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Survival trends (2008–2020) of three tree species in response to elephant impact, environmental variation, and stem wire-netting protection in an African savanna

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ABSTRACT

Reduced levels of the survival of large trees (≥5 m height) in Africa's savannas are a conservation concern, particularly where large trees co-occur with African elephants (*Loxodonta africana*). Elephants, as ecosystem engineers, can structurally modify and lesson the savanna large tree component. Wire-netting, which involves wrapping chicken-mesh around a tree's main stem, has been used as a mitigation method to increase tree survival. We assess the trends in survival of three large tree species of conservation importance, namely *Lannea schweinfurthii*, *Senegalia nigrescens* and *Sclerocarya birrea*, within the Associated Private Nature Reserves (APNR) on the western boundary of the Kruger National Park, South Africa. We consider survival trends linked by both elephant impact, as well as external environmental factors. We conducted four field assessments on 2,758 trees in 2008 (baseline), 2012, 2017, and 2020, where we recorded i) elephant impact levels on each tree, ii) whether the tree had wire-netting, and iii) the tree's survival status. We then modelled tree survival status as a dependent variable against multiple environmental factors. We found that tree survival was lowest when mean annual rainfall was lowest due to the drought, particularly amongst *L. schweinfurthii* and *S. nigrescens*. Wire-netting significantly increased large tree survival in comparison to control trees over the 12-year period, however, this effect decreased after four years if the wire-netting had lost its structural integrity. We illustrate how various environmental factors, in combination with elephant impact, affect large tree survival in an African savanna with a high density of artificial water points. We also provide results on the longest known study on wire-netting as a mitigation method for elephant impact on large trees and provide evidence on how a period of drought may have accelerated large tree decline in a southern African savanna.

1. Introduction

There has been a continental decline in the number of savanna elephants (*Loxodonta africana*) across Africa over the past two decades (Chase et al., 2016), principally due to the poaching of elephants for ivory (Schlossberg et al., 2020), as well as human-elephant conflict (HEC) (Shaffer et al., 2019) and loss of habitat (Robson et al., 2017). However, in most of the southern African states, elephant numbers and subsequent densities have either stabilised or increased in the same period (Chase et al., 2016). Concerns have been raised though over the impact that increased elephant densities may have on their environment (Owen-Smith et al., 2006). Elephants are both selective of the tree species (Shannon et al., 2008, Abraham et al., 2021) and tree heights (Helm et al., 2009, Cook et al., 2017). Elevated elephant impact levels may therefore potentially eliminate certain tree species (Boundja and Midgley, 2009, Venter and Witkowski, 2010) or height classes (Helm and Witkowski, 2012, Midgley et al., 2020) from a particular habitat over time, thereby affecting dependent fauna species in the process, such as vultures nesting in tall trees (Rushworth et al. 2018). Elephants are also a water-dependent species and generally forage within 15 km of water (Conybeare, 2004). This foraging pattern causes a piosphere effect around the surface water, where elephant impact lessens as the distance to water increases (Gaylard et al., 2003, Van Langevelde et al., 2017). Therefore, in PAs where water is readily available and does not constrain

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elephant habitat use, elephant impacts are relatively homogeneous (Linden et al., 2022).

The debates surrounding elephant densities and large tree survival have largely dominated elephant management plans and research strategies within southern Africa (Owen-Smith et al., 2006, Kerley et al., 2008, Young and Van Aarde, 2011, Henley and Cook 2019), with a range of mitigation strategies, ranging in degrees of severity, success, and ethical concerns, having been implemented in PAs to either limit or redistribute elephant impact both spatially and temporally, to protect large trees, (van Aarde and Jackson, 2007, Ferreira et al. 2017, Henley and Cook, 2019). However, in PAs where elephant impact on trees cannot be spatially manipulated, direct tree protection methods, such as wire-netting trees by placing chicken-mesh around the tree's main stem, have been applied (Derham et al., 2016). Wire-netting has been found to significantly increase large tree survival in PAs containing elephants, by protecting trees from being bark-stripped by elephants (Derham et al., 2016), which leave trees vulnerable to mortality by desiccation (Michaletz and Johnson 2007), fire damage (Helm et al., 2011a), and insect infestation (Wigley et al., 2019). Wire-netting, due to its low costs (Derham et al., 2016), presents PA management with an option to protect many large trees. However, little is known regarding the lifespan of wire-netting if not maintained, and thereby how effective it is as a long-term tree-protection solution.

Besides elephants, however, tree survival in African savannas can be affected by various other ecological factors such as fire frequency and intensity (MacFadyen et al., 2019, Das et al., 2022), termite infestation (N'Dri et al., 2011), as well as drought stress (Jones et al., 2022, Coetsee et al., 2023). In South Africa's Greater Kruger National Park (Greater KNP) for example, long-term data on the effect of fire intensity on trees has revealed that high fire frequencies can have a negative effect on woody biomass (Pellegrini et al., 2017), as well as affecting the recruitment of larger tree species by supressing individuals < 2 m in height (Jacobs and Biggs, 2001). The impact of fires on tree survival is further compounded when combined with previous elephant impact such as bark stripping, as these trees are most vulnerable to being burnt through (Das et al., 2022). Drought stress, conversely, can affect large trees by causing hydraulic failure and the loss of stored carbohydrates, as well as by increasing a tree's vulnerability to biotic attacks due to the low carbon-storage in the plant tissue (Anderegg et al., 2012, Gessler et al., 2017). Studies on the effect that the 2015–2016 *El Niño* Southern Oscillation phenomenon had on large tree species in southern Africa have shown that even without the presence of elephants, there were significant large tree declines due to drought stress (Jones et al., 2022).

Therefore, the aim of this paper was to investigate the trends in survival of three large tree species, namely *Lannea schweinfurthii* (false marula), *Senegalia nigrescens* (knobthorn) and *Sclerocarya birrea* subsp. *caffra* (marula) over a 12-year period within South Africa's Associated Private Nature Reserves (APNR), a savanna system where due to the high density of artificial water points (e.g. Parker and Witkowski 1999), water is readily available to elephants throughout the APNR. These three tree species were selected as iconic tree species and because APNR stakeholders had expressed concerns over decreasing tree numbers due to elephant impact (Henley, 2013). Therefore, our objectives were to i) investigate the survival proportions of the three tree species in the APNR across a 12-year period, ii) to investigate the effectiveness of wire-netting on trees in the APNR across a 12-year period, and iii) to investigate how various environmental factors, in combination with elephant impact, have affected tree survival across three temporal surveys within the 12-year period.

2. Materials and methods

2.1. Study site

The study was conducted in the APNR (24°04 − 24°55 S; 30°82′-31°48′ E), a protected area of 2,089 km^2 sharing an open boundary with the Greater KNP in the north-eastern corner of South Africa (Fig. 1). The APNR is comprised of five private nature reserves, namely the Balule-, Klaserie-, Thornybush-, Timbavati-, and Umbabat Private Nature Reserves, and forms a part of the Great Limpopo Transfrontier Conservation Area Co-Operative Agreement, thereby aligning its management objectives with those of the KNP and surrounding national and international protected areas (GLTFCA, 2020). Mean annual rainfall in the APNR ranges between 400 mm–650 mm, with an average temperature of 22 °C (Greyling, 2004, Peel et al., 2007). The altitude ranges from 300 m–500 m above sea level (Zambatis, 1994). The underlying geomorphology is predominantly comprised of the Basement Complex, made up of gneiss, granite and migmatite rock forms (Venter, 1990). Broadly, the APNR falls within the Savanna Biome of South Africa, specifically located in the Granite Lowveld (SVI 3) and the Phalaborwa-Timbavati (SVI 7) vegetation units (Mucina and Rutherford, 2006). The APNR is considered an environment with excess artificial water points. The mean density of 2.5 waterholes per km^2, is substantially higher than the neighbouring central region of the KNP with a waterhole density of 0.1 per km^2 (Child et al., 2013, Henley, 2014).

Before the fence-line between the APNR and KNP was dropped in 1993, the APNR had an estimated elephant population of 500 individuals (Greyling, 2004). With the fence-line now removed, and the APNR forming part of an open system with the KNP, elephant densities have gradually increased, ranging in density from 0.69 to 2 elephants per km^2 (Peel, 2015). The combined elephant census count for the KNP and APNR is estimated at above 30,000 individuals (GLTFCA, 2022), of which the APNR elephant numbers range between 2,000 and 3,000 individuals (Peel, 2015). As many as 1,200 elephants are predicted to move in between the KNP and APNR on an annual basis (Smit et al., 2020).

2.2. Site and tree selection

Assessments took place on five properties within the APNR, namely Charloscar, De Luca, N'tsiri, Sumatra and Vlakgezicht (Fig. 1). Properties were selected based on the property owners' willingness to be a part of the study (Henley, 2013). Following consultation with the property owners in 2003, the following three tree species were selected as trees of concern due to observed elephant impact on adult trees: *Lannea schweinfurthii* Engl. (false marula), *Senegalia nigrescens* Oliv. (knobthorn), and *Sclerocarya birrea* subsp. *caffra* A. Rich. (marula) (Henley, 2013). We had tagged 2,807 live trees across all properties in 2008, of which 2,758 were used for the analyses of this study as 49 trees could not be reliably relocated in 2012, with variation in tree numbers across species and properties (Table 1) (Henley, 2013). Individuals of these three species had a height of ≥ 5 m (or a reduced height of ≥ 2 m due to previous elephant impact) had their coordinates recorded using a Global Positioning System (GPS) (Henley, 2013). Of these trees, wire-netting was applied to approximately half or 1,395 trees (Table 1). The wire-netting (chicken mesh of 1.8 m length) was wrapped around the main stem of the tree, approximately 50 cm above the ground after measuring the tusk entry heights of impacted trees with no protection (Derham et al., 2016) (Fig. 2). Small holes were cut within the wire where the wire-netting covered hollows within each tree's main stem, ensuring no small fauna would be trapped beneath the wire (Henley, 2013).

2.3. Field surveys and elephant impact assessments

All 2,758 trees were surveyed during the following years: 2008, 2012, 2017, and 2020. All living trees in 2008 were used as the baseline sample size for subsequent surveys. Trees that were recorded as dead in a particular survey were reassessed in the following survey to ensure that the tree's survival status (dead or alive) was correctly recorded.

The following field methodology was carried out on each tree during each survey year: the tree was reassessed by locating it from its previously recorded GPS coordinates. The tree's main stem diameter at breast

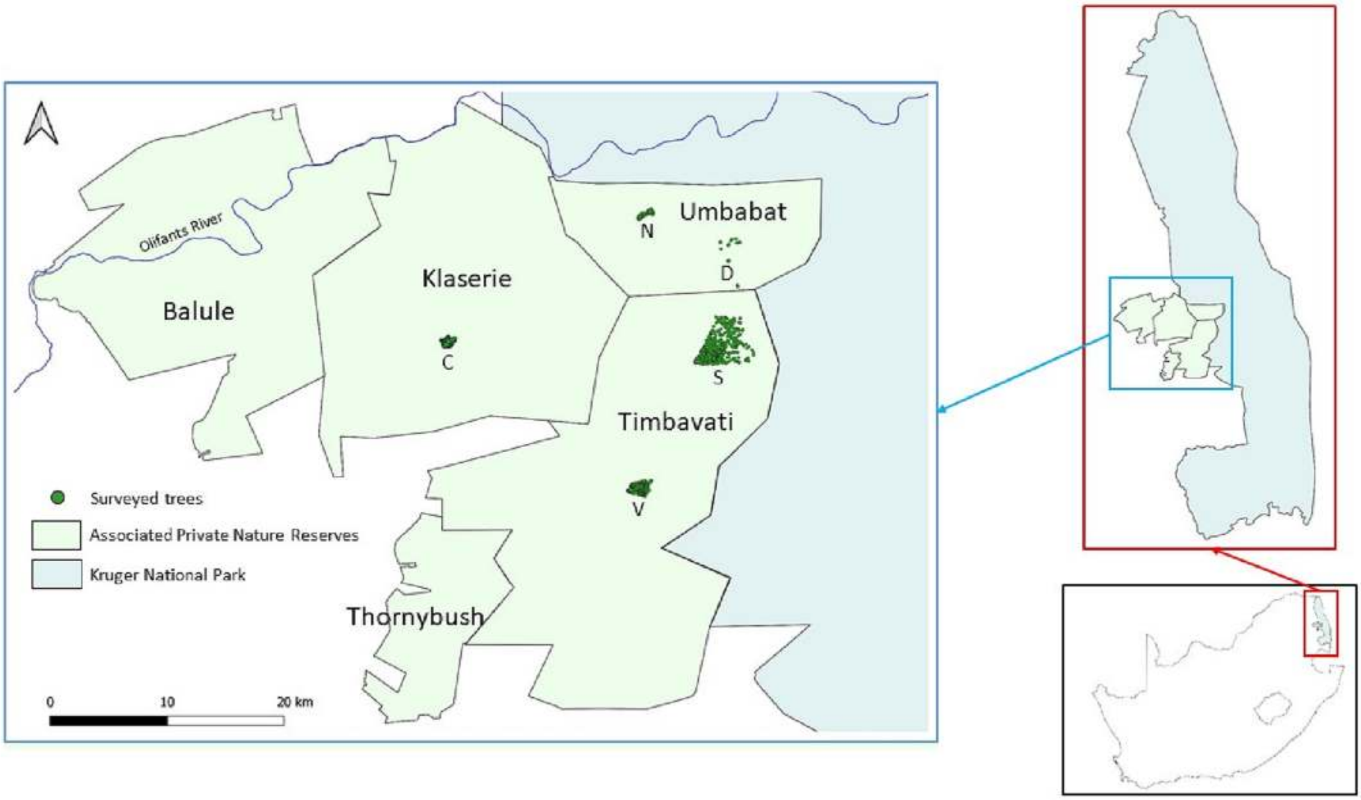

Fig. 1. Location of the surveyed tree species within the Associated Private Nature Reserves (APNR), South Africa from 2008 to 2020. Trees were located on the Charloscar (C), De Luca (D), N'tsiri (N), Sumatra (S) and Vlakgezicht (V) property study sites within three of the five private reserves.

Table 1
Total trees (and those which were wire-netted) recorded across species and properties within the Associated Private Nature Reserves (APNR) by 2008 (the baseline numbers).

	Charloscar (Klaserie)	De Luca (Umbabat)	N'tsiri (Umbabat)	Sumatra (Timbavati)	Vlakgezicht (Timbavati)	Species total
Lannea schweinfurthii	87 (29)	0 (0)	1 (0)	123 (10)	285 (11)	495 (50)
Senegalia nigrescens	323 (185)	3 (3)	69 (40)	323 (284)	115 (19)	833 (531)
Sclerocarya birrea	210 (106)	17 (11)	38 (20)	804 (503)	361 (174)	1,430 (814)
Property total	620 (320)	20 (14)	108 (60)	1,250 (797)	761 (204)	2,758 (1,395)

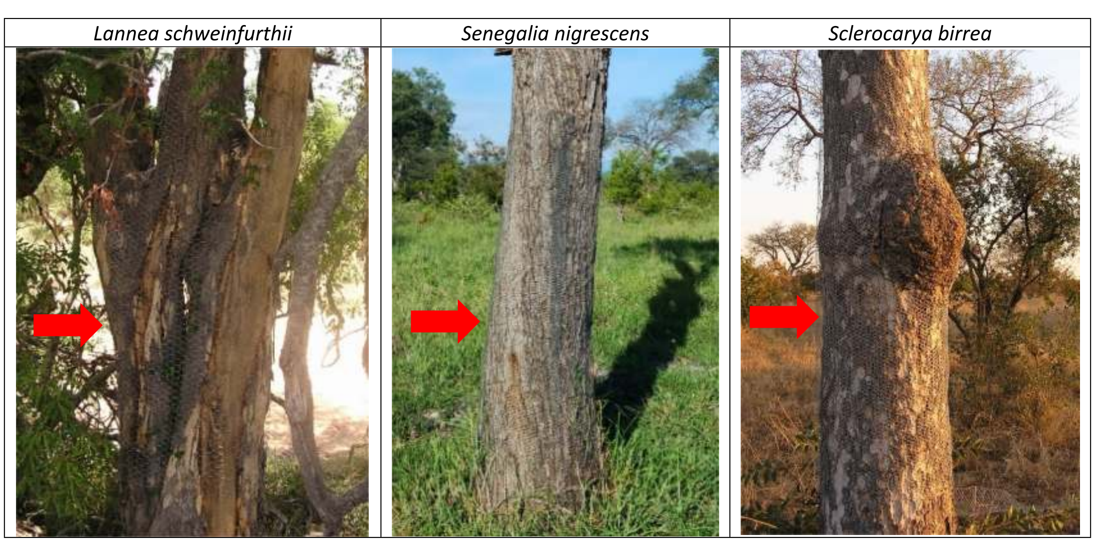

Fig. 2. Examples of wire-netted *Lannea schweinfurthii*, *Senegalia nigrescens* and *Sclerocarya birrea* trees in the Associated Private Nature Reserves (APNR). The wire-netting extends 1.8 m upwards, starting 0.5 m above the ground. Arrows indicate the placement of the wire-netting around the tree's main stem.

height (DBH) was recorded (cm), as well as the presence of termites (*Coptotermes* species) in the tree's main stem. As bracket fungus can lead to the eventual weakening of a tree (Hood 2006), its presence was recorded as an additional factor for the survival analyses. The presence or absence of wire-netting was recorded, as well as the condition of the wire-netting (good, torn, fallen off). A photograph of the full tree was taken, and a 1 m stick was placed next to the tree as a size reference. Tree height was then digitally measured using *VolCalc*, a software program for measuring tree morphometrics (Barrett and Brown, 2012). Elephant impact scores were assessed using published impact scoring methodology (Walker, 1976, Helm and Witkowski, 2013) (Table 2). Previous fire scars on the tree's main stem were also recorded as well as the levels of insect attack (presence and absence) of termites (*Coptotermes* species), and ants (*Crematogaster* species) within the tree' main stem.

Historical mean annual rainfall (mm) records were provided by the APNR management, having been collected from the nearest rainwater gauge within each property, whilst mean elephant bull and breeding herd densities (presented as the mean individuals per km^2 across each survey period) were calculated from the annual census data collected by APNR management (Table 3). Each tree's distance to the nearest surface waterhole (m) was recorded on ArcGIS in three separate measurements using the distance to neighbour tool: distance to any water body, distance to perennial water, and distance to seasonal water. Waterhole layers were provided by Elephants Alive. Perennial and seasonal waterholes were further distinguished using the European Commission's Joint Research Centre's Global Surface Water Mapping Layers (Pekel et al., 2016). Surface water was readily available to elephants during the 2015–2016 *El Niño* Southern Oscillation phenomenon (Smit et al., 2020).

2.4. Statistical analysis

Statistical analyses were performed using R version 4.2.1 (R Development Core Team, 2012) and were considered significant at $p < 0.05$. A Cox proportional-hazards model (Cox model, *coxme* package, Therneau and Therneau, 2015) was used to analyse tree survival over time. A Cox model is a multivariable model used to measure time-to-event outcomes with a set of co-variates (Fisher and Lin, 1999). A Cox model includes a hazard function, or the risk of an event taking place, as well as a time component and an event component with truncated (1) and censored (0) events (Kleinbaum et al., 2012). For our analysis, the death of a tree represented a truncated event, whilst the number of years that a tree survived since project commencement represented the time component.

The following co-variates were originally used in our Cox model: wire-netting presence (categorical), tree species (categorical), stem DBH (categorical), fire scar presence (fire history) (categorical), termite presence (categorical), bull density (continuous), breeding herd density (continuous), distance to perennial water (continuous), and distance to non-perennial water (continuous). Furthermore, the interaction effect of tree stem diameter and wire-netting presence was tested, as wire-netting only protects trees from bark-stripping (Derham et al., 2016), whilst smaller trees are more vulnerable to uprooting and stem snapping by

Table 2
Scoring system for elephant impact on large trees (Helm & Witkowski 2013).

Score	Score Description
0	No impact
1	<50% of the bark around the main stem's circumference has been removed and/or secondary branches have been broken off
2	>50% of the bark around the main stem's circumference has been removed, or one primary branch has been broken off
3	>50% of the bark around the main stem's circumference has been removed and one primary branch has been broken off, or more than one primary branch has been broken off
4	The tree has had its main stem snapped but is coppicing or alive
5	Tree is dead

Table 3
Description of key variables of five properties within the Associated Private Nature Reserves (APNR).

	Charloscar			De Luca			N'tsiri			Sumatra			Vlakgezicht		
	2008–2012	2013–2017	2018–2020	2008–2012	2013–2017	2018–2020	2008–2012	2013–2017	2018–2020	2008–2012	2013–2017	2018–2020	2008–2012	2013–2017	2018–2020
Elephant bull density (elephants/km^2)	0.07	0.28	0.08	0.23	0.25	0.28	0.23	0.25	0.28	0.19	0.14	0.07	0.19	0.14	0.07
Elephant breeding herd density (elephants/km^2)	1.06	0.84	1.15	0.46	1.13	1.22	0.46	1.13	1.22	0.64	1.09	1.35	0.64	1.09	1.35
Mean annual rainfall (mm)	568	415	769	480	406	368	480	406	368	471	367	467	470	424	354
Fire present on property	No	Yes	No	No	No	No	No	Yes	No	No	Yes	Yes	No	Yes	Yes

elephants (Helm et al., 2009). We divided our data into trees with a DBH of < 40 cm and ≥ 40 cm, based off previous research which has shown that trees with a DBH of < 40 cm are more vulnerable to elephant-induced mortality (Cook et al., 2017). We decided to exclude tree height as a covariate for the Cox model, because although tree height and DBH had low correlation scores per species (Pearson's correlation: *L. schweinfurthii* $r^2 = 0.32$, *S. nigrescens* $r^2 = 0.21$, *S. birrea* $r^2 = 0.45$), we selected only DBH for the model to avoid potential collinearity of the factors on the model outcome (Babalola and Yahya, 2019), whilst taking into account that DBH is a more accurate predictor of tree strength (Van Gelder et al., 2006). To reduce the effect that larger continuous data values may have on the Cox model, we log-transformed the bull density, breeding herd density, and both distance to water co-variates. To obtain the final model, stepwise backward selection modelling was used, where the co-variate with the highest p-value was eliminated from the model, before repeating the modelling process. Furthermore, to confirm the final model, we performed a forward selection process, whereby p-values were obtained through likelihood ratio tests of the full model with the selected co-variate against the model without the co-variate, to provide consistent estimates for regression parameters (West et al., 2007).

Classification trees (CT), based on conditional inference (*party* package, Hothorn et al., 2023) were also constructed for each survey period (2008–2012; 2013–2017; and 2018–2020). Using the same co-variates as the Cox model, and here we were able to add elephant impact scores from the previous survey period (Table 2) to model its effect on tree survival. This division allowed for more detailed analyses on how the various predicting variables influenced tree survival across each survey period (see Das et al., 2022). We selected conditional inference for our CT analyses, as this prevents bias towards factors with multiple categories (Strobl et al., 2009). The Breiman and Cutler's Random Forests for Classification and Regression analysis was then used to test which factors carried the most statistically significant importance for each CT (*randomForest* package, Breiman and Cutler. 2022).

3. Results

3.1. General elephant impact and mortality

After 12 years, 66.93% of the trees had died, leaving 912 alive after the 12-year survey (Table 4). A total of 64 trees (2.32% of monitored trees) were recorded as dead due to factors other than elephant impact. These factors included fire ($n = 44$) and insect/other damage ($n = 20$). No elephant impact was recorded on 3.95% of the surveyed trees ($n = 109$) by the end of the surveys (2020). The most common form of elephant impact on trees was branch breakage (25.35%), followed by bark-stripping (17.58%), main stem snapping (12.1%), and uprooting (9%).

Table 4
Mortality levels of monitored trees between 2008 and 2020 in the Associated Private Nature Reserves (APNR), South Africa.

Survey year	Trees classified as living	Trees classified as dead from previous survey	Percentage dead trees (%)	Percentage dead trees per annum (%)	Cumulative dead trees (%)
2008	2758				
2012	2254	504	18.27	4.57	18.27
2017	1440	814	36.11	7.22	47.79
2020	912	528	36.67	12.22	66.93

3.2. Tree survival trends

3.2.1. Wire-netting

After 12 years, 61.65% of the wire-netted trees had died, in comparison to 73.24% of the control trees. Of the surviving wire-netted trees, 81.5% still had their wire-netting in good condition, however, this percentage varied across tree species, with 100% of surviving *L. schweinfurthii* in good condition, versus 85.85% and 77.28% of the surviving *S. nigrescens* and *S. birrea* respectively. According to the Cox model, we found that the presence of wire-netting significantly increased tree survival over the study period (hazard ratio = 0.72, $p < 0.001$, Table 5), whilst survival proportions of trees significantly increased for trees with larger DBHs (hazard ratio = 0.39, $p < 0.001$, Table 5). The interaction of wire-netting presence and trees with a larger DBH (>40 cm) had the greatest effect on improving tree survival (hazard ratio = 0.29, $p < 0.001$, Table 5). Trees with wire-netting that had DBHs ≥ 40 cm had the greatest survival proportions (Fig. 3). Interestingly, the CT analysis showed that wire-netting was a significant co-variate of tree survival during the 2008–2012 survey period, after which it did not feature in the 2013–2017 and 2018–2020 CTs (Table 6). During the 2008–2012, 23.87% of the control trees had died in comparison to only 4.94% of the wire-netted trees.

3.2.2. Tree species

After 12 years, the total number of dead trees for each tree species included 496 of 833 *S. nigrescens* (59.5% of species sample or 4.9% dead per annum), 336 of 495 *L. schweinfurthii* (67.8% of species sample or 5.7% dead per annum), and 1,014 of 1,430 *S. birrea* (70.9% of species sample or 5.9% dead per annum). According to the Cox model, the species of tree had a significant effect on the trees' survival proportion ($p < 0.001$), with *S. nigrescens* having a higher survival proportion in comparison to *L. schweinfurthii* (hazard ratio = 1.23, $p < 0.001$, Table 5) and *S. birrea* (hazard ratio = 1.47, $p < 0.001$, Table 5, Fig. 4) for the 12-year period. When analysing the individual survey periods, the CT analyses identified tree species as significant co-variate during the 2018–2020 CT analysis ($p < 0.001$, Table 6), whereby the survival proportion of *S. birrea* was significantly lower in comparison to *L. schweinfurthii* and *S. nigrescens*.

3.2.3. External ecological co-variates

Previous fires had occurred on four of the five study properties (Table 3), and the Cox model showed that exposure to fire significantly decreased tree survival proportions (hazard ratio = 1.27, $p < 0.001$, Table 5). According to the CT analyses, fire was a significant co-variate ($p < 0.001$) negatively affecting tree survival during the 2008–2012 survey period (Table 6), particularly on the N'tsiri and Vlakgezicht properties. The trees on the Sumatra and Vlakgezicht properties were

Table 5
The reduced Cox proportional-hazards model (with coefficients, hazard ratios, standard errors, and z- and p-values) for tree survival between 2008 and 2020 in the Associated Private Nature Reserves (APNR). n = 2,758, number of events = 1,510 (dead trees).

Variable	Coefficient	Exp (Coefficient)/ Hazard ratio	Standard error	*z*-value	*p*-value
Wire-netting (WN)	−0.32	0.72	0.05	−6.24	<0.001
Diameter at breast height (DBH)	−0.94	0.39	0.16	−5.94	<0.001
Fire	0.23	1.27	0.07	3.58	<0.001
Tree species	0.12	1.31	0.31	4.03	<0.001
Mean annual rainfall	−1.16	0.31	0.29	−4.07	<0.001
WN × DBH	−1.25	0.29	0.33	−3.76	<0.001

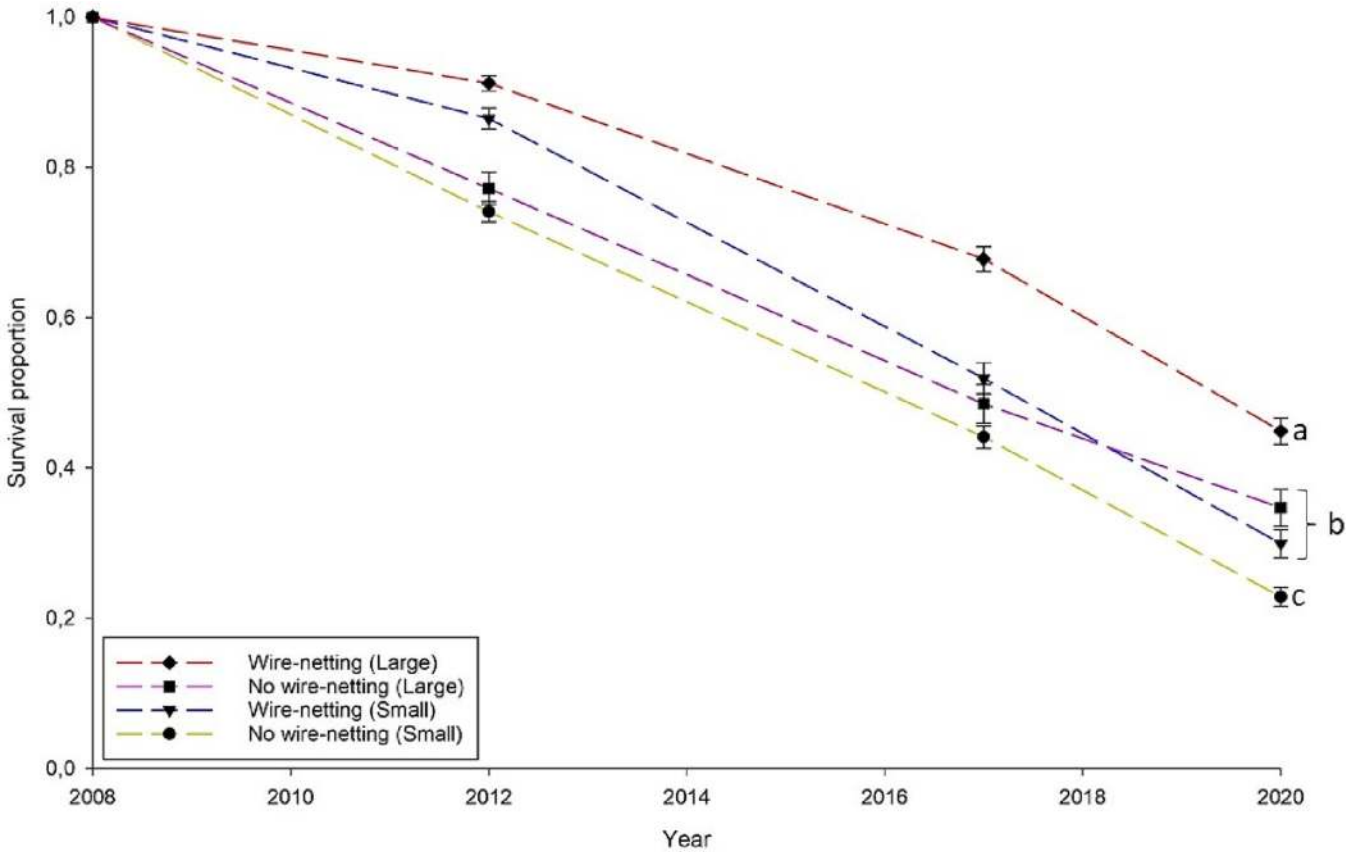

Fig. 3. Survival proportions of wire-netted and control (no wire-netting) trees of small (<40 cm) versus large (≥40 cm) stem diameters (diameter at breast height) over three time periods between 2008 and 2020 in the Associated Private Nature Reserves (APNR), South Africa. Different letters (a,b) indicate a significant difference in survival proportions.

Table 6
Classification tree analyses of the significant co-variates affecting the survival proportions of three large tree species within the Associated Private Nature Reserves (APNR) across the three survey periods.

Survey period	Significant co-variates	p-value
2008–2012	Wire-netting	<0.001
	Fire presence	<0.001
2013–2017	Previous elephant impact	<0.001
	Mean annual rainfall	<0.001
2018–2020	Previous elephant impact	<0.001
	Mean annual rainfall	<0.001
	Tree species	<0.05

also exposed to fire in both the 2013–2017 and 2018–2020 survey periods. The Cox model also found that tree survival proportions significantly increased where MAR was higher (hazard ratio = 0.31, $p < 0.001$, Table 5). According to the CT analyses, an increase in MAR had a significantly positive effect ($p < 0.001$) on tree survival during both the 2013–2017 and 2018–2020 survey periods (Table 6). These survey periods occurred during and after the 2015–2016 *El Niño* Southern Oscillation phenomenon respectively. The CT analyses also found that trees which had high levels of elephant impact (impact score = 4, Table 2) had significantly lower survival proportions ($p < 0.001$) during the following survey period than if elephant impact scores were between 0 and 3 (Table 6).

4. Discussion

4.1. Wire-netting as a mitigation method

To our knowledge, this represents the longest study focussed on the efficacy of wire-netting as an elephant mitigation method. We found that wire-netting significantly increased the survival proportions of all three tree species across the 12-year study period. However, the difference between the mortality rates of the wire-netted and control trees was greatest during the first four years of the study, with relatively similar rates of declines for the remaining eight years. Wire-netting can be highly effective at mitigating against bark-stripping, as elephants cannot chisel an edge of bark with their tusks to rip the bark off further (Derham et al., 2016). However, the trees do remain vulnerable to heavier, albeit less frequent forms of elephant impact such as stem snapping and uprooting (Derham et al., 2016, Cook et al., 2018). Both stem snapping and uprooting are most common on smaller trees, which are easier for elephants to push over (Helm et al. 2009), and our results highlight that wire-netting is most suitable for larger-stemmed trees.

Whilst both Derham et al. (2016) (a four-year study) and Cook et al. (2018) (a one-year study) provide evidence for the effectiveness of wire-netting at increasing tree survival, our study provides evidence on how wire-netting can also lose its effectiveness if not maintained. At our study sites, over one fifth of the wire-netted trees had chicken mesh which had either been torn, rusted, or fallen off the trees' main stems, rendering the wire-netting ineffective at protecting the tree against bark-stripping. Cook et al. (2018) predicted that wire-netting would be effective for up to five years, after which the chicken-mesh may need replacing. Our results suggest that after four years, conservation managers should consider replacing the chicken-mesh on the trees where

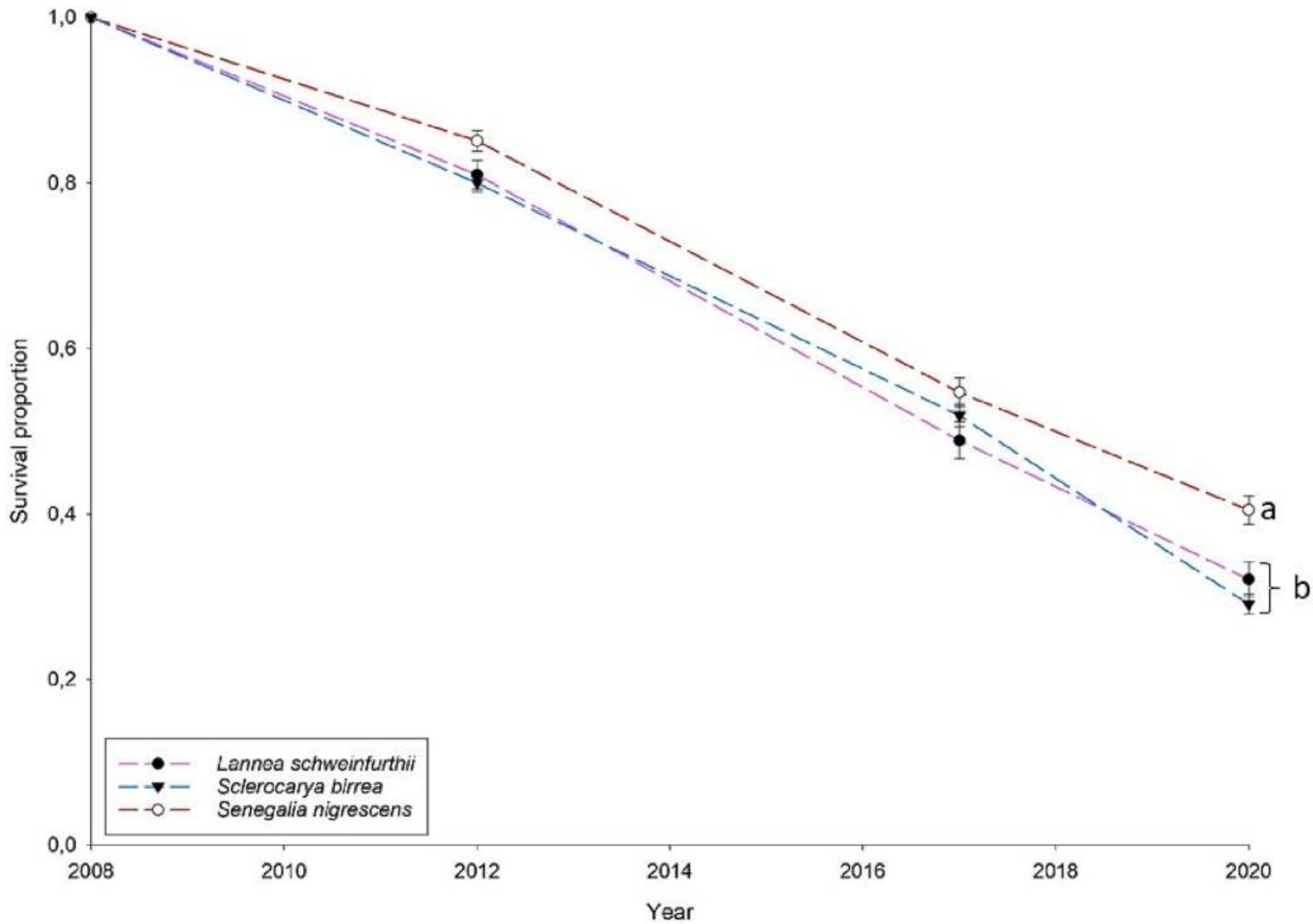

Fig. 4. Survival proportions of three tree species over three time periods between 2008 and 2020 in the Associated Private Nature Reserves (APNR), South Africa. Different letters (a,b) indicate a significant difference in survival proportions according to the Cox proportional hazards model.

required to maintain the wire-netting's effectiveness.

4.2. Tree species survival with environmental factors

The numbers of adult *L. schweinfurthii*, *S. nigrescens* and *S. birrea* have been steadily declining in the APNR since 2008. The overall percentage of dead trees per annum for our study was 5.58% (range = 4.6-12.2%). These percentage rates are higher than those recorded over a 12-year study by Das et al. (2022) further east within the Greater KNP on ten different species, where the percentage of dead trees per annum ranged between 3% and 5%. All three tree species experienced increased rates of decline after the initial 2008 – 2012 survey. This initial survey took place before the 2015–2016 *El Niño* Southern Oscillation phenomenon, after which mean annual rainfall largely decreased across the APNR (Table 3). Elephants, in general, increase their browse intake, and hence tree impact, during the drier months when grass quality decreases (Greyling 2004, Codron et al., 2006), and their impact on large trees may be further amplified during times of drought (Thornley et al., 2020).

Regardless of elephants, however, recent studies have shown that the 2015–2016 *El Niño* drought phenomenon caused a decline in large tree densities in southern Africa (Jones et al., 2022, Trotter et al., 2022, Coetsee et al., 2023). Die-back of trees can occur when there is reduced surface water availability (MacGregor and O'Connor, 2002). Both *L. schweinfurthii* and *S. nigrescens* have shallow rooting systems (Midgley et al., 2005, Zhou et al., 2020), and would be vulnerable to water stress and competition for soil water in comparison to trees with deeper rooting systems (Jones et al., 2022).

The increased percentage of dead *S. birrea* during the final survey period (2018–2020) may be explained by a fire which moved through the Sumatra and Vlakgezicht properties, where a large percentage of the sampled *S. birrea* occurred. Adult *S. birrea* are vulnerable to intense fires (Jacobs and Biggs, 2001, Helm et al., 2011b; Helm et al., 2011a), particularly after receiving elephant impact (Das et al., 2022). Bark-stripped trees, for example, are more susceptible to fires and subsequent desiccation, which would decrease tree survival (Moncrieff et al., 2008, Helm et al., 2011a). Our results emphasize how historical elephant impact can have a significant effect on tree survival in future years, particularly in relation to fire.

Distance to both perennial and non-perennial water did not show up as significant factors for tree mortality in our models, and we suggest that this is because surface water had a uniform effect on tree survival (Linden et al., 2022). In a savanna system where water is readily available to elephants through the provision of artificial waterholes, a piosphere gradient cannot be maintained (Lange, 1969), and thus elephant impact may be homogenised across the system (Linden et al., 2022). As elephants are a water-dependent species, their distribution is closely linked to the distribution of water, which may explain why neither bull nor breeding herd density stood out as significant factors in our model.

4.3. Management implications and recommendations

For savanna systems where water is readily available to elephants, the options that managers have to decrease or distribute elephant impact gradients across the system are limited (Henley and Cook, 2019).

Elephants are selective feeders (Greyling, 2004), and tree densities are decreasing in PAs where elephant impact cannot be spatially and temporally managed (Cook et al., 2017). Therefore, mitigation methods which directly protect large trees, such as wire-netting, may be effective at prolonging the trees' survival proportions in these PAs (Henley and Cook, 2019). Maintencance of wire-netting though, will be required after four years. However, our data also shows that other environmental factors such as fire, particularly in areas of low MAR or during a drought period, may be consequential to decreasing large tree densities, especially on trees with previous elephant impact. Whilst beyond the scope of this study, understanding how tree survival is affected by different fire regimes across various rainfall gradients and soil profiles will help provide management with a better understanding when planning regional fires (Coetsee et al., 2023). Future studies into the recruitment rates of these three species would better help conservation managers understand whether new saplings are replenishing the loss of these large adult trees.

5. Conclusion

Our study provides evidence on how a complexity of environmental factors have affected the mortality trends of three large tree species within the APNR savanna system over a 12-year period. Our results suggest that wire-netting can be used as a mitigation method to significantly increase tree survival proportions by reducing elephant impact on these trees. However, as our survey data stretches over a 12-year period, our results suggest that conservation managers will need to look at replacing wire-netting four years after wrapping the trees to ensure that the wire-netting has not lost its structural integrity. Our results have also shown that tree survival was positively affected by an increase in mean annual rainfall, and negatively affected by fire events. These results provide important insights into how various environmental factors have influenced large tree survival where trees co-occur with elephants.

CRediT authorship contribution statement

Robin M. Cook: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Ed T.F. Witkowski** Formal analysis, Supervision, Validation, Writing – review & editing. **Michelle D. Henley:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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