069$, $p < 0.001$ (Figure 4d). That is, bull groups are generally moving closer to rivers (darker shades of blue in Figure 4d), while herd groups are moving further away from major rivers (lighter shades of blue in Figure 4d) than historically expected.

4 | DISCUSSION

4.1 | Elephant point patterns

Recent reports indicate that Kruger's elephant numbers have exponentially increased since 1995 but also argue that growth rates are slowing in response to less intensive elephant management practices implemented after 1994 (Ferreira et al., 2017). Namely, since the cessation of culling in Kruger managers expect elephant populations to start self-regulating through reduced birth rates. From a biogeographical perspective however, our results show Kruger's elephant distribution patterns have homogenized with a clear decrease in available empty space from 2000 (Supporting Information Figure S1). In addition, while bull and herd groups were initially significantly segregated, this pattern changed from 2006 onwards (Supporting Information Figure S2). As a result, groups are no longer showing significant levels of segregation and little clustering behaviour from distances >4 km (Supporting Information Figure S2). Since Shannon, Page, Mackey, Duffy, and Slotow (2008) describe this type of segregation as a natural behavioural response to social stimuli (e.g., breeding) and/or different habitat requirements of male versus female body sizes, we suggest the implications of this change may be far-reaching. We argue that bull and herd groups are being forced into closer proximity as empty space constricts and may no longer be able

to select for preferred resources and maintain the natural heterogeneous distribution patterns proposed by Ferreira et al. (2012). Anthropogenic factors like Kruger's perimeter fence may also have exacerbated this homogenization effect. Grant, Bengis, Balfour, and Peel (2008) for example, outline how fences can affect elephant ecology and population dynamics by restricting natural movement functions triggered by ecosystem cues. In this way, increasing populations may place more pressure on habitats and resources that may ultimately compromise other species (Owen-Smith, Kerley, Page, Slotow, & Aarde, 2006). This concept is supported by numerous multinational (e.g., Loarie et al., 2009) and local scale studies (e.g., Vanak, Thaker, & Slotow, 2010), and thus requires careful consideration by managers in future.

4.2 | Elephant resource selection

Recognizing the need for a holistic landscape management approach to elephant conservation in Kruger, Ferreira et al. (2017) call for a deeper understanding of the spatiotemporal response of elephants to resource heterogeneity. Using point pattern analysis, our study reveals divergent resource selection functions for bull versus herd groups. Both bull and herd elephants were found in higher concentrations closer to rivers (Table 1), a response driven by an elephant's general preference for natural water sources and optimal foraging conditions in riparian vegetation (Gaylard, 2015). However, the stronger response of herds to rivers suggests they may be more dependent on riverine habitats (Stokke & du Toit, 2002) for shelter (Smit et al., 2007) and potentially to fulfil browse requirements during the dry season (Shannon, Mackey, & Slotow, 2013). This effect is less apparent in bulls as they roam over larger areas (Stokke & du Toit, 2002) and will reportedly switch their diets to grass earlier in the season (Shannon et al., 2013).

Coupled to this, we expected rainfall-driven vegetation dynamics or ancillary increases to surface water availability to emerge as important drivers of elephant distribution and abundance, as has been suggested by Chamaillé-Jammes et al. (2007) and Loarie et al. (2009). However, we found this relationship only held for bulls and not herds. We speculate this may be an artefact of the winter view of elephant distribution and abundance patterns derived from July/August census data. Elephants may therefore not be responding strongly to rainfall while in their dry season winter home ranges. Unfortunately, data are not available for the summer distribution patterns of elephants in Kruger. Interestingly though, bulls had a strong negative response to rainfall, which could be explained by bull elephant's dependence on artificial water sources described by Smit et al. (2007) and later by Gaylard (2015).

Fire return period also influenced elephant distribution patterns, as herds selected for areas with lengthier fire return intervals, whereas bulls selected areas with shorter fire return intervals, albeit less clearly (Table 1). Bulls, being more dependent on grass during the winter months (Shannon et al., 2013; Smit et al., 2007), may respond to more frequent fires as they improve grass quality (Trollope, 1996). This supports a cause and effect synergy between fires and elephants as seen by Dublin et al. (1990) and others (Shannon et al., 2011). This synergistic relationship is expressed in habitat structure, where elephants may reduce woody cover, allowing fires to maintain the landscape in a grassland state. In an outdoor laboratory like Kruger however, it is difficult to discern the directionality of cause and response, that is whether fire is driving elephant distribution and abundance (cause) or if the distribution and abundance of elephants is forming and/or maintaining fire regimes (effect) or both (Asner et al., 2015; Levick et al., 2015). In other words, are higher fire frequencies changing elephant space-use intensity or are changing elephant distribution and abundance patterns shifting fire frequencies as they alter tree-grass dynamics? Dublin et al.'s (1990) work in the Serengeti highlighted both elephants and fire as mechanisms of multiple stable states in that ecosystem. In their study, fire was identified as the catalyst of vegetation change from woodland to grassland but that elephants were the maintenance agents of this state change (Dublin et al., 1990). In Kruger, decision makers can use the resource selection functions presented here to glimpse potential future elephant distribution and abundance scenarios under different climate change projections, available surface water changes and/or fire regime shifts. Results may also be used to guide management decisions surrounding possible space-use manipulation experiments described by Ferreira et al. (2012).

4.3 | Elephant space-use intensity change

Long-term distribution and abundance patterns of elephants in Kruger have without question changed from 1985 to 2012 (Figure 3b). Areas identified as significantly increasing or decreasing in densities are however spatiotemporally dynamic (Figure 3a). Significant changes were strongly associated with distance to rivers, with the majority of marked increases happening <1 km from major rivers (Supporting Information Figure S4b). This could suggest that density-dependant changes are being felt more strongly than suggested by Ferreira et al. (2017).

Fire is also a potentially significant agent of change, where the magnitude of density increase appears to shrink as fire frequencies increase (Supporting Information Figure S4a). This may however be an artefact of elephant densities increasing in riparian areas, which are inherently less likely to burn and therefore have low fire frequencies. Nevertheless, drawing on Figure 3b managers may be able to identify possible "impact hotspots" and focus research into the more empirical effects of increased elephant densities, like changes to vegetation structure and associated species diversity, and potential ecosystem regime shifts (Ferreira et al., 2012; Kerley et al., 2008; Scholes & Mennell, 2008).

4.4 | Elephant group-type distribution change

Over the same period (1985–2012), the probability of encountering bull versus herd groups has also changed, suggesting that there is strong evidence of more pervasive density-dependent effects. From Figure 5, one can see herd groups moving north of the Olifants River

while bulls shift further south. In synchrony, bull groups are now also occupying areas closer to rivers as herds expand outwards into the uplands (Figures 4d and 5). This strongly supports the hypothesis that as elephant numbers grow, empty space becomes more limiting and elephants bleed into previously unoccupied areas. Added to this, the probability of encountering bull groups has increased in areas with shorter fire return intervals, while the probability of encountering herd groups has increased in areas experiencing more intermediate fire frequencies (Figure 4c). Since bull elephants generally cause more damage to larger tree species (Guy, 1976; O'Connor, Goodman, & Clegg, 2007) and coupled with the impacts of fires, we can only speculate as to the long-term effects these shifts in bull dominance may have on the ecosystem as elephant numbers continue to grow. For example, have elephants and fire acted together to change the system significantly enough to detect changes in elephant distribution patterns, and are these changes in response to changing fire frequencies driven by increasing elephant densities? If this is the case, these interacting effects may result in similar state changes as were seen by Dublin et al. (1990) in the Serengeti. Further exploration of our results may also help disentangle drivers of tree mortality in Kruger. That is, does tree mortality occur in response to elephant-fire interactions (Shannon et al., 2011; van Wilgen et al., 2014) or does fire act alone to accelerate tree loss in elephant populated areas (Levick et al., 2015)? Either way, tree loss may be more intrinsically linked to changes in elephant space-use intensity than originally expected. A deeper understanding of Figure 5 and the recently bull-dominated areas identified therein, may help managers determine whether large trees are lost at a faster rate in these areas or not.

4.5 | Limitations

Causes and effects are difficult to disentangle in ecological studies, making it almost impossible to identify primary drivers or mechanisms with only simple regression techniques (MacFadyen, Hui, Verburg, & Van Teeffelen, 2016). Future studies may wish to employ techniques like Structural Equation Models (SEM) to help tease apart cause and effect relationships affecting elephant distribution and abundance patterns. The ability to include interaction terms into MPPM's in future would also allow us to interrogate how these resource selection functions change with increasing densities. Furthermore, the roles played by rivers in elephant distribution patterns could also be explored further by classifying rivers into functional classes, that is does River A act primarily as a water or a riparian vegetation resource? Artificial waterholes should also be considered in future. Despite previous studies highlighting elephant breeding herds tendencies to favour rivers over artificial waterholes (Gaylard, 2015; Smit & Ferreira, 2010; Smit et al., 2007), a recent study by Purdon and van Aarde (2017) presents evidence that artificial water provisioning in Kruger does in fact alter elephant spatial utilization patterns. Using telemetry data from 26 collared female elephants between June 2012 and March 2014, they discuss visitation trends and explore management options in more detail (Purdon & van Aarde, 2017). Understanding how artificial water provision has influenced population-level distribution patterns will make an interesting addition to Kruger management strategies in future. However, long-term data on waterhole open and closure schedules are not yet available. Although, interestingly only seven out of the currently 147 boreholes are greater than three kilometres from a major river (Zambatis, 2012).

5 | CONCLUSION

Kruger's patterns of elephant group-type (bulls vs. herds) segregation, distribution and abundance have shifted in response to increasing space limitations and possible elephant-fire induced regime shifts. Specifically, bull and herd groups are no longer clearly segregated as available empty space becomes more limited. Despite this, bull and herd elephants have dichotomous resource selection functions, in that bulls concentrate in areas receiving lower rainfall but more frequent fires while herds concentrate in higher rainfall areas experiencing less frequent fires. Both bull and herd groups continue to concentrate closer to major rivers, emphasizing rivers as important spatial drivers. Over the study period, densities increased most significantly closer to rivers and in areas experiencing fewer fires. Fire was identified as a strong agent of group-type change, as the probability of finding bulls, instead of herds, increased significantly with increasing fire frequency.

Recognizing the challenges southern African protected areas face to produce practical management solutions for healthy and growing elephant populations, this work aimed to fill some of the biogeographical gaps on what drives the population-level distribution and abundance patterns of Kruger's elephants. Future challenges lie in digesting these insights into a guiding principle for management action and the prioritization of finer scale research into the cascading effects of different elephant space-use intensities. Ideally, this work should help guide experimental management strategies, which aim to alter elephant density and distribution patterns. For example, by manipulating artificial water sources (opening/closing windmills), in areas experiencing fewer fires and which are further than three kilometres from a major river. Ultimately, we encouraged South African National Parks to use the spatiotemporal results herein to focus research into the more empirical effects of high elephant densities.

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DATA ACCESSIBILITY STATEMENT

All data will be made freely available on the South African National Parks (SANParks) online data repository at http://dataknp.sanparks.org/sanparks/

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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