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Persistence of the African baobab (*Adansonia digitata* L.) in a system experiencing chronic utilization by elephants

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Abstract

Chronic utilization of woody vegetation by African savanna elephants may transform woodland vegetation to open savanna and threaten the extirpation of targeted species. This situation has arisen in Gonarezhou National Park (GNP), Zimbabwe, where a large elephant population (>2 km^{-2}) threatens the persistence of the long-lived baobab (*Adansonia digitata*) tree, through elevated mortality levels. This study investigated whether complete or partial refugia from elephant utilization existed for baobabs, and whether protection of trees by management, using wire netting or log- or rock-packs around a tree base, had been effective. A total of 563 baobabs were sampled across northern GNP. Elephants had debarked 99% of trees to some degree, and gouged holes in the stem of 22% of trees. The probability, and severity, of debarking and gouging decreased with increasing distance to permanent water, increasing slope, and the amount of boulder cover. Slope gradient had the greatest effect on elephant impact, with trees located on steep slopes being less affected by elephants than those on flat ground. Distance to water had an effect despite the farthest tree, at 9 km from water, being within the 15 km foraging range of bull elephants. Large boulders partly protected trees even on gentle terrain. None of these factors provided a complete refuge from elephant impact within GNP, but, individually and collectively, provided a partial refuge at current elephant densities. Protection measures doubled tree survival over approximately 5 years, with fencing wire wrapped around baobab stems proving to be the most effective method. Assessment of the future security of baobabs in GNP requires knowledge of their distribution and that of the refugia provided by distance from permanent water, slope, and boulder cover.

KEYWORDS

baobab refugia, debarking, elephant impact, plant–animal interactions, wildlife management

1 | INTRODUCTION

Natural systems are experiencing unprecedented pressures that threaten their configuration (Millennium Ecosystem Assessment, 2005; Shukla et al., 2019). While research efforts in natural areas have increasingly focused on the impacts of global scale drivers in recent decades, particularly global climate change, the effects of

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local scale drivers remain important. However, the impact of local drivers may potentially exceed those of global drivers in some circumstances, especially for species constrained to an island-like system. Protected areas should serve as the mainstay of biodiversity conservation, but many of these have become islands in a human-transformed landscape. Many protected areas in Africa now function as a closed system, with reduced movement of many species between the park and the outside area (Boone & Hobbs, 2004; van Aarde & Jackson, 2007). For protected areas, the effect of species that can drive conspicuous changes in ecosystem structure and functioning is expected to be of critical importance in the medium term. An example for African parks is change in the abundance of the African savanna elephant (*Loxodonta africana*) that can transform the composition, structure, and functioning of woodland (Cumming et al., 1997; Guldemond & van Aarde, 2008; Ripple et al., 2015; van Langevelde et al., 2003).

The range of the African elephant has contracted to 15% of its former extent (Chase et al., 2016), and populations over most of this range have declined conspicuously as a consequence of poaching and habitat loss (Bouché et al., 2011; Douglas-Hamilton, 1987). By contrast, elephant populations have increased in many southern African protected areas over the past few decades (Stephenson, 2004). Impacts of this ecosystem engineer (Fritz, 2017; Western, 1989), which can convert forests and woodland into open savanna or grassland (Laws et al., 1975), have increased in protected areas over the last few decades owing to an increase in elephant density (Hanks, 1979; Laws et al., 1975). Local elephant densities may exceed 0.5–1 elephant km^{-2}, above which conspicuous changes in woodland structure occur (Baxter & Getz, 2005; Cumming et al., 1997; Thomson, 1975), noticeably around artificial water points (Gaylard et al., 2003; Tafangenyasha, 1997a; Wilson et al., 2021).

Chronic elephant impact on woody vegetation may lead to extirpation of vulnerable plant species (Laws et al., 1975; O'Connor et al., 2007), and animal species reliant on woody vegetation (Cumming et al., 1997; Fenton et al., 2008). The iconic African baobab (*Adansonia digitata* L.), widely distributed across sub–Saharan Africa (Wickens, 1982), is a species of concern. Baobabs provide habitat and food for birds, bats, baboons, elephants, antelope, and many invertebrate species (Wickens, 1982). Although the deciduous character and height (>20 m) of trees limit the availability of their foliage to elephants, baobabs are extensively debarked, and often ringbarked, by elephants (Barnes, 1980; Wickens, 1982; Figure S1). Unlike most other woody savanna species, ringbarking is not necessarily fatal because baobabs can regenerate new bark (Barnes, 1980; Kotina et al., 2017; Wickens, 1982). However, elephants may also gouge the trunk to consume the moist pulp, enlarging the cavity until the tree collapses and dies, an activity that is executed mostly by bulls during the dry season (Barnes, 1980; Swanepoel, 1993; Swanepoel & Swanepoel, 1986; Weyerhaeuser, 1985; Figure S1). Elephants have been found to cause between 1.1% and 3.0% annual mortality of adult baobabs, at elephant densities of 1.6–4.9 elephants km^{-2} (Barnes, 1980; Barnes et al., 1994; Caughley, 1976; Kupika et al., 2014; Ndoro et al., 2015; Swanepoel, 1993; Swanepoel & Swanepoel, 1986; Weyerhaeuser, 1985).

Low, episodic recruitment (Mayne et al., 2022; Venter & Witkowski, 2010, 2013), slow growth (Barnes, 1983; Wilson, 1988), and the ease of destruction by elephants are attributes of the long-lived baobab (up to 1835 years, Patrut et al., 2013) which threaten their persistence in protected areas that support high elephant densities (Barnes, 1980; Edkins et al., 2007; Swanepoel, 1993). However, spatial refugia that preclude or limit elephant access may ensure their persistence in the face of increasing elephant pressure (O'Connor et al., 2007). An absolute refuge confers complete protection, which may be an inaccessible area (cliffs; Weyerhaeuser, 1985), or the area beyond an elephant's foraging range from water, approximately 15 km (Conybeare, 2004). A partial refuge occurs with increasing distance from water because a baobab has a decreasing probability of encounter with an elephant (O'Connor et al., 2007). Accordingly, baobabs closer to permanent water show greater elephant damage, lower survival, and a lower population density than baobabs farther away (Kupika et al., 2014; Ndoro et al., 2016; Swanepoel, 1993). However, the effectiveness that distance from permanent water serves as a refuge may be compromised if the fleshy pulp of a baobab's trunk is used as a water source by elephants (Fenner, 1980; Tsoumis, 1991; Wickens, 1982). The provision of permanent artificial water may promote access to previous complete refugia by elephants, or increase the frequency with which elephants can access partial refugia (O'Connor et al., 2007; Western, 1975; Wilson et al., 2021).

Baobabs in rugged terrain may be less likely encountered by elephants because they prefer gentle terrain (Nellemann et al., 2002; Thomson, 1975; Weyerhaeuser, 1985), consistent with elephant impact decreasing as slope steepness and rockiness increased at one location (Edkins et al., 2007). Large boulders on level terrain can therefore be expected to reduce elephant impact. The nature of refuges may also differ between the elephant sexes. First, calves constrain cow-calf herds to within 5 km from water, whereas bulls can forage up to about 15 km (Stokke & du Toit, 2002). Second, bulls may

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experience greater difficulty in negotiating rugged terrain because they are twice the mass of cows (Laws, 1966). Elephants often use roads, such that their impact is expected to decrease with increasing distance from a road (van Wyk & Fairall, 1969), although this pattern was not found for *Sclerocarya birrea* in one park (Gadd, 2002). Elephants actively select for plant communities (van Wyk & Fairall, 1969; Viljoen, 1989), and a baobab within an unfavorable plant community may receive less attention than one within a preferred community (Baraza et al., 2006). Soil fertility influences patterns of elephant utilization (Asner & Levick, 2012; Pretorius et al., 2011), such that baobabs growing on less fertile soils may receive less attention from elephants.

Gonarezhou National Park (GNP), Zimbabwe, provides a useful case study for examining whether baobabs can persist under high elephant densities. Since the proclamation of the park in 1975, elephant numbers have risen from <1 elephant km^{-2} before 1992 to >2 elephants km^{-2} since 2009 (Dunham, 2012, 2022). Current density is four times higher than the threshold of 0.5 elephant km^{-2} above which elephants are considered to transform woodlands (Baxter & Getz, 2005; Cumming et al., 1997; Thomson, 1975). Consequently, elephants have severely impacted the woody vegetation of GNP (Cunliffe et al., 2012), and have damaged 71%–84% of baobabs across GNP, especially targeting large individuals closer to permanent water (Kupika et al., 2014; Mashapa et al., 2014; Mpofu et al., 2012). Park management has responded since 2015 by protecting individual baobab trees using methods which include the wrapping of stems with wire fencing, or packing a band of rocks or logs around a tree base (Derham et al., 2016; Henley & Cook, 2019). The success or efficacy of these methods has not been assessed.

Baobabs are an iconic component of African savannas, support considerable faunal diversity, and contribute to ecosystem functioning. If current levels of elephant utilization persist, baobabs may become extirpated within GNP, unless absolute or partial refugia from elephant impact exist. Protecting individual trees may prove fruitless if the methods of protection do not improve chances of survival. Defining potential refugia from elephant impact would further assist in identifying particularly vulnerable baobabs and guide the selection of trees for protection. This study therefore addressed two main questions. The first was whether increasing distance from permanent water, increasing slope, and greater protection from boulders or other vegetation, afford baobabs a partial or complete refuge from elephant impact. The second was whether protection increases baobab survival and, if so, which method is the most effective?

2 | METHODS

2.1 | Study area

Gonarezhou National Park (GNP) (21° 00′ to 22° 15′ S; 30° 15′ to 32° 30′ E) covers 5053 km^2 in the southeast lowveld of Zimbabwe (Figure 1), and ranges in altitude from 165 to 578 m above sea level. GNP was proclaimed as a national park in 1975. The park has a semi-arid climate, with a mean annual rainfall of 500–600 mm. The northern and western boundaries of the park are fenced, but the eastern boundary remains unfenced (Dunham, 2022). The study was restricted to northern GNP (Figure 1). Geology of this region consists of a basalt plain in the north-west, a granophyre igneous intrusion forming the higher-lying central area, the Malvernia sedimentary beds under much of the remainder, and alluvial deposits adjacent to non-rocky portions of the main rivers (Cunliffe et al., 2012). Basalt-derived soils are fertile, granophyre-derived soils are of intermediate fertility, sandveld derived from the Malvernia beds is relatively infertile, and alluvial deposits contain both fertile clay-rich areas and infertile sandy areas (Cunliffe et al., 2012). The distribution of the woodland vegetation types of GNP is determined largely by geology (Cunliffe et al., 2012).

The perennial Runde and Save Rivers drain northern GNP. Massasanya and Bhenji Dams, built in the 1970s, are the only artificial water sources (Tafangenyasha, 1997a). Some seasonal tributaries of the Runde River usually hold water throughout the year, while several seasonal pans hold water for variable durations during the dry season (Figure 1).

Elephant density was maintained at <1 elephant km^{-2} between 1969 and 1992 through population reduction and the impact of the 1991/1992 drought, whereafter the population increased at a mean annual rate of 6.2% until 2009 (Dunham, 2012) and has maintained a density of >2 elephants km^{-2} until 2022 (Dunham, 2022). Elephants, in concert with fire and drought, have transformed closed woodland to open woodland or grassland (Cunliffe et al., 2012; Tafangenyasha, 1997b). By 2012, 71%–84% baobabs in GNP had been damaged by elephants (Kupika et al., 2014; Mashapa et al., 2014; Mpofu et al., 2012), and this level is expected to have increased after another decade of chronic elephant utilization. A program of protecting individual baobabs commenced in 2015, initially by packing rocks or logs around the tree base (Henley & Cook, 2019), then in later years by wrapping the trunk with wire fencing, a technique which is effective for other species (Derham et al., 2016).

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2.2 | Sampling strategy

Baobabs were sampled between September and November 2022, recording the GPS position of each tree using a Garmin® eTrex 10 GPS. The height of each tree was determined using a laser rangefinder (Vortex Impact 1000). For a mostly dead tree, the height of the highest living coppice and the height of the tallest dead stem were measured. Tree circumference was measured at 1.3 m above ground, or as close as possible depending on branching, from which stem diameter was calculated. For multi-stemmed trees, stem diameter was calculated from the sum of stem areas.

2.2.1 | Potential refugia from elephant impact

A total of 377 live, unprotected trees was sampled to investigate the factors influencing elephant impact (Figure 1). For security reasons, sampling was restricted to the road network, hill ridges and adjoining slopes. The approach covered the main gradients of distance from permanent water, macro-topography and variability in local terrain. Smaller individuals were also included in the sample but no active search was made for baobab seedlings.

2.2.2 | Survival of protected and unprotected trees

A total of 232 known, live individuals recorded from 2013 to 2020 (geotagged when first sampled) were revisited in 2022 (Figure 1), of which 107 had been protected in various ways (Table 1) between 2015 and 2020, and 125 were left unprotected. Fencing involved wrapping diamond-mesh wire around the trunk from the ground up to approximately 3 m. Rock and log packing involved tightly packing a 2–3 m wide band of rocks or logs around the base of a tree. Upon revisiting an individual, life state was recorded, and apparently dead individuals were checked for any coppice growth. Dead, non-standing individuals were identified as a depression in

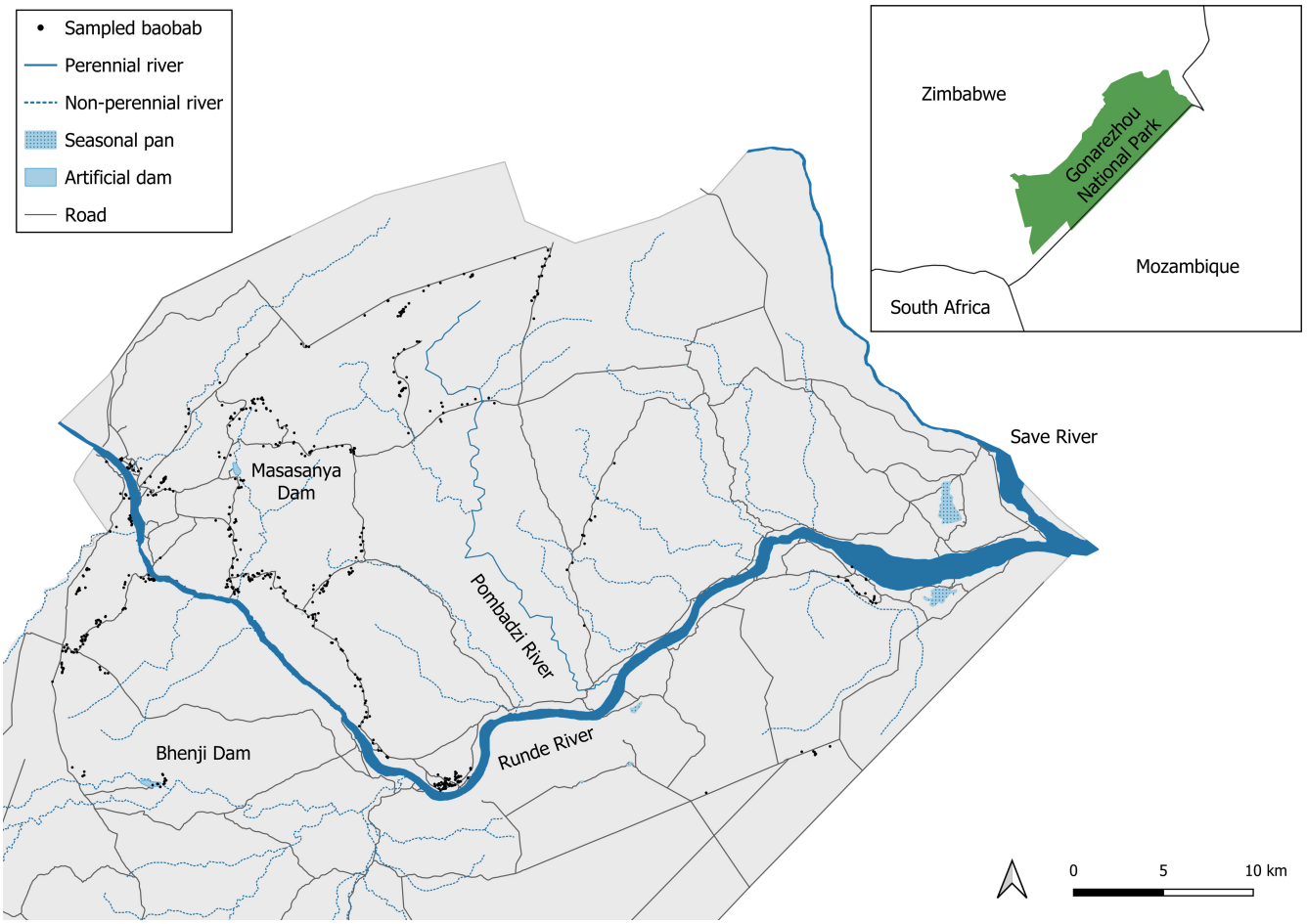


FIGURE 1 Map showing the distribution of sampled baobabs in northern Gonarezhou National Park, Zimbabwe, with the inset showing the location of the park.

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TABLE 1 Breakdown of the number of known trees that received protection between 2015 and 2020, and the number of trees protected in each manner.

	Protected known baobabs						Unprotected known baobabs
	107						125
	Protection method						
	Fence	Rocks	Logs	Fence + rocks	Fence + logs	Rocks + logs	
Year of protection	20	72	3	7	1	4	
2015	1	31	0	5	0	2	
2018	2	24	0	0	0	0	
2019	3	4	0	0	0	0	
2020	2	0	0	0	0	0	
Unknown	12	13	3	2	1	2	

the ground, usually containing some fibrous material. Included in the database for determining survival was a set of 33 landscape photographs that each showed one or more baobabs, taken in September 2013 and rephotographed in August 2022. A non-visible baobab was assumed to have died.

Intactness of the protection applied to a tree was assessed. Fencing was assessed in terms of holes or wire pulled from either end, and the amount of bark growth over fencing was estimated using a five-point scale (0 = none; 4 = bark had completely grown over sections). Rock or log packing was considered intact if there were no obvious paths through the packing. An average width and height of a rock or log band around a tree was measured along four perpendicular transects radiating from the tree.

2.3 | Quantifying elephant utilization

Elephant damage by canopy loss, debarking, or gouging was estimated for each tree. For multi-stemmed trees, estimates were the average of each stem.

2.3.1 | Canopy loss

The percentage canopy volume lost to elephants was estimated using an eight-point scale (Anderson & Walker, 1974): 0, 0%; 1, 1%–10%; 2, 11%–25%; 3, 26%–50%; 4, 51%–75%; 5, 76%–90%; 6, 91%–99%; 7, 100%. This included "near-dead" trees with coppice.

2.3.2 | Debarking

The extent of debarking was quantified as the proportion of the circumference that had been debarked (measured to the nearest decimeter). Debarking was categorized as either recent (<1 year) or old (>1 year). Recent debarking is paler in color than older debarking, and fibrous tissue usually remains (Edkins et al., 2007). Bark reforming was noted, as was the position of debarking in relation to the immediate slope around a tree (upslope, downslope, contour).

2.3.3 | Gouging

The width, depth, and vertical length of a gouged hole were measured. Volume of each gouge was calculated based on an elliptic cone, and a total was summed for trees with multiple gouges. This total was used to calculate a "relative gouge volume" as a percent of a cylindrical stem volume up to 4.5 m, which is 1 m above the average height of an adult elephant bull (Laws, 1966).

2.3.4 | Environmental variables

Using the GPS coordinates of each tree, the following variables (i)–(iii) were quantified using a digital elevation model (DEM) of GNP with a spatial resolution of 12 m and produced by ALOS PALSAR (ASF DAAC, 2015), and ArcGIS Desktop® (ESRI, 2021) (Table 2). (i) Perennial surface water available in the late dry season (September–October) was mapped from 1991 to 2019 using satellite images from Landsat 5, 7 and 8 (U.S. Geological Survey), Sentinel-1 (ESA, 2015), and Sentinel-2 (ESA, 2020). An average distance-to-water raster file was created using the modified normalized difference water index (Xu, 2006) for each year and then averaged over years, from which the distance of each sampled tree to perennial surface water was extracted. (ii) The minimum distance of each sampled tree to a road was determined using a line shapefile of roads in GNP. (iii) The macro-

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TABLE 2 Quantified macro-terrain and landscape variables for each sampled tree.

Variable	Units	Minimum value	Maximum value	Sources
Distance to perennial surface water	Meters	132	9050	U.S. Geological Survey; ESA (2015, 2020); B. Clegg (unpublished data)
Distance to a road	Meters	246	1300	Gonarezhou Conservation Trust
Macro-slope gradient	Degrees	0.01	29.50	ASF DAAC (2015)
Topographic wetness index	Unitless	−0.43	19	ASF DAAC (2015); B. Clegg, unpublished data
Geological substrate	Categorical	Not applicable	Not applicable	Cunliffe et al. (2012)

Note: The minimum and maximum values are of the extracted values and not the base layer. Sources refer to the origin of the input layers and the person responsible for the creation of base layers, where applicable.

slope gradient (degrees) was extracted from the DEM for each sampled tree. (iv) The topographic wetness index (TWI) is a DEM-based, relative measure of soil-moisture availability based on how likely an area is to accumulate water (Beven & Kirkby, 1979; Kopecký & Čížková, 2010). TWI values typically range from −3 to 30, with higher values indicating a greater soil moisture availability. A TWI image file was created in SAGA GIS (Conrad et al., 2015), with the final image smoothed by running the mean filter 10 times. A TWI value was extracted for each sampled tree. (v) Rock cover under each tree canopy was estimated using the eight-point ranking scale (Anderson & Walker, 1974), and by the average height of rocks. (vi) Geological substrate type was excluded because most of the trees occurred on one type. (vii) Estimates were made of protection of a baobab's trunk by other woody plants, and grass cover under each baobab canopy as an index of potential fire impact, but neither variable proved useful.

2.4 | Data analysis

Statistical analyses were mainly forms of regression analysis, conducted using R version 4.2.2 (R Core Team, 2022). Models were built by starting with a full set of relevant explanatory variables, and thereafter using an Akaike's Information Criterion (AIC) information theoretic approach to select a best model based on AIC (Anderson & Burnham, 2002). For all regression models, apart from the ordinal linear regression (see next paragraph), we used the dredge function from the package *MuMIn* (Bartoń, 2020) to evaluate all possible model alternatives to select the best model. For the ordinal linear regression model we used backward-stepwise selection using the *step4vglm* function from the package, *VGAM* (Yee, 2010). Chi-square statistics were calculated for each explanatory variable in the final models (Fox & Weisberg, 2019). Stem circumference or stem volume was included as a covariate in the analyses to control for tree size, where appropriate. The values of distance to water, distance to road, macro-slope gradient, TWI, boulder cover and stem circumference and volume were first standardized to a mean of zero and a standard deviation of one to assist with the interpretation of the regression coefficients (Schielzeth, 2010). These variables were examined for collinearity using Pearson's correlation coefficient, of which there was no notable evidence (maximum $r = 0.50$).

A set of eight regression analyses were undertaken (Table 3). The first six listed models determined factors which influence elephant impact on unprotected baobabs. Specifically, the probability and extent of the different forms of damage to a tree (canopy loss, recent or old debarking, gouging) were analyzed. Ordinal linear regression was used to analyze canopy loss; trees with a rank ≥2 for elephant damage (3% of the sample) were ranked as 2+. All other analyses used logistic regression models (LRMs). To control for tree size, debarking was weighted by stem circumference, and gouge volume was weighted by stem volume.

To test whether protection status affected b149aobab survival, an LRM with protected status as the only explanatory variable was run (Table 3—LRM7). To control for a possible effect of time since protection, only trees recorded before 2020 ($n = 101$; 39 not protected) were included (Table 1). The sample of unprotected trees was drawn from the same range of distance to water, distance to road, and macro-slope gradient, and included only those trees that fell within 95% of the protected-tree range of each variable. This yielded a total of 62 protected and 39 unprotected trees. To control for the potential biases in the selection of baobabs for protection, distance to water, distance to road, and the gradient of the macro-slope were included as explanatory variables in the regression analysis (Table 3—LRM8). To test which protection method was most effective (Table 1), a Fisher's exact test of independence was conducted on counts of trees grouped by tree survival status and protection method.

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TABLE 3 Final models (post model selection) that were used to understand the factors potentially influencing the impact of elephants on baobabs, and to test for differences in the survival of protected and unprotected baobabs.

Model	Response variable	Nagelkerke R^2	Explanatory variable	χ^2	df	*p*-value
ORM1	Canopy loss	0.02	Boulder protection	2.55	1, 750	.11
			Stem circumference	3.45	1, 750	.06
LRM2	Recent debarking (yes or no)	0.16	**Distance from water**	**4.05**	**1, 370**	**.04**
			Boulder protection	0.93	1, 370	.33
			Stem circumference	**22.88**	**1, 370**	**<.001**
			Macro-slope gradient	**6.07**	**1, 370**	**.01**
			Distance from water: boulder protection	**20.63**	**1, 370**	**<.001**
			Boulder protection: slope gradient	2.70	1, 370	.10
BRM3	Extent of recent elephant debarking (weighted by stem circumference)	NA	Boulder protection	3.61	1, 369	.06
LRM4	Extent of old elephant debarking (weighted by stem circumference)	0.12	**Macro-slope gradient**	**16.76**	**1, 374**	**<.001**
			Topographic wetness index	0.42	1, 374	.51
LRM5	Gouged (yes or no)	0.13	Distance from water	3.57	1, 370	.06
			Distance from roads	**4.50**	**1, 370**	**.03**
			Macro-slope gradient	**14.71**	**1, 370**	**<.001**
			Stem volume	**12.75**	**1, 370**	**<.001**
LRM6	Extent of gouging (weighted by stem volume)	0.002	**Topographic wetness index**	**0.02**	**1, 375**	**.01**
LRM7	Tree status (alive or dead)		Protection status	0.008	1, 99	.90
LRM8	Tree status (alive or dead)	0.40	**Protection status**	**10.85**	**1, 96**	**.001**
			Distance from water	**8.94**	**1, 96**	**.003**
			Distance from roads	**16.73**	**1, 96**	**<.001**
			Macro-slope gradient	**13.04**	**1, 96**	**<.001**

Note: Factors in bold have *p* values lower than .05.
Abbreviations: BRM, beta regression model; LRM, logistic regression model; ORM, ordinal regression model.

The overall fit of a final LRM was assessed using the Hosmer–Lemeshow goodness-of-fit test (Lele et al., 2019). Each model was re-assessed for collinearity among explanatory variables using variance inflation factors (VIF), but none was found. Models were checked for overdispersion (Carruthers et al., 2008) and zero inflation, and if detected, a beta-regression model with zero-inflation component was used (Harrison, 2015). The explanatory power of each model was assessed using adjusted Nagelkerke pseudo-R^2 values (Zhang, 2022).

3 | RESULTS

3.1 | Description of trees and environment

A total of 563 baobabs, protected and unprotected, were sampled in northern GNP (Figure 1) that covered a wide range of environmental conditions and tree size (Table 2). In terms of geology, 86 trees were on alluvium, 422 on granophyre, 32 on basalt, and 23 on the Malvernia Formation. Boulder cover was absent for 21% of trees, but covered 26%–50% of the surface area for 28% of trees, and 76%–90% for only 2% of trees. Boulders were about 50 cm in height at 52% of trees; with one tree surrounded by boulders up to 250 cm in height. Other woody plants offered protection to 14% of baobabs, occluding on average only 5% (±0.7 SE) of tree circumference and 7% (±0.6 SE) of tree height. The potential fuel load was mostly sparse, with a median grass cover of 26%–50%.

A total of 149 protected trees were sampled: 88 rock-packed, 43 fenced, three log-packed, five rock and log-packed, nine fenced and rock-packed, and one fenced and log-packed. Bark growth over fencing was minimal or absent for 75% of fenced trees, and bark had not completely grown over sections of the fence of any tree. Rock packs were on average 2.5 m (±0.07 m SE) wide (range 1.6–3.4 m), and

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consistently about 0.5 m in height. In only one case each had rocks or logs been moved, creating a path to the tree.

3.2 | Environmental influences on elephant utilization

3.2.1 | Canopy loss

Most trees lost less than 10% of their canopy to an unknown cause; only 12% of unprotected trees lost canopy to elephants, the low value attributed to the height of the canopy. There was weak evidence that increasing boulder protection reduced canopy loss, and that increasing stem diameter resulted in less canopy lost (Table 3—ORM1; Table S1).

3.2.2 | Recent debarking

Sixty-four percent of 377 unprotected trees had recent elephant debarking, with an average extent of 8% (±0.6% SE) (maximum 85%) of tree circumference recently debarked. The probability of recent debarking (Table 3—LRM2) was 95.5% for the largest trees and 34.6% for the smallest trees (Figure 2a), and decreased linearly with increasing distance from water, from 76.6% for trees closest to 45.8% for trees farthest from water (Figure 2b). Boulder protection had no effect on its own (Figure 2c), but it amplified the effect of increasing distance from water (Figure 2e). The probability of recent debarking decreased with increasing slope, but there was no evidence for an interaction with boulder protection (Table 3; Figure 2f). The extent of recent debarking weakly declined with increasing boulder protection, from 15% of a stem with no boulder protection to 11% of a stem with surrounding boulder cover of 76%–90% (Figure 2g).

3.2.3 | Old debarking

Nearly all (99.7%) unprotected trees ($n = 377$) had been historically debarked by elephants by an average extent of 95% (±0.9% SE) of tree circumference, with 83% of trees having been ringbarked. A model with modest explanatory power revealed that the extent of old debarking decreased in a linear manner with increasing slope gradient, from 99.4% for trees on the gentlest slopes to 67.7% for trees on the steepest slopes (Figure 3; Tables 3, S1—LRM4).

3.2.4 | Gouging

Twenty-two percent of unprotected trees ($n = 377$) had been gouged, with an average loss of trunk volume (up to 4.5 m) for gouged trees of 0.45% (±0.12% SE), and a maximum of 36%. Bark had reformed around the edge of some old gouges, but most gouges showed little sign of healing, and most older gouges had decaying fibrous tissue. The probability of gouging was influenced by distance from roads, stem size, and slope gradient, with some evidence for distance from water having an effect (Figure 4; Tables 3 and S1—LRM5). Tree stem size had the strongest influence, with the probability of gouging increasing from 12.6% for the smallest trees to 71.5% for the biggest trees (Figure 4a). The probability of gouging increased non-linearly from 15.1% for trees closest to roads to 42.0% for trees farthest from roads (Figure 4b); decreased non-linearly from 33.3% for trees on the gentlest slopes to 3.0% for trees on steepest slopes (Figure 4c); and decreased linearly from 27.1% for trees closest to water to 8% for trees farthest from water (Figure 4d). None of the factors investigated were significant predictors of relative gouge volume (Tables 3 and S1—LRM6).

3.3 | Protected versus unprotected trees

By the time of this study, 42% ($n = 62$) of the trees protected before 2020 had died, which was not different to the 41% ($n = 39$) of known unprotected trees which had died (Tables 3 and S1—LRM7). However, controlling for environmental variables showed that protection more than doubled survival—78.4% (95% CI [63.7, 88.3]) for protected trees versus 31.9% (95% CI [15.2, 55.1]) for unprotected trees (Figure 5a; Tables 3 and S1—LRM8). Increasing slope gradient had the strongest influence on increasing the probability of baobab survival, from 17.5% for trees on the gentlest slopes to 93.5% for trees on the steepest slopes (Figure 5b). The probability of survival also increased, from 32.5% to 91.5%, with increasing distance from water (Figure 5c), but decreased from 83.6% to 0.04% with increasing distance from a road (Figure 5d).

There was some evidence that protection method influenced tree survival (Fisher's exact test, $p = .056$; Figure 6). Fencing appears to have resulted in higher survival if the small sample size is recognized (Figure 6).

4 | DISCUSSION

4.1 | Baobab refugia from elephant impact

Elephants have made extensive use of baobabs in GNP (Kupika et al., 2014; Mashapa et al., 2014; Mpofu et al., 2012). This study identified no absolute refuge of baobabs from elephant use. However, distance to

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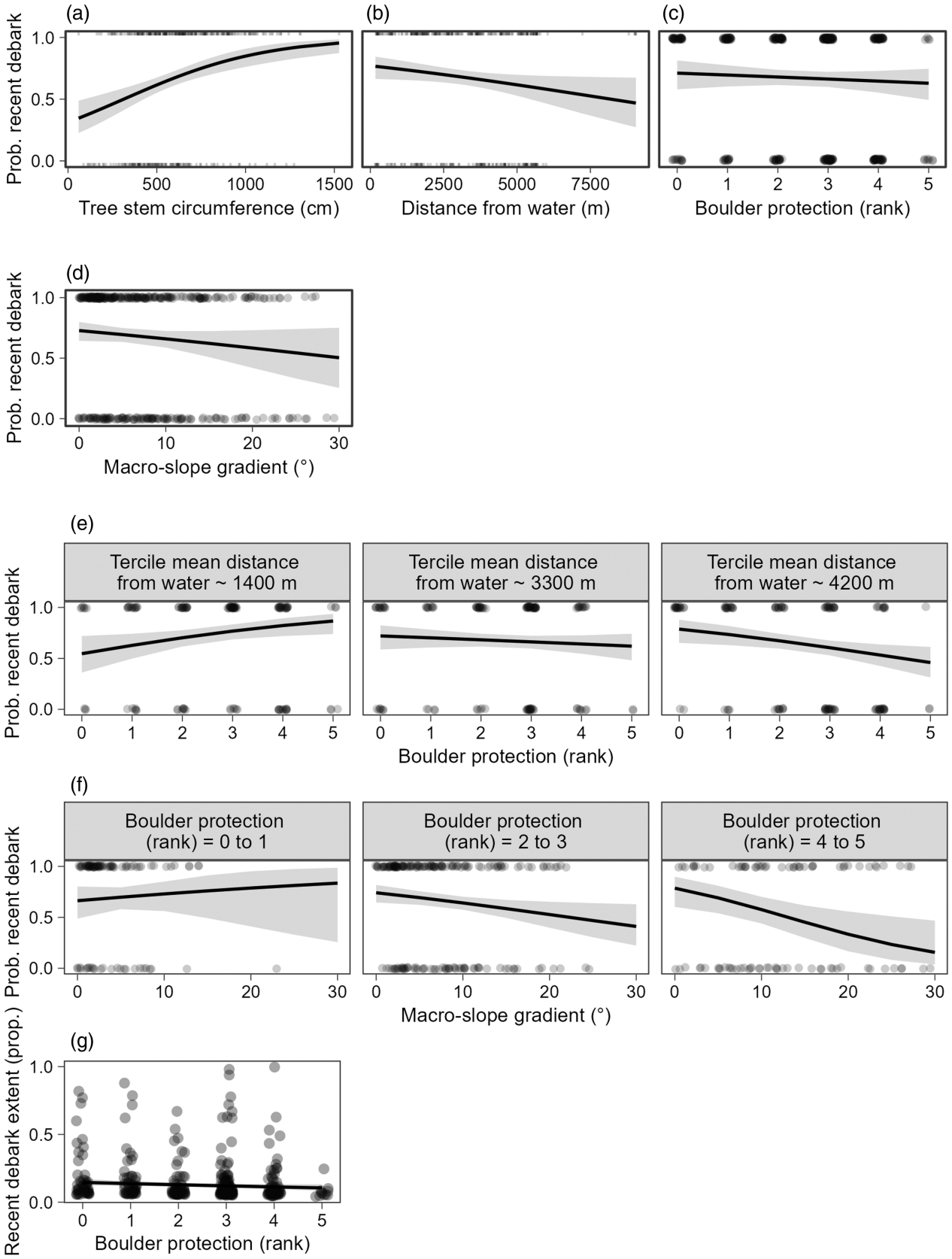


FIGURE 2 Legend on next page.

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permanent water, slope gradient, or boulder cover offered partial refugia, all of which are broadly consistent with elephant biology (Conybeare, 2004; O'Connor et al., 2007), previous findings (Edkins et al., 2007; Kupika et al., 2014; Swanepoel, 1993), and the well-recorded influence of distance to water on elephant impact (Gaylard et al., 2003; Tafangenyasha, 1997a). All our sampled baobabs in northern GNP were within 10 km of water, thus within the ~15 km foraging range of bull elephants (Conybeare, 2004). A complete refugium in terms of distance from water was, therefore, not identified. However, the consistent relationships with distance from water shown for elephant impacts (Figures 2b and 4d) and baobab survival (Figure 5c; Table 3) clearly identified that distance from water offered a partial refuge. Whether the sandveld of central GNP, which contains only seasonal water but apparently support a low baobab density (Mashapa et al., 2014), offers an absolute refuge based on distance from permanent water warrants investigation via mapping baobab distribution across GNP. The nature of refugia identified for baobabs in this study is expected to apply to other woody species utilized by elephants and which show a similar distribution across habitats. For example, the rock fig (*Ficus abutilifolia*) is distributed along the gorge section of the Runde River and is potentially easily accessible to elephants. However, a proportion of the population is not impacted because some trees are sited in patches where the boulders are too large or the slope is too steep for elephants to maneuver (TG O'Connor, unpublished data).

The decreased probability of gouging with increasing distance from water (Figure 4d) suggests that elephants were not using the fleshy pulp of the trunk as a water source in GNP (see Fenner, 1980; Tsoumis, 1991; Wickens, 1982), but this needs to be evaluated by assessing baobabs farther than the 15 km foraging range of elephants.

Elephants can find it difficult to negotiate rugged terrain (Nellemann et al., 2002; Thomson, 1975), such that steep slopes combined with boulder cover can deter elephant utilization of baobabs (Edkins et al., 2007; Weyerhaeuser, 1985). Our findings were consistent with this understanding. At intermediate and high levels of boulder protection we found that baobabs on steeper slopes were less likely to have experienced recent debarking (Figure 2f; Table 3). Boulder cover of northern GNP is high owing to extensive faulting and fracturing of the widespread granophyre geology (Cunliffe et al., 2012). Most (79%) baobabs had some boulders around them, underscoring the importance of rocky areas in potentially ensuring the persistence of baobabs. Slope gradient emerged as the most important partial refuge because it influenced the probability of gouging (Figure 4c), the most destructive form of baobab use (Barnes, 1980; Weyerhaeuser, 1985), the extent of old debarking done by elephants (Figure 3) and the probability of survival (Figure 5b). In Kruger National Park, South Africa, baobabs on slopes of >18° always had less than 20% of their circumference debarked by elephants (Edkins et al., 2007), paralleled in this study by the probability of

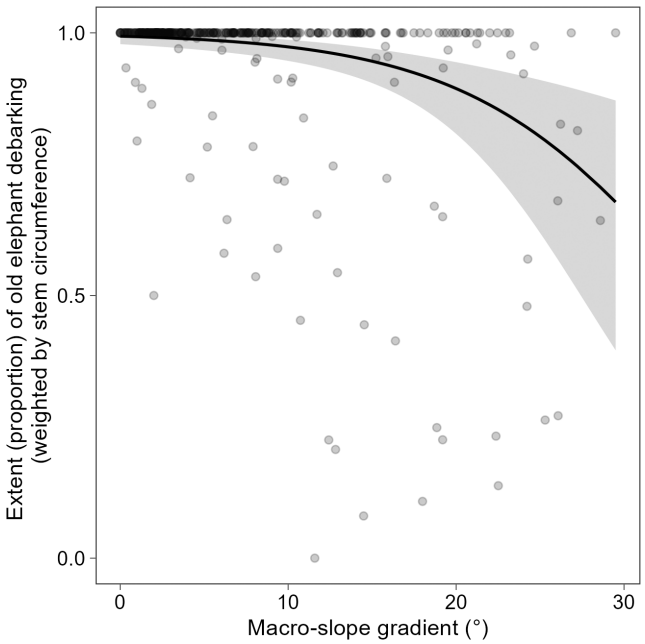


FIGURE 3 The predicted relationship from logistic regression model 4 (LRM4) of the extent (percent of circumference) of a tree having old debarking in relation to the macro-slope gradient (shaded area represents the 95% confidence interval; dots represent observations).

FIGURE 2 The predicted relationship from logistic regression model 2 (LRM2) of the probability of a tree being recently debarked in relation to (a) tree stem circumference, (b) distance from water, (c) boulder protection, (d) macro-slope gradient, (e) an interaction between distance from water and boulder protection (the three panels show the relationship between boulder protection and the probability of being recently debarked for the lower, middle and upper terciles of distance from water), and (f) an interaction between macro-slope gradient and boulder protection (the three panels show the relationship between macro-slope gradient and the probability of being recently debarked for low (0 to 1), intermediate (2 to 3) and high (4 to 5) levels of boulder protection). The predicted relationship from beta regression model 3 (BRM3) of the extent of recent elephant debarking (controlling for tree size) in relation to boulder protection (g). (shaded area represents the 95% confidence interval; dots or rug lines represent observations).

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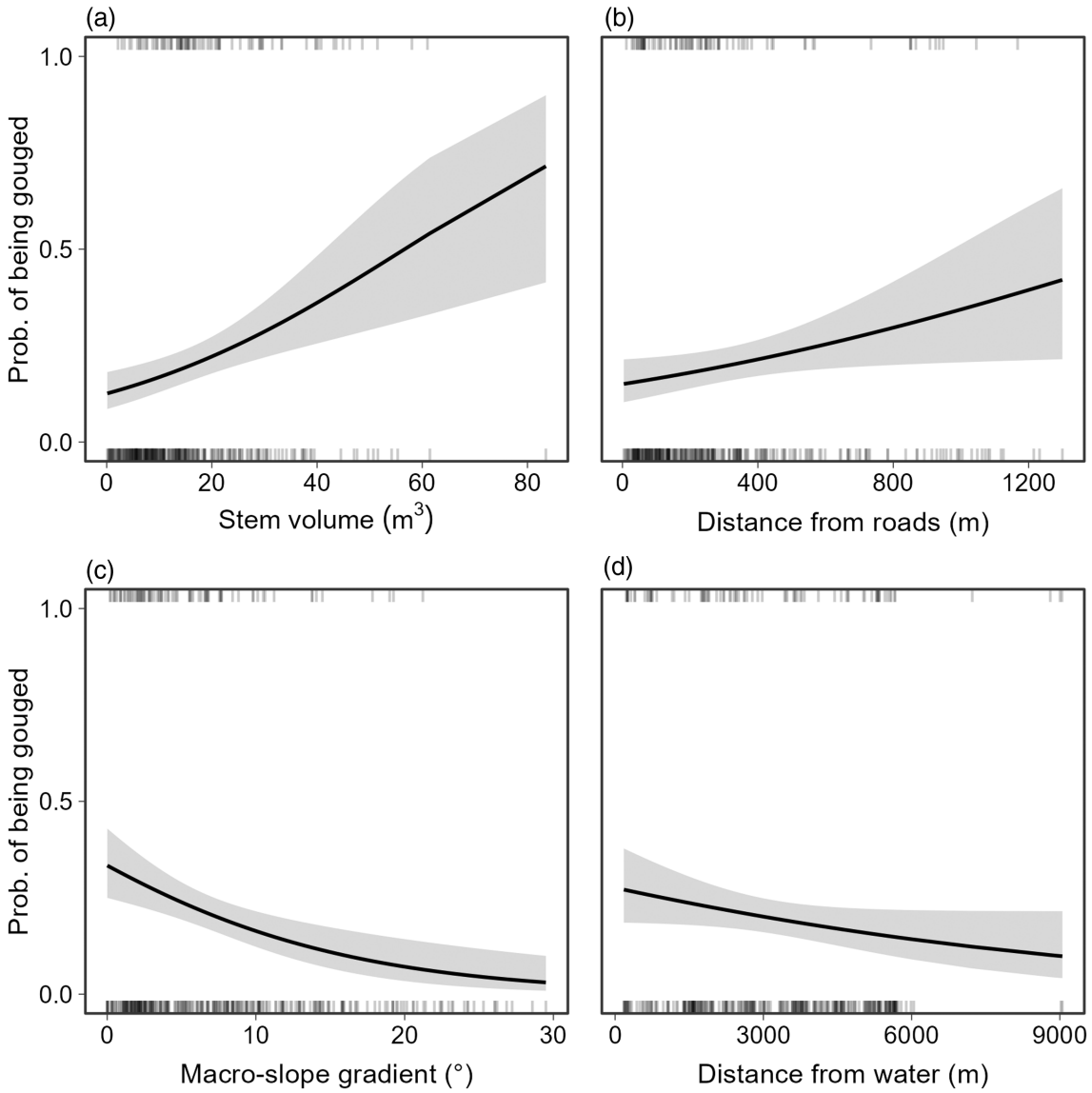


FIGURE 4 The predicted relationship from logistic regression model 5 (LRM5) of the probability of a tree being gouged in relation to (a) tree stem volume, (b) distance from roads, (c) macro-slope gradient, and (d) distance from water. (shaded area represents the 95% confidence interval; rug lines represent observations).

gouging falling below 10% on slopes >18°, and approaching 0% on slopes >25° (Figure 4c). Steep slopes (>25°), on which baobabs occurred, may therefore be the most effective refuge for baobabs within GNP.

An increasing probability of gouging (Figure 4b) and a decreasing probability of survival (Figure 5d) with increasing distance from a road were unexpected findings, especially as the converse pattern was shown for *Sclerocarya birrea* (Gadd, 2002). No explanation can be offered until it is understood why some trees are gouged and adjacent trees are not. An explanation based on vehicle traffic seems implausible for GNP on account of its low tourist patronage (Mutanga et al., 2017), and that some trees next to roads were gouged.

It was expected that TWI might affect elephant utilization because higher soil moisture promotes biomass growth that stays green for longer into the dry season (Coe et al., 1976). One explanation is that the deep fissures within granophyre geology, on which most baobabs were recorded, accumulate water, even on the crests of slopes. Such areas would be recorded as having low TWI (Stothoff et al., 1999) but this would not reflect the actual amount of water available to a baobab. In addition, the influence of TWI is mainly through the availability of foliage during the dry season, but baobabs are obligately deciduous. The preponderance of the baobab population occurring on granophyre geology further precluded investigation of an effect of soil fertility on utilization by

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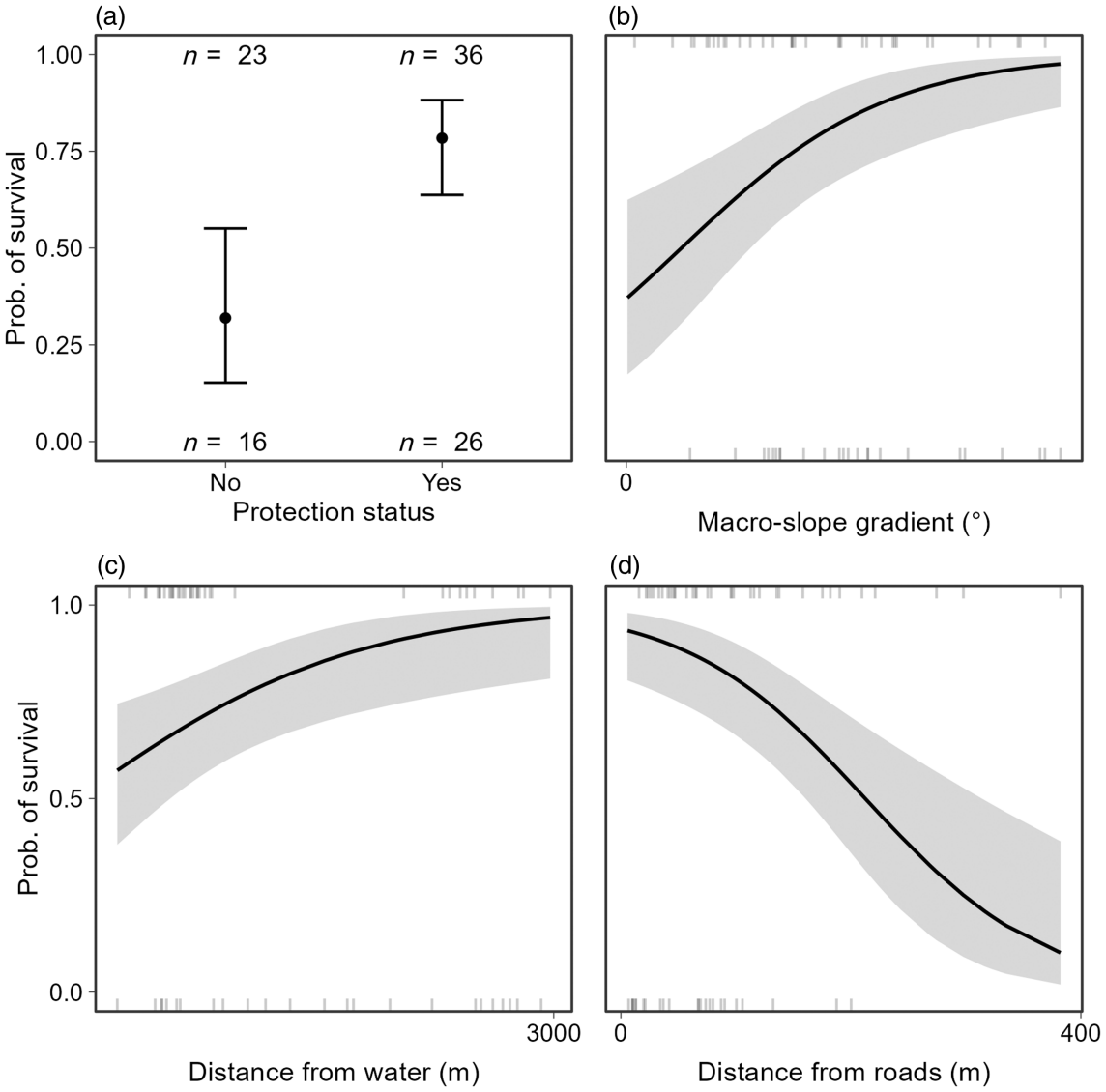


FIGURE 5 The predicted relationship from logistic regression model 8 (LRM8) of the probability of tree survival in relation to (a) protection status (yes or no), (b) macro-slope gradient, (c) distance from water, and (d) distance from roads. (shaded area represents the 95% confidence interval; counts, *n*, in (a) and rug lines represent observations).

elephants (Asner & Levick, 2012; Pretorius et al., 2011), although it needs to be recognized that elephants use baobabs less for their leaves than for their bark or pulp (Barnes, 1980; Weyerhaeuser, 1985). It is unclear whether soil characteristics affect the palatability of baobab bark and wood in a manner similar to its effect on leaf palatability (see Anderson & Walker, 1974).

The increased probability of recent debarking and gouging with increasing tree size (Table S1, LRM2 and LRM5) is consistent with current understanding that tree size influences elephant use (Asner & Levick, 2012; Weyerhaeuser, 1985). This may be because elephants frequently return to known foraging sites, as shown for Bornean elephants (English et al., 2014), or preferentially use baobabs for shade in GNP (personal observation). Large trees may also be more resilient to repeated use by elephants than smaller adults; as observed in Lake Manyara National Park, Tanzania, where although damage increased with tree size, mortality decreased (Weyerhaeuser, 1985). Larger trees experienced lower levels of canopy loss because most branches of large trees are beyond (>6 m) the reach of elephant bulls, whereas small baobabs are vulnerable to mortality resulting from near entire loss of canopies to elephants.

4.2 | Protection of baobabs

Protection of baobabs using fencing, rock packing and log packing more than doubled the probability of their

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survival compared with unprotected baobabs. Elsewhere, fencing has reduced elephant debarking of several tree species (Cook et al., 2018; Derham et al., 2016). For most woody species, a greater extent of debarking results in increased tree mortality (Ihwagi et al., 2010; Savidge, 1968). Although debarking per se is not a threat to the survival of baobab trees owing to their ability to regenerate bark (Kotina et al., 2017), it may presage gouging which, in turn, leads to mortality. This study is the first to show that protection methods improve the survival of baobabs, despite having been employed for less than seven years. Considering the limited managementoptions available for reducing elephant impact in protected areas (Henley & Cook, 2019; van Aarde & Jackson, 2007), the measures examined in this study offer management a means of maintaining large trees, intrinsic to ecosystem functioning (e.g., Ludwig et al., 2008; Vogel et al., 2014), in areas exposed to chronic elephant use.

Fencing appeared to be the most effective protection method for ensuring baobab survival, although a larger sample size is desirable (Figure 6). Fencing was also observed to be the most durable form of protection as rock or log bands were vulnerable to being moved by elephants or baboons. This has also been noted by Henley and Cook (2019), and usually promotes access of the compromised side of a baobab to elephants. Rock or log bands were noted not to be sufficiently wide for some trees to deter elephants, whereas elephants could not access fencing if it was securely wrapped around a trunk. African honeybees (*Apis mellifera* subsp. *scutellata*) are a recognized deterrent to elephants, whose presence in hives can mitigate elephant impact (Cook et al., 2018). However, bees appear to be ineffective for protecting baobabs from elephants (Cook et al., 2018) and baobabs commonly harbor wild beehives (Wickens, 1982), and in this study 31% of the sampled baobabs had a bee swarm present but had been used by elephants.

Fencing is concluded to be the best option for protecting baobabs. When trees are protected in this way they maintain their ecological functionality with other organisms still able to access them for shade, forage, or other uses (Derham et al., 2016). By contrast, the use of exclosures to prevent access by elephants also precludes access by other larger herbivores (Western & Maitumo, 2004). Collection of rocks and logs disturbs their micro-habitat and the fauna associated with rocks and logs (Henley & Cook, 2019). Fencing is cost-effective to deploy on a large scale, typically requires little maintenance, and lasts at least eight years (Derham et al., 2016; Henley & Cook, 2019). This study found no evidence for "suffocation" of tree growth by fencing, and, in addition, the slow growth of baobabs (Barnes, 1983; Wilson, 1988) allows for extended intervals between refencing of individual

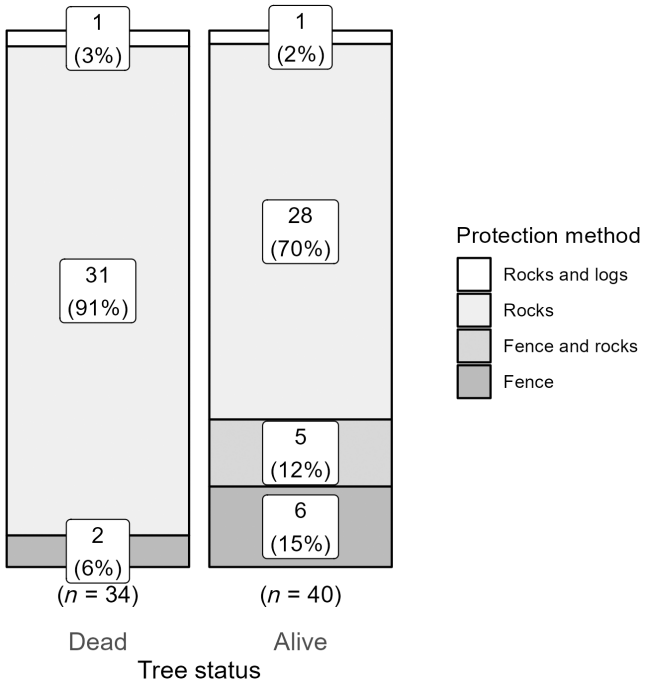


FIGURE 6 Survival (tree status) in relation to four different protection methods. A Fisher's exact test provided some evidence that there is an association between tree status and protection method ($p = .056$). The percentage of alive trees protected by fences was higher than that for dead trees relative to other protection methods, but sample sizes were small for most protection methods. (Upper number in boxes represents sample size and lower number is the percentage of trees for each tree status—dead or alive).

baobabs. A caveat for these prescriptions is that they apply primarily to adult baobabs, whereas smaller baobabs are subject to extensive canopy use, branch breaking, or uprooting (Barnes, 1980; Caughley, 1976; Weyerhaeuser, 1985) which cannot be prevented by fencing.

4.3 | Management recommendations

The three baobab refugia identified in this study are partly shared by baobabs in areas of high elephant density across Africa (Edkins et al., 2007; Ndoro et al., 2016; Swanepoel, 1993; Weyerhaeuser, 1985). Persistence of the baobab population in GNP cannot be predicted because the extent of these refugia within the park is unknown. In order to assess the security and long-term survival of baobabs across the park, the distribution of the baobab population and these refugia should be mapped. The increase in elephant density within GNP since 1992 (Dunham, 2012, 2022) threatens to erode the effectiveness of these refugia, for which surveillance of the trend

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in baobab condition is required. Furthermore, an improved understanding about the regeneration and growth rate of baobabs would improve prediction but this facet of baobab population ecology is not easily uncovered. A shift in the long-term spatial distribution of elephants within GNP, as a result of the provision of permanent artificial water points, would further compromise the current distribution of refugia (Owen-Smith, 1996; Wilson et al., 2021). GNP has a valuable role to play in baobab conservation because it occupies a modal position within the climate space in which baobabs are distributed (Wickens, 1982), and should be buffered to a degree against climatic variability anticipated with climate change (Mayne et al., 2022; Sanchez et al., 2011). An improved strategy for selecting trees to be protected could improve effectiveness of this approach. Baobabs are used by elephants mainly during the dry season, when gouging is likely to be initiated usually on a single tree (Barnes, 1980; Swanepoel, 1993; Swanepoel & Swanepoel, 1986). Trees with fresh gouge damage are likely to be baobabs growing outside of refuge areas and should, therefore, receive priority. Even if the mapping of refugia identify that a large portion of GNP's baobab population is secure, protection of individuals in high-use areas would ensure this iconic species remains widely distributed throughout the park.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are publicly available on ZivaHub, the University of Cape Town's online data repository, at https://doi.org/10.25375/uct.25968445.

ETHICS STATEMENT

Not relevant.

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