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RESEARCH ARTICLE

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Local extirpation of woody species in *Colophospermum mopane* woodland under chronic utilisation by elephants

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Abstract

The hypothesis that certain woody species may be prone to local extirpation under chronic elephant utilisation was examined for *Colophospermum mopane* open woodland, for an area within the foraging range of elephants from permanent water. Elephant density increased from nearly absent in the 1970s to >3 elephants km^{-2}, with 0.62 adult bulls km^{-2}, by 2022. Study components of vegetation impact included a long-term elephant exclosure, a fence-line contrast with an adjacent communal area, comparison with an adjacent wildlife reserve carrying a fifth of the elephant density and the use of historical studies of the vegetation. A history of elephant utilisation resulted in woodland becoming hedged through pollarding of tree stems by elephants. Impacted woodland was characterised by a slightly lower tree density, reduced average height of trees, altered shrub composition and lower species richness. The dominant *C. mopane* and sub-dominant species had persisted. However, about 14 species were potentially trending towards local extirpation on account of very high levels of adult mortality, but had persisted because of a low level of seedling recruitment. Fleshy fruits were a shared attribute among most extirpation-trending species, which, together with a reduction in woody species richness that affects browsers, has ramifications for trophic flows.

KEYWORDS
biodiversity conservation, elephant density, fence-line contrast, fleshy fruit, semi-arid savannah

Résumé

L'hypothèse selon laquelle certaines espèces ligneuses sont susceptibles de disparaître localement en cas d'utilisation chronique par les éléphants a été examinée pour la forêt ouverte de *Colophospermum mopane*, dans une zone située à l'intérieur de la zone d'alimentation des éléphants à partir d'un point d'eau permanent. La densité des éléphants est passée d'une quasi-absence dans les années 1970 à plus de 3 éléphants au km^{-2}, avec 0,62 mâle adulte au km^{-2}, en 2022. Les éléments de l'étude de l'impact sur la végétation comprenaient un enclos à long terme pour les éléphants, un contraste entre la clôture et une zone communale adjacente, une comparaison avec une réserve de faune adjacente présentant un cinquième de la densité d'éléphants et l'utilisation d'études historiques de la végétation. L'histoire de l'utilisation des éléphants a transformé les bois en haies à cause de l'écimage des tiges des arbres par les éléphants. Les zones boisées touchées se caractérisaient par une densité d'arbres légèrement inférieure, une hauteur moyenne des arbres réduite, une composition d'arbustes modifiée et une richesse d'espèces plus faible. L'espèce dominante *C. mopane* et les espèces sous-dominantes ont subsisté. Cependant, environ 14 espèces étaient potentiellement en voie de disparition locale en raison des niveaux très élevés de la mortalité des adultes, mais avaient subsisté en raison d'un faible niveau de recrutement des semis. Les fruits charnus étaient un attribut commun à la plupart des espèces ayant tendance à disparaître, ce qui, associé à une réduction de la richesse en espèces ligneuses qui affecte les brouteurs, a des ramifications pour les flux trophiques.

1 | INTRODUCTION

Savannah elephants (*Loxodonta africana*) have attracted more attention than any other large mammal species across the protected areas of the savannah regions of sub-Saharan Africa owing to concern about their ability to transform vegetation (Laws et al., 1975). Concern about vegetation lessened across West, Central and East Africa, from the 1980s to the present, following dramatic population declines throughout this region (Thouless et al., 2016). Southern Africa contained 70% of an estimated 415,000 elephants in Africa in 2016 (Thouless et al., 2016), mostly in protected areas, in many of which elephant densities are high and their impacts are conspicuous (e.g. Skarpe et al., 2004). Protected areas are further faced with meeting the challenge of maintaining their full complement of biodiversity. Concern about elephant impacts on woodlands has grown to encompass the consequent implications of this impact on other components of biodiversity, of which a foundation is the species richness of primary producers (Cumming et al., 1997).

One hypothesis proposes that woody species which are selected by elephants experience elevated adult mortality resulting from ringbarking, pollarding or uprooting by elephants, and exhibit low levels of regeneration. These woody species are likely to trend towards local extirpation under chronic elephant utilisation, defined as severe utilisation sustained over time (O'Connor et al., 2007). Adult bulls rather than cow–calf groups are recognised to be the cause of a disproportionate amount of woody plant mortality, owing mainly to their size and nutritional needs although behavioural factors also play a role (Clegg, 2010; O'Connor et al., 2007). A trend towards local extirpation may, therefore, be expected in regions where bulls accumulate. Evidence in support of elephants driving selected woody species towards local extirpation has been forthcoming from medium-sized (<500 km^2) protected areas in southern Africa (O'Connor, 2017; O'Connor & Page, 2014), where the entire area is within 15 km of water and, therefore, accessible to elephant bulls year-round (Conybeare, 2004). Whether local extirpation of impacted species might occur in large protected, semi-arid areas in which elephants undertake seasonal movements has not been examined. Seasonal movements may offset any trend towards local extirpation, or, alternatively, local extirpation may be facilitated by elephant concentrations around permanent water during the dry season.

Providing evidence about elephants driving certain plant species towards local extirpation is more difficult than showing their impact on woodland structure and composition, which has been closely studied since the 1950s to the present (e.g. Buechner & Dawkins, 1961; Guldemond & Van Aarde, 2008; Laws et al., 1975). Plot-based sampling is sufficient to show compositional and structural changes in vegetation units of interest, but it is inadequate for investigating whether certain species are trending towards local extirpation for three main reasons. First, many of the species potentially threatened with local extirpation are uncommon or rare, and are, therefore, unlikely to be encountered using plot-based sampling resulting in small sample sizes which are inadequate for quantitative analysis. Second, local extirpation must be assessed at a landscape scale (e.g. in this study, the foraging distance of elephants from permanent water [~15 km; Conybeare, 2004]). Plot-based sampling covers a minute fraction of a landscape. Third, a study assessing a trend towards local extirpation is retrospective of a dynamic that may have unfolded over a long period of time – a forensic approach that seeks appropriate supporting evidence is, therefore, required.

The diet of savannah elephants is catholic – they consume the order of 100 plant species at any one locality (e.g. Clegg, 2010; Laws et al., 1975). Foraging elephants will encounter a large number of vegetation types over an annual cycle on account of their large foraging ranges, which vary from 50 km^2 to >6000 km^2 depending on the environment (Dolmia et al., 2007; Leggett, 2006). Elephants show pronounced selection for vegetation types and for plant species within a vegetation type that varies on a seasonal basis (Clegg, 2010; Pretorius et al., 2011). *Colophospermum mopane* (mopane) woodlands, which are widespread across southern Africa (Timberlake, 1995), are well used by elephants because mopane is a staple species in the diet of elephants where it occurs (Clegg, 2010;

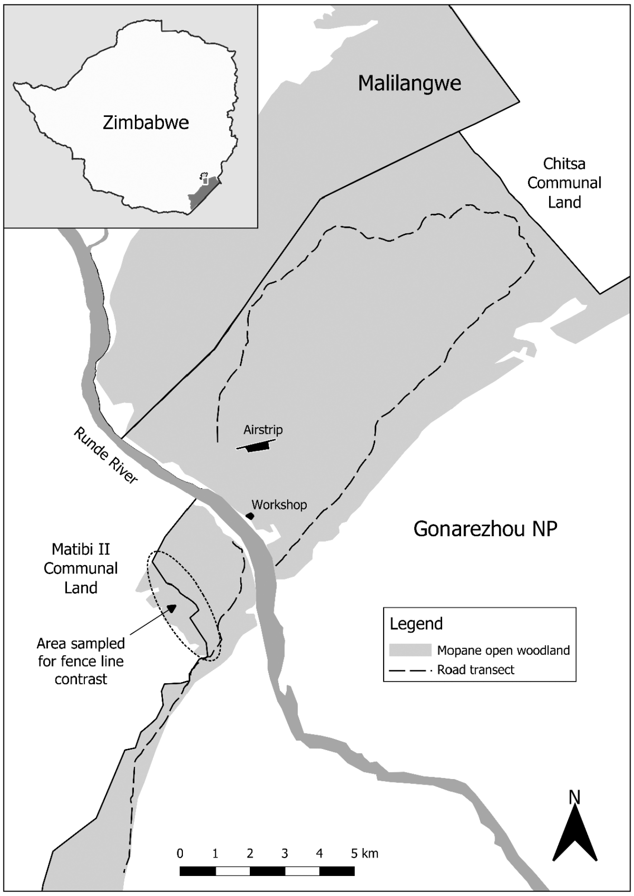

FIGURE 1 The location of the study areas in the Chipinda Pools region of Gonarezhou National Park, and the adjacent Malilangwe Wildlife Reserve and Matibi II Tribal Trust Land. Key to sampling: Airstrip, six pairs of plots along the southern and eastern border; Fence-line contrast between Matibi II communal land and Gonarezhou National Park (NP), six pairs of plots in the area indicated; Road transect along the Gulugi Loop (north of the river) and the road south from the river, broken line; Workshop exclosure, a pair of plots inside and outside the area for both the south-east and the north sides (Kelly's study plots (Kelly, 1973; Kelly & Walker, 1976) are situated approximately adjacent to the airfield).

Lewis, 1991; Styles & Skinner, 2001). Mopane is characteristically mono-dominant throughout its range, and mopane woodlands are relatively species poor (Timberlake, 1995). A poor species richness of mopane woodland, therefore, enables assessment of the other woody species which occur in this woodland type.

Gonarezhou National Park (GNP) offered an opportunity to examine whether chronic utilisation of mopane woodland by elephants had driven some woody species towards local extirpation. Subsequent to the establishment of the park in 1975, the elephant population attained a density of >2 elephants km^{-2} (Dunham, 2022), considered to be a density greater than that at which woodland can be sustained (Cumming et al., 1997). A large area of GNP is dominated by mopane (Cunliffe et al., 2012). The aim of this study was to evaluate whether observed trends in GNP were consistent with the hypothesis of elephants driving selected woody species in mopane woodland towards becoming locally extirpated (O'Connor et al., 2007). This aim can be addressed by contrasting the persistence of woody species in areas subjected to chronic utilisation by elephants within GNP with those from which elephants have been excluded, or areas in which elephants occur at considerably lower density. This aim was investigated through examination of a set of independent, yet inter-related, studies. The key questions addressed were the following. (1) Has the study area experienced a sustained increase in occupation by elephants, for both cow–calf groups and adult bulls? (2) If so, has chronic utilisation of woody vegetation by elephants transformed woodland structure or composition? (3) Have certain woody species been extirpated, or are they trending towards local extirpation? (4) Do extirpation-prone species share any attributes? The question on elephant trends was addressed using census data collected over four decades. The questions concerning vegetation were addressed using separate, yet related, studies of a long-term exclosure, a fence-line contrast of GNP with a communal area with very few elephants, a fence-line contrast of GNP with a neighbouring reserve with elephants at low density, and consideration of historical descriptions of vegetation.

2 | STUDY AREA

GNP, the neighbouring Matibi II communal area, and Malilangwe Wildlife Reserve are situated in the semi-arid, south-east lowveld of Zimbabwe (Figure 1). GNP covers an area of 5335 km^2. Rain falls during the hot summer months of November to April. Mean annual rainfall is approximately 550 mm but it is conspicuously variable over seasons, and has varied from 93 mm in 1991/92 to 1118 mm in 1999/2000 at Chipinda in GNP. Maximum daily temperatures exceed 30°C during every month of the year. The topography, geology and vegetation of the park have been described in detail by Cunliffe et al. (2012). This study was concerned with *Colophospermum mopane* woodland that is underlain by basalt geology (vegetation type 4.1 of Cunliffe et al. (2012)), which occurs along the north-west boundary of the park, delimited to the east by the Chuwonja-Sibonja Hills. Soils are predominantly sandy loams when freely drained but are of vertic character in depressions (Kelly & Walker, 1976). Fire has not been a factor in the study area within 5 km of the Runde River for the last decade because of heavy grazing, especially by hippopotami (*Hippopotamus amphibius*) (e.g., Mackie, 1973). The area of the Gulugi drainage (Figure 1) last experienced a wildfire in 2009, and, thereafter, firebreaks were burnt twice following two particularly wet seasons. The other main browser and mixed feeder species in GNP are black rhinoceros (*Diceros bicornis*), giraffe (*Giraffa camelopardalis*), eland (*Tragelaphus oryx*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), impala (*Aepyceros melampus*), grey duiker (*Sylvicapra grimmia*), steenbok (*Raphicerus campestris*) and Sharpe's grysbok (*Raphicerus sharpei*) (Dunham, 2012; Gandiwa et al., 2013).

The size of the elephant population in GNP was controlled through population reduction exercises during the 1970s and the 1980s, and the population experienced additional mortality as a result of the exceptionally severe 1991/92 drought (Dunham, 2012). Consequently, from a density of less than one elephant km^{-2} in 1991/92, the population grew at 6.2% per annum to exceed a density of two elephants km^{-2} by 2014 (Dunham, 2012, 2022). Prior to the proclamation of the national park in 1975, the study area fell within a fenced corridor established by Tsetse and Trypanosomiasis Control that existed from 1964 to 1972, and from which all wildlife, including elephants, was eliminated by shooting (Kelly & Walker, 1976).

3 | METHODS

3.1 | Elephant population

Using standard aerial survey techniques (Dunham, 2012), 20 aerial surveys of the elephant population of GNP were conducted from 1980 to 2022 (Bowler, 1995; Coulson, 1980, 1981; Davies, 1996; Dunham, 2002, 2022; Dunham et al., 2007, 2010, 2013, 2021; Dunham & Van der Westhuizen, 2015, 2016, 2018; Gibson, 1989; Jones, 1991; Mackie, 1999; Sharp, 1982, 1983, 1984, 1986, 1987). The study area was contained in one of the strata. Density is used because the area of this stratum changed over time (maximum = 1167 km^2; minimum = 196 km^2). Up until 1995, only the total number of elephants was recorded, but thereafter the density of all elephants and adult bulls per stratum was recorded for each survey.

3.2 | Vegetation sampling

Plant nomenclature follows the Flora of Zimbabwe (2024). Individual plants were categorised based on a combination of height and state resulting from history of use. Any multi-stemmed species (e.g. *Grewia* spp.) was defined as a shrub irrespective of its height. Three categories were defined for species with one or a few stems: a tree was defined as a plant >3 m, a shrub as ≤3 m in height and a transformed tree was a pollarded tree >1.5 m but ≤3 m in height, and with a stem circumference >25 cm.

3.2.1 | Fence-line contrast

A fence-line contrast (sensu Noy-Meir et al., 1989) between GNP and the adjacent Matibi II communal area, south of the Runde River (Figure 1), was sampled during May and June, 2023. This boundary was fenced for the control of tsetse fly from 1964 to 1972 (Kelly & Walker, 1976), the fence subsequently fell into disrepair but was restored in 2012. Even when unfenced, establishment of relatively dense human settlement within the Matibi II area along the boundary ensured that elephants did not make persistent use of the communal area. Six paired plots were located along 4 km of fence line, no pair closer than 500 m from one another to ensure spatial independence, and placed at least 5 m from the fence to avoid edge effects (edge distance was determined on-site). All plots in GNP were <2.5 km from the Runde River. A plot was 30 by 30 m. A count was made per plot of the number of trees, transformed trees and shrubs. The height of all individuals was measured. For trees and transformed trees, the number of main stems and the number which had been pollarded or pushed over was counted. Plant height and height of pollarded main stems were measured. The number of shrubs was counted in a belt transect within the 30 by 30 m plot, whose width depended on shrub density, but it was ensured that at least 15 individuals per plot were sampled.

3.2.2 | Workshop exclosure

A workshop area of 1.8 ha at park headquarters (Figure 1) was fenced in 2008. This area contained patches of natural vegetation amounting to 1 ha in area in 2022. Prior to fencing, elephant visitation to the now enclosed area was reduced on account of ongoing human disturbance. The workshop was 200 m from the Runde River, and elephants had free access to the area outside the exclosure opposite the patches. Two sets of paired plots were measured in August 2022; plot size was determined by patch size – plots of one pair were 35 m by 35 m, and of the other were 20 m by 20 m. Plots were placed 2 m from the fence to allow for edge effects (edge distance was determined on site). All woody individuals were measured for their height, and the stem circumference of all trees and transformed trees was measured above any basal swelling. All individuals were ranked for recent (<1 year, distinguished by wood colour) or old (>1 year, wood has gone grey) loss of canopy volume taken by elephants or unknown agents, using an 8-point scale (Walker, 1976). The same scale was used to estimate the percentage to which each tree stem had been debarked, distinguishing old and recent debarking. It was recorded whether a tree stem had been pollarded. Outside plots were increased to a size of 1 ha in order to increase the sample size of trees other than *C. mopane* (cf. Walker, 1976).

3.2.3 | Historical information and landscape pattern

Historical information was derived from two main sources. Kelly studied primary productivity of mopane woodland on basalt-derived soils, south-east Zimbabwe, across three land uses during the 1970/71 and 1971/72 growing seasons (Kelly, 1973; Kelly & Walker, 1976). Two of his nine plots were located in GNP in the vicinity of Chipinda Pools, but his map was not detailed enough to relocate the plots. However, Kelly and Walker (1976, p. 558) state "The tree species *Colophospermum mopane*, *Sclerocarya caffra*, and *Commiphora pyracanthoides* ssp. *glandulosa* and the shrub species *Cissus cornifolia*, *Grewia bicolor* and *G. monticola* were present at all sites." They specifically state further that they used the presence of *Sclerocarya birrea* (*S. caffra*) and *Commiphora glandulosa* (*C. pyracanthoides* ssp. *glandulosa*) to ensure all their plots were positioned on flat or gently sloping ground. On the basis of this evidence, a census was conducted along 37.7 km of the road system on basalt-derived soils within 10 km north and south of Chipinda Pools in November, 2023 (Figure 1). Plants of interest were counted from the back of an open vehicle moving at 8 km hr^{-1} following spring flush: shrubs were counted within 5 m on either side of the road, and the distance to each adult tree was visually estimated (visibility was good because the mopane woodland had been hedged). One site sampled by Kelly and Walker (1976) was known to be in the proximity of the airfield (Figure 1). The composition of trees (>3 m in height) and shrubs (≤3 m in height) around the Chipinda airfield was sampled in 2022. Six pairs of plots, each plot 30 by 30 m in size (1.08 ha in total), were located on either side of a newly constructed fence enclosing the airfield. A pair of plots was randomly placed within each of seven sections of equal distance along the south and south-east perimeter of the fence line (Figure 1).

The second source was from Clegg (2010), who mapped and described the vegetation types of Malilangwe Wildlife Reserve (MWR) adjacent to GNP. The vegetation types on the boundary of MWR would have extended into GNP prior to chronic elephant impact. The two types are number 23 '*Colophospermum mopane – Enneapogon scoparius* open woodland' and number 38 '*Colophospermum mopane – Endostemon tenuiflorus* open woodland'. Sample size was ten and four plots respectively. Both occur on basalt-derived soils – type 23 on shallow (25 cm mean depth), calcareous, gravelly soil, and type 38 on very shallow (17 cm mean depth), rocky, loam soils (Clegg & O'Connor, 2012). These two vegetation types were used as a benchmark for assessing compositional variation across the data set assembled in this study. Clegg (2010) defined trees as >3 m in height, and shrubs as ≤3 m in height.

3.3 | Data analysis

All analyses were done using R (R Core Team, 2022).

A linear regression was the most appropriate fit for the trend of elephant density (adult bulls, total population) over time; any non-linear fit was discounted after examining the distribution of residuals. In order to determine if the rate of change in the density of adult bulls and the total population differed, a regression model of the combined data for the two groups was run, for which a significant interaction term between 'year' and 'group' would indicate the regressions are different. This model used data from 1995 onward, the year in which adult bulls were first separately counted. The rate of increase of the total population is expected to be greater than that of adult bulls because the total population contains reproductive output, whereas the numbers for adult bulls have been affected by calf and juvenile mortality, which can be high (Moss, 2001).

For the fence-line contrast, a paired t-test ($n = 6$) was used to test for differences across the fence line in the density of trees, transformed trees, shrubs or common tree or shrub species; tree height;

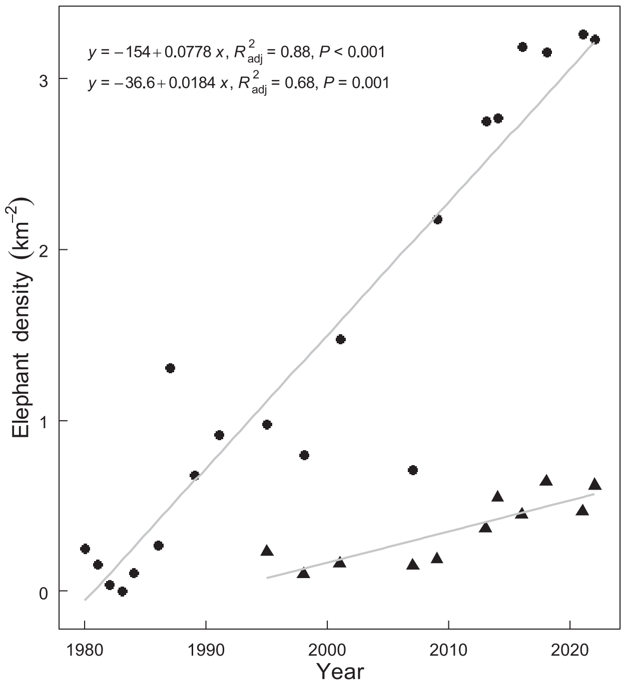

FIGURE 2 Trend of elephant density in the Chipinda Pools region, Gonarezhou National Park, Zimbabwe, between 1976 and 2021. Estimates are derived from stratified aerial sampling. Key: ● total elephants; ▲ adult elephant bulls. The top equation is for the relation between year and the total number of elephants, the bottom equation is that for adult bulls only (Bulls were counted as a separate group from 1995).

and the proportion of pollarded stems. A Kolmogorov–Smirnov test (D) was used to test for differences in the distribution of tree height. For testing whether shrub composition was different across the fence, the difference in composition of each pair was measured using Bray–Curtis dissimilarity (*vegan* package in R; Oksanen et al., 2022), and the effect of the fence line on compositional dissimilarity was tested with a one-sample t-test. Differences in species richness of trees, shrubs and both combined were tested with a χ^2 test (assumption of parity).

Each pair of plots of the workshop exclosure was analysed separately because pairs differed in plot size and landscape position. The difference in composition between each pair was calculated using the Bray–Curtis measure (Oksanen et al., 2022), using density for shrubs and basal area for trees. Differences in structure were summarised using a t-test for average tree height (all species), and a Kolmogorov–Smirnov test (D) for differences in the distribution of tree height. Difference in woody species richness (trees plus shrubs) inside the workshop (~1 ha) versus the two outside plots combined (2 ha) was tested with a χ^2 test (assumption of parity).

In order to illustrate compositional variation in relation to the degree of exposure to chronic elephant utilisation, a non-metric multidimensional scaling (nmds) ordination was undertaken of the seven sampled locations, using two stress levels (*vegan* package in R; Oksanen et al., 2022). These locations were inside and outside

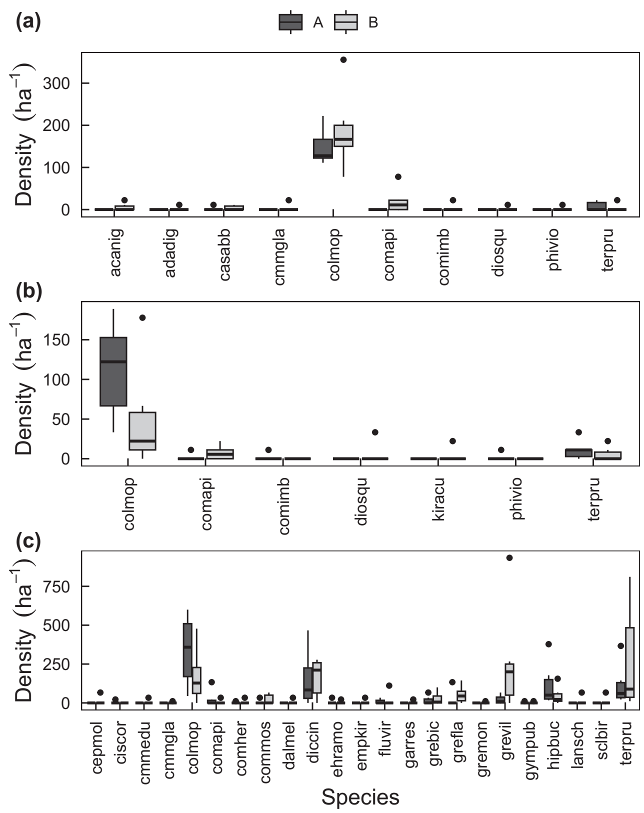

FIGURE 3 Paired box-and-whisker plots of the density of each species on either side of a fence line separating Gonarezhou National Park (left column) and Matibi II communal area (right column) for (a) trees >3.0 m in height, (b) transformed trees >1.5 height ≤3.0 m; and (c) shrubs ≤1.5 m in height. Key to the species: acanig, *Acacia* (*Senegalia*) *nigrescens*; adadig, *Adansonia digitata*; casabb, *Cassia abbreviata*; cepmol, *Cephalocroton mollis*; ciscor, *Cissus cornifolia*; cmmedu, *Commiphora edulis*; cmmgla, *Commiphora glandulosa*; colmop, *Colophospermum mopane*; comapi, *Combretum apiculatum*; comher, *Combretum hereroense*; comimb, *Combretum imberbe*; commos, *Combretum mossambicense*; dalmel, *Dalbergia melanoxylon*; diccin, *Dichrostachys cinerea*; diosqu, *Diospyros squarrosa*; ehramo, *Ehretia amoena*; empkir, *Empogona kirkii*; fluvir, *Flueggea virosa*; garres, *Gardenia resiniflua*; grebic, *Grewia bicolor*; grefla, *Grewia flavescens*; gremont, *Grewia monticola*; grevil, *Grewia villosa*; gympub, *Gymnosporia pubescens*; hipbuc, *Hippocratea buchananii*; kiracu, *Kirkia acuminata*; lansch, *Lannea schweinfurthii*; phivio, *Philenoptera violacea*; sclbir, *Sclerocarya birrea*; terpru, *Terminalia prunioides*.

the workshop exclosure on either side of the GNP – Matibi II fence-line, airfield and vegetation types 23 and 38 of Clegg (2010). Data for each location were the mean values of species density (plants ha^{-1}). Singletons were deleted. Trees and shrubs of the three dominant species (*C. mopane*; *Combretum apiculatum*; *Terminalia prunioides*) were treated as pseudo-species in order to represent structural differences. Default settings of the metaMDS function in the *vegan* package (Oksanen et al., 2022) were used, specifically, the transformations applied were a square-root transformation of data and a Wisconsin double standardisation of the data matrix.

4 | RESULTS

4.1 | Elephant population

The density of all elephants increased linearly from 1980 to 2022, from close to 0 elephants km^{-2} to 3.23 elephants km^{-2} in 2022 (Figure 2), compared with an average density of 2.22 elephants km^{-2} for GNP in 2022. The density of adult bulls increased linearly between 1995 and 2022, from about 0.2 to 0.62 adult bulls km^{-2} (Figure 2), compared with the park average in 2022 of 0.37 adult bulls km^{-2}. Densities of >2.7 elephants km^{-2} and about 0.5 adult bulls km^{-2} were supported from 2013 onward. As expected, the total population showed a greater rate of increase in density than adult bulls from 1995 onward ($F_{3,18}=86.67$; $p<0.0001$; $R^2_{adj}=0.9245$) for the interaction between 'year' and 'group'.

4.2 | Vegetation

4.2.1 | Fence-line contrast

Mopane was the dominant species on either side of the fence, contributing 97.0% and 84.3% of trees plus transformed trees for GNP and Matibi II respectively; *Combretum apiculatum* and *Terminalia prunioides* were the only other slightly conspicuous species of tree or transformed tree (Figure 3, Table 1). The dominant shrub species were mopane, *Terminalia prunioides*, *Dichrostachys cinerea*, *Grewia villosa* and *Hippocratea buchananii* (Figure 3, Table 1). Twice as many stems (42.8% vs. 21.3%) had been pollarded in GNP than in Matibi II (Table 2). Pollarding was the main form of damage – only ten trees had been pushed over. There was no difference across the fence line in the density of transformed trees, trees plus transformed trees of mopane or shrubs (Table 2). However, in GNP compared with the communal area, the density of trees was marginally less, mopane trees were on average 1.3 m shorter (Table 2), and the maximum height of mopane trees had been reduced to <5.5 m compared to <9 m (Figure 4). Mopane woodland in both areas had, therefore, been hedged but recent protection afforded by fencing of the communal area had allowed regrowth of mopane trees. Richness of woody species was marginally lower in the park versus Matibi II (16 vs. 29), but there was no difference in the species richness of shrubs or of trees plus transformed trees (Table 2). Noteworthy differences were the absence from GNP of *Commiphora glandulosa* and *Sclerocarya birrea*, and the scarcity of *Grewia* shrubs, with the exception of *G. villosa* (Table 1). Shrub composition on either side of the fence was also different, as shown by a Bray–Curtis Dissimilarity measure of 0.735 (Table 2).

4.2.2 | Workshop exclosure

A total of 31 woody species was recorded within the exclosure, compared with only 12 species outside ($\chi^2=8.395$; $df=1$;

TABLE 1 Woody composition (density ha^{-1}) of *Colophospermum mopane* woodland in the Chipinda Pools region of Gonarezhou National Park: (a) within a fenced workshop area which served as an elephant exclosure, with ~1 ha of remaining natural vegetation, and an area immediately adjacent to the workshop freely accessible to elephants; (b) fence-line contrast between the park and the adjacent Matibi II communal area; and (c) around the airfield in 2022, which is for comparison with the non-quantitative description of *C. mopane* woodland given by Kelly and Walker (1976) in 1971/72 (see section 'Historical information and landscape pattern'); and (d) two types of *C. mopane* woodland on the adjoining Malilangwe Wildlife Reserve.

Species	Plant form	Workshop inside density (ha^{-1})	Workshop outside density (ha^{-1})	GNP density (ha^{-1})	Matibi density (ha^{-1})	Airfield density (ha^{-1})	Clegg type 23[a] density (ha^{-1})	Clegg type 38[b] density (ha^{-1})
Acacia (Senegalia) nigrescens	Tree	3.0	1.0		5.6		1.6	
	Shrub						7.5	0.8
Cassia abbreviata	Tree			1.9	3.7			1.0
Cephalocroton mollis	Shrub				11.1		29.3	
Cissus cornifolia	Shrub			3.70		5.9	18.1	25.3
Colophospermum mopane	Tree	485.7	260.7	298.2	257.4	236.0	159.4	203.8
	Shrub	382.7	1491.7	300.9	151.9	814.6	255.9	190.0
Combretum apiculatum	Tree	49.0	0.0	1.9	27.8			38.0
	Shrub	29.1	49.5	25.9	55.6	6.4	1.0	54.0
Combretum hereroense	Tree			1.9				
	Shrub			0	5.6		1.0	
Combretum imberbe	Tree	10.0	4.5	1.9	3.7	3.3	0.7	
Combretum mossambicense	Shrub	4.1	0.0	5.6	22.2	3.5		20.0
Commiphora africana	Tree	12.3	0.0				0.3	
	Shrub	8.2	0.0			1.7	64.5	
Commiphora edulis	Tree	3.0	0.0					
	Shrub	8.2	0.0		5.6			
Commiphora glandulosa	Tree	11.0	0.0		5.6		0.4	2.7
	Shrub	4.1	0.0					
Commiphora pyracanthoides	Shrub					1.9	169.9	4.0
Dalbergia melanoxylon	Shrub				5.6		19.3	
Dichrostachys cinerea	Shrub	143.6	20.7	152.8	164.8	27.9	15.6	17.3
Diospyros squarrosa	Tree				7.4			0.26
	Shrub							1.0
Ehretia amoena	Shrub			5.6	3.7		0.8	
Empogona kirkii	Shrub	16.6	37.5		5.6		3.6	73.3
Flueggea virosa	Shrub	16.6	0.0	9.3	18.5		1.0	0.8
Gardenia resiniflua	Shrub				3.7			6.8
Grewia bicolor	Shrub	323.0	24.3	16.7	27.8		25.4	70.3

(Continues)

TABLE 1 (Continued)

Species	Plant form	Workshop inside density (ha^{-1})	Workshop outside density (ha^{-1})	GNP density (ha^{-1})	Matibi density (ha^{-1})	Airfield density (ha^{-1})	Clegg type 23[a] density (ha^{-1})	Clegg type 38[b] density (ha^{-1})
Grewia flavescens	Shrub	86.0	12.3	22.2	53.7			8.0
Grewia monticola	Shrub	12.3			1.9		13.0	11.8
Grewia villosa	Shrub			21.3	266.7		28.9	
Gymnosporia pubescens	Shrub			1.9	1.9		97.6	
Hippocratea buchananii	Shrub	460.0	24.3	115.7	46.3	8.7	39.7	34.0
Kirkia acuminata	Tree	15.0	0.0	0	3.7			1.0
	Shrub	8.2	0.0					
Lannea schweinfurthii	Tree	5.0						
	Shrub				11.1			
Markhamia zanzibarica	Tree							1.8
	Shrub	0.0	12.3					186.8
Philenoptera violacea	Tree	1.0		1.9	1.9		0.4	
	Shrub						7.6	
Pterocarpus brenanii	Tree	12.3	0.0				0.2	1.5
	Shrub						20.1	16.3
Sclerocarya birrea	Tree	2.0					0.8	2.0
	Shrub				11.1		6.2	3.3
Terminalia prunioides	Tree	28.6	4.1	25.9	42.6			3.0
	Shrub	53.0	135.0	107.4	238.9			17.8
Vitex ferruginea	Tree	20.4	0.0					
	Shrub	8.2	25.0					
Other[c]	Tree	3.0	0.0		1.9			0.64
	Shrub	12.6	12.3			5	6.2	1.0

Note: Columns shaded light grey represent sites which have been subjected to chronic elephant utilisation.

[a]*Colophospermum mopane – Enneapogon scoparius* open woodland (Clegg, 2010);

[b]*Colophospermum mopane – Endostemon tenuiflorus* open woodland (Clegg, 2010).

[c]Occurred on only one site: an additional three tree and 12 shrub species.

TABLE 2 Differences in mean vegetation structure (± SE) across a fence line between Gonarezhou National Park (GNP) and Matibi II communal area.

Variable	GNP	Matibi	Test statistic[a]	*p*
Tree density (ha^{-1})	157.4 ± 15.29	233.3 ± 40.06	$t = 2.49$	0.0555
Transformed tree density (ha^{-1})	129.6 ± 26.71	72.2 ± 25.62	$t = 1.92$	0.1127
Density (ha^{-1}): mopane trees plus transformed trees	298.1 ± 31.87	257.4 ± 68.10	$t = 0.9$	0.4218
Shrub density (ha^{-1})	835.2 ± 101.7	1118.5 ± 124.5	$t = 1.51$	0.1903
Mopane tree height (m)	3.9 ± 0.08	5.2 ± 0.33	$t = 4.8$	0.0047
Mopane pollarded stems (%)	42.8	21.3	$t = 2.78$	0.0387
Species richness – total	16	29	$\chi^2 = 3.76$	0.0526
Species richness – trees	5	11	$\chi^2 = 2.25$	0.1336
Species richness – shrubs	14	22	$\chi^2 = 1.78$	0.1824
Bray–Curtis dissimilarity	0.7354		$t = 16.03$	0.00002

[a] $df = 5$ for all t-tests.

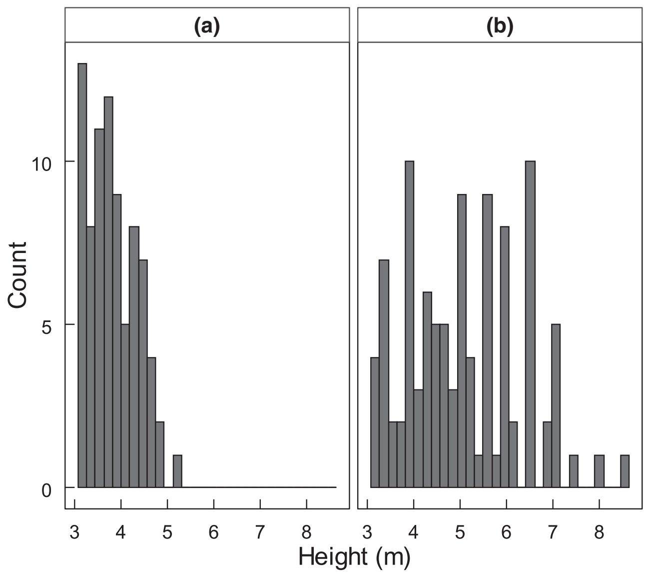

FIGURE 4 Height distribution of *Colophospermum mopane* trees (individuals >3.0 m in height) on either side of the fence separating (a) Gonarezhou National Park and (b) the adjacent Matibi II communal area (Kolmogorov–Smirnov two-sample test: D = 0.52686; $p = 3.4e{-}11$).

$p = 0.0038$), a difference of 61%. All species recorded on the outside, except for one, were found within the exclosure (Table 1). Mopane was the dominant shrub species outside the exclosure, with nine other species recorded at low density. By contrast, inside the exclosure, the density of *Grewia bicolor* or *Hippocratea buchananii* was equivalent to that of mopane shrubs, with 21 shrub species recorded in total (Figure S1). The differences in shrub composition were distinct between each pair of plots (D = 0.734; 0.525), but the differences in tree composition were less distinct (D = 0.985; 0.663). Mopane was the mono-dominant tree species outside the exclosure, with only three other tree species represented (Table 1), whereas mopane was the dominant tree species of only one plot inside the exclosure (Figure S2). Chronic elephant utilisation of the area immediately adjacent to the workshop

TABLE 3 Indicators of plant utilisation outside the workshop exclosure (average of two plots).

Variable	Mopane trees	Other trees	Mopane shrubs	Other shrubs
n	82	16	164	59
Old elephant damage (% stems)				
No impact	2.4	6.8	38.4	37.3
Leaves/branches	9.8	0	20.1	0
Pollarded	78.0	86.7	40.9	57.6
Pushed over	9.8	6.8	0.6	5.1
Biomass removed per plant (%)	53.0	72.1	23.4	47.6

exclosure was confirmed (Table 3). Transformed trees (reduced to <3 m in height) constituted 33.3% of the *Combretum imberbe* trees and 5.7% of the mopane trees recorded. In terms of old elephant damage, >88% of tree main stems had been pollarded or pushed over by elephants, and a tree had lost on average more than half of its biomass. Impact recorded for old unknown damage or new elephant damage on trees was minor and disregarded. The average height of all trees, and of mopane, was reduced by approximately 2 m (Table 4), and the distribution of tree height was truncated from 3 to 12 m inside to <7.5 m outside the exclosure (Figure 5). Impact on shrubs was also conspicuous: >40% of shrubs had been pollarded or pushed over, a shrub had lost >23% of its biomass (Table 3), and shrub height was reduced by 0.8–1.7 m (Table 4). In summary, the area outside the exclosure had been transformed into a hedged mopane woodland by chronic elephant use.

4.2.3 | Historical information

The road census revealed the nature of vegetation change over 50 years since the vegetation was described by Kelly and

TABLE 4 Vegetation differences (mean, SE) between the two sides of the workshop exclosure for two separate plots.

	Plot 1 in	Plot 1 out	Difference	Plot 2 in	Plot 2 out	Difference
Shrub height (m)	2.6 ± 0.08	0.9 ± 0.03	t = 19.2; p = 1.98e−54	2.4 ± 0.21	1.6 ± 0.15	t = 3.3; p = 0.0015
Tree height (m)	5.6 ± 0.26	3.7 ± 0.17	t = 6.02; p = 1.43e−07	5.9 ± 0.31	3.8 ± 0.29	t = 5.2; p = 6.11e−06
Mopane tree height (m)	5.9 ± 0.42	3.7 ± 0.18	t = 4.7; p = 0.00008	5.6 ± 0.29	3.8 ± 0.29	t = 4.4; p = 0.00008

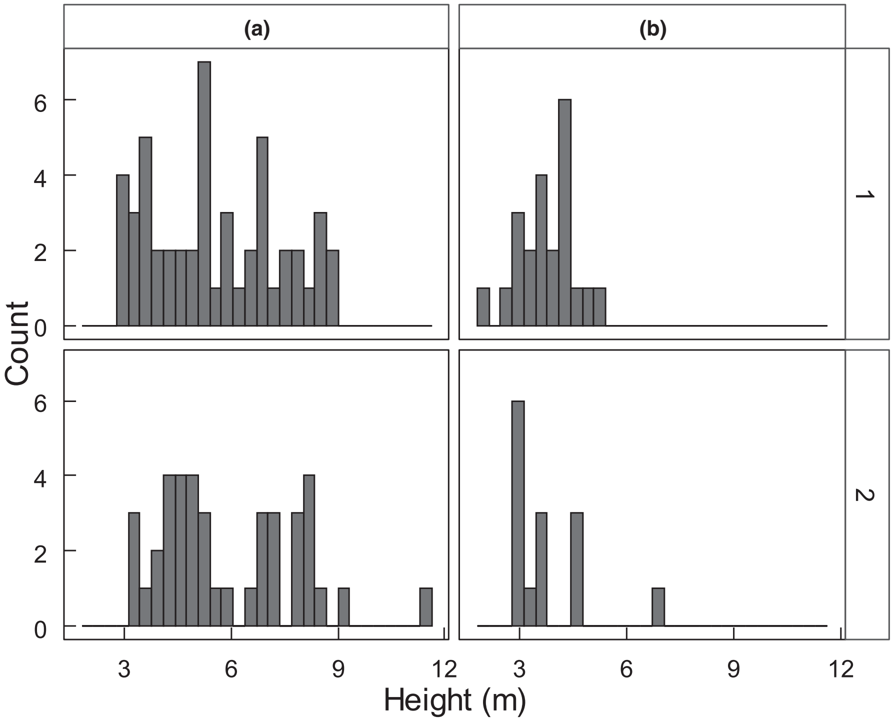

FIGURE 5 The effect of exclosure on the distribution of tree height: inside the exclosure (left-hand column a) differed from outside the exclosure (right-hand column b) for both plot 1 (top row; D = 0.58364; p = 0.00006) and plot 2 (bottom row; D = 0.61429, p = 0.0008).

TABLE 5 Density of trees and shrubs of selected species occurring on basalt geology within 10 km north and south of the Runde River.

		Density (ha^{-1})		
Species	Plant form	North bank	South bank	Average
Acacia nigrescens	Tree	0	0.015	0.01
Cissus cornifolia	Shrub	3.24	0.96	2.10
Commiphora africana	Shrub	0.53	0.26	0.40
Commiphora glandulosa	Shrub	0.04	0	0.02
Commiphora pyracanthoides	Shrub	0.31	0.44	0.38
Diospyros squarrosa	Shrub	0	0.09	0.05
Grewia bicolor	Shrub	0	1.84	0.92
Grewia flavescens	Shrub	0	0.07	0.04
Grewia lepidopetala	Shrub	0	0.07	0.04
Grewia monticola	Shrub	0.04	0	0.02
Kirkia acuminata	Tree	0	0.03	0.02
	Shrub	0.04	0.17	0.11
Lannea schweinfurthii	Shrub	0.11	0.04	0.08
Sclerocarya birrea	Shrub	0.46	0.35	0.41
Sterculia rogersii	Shrub	0.04	0	0.02
Vitex ferruginea	Shrub	0	2.36	1.18

Walker (1976). Adults of *Acacia nigrescens* and *Kirkia acuminata* occurred at low density, no adult trees of *Sclerocarya birrea* or *Commiphora glandulosa* had persisted, but small shrubs of *S. birrea*, *K. acuminata*, *Lannea schweinfurthii*, three *Commiphora*, four *Grewia* and other shrub species were present at very low density (Table 5). By contrast, *Cissus cornifolia*, a shrub not used much by elephants,

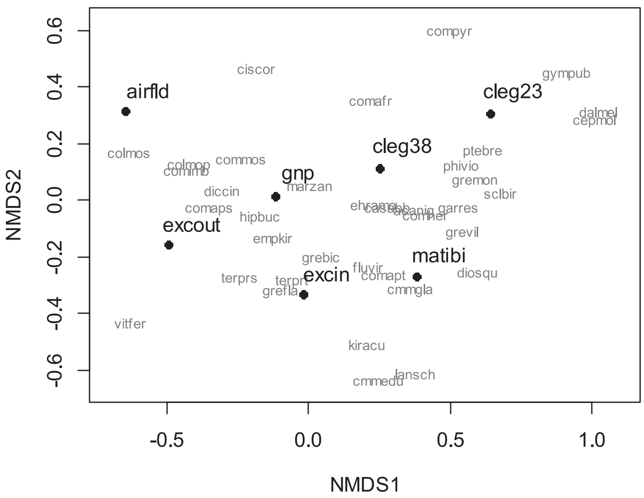

FIGURE 6 The first two axes of a non-metric multidimensional ordination using two stress levels (stress = 0.0682834, a good fit). Key to the sites (see Figure 1 for the locations): airfld, airfield; cleg23, vegetation type 23 (Clegg, 2010); cleg38, vegetation type 38 (Clegg, 2010); excin, exclosure plot inside; excout, exclosure plot outside; gnp, fence-line contrast park side; matibi, fence-line contrast communal area. Key to the species: acanig, *Acacia (Senegalia) nigrescens*; casabb, *Cassia abbreviata*; ciscor, *Cissus cornifolia*; colmos, cmmafr, *Commiphora africana*; cmmedu, *Commiphora edulis*; cmmgla, *Commiphora glandulosa*; cmmpyr, *Commiphora pyracanthoides*; colmos, *Colophospermum mopane* shrub; colmot, *Colophospermum mopane* tree; comaps, *Combretum apiculatum* shrub; comapt, *Combretum apiculatum* tree; comher, *Combretum hereroense*; comimb, *Combretum imberbe*; commos, *Combretum mossambicense*; dalmel, *Dalbergia melanoxylon*; diccin, *Dichrostachys cinerea*; diosqu, *Diospyros squarrosa*; ehramo, *Ehretia amoena*; empkir, *Empogona kirkii*; fluvir, *Flueggea virosa*; garres, *Gardenia resiniflua*; grebic, *Grewia bicolor*; grefla, *Grewia flavescens*; gremon, *Grewia monticola*; grevil, *Grewia villosa*; gympub, *Gymnosporia pubescens*; hipbuc, *Hippocratea buchananii*; kiracu, *Kirkia acuminata*; lansch, *Lannea schweinfurthii*; marzan, *Markhamia zanzibarica*; phivio, *Philenoptera violacea*; ptebre, *Pterocarpus brenanii*; sclbis, *Sclerocarya birrea* shrub; sclbit, *Sclerocarya birrea* tree; terprs, *Terminalia prunioides* shrub; terprt, *Terminalia prunioides* tree; vitfer, *Vitex ferruginea*.

occurred at more than twice the density of any other shrub species. The composition of the airfield plots was consistent with this pattern of change (Table 1), where the only tree species were mopane and one individual of *Combretum imberbe*. Mopane was the strongly dominant species of the 12 shrub species recorded in these plots, but no *Grewia* shrubs, or shrubs or saplings of *S. birrea* or *C. glandulosa* were encountered, although two shrub species of *Commiphora* occurred at low density (Table 1).

Compositional variation was adequately described by an nmds ordination with two stress levels (stress = 0.068283, a good fit). The ordination successfully illustrated a gradient in composition from sites associated with low elephant density (right-hand side of the ordination diagram) through to sites subjected to chronic elephant pressure (left-hand side of the ordination diagram) (Figure 6). Species characteristic of the first mentioned group of sites included *Grewia* shrub species, *Commiphora* tree species, *K. acuminata*, *L. schweinfurthii*, *P. violacea* and *S. birrea*. Species associated with chronic utilisation by elephants included mopane shrubs and trees, shrubs of *C. apiculatum* and *T. prunioides*, *C. imberbe* trees and the shrub species *Combretum mossambicense*, *Cissus cornifolia* and *Dichrostachys cinerea*. Paired plots (GNP vs. Matibi; outside vs. inside exclosure; airfield vs. Clegg vegetation types 23 and 38) were consistently arranged in ordination space in accordance with this gradient (Figure 6). However, some sites associated with low elephant density were more dissimilar in composition with one another than they were to sites which had experienced chronic elephant use, attributed to additional environmental influences on composition. Small sample size precluded investigation of these additional influences.

5 | DISCUSSION

5.1 | Chronic elephant utilisation of the study area

The stratum surveyed constituted between 3.9% and 23.1% of the total area of the national park, and GNP constitutes <10% of the area of the Greater Limpopo Transfrontier Conservation Area that is potentially accessible by elephants from GNP. Home range areas of adult bulls and breeding herds in GNP can be, respectively, as large as 7000 and 2500 km^2 (pers. comm., B. Mandinyenya, Ecologist, GNP). Figure 2, therefore, shows the changes in occupancy of the study area by elephants which use a far larger area, and does not necessarily reflect the >6% rate of population growth evident between 1992 and 2021 (Dunham et al., 2021). Indeed, the pattern of occupancy of a stratum need not show any directional pattern of change over time, as was evident for the Mabalauta stratum in southern GNP (O'Connor & Shimbani, 2024). There is no obvious explanation of why the Chipinda but not the Mabalauta stratum of survey has experienced an increasing pattern of occupancy by elephants since 1990, but the pattern shown (Figure 2) underscores that the study area has been subject to increasing use by elephants over time. The density of >2.7 elephants km^{-2} recorded for the Chipinda region was above the average across all strata of the park of approximately 2.2 elephants km^{-2} (Dunham et al., 2021), both of which are among the highest densities recorded for semi-arid savannahs (Cumming, 1981). Elephant density had exceeded one elephant km^{-2} for the previous decade, a density in excess of that conventionally considered to ensure the persistence of woodlands (Cumming et al., 1997). The density of adult bulls has risen at a slower rate than that of breeding herds over the last two decades (Figure 2), which is attributable to mortality experienced during the calf and juvenile periods (Moss, 2001) and the greater area used by adult bulls. Nonetheless, the density of adult bulls was also greater than the park's average (Dunham et al., 2021), which is cause for concern because adult bulls are responsible for a disproportionate amount of the damage inflicted on woody plants in terms of pollarding, ringbarking and uprooting (Clegg & O'Connor, 2016). In summary, the Chipinda region of GNP has experienced chronic use by elephants over the last two decades.

5.2 | Vegetation transformation

Studies of a fence-line contrast and an exclosure plot confirmed that mopane woodland in the Chipinda region has been transformed from a woodland structure of trees to a shrubland, although mopane remained abundant and increased its dominance (Figures 3–5; Tables 1 and 2). Elephants transformed mopane woodland almost exclusively by pollarding tree stems rather than by pushing over, ringbarking or uprooting main stems (Table 3). This 'hedged' mopane shrubland resulting from pollarding of trees has been consistently observed for mopane woodland subjected to sustained elephant utilisation across southern Africa (O'Connor et al., 2024; Smallie & O'Connor, 2000; Styles & Skinner, 2001). By contrast, elephants impact many other species mainly through ringbarking, pushing over or uprooting of stems that, by contrast with pollarding, usually results in the death of a tree (Jacobs & Biggs, 2002b; Laws et al., 1975; O'Connor, 2017). Mopane is further distinguished by its ability to coppice prolifically following pollarding (Mushove & Makoni, 1993) compared to trees of some species when pollarded which coppice weakly and then die (e.g. MacGregor & O'Connor, 2004). Mopane woodland, therefore, persists under sustained elephant impact whereas most other woodlands are usually radically transformed into a very open woodland structure or even grassland (Guldemond & Van Aarde, 2008; Laws et al., 1975). A consequence of the persistence of hedged mopane is improved food availability for elephants because coppicing increases the amount of suitable forage (O'Connor et al., 2024; Smallie & O'Connor, 2000; Styles & Skinner, 2001). Mopane is tolerant of repeated utilisation, continuing to replace defoliated foliage through coppicing (Mushove & Makoni, 1993), such that elephant utilisation of mopane woodlands can be sustained year upon year but other species growing in mopane woodland may not be tolerant of repeated and severe utilisation. The compositional differences recorded between inside and outside the exclosure (Table 2), and either side of the fence-line contrast, are attributed to the differences in the abundance of species other than mopane, which is starkly shown by a 45–61% decrease in woody species richness accompanying the hedging of mopane woodland.

5.3 | Trend towards local extirpation or persistence

Identifying which species in this study might be trending towards local extirpation requires an evaluation of whether the adult population was being lost, and whether adult recruitment from saplings or sapling recruitment from seedling regeneration has been curtailed, through direct or indirect elephant impacts. A challenge is reaching a conclusion about rare or uncommon species that would be at high risk if used by elephants, but which are usually poorly represented in plot-based sampling. In this study, the use of a set of separate, yet related, exercises assisted in addressing the fate of such species. Tables 1 and 5 summarise the complementary information of an exclosure plot, a fence-line contrast and comparison of GNP with an adjacent wildlife reserve supporting a low elephant density. No adult populations of the tree species *Sclerocarya birrea*, *Commiphora* spp. (*C. glandulosa*, *C. edulis*), *Lannea schweinfurthii* or *Sterculia rogersii* remained in the area, and those of *Kirkia acuminata* and *Senegalia nigrescens* were present at a low density, but regeneration of all these species was present at a low density. A similar pattern was evident for shrub species of *Commiphora* (*C. africana*, *C. pyracanthoides*) or *Grewia* (*G. bicolor*, *G. flavescens*, *G. monticola*). Thus, although adult populations had been eliminated, local extirpation of these populations had been prevented by regeneration at low density. Of note was that an extensive road census (Table 5) rather than plot-based sampling (Table 1) revealed regeneration of these species. The uncommon species of *Dalbergia*, *Diospyros*, *Pterocarpus* and *Vitex* also appear to have been nearly extirpated. Baobab density is shown elsewhere to have been considerably reduced in the proximity of the Runde River in GNP (Foster et al., 2024).

Species shown in this study to be vulnerable to chronic elephant utilisation have experienced a similar fate elsewhere. A similar loss of *S. birrea* has been recorded in Kruger National Park, South Africa (Jacobs & Biggs, 2002a, 2002b). Different species of *Commiphora* were once eliminated over a wide area in Tsavo National Park, Kenya (Leuthold, 1977), and in Ruaha National Park, Tanzania (Barnes, 1983, 1985) – adults of all species of *Commiphora* apparently experience high levels of mortality from pollarding when exposed to chronic elephant utilisation (O'Connor, 2017). *Grewia flavescens* was eliminated from certain habitats in Sengwa Wildlife Reserve, Zimbabwe, through uprooting by elephants (Anderson & Walker, 1974; Conybeare, 2004), which is presumed to be the main means whereby the populations of *Grewia* species in Gonarezhou were depleted (Table 1).

Some species were relatively unaffected under a regime of chronic elephant utilisation, examples of which were the shrub species *Combretum mossambicense*, *Cissus cornifolia*, *Ehretia amoena*, *Flueggea virosa*, *Grewia villosa* and *Gymnosporia pubescens*, and the tree species *Cassia abbreviata* and *Philenoptera violacea*. Elephants similarly avoided some shrub species of riverine mopane woodland in GNP (O'Connor et al., 2024). The basis for elephants avoiding most of these species has not been established. For example, *F. virosa* is eaten by other browsers (Anderson & Pooley, 1977; Du Toit, 1988, 1993; Hall-Martin, 1974; Owen-Smith, 1979); *G. villosa* has large, soft leaves, a leaf type which is usually selected by elephants (Clegg, 2010) but was untouched although its congeners were heavily utilised; whereas *Thilachium africanum* and *Maerua edulis* in riverine mopane woodland (O'Connor et al., 2024) are not browsed on account of toxic properties. The basis for avoidance or selection of forage items requires pursuit of a functional approach towards studying foraging decisions (Clegg, 2010), and closer study of forage properties in relation to the stomach type of elephants (O'Connor et al., 2007).

A third set of species were those which were impacted by elephant utilisation but were apparently persisting albeit at a reduced density, examples of which were the tree species *Combretum apiculatum*, *Combretum hereroense* and *Terminalia prunioides*, and the shrub species *Dichrostachys cinerea* and *Empogona kirkii* and the tree climber *Hippocratea buchananii* which was partially protected by usually growing adjacent to a tree. Elucidation of traits which may have influenced some species trending towards extirpation and others persisting is beyond the scope of this paper, but the affected species describe a marked range in growth form, life-history strategy, attractiveness to elephants and manner of use by elephants.

5.4 | Consequences for trophic patterns

The vegetation changes resulting from sustained elephant impact recorded in this study were transformation of woodlands to shrublands, changes in composition which increased the dominance of mopane, and a possible trend towards local extirpation of about 14 woody species. These changes are expected to have had conspicuous impacts on forage availability for many other animal species. Hedging of mopane resulting from sustained elephant utilisation may increase forage availability for elephants (O'Connor et al., 2024; Smallie & O'Connor, 2000). Other large mammalian browsers may also benefit from vegetation structural changes wrought by elephants, although only black rhinoceros (Van der Westhuizen et al., in preparation) and giraffe (Hall-Martin, 1974) are recorded to consume substantial amounts of mopane. Arguably, giraffes do not benefit from canopy height being lowered. However, the reduction or loss of other woody species is expected to have a negative effect on other large mammalian browser or mixed feeder species in GNP, which includes black rhinoceros, giraffe, eland, greater kudu, nyala, impala, steenbok, grey duiker and Sharpe's grysbok, because all of these species rely on a richness of plant species (Anderson & Pooley, 1977; Du Toit, 1988, 1993; Hall-Martin, 1974; Owen-Smith, 1979; Van der Westhuizen et al., in preparation).

Fleshy fruits offer a high-quality food resource for primates and frugivorous birds, and were a shared attribute of many species concluded to be trending towards local extirpation (Table S1). This group includes *S. birrea*, *L. schweinfurthii* and species of *Commiphora*, *Grewia*, *Vitex* and *Diospyros*. Of the species not noticeably impacted by elephants, only *Cissus cornifolia*, *F. virosa* and *Grewia villosa* have fleshy fruits. In eliminating *Sclerocarya birrea*, elephants have eliminated a species whose fruits they relish (Jacobs & Biggs, 2002a, 2002b) and one for which they are one of the few dispersal agents owing to the size of its fruit, about 3.5 cm in diameter (Lewis, 1987). The fruits of the other species which have been nearly extirpated range in size from about 6–8 mm diameter for *Grewia* species to about 2 cm in diameter for *Diospyros squarrosa*, thus potentially affecting a broad range of vertebrates, especially birds, which are partly frugivorous.

5.5 | Conclusion

It has long been recognised that elephants are capable of transforming closed woodland to open savannah, such as *Brachystegia* woodland to *Combretum* savannah (Cumming, 1981; Thomson, 1975), or even forest to grassland (Laws et al., 1975). In this study of mopane woodland, chronic elephant utilisation has resulted in a stark structural change of the woodland, but mopane remains a dominant, relatively abundant species. However, this study has increased the list of putative examples of potential local extirpation of woody species by elephants (O'Connor et al., 2007). The mopane woodlands on basalt in GNP have become simplified, as observed for mopane woodland in another semi-arid region (O'Connor & Page, 2014). The study was conducted well within the foraging range of elephants, yet the abundance of these impacted species needs to be determined for areas beyond this range in order to assess the threat of local extirpation at a park level.

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No funding was received for this research; it was part of operational responsibilities.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request.

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SUPPORTING INFORMATION

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

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