

ARTICLE

Elephant rewilding affects landscape openness and fauna habitat across a 92-year period

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Abstract

Trophic rewilding aims to promote biodiverse self-sustaining ecosystems through the restoration of ecologically important taxa and the trophic interactions and cascades they propagate. How rewilding effects manifest across broad temporal scales will determine ecosystem states; however, our understanding of post-rewilding dynamics across longer time periods is limited. Here we show that the restoration of a megaherbivore, the African savannah elephant (*Loxodonta africana*), promotes landscape openness (i.e., various measures of vegetation composition/complexity) and modifies fauna habitat and that these effects continue to manifest up to 92 years after reintroduction. We conducted a space-for-time floristic survey and assessment of 17 habitat attributes (e.g., floristic diversity and cover, ground wood, tree hollows) across five comparable nature reserves in South African savannah, where elephants were reintroduced between 1927 and 2003, finding that elephant reintroduction time was positively correlated with landscape openness and some habitat attributes (e.g., large-sized tree hollows) but negatively associated with others (e.g., large-sized coarse woody debris). We then indexed elephant site occurrence between 2006 and 2018 using telemetry data and found positive associations between site occurrence and woody plant densities. Taken alongside the longer-term space-for-time survey, this suggests that elephants are attracted to dense vegetation in the short term and that this behavior increases landscape openness in the long term. Our results suggest that trophic rewilding with elephants helps promote a semi-open ecosystem structure of high importance for African biodiversity. More generally, our results suggest that megafauna restoration represents a promising tool to curb Earth's recent ecological losses and highlights the importance of considering long-term ecological responses when designing and managing rewilding projects.

KEYWORDS

elephant, megafauna, reintroduction, savannah, temporal scale, trophic rewilding

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INTRODUCTION

Trophic rewilding is a nature-based solution that advocates the restoration of historically depleted fauna assemblages as a means to facilitate self-managing biodiverse ecosystems (Bakker & Svenning, 2018; Svenning et al., 2016). By restoring fauna assemblages to resemble those present at some evolutionary baseline, trophic rewilding aims to increase biodiversity and restore lost ecological processes. In particular, trophic rewilding has focused on the restoration of large-bodied megafauna that strongly moderate ecological interactions and processes via trophic cascades or through ecosystem engineering activities (Svenning et al., 2016). Although empirical studies testing rewilding effects are becoming more common (e.g., Guyton et al., 2020), more work is required to determine how rewilding effects manifest at larger spatial and temporal scales (Bakker & Svenning, 2018). This knowledge will be of paramount importance to optimize large-scale rewilding projects, particularly because such initiatives impose considerable financial costs and their widespread application depends on community support.

The effects that megafauna species have on ecosystem dynamics are difficult to quantify because large-bodied species have wide-reaching impacts on multiple ecological responses (here defined as any aspect of the ecology and environment impacted by elephants) that manifest at different spatial and temporal scales (Schweiger et al., 2019; Van Meerbeek et al., 2019). Megafauna restorations themselves are almost always logistically and ethically challenging (Lorimer et al., 2015), which provides a further complication for studies quantifying megafauna effects because classical experiments are difficult. In light of these challenges, case studies are needed that (1) concurrently assess multiple ecological responses and disentangle their correlated impacts on unifying ecosystem processes and (2) draw on multiple data sources and a priori knowledge of predefined ecological interactions to draw inferences about causal ecological effects (Davies & Gray, 2015).

Here, we use such an approach to determine how *de facto* trophic rewilding through the restoration of a charismatic megaherbivore, the African savannah elephant (*Loxodonta africana*), impacts ecological responses across temporal scales that are difficult to manipulate using experimental approaches. We focus on assessing rewilding effects across temporal scales (a 92-year sample period) because there is a strong need for rewilding ventures to achieve ecological gains in both the long and short term (Svenning et al., 2016). Further, a longer-term perspective will allow environmental managers to better predict what kinds of ecological dynamics and states to expect at any point after species reintroduction. Specifically, we contrast

how different ecological responses associated with, and affecting, landscape openness (here defined as various measures of vegetation composition/complexity) and fauna habitat vary across nature reserves with different elephant reintroduction times.

The African savannah elephant is a highly relevant species for testing ideas surrounding rewilding because they are known to act as “ecosystem engineers” that strongly impact ecosystem states (Guldmond et al., 2017). Despite their strong ecological effects, African elephants have recently experienced widespread extirpations (Chase et al., 2016), as have Asian elephants (*Elephas maximus*; Corlett, 2017). At the same time, elephants and other proboscideans represent the evolutionary norm for extant ecological communities across Africa, as well as Eurasia and the Americas (Faurby & Svenning, 2015; Lister, 2013). Therefore, their restoration should restore lost ecological interactions and processes at landscape scales (Galetti et al., 2018).

In sub-Saharan savannah, elephants actively promote herbaceous vegetation cover and increase landscape openness by reducing tree and shrub density and canopy size (Guldmond et al., 2017), which should indirectly impact fauna by selecting for species that prefer “open” rather than “closed” savannah (Gordon et al., 2021; Nasser et al., 2011). By breaking tree branches and toppling trees, elephants are thought to promote herbaceous plant cover/diversity through nursery effects (Coverdale et al., 2016); however, they may compromise the abundance of some larger tree species, which may then negatively affect fauna requiring larger trees (Rushworth et al., 2018). Elephants’ impacts on tree persistence also moderates the amount of coarse woody debris, which may impact fire regimes (Kimuyu et al., 2014) and advantage smaller mammalian fauna, such as rodents or lagomorphs, by creating habitat refugia (Manning et al., 2013) but disadvantage larger species such as antelope by reducing predator detection (Kuijper et al., 2013). By breaking tree branches, elephants can facilitate the formation of tree crevices and hollows (which are an important habitat resource used by a variety of taxa; Pringle, 2008) by allowing primary hollow forming taxa (termites, fungi, some vertebrates) into tree heartwood, which indirectly benefits many hollow-using fauna (Gibbons et al., 2002; Gibbons & Lindenmayer, 2002). Although much is known about elephants’ positive and negative ecological effects, our understanding of how the magnitude and trajectory of these impacts manifest across longer temporal (and spatial) scales is limited.

We used a landscape-scale field survey and a space-for-time approach to understand how vegetation composition and the occurrence of 17 ecological responses varied across five protected areas with different elephant

reintroduction times: no elephants, 2003, 1995, 1972, and 1927. We focused on ecological responses associated with woody vegetation density and impact/damage and size-specific coarse woody debris abundance and tree hollow density. Given a priori knowledge of elephants' ecological effects, we made the following predictions:

1. Woody vegetation density and cover will be highest with no elephants present and will decrease with elephant reintroduction time due to persistent elephant impacts.
2. Tree hollow density and woody vegetation impact will be lowest with no elephants and will increase with elephant reintroduction time due to elephant branch breaking and tree impact. These effects will be strongest for large hollows, which take longer periods to form.
3. Coarse woody debris will be lowest without elephants and will decrease with elephant reintroduction time because elephant impacts are high where elephants are present and woody vegetation densities are higher at younger than older reintroduction times. These effects will be strongest for large coarse woody debris items that are strongly impacted by elephant branch breaking and tree felling.

In addition to assessing reserve-level elephant impacts on ecosystem patterns and processes, we also use telemetry to consider the effects of elephant site occurrence between 2006 and 2018 (here used as a measure of visitation frequency) on various ecological responses to assess patterns at a more local scale. This assessment allowed us to determine whether elephants' shorter-term effects could explain their longer-term impacts. Specifically, we predicted that elephant site occurrence would be positively associated with woody plant density in the short term (i.e., our assessment between 2006 and 2018) because woody plants are an important food resource. Over longer time periods, it is probable that such a response, in association with consistent site visitation over decades (even at lower visitation frequencies), would result in a more open savanna.

METHODS

Study area

The study was conducted in Kruger National Park (KNP; 19,485 km²) and the adjoining Association of Private Nature Reserves network (APNR; 2011 km²) in northeast South Africa (Figure 1). The study area is dominated by lowveld savannah (low-elevation savannah with a

herbaceous understory), nutrient-poor granitic soils, and a subtropical climate (Table 1). The vegetation is dominated by *Sclerocarya birrea* and *Senegalia nigrescens* overstorey trees, *Combretum* spp., *Commiphora* spp., *Grewia* spp., and *Terminalia* spp. midstorey woody plants, and a continuous grassy understory. Fire is historically rare in the APNR network, and median and maximum fire return intervals of 3.8–6.7 and 9–15 years (respectively) have been reported for our study area in KNP (Smit et al., 2013). We conducted a comparative analysis of MODIS satellite imagery (~500 m resolution), which suggested that 64% and 19% of our KNP (mean 11 years-since-fire at burnt sites) and APNR (mean 18 years-since-fire at burnt sites) sites experienced fire between 2000 and 2019, respectively (Table 1).

Reserve history

The study was conducted across five nature reserves that differed in their elephant reintroduction times (Table 1, Figure 1). Elephants were historically common across all reserves before their extirpation in the late 1800s (Hall-Martin, 1992). Cattle and native game were present at varying densities across all reserves (excluding KNP) before their establishment when cattle grazing stopped. A similar and diverse assemblage of native herbivores and carnivores occurs across all reserves (Schütze, 2013). Fauna biomass (Appendix S1: Table S1) and elephant densities (Table 1) were generally comparable across reserves.

The KNP was established in 1927 and a boundary fence erected in 1959. Elephants were rare upon establishment; however, they have experienced dramatic population recovery since then (Ferreira et al., 2017). Elephant densities have increased by zero to one individual/km² at our study sites since 2000 (MacFadyen et al., 2019). We treat 1927 as the elephant reintroduction time for KNP.

The Klasierie Private Nature Reserve (KPNR) was an unprotected nature area before its establishment in 1972. Fences with adjoining APNR and KNP were removed from 1993. Elephants were rare prior to 1972; however, they experienced rapid population increases over the following decades. We treat 1972 as the elephant reintroduction time for KPNR.

Balule Nature Reserve (BNR) was established in 1993, and new properties have been added to the reserve since then. The reserves' eastern fences with adjoining APNR were removed in 2006. Elephants were first detected at our field sites in 2003, and we treat this as the elephant reintroduction time for BNR.

Two properties adjoining BNR were afforded conservation status in 1993 (henceforth the BNR "Buffer Zone"). The reserves are fully fenced. A similarly diverse

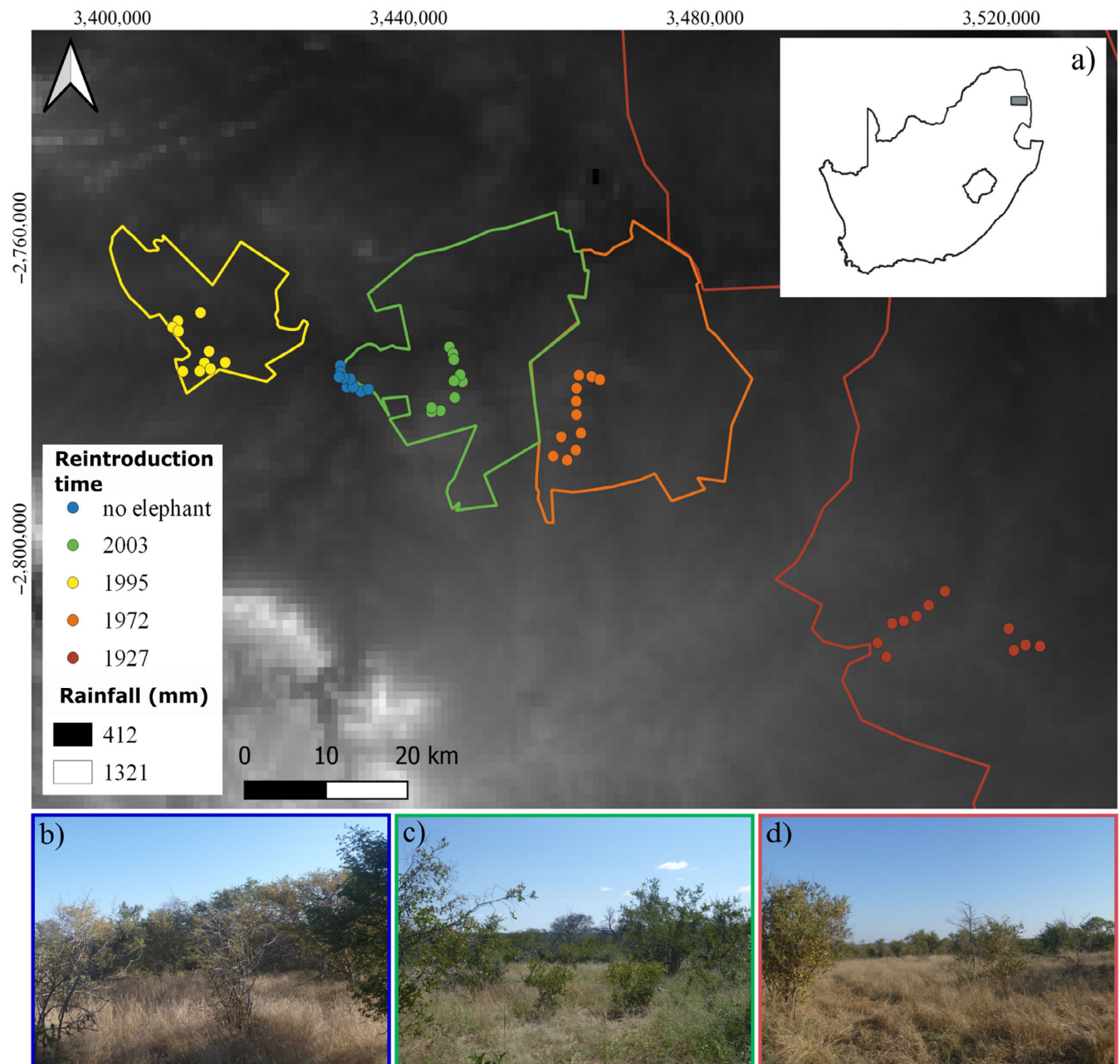


FIGURE 1 (a) Map of study area in northeast South Africa and the location of 52 sites (colored points) where field surveys were conducted. Sites were stratified between five nature reserves with different elephant reintroduction times (colored lines show reserve extent): no elephants (blue), 2003 (green), 1995 (yellow), 1972 (orange), and 1927 (red). The underlying grayscale map shows mean annual rainfall (mm). Coordinates are Universal Transverse Mercator WGS84 projection. (b–d) Images of a typical field site at the reserve where elephants are absent (blue) (b) and where elephants were introduced in 2003 (green) (c) and 1927 (red) (d). Photo credits: Christopher E Gordon.

assemblage of herbivores and carnivores occurs in these reserves compared with APNR and KNP; however, black and white rhinoceros (*Ceratotherium simum*, *Diceros bicornis*), cape buffalo (*Syncerus caffer*), elephants, and lions (*Panthera leo*) are absent. We treat the BNR Buffer Zone as a “control” reserve where elephant reintroductions have not occurred.

Greater Makalali Private Nature Reserve (GMPNR) was established in 1995, and additional properties have

been added to the reserve network since then. The reserve is fully fenced. Elephants were introduced to GMPNR in 1995, and elephant densities of 0.2–0.3 individuals/km² have been maintained since 2000. Elephants were first detected at most of our field sites in 1995, and we treat this as the elephant reintroduction time for GMPNR.

The aforementioned elephant reintroductions were not implemented with a focus on trophic rewilding. However, elephants’ potential for strong ecological effects

TABLE 1 Variables thought to impact fauna and vegetation dynamics within five reserves with different elephant reintroduction times.

Reserve	Size (km ²)	Elephants introduced (year)	Access to other reserves	Elephant density (ind/km ²)	MAP (mm)	MPWM (mm)	Elevation (m)	Distance to water (m)	No. fires: 2000–2016 (count)
Balule Nature Reserve (Buffer Zone)	7.5	None	No	0	507 (507–507)	87 (87–87)	429 (413–456)	1.5 (0.5–3.3)	0
Balule Nature Reserve	559	2003	Yes	1.24 (0.7–1.62)	459 (445–465)	85 (84–86)	459 (419–512)	3.0 (1.9–4.2)	0
Greater Makalali Private Game Reserve	210	1995–2006	No	0.03 (0.02–0.03)	545 (539–565)	96 (95–98)	500 (488–514)	2.4 (1.2–3.4)	0.2 (0–1)
Klaserie Private Nature Reserve	604	1972	Yes	1.49 (0.96–2.22)	422 (416–435)	86 (85–89)	443 (398–504)	1.9 (0.6–3.3)	0.5 (0–1)
Kruger National Park	19,485	1927	Yes	0.56 (0.37–0.75)	544 (541–548)	98 (96–99)	412 (359–463)	8.6 (1.9–1.3)	1 (0–2)

Note: Mean values (± central 95th percentiles) were extracted at field sites within each reserve using the approach described in Appendix S6: Section S1. All sites were located in Granite Lowveld savannah (Mucina et al., 2018).

Abbreviations: MAP, mean annual precipitation; MPWM, mean precipitation in the wettest month.

are allowed to manifest with minimal human intervention, with approximately self-sustaining elephant populations (Robson & van Aarde, 2018). Therefore, we here treat them as de facto cases of trophic rewilding.

Vegetation composition and ecological responses to elephant reintroduction time

We conducted field surveys at 10–11 sites (52 sites total) located in Granite Lowveld savannah with granite lithology and sandy soils (Mucina et al., 2018) within each of the five reserves between April and June 2019. Sites were spaced at 1- to 4-km intervals on catena hilltops and were located 100–200 m from small access roads. To control for confounding factors, all sites were located within the same biophysical and bioclimatic settings (Table 1).

At each site, all live woody plants ≥1 m in height above the ground (excluding taller tree species, see subsequent discussion; henceforth “woody plants”) were identified to species within a 50 × 10 m quadrat. The presence of trunk damage (henceforth “impact”; main stem broken or severed) or uprooting (plants toppled exposing roots) was noted for each plant and its canopy dimensions were measured using a 4-m measuring pole. The surface area (m²) of each canopy was calculated as an ellipsoid using the relevant equation: $SA = 4\pi((ab)^{1.6} + (ac)^{1.6} + (bc)^{1.6}/3)^{1/1.6}$, where *a* = radius canopy width one, *b* = radius canopy width two, and *c* = radius canopy height.

The density of all woody plants per 0.05 ha and the two most common taxa across all reserves, *Combretum*

apiculatum (39% of all woody plants) and *Grewia* spp. grouped (*G. bicolor*, *G. caffra*, *G. flava*, *G. hexamita*, *G. inaequilatera*, *G. monticola*; 27% of all woody plants), were calculated at each site. The canopy surface area measures were summed within sites for all woody plants (excluding taller trees, see subsequent discussion) and for *C. apiculatum* and *Grewia* spp. separately. The percentage of all woody plants with trunk or uprooting impact was also calculated as a measure of overall elephant-mediated woody plant impact, inclusive of compositional changes between sites.

Tree and hollow bearing tree density was assessed at all sites via walking transects conducted along a road (mean length 247 m, range 76–563 m) and a bearing 200 m parallel to the road (mean length 234 m, range 93–395 m). Because tree distribution was often patchy and some tree species and hollow bearing trees were rare, the walking tree transects provided a more appropriate scale to estimate tree and hollow bearing tree density than quadrats. Trees were defined as woody plants with a maximum adult height of ≥15 m and included *Balanites maughamii*, *Combretum imberbe*, *Lannea schweinfurthii*, *Philenoptera violacea*, *S. birrea*, and *S. nigrescens*.

To account for differences in tree density and tree detection between reserves, all trees were counted ≤20 m from one side of each transect at the reserves with “thick” vegetation (no elephants, elephant reintroduction times of 1995, 2003) and ≤40 m at the reserves with “sparse” vegetation (elephant reintroduction times of 1972 and 1927; Table 2). Only trees >5 m in height and 10 cm in width at 130 cm in height above the ground

TABLE 2 Ecological attributes assessed during field surveys, their predicted and observed response to elephant reintroduction time, and the range of site values (median \pm central 95th percentiles) observed at nature reserves with (Elephants) and without elephants (No elephants).

Ecological attribute	Description	Response: Elephant reintroduction time		Site values	
		Predicted	Observed	Elephants	No elephants
All trees	Tree density (>5 m height; 10 ha) from line transects	Decrease due to elephant browsing/impact	Decrease	62 (15–155)	176 (59–279)
<i>S. nigrescens</i>	As above for <i>S. nigrescens</i> trees	As above	Decrease	30 (0–149)	63 (4–141)
<i>S. birrea</i>	As above for <i>S. birrea</i> trees	As above	No effect	13* (5–31)	83* (14–220)
Tree impact	Percentage of trees with ≥ 1 primary stem broken	Increase due to elephant browsing/impact	Increase	33 (0–100)	2 (0–12)
Tree hollows: small	Density (10 ha) trees bearing hollows (2–5 cm width) from line transects	Decrease due to lower tree densities via elephant impact	Decrease	14 (0–39)	18 (0–51)
Tree hollows: medium	As above for hollows >5–10 cm width	As above	No effect	25 (0–47)	24 (0–43)
Tree hollows: large	Presence of trees bearing hollows (>10 cm width) from line transects	Increase due to elephant mediated hollow formation via branch breaking	Increase	0 (0–10)	0 (0–6)
Coarse woody debris (CWD): small	Counts CWD (<5 cm diameter) intercepts at 150 points	Decrease due to lower plant densities via elephant impact	No effect	26* (11–47)	49* (23–74)
CWD: medium	As above for CWD ≥ 5 cm diameter	As above	Decrease	36 (19–55)	8 (1–18)
CWD: large	Presence of CWD (≥ 200 cm length, 20 cm diameter) at 150 points	As above	Decrease	1 (0–7)	0 (0–1)
All woody plants	Density (0.05 ha) woody plants (>1 m height; no trees)	Decrease due to elephant browsing/impact	No effect	38 (16–66)	41 (27–58)
<i>C. apiculatum</i>	As above for <i>C. apiculatum</i>	As above	No effect	17* (4–42)	9* (3–16)
<i>Grewia</i> spp.	As above for <i>Grewia</i> spp.	As above	Decrease	7 (0–33)	17 (6–34)
All woody plant impact	Percentage of woody plants (no trees) with trunk or uprooting damage	Increase due to elephant browsing/impact	No effect	30* (2–62)	9* (0–16)
All woody plant canopy	Sum canopy surface area (m ²) of all woody plant	Decrease due to lower plant densities via elephant impact	Decrease	552 (232–1121)	1037 (666–1265)
<i>C. apiculatum</i> canopy	As above for <i>C. apiculatum</i>	As above	No effect	326 (88–766)	284 (56–505)
<i>Grewia</i> spp. canopy	As above for <i>Grewia</i> spp.	As above	Decrease	66 (0–358)	331 (153–584)

Note: Asterisks denote attributes that differed between nature reserves with and without elephants but did not differ with elephant reintroduction time.

were included in counts. The following attributes were also noted for each tree: perpendicular distance from transect, the presence of at least one primary stem broken at the tree trunk, and the presence of small (2–5 cm minimum entry width), medium-sized (>5–10 cm minimum entry width), and large (>10 cm minimum entry

width) tree hollows (Gibbons et al., 2002). The density of trees and hollow bearing trees were assessed at each site using the methods described in what follows and in Gordon et al. (2021). The percentage of trees with at least one primary stem broken was calculated at each site as a measure of elephant-mediated tree impact.

Thick vegetation may have reduced tree detectability along our line transects, especially at the reserve without elephants and younger (1995, 2003) reintroduction times. Therefore, tree and hollow bearing tree densities (individuals per 10 ha) were calculated at sites using distance sampling (Thomas et al., 2010; Appendix S2: Section S1, Table S1). Density estimates were calculated for all trees combined, the two most common tree species (*S. nigrescens* [54% of trees across sites] and *S. birrea* [31% of trees observed across sites]) and trees bearing at least one small-, medium-, and large-sized hollow. The on- and off-road transects were combined for analysis.

A line-intercept method was used to index the relative abundance of small- (<5 cm in diameter), medium- (≥5 cm in diameter), and large-sized (≥200 cm in length and ≥20 cm in diameter) coarse woody debris items. To do this, the occurrence of coarse woody debris items was noted at 1-m intervals along 3 × 50 m measuring tapes located at the ends and middle of the 50 × 10 m woody vegetation sampling quadrat (see preceding discussion) using a 1-m pole. The total number of small, medium, and large coarse woody debris point intercepts was then counted within each site as a measure of relative abundance. Coarse woody debris is not collected by humans at the study sites.

Woody vegetation composition across elephant reintroduction times: Data analysis

The floristic survey and Bayesian multivariate models were used to determine whether the presence of woody plants within vegetation communities varied across nature reserves with different elephant reintroduction times. The analysis simultaneously fit separate generalized linear models with a binomial distribution for each species, accounting for unmeasured interspecific species interactions and/or environmental effects via the inclusion of two latent variables (Hui, 2016). The five reserves were included as separate binary variables in the model (1 = each reserve, 0 = all other reserves), and therefore reserve-specific responses were made in relation to all other reserves. Species presence was included as a response matrix. Presence data were preferred over counts because few species were ubiquitous across the study region; that is, only 11% of species occurred at >50% of sites. Only species occurring at >5% of sites were considered.

Latent variable biplots were used to visualize community responses between the reserve treatments, whereby similar vegetation communities are observed within discrete site groupings. Species-specific responses within each reserve were assessed using the distributions of

zero-centered model coefficient estimates. A species was more or less likely to occur within a reserve if the median and 95% credible interval (CI) deviated from zero, with a “significant” effect observed if the CI did not cross zero. All analyses were conducted using the *boral* package (Hui, 2016) in R.

Ecological responses to elephant reintroduction time: Data analysis

Separate Bayesian generalized linear models were used to compare how specific ecological responses (Table 2) varied between nature reserves with different elephant reintroduction times. Elephant reintroduction time was included as a categorical variable with five levels (i.e., one for each nature reserve; Table 1) due to the relatively small number of reserves included in the study. The reserve where elephants were absent was treated as the control “reference” group for model inference; that is, the distributions of coefficient estimates and model predictions from the four reserves with different elephant reintroduction times were each compared with those from the reserve where elephants were absent. This approach allowed us to infer a continuous response of each ecological response along a gradient of increasing elephant reintroduction time, given the categorical nature of the reserve-level data (see preceding discussion). The ecological responses were selected based on our understanding of the ecological impacts of elephants within the study area (Table 2).

Models were fit with four parallel chains of 2000 iterations and weakly informative priors (mean 0, SD 20), with the first 1000 iterations discarded from each chain. The posterior predictions from the fit models were used to calculate distributions representing the predicted difference between each of the reserves with different elephant reintroduction times when compared to the reserve without elephants (i.e., four separate effect size measures, one for each reserve where elephants were present). The magnitude of the ecological effects were visualized by comparing the predicted median difference/effect size values ($\pm 50\%$ and 95% CI) between reserves with and without elephants, with stronger effects observed when these values deviated from zero. A “significant” effect was observed if the 95% CI did not cross zero. To qualitatively highlight the trajectory of the ecological effects between reserves with different elephant reintroduction times in our figures, we fit second-order quadratic trend lines ($\pm 95\%$ CI) through the median effect size difference values described earlier. These trend lines were purely illustrative, and no statistical analyses were associated with them.

Gaussian models were used for the small and medium-sized coarse woody debris, all woody vegetation

density, all woody vegetation canopy size and impact, and *C. apiculatum* canopy size analyses. Binomial models were used for the presence of trees bearing large-sized hollows (observed at 36% of sites) and large-sized coarse woody debris (observed at 38% of sites) analyses. Negative binomial models were used for all other analyses to account for overdispersion within the right-skewed data sets.

Ecological responses to long-term elephant site occurrence

The annual core home range of nine to 18 elephants (6–12 bulls occurring in bachelor herds; 3–6 adult females occurring in large family herds) was assessed for 11 years between 2006 and 2018 using movement data from Global Positioning System (GPS) collars (African Wildlife Tracking, Pretoria, South Africa). GPS locations were recorded every 1–4 h each day within reserves with elephant reintroduction times of 1972 (KPNR) and 2003 (BNR). The number and proportion of collared elephants varied between years; however, this did not influence the collective area of elephant home ranges (Appendix S3: Figure S1). Therefore, we are confident that the annual home-range data were comparable across the sample period.

Elliptical time-density models (Wall et al., 2014) were used to calculate the core home range (central 50th percentile of habitat use) of each elephant annually at a 500-m pixel resolution. The individual annual home-range maps were then overlaid to create maps representing the total core annual home range of all collared elephants. Long-term site-occurrence maps were calculated by summing the number of times an annual core home range fell within a pixel (Appendix S4: Figure S1). To reduce edge effects, long-term site occurrence was assessed at each of our field sites by averaging all pixel values within 500 m of a site.

Data analysis

Bayesian generalized linear models were used to compare how a subset of the ecological responses that were common and shown to vary across reserves with different elephant reintroduction times differed with long-term elephant site occurrence at BNR (2003 reintroduction time; 10 sites) and KPNR (1972 reintroduction time; 11 sites). The ecological responses were density of all trees, *S. nigrescens* density, tree impact, density of trees with small-sized hollows, medium- and large-sized coarse woody debris abundance, *Grewia* spp. density, and the size of all woody vegetation canopies. Analyses were not

conducted for large-sized tree hollows because they were rare. Likewise, the size of all *Grewia* spp. canopies was not analyzed because it showed a similar response to that of all woody plant canopies.

Two separate models were fit for each ecological response. First, elephant site occurrence was included as a continuous variable to determine its independent effect on the response variables. Second, site occurrence (continuous) and reserve treatment (categorical) were included as interacting variables to compare responses between the two different nature reserves. Gaussian models were used for the tree impact and medium-sized coarse woody debris analyses, a Poisson model was used for the large-sized coarse woody debris analysis, and negative binomial models were used for the remaining analyses. All models were fit using the protocol described earlier. The distributions of zero-centered coefficient estimates were used to infer the effects of the predictor variables on the ecological responses, with stronger effects observed when the coefficient estimates deviated from zero. A “significant” effect was observed if the 95% CI did not cross zero. The distributions of zero-centered coefficient estimates were used to calculate sets of predicted values at sites, which were used to visualize the trajectory of ecological effects.

All statistical analyses were conducted in R using the `rstandarm` package, and diagnostic checks were made using the `shinytan` package (Muth et al., 2018).

RESULTS

Vegetation composition across elephant reintroduction times

Sixty-one woody plant species were observed across the study region, and 31 were observed at >5% of sites. *Combretum apiculatum* (98% of sites), *S. nigrescens* (75% of sites), *Grewia monticola* (69% of sites), *Cissus cornifolia* (56% of sites), *Grewia flava* (52% of sites), and *S. birrea* (52% of sites) were the most common species across sites. Collectively, the composition of woody vegetation communities was similar across the study region, and no discrete site groupings were observed within the different nature reserves (Figure 2a). Although rare, some species-specific differences were evident (Figure 2b).

Ecological responses to elephant reintroduction time

Two of the ecological responses increased across reserves with increasing elephant reintroduction time (i.e., were higher at reserves with older than younger reintroduction

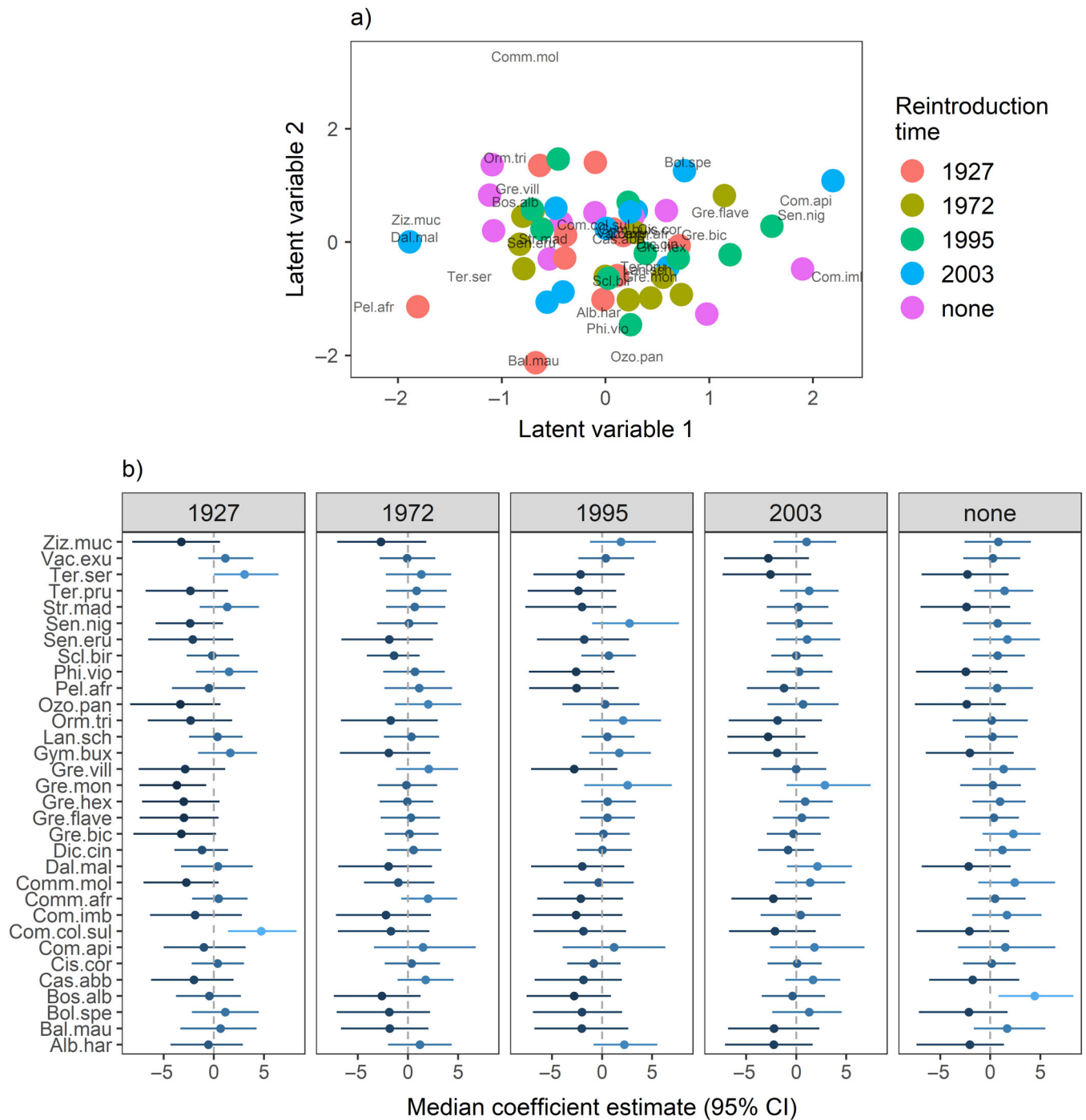


FIGURE 2 (a) Latent variable biplot showing variations in site-level woody vegetation composition (points) between five nature reserves with different elephant reintroduction times (colors). Distinct vegetation communities are present if site-level points are located within discrete reserve groupings, which is not the case here. (b) Caterpillar plots showing how species-specific site occurrence varied between the five nature reserves. For each reserve, the plots show how species occurrence was more (positive) or less (negative) likely to occur at each reserve compared with species occurrence trends across all other reserves collectively. Points show zero-centered coefficient estimates $\pm 95\%$ (credible interval; lines). Darker and lighter colors show greater negative and positive effects, respectively. Species acronyms and full names are shown in Appendix S7: Table S1.

times compared to the reserve without elephants): tree impact (Figure 3b) and the occurrence of trees bearing large-sized hollows (Figure 3d).

Eight of the ecological responses showed a general decrease across reserves with increasing elephant reintroduction time; that is, they were lower at reserves

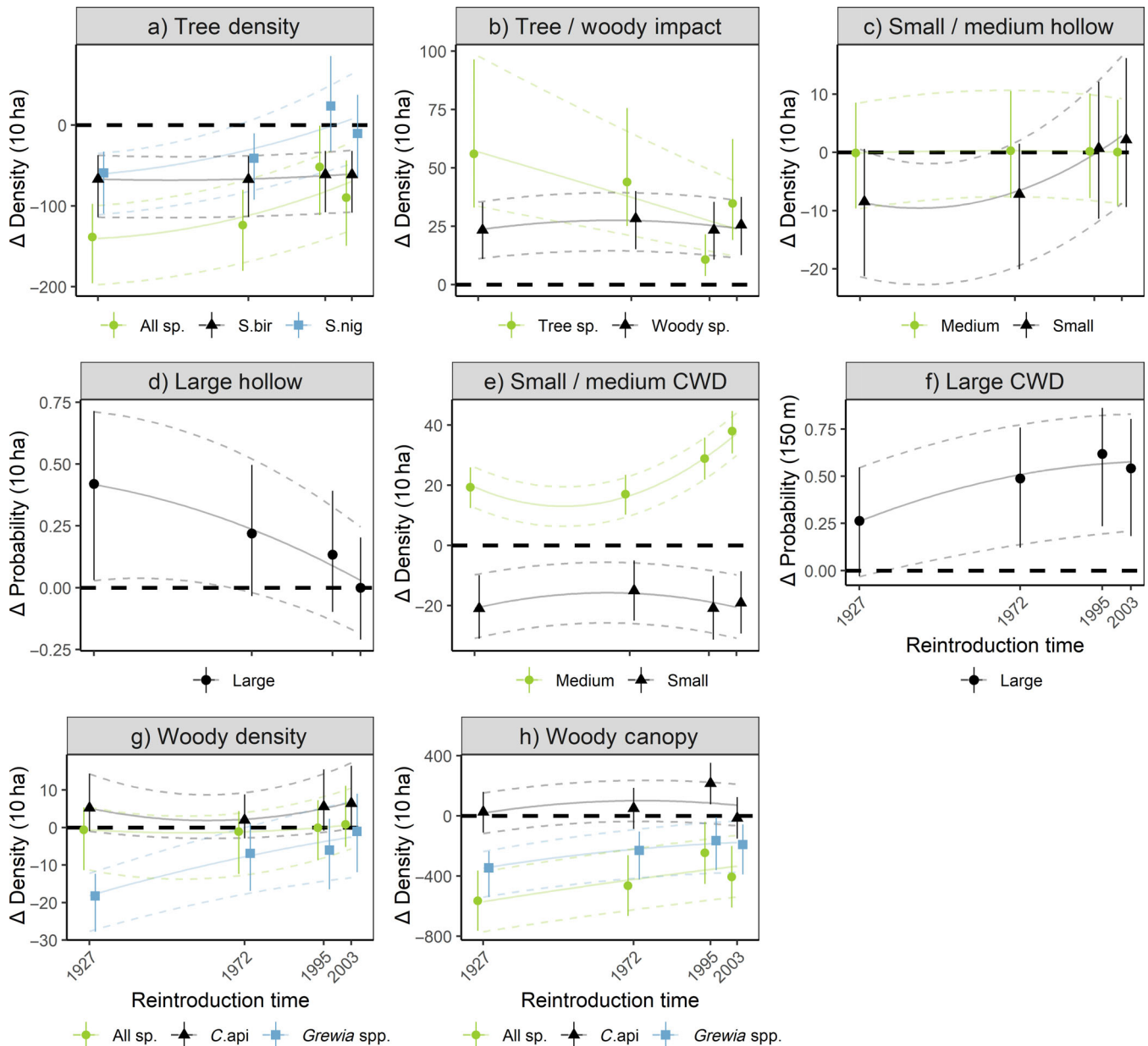


FIGURE 3 Predicted differences for each “ecological response” between four reserves with different elephant reintroduction times and a reserve where elephants are absent. (a) All tree density (>5 m height; green circles) and *Senegalia nigrescens* (black triangles) and *Sclerocarya birrea* density (blue squares). (b) Percentage tree (green circles) and woody vegetation (>1 m height, excluding tree species; black triangles) impact. (c) Small- (black triangles) and medium-sized (green circles) tree hollow density. (d) Large-sized tree hollow probability. (e) Small- (black triangles) and medium-sized (green circles) coarse woody debris density (CWD). (f) Large-sized CWD probability. (g) All woody vegetation density (green circles) and *Combretum apiculatum* (black triangles) and *Grewia* spp. (blue squares) density. (h) All woody vegetation canopy size (green circles) and *Combretum* api. (black triangles) and *Grewia* spp. (blue squares) canopy size. Areas above dashed lines show values that are larger at the reserves with than without elephants. Points show median predictions $\pm 95\%$ (vertical bars) credible intervals (CI). A “significant” effect is observed when the 95% CI do not cross zero. To further visualize how each ecological response varied between reserves with different reintroduction times, second-order quadratic trend lines (\pm central 95% CI; dashed lines) are plotted through the median point predictions.

with older versus younger reintroduction times compared to the reserve without elephants. Tree density (Figure 3a), *Grewia* spp. canopy size (Figure 3h) and all woody plant canopy size (Figure 3h) were always lower at the reserves

with elephants when compared to the reserve without elephants. Medium-sized coarse woody debris abundance (Figure 3e) and large-sized coarse woody debris occurrence (Figure 3f) were always higher at the reserves

compared to the reserve without elephants. The remaining three responses were only lower at the reserves with elephant reintroduction times of 1927 and 1972 when compared with the reserve without elephants: *S. nigrescens* density (Figure 3a), the density of trees bearing small-sized hollows (Figure 3c), and *Grewia* spp. density (Figure 3g; this was also slightly lower at the reserve with an introduction time of 1995).

Seven of the ecological responses did not differ between reserves with different elephant reintroduction times, but four of these nevertheless differed between reserves with and without elephants. *Sclerocarya birrea* density (Figure 3a) and small-sized coarse woody debris abundance (Figure 3e) was always higher at the reserve without than the reserves with elephants. Woody plant impact (Figure 3b) and, to a lesser degree, *C. apiculatum* density (Figure 3g) were always higher at the reserves with than without elephants. The density of trees bearing medium-sized hollows (Figure 3c), all woody plant density (Figure 3g), and *C. apiculatum* canopy size (Figure 3h) were similar across all reserves.

Ecological responses to long-term elephant site occurrence

A positive relationship was observed between long-term elephant site occurrence and the density of all tree species, medium-sized coarse woody debris abundance, and *Grewia* spp. density (Figure 4; Appendix S5: Figure S1). There was no evidence of an interaction between long-term elephant site occurrence and nature reserve; however, there was a tendency (i.e., the 95% CI marginally crossed zero) that site occurrence versus tree impact (and to a lesser degree woody plant canopy size) effects varied between the different reserves (Appendix S5: Figure S1).

DISCUSSION

Elephant rewilding, landscape openness, and fauna habitat

Our study suggests that trophic rewilding with elephants strongly drives multiple ecological responses associated with landscape openness and the availability of fauna habitat. Specifically, we show that habitat attributes associated with closed savannah (e.g., high tree density, large collective canopy size, high abundance of large-sized coarse woody debris) were more common where elephants were absent and at younger reintroduction times. Conversely, attributes associated with open wooded savannah (e.g., opposite of the aforementioned closed

savannah plus large-sized tree hollows) were more common at older reintroduction times. This finding is supported by studies showing that elephants can increase landscape openness (Stevens et al., 2016), impact vegetation structure (Davies et al., 2018), and moderate fauna habitat (Pringle, 2008). However, to date, such studies have not considered the recovery dynamics of such effects across longer temporal scales.

Only three of the 17 responses did not vary between areas where elephants were present and absent: *C. apiculatum* canopy size, the density of trees bearing medium-sized hollows, and total woody plant density. Regarding the latter, elephants are known to reduce woody vegetation cover in savannah landscapes (Stevens et al., 2016); however, the magnitude of these impacts vary between species due to food preferences (De Boer et al., 2000). *Combretum apiculatum*, which was the most common species across our study region, is not a preferred elephant browse (Kos et al., 2012). Therefore, it is likely that the muted response of the total woody plant category can be attributed to the spatial distribution of *C. apiculatum* and other common woody species that elephants do not readily consume. Despite similar woody plant densities, the total area covered by their canopies was always higher in areas where elephants were absent than present and decreased with increasing reintroduction time. This trend highlights that, despite having similar woody stem densities, the savannah landscapes studied here were still much more open at older than younger reintroduction times.

Four of the ecological responses strongly differed between the reserves where elephants were present and the one where elephants were absent, but the magnitude of these effects did not differ between the four reserves with different elephant reintroduction times: *S. birrea* density, woody plant impact, abundance of small-sized coarse woody debris, to a lesser degree *C. apiculatum* density. It is likely that many of these responses had reached a steady-state dynamic within our youngest post-reintroduction reserve (i.e., 16-years) and remained at similarly low densities thereafter. Support for this hypothesis comes from studies showing heavy elephant impacts in the years following reintroduction, especially on preferred food resources (Cook et al., 2017).

Only two of the responses increased with elephant reintroduction time (i.e., the magnitude/direction of the pairwise difference between the reserve where elephants were absent and the four where elephants were present increased with elephant reintroduction time): density of trees with large-sized hollows and tree impact. Tree hollows form when invertebrates and fungi are able to access tree heartwood via bark scars (Gibbons et al., 2002; Gibbons & Lindenmayer, 2002). The size of these scars

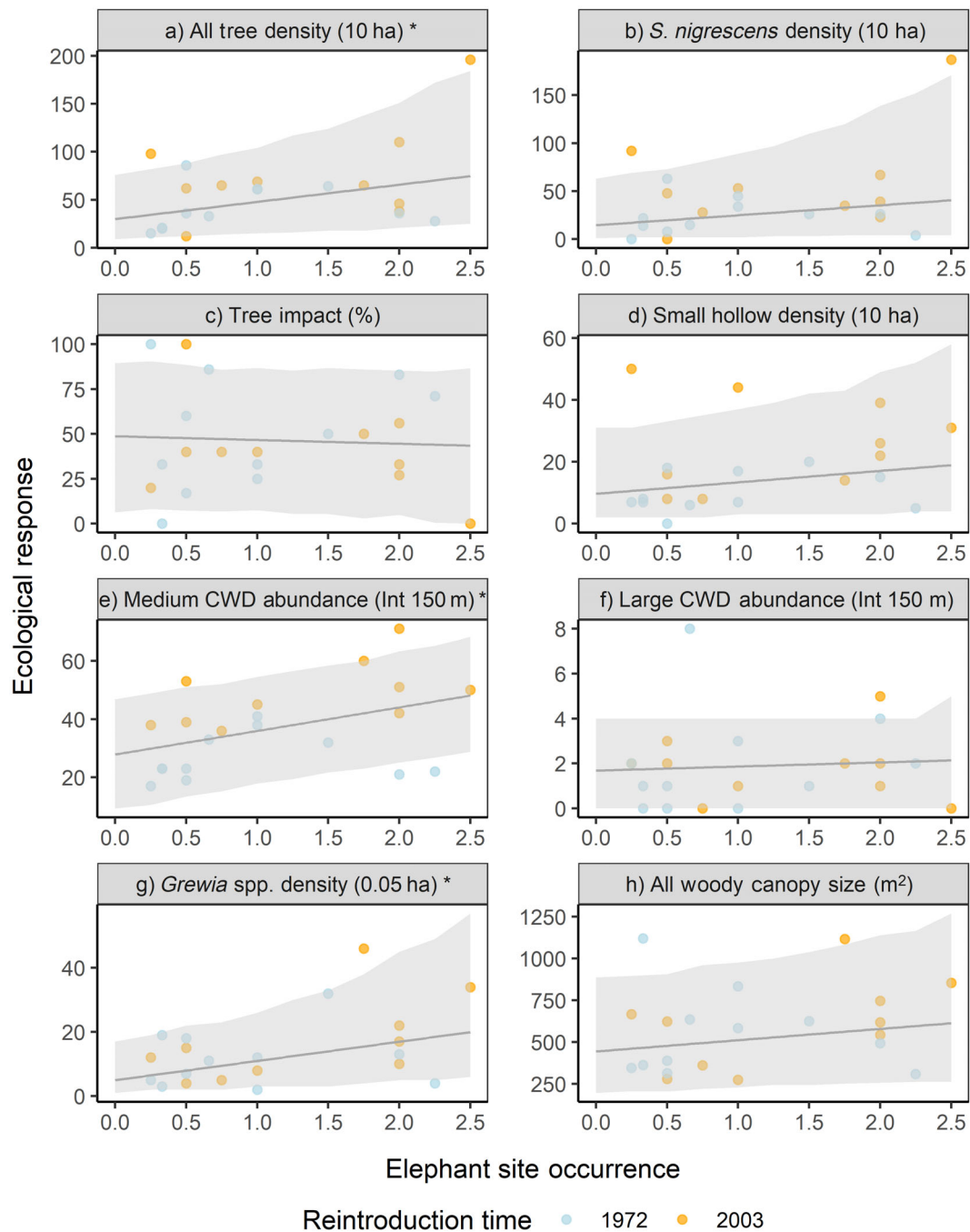


FIGURE 4 Response of (a) tree density, (b) *Senegalia nigrescens* density, (c) tree impact, (d) density of trees bearing small-sized hollows, (e) medium-sized coarse woody debris (CWD) abundance, (f) large-sized CWD abundance, (g) *Grewia* spp. density, and (h) collective canopy size of all woody plant species (excluding trees) to long-term elephant site occurrence. The dark gray line represents predicted median predictions \pm 80% credible interval (light gray band). Colored points show raw data values from sites at two nature reserves with different elephant reintroduction times: 1972 = blue; 2003 = orange. Asterisks represent “significant” responses.

limits hollow size because tree cambium contains a range of chemical defenses to combat invertebrate damage (Gibbons & Lindenmayer, 2002). Therefore, it is not surprising that we observed concomitant trends in tree impact and the density of trees bearing large-sized hollows. This is particularly so because elephants are a leading cause of large branch damage in savannahs where

they are common (Cook et al., 2017; Guldmond et al., 2017), which suggests that elephant damage may be a key driver of large-sized hollow density.

However, tree impact cannot fully explain the spatial variability in large-sized tree hollows because levels of impact were also relatively high at the reserve where elephants were reintroduced in 2003. Interestingly, trees

bearing small-sized hollows were common at the reserve without elephants and a negative association was observed between elephant reintroduction time and the density of trees bearing small hollows. Small hollows can form rapidly due to abiotic disturbances (e.g., wind damage) because there is a smaller space to excavate (Gibbons & Lindenmayer, 2002). Therefore, it is likely that both elephant damage and longer time periods are required to form and promote the density of large-sized hollows. Conversely, small-sized hollows may form in the absence of elephant damage and at younger reintroduction times (i.e., via abiotic processes); however, their absolute density will be moderated by elephants at older reintroduction times due to elephants' negative effects on tree density. This hypothesis is supported by a recent study showing that tree damage by various megaherbivore species is a key hollow-forming process in European forests (Broughton et al., 2022).

The remaining responses decreased with elephant reintroduction time, and most were associated with increasing landscape openness (i.e., the magnitude/direction of the pairwise difference between the reserve where elephants were absent and the four where elephants were present decreased with increasing elephant reintroduction time), notably tree density and overall woody plant canopy size, which showed near linear decreases with time. A key question that remains untested here is whether these decreases will continue at even older reintroduction times within our study system. Unlike the basaltic savannah in eastern KNP or many savannah in areas such as East Africa (e.g., Maasai Mari–Serengeti system), which can be extremely open, woody vegetation is a more common and ubiquitous component of the granitic lowveld savannah assessed here (Gertenbach, 1983). Therefore, assuming that ecosystems will tend toward a historical baseline where elephants are present, it is unlikely that elephant reintroduction would result in a completely open landscape (Abraham et al., 2021). It is more likely that extensive open areas would occur within a mosaic of woody vegetation patches, as determined by fine-scale variations in water and nutrient variability, terrain, and/or the distribution of microhabitats inaccessible to elephants (Davies et al., 2018).

Medium-sized and large-sized coarse woody debris abundance decreased with increasing reintroduction time in a similar fashion to tree density. Elephants readily topple trees and break tree branches when foraging and are a leading cause of tree death (Cook et al., 2017; Guldemond et al., 2017). Therefore, it is likely that elephant impact was the primary cause of the coarse woody debris dynamics reported here. Interestingly, very small-sized coarse woody debris items were much more common at the reserve where elephants were absent than present, and again, this trend was associated with

increased tree density and woody plant canopy size. This may have occurred because abiotic disturbances, primarily wind, broke smaller tree branches, which then fell to the ground. Elephants are also known to “prune” woody plants and, as a result, reduce the density of smaller branchlets via browsing or through their movements (Fornara & Toit, 2007), and this could have also contributed to this trend in areas where elephants are present.

In general, long-term elephant site occurrence had a variable effect on the ecological responses; however, some important effects were observed. In contrast to our prediction, tree and *Grewia* spp. density and medium-sized coarse woody debris abundance increased with long-term site occurrence. Elephants readily consume *Grewia* spp. and trees (Guldemond et al., 2017; Kos et al., 2012) and disperse their seeds (Bunney et al., 2017). Therefore, it is possible that elephants may have frequently visited more closed than open areas to feed within underexploited areas, and/or their feeding may have promoted woody plant recruitment through seed dispersal. Our longer-term assessment of elephant impacts (over the 92-year sample period) suggested that elephants can contribute to reductions in woody vegetation cover through time, and numerous studies have shown that elephants strongly moderate tree and woody plant densities, with their impacts heterogeneously distributed across landscapes (Abraham et al., 2021; Asner et al., 2016). Collectively, these findings provide partial support for the former hypothesis. If elephants are selecting more closed landscapes to optimize foraging, this may provide a mechanism accounting for the decreasing woody plant cover and tree density with time observed in our longer-term assessment. That is, elephants are attracted to dense vegetation in the short term, and this reduces woody vegetation cover in the longer term. The positive association observed here with medium-sized coarse woody debris may be explained by increased elephant impacts on primary branches (which presumably accounted for many medium-sized items) where woody vegetation was common, which subsequently increased coarse woody debris abundance through time.

It is possible that differences in land use could have also contributed to our results, in particular, differences in fauna densities and reserve sizes, historical livestock grazing (e.g., Stevens et al., 2016; Venter et al., 2018), and fire regime differences between KNP and the other reserves (Table 1). However, we expect these biases to be minimal because (1) herbivore composition and biomass were similar between reserves of different sizes (Appendix S1: Table S1; Schütze, 2013), (2) the effects of historical livestock grazing were accounted for in our study design by placing field sites away from artificial water sources (Landman et al., 2012), and (3) the trajectory of the “rewilding effects” were still apparent across the four

reserves where wildfire was relatively uncommon. It is also possible that elevated CO² concentrations associated with anthropogenic climate change may have led to a general densification of the savannah landscapes assessed here (Higgins & Scheiter, 2012). However, our reserves were located in climatically similar landscapes, and hence, such an effect would have been ubiquitous across the study region. Collectively, these observations suggest that our results were largely due to differences in elephant residency time at each reserve.

Elephant rewilding and fauna dynamics

By moderating vegetation and habitat quality, trophic rewilding with elephants has the potential to propagate indirect-effect pathways affecting fauna community dynamics and ecosystem processes more generally (Kuijper et al., 2013; Pringle, 2008). In particular, our study suggests that differences in elephant reintroduction time will impact fauna community dynamics by increasing landscape openness, presumably by moderating food availability and rates of predation pressure. In this context, the “open” savannah that typically occur at older reintroduction times, may benefit larger herbivores which require long lines-of-sight for predator detection, and particularly grazers which also require herbaceous vegetation to meet their metabolic demands. Conversely, the densely wooded savannah that typically occurs at younger reintroduction times and where elephants are absent may benefit smaller herbivores and omnivores that require cover for predator avoidance,

smaller predators that prey on smaller herbivores/omnivores, and browsers that require woody plants to meet their metabolic demands. A conceptual diagram that provides an overview of how elephant reintroduction time may indirectly impact fauna community dynamics by moderating landscape openness is shown in Figure 5. Future research will be required to accept or refute the predictions shown in this diagram.

In addition to the broader habitat preferences discussed earlier, elephants may additionally impact fauna at finer scales by moderating habitat quality and/or predation risk (Gordon et al., 2021). Our cross-reserve comparisons showed that larger coarse woody debris items were more common at younger than older reintroduction times. It is likely that this coarse woody debris will benefit smaller species at younger reintroduction times by providing habitat and predator refugia (Manning et al., 2013); however, it will negatively impact larger species by reducing predator detection and escape (Kuijper et al., 2013). The latter effect may be compounded by the relatively closed savannah landscapes present at younger reintroduction times.

Our cross-reserve comparisons also showed that the density of trees bearing small-sized hollows decreased and large-sized hollows increased with elephant reintroduction time. Fauna’s use of hollows is size dependent, with larger species limited to larger hollows (Gibbons et al., 2002). Therefore, the trends in hollow density shown here suggest that smaller hollow-using species will be benefited at both older, but particularly younger, reintroduction times and that larger species will be benefited at older reintroduction times only. Larger hollows are rare and provide a limiting

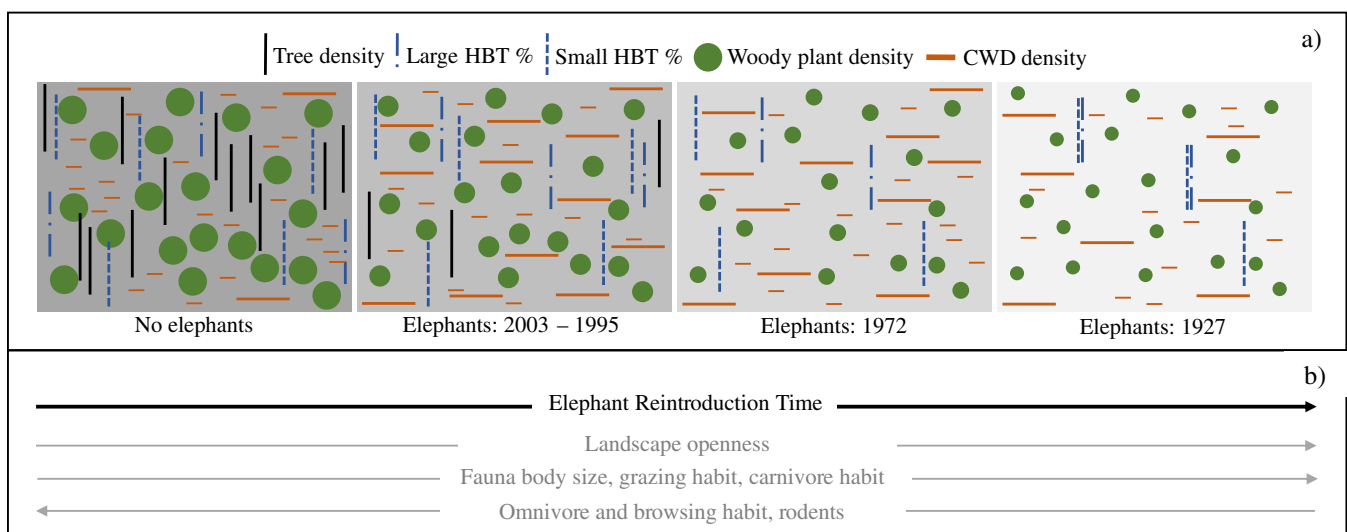


FIGURE 5 Overview of how ecological responses associated with landscape openness and fauna habitat assessed in our study (a) varied between reserves with increasing elephant reintroduction times (left to right) and (b) how this is predicted to impact fauna community dynamics. For (a), the number and size of polygons within each elephant reintroduction time are weighted by the predicted responses shown in Figure 2 (see Appendix S8: Section S1 for a description of the weighting protocol). HBT, hollow bearing tree.

resource for many larger species, for example, ground hornbills (*Bucorvus leadbeateri*). Therefore, it is possible that elephant-mediated hollow formation is an important factor limiting the population viability of these species.

CONCLUSIONS

Our correlative data sets support the hypothesis that elephant restoration mediates flora and fauna state changes that continue to manifest 16–92 years following reintroduction. Our space-for-time field survey suggests that landscape openness and some habitat attributes (e.g., large-sized hollows) increased with elephant reintroduction time, but other attributes (e.g., large-sized coarse woody debris) decreased with reintroduction time. These changes are likely to propagate indirect effects pathways affecting fauna community dynamics more generally; for example, smaller omnivores and browsers may be favored in the closed woody savannah present at younger reintroduction times, and larger carnivores and grazers may be favored in the open savannah present at older times (Figure 5).

Large-bodied megafauna, including African savannah and bush and Asian elephants, are often keystone species (Ripple et al., 2015) and represent the evolutionary norm across much of Earth's terrestrial landscapes (Faurby & Svenning, 2015; Svenning et al., 2016). Therefore, our results support the idea that trophic rewilding through elephant restoration (and the restoration of megafauna in general) provides a promising tool to mitigate biodiversity and ecological losses by restoring lost ecological processes and the open savannah mosaic. Further, elephant rewilding may represent a promising tool to combat novel global changes, notably woody plant densification in savannah resulting from anthropogenic climate change (Stevens et al., 2016).

Elephant restorations may compromise biodiversity locally in some instances (Cook et al., 2017; Midgley et al., 2020), and active population control may be argued in these cases (Bertschinger et al., 2018), for example, when elephants completely prohibit tree recruitment throughout a conservation area (Cook et al., 2017). However, this is a limited overall challenge due to the widespread depression of elephant populations (Chase et al., 2016). The implementation of elephant rewilding as a nature-based solution to ecological restoration would require community support, and issues of human–wildlife coexistence would need to be considered in future elephant (and megafauna) rewildings (i.e., being more appropriate in areas of low human population density or where infrastructure, such as fences, can mitigate the potential for negative interactions; Pedersen et al., 2020; Vogel et al., 2022). More generally, our results are relevant for the design and management of trophic

rewilding projects assessing transient dynamics across multidecade time scales.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Gordon et al., 2022) are available in Figshare at <https://doi.org/10.6084/m9.figshare.21710066>.

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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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