The value of large trees and their protection where elephants and trees co-exist

by

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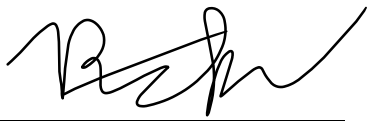
DECLARATION

I declare that this Thesis is my own work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted by me before for any other degree, diploma or examination at any other University or tertiary institution.



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23rd day of May 2024 at Hoedspruit, South Africa.

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Prof. Ed T.F. Witkowski (*University of the Witwatersrand*)

Dr. Michelle D. Henley (*University of South Africa, and Elephants Alive*)

Dedication

This Degree of Doctor of Philosophy is dedicated to four special people who played a significant role in my life and sadly passed away during the interim of my PhD research, and thus were not able to see me finish.

"When someone you love becomes a memory, that memory becomes a treasure."

- **Agnes Joubert** – Thank you, Gran, for everything you did for me growing up. You were so proud of me when I started this degree. I know you would feel the same seeing me finish.
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ABSTRACT

Increasing African elephant (*Loxodonta africana*) numbers in many southern African protected areas have raised concerns about their impact on large tree species and subsequent effects on biodiversity. However, sustainable strategies for managing elephant impact on particular large trees of concern require stakeholder support. Concerned stakeholders in South Africa's Associated Private Nature Reserves (APNR), a protected area containing a high density of waterholes and elephants, are implementing tree protection methods to protect large trees from elephant impact, but few studies have assessed these methods' efficacy. This thesis aimed to understand stakeholder perception of the value of large trees. Thereafter, I investigate elephant impact on the large tree component within the APNR over a 12-year period while also assessing the relationship between the persistence of the nests of large tree nesting birds and that of the trees themselves. Lastly, I assessed the effectiveness of various implemented tree protection methods to mitigate against elephant impact.

A combination of qualitative and quantitative analysis was used to measure stakeholders' values on large tree and elephant population dynamics, as well as management strategies to reduce the impact on large trees. The results show that stakeholders were concerned about the loss of large trees and its impact on other species. However, they disagreed on the most effective management strategy to minimise elephant impact, with varying values across stakeholder generations and professions.

The persistence trends of 2,758 large trees comprising three species of concern were analysed between 2008-2020 to understand the impact of elephants and other environmental factors on tree mortality. The annual large tree mortality rate from 2008-2020 was 5.6%, with varying declines among tree species and the most significant declines occurring during dry periods. Furthermore, the long-term impact of elephants on trees nested in by the critically endangered white-backed vulture (WbV, *Gyps africanus*) was studied in riparian and woodland habitats to investigate both tree and nest persistence. Ten tree species were utilised for nesting sites, with woodland trees more at risk to elephant impact verses those in the riparian habitat. However, there was no direct correlation between WbV nest loss and tree fall.

Lastly, when considering tree protection methods, about half of the 2,758 trees surveyed were wire-netted as potential elephant impact mitigation strategy. Trees with a stem diameter $\geq$40 cm that were wire-netted had the highest persistence rates, but the wire-netting needed replacing after four years. Overall, wire-netting was the most practical method for larger-scale implementation, particularly on larger trees elephants cannot push over. Of the four tree protection methods evaluated in this study in terms of their effectiveness and practicality as a mitigation strategy, beehives were found to be the most effective at protecting trees but proved to be the most expensive in comparison to wire-netting, concrete pyramids and creosote jars.

Elephant impact on large trees is complex and varied, with vulnerability differing based on tree species and size across rainfall gradients. The correct implementation of protection methods provides stakeholders with a management strategy to protect large trees. The findings from this thesis have great value for the management and conservation of large trees in the APNR and may provide guidance for other protected areas facing similar challenges with increasing elephant populations.

GLOSSARY OF TERMS & ABBREVIATIONS

APNR – 'Associated Private Nature Reserves', a collective term for the joint association of the Balule, Klaserie, Thornybush, Timbavati, and Umbabat Private Nature Reserves.

Culling – The practice of controlling elephant populations through large scale killings of both breeding herds and bulls.

Elephant impact/impact type/effects – For the purpose of this thesis, these terms refer to the actions of bark-stripping, branch breakage, main stem snapping (pollarding), and uprooting of trees by elephants.

Encounter rate – The probability of an elephant encountering a tree species. This can be increased by environmental factors that will restrict elephants' spatial movements, including increased waterholes and fencing off reserves.

GLTFCA – 'Great Limpopo Transfrontier Conservation Area', a protected area incorporating a collection of national parks, provincial reserves and privately-owned protected areas in Mozambique, South Africa and Zimbabwe.

Greater KNP – 'Greater Kruger National Park', a collective term for the Kruger National Park and all adjoining South African governmental- and privately-owned protected areas that are unfenced with the Kruger National Park.

Heterogeneity – Environmental concept describing a degree of non-uniformity in land cover, vegetation, and species composition, as opposed to a homogenised system where there is a decrease in the species and functional composition.

KNP – 'Kruger National Park', referring to the protected area under the jurisdiction of the South African National Parks.

Large tree – A multi- or single-stemmed tree species that grows to at least 5 m in height.

Lowveld savanna – The savanna system located in the north-eastern portion of South Africa at an altitude range of 150-600 m above seas level.

Protected area – "A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.”. Definition sourced from the International Union for Conservation of Nature (Dudley 2008).

Stakeholder – Any individual or group of individuals that can affect or be affected by the conservation work in the Associated Private Nature Reserve.

WbV – ‘White-backed vulture (*Gyps africanus*)’, a critically endangered vulture species.

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CHAPTER 1:

GENERAL INTRODUCTION

Ecological value of large trees

Large trees as foundational species in savannas

Savanna landscapes are characterised by a co-dominance of trees and grasses (Scholes and Archer 1997). These savanna landscapes are primarily determined by water and nutrient availability (Sankaran *et al.* 2004, February *et al.* 2013), as well as fire (Scholes and Archer 1997, Touboul *et al.* 2018) and herbivory pressure (Smit and Coetsee 2019).

Within savanna landscapes, species of large trees ($\geq$ 5 m in height, Shannon *et al.* 2008), dispersed across the landscape, have been termed foundational species, help maintain the stability of fundamental ecosystem processes, including decomposition rates, energy and nutrient flow, and carbon sequestration (Figure 1, Ellison *et al.* 2005).

Local-scale effect

At a local-scale, large trees provide a uniquely cooler, wetter microclimate underneath the canopy layer (Joseph *et al.* 2018). Water concentration is enhanced through stem flow and increased water infiltration around the root system (Belsky *et al.* 1989, Eldridge and Freudenberger 2005). Shade provided by a large tree canopy further reduces the soil temperature and rate of water evaporation, increasing the soil moisture content in comparison to outside of the canopy (Belsky *et al.* 1989, Joseph *et al.* 2018). Large trees can also increase the soil fertility under the canopy (Tessema and Belay 2017). Root systems transport nutrients upwards from deep soil layers, eventually dispersing these nutrients on the soil surface in the form of litter (Ward *et al.* 2018). Nutrients are also accumulated when large trees serve as foci for animal activity (Belsky and Canham 1994). This nutrient enrichment may be in the form of faecal droppings from both ground-dwelling- and avifauna, fallen nesting material, or carcass remains (Dean *et al.* 1999, Ligeza and Smal 2003). Grass species growing underneath a tree's sub-canopy in southern Africa's nutrient poor savannas have been found to be more nutrient rich in comparison to grass species outside of the canopy, further attracting grazing herbivores to the tree's sub-canopy (Treydte *et al.* 2008).

Large trees also provide structural complexity (Manning *et al.* 2006), serving important habitat functions within ecosystems due to their horizontal and vertical structuring, and thus creating spatial heterogeneity (Dean *et al.* 1999, Pringle *et al.* 2016). On the ground, the increased shade, nutrient-, and water- levels surrounding large trees can improve the survival of more shade-tolerant species (Ludwig *et al.* 2004, Ward *et al.* 2018), as well as other distinct plant assemblages that are adapted to these shaded fertile patches (Belsky and Canham 1994, Ludwig *et al.* 2004). In the arid Kalahari savanna of South Africa for example, shade-adapted fleshy fruit-bearing plants (*Boscia, Grewia, Lycium* and *Solanum* spp.) have only been recorded growing under the canopy of *Vachellia erioloba*, in comparison to outside of the tree canopy (Dean *et al.* 1999).

Large trees are also important habitat and nesting sites for bats (Froidevaux *et al.* 2022), and other ground-dwelling and arboreal mammals (Viljoen 1986), invertebrates (Horák 2017), birds (Rushworth *et al.* 2018), and reptiles (Hopkins and Tolley 2011). In senescing trees, naturally formed cavities are also used as nesting localities for a number of species (Combrink *et al.* 2017, Gordon *et al.* 2023). These senescing trees can have a positive effect on bird and invertebrate diversity by increasing habitat complexity (Stagoll *et al.* 2012). A large tree's leaves, bark and roots also provide important forage for many herbivores (Greyling 2004, Namah *et al.* 2019).

Tree species including large individuals can however be problematic to other species. Eucalypts, for example, extract vast amounts of water and nutrients from the soils in which they grow, which can affect the persistence of surrounding plant species (Forsyth *et al.* 2004). Large trees can also outcompete small plant species for light, reducing the persistence of light-demanding species (Velázquez and Wiegand 2020).

<u>Landscape-scale-effects</u>

On a landscape-scale, large trees increase landscape heterogeneity through horizontal patchiness (Manning *et al.* 2006, Wiegand *et al.* 2006). For species reliant on large trees as habitat, these trees play an important role in landscape connectivity, providing a "life-boating" function for species which would otherwise not exist in that particular ecosystem

(Monadjem and Garcelon 2005, Tiang *et al.* 2021). For example, large senescent trees with natural cavities provide important nesting sites for endangered Southern ground hornbills (*Bucorvus leadbeateri*, Zoghby et al. 2016).

Figure 1. Large trees provide important ecological services to savanna systems, including nutrient recycling, habitat provision, forage, and shade (Photo credit: Robin Cook).

Large trees can be viewed as biological legacies within a landscape if they persist after a disturbance (Manning *et al.* 2006), whether this disturbance is from human activity (Stagoll *et al.* 2012), herbivory (Asner *et al.* 2016) or fire (Werner and Peacock 2019). The trees' persistence thus enables species from the unaltered landscape to persevere within the altered landscape (Moreira-Arce *et al.* 2021, Tiang *et al.* 2021). The presence of large trees can also determine the spatial and temporal movements of species within a landscape. In South Africa's Kruger National Park (KNP) for example, male African savanna elephant (*Loxodonta africana*) prefer areas of high tree canopy and low herbaceous biomass at a large scale, whilst female elephants selected for areas of high herbaceous biomass and low tree canopy (De Knegt *et al.* 2011). The distribution of white-backed vultures (*Gyps africanus*), on the other hand, can be influenced by anthropogenic activities that limit the availability of large trees used as nesting sites outside of protected areas (Bamford, Monadjem, and Hardy 2009).

African savanna elephants as ecosystem engineers and a keystone species

Spatial distribution of African savanna elephants

African savanna elephants (*Loxodonta africana*) occupy a wide range of habitats across sub-Saharan Africa, from the dry desert regions (Viljoen 1989) through to the tropical rainforests in central and western Africa (Mondol *et al.* 2015), although the majority occur within the savanna biome (Robson *et al.* 2017). In southern Africa, between 70-80% of elephant home ranges occur outside of protected areas, demonstrating the need for landscape management (Van Aarde and Jackson 2007, Henley *et al.* 2023, Huang *et al.* 2024). Elephant management in South Africa is very different though, with elephants being confined to fenced-off protected areas across the country (Slotow 2012).

Elephant home ranges vary in time and space, driven by factors including resource availability (O'Connor *et al.* 2007, Smit *et al.* 2007, Purdon and Van Aarde 2017, MacFadyen *et al.* 2019, Sach *et al.* 2020, Louw *et al.* 2021) and fear landscapes (Wittemyer *et al.* 2017, Ihwagi *et al.* 2019). Elephant home ranges can vary from several square kilometres to over 2000 km^2 (Galanti *et al.* 2006). Therefore, with such wide-ranging home range sizes, the effects that elephants have on ecosystems are complex, varying over spatial and temporal scales (Guldemond *et al.* 2017, Henley and Cook 2019, Abraham *et al.* 2021).

Elephant forage consumption and sexual dimorphism

The ability of African elephants to move over expansive home ranges (Van Aarde and Jackson 2007), consume large amounts of forage (up to 180 kg of wet mass for an adult bull, Owen-Smith 1988), and manipulate the environment to their choosing has resulted in elephants being termed a keystone species and ecosystem engineer (Owen-Smith 1988). The low digestive efficiency of elephants means that large amounts of fibre can be consumed without slowing the rate of forage intake (Janis 1976). Elephants are therefore able to alter the structure and survival of plant species at a greater magnitude than most other herbivores because of their large size, feeding habits and habitat range (Owen-Smith 1988).

Before understanding how elephants affect their ecosystems, it is important to highlight sexual dimorphism within elephants. African elephants are the largest land-dwelling mammal on Earth, with adult females weighing up to 3 tons and males exceeding 6 tons (Lee and Moss 1995). Sexual dimorphism in elephants leads to differences in the nutrient requirements and foraging behaviour (Greyling 2004, Shannon *et al.* 2006). Male elephants feed on a wider range of plant parts in comparison to females, whilst also feeding in a more vigorous manner (Stokke and du Toit 2000, Greyling 2004). Female elephants have been frequently recorded debarking trees and removing their leaves in the Associated Private Nature Reserves of South Africa, whilst male elephants uproot and fell trees more often, digging for roots in the process (Henley 2013). The robust feeding nature of male elephants means that their effects on the environment are often larger than those of females (Greyling 2004, Shannon *et al.* 2006).

Importance of elephants for ecosystem processes

Elephants can produce at least 150 kg of dung each day, with around 50% of the consumed forage material passing undigested through their gut (Owen-Smith 1988). Elephants therefore recycle nutrients in savannas, and importantly, transport nutrients uphill or against the nutrient-leaching gradient (Gross 2016). The large amounts of dung deposited act as fertilizer that increases the nitrogen content in plants, providing increased nutrient content for herbivores (Sitters *et al.* 2020). Elephants also facilitate biomass recycling through their robust feeding nature of leaving plant material toppled along the soil, as well as by feeding on the bark and roots of trees (Owen-Smith 1988, Greyling 2004).

Elephants are important seed dispersal agents, transporting seeds up to 65 km from the parent tree through the process of endozoochory (Bunney *et al.* 2017). In the forests of Uganda, elephant endozoochory is essential for *Balanites wilsoniana* regeneration, as seedlings cannot germinate and survive underneath their parent's canopy (Babweteera and Ssekuubwa 2017). Acid in the digestive systems of elephants can also help with the seed germination of some plant species, whilst the dung boli provides a fertile environment for germination (Cochrane 2003). *Sclerocarya birrea* seeds germinate at a more rapid pace if passed through an elephant's digestive system, as the acid treatment weakens the operculum surrounding each seed, promoting germination (Lewis 1987).

Elephant browsing activities also stimulate compensatory regeneration of leaves, thereby improving forage quality (Jachmann and Bell 1985). By felling or pulling down branches, elephants can also create browsing lawns of reduced height and increased forage quality through the growth of new coppicing shoots, as observed in mopane woodlands (Jachmann and Bell 1985, Kohi *et al.* 2011). Furthermore, the reduced height enables forage material to be more accessible to mesobrowsers (5-1000 kg) (Styles and Skinner 2000, Rutina *et al.* 2005). Elephants also create pathways to waterholes, which in turn are used by other species, and they can dig for water in dry riverbeds, exposing surface water that would otherwise be unavailable to other species (Ramey *et al.* 2013).

Elephant impact on large trees

Recent historical perspective – the 'elephant problem' in the mid to late 20th century

Concerns have been raised over the last few decades about the decline of large trees in savannas containing elephants across sub-Saharan Africa (Leuthold 1977, Fenton *et al.* 1998, Helm *et al.* 2009, Asner *et al.* 2016, Das *et al.* 2022). The idea of 'too many elephants' was historically referred to as the 'elephant problem' and was termed so after a combination of a drought and high elephant densities resulted in the woodland reduction of Kenya's Tsavo National Park's (Glover 1963, Caughley 1976). The 'elephant problem' is centred around the concept that there is no natural equilibrium between elephant and tree densities but rather one stable cycle between states of high and low elephant densities (Caughley 1976). It was thus proposed that protected areas containing elephants should have a "safe" carrying capacity of elephants, and culling programs were initiated in various protected areas that contained elephants (Laws 1970, Whyte *et al.* 1998, Child 2004). In South Africa's KNP for example, over 14,000 elephants were culled between 1967 and 1994 to try preserve the large tree flora and biodiversity, maintaining the elephant population between 6,000-8,000 elephants (Whyte *et al.* 1998).

However, whilst elephant culling was being initiated by various southern African countries, large-scale poaching of elephants occurred in east Africa during the 1970s and 1980s (Blanc *et al.* 2002), which began to place societal-driven pressure on southern Africa to seek alternative elephant management strategies (Dickson and Adams 2009). Concerns were also raised around the ethics of culling elephants due to their complex social structures (Lee and Moss 2014), and whether the means of culling justified the ecological outcome, particularly in the KNP (Gillson and Lindsay 2003, IFAW 2005).

Since the cessation of culling in the KNP, elephant numbers have exponentially increased in the KNP, causing a continuation of debates surrounding their environmental impact and subsequent management (Figure 2, Gillson and Lindsay 2003, Owen-Smith *et al.* 2006, Dickson and Adams 2009, Ferreira *et al.* 2017). It has however become increasingly clear that the relationship is not linear, rather being influenced by an array of ecological processes (O'Connor *et al.* 2007, Vanak *et al.* 2012, Abraham *et al.* 2021, Das *et al.* 2022).

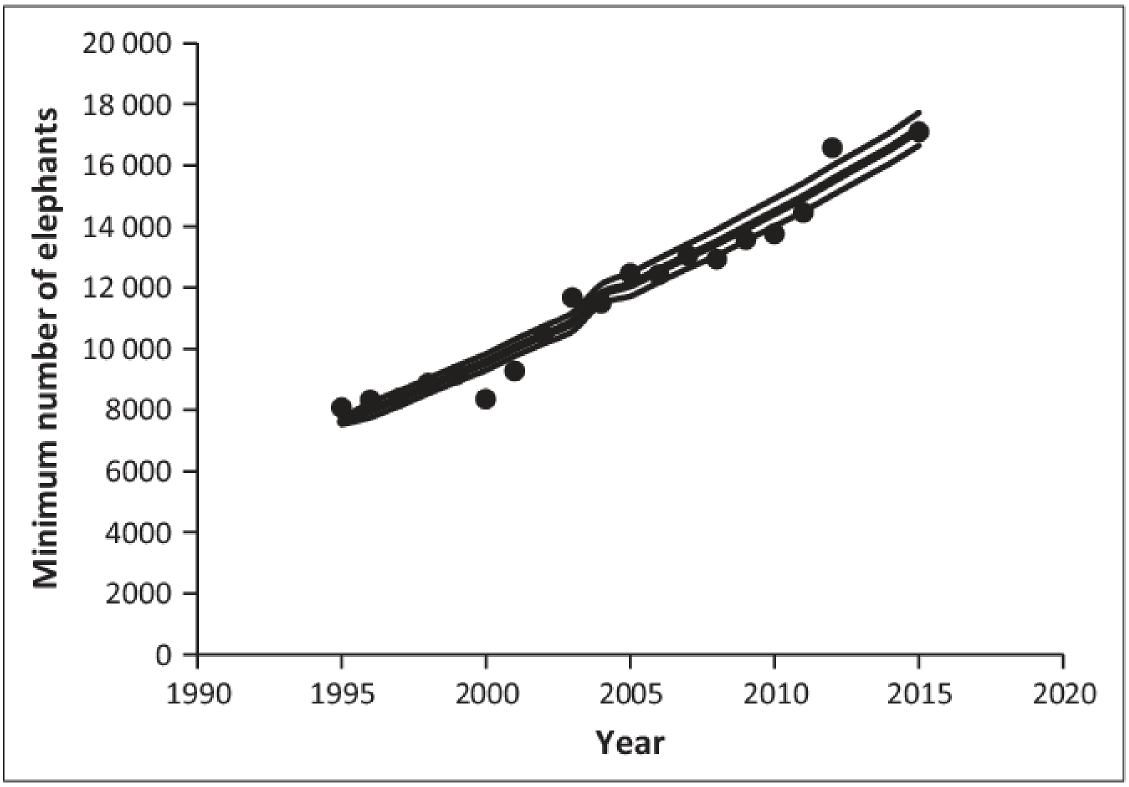

Figure 2. Population growth of African elephants in the Kruger National Park, South Africa, following the cessation of elephant culling in 1994 (Figure credit: Ferreira *et al.* 2017).

There is an argument that certain savannas are returning to conditions that previously existed before the ivory trade decimated elephant populations across the continent, whilst the rinderpest plague in the late 19th century eliminated many tree seedling herbivores as well (Gillson and Lindsay 2003, Skarpe *et al.* 2004, but see Wilkinson *et al.* 2022). There is a consensus though that elephants should be spatially and temporally distributed at varying densities, thereby creating regions containing high and low elephant impact, which promotes a heterogenic system (Figure 3, Owen-Smith *et al.* 2006, Ferreira *et al.* 2017, Louw *et al.* 2021, Wang *et al*. 2023).

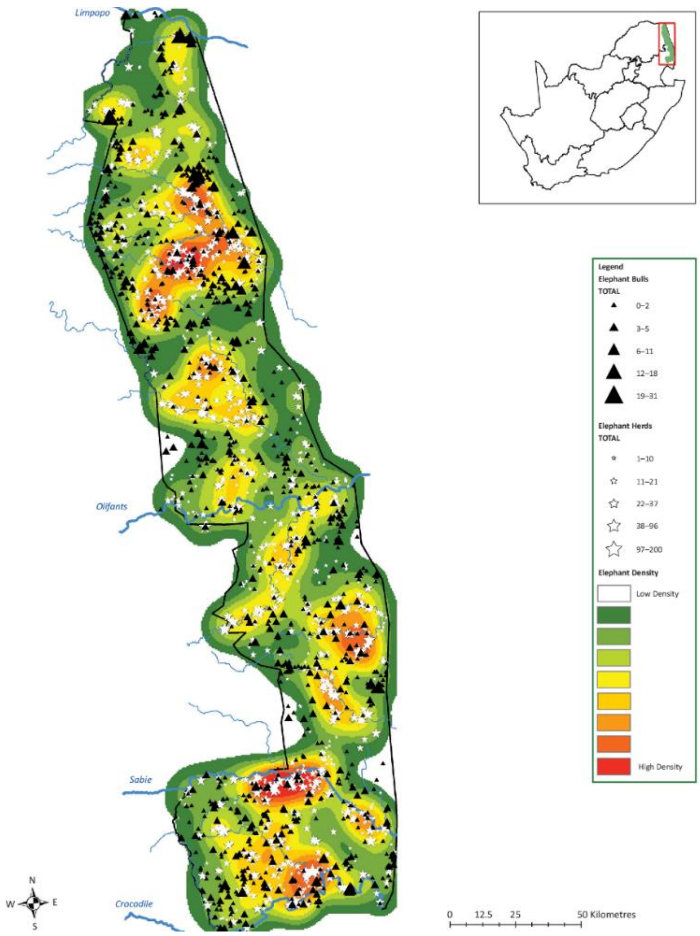

Figure 3. Distribution of African elephants in the Kruger National Park, South Africa, based on averaging annual census data collected during the dry season, illustrating regions of high and low elephant densities that are spatially and temporally dynamic (Figure credit: Ferreira *et al.* 2017).

<u>Elephant impact-types on large trees</u>

Elephant impact on large trees can range in both impact type and severity, affecting trees' structural components (Owen-Smith 1988, Greyling 2004, Landman *et al.* 2019). The most common impact types on savanna trees include bark-stripping (Figure 4) and branch breakage (Greyling 2004, Henley 2013). Elephants will bark-strip trees to access the sugar-containing phloem tissue inside of the bark, usually in the early spring when the sap flow is most active (Owen-Smith 1988). The bark structure of a tree species can determine how vulnerable the tree is to bark-stripping, as species with stringy bark such as knobthorn (*Senegalia nigrescens*) are the most vulnerable to being bark-stripped (O'Connor *et al.* 2007). A tree that has been bark-stripped can suffer from moisture stress because of a lack of photosynthetic material being transported down to the roots (Michaletz and Johnson 2007). Bark-stripping can also leave trees exposed to fire damage (Helm, Wilson, *et al.* 2011, Henley 2013) and insect infestation (Cook and Henley 2019, Wigley *et al.* 2019), which results in the trees being rotten or hollow on the inside and vulnerable to strong winds or further elephant impact (Hofmeyr 2003, Henley 2013).

Elephants also break off the primary and secondary branches to feed on the twigs and foliage within the crown canopy (Owen-Smith 1988, Codron *et al.* 2006). Branch breakage may not directly kill a tree, with species such as marula trees sometimes requiring up to 100% of their primary branches broken off to be killed (Gadd 2002). However, a tree's response to branch breakage is species specific, with trees such as *S. birrea* (Coetzee *et al.* 1979) and *Colophospermum mopane* (Styles and Skinner 2000) having greater coppicing abilities in comparison to species such as *Vachellia tortilis* (MacGregor and O'Connor 2004). Impacted trees in a resprouting condition may be prevented from reaching sexual maturity, as observed in the KNP's *Hyphaene petersiana* population, where elephant impact prevented trees from producing seeds (Midgley *et al.* 2020).

Two of the more severe forms of elephant impact include uprooting and felling (main stem snapping). Both impact types allow for elephants to access a large tree's foliage crown, whilst uprooting also enables access to the roots (Jachmann and Bell 1985, Greyling 2004). Elephants have been observed felling trees and sampling the now more accessible foliage before moving on to the next tree (Gadd 2002, Ihwagi *et al.* 2012). Uprooting and felling may also occur as social displays of dominance and hierarchy between elephant bulls (Midgley and Kerley 2005).

The size of a tree may also influence its vulnerability to impact, as smaller size classes (<11 m in height) are easier to uproot and fell in comparison to larger classes (Cook *et al.* 2017). Trees with deep extensive root systems and strong bark are also more resilient to this form of impact (O'Connor *et al.* 2007). Large riparian trees display a significant degree of resilience due to their deep roots that are adapted to withstanding flood conditions (Turner *et al.* 2022).

<u>Probability of encounter and factors influencing elephant-tree encounter rates</u>

Encounter rate, or the probability of an encounter between a particular large tree and elephants, is important for predicting elephant impact levels on large trees. Trees are more likely to be impacted if elephants encounter them at a high frequency or for a longer duration (O'Connor *et al.* 2007). In open systems, elephants can migrate seasonally, providing relief to vegetation in the dry season when elephant impact on large trees is most prolific (Leggett *et al.* 2003, Smit *et al.* 2020). In smaller fenced-off protected areas (<1000 km, Owen *et al.* 2006), elephant home ranges are compressed, resulting in a higher frequency and longer duration of time spent around the same trees (O'Connor *et al.* 2007). In South Africa's Pilanesberg National Park, elephants have been recorded foraging more intensely in the centre of the reserve and away from the fence-line, with an edge-effect occurring and influencing the elephants' spatial use (Vanak *et al.* 2010). In contrast, in a review of six southern African countries, Loarie *et al.* (2009) found elephants bunching up against fences, increasing impact on the surrounding vegetation. In Karongwe Private Game Reserve (South Africa), elephant impact was homogenised across the assessed trees within the protected area (Thompson *et al.* 2022). The increased foraging pressure and repeated encounter rates of elephants onto large trees can homogenise the habitat structure of a small protected area, simultaneously decreasing the biological diversity (Owen-Smith *et al.* 2006, Guldemond and Van Aarde 2008).

Figure 4. Bark-stripping activities by elephants may not directly kill a tree but will leave a tree vulnerable to insect infestation, fire-related mortality, and eventual desiccation (Photo credit: Robin Cook).

Roads, such as those found within the Kruger National Park (KNP) of South Africa, can increase encounter rates between elephants and trees, as elephant bulls tend to make use of roads in protected areas (Pienaar 1968). For example, higher elephant impact levels were recorded on *S. birrea* trees within 10 m of a road’s edge in the KNP, versus trees within 50 – 100 m (Coetzee *et al.* 1979). However, this pattern was not observed by Gadd (2002), whilst Cook and Henley (2019) hypothesised that this pattern of impact may be uniform in smaller protected areas with an high abundance of roads. Smit and Asner (2012) have also used Airborne Light Detection and Ranging (LiDAR) imagery to show that woody vegetation coverage is also more prominent within 15 m of roads in the KNP because of increased runoff of rainfall, making these road edges potentially more attractive for browsing herbivores..

Terrain ruggedness can also create spatial refuges for trees, limiting the frequency of encounters between elephants and trees in these terrains, as elephants are less likely to move over steep slopes (Wall *et al.* 2006). In northern KNP for example, steep rocky slopes appear to provide a spatial refuge for *Adansonia digitata* (Edkins *et al.* 2008).

The provision of artificial surface water, a common practice in South Africa’s protected areas, allows for elephants to access a greater range of vegetation within a protected area than they would have without water provision (O’Connor *et al.* 2007, Smit *et al.* 2007, Purdon and Van Aarde 2017). Elephants generally forage within 15 km of water (Conybeare 2004). This intense foraging causes a piosphere effect around the surface water, where elephant impact is highest closest to water and decreases with increasing distance from water (Figure 5, Gaylard *et al.* 2003, van Langevelde *et al.* 2017, Wilson *et al.* 2021).

In small protected areas, or reserves with an abundance of artificial surface water such as South Africa’s APNR, no single location is usually further than a few kilometres from water (Henley 2014). This means that elephants have access to more vegetation across the APNR, which has led to concerns that elephant impact may become homogenised across the APNR (Edge *et al.* 2017). Closing artificial waterholes could therefore influence the spatial distribution of elephants, influencing their resource use and providing important spatial refuges for tree species further away from the remaining waterholes (Smit 2013, Robson and Van Aarde 2018, Louw *et al.* 2021).

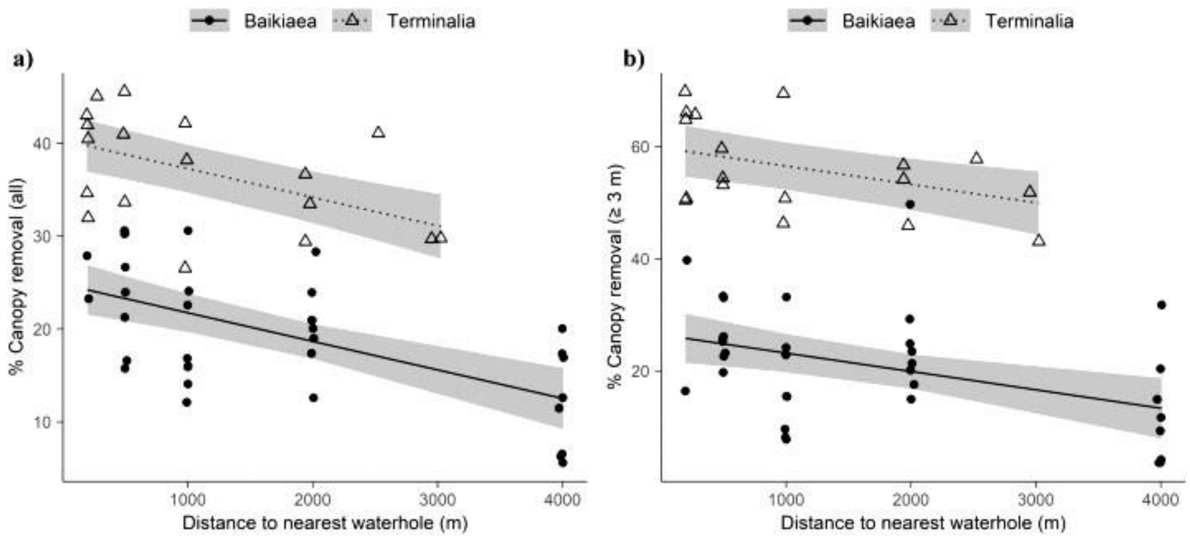

Figure 5. Evidence of a piosphere effect (decreased vegetation cover closer to waterholes) for *Baikiaea* and *Terminalia* woodland around waterholes in Zambezi National Park (Figure credit: Wilson *et al.* 2021).

<u>Elephant selectivity and large tree persistence</u>

Elephants are selective in foraging nature, and hence certain tree species appear to be more vulnerable to impact than others (Greyling 2004, Shannon *et al.* 2006). Teren *et al.* (2018) recorded heavy impact on *S. nigrescens* and *V. erioloba* in the Linyanti region of Northern Botswana, whilst a high percentage of *V. tortilis* had been impacted in South Africa's Hluhluwe-Imfolozi Game Reserve (Boundja and Midgley 2010). In the KNP, studies have shown heavy elephant impact levels on *Lannea schweinfurthii* (Das *et al.* 2022), *A. digitata* (Edkins *et al.* 2008), *S. birrea* (Helm *et al.* 2009), and *V. tortilis* (Abraham *et al.* 2021). Tree species less impacted on by elephants include *Terminalia sericea*, *Spirostachys africana*, and *Combretum imberbe* (Abraham *et al.* 2021, Das *et al.* 2022).

Increased levels of elephant impact may also occur during severe droughts, as elephants forage on large trees for extended periods of time due to a lack of available grasses (O'Connor *et al.* 2007). In Pongola Private Game Reserve, South Africa, the severity of elephant impact significantly increased during the 2015-2016 *El Niño* drought, with the probability of tree mortality and crown alterations increasing from the pre-drought levels (Thornley *et al.* 2020). This may hold implications for future climate change research, as droughts are expected to occur more regularly in southern Africa (Trenberth *et al.* 2014).

The persistence of trees in a landscape containing elephants is also highly dependent on the species' rate of recruitment and regeneration, versus its rate of mortality (O'Connor *et al.* 2007). Therefore, the establishment of saplings is vital for large tree species that are actively selected for by elephants (Moe *et al.* 2009, Helm, Scott, *et al.* 2011, Trotter *et al.* 2022). Recruitment can be negatively affected by factors such as strong fires (Jacobs and Biggs 2001, Helm, Wilson, *et al.* 2011), high levels of seed predation (Helm, Scott, *et al.* 2011, Cook *et al.* 2017), soil geochemistry (Mills *et al.* 2023), seedling herbivory (Skarpe *et al.* 2004), as well as changing climatic conditions (Sankaran *et al.* 2004, Venter and Witkowski 2013). The foraging and trampling of seedlings by elephants further exacerbates the concern (Edkins *et al.* 2008). Where species may be experiencing a bottleneck effect due to one of the abovementioned factors, further emphasis needs to be placed on the survival of adult trees as being potential seedbanks for when narrow windows of recruitment may occur (Sankaran *et al.* 2004).

Direct and indirect effects on fauna from elephant presence and impact on trees

The ability of elephants to alter habitat-structure and affect the availability of resources has both a direct and indirect positive and negative effects on other fauna (Valeix *et al.* 2007, Guldemond *et al.* 2017). Several studies have focused on quantifying these effects. In a comprehensive review of 367 peer-reviewed papers spanning 67 years of studies, Guldemond *et al.* (2017) concluded that although elephants lessened the abundance of trees and altered trees' structural components, there were no cascading impacts on vertebrates, invertebrates, and soil properties. A collection of studies will be discussed below.

Elephant impact on tree structure and density can have several positive effects on species richness and abundance. In south-east Zimbabwe for example, elephants were found to be important transport vectors of aquatic invertebrates, transporting invertebrates between mud-wallowing localities (Vanschoenwinkel *et al.* 2011). In northern Tanzania, Nasseri *et al.* (2011) found that herpetofaunal species richness increased in areas with high elephant impact due to the habitat complexity created in the elephant-modified woodlands. In Kenya, recent research by Krell and Krell-Westerwalbesloh (2024) emphasizes the importance of elephants and their faeces for supporting high abundances and diversities of coprophagous beetles such as dung beetles. High elephant densities have also been correlated with increased numbers of impala (*Aepyceros melampus*) and kudu (*T. strepsiceros*, Skarpe *et al.* 2004), with both species appearing to favour the newly coppiced shoots on woody vegetation that has been trimmed to lower height by elephants (Makhabu *et al.* 2006). Rode (2010) also found that the gum produced by elephant-induced bark-stripping was fed on by species of bushbabies (*Galago moholi* and *Otolemur crassicaudatus*) in South Africa.

A broad-scale analysis on elephant impact on invertebrate assemblages in the KNP found that elephant impact may have negatively affected the diversity of invertebrate species across a savanna catena slope in comparison to a neighbouring control site without elephants (Jonsson *et al.* 2010). Furthermore, a reduction in tree cover from homogenised elephant impact on vegetation in the KNP may have decreased the density and species richness of small terrestrial mammals and bats (McCleery *et al.* 2018). The density of small rodents was also lower in protected areas where elephants, fire and human activity had reduced the number of woody patches available in a grassy biomass (Loggins *et al.* 2019).

For grazing herbivores, Fritz *et al.* (2002) recorded no significant effect of elephants on grazers in 31 natural ecosystems in eastern and southern Africa, whilst Owen-Smith (1989) cautioned that a decline in grazer-diversity may occur in areas with no elephants, as elephants play an important function in preventing the encroachment of woody species. Elephants can also impact other megaherbivores such as white rhinos (*Ceratotherium simum*), with Prinsloo (2017) suggesting that the fallen woody-debris from elephant-related foraging may affect the white rhino grazing potential.

Browsers can be influenced by elephant impact by resource reduction and increased visibility through the removal of vegetation by elephants (Owen-Smith 1988, Valeix *et al.* 2007). In their meta-analyses of how elephants influence the distribution of ungulates, Fritz *et al.* (2002) reported a negative correlation between elephant and browser biomass. However, these patterns appear to be species specific. An increase in elephant numbers in Botswana's Chobe National Park was negatively correlated with the number of Chobe bushbuck (*Tragelaphus sylvaticus*, Dipotso *et al.* 2007). By pushing down large trees, elephants may both positively and negatively influence the ambushing opportunities of predators such as lions (*Panthera leo*) and leopards (*Panthera pardus*), as well as affecting the spatial distribution of their prey among the potential ambushing sites (Fležar *et al.* 2019, Ferry *et al.* 2021).

Birds, especially those requiring trees for nesting, perching or foraging spots, may be both positively and negatively influenced by high levels of elephant impact (Rushworth *et al.*

2018, Gordon *et al.* 2023). Cumming et al. (1997) recorded an overall decrease in bird diversity in Zimbabwe's miombo woodlands in sites containing elephants versus those without. In South Africa's Albany thicket biome, songbird assemblages were both negatively and positively influenced by the length of time that elephants had been present in each selected study site (Parker 2019). Interestingly, there was an equal split between songbird species benefiting from the structural changes to vegetation, and songbird species negatively affected by these changes (Parker 2019).

Gordon et al. (2023) have shown that elephant presence is positively associated with large-sized tree hollows, which would be suitable for tree nesting species such as southern ground hornbills (*Bucorvus leadbeateri*, Combrink *et al.* 2017). Concerns have been raised though by Combrink *et al.* (2017) that elephants may have a negative impact on tree availability for southern ground hornbills as potential nesting sites. Henley and Henley (2005), however, have suggested that elephants usually impact trees with smaller stem diameters than what would be selected for by southern ground hornbills as nesting sites. Concerns have also been raised over the negative influence that elephant impact may have on the breeding success of tree-nesting raptors and vultures, with special reference to the critically endangered and tree-nesting white-backed vulture (WbV, *Gyps africanus*, Monadjem and Garcelon 2005, Rushworth *et al.* 2018). This ecologic relationship requires more data and will be further discussed below.

Elephant impact on trees nested in by white-backed vultures (WbVs)

General threats to WbVs

There has been a continual decline in the number of WbVs on both a continental scale (Ogada *et al.* 2016) and regionally in South Africa (Taylor *et al.* 2015). For long-lived bird species, understanding how factors affect adult survival is critical before focusing on breeding success and tree availability (Bamford, Monadjem, Anderson, *et al.* 2009, Monadjem *et al.* 2013).

Poisoning events have largely contributed to the decline of adult WbVs across Africa (Ogada *et al.* 2016). 'Sentinel poisoning' has been a major threat, where carcasses (often rhino and elephant) are poisoned to deliberately kill scavenging vultures, thereby decreasing the chances of law enforcement authorities being alerted to the carcass' locations (Kendall and Virani 2012, Ogada 2014, Murn and Botha 2018). Elephant carcass poisonings, particularly around the KNP, are one of the biggest threats to the lowveld savanna's WbV population (Murn and Botha 2018). Lead poisoning has increasingly become a concern for WbVs too (Plaza and Lambertucci 2019, Van den Heever *et al.* 2023), whilst the threat of veterinary drugs in livestock carcasses at supplementary feeding stations for scavenging birds have recently been highlighted as a potential threat (Brink *et al.* 2020). Poaching and the trading of WbV body parts for traditional medicinal use is also a growing concern (Mashele *et al.* 2021, Manqele *et al.* 2023), whilst collisions with pylons and wind turbines, as well as pylon electrocutions have affected WbV populations (Anderson and Hohne 2008).

Lastly, human alterations to land-use outside of protected areas have brought about a decline in the available habitat and food for WbVs (Bamford, Monadjem, and Hardy 2009). Human disturbances by nesting sites can also negatively affected WbV breeding success (Chomba and M'Simuko 2013). Therefore, as human alterations continue to limit the availability of nesting sites outside of protected areas, greater pressure is being placed on ensuring that WbV nesting sites within protected areas are available (Monadjem and Garcelon 2005, Rushworth *et al.* 2018).

Tree selection for nesting sites in protected areas by WbVs

WbVs usually nest in loose clusters of high nest densities along rivers and drainage lines, and low nest densities in woodland habitat (Virani *et al.* 2010, Kendall *et al.* 2018, Johnson and Murn 2023). The availability of tall trees around river systems appears to be the leading factor for the higher densities in riverine vegetation, rather than distance to water itself (Bamford, Monadjem, Anderson, *et al.* 2009, Virani *et al.* 2010, Kendall *et al.* 2018). In riverine vegetation, WbV nests have been recorded in trees such as *Ficus sycomorus*, *Diospyros mespiliformis*, *Schotia brachypetala* and *Boscia albitrunca* among others (Virani *et al.* 2010, Kendall *et al.* 2018), whilst in woodland habitat, *S. nigrescens* is the most common species for nesting sites, as they are usually the tallest trees in this habitat (Vogel *et al.* 2014, Rushworth *et al.* 2018). *S. nigrescens* also form rounded canopy crowns as they mature (Ross 1968), providing a larger canopy area for nest construction in comparison with smaller trees (Kendall *et al.* 2018).

Elephant impact on trees nested in by WbVs

The importance of protected areas as safe breeding locations for WbVs has been linked with concerns over how increasing elephant densities may impact tree availability for WbVs (Figure 6, Rushworth *et al.* 2018). However, few studies have focused on this interaction. In Kenya's Masai Mara National Reserve, amidst concerns surrounding elephant impact on large trees, scientists modelled the available trees for WbVs using morphological data on the trees utilised as nesting sites and found that tree availability for WbVs was not a concern due to the high number of available nesting trees (Kendall *et al.* 2018). However, in smaller protected areas where elephants may be fenced off and their densities increased, tree impact may increase and limit the availability of nesting sites (Rushworth *et al.* 2018). In their assessment on WbV nesting sites across Eswatini, Monadjem and Garcelon (2005) reported no vulture nests in the protected areas that did contain elephants among the study sites.

In the KNP, elephant impact on large trees was hypothesised to be affecting vulture numbers in the 1980s (Tarboton and Allan 1984). A five-year study by Vogel *et al.* (2014) in the APNR then found that overall elephant impact on *S. nigrescens* containing vulture nests was low, with tree persistence significantly higher than nest survival. However, no longer-term study, comprising of a multitude of tree species, has been conducted to investigate elephant impact and its potential effect on vulture nest persistence. It is worth noting though that vulture faeces are high in acidity (Chung *et al.* 2015), which may result in the breakdown of branches surrounding the nest and eventual nest collapse (Andre Botha, personal communication, 27 July 2020).

Protecting large trees against elephant impact

Management dilemma: elephant and large tree co-existence

Managers of protected areas containing elephants are faced with the dilemma of managing an area that meets stakeholder expectations for financial revenue (Ballantyne *et al.* 2011), but also one that has ecological integrity as a functioning ecosystem (Treves 2006). Tourists, for example, visiting protected areas may expect to see a landscape that resembles the modified, aesthetically pleasing images advertised to them (Barretto 2013), whilst private landowners may feel a sentimental attachment to large trees within their properties (Edge *et al.* 2017). The type of landscape that stakeholders find appealing may therefore influence the number of elephants a protected area may contain (Owen-Smith *et al.* 2006), as well as the elephant management strategies put in place by conservation managers (Henley and Cook 2019, Manfredo *et al.* 2021). The challenges are further complicated when a mixed array of stakeholder values need to be considered for management decisions surrounding socially complex elephant populations (Lee and Moss 2014).

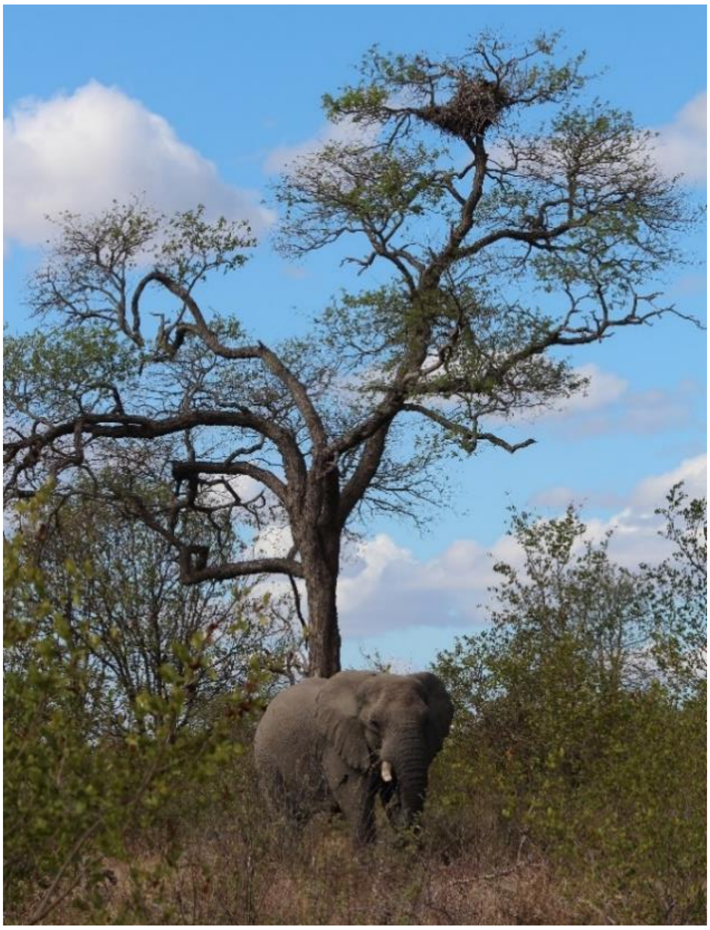

Figure 6. An African elephant stands beside a *Senegalia nigrescens* tree containing a white-backed vulture nest. Concerns exist over the impact that elephants may be having on trees nested in by these critically endangered birds (Photo credit: Robin Cook).

Stakeholders can also have divergent viewpoints around elephant impact on large trees (Edge *et al.* 2017). Private landowners in the APNR for example had a lower tolerance to elephant impact on large trees in comparison to tourists, whilst also being more in favour of elephant population reduction methods such as culling (Edge *et al.* 2017). Furthermore, in Africa, elephant numbers are declining continentally (Chase *et al.* 2016) but are predominantly stable or increasing in protected areas in southern Africa (Huang *et al.* 2024). Managers therefore must balance the views of their stakeholders, adopting management plans that cater to both the ecological integrity and social acceptability of a protected area and its management approaches (Edge *et al.* 2017, Henley and Cook 2019).

Overview of elephant population reduction strategies

A range of elephant management strategies, ranging in degrees of severity and ethical concerns, have been implemented in protected areas in an attempt to protect large trees, and biodiversity in general, against homogenised high levels of elephant impact (see Lotter (2006) and Henley and Cook (2019) for a review). As previously discussed, culling operations were carried out historically in the KNP to manage elephant impact on the environment (Whyte *et al.* 1998). However, culling elephants in KNP prevented density-dependent feedback systems from occurring on the population (Robson and van Aarde 2018), whilst a vacuum effect can also occur where other elephants from other regions of KNP occupy spaces where elephants had previously been culled (Van Aarde *et al.* 1999). Furthermore, these culling operations were carried out when the KNP had a high density of artificial waterholes, and hence elephants were able to access vast regions of KNP which had previously only been available to them during the wet season (Pienaar *et al.* 1997, Whyte *et al.* 1998). With the culling of elephants in KNP having ceased in 1995, recent research suggests that zones within the KNP that historically contained high densities of elephants are showing signs of density-dependent growth (Louw *et al.* 2021).

Hunting as a population control option is too selective in terms of desired traits on elephant bulls (Stalmans *et al.* 2002), whilst also creating the potential for a skewed-population in terms of both sex ratios and age-groups (Milner *et al.* 2007). Hunting will therefore not be discussed further as a management option in an open system for controlling elephant impact on large trees.

Immunocontraception of elephants, through non-invasive, native porcine zona pellucida (PZP) vaccinations have been used on elephant populations across 43 protected areas in South Africa in an attempt to decrease elephant reproductive output (Delsink *et al.* 2023). This method has been proven to be effective at reducing the growth rate of elephant populations in small, fenced-off protected areas by preventing female elephant from conceiving, or by increasing the inter-calving intervals (Fayrer-Hosken *et al.* 2000, Druce *et al.* 2011). Regarding the behavioural effects on elephants following the sustained usage of immunocontraceptions, Delsink *et al.* (2013) reported no detectable behavioural, social or spatial changes over an 11-year study. Whilst effective for small protected areas, this method has, however been criticised for not being practical for protected areas containing large elephant populations, where the practically of repeatedly locating individual female elephants can decrease the method’s effectiveness (Van Aarde and Jackson 2007). This has changed with the introduction of a blanket contraceptive treatment method, where many female elephants are treated and the small proportion that may escape retreatment allows for an acceptable number of calves to come through the system (Delsink *et al.* 2013, Bertschinger *et al.* 2018). The few females that do give birth within the population have also been found to be important in terms of perpetuating the allomothering mothering skills needed within elephant society (Lee 1987).

Translocating elephants from one protected area to another can also be used to reduce elephant numbers (Pinter-Wollman 2012). However, space for elephants is limited in countries such as South Africa (Whyte 2007), whilst removing elephants may create the same vacuum effects experienced during culling operations, promoting high elephant breeding rates (Caughley 1993). Furthermore, precautions are required in the social demographic make-up of the transported populations. Previously transported young elephant bulls from the KNP to smaller protected areas were found to come into musth at a younger age (<10 years old) without the presence of older established bulls, and up to 49 white rhinos were killed in South Africa’s Pilanesberg National Park by these abnormally aggressive elephant bulls (Slotow and Dyk 2001). Furthermore, the logistics and financial costs associated with a required in-depth and highly regulated elephant management plan may also deter some protected areas from accepting elephants (DFFE 2004).

Overview of spatial and temporal elephant management strategies

The spatial manipulation of elephant densities focuses on altering the spatial and temporal locations of elephants across protected areas (see Henley and Cook (2019) for a review). As previously discussed in this literature review, this method is applicable to large, protected areas where the manipulation of surface water can restrict elephant access from certain areas, thereby attempting to regulate where and when elephants will impact certain vegetation-types (Ferreira *et al.* 2017, Robson and Van Aarde 2018, MacFadyen *et al.* 2019). The KNP, for example, have destroyed many historical artificial waterholes to restore natural process affecting the elephant population (Figure 7, Purdon and van Aarde 2017). A reduction in waterholes can promote density-dependent habitat selection, whereby increased elephant densities in favoured habitats can lead to increased intraspecies competition, which could displacing subordinate herds to suboptimal habitats (MacFadyen *et al.* 2019, Louw *et al.* 2021).

The expansion of protected areas through the removal of fences can also help alleviate elephant densities, especially as bulls are usually the first to expand their home ranges (Druce *et al.* 2008). In the KNP, the removal of international border fence-lines and the promotion of Transfrontier conservation areas, such as the Great Limpopo Transfrontier Protection Conservation Area (GLTFCA), has promoted the movement of elephants from KNP into both protected and unprotected areas in eSwatini, Mozambique and Zimbabwe (Cook *et al.* 2015, Henley *et al.* 2023). However, careful planning is required, as an expansion of elephant populations into new ranges may also lead to increased or new levels of human-elephant conflict (Witter 2013, Henley *et al.* 2023).

Figure 7. The demolition of Wik-en-Weeg dam in the Kruger National Park, South Africa, as a part of the new water policy of the South African National Parks (Pienaar *et al.* 1997, Photo credit: www.krugerpark.co.za).

Elephants may also be deterred from areas where landscapes of fear exist, either because of human-elephant conflict (Ihwagi *et al.* 2019, Wall *et al.* 2021), or the proposed use of disturbance shooting and localised culling, which differs from hunting as it focuses on both bulls and breeding herds and is not driven by an elephant's selective physical traits (Pienaar 2012). The concept of inducing fear within a landscape has been promoted to regulate large herbivore distribution and numbers to divert herbivores away from undesired areas (Cromsigt *et al.* 2013). The ecology of 'fear' is a significant regulator of herbivore movements (Pringle 2018, Davies *et al.* 2021), with the fear of humans being shown to be a significant factor for regulating herbivore spatial and temporal distributions (Doherty *et al.* 2021). This concept is currently being explored as a driver of elephant spatial and temporal distributions (Zanette *et al.* 2023).

<u>Directly protecting the resource –tree protection methods</u>

Tree protection methods have been developed to directly protect large trees from elephant impact in protected areas that are either too small to manipulate elephant movements spatially or have an abundance of artificial waterholes (Henley and Cook 2019). Although mitigation methods have been criticised as not directly addressing the problem of potentially high elephant densities threatening large tree survival (Rushworth *et al.* 2018), protecting individual large trees can help protect the seedbanks of future large trees (Western and Maitumo 2004). Furthermore, they can be viewed as 'tools' in a 'toolbox' for helping mitigate against the impact that elephants may have on certain tree species (Enterprises University of Pretoria 2022). Several elephant mitigation methods have been proposed to protect large trees, of which a selection have been reviewed. This section will provide a review on the current information available for each mitigation method.

<u>Wire-netting</u>

Wire-netting involves placing chicken-mesh around the main stem of a large tree to protect the tree against bark-stripping (Derham *et al.* 2016). It can be a highly successful method for improving tree survival, if applied correctly as in the APNR (Henley and Cook 2021), only 1.7% of 1,387 large trees with wire-netting were bark-stripped in comparison to 25% of 1,281 large trees with no protection (Derham *et al.* 2016). Wire-netting is a relatively easy to use, cost-effective method in comparison to other proposed mitigation methods (Derham *et al.* 2016, Cook *et al.* 2018).

Wire-netted trees, however, are still vulnerable to heavier forms of impact such as main stem snapping and uprooting (Derham *et al.* 2016). Tourists in general do not appear to mind the sight of wire-netted trees (Edge *et al.* 2017) and wire-netting can be applied to a large number of trees due to its relatively low costs (Derham *et al.* 2016).

Beehives and honeybees

Active beehives have been used as mitigation methods for preventing elephants from crop raiding in both Africa (King *et al.* 2017) and Asia (Van de Water *et al.* 2020). Elephants are sensitive to bee stings around their ears, eyes, as well as inside of their trunks (Vollrath and Douglas-Hamilton 2002) and display a fear response to the sounds of swarming honeybees (King *et al.* 2007, 2018).

African honeybees (*Apis mellifera scutellata*) have been used to protect large trees against elephant impact as well. In the Laikipia Plateau in Kenya, one third of the *Vachellia xanthophloea* trees with beehives received no elephant impact during a 40-day experimental trial (Vollrath and Douglas-Hamilton 2002). In Jejane Private Nature Reserve (within the APNR), beehives have been used to protect *S. birrea* trees from elephant impact, where the presence of beehives alone significantly decreased the likelihood of a tree receiving elephant impact (Figure 8, Cook *et al.* 2018). A drawback to the beehive mitigation method however, is the relatively high cost involved in purchasing beehives and maintaining colonies in the dry season, limiting the scale of use for this method (Cook *et al.* 2018). The aggressive nature of African honeybees to swarm and attack when threatened can also limit their usage in the absence of a trained beekeeper (Alaux *et al.* 2009). African honeybees, as an aggressive generalist pollinator, may also outcompete other pollinator species, both spatially and temporally (Martins 2004).

This mitigation method does, however, have the potential to generate income in the form of honey production and other bee-related products (King *et al.* 2017), as well as promoting pollination services within an area (Chirwa and Akinnifesi 2008).

Rocks and concrete pyramids

The placement of natural rocks or artificial concrete pyramids around a tree’s main stem have been used to protect trees against elephant in the form of a barrier (Pienaar 2012).

Whilst this method is a part of the KNP elephant management plan (Pienaar 2012) and has been applied on various properties within the APNR (personal observation), no scientific evaluations on its effectiveness as an elephant mitigation method have been conducted. Furthermore, an evaluation would need to identify the distance required to keep an elephant away from the tree's main stem, as no standardised diameter size has been applied around the trees in the APNR (personal observation). I discuss the requirement in the last chapter.

Figure 8. An active beehive hung in a *Sclerocarya birrea* keeps a small bachelor group of African elephants away from impacting the tree (Photo credit: Robin Cook).

Creosote jars

Creosote is a residue created by the distillation of coal-tar (Bernstein and Reh 2023). The thick and oily composition of creosote does not allow it to dissolve easily in water, whilst it is highly flammable as well (Van Zyl 2013, Bernstein and Reh 2023). Creosote has been used as an olfactory tool to mitigate human-elephant conflict in Zimbabwe (La Grange *et al.* 2022) but has never been tested as a tree-protection method. In 2017, some individual landowners in the APNR placed coal-creosote inside of glass jars and nailed the jars on platforms to the main stems of large trees (personal observation). Since the method's implementation, creosote stains have been observed on elephants within the APNR (Elephants Alive, unpublished data). Scientific evaluations are thus required on this mitigation method before it is replicated elsewhere, which I elaborate on in the last chapter of the thesis.

Research rationale

Conservation managers across certain protected areas containing African elephants (*Loxodonta africana*) are faced with stakeholder concerns about the decline of large trees (≥ 5m in height, Shannon *et al.* 2008) due to elephant impact. Both large trees and elephants provide important ecosystem services and act as keystone species in their environments (Manning *et al.* 2006, De Boer *et al.* 2015). However, heavy levels of elephant impact on large trees in protected areas where water is readily available to elephants can threaten the persistence of certain tree species (Helm *et al.* 2009, Boundja and Midgley 2010), as well as species that may be reliant on large trees for breeding purposes (Combrink *et al.* 2017, Rushworth *et al.* 2018). For example, the loss of large trees may limit the number of nesting species such as the critically endangered white-backed vulture (*Gyps africanus*) (Monadjem and Garcelon 2005, Rushworth *et al.* 2018).

In South Africa's Associated Private Nature Reserves (APNR), there are stakeholder concerns over the loss of large trees from the landscape (Edge *et al.* 2017). The APNR is a protected area with a high density of waterholes, sharing an open boundary with the Kruger National Park (KNP), and is used by a multitude of stakeholders (Child *et al.* 2013, Edge *et al.* 2017). Previous research in the APNR has shown that large trees densities are continually declining (Henley 2013, Cook *et al.* 2017) and that elephant impact can negatively influence the perceptions of stakeholders if they perceive the impact to be aesthetically unappealing or of ecological concern (Edge *et al.* 2017). Tourists and landowners of the APNR have shown support for the use of tree protection methods for minimising elephant impact (Edge *et al.* 2017). Although tree protection methods have been recorded in previous national management plans (Pienaar 2012, Enterprises University of Pretoria 2022), only two methods have been published in scientific literature (Derham *et al.* 2016, Cook *et al.* 2018). Furthermore, understanding stakeholder values surrounding large tree and elephant population dynamics and management is important for the sustainability of conservation efforts (Manfredo *et al.* 2021).

The APNR therefore provides an ideal landscape where tree protection methods can be tested, and an array of stakeholders' conservation-based values measured. Therefore, the purpose of this research is to investigate the value of large trees in the APNR, as well as to assess their protection methods against elephant impact. This will be explored by i) exploring the diversity of values held by stakeholders of the APNR regarding the ecology and management implications of elephant impact on large trees, ii) investigating the survival trends of three iconic tree species in relation to elephant impact in the APNR over a 12-year period, iii) examining the impact that elephants have on large trees containing white-backed vulture nests over a 12-year period, and iv) testing the effectiveness of mitigation methods for protecting large trees against elephant impact.

Study aim and objectives

To understand how APNR stakeholders perceive the value of large trees and to investigate the level of elephant impact within the APNR, whilst assessing which tree protection methods effectively protect large trees from such impact.

Objective 1. Identify the diversity of values held by stakeholders of the APNR regarding the ecology and management implications of elephant impact on large trees.

Objective 2. Investigate the survival trends of three iconic tree species in relation to elephant impact in the APNR over a 12-year period.

Objective 3**.** Examining the impact that elephants have on large trees containing white-backed vulture nests over a 12-year period.

Objective 4**.** Test the effectiveness of mitigation methods for protecting large trees against elephant impact.

Thesis Outline*

The first chapter of this thesis consists of a general introduction, which includes a literature review of ecological importance of elephant and large tree population dynamics, interactions, as well as management strategies that have been implemented to manage elephant impact on the environment. Chapter 2 identified which conservation values and elephant management strategies promoted unity and polarisation among stakeholders of the Associated Private Nature Reserves (APNR) (Objective 1). Chapter 3 is a published paper investigating the effect that elephants and other environmental factors have had on the survival of three large tree species in the APNR over a 12-year period and investigated the effectiveness of wire-netting as a tree protection method (Objective 2). Chapter 4 investigated the impact that elephants have on trees nested in by white-backed vultures in the APNR across a 12-year period (Objective 3). Chapter 5 is a published paper that examined the effectiveness of four mitigation methods that have been applied to protect large trees from elephant impact across the APNR (Objective 4). The final chapter (Chapter 6) provides an overview of the impact that elephants have had on large trees in the APNR, as well as the potential for tree mitigation methods given stakeholder values and opinions. This chapter also provides a decision-making diagram for when and how to apply mitigation methods to trees for protection purposes. The thesis also contains an Appendix section, containing three scientific publications to which the PhD candidate has been a part of during the years he was conducting the PhD research, and to which are referenced in the final chapter.

** This thesis has been prepared and written in the format of scientific papers. Some repetition of information, given this format, is unfortunately unavoidable but has been minimised as much as possible.*

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CHAPTER 2:

Stakeholder values on the ecology and management of African elephants in relation to trees

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Abstract

Societal values significantly influence conservation decisions, particularly related to keystone and charismatic species such as the African savanna elephant (*Loxodonta africana*). Whilst subject to illegal hunting and habitat-loss continentally, increased elephant numbers in South Africa have caused concern and debate among stakeholders as to how socially complex elephant populations should be managed in relation to their impact on ecologically important large trees. We conducted a Likert scale survey with stakeholders of a protected area containing elephants in South Africa's semi-arid savanna, to identify level of agreement or polarization on large tree and elephant dynamics, as well as lethal and non-lethal management strategies. We found that tourists and property owners showed the greatest levels of support for tree protection methods, whilst stakeholders in conservation management were most highly supportive of waterhole closures. Tourists were significantly less likely to support the culling of elephants in comparison to conservation management stakeholders. We illustrate how stakeholder profession, age, and gender can influence the likelihood of supporting particular management strategies, as well as the complexities facing conservation managers in managing stakeholder expectations regarding sustainable large tree and elephant populations.

Keywords: Culling, Elephant management strategies, Likert scale survey, The elephant problem, Tree protection methods, Conservation policy

Introduction

Conservation and societal values

Conservation decision-making is expected to be based on scientifically-sound principles, learnt through experimentation or a review of accumulative evidence (Pullin *et al.* 2004). However, these decision-making processes are also influenced by societal values regarding where, what, and how we should conserve biodiversity (Kareiva and Marvier 2012). Human values, which are our fundamental goal structures (Schwartz and Bilsky 1990), provide us with benchmarks as to whether activities are deemed acceptable or not (Manfredo *et al.* 2017). Gathering and synthesising data on societal values helps policy-makers find common values among a diversity of stakeholders (Madden and McQuinn 2014), as well as to anticipate how stakeholders may respond to conservation policy-decisions in protected areas (Manfredo *et al.* 2021). The International Union for the Conservation of Nature describe a protected area as "A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values." (Dudley 2008).

The 'elephant problem' and continental elephant number trends

Societal values have played a significant role in the management of Africa's savanna elephant (*Loxodonta africana*) populations, particularly in relation to elephant numbers and their impact on the environment (Gillson and Lindsay 2003; Dickson and Adams 2009). Expanding elephant populations in certain protected areas with so-called 'too many elephants' is referred to as the 'elephant problem' (Glover 1963). A concept such as a "safe" elephant carrying capacity, was also first termed after a combination of a drought and high elephant densities were deemed responsible for the declining woodland in Tsavo National Park, Kenya, particularly around waterholes (Glover 1963). Similar concerns were realised in other protected areas across eastern and southern Africa, and the practice of reducing elephant numbers by means of culling was initiated (Laws 1970, Whyte *et al.* 1998).

Elephants, as a megaherbivore and keystone species (Owen-Smith 1988), have the capability to significantly alter their environment, often through the reduction of tree cover and promotion of landscape openness (Asner *et al.* 2016). Tree cover reduction and structural alteration can have both beneficial and nonbeneficial effects on a protected area's fauna and flora (Guldemond *et al.* 2017). A large-scale loss of trees however would decrease important ecological roles provided by trees to a landscape such as nutrient recycling, shade and food provision, and habitat creation, including nests (Dean *et al.* 1999, Ward *et al.* 2018). Large trees also provide positive landscape aesthetics for human stakeholders (Edge *et al.* 2017).

Concerns over tree loss meant that elephant culling was maintained as a precautionary measure to limit the negative impacts that elephants may have on biodiversity (Pienaar *et al.* 1966, Laws 1970). However, scientific opinions as to how elephant impact on the environment should be managed have changed over time, influencing societal views in the process (Dickson and Adams 2009). An alternative hypothesis to the 'elephant problem' was proposed by Caughley (1976), who stated that no natural equilibrium between elephant and tree densities existed, but rather that of two stable limit cycles. Here, elephant numbers would rise, and tree numbers would decline until density-dependent feedbacks would result in elephant population declines, and therefore tree numbers would increase once more. Recent scientific studies have further suggested that management should focus on the spatial and temporal distributions of elephants, moving away from directly managing elephant numbers, towards managing elephant effects instead (Ferreira *et al.* 2017).

Additionally, societal values surrounding elephant numbers have been influenced by the large-scale poaching of elephants (defined as the illegal taking of animals in line with a country's rules, Eliason 2004), particularly in central- and east Africa, where elephant numbers were decimated in the 1970s and 1980s (Blanc *et al.* 2002), as well as between 2005-2011 (Schlossberg *et al.* 2020). The large-scale reduction in the continent's elephant numbers placed further societal-driven pressure on any conservation management decisions aimed at reducing elephant numbers (Dickson and Adams 2009).

Research into the sentient nature and complexity of elephant social structures have added further debate as to how elephant populations should be managed (Lee and Moss 2014), bringing in an animal welfare component into the discussions (IFAW 2005, Slotow *et al.* 2021), with evidence suggesting long-lasting stress levels in surviving populations where culling took place (Shannon *et al.* 2013).

There currently exists an overall stabilisation of the population (Huang *et al.* 2024), although these trends differ on a regional basis, with southern Africa's elephant numbers generally increasing, whilst there are declines in eastern, central and western Africa (Chase *et al.* 2016). Variation in these population trends has caused global debate regarding how Africa's elephants should be managed when the conservation concerns surrounding the individual populations are often polarised (Lindsay *et al.* 2017).

Case study: Kruger National Park and the Associated Private Nature Reserve, South Africa

A key example of societal debates surrounding managing elephant impact on trees can be found in South Africa's Kruger National Park (KNP), where over 14,000 elephants were culled from 1967-1994, before the implementation of an internationally-pressured moratorium (Whyte *et al.* 1998). Post-moratorium elephant numbers in both the KNP and the adjoining protected areas has increased from an artificially controlled number of 6,000-8,000 elephants, to over 30,0000 (GLTFCA 2022).

This increase in elephant numbers has also been observed in one of the large adjoining protected areas to KNP, the Associated Private Nature Reserves (APNR). The APNR, a collection of privately owned protected areas, dropped its fence-line with the KNP in 1993, and has since had its elephant population rise from 500 elephants to a fluctuation of 2,000-3,000 (Greyling 2004, Peel 2015). This increase, coupled with the APNR's high waterhole density in comparison to the neighbouring KNP, has resulted in a steady decline in the numbers of large (≥5 m in height) trees (Cook *et al.* 2023a). A high density of artificial waterholes results in elephants contracting their spatial and temporal distributions, thereby increasing the likelihood of tree impact (O'Connor *et al.* 2007). Given the complexity of ecological systems, aspects of the decline in large trees can thus directly be attributed to elephant effects on older age classes of trees while mesoherbivore densities and other environmental elements such as topography, fire and climatic events are also known to affect tree dynamics (Henley and Cook 2019).

Irrespective of the causal links, the combination of rising elephant numbers and declining large trees has induced the construction of proposed management plans on how to manage elephant effects on large trees in a protected area that contains a range of stakeholder groups including photographic safaris, trophy hunting, research facilitation, and shareblock incorporations (Child *et al.* 2013).

Conflictions over elephant management strategies

Balancing conservation decisions with diverse stakeholder groupings is a global challenge and one that can affect conservation revenue (Bushell 2003). Proposed methods to managing elephant impact on large trees in the APNR include: spatial and temporal manipulation methods (artificial waterhole closure, translocation of elephants), methods for directly protecting trees against elephant impact, as well as elephant population control measures (contraception and culling) (Henley and Cook 2019).

The closure of artificial waterholes has been carried out in the KNP to limit the temporal and spatial distributions of elephants, thereby promoting density-dependent habitat selection and competition for resources (Robson and Van Aarde 2018). It is argued though, that large-scale waterhole closures could be detrimental to tourism (Van Wyk 2001).

Tree protection methods, such as wrapping up trees with wire-netting (to prevent bark-stripping), or hanging beehives in tree branches to scare off elephants, have been used to protect individual trees from elephant impact (Derham *et al.* 2016). However, these methods only provide small-scale protection, limiting their effectiveness in large protected areas (Henley and Cook 2019).

Contraception of elephant cows with native porcine zona pellucida (PZP) has been used to decrease the growth rate of elephant populations by either preventing female elephants from conceiving, or by increasing the intervals between calving (Delsink *et al.* 2023). Opponents however have observed its limitations to large populations where follow-up treatments may be logistically unattainable (Whyte 2007), however effectiveness within a number of reserves has recently been cited (Delsink *et al.* 2023).

Culling elephants directly lowers the number of elephants in a protected area and is indiscriminate of sex and age (Whyte *et al.* 1998). Whilst proponents of culling argue that a reduction in elephant numbers will lower impact on large trees (Whyte *et al.* 1998), opponents cite animal welfare concerns (Slotow *et al.* 2021) and evidence that elephant densities are not directly linked to tree losses (Abraham *et al.* 2021). Although trophy hunting generates an income, it has limited applicability as an ecological management tool as it is directed towards bulls and is selective of certain phenotypic traits, making it ineffective as a population control method and in need of effective management to prevent evolutionary consequences over time (Harris *et al.* 2002).

The diversity of available methods, combined with the variety of views held by stakeholders, means that selecting for the best method that appeases both the concern over the loss of large trees and satisfies stakeholder perceptions is critical for conservation managers. For the APNR, with its highly diverse array of stakeholders, quantifying stakeholders' values on elephant management strategies is essential. Our study therefore aimed to identify and quantify the diversity of values held by stakeholders of the APNR, regarding the ecological theory and management strategies related to elephant impact on large trees in the form of a questionnaire with a Likert scale. Our objectives were to i) identify which values promoted agreement and non-agreement amongst stakeholders, and ii) investigate how stakeholder demographics may influence stakeholder agreement for the implementation of culling, contraception, waterhole closures, and tree protection methods as management methods to reduce elephant impact on large trees.

Conservation managers are thus faced with a toolbox of elephant management methods, each with its societal proponents and opponents, as well as conflicting ideologies as to how, or if, elephant populations should be managed. Identifying where agreements and nonagreements occur among stakeholders is therefore necessary (Dickson and Adams 2009). Likert scales are a frequently used tool in fields such as psychology and sociology for measuring respondent values in an ordinal quantitative format (Sandiford and John 2003, Taherdoost 2022). Likert scales allow for data to be collected relatively quickly and from a large group of respondents (Sandbrook *et al.* 2019), and allow for quantitative data to be compared and combined with qualitative data-gathering techniques (Nemoto and Beglar 2014). Likert scales can however be subject to central tendency and social desirability biases (Westland 2022).

Materials and methods

Study area

The APNR (size: 2,089 km^2) is situated in the north-eastern region of South Africa (24˚04-24˚55′ S; 30˚82′-31˚48′ E), sharing an open boundary with the KNP since 1993 and forms a part of the Great Limpopo Transfrontier Conservation Area (GLTFCA 2022, Figure

1). Five privately owned PAs make up the APNR, including the Balule-, Klaserie-Thornybush-, Timbavati-, and Umbabat-Private Nature Reserves. Each of these PAs are comprised of delineated properties owned by private (non-State) individuals who have made the choice to operate the activities on their properties for commercial (e.g. photographic or hunting safaris) or for private usage only. APNR stakeholder groups were categorised as the following: conservation management (reserve management and biological scientific researchers), tourism and hospitality (tourist lodge personnel, tour operators and field guides), property owners (landowners and shareholders), and tourists (leisure travellers). The APNR has a waterhole density of 2.5 waterholes per km^2, which means that water is far more available to animals there than the neighbouring regions of the KNP, which have a waterhole density of 0.1 per km^2 (Child *et al.* 2013). Whilst elephant densities across the APNR and KNP fluctuate throughout the year, census data in the dry season estimate the APNR elephant density at 1.67 elephants per km^2 (2022 census) and the KNP elephant density at 1.54 elephants per km^2 (2022 census) (GLTFCA 2022).

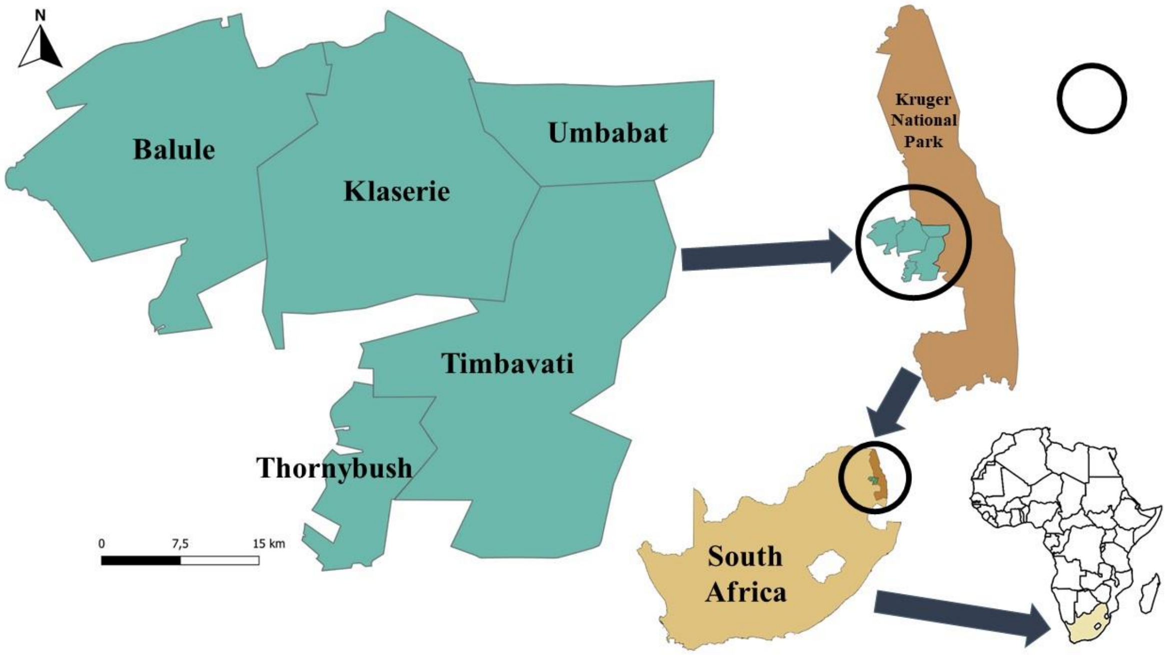

Figure 1. Location of the Associated Private Nature Reserves (APNR), South Africa, comprised of five private protected areas sharing an open boundary with the Kruger National Park (KNP).

Survey design and sampling

Non-medical human ethics clearance for this survey was granted by the University of the Witwatersrand's Human Research Ethics Committee (protocol number: H22/11/54). A participatory consent sheet was emailed to all potential participants explaining the purpose and content of the questionnaire (Participatory information sheet S1).

We constructed 36 Likert items from existing scientific literature on the debates surrounding the management of elephants in the KNP and APNR, covering a broad base of elephant-large tree ecological and societal values (Tables S1 and 2). Conservation managers of the APNR were also consulted to ensure that current management issues were represented. We then conducted a thematic analysis (*Taguette* software, Rampin and Rampin 2021) to identify common themes across the Likert items and divided them into two sections (Sections 1 and 2) of 18 items each. Section 1 referred to the theory of elephant and large tree population dynamics (Table S2) and Section 2 referred to management practices of protecting large trees where they co-occur with elephants Table S3).

We then constructed a web-based questionnaire (KoBoToolbox 2023), placing the Likert items in a 5-option Likert framework (Strongly disagree, Disagree, Neutral, Agree, Strongly agree). Demographic data of each participant was also collected, which included: nationality, gender, age class, education level, number of years as a stakeholder (number of years since the participant first assumed their stakeholder title within the APNR), visitation rate to the APNR, and stakeholder group (Table 1). Demographic details were used for Section 2 of the analyses. Each Likert item had an open-ended comments section where participants could voluntarily elaborate on their answer if they so wished.

The Likert items were first piloted with 6 participants (both South African and international). Upon feedback minor alterations were made to Likert items that required clarification. The survey was launched on 26 July 2023 and distributed to all conservation managers of the APNR, as well as a subgroup of lodge owners, private landowners, and shareblock representatives (total of 127 submitted surveys) whose contact details were available due to historical communication and in compliance with the South African Protection of Personal Information Act (POPIA). From there on, the survey was distributed through targeted snowball sampling (Burger and Silima 2006), whereby respondents were asked to pass on the online survey to relevant stakeholder associates, bringing the survey total to 170 participants responses. The survey was closed on 17 November 2023.

Data cleaning and preparation

A total of 170 APNR stakeholders responded to the survey (Table 1). Due to the relatively small number of available participants, we combined the age classes of those below 50 years and those above 50 years of age, whereby those $\geq$50 years would have had a minimum period of 20 years during the 'command-control-era' (management focused on the direct manipulation of animal numbers through human intervention) when culling was permitted (Whyte *et al.* 1998). Respondents in the above 50 years cohort would have spent their early to middle age years at a time when culling was operational (years 1973-1994). We also combined the representatives of all non-South African respondents (13 different countries), as international stakeholders for statistical purposes. Participant education classes were not included in the analyses due to the small sample sizes per category.

Statistical analyses

Statistical analyses were carried out in R version 4.3.1 (Development Core Team 2012) and were considered significant at $p<0.05$. Responses to the Likert items were displayed in a Likert chart in order of responses with the highest cumulative percentages of 'Agree' and 'Strongly agree' (*Likert* package, Bryer and Speerschneider 2016).

Polarisation tests were performed on each Likert item (*agrmt* package, Ruedin and Aeppli 2023). This test measures the level of dispersion amongst data in an ordered rating scale, providing an output from 0 and 1, where an output of 0 signifies perfect agreement amongst respondents; an output of 0.5 signifies no agreement; whilst an output of 1 signifies perfect polarisation (Ruedin and Aeppli 2023). No agreement consequently signifies a lack of agreement and a lack of polarisation amongst participant responses. Polarisation scores are calculated using the following formula: Polarisation score (Pol) = (1-*agreement*)/2, whereby *agreement* is calculated using Cohen's Kappa coefficient:

$$K = P_o\text{-}P_e/1\text{-}P_e$$

Where: P_o is the observed agreement and Pe is the expected agreement by chance (Ruedin and Aeppli 2023).

Table 1. Participant sample size and demographic information, separated by stakeholder group for the Associated Private Nature Reserves (APNR), South Africa.

Demographic factor	Category	Conservation management (n=54)	Hospitality and tourism (n=42)	Property owner (n=41)	Tourist (n=33)	Total (n=170)
Nationality	South African	38 (70.4%)	31 (73.8%)	30 (73.2%)	26 (78.8%)	125 (73.5%)
	International	16 (29.6%)	11 (26.2%)	11 (26.8%)	7 (21.2%)	45 (26.5%)
Gender	Female	18 (33.3%)	21(50%)	17 (41.5%)	25 (75.8%)	81 (47.6%)
	Male	36 (66.7%)	21 (50%)	24 (58.5%)	8 (24.2%)	89 (52.4%)
Age class	<50 years	40 (74.1%)	34 (81%)	14 (34.1%)	18 (54.5%)	106 (62.4%)
	>50 years	14 (25.9%)	8 (19%)	27 (65.9%)	15 (45.5%)	64 (37.6%)
Education	High school	4 (7.4%)	5 (11.9%)	5 (12.2%)	1 (3%)	15 (8.8%)
	Tertiary certificate	0 (0%)	4 (9.5%)	1 (2.4%)	0 (0%)	5 (2.9%)
	College diploma	4 (7.4%)	13 (31%)	5 (12.2%)	10 (30.3%)	32 (18.8%)
	Bachelor’s degree	14 (25.9%)	12 (28.6)	21 (51.2%)	14 (42.4%)	61 (35.9%)
	Master’s degree	20 (37%)	8 (19%)	8 (19.6%)	7 (21.2%)	43 (25.3%)
	Doctorate	12 (22.3%)	0 (0%)	1 (2.4%)	1 (3%)	14 (8.2%)
Residency period (number of years as a stakeholder)	<10 Years	32 (59.3%)	30 (71.4%)	19 (46.3%)	16 (48.5%)	97 (57.1%)
	>10 Years	22 (40.7%)	12 (28.6%)	22 (53.7%)	17 (51.5%)	73 (42.9%)
Visitation rate	Less than once a year	7 (10.7%)	1 (2.4%)	1 (2.4%)	8 (24.2%)	17 (10%)
	Once a year	11 (21.4%)	2 (4.9%)	3 (7.3%)	11 (33.3%)	27 (15.9%)
	At least once every 6 months	7 (3.6%)	6 (14.3%)	17 (41.5%)	9 (27.3%)	39 (22.9%)
	At least once a month	10 (10.7)	5 (11.9%)	11 (26.8%)	2 (6.1%)	28 (16.5%)
	resident	19 (53.6%)	28 (66.5%)	9 (22%)	3 (9.1%)	59 (34.7%)

We then ran four separate ordinal logit models (*MASS* package, Ripley *et al.* 2023) to examine how stakeholder demographics influenced stakeholder values surrounding the effectiveness of the four elephant management strategies of interest, using results from the following four Likert items:

i) I think that a decrease in APNR waterholes would limit elephant movements and their consequential impact to large trees in proximity to waterholes (*Waterhole closure*).

ii) I think that tree protection methods (such as wire-netting/rocks/beehives) should be used to protect individual trees from elephant impact (*Tree protection methods*).

iii) I think that the contraception of elephants is a viable management tool for lessoning elephant impact on large trees within the APNR (*Contraception*).

iv) I believe that culling elephants will reduce elephant impact on large trees (*Culling*).

Ordinal logit models (OLMs) are useful for social surveys that make use of ordered categorical response variables (Zheng *et al.* 2014). We scored the discrete ordered response variable as follows: 1= Strongly disagree, 2= Disagree, 3= Neutral, 4= Agree, 5= Strongly agree. The following categorical predictor variables from Table 1 were included: stakeholder group, nationality, gender, age class, residency period, and visitation rate. Predictor variables were removed in succession from the model through likelihood ratio tests, allowing us to test whether the removal of a variable significantly increased the model variance (Guisan and Harrell 2000).

We lastly constructed a chord diagram (*circlize* package, Gu 2022) to visually illustrate the interrelationships between stakeholder groups and their collective agreements on one or more of the four elephant management strategies to reduce elephant impact on large trees, and performed a thematic analysis (*Taguette* software, Rampin and Rampin 2021) on the comments provided by participants to identify common response themes. Each management method's comments were entered into the *Taguette* software and a list of common themes were highlighted from the provided comments, and comments may also have contained multiple themes. These common themes were then reduced to 2-3 overall themes per management method which best represented all of the participants' comments.

Results

Section 1: Large tree and elephant population dynamics

We analysed the results of 170 participants, comprising both South African and international stakeholders and spread across four specified stakeholder groups (Table 1). Most participants (82%) identified with having a good understanding of the effects that elephants have on large trees and identified that both elephants (97% in agreement) and large trees (81% in agreement) added significant tourism value (Figure 2).

We calculated high levels of agreement (Pol=0.02) for the Likert items ‘Elephants add significant tourism value to the landscape’ and ‘Functioning ecosystems should be a primary goal of conservation’, as well as high levels of non-agreement for the Likert items ‘I have negative feelings when I see an elephant push over a tree’ (Pol=0.53) and ‘Pushed over large trees decrease a landscape’s beauty’ (Pol=0.59, Figure 2).

We found that 69% of participants were concerned about the current levels of elephant impact on large trees (Pol=0.21), but only 48% felt that there were too many elephants (Pol=39, Figure 2). Regarding how elephant impact may affect other faunal species, 79% agreed that elephant impact can increase habitat for lizards and insects (Pol=0.15), whilst 76% felt that that elephant impact could also decrease habitat availability for tree-nesting birds (Pol=0.16, Figure 2).

Section 2: Management practices for protecting large trees

Polarisation scores ranged from a high agreement level for the Likert item ‘Conservation decision-making around elephants and trees should be informed by scientific studies (Pol=0.02), to high levels of non-agreement for ‘Contraception of elephants is a viable management tool for reducing elephant impact’ (Pol=0.57) and ‘A large-scale closure of waterholes would decrease tourism’ (Pol=0.57, Figure 3). There was general agreement though (59%, Pol=0.23), that large tree densities have decreased over time (Figure 3).

We also wanted to know whether stakeholders felt that external population trends compared to that of the APNR (i.e. declining elephant numbers elsewhere in Africa, or a tree species decreasing within the APNR might be flourishing beyond the borders of the APNR) should influence APNR management decisions. Here we found relatively high levels of nonagreement for both elephant (Pol=0.5) and tree trends (Pol=0.41).

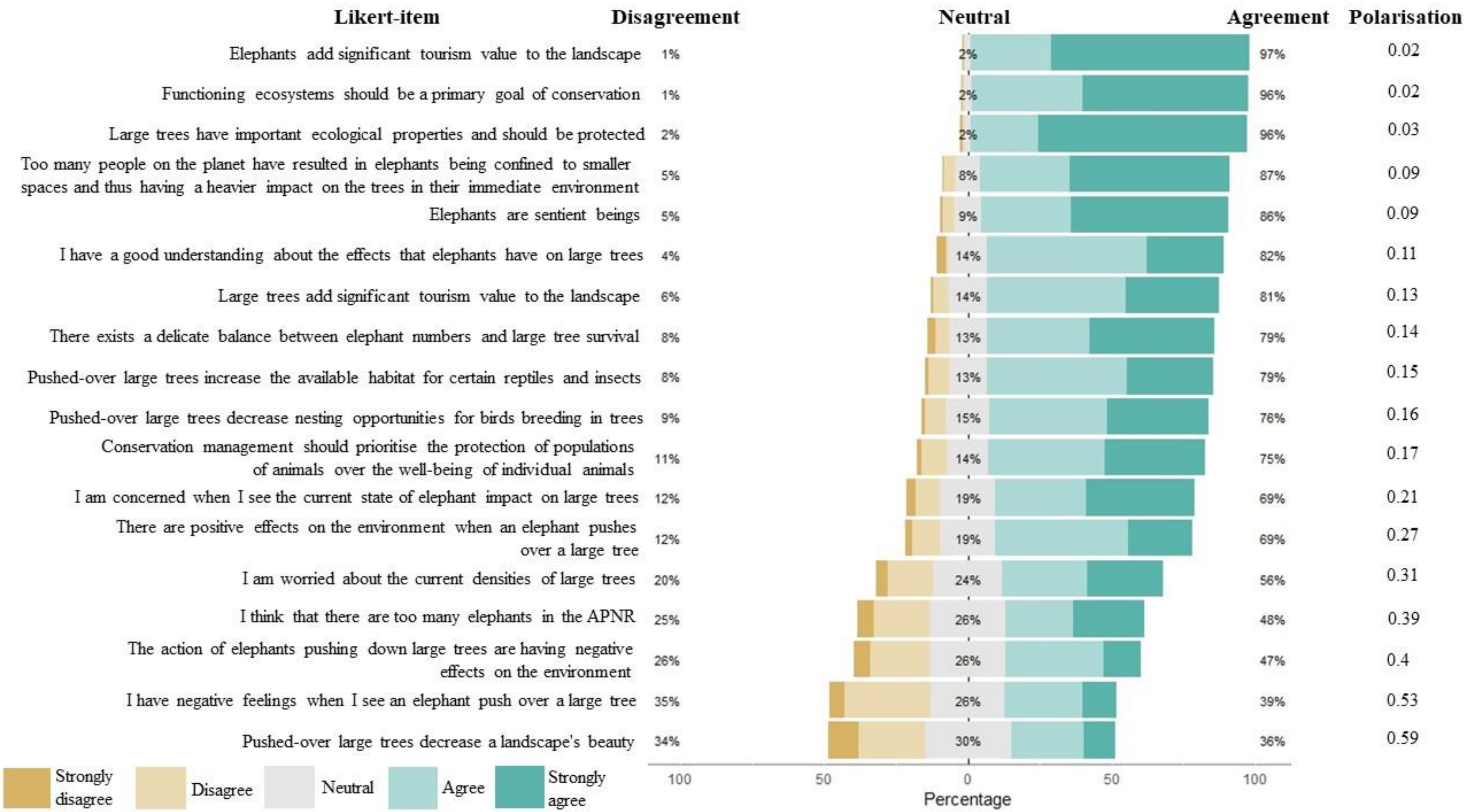

Figure 2. Section 1: The views of stakeholders on value statements related to elephant and large tree population dynamics in the Associated Private Nature Reserves (APNR), South Africa.

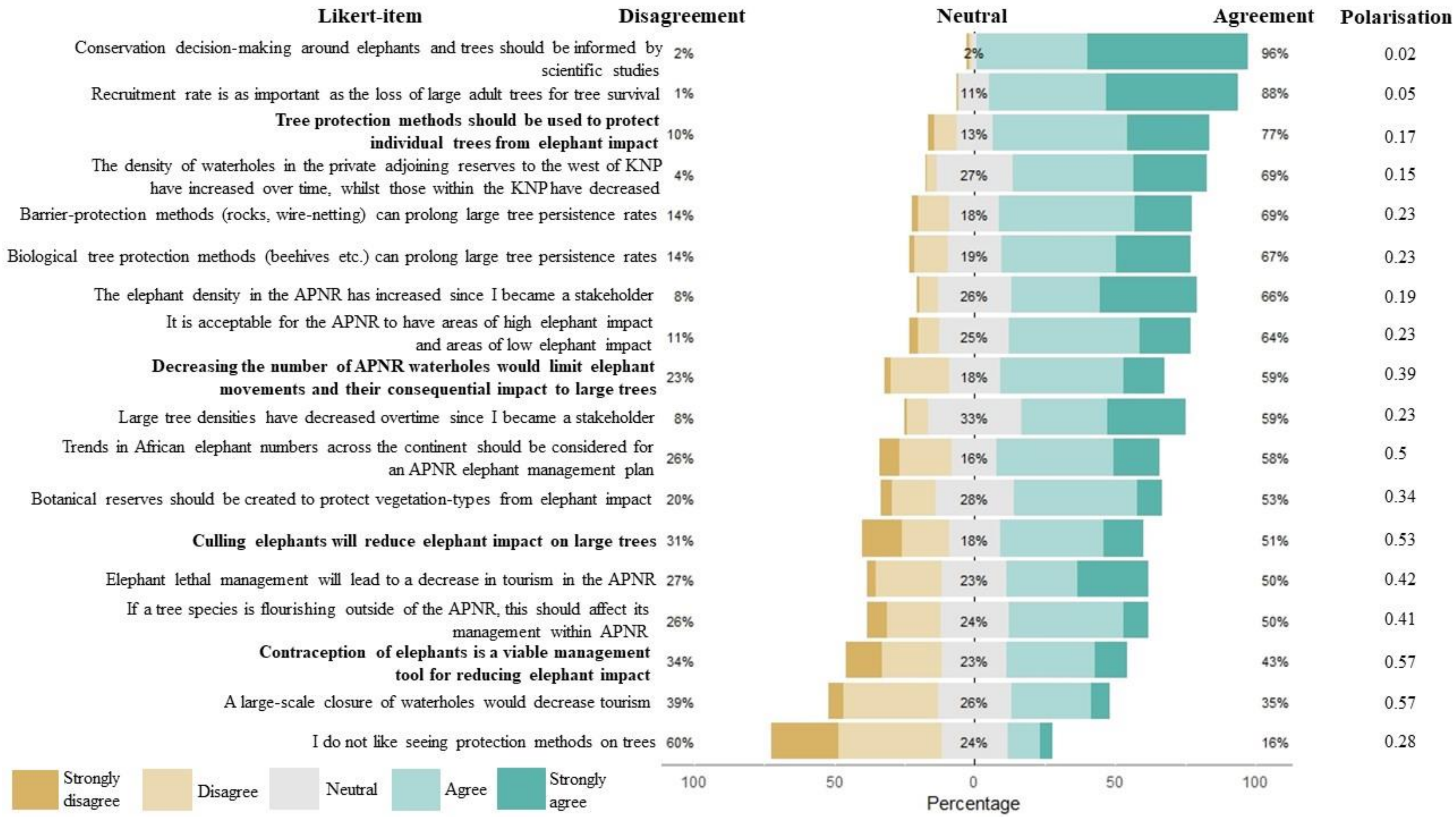

Figure 3. Section 2: The views of stakeholders on value statements related to management practices for protecting large trees where they co-occur with elephants in the Associated Private Nature Reserves (APNR), South Africa. Bold Likert items represent terms used in the ordinal logit models.

Management practices

Waterhole closure

69% of the participants (Pol=0.15) felt that the waterhole density in the APNR, relative to that of the KNP, had increased over time (Figure 3), whilst 59% (Pol=0.39) agreed that 'Decreasing the number of APNR waterholes would limit elephant movements and their consequential impact to large trees' (Figure 3). The OLM for this Likert term retained the variable 'Age', whereby participants >50 years of age, in comparison to those who were <50 years, were significantly less likely to agree that waterhole closure would reduce elephant impact on large trees ($t_{(1)}$=-2.56, $p<0.05$, Table 2). Whilst not significant according to the OLM, the greatest support for the closure of waterholes to reduce elephant impact came from tourists (66.7%) and conservation management (63%), in comparison to stakeholders in tourism and hospitality (57.1%) and property owners (46.3%, Figure 4). There was also a high level of non-agreement (Pol=0.57) on whether participants believed that large-scale closure of waterholes would decrease tourism (Figure 3).

The most common themes (with examples of participant quotes) in the waterhole thematic analysis included:

1) Expanded elephant movements: - [*It would increase their* (elephants) *movements as they would be forced to move further to another* (water) *source.*]
2) Localised impact concerns - [*You would reduce excessive elephant activity* (impact across the whole system)*, but you may also then create greater impact in areas where waterholes are not closed* (high levels of localised impact).]

Tree protection methods

The implementation of tree protection methods to reduce elephant impact was supported by 77% of the participants (Pol=0.17), with 69% of participants believing that barrier-protection methods were effective at protecting trees (Pol=0.23) and 67% believing the same for biological methods (Pol=0.23, Figure 3). Only 16% of participants did not like seeing protection methods on trees in the APNR (Pol=0.28, Figure 3).

Our OLM focused on the Likert term 'Tree protection methods should be used to protect individual trees from elephant impact' retained the variables 'Age' and 'Shareholder group' in the reduced model (Table 2). Participants who were >50 years of age were significantly less likely to believe that tree protection methods should be implemented for tree protection in comparison to participants <50 years of age ($t_{(1)}$=-2.16, p<0.05, Table 2). Property owners ($t_{(3)}$=2.89, p<0.01) and tourists ($t_{(3)}$=2.88, p<0.01) were significantly more likely to be in favour of the implementation of tree protection methods in comparison to conservation managers (Table 2). Overall, tree protection methods received relatively high levels of support as an elephant management strategy (Figure 4).

The most common themes (with examples of participant quotes) in the tree protection thematic analysis included:

1) Small-scale effectiveness concerns - [*Appropriate in small properties with "artificially" high densities of elephants, but it is not feasible at a large landscape level.*]
2) Importance for iconic trees - [*Applicable with certain species such as baobab. This makes sense if they are rare or occur at low densities or are simply of high tourism value.*]
3) Limitations of success: - [*If an elephant really wants to get to the tree, it does not matter what you do, they will push it over.*]

Contraception

Contraception as a means of managing elephant impact on large trees was supported by 43% of the participants, with a high level of non-agreement (Pol=0.57, Figure 3). The OLM for the Likert term 'I think that the contraception of elephants is a viable management tool for lessoning elephant impact on large trees within the APNR' retained the variables 'Residency period' and 'Stakeholder group' (Table 2). Participants who classified themselves as having been stakeholders for ≥10 years (of which 75.6% of them were also ≥50 years of age) were significantly less likely to support contraception as a means of reducing elephant impact on large trees ($t_{(1)}$=-1.98, p<0.05), whilst tourists, in relation to conservation management, were significantly more likely to support the use of contraception ($t_{(3)}$=1.95, p<0.05, Table 2). Contraception also had the lowest number of participants supporting its effectiveness to protect large trees (Figure 4).

The most common themes (with examples of participant quotes) in the contraception thematic analysis included:

1) Concern over behavioural modifications to elephants - [*Too many negative/unknown biological consequences for elephant society and may just create other behavioural problems.*]
2) Scale of application requirements - [*It will be impossible to treat a sufficient proportion of* (elephant) *cows regularly to have any meaningful effect.*]

Culling

High non-agreement scores were calculated for both Likert terms related to culling elephants (Figure 3). Of the participants, 51% agreed the culling of elephants would decrease impact on large trees (Pol=0.57), whilst 50% also believed that culling would lead to a decrease in tourism (Pol= 0.53, Figure 3). The OLM showed that male participants were more likely than female participants to be in favour of culling as a strategy to reduce impact on large trees ($t_{(1)}=3.44$, $p<0.001$, Table 2). There was also a non-significant ($t_{(1)}=1.72$, $p=0.09$) but noteworthy trend that participants with a stakeholder residency of ≥ 10 years were more likely to be in favour of culling in comparison to newer stakeholders (Table 2). The greatest support for culling came from conservation managers (Figure 4), who were significantly more likely to support culling in comparison with tourists ($t_{(3)}=-2.31$, $p<0.05$, Table 2).

The most common themes (with examples of participant quotes) in the culling thematic analysis included:

1) Questioning the ethics of culling elephants - [*It would reduce impact; however, I do not believe culling is the answer. Other humane efforts should be implemented.*]
2) Reluctant agreement - [*Elephants are so intelligent that I hate the idea of this but if it helps the greater good of the species then yes.*]
3) Large-scale culling requirements – [*Agreed but provided that a sufficient number of elephants are removed and that their population is continuously maintained within predefined bounds.*]

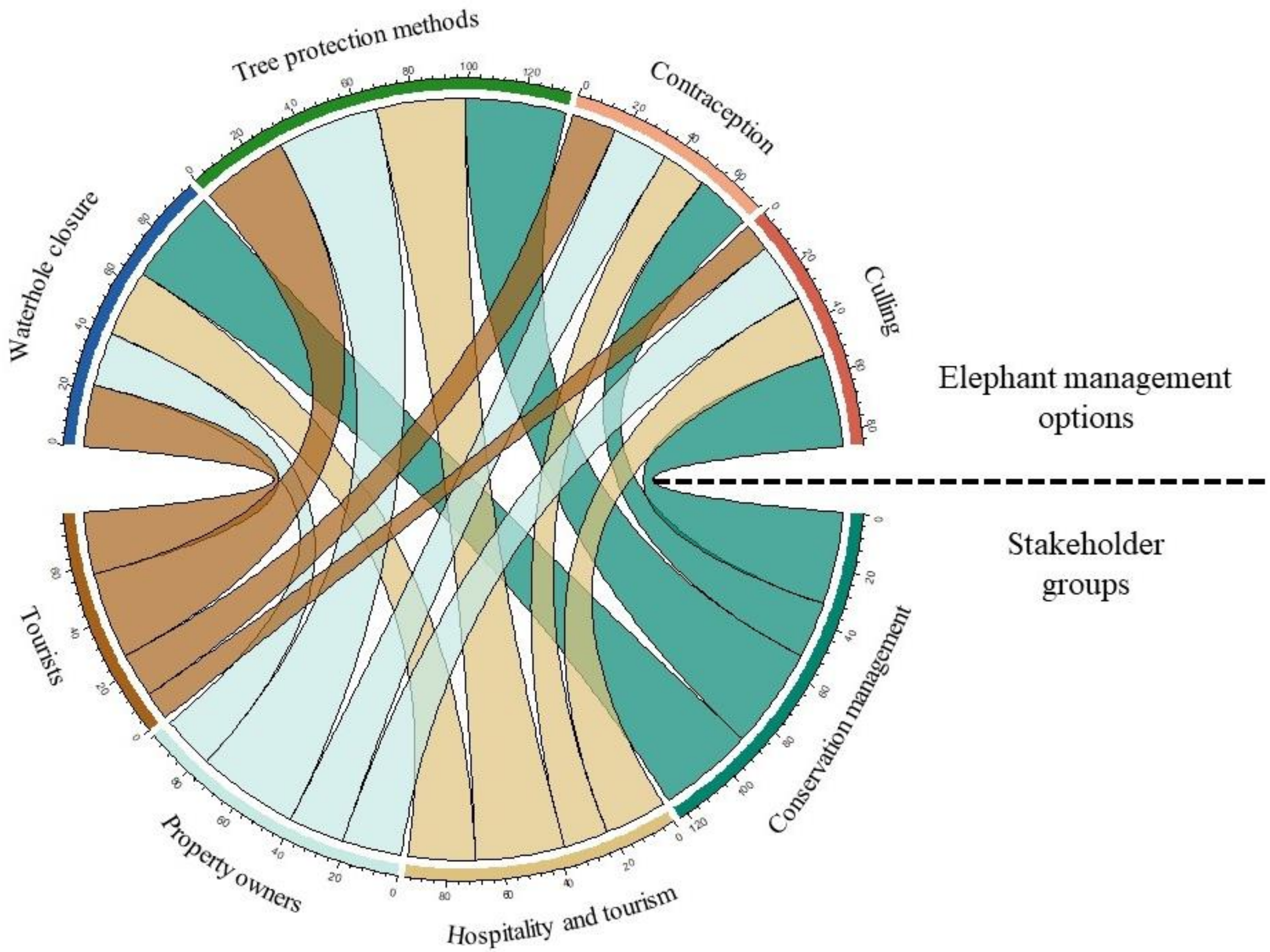

Figure 4. Chord diagram representing stakeholder agreement support for four potential elephant management methods in the Associated Private Nature Reserves (APNR), South Africa, based on responses by participants to Likert items suggesting the effectiveness of each method to reduce elephant impact on large trees. Larger arcs represent stronger levels of agreement support.

Table 2. Retained variables of the four ordinal logit models (OLMs) for stakeholder values on four potential elephant management strategies to reduce elephant impact on large trees in the Associated Private Nature Reserves (APNR), South Africa. The following baseline variables are used for comparison: Age: <50 years; Gender: Female; Residency period: <10 years; Stakeholder: Conservation management.

Elephant management method	Factors	Estimate	Standard error	t-value	p-value
Waterhole closure	Age: $\geq$50 years	-0.86	0.33	-2.56	*
	α_1	-1.66	0.32	-5.08	***
	α_2	-0.81	0.3	-2.65	**
Tree protection methods	Age: $\geq$50 years	-0.96	0.45	-2.16	*
	Stakeholder: Property owners	1.74	0.6	2.89	**
	Stakeholder: Tourism and hospitality	0.4	0.46	0.85	0.4
	Stakeholder: Tourists	2.33	0.81	2.88	**
	α_1	-2.19	0.39	-5.67	***
	α_2	-0.96	0.32	2.99	**
Contraception	Residency period: $\geq$10 years	-0.6	0.31	-1.98	*
	Stakeholder: Property owners	0.7	0.4	1.74	0.08
	Stakeholder: Tourism and hospitality	0.15	0.39	0.38	0.7
	Stakeholder: Tourists	0.82	0.42	1.95	*
	α_1	-0.54	0.3	-1.84	0.07
	α_2	0.44	0.3	1.5	0.13
Culling	Gender: Male	1.12	0.32	3.44	***
	Residency period: $\geq$10 years	0.57	0.33	1.72	0.09
	Stakeholder: Property owners	-0.34	0.42	-0.82	0.41
	Stakeholder: Tourism and hospitality	-0.27	0.42	-0.64	0.52
	Stakeholder: Tourists	-1.11	0.48	-2.31	*
	α_1	-0.47	0.35	-1.33	0.18
	α_2	0.41	0.35	1.15	0.25

p-values: * <0.05; ** <0.01, *** <0.001

α_i indicates the intercepts estimated to predict the different ordinal classes.

Discussion

Large tree and elephant population dynamics

Conservation managers are faced with striving to achieve sustainable and effective biodiversity goals whilst managing and balancing varied stakeholders' values and interests

(Manfredo *et al.* 2021). An effective understanding and integration of these values and interests are however required for the longevity of conserving protected areas (Mushove and Vogel 2005). Recognising and integrating scientific knowledge and stakeholder values has been identified as a key approach for elephant management (Cassidy and Salerno 2020).

In Section 1, we found high levels of agreement for value statements related to the ecologic- and economic- importance of both large trees and elephants, however, nonagreements existed over how stakeholders valued large trees pushed over by elephants and the impending effect on the landscape's aesthetics and ecologic-functioning. Edge *et al.* (2017) identified that stakeholders ranked unimpacted large trees as more aesthetically attractive versus impacted trees, emphasizing the importance of landscape aesthetics in stakeholders' perceptions. Duvall *et al.* (2018) has argued that the perception of a healthy African savanna, constituting an array of mixed grasses and large standing trees, has been shaped by social constructs, often through simplification and generalisations. In our survey though, respondents were more concerned about excessive numbers of pushed over trees and how this could affect other species.

Participant: "*I do not see them* (pushed over trees) *as a positive or negative aspect in terms of visual beauty. It is more linked to the potential damage to any wildlife that has nested in the tree.*"

Elephant impact on trees can thus evoke biospheric concerns, where stakeholders are concerned about the potential looming concerns about tree loss, going over and beyond general aesthetic concerns (Schultz 2000).

<u>Management practices</u>

Most APNR stakeholders (96%) agreed that elephant management strategies should be informed by scientific studies. However, different scientific studies have been used by stakeholders of contrasting value-systems to support contrasting elephant management strategies (Dickson and Adams 2009). This was observable from our results, where there was relatively high levels of agreement by stakeholders for tree protection methods and waterhole closures in comparison to higher levels of no agreement for contraception and culling.

Our study notably found that stakeholders' age and residency period in the APNR were significant predictors of which management strategies they were most likely to support.

Elephant culling was the only management strategy with a higher likelihood of support from participants with greater residency longevity as stakeholders in the APNR ($\geq$10 years residency, of which 75.6% of this group were $\geq$50 years of age). Culling has been practiced across multiple African countries containing elephants since the introduction of the 'elephant problem' (Glover 1963), which may explain why stakeholders of a longer residency period would have more trust in a well-known and established strategy that was generally accepted and conducted until the late 20th century (Whyte *et al.* 1998). Manfredo *et al.* (2009) propose that societal-intergeneration shifts of conservation values are promoted by dramatic paradigm shifts, but that individual-level change is more delayed by individual values formed early in life settings. Non-lethal strategies such as waterhole closures (Pienaar *et al.* 1997), contraception (Fayrer-Hosken *et al.* 2000) and tree protection (Derham *et al.* 2016) are i) more recently developed and implemented strategies, ii) more relatable with modern ethical concerns in conservation (Ramp and Bekoff 2015), and iii) would be more appealing to younger APNR stakeholders unaccustomed to culling.

Support of the four management strategies also varied across the stakeholder groups. Property owners, for example, were generally likely to agree that tree protection methods could be used to protect iconic trees from elephant impact, which may be explained by property owners having sentimental value for the individual trees surrounding their properties, thereby being more likely to actively protect them (Henley 2013). Tree protection methods are also suitable for protected areas with high densities of water, as elephant residency time around trees is increased (O'Connor *et al.* 2007). However, property owners and stakeholders involved in tourism and hospitality did not show high levels of support for waterhole closures. There may be underlying concerns that closing waterholes around their own properties and lodges could lead to a reduction in wildlife sightings. Artificially high densities of waterholes in the APNR in comparison to the neighbouring KNP are a concern though, as this leads to increased encounter rates between elephants and trees (O'Connor *et al.* 2007), and therefore high tree mortality rates (Cook *et al.* 2017). A relaxation of traversing rights that dictate where stakeholders may or may not travel in the APNR may positively influence the willingness of stakeholders to close waterholes, as they would still have access to regional waterholes, albeit at lower densities.

Contracepting elephant cows had the lowest levels of agreement amongst APNR stakeholders, with stakeholders in conservation management the least likely to agree with this strategy. Concerns raised were the high associated costs and impracticality of covering an area as large as the APNR, as well as potential behavioural changes to complex elephant societies. Recent studies have shown that blanket treatments are now available for larger elephant populations, reducing the financial costs (Bertschinger *et al.* 2018), and that no behavioural or spatial changes to contracepted elephants have currently been recorded (Delsink *et al.* 2013). Our results indicate that this knowledge is not yet widely known and may be influencing stakeholder perceptions on the logistics surrounding elephant contraception.

Lastly, culling elephants to protect large trees was most agreed upon by stakeholders in conservation management with conservations managers of reserves in particular showing 81% agreement versus 54.2% of biological scientists. Tourists though were significantly less likely to agree with culling. Whilst conservation management may be seeking a rapid solution to reduce elephant numbers with the hope of reducing elephant impact, international societal views are moving away from population reduction strategies towards more humane approaches. International tourism boycotts may be a concern for protected areas which invest in elephant culling (Sutton and Taylor 2019), and transparency will be imperative for any planned culling initiative as public scrutiny will be expected.

Furthermore, conservation managers will also need to consider the financial costs associated and the associated unintended consequences with each of the four management strategies, in combination with the stakeholder perceptions, to assess the overall practicality of each strategy.

Recommendations for balancing stakeholder values

Conservation managers in the APNR are faced with the challenge of serving stakeholder interests whilst striving towards long-term ecologic- and economic-sustainability. An adaptive management approach, whereby adjustments to management strategies based on scientific studies is required (GLTFCA 2022). Additionally, a participatory process should be implemented by conservation management whereby stakeholders are i) provided with scientifically-based educational material surrounding large tree and elephant population dynamics and management strategies, ii) are given the opportunity to give input into elephant management strategies, and iii) are provided with transparent feedback regarding the outcomes of these strategies (Sterling *et al.* 2017).

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Supplementary section for Chapter 2

Participatory information sheet S1

Good day,

My name is Robin Cook, a PhD-candidate at the University of the Witwatersrand, Johannesburg (Wits), and the Big Trees Projects Manager at Elephants Alive. I am conducting my PhD research on 'The Value of Large Trees and Their Protection where Elephants and Trees Co-exist', under the supervision of Prof. Ed Witkowski and Dr. Michelle Henley. My research is being conducted through the School of Animal, Plant and Environmental Sciences (Wits).

There are four components to this research:

1) examining what determines the value of a tree to a stakeholder within protected areas where they co-occur with elephants;
2) investigate the trends in mortality of three large tree species within the Greater Kruger National Park;
3) testing the effectiveness of mitigation methods for protecting large trees against elephant impact;
4) examining the impact that elephants have on large trees containing raptor and southern ground hornbill nests.

You are being invited to consider participating in this research to better understand what determines the value of a tree to a stakeholder within protected areas where they co-occur with elephants. This research aims to 1) identify which groupings of stakeholders share similar values pertaining to large trees in an environment containing elephants; 2) identify which values promote consensus amongst stakeholders; and 3) identify which values promote polarisation among stakeholders.

This will be conducted in the form of an online questionnaire, where value-statements will be presented to the Stakeholder/Participant, with various agreeable and disagreeable options. A further option for additional notes will be provided for each value-statement. This is to allow you to further explain your answer in detail if you so wish. There is no right or wrong answer. Answers should reflect your own values.

Statements will focus on how a tree's ecological, economic and cultural importance can affect a stakeholder's value of that tree. Aspects such as landscape beauty (the aesthetics of a landscape with many large trees standing, versus a landscape with many large trees pushed over) will be explored, as well as a tree's functional output (nesting sites, shade, browse for species). The questionnaire will also explore stakeholder values surrounding the co-existence of large trees and elephants in an environment, particularly focusing on the hierarchical value of elephants and trees, as well as management methods focused on preserving trees in an environment with elephants. All value-based statements are related to the Greater Kruger National Park (Greater KNP).

Note that participation in this research is voluntary and that participants may withdraw participation at any point. During the research activity, I will need to ask for some personal information about you, including age, gender, nationality, education background, and to which stakeholder group you belong. Whilst these various stakeholder demographic options will be asked at the start of the questionnaire, the Stakeholder/Participant will remain anonymous. The researcher will make every effort to protect the confidentiality of personal information, and the limits of confidentiality if applicable. This data will be stored in an internal, password-protected, online system, to which only the researcher and his two supervisors will have access.

This research study will be written up as a doctoral thesis and a scientific publication research report. The thesis will be available on the university library website. If you would like to read the thesis upon completion, I will be happy to send it to you.

If you decide to take part, your participation in this research study will last about 15 minutes. Completing and submitting the online questionnaire is taken to mean consent to participate. For any further queries, please contact Robin Cook at robincook@elephantsalive.org. If you have any concerns or complaints about the ethical procedures of this research study, you are welcome to contact the University Human Research Ethics Committee (Non-Medical), telephone +27(0) 11 717 1408, email hrecnon-medical@wits.ac.za

Yours sincerely,

Robin Cook

Table S2. Likert items for Section 1: Large tree and elephant ecological principles.

Theme	Number	Likert statement	Literature
Landscape and population principles	1	I think that functioning ecosystems should be a primary goal of conservation.	Gaylard and Ferreira 2011
	2	I think that conservation management should prioritise the protection of populations of animals over the well-being of individual animals.	Williams *et al.* 2002
	3	I think that too many people on the planet have resulted in elephants being confined to smaller spaces and thus having a heavier impact on the trees in their immediate environment.	Shaffer *et al.* 2019
Large tree importance and density	4	I think that large trees have important ecological properties and should be protected.	Manning *et al.* 2022
	5	I think that large trees add significant tourism value to the landscape.	Edge *et al.* 2017
	6	I am worried about the current densities of large trees in the Associated Private Nature Reserves.	Cook *et al.* 2023a
	7	I believe that pushed-over large trees decrease a landscape's beauty.	Edge *et al.* 2017
Elephant importance and density	8	I would classify elephants as sentient beings.	Wallach *et al.* 2020
	9	I think that elephants add significant tourism value to the landscape.	Edge *et al.* 2017
	10	I think that there exists a delicate balance between elephant numbers and large tree survival.	Morrison *et al.* 2016
	11	I think that there are too many elephants in the Associated Private Nature Reserves.	Moore 2015
Elephant impact on trees	12	I feel that I have a good understanding about the effects that elephants have on large trees.	Owen *et al.* 2006
	13	I am concerned when I see the current state of elephant impact on large trees.	Edge *et al.* 2017
	14	I think that there are positive effects on the environment when an elephant pushes over a large tree.	Kohi *et al.* 2011
	15	I think that pushed-over large trees increase the available habitat for certain reptiles and insects.	Pringle 2008
	16	I have negative feelings when I see an elephant push over a large tree.	Edge *et al.* 2017
	17	I believe that the action of elephants pushing down large trees are having negative effects on the environment.	Fritz *et al.* 2002
	18	I think that pushed-over large trees decrease nesting opportunities for birds breeding in trees in the Associated Private Nature Reserves.	Vogel *et al.* 2014

Table S3. Likert items for Section 2: Managing elephant impact on large trees.

Theme	Number	Likert statement	Literature
Spatial and temporal trends	1	I think that conservation decision-making around elephants and trees should be informed by scientific studies.	Owen *et al.* 2006
	2	I think that the trends in African elephant numbers across the continent should be considered for an Associated Private Nature Reserves elephant management plan.	Chase *et al.* 2016
	3	If a tree species is flourishing outside of the Associated Private Nature Reserves, this should be considered when deciding on a management plan for elephants and their impact on the tree species within the Associated Private Nature Reserves.	Helm and Witkowski 2012
	4	I think that the density of large trees in the Associated Private Nature Reserves has decreased overtime since I started visiting.	Cook *et al.* 2023a
	5	I think that it is acceptable for the Associated Private Nature Reserves to have areas of high elephant impact and areas of low elephant impact.	Abraham *et al.* 2021
	6	I think that botanical reserves (areas of varying sizes within a protected area where elephants are excluded to preserve vulnerable vegetation-types that have high conservation value and are at risk to elephant impacts) should be created within the Associated Private Nature Reserves.	Lombard *et al.* 2001
	7	I think that the recruitment rate (growth of smaller trees or seedlings into adult trees) is as important as the loss of large adult trees for tree survival.	Helm *et al.* 2011
Waterhole closure	8	I think that the density of waterholes in the private adjoining reserves to the west of Kruger National Park have increased over time, whilst those within the Kruger National Park have decreased.	Smit *et al.* 2020
	9	I think that a decrease in Associated Private Nature Reserves waterholes would limit elephant movements and their consequential impact to large trees in proximity to waterholes.	Purdon and van Aarde 2017
	10	I believe that a large-scale closure of waterholes would decrease tourism.	Van Wyk 2001
Controlling elephant numbers	11	I feel that the elephant density in the Associated Private Nature Reserves has increased since I started visiting.	GLTFCA 2022
	12	I think that the contraception of elephants is a viable management tool for lessoning elephant impact on large trees within the Associated Private Nature Reserves.	Delsink *et al.* 2023
	13	I believe that culling elephants will reduce elephant impact on large trees.	Whyte *et al.* 1998
	14	I believe that elephant lethal management will lead to a decrease in tourism in the Associated Private Nature Reserves.	Dickson and Adams 2009

Tree protection methods	15	I think that tree protection methods (such as wire-netting/rocks/beehives) should be used to protect individual trees from elephant impact.	Cook *et al.* 2023b
	16	I think that barrier-protection methods (rocks, wire-netting) are viable options for prolonging the survival rate of large trees.	Cook *et al.* 2023b
	17	I think that biological tree protection methods (beehives etc.) are viable options for prolonging the survival rate of large trees.	Cook *et al.* 2023b
	18	I do not like seeing protection methods on trees in the Associated Private Nature Reserves.	Cook *et al.* 2023b

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

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ABSTRACT

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

1. Introduction

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

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

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

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

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

2. Materials and methods

2.1. Study site

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

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

2.2. Site and tree selection

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

2.3. Field surveys and elephant impact assessments

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

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

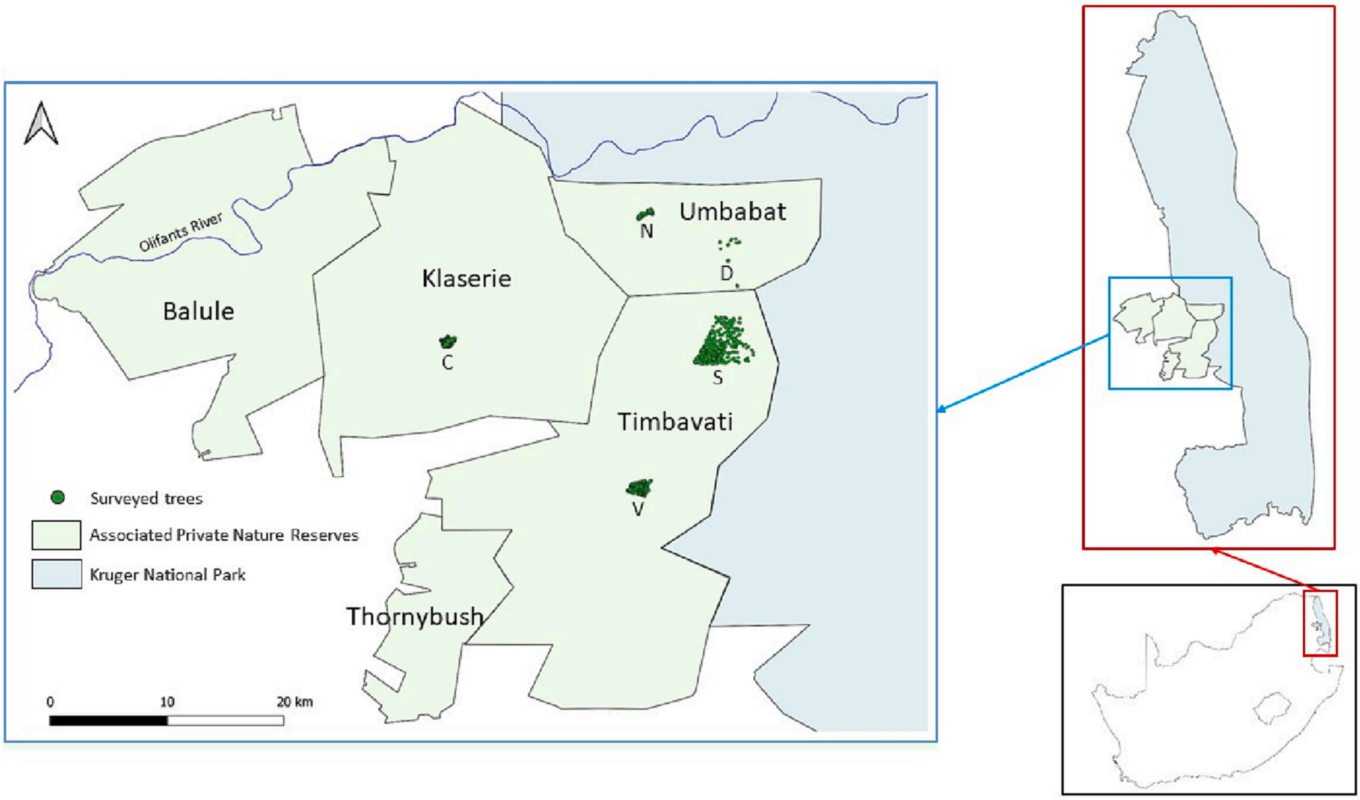

Fig. 1. Location of the surveyed tree species within the Associated Private Nature Reserves (APNR), South Africa from 2008 to 2020. Trees were located on the Charloscar (C), De Luca (D), N'tsiri (N), Sumatra (S) and Vlakgezicht (V) property study sites within three of the five private reserves.

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

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

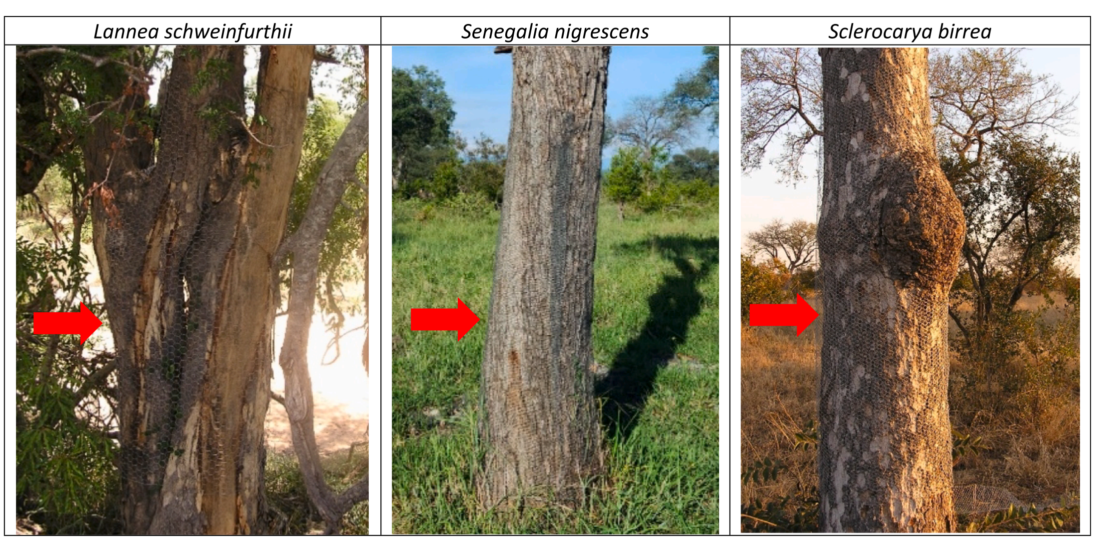

Fig. 2. Examples of wire-netted *Lannea schweinfurthii*, *Senegalia nigrescens* and *Sclerocarya birrea* trees in the Associated Private Nature Reserves (APNR). The wire-netting extends 1.8 m upwards, starting 0.5 m above the ground. Arrows indicate the placement of the wire-netting around the tree's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

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

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

2.4. Statistical analysis

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

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

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

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

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

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

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

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

3. Results

3.1. General elephant impact and mortality

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

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

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

3.2. Tree survival trends

3.2.1. Wire-netting

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

3.2.2. Tree species

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

3.2.3. External ecological co-variates

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

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

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

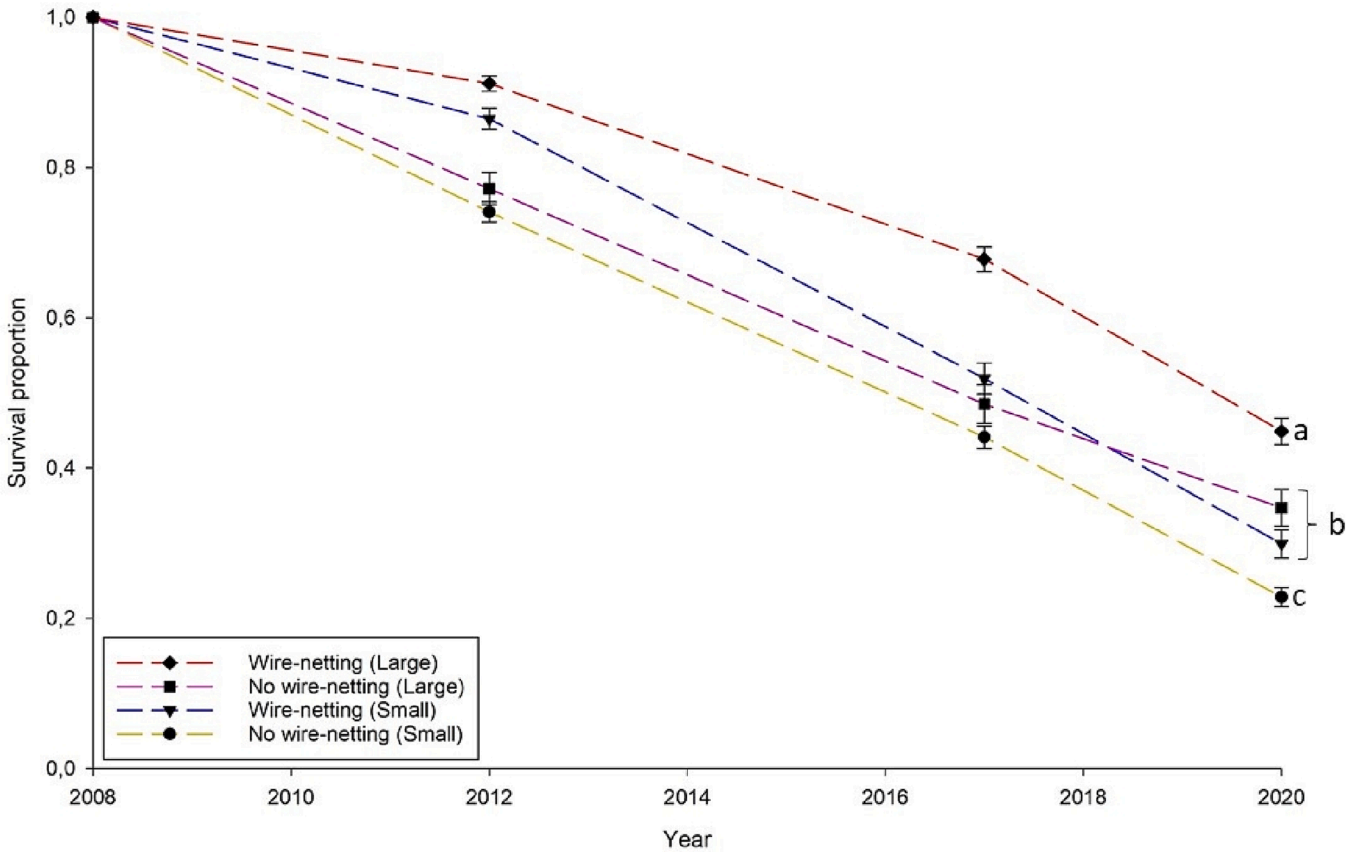

Fig. 3. Survival proportions of wire-netted and control (no wire-netting) trees of small (<40 cm) versus large (≥40 cm) stem diameters (diameter at breast height) over three time periods between 2008 and 2020 in the Associated Private Nature Reserves (APNR), South Africa. Different letters (a,b) indicate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

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

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

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

4. Discussion

4.1. Wire-netting as a mitigation method

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

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

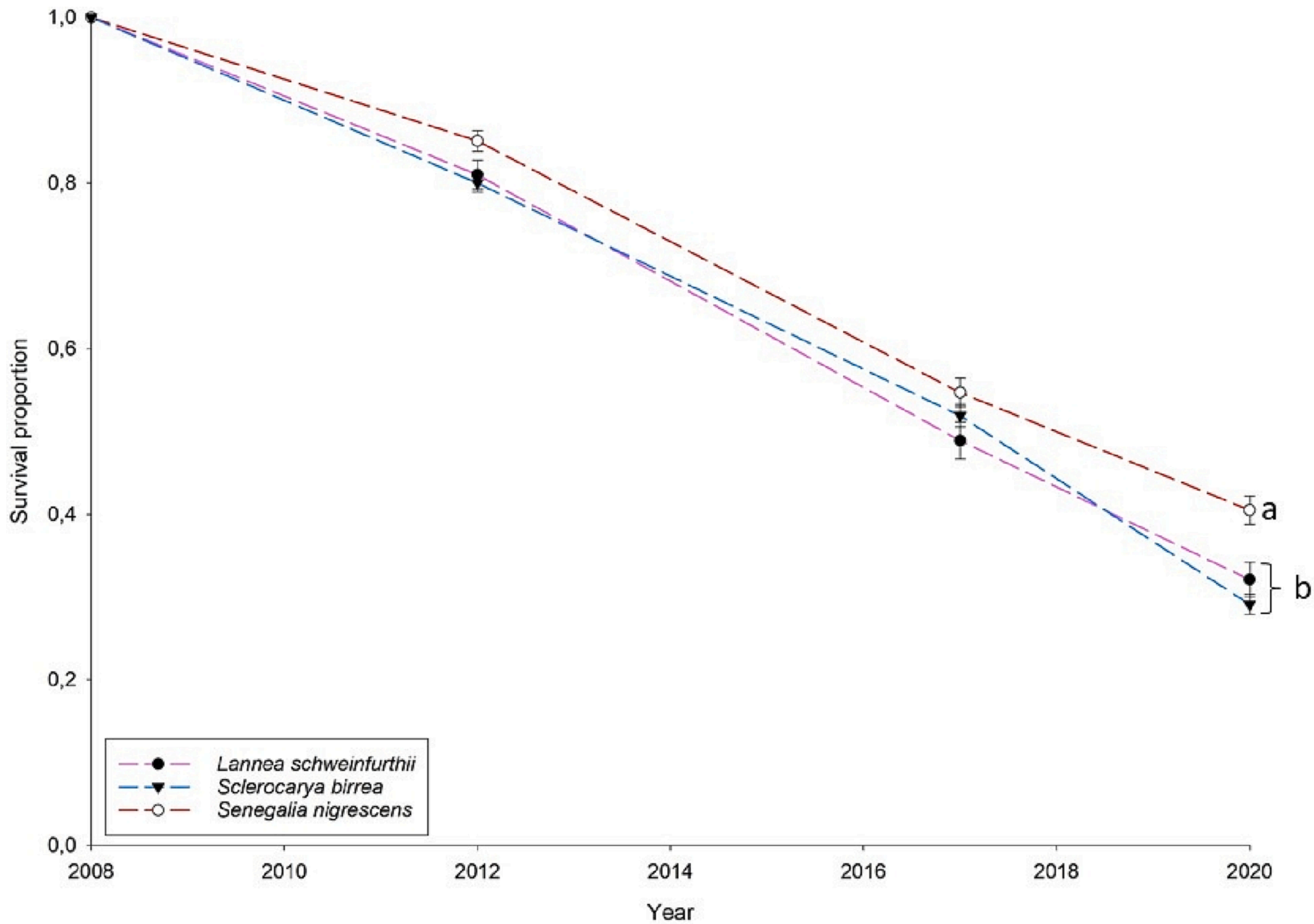

Fig. 4. Survival proportions of three tree species over three time periods between 2008 and 2020 in the Associated Private Nature Reserves (APNR), South Africa. Different letters (a,b) indicate a significant difference in survival proportions according to the Cox proportional hazards model.

required to maintain the wire-netting's effectiveness.

4.2. Tree species survival with environmental factors

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

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

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

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

4.3. Management implications and recommendations

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

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

5. Conclusion

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

CRediT authorship contribution statement

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

Declaration of Competing Interest

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

Data availability

The authors do not have permission to share data.

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CHAPTER 4:

Impacts of African elephants on trees nested in by critically endangered white-backed vultures

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Abstract

The continual decline in the number of white-backed vultures (*Gyps africanus*) on both a continental scale across Africa, as well as regionally within South Africa, means that understanding how factors affect individual vulture survival is critical. There has been an emphasis from conservation bodies to understand the habitat and nesting requirements of white-backed vultures (WbVs) in protected areas, particularly where African elephants (*Loxodonta africana*) can impact trees containing WbV nests. The aim of our study was to assess the impact that elephants have on large trees containing WbV nests in a South African savanna system through three separate but interlinked assessments. We first assessed the variety of tree species utilised by WbVs as nesting sites and compared the size morphometrics and elephant impact scores of these trees in the riparian and woodland habitats. We then assessed how the presence and absence of elephants affects the size morphometrics of the most abundantly utilised tree species, *Senegalia nigrescens*, by also assessing WbV nests on trees in a neighbouring protected area with no elephants. Lastly, we modelled how a variety of environmental factors have influenced the persistence rate of WbV nests and the trees in which they nest using long-term data from 2008-2020. We found that WbVs utilised 10 tree species and a range of tree heights (7.4-22.8 m) in both riparian and woodland habitats, with woodland trees receiving higher overall elephant impact scores. Our results show that the large trees nested in by WbVs were most at risk of bark-stripping by elephants but were mostly too large to be toppled or stem snapped. We suggest that elephants may be having a trimming effect on the availability of tree heights available to WbVs but that strong gusts of wind have been a strong negative contributor to WbV nest persistence and that only a relatively small number of trees died during the 12-year study in comparison to fallen nests. We highlight that the risk of WbV nesting sites to elephant impact depends on the species of tree utilized, as well as the size of the tree.

Keywords: *Gyps africanus*; increasing elephant numbers; *Senegalia nigrescens*, strong winds; tree mortality; vulture nests

Introduction

White-backed vultures (*Gyps africanus*) provide critical ecosystem services to savanna systems as a scavenging species (Ogada *et al.* 2012), and are important regional avian biomonitors and an umbrella species for African vultures (Thompson *et al.* 2021). There has, however, been significant declines in white-backed vulture (WbV) numbers, both continentally (Ogada *et al.* 2016) and regionally within South Africa (Birdlife International 2021). WbVs are now listed as 'Critically Endangered' globally (Birdlife International 2021). Poisoning events have largely contributed to the decline of adult WbVs (Ogada *et al.* 2016, Peters *et al.* 2023), whilst collisions with pylons and wind turbines, pylon electrocutions, as well as the acquisition and trade of vulture body parts within traditional medicines have further exacerbated WbV mortality (Jenkins *et al.* 2010, Rushworth and Krüger 2014, Mashele *et al.* 2021).

As a long-lived species, adult survival is essential for population endurance (Monadjem *et al.* 2013). However, habitat loss, and thus a loss from human alterations has increased the pressure on protected areas (PAs) to preserve WbV nesting sites (Rushworth *et al.* 2018). Currently, >50% of the distribution range of WbVs overlaps with PAs in southern Africa (Kane *et al.* 2022), where, as a tree-nesting vulture species, WbVs are reliant on tall trees (>7 m; Johnson and Murn 2023). Tall trees may provide WbVs with either social foraging cues (Kendall *et al.* 2012), or an escape from nest predators (Kemp and Kemp, 1975).

In South Africa's savanna system, high densities of nests occur on top of tall trees within the riparian habitat along major river systems (Virani *et al.* 2010, Kendall *et al.* 2018), whilst lower densities of nests are found in the woodland habitat away from river systems, usually on top of *Senegalia nigrescens* trees (Vogel *et al.* 2014). Riparian tree species are generally very large in comparison to woodland trees due to increased levels of soil moisture and nutrients (Scholes and Archer 1997). However, concerns exist in South Africa regarding the decline of large trees due to African elephant (*Loxodonta africana*) feeding habits (Asner *et al.* 2016, Cook *et al.* 2023) and the implications to WbV populations inside of PAs through tree loss (Monadjem and Garcelon 2005, Rushworth *et al.* 2018).

Elephants, as ecosystem engineers (Owen-Smith 1988) can alter the structural landscape of savannas through the trimming and removal of the large tree component (Guldemond *et al.* 2017), thereby promoting landscape openness (Gordon *et al.* 2023). However, in small fenced-off PAs, or PAs with high waterhole densities, impact on large trees may be exacerbated due to increased probability of encounters between elephants and large trees (O'Connor *et al.* 2007). Reduced availability of suitable nesting trees for WbVs may have negative consequences for the breeding success and sustainability of WbV populations (Rushworth *et al.* 2018).

Very few studies have specifically focused on the impact that elephants have on the trees in which WbVs nest, with varying results. Monadjem and Garcelon (2005) found that WbV were not nesting in PAs in Eswatini that contained elephants. However, in Kenya's Maasai Mara National Park with an elephant density of 1.65 elephants per km^2, Kendall *et al.* (2018) modelled that suitable tree numbers for WbV nests far outnumbered the number of WbV nesting pairs in the region. Furthermore, in South Africa's Associated Private Nature Reserves (APNR), elephant impact on *S. nigrescens* containing WbV nests did not affect nest persistence over a five-year monitoring period but did facilitate the long-term decline of the trees' structural integrity to support nests (Vogel *et al.* 2014).

Given that WbVs nest in a variety of tree species in both woodland and riparian habitats (Virani *et al.* 2010), and that elephant impact varies across tree species (Abraham *et al.* 2021), it is important to assess the vulnerability of the trees in which WbVs nest versus elephant impact across a multitude of tree species. Furthermore, as previous studies have highlighted the importance of *S. nigrescens* as a significant nesting tree for WbVs in southern Africa's savannas (Monadjem and Garcelon 2005, Vogel *et al.* 2014), additional studies are required to understand the ecological relationships between elephants and WbV nests on *S. nigrescens* trees.

Therefore, our study aimed to assess elephant impact on trees containing WbV nests in the South African savanna system through three separate but interlinked assessments. Our objectives were to 1) measure the dimensions of nesting trees selected for by WbVs, as well as the elephant impact scores on these trees (termed: *multispecies assessment*), 2) assess the influence that the presence and absence of elephants have on the morphometrics of *S. nigrescens* trees containing WbV nests (termed: *elephant effect*), and 3) investigate the long-term (2008-2020) changes of *S. nigrescens* containing WbV nests that co-occur with elephants (termed: *persistence trends*).

Materials and methods

<u>Study area</u>

The study was conducted in the Associated Private Nature Reserves (APNR) (24˚04'-24˚55' S; 30˚82'-31˚48' E) and the neighbouring Air Force Base Hoedspruit (AFB) (24˚19'-24˚23' S; 31˚01'-31˚03' E) in the north-eastern region of South Africa (Figure 1). The APNR (size: 2,089 km^2) is a protected area, sharing an open boundary to the Kruger National Park, and includes the private nature reserves of Balule-, Klaserie-, Thornybush-, Timbavati- and Umbabat Private Nature Reserves (Figure 1). The AFB (size: 25 km^2) shares a closed elephant-proof boundary along the south-western border of the Klaserie Private Nature Reserve (PNR, Figure 1), and hence has no elephants. The region's mean annual rainfall range is between 400 mm-600 mm, with an average maximum temperature of 22 ^{o}C (Peel *et al.* 2007). Both the APNR and AFB are located within the Granite Lowveld (SVl 3) vegetation unit of South Africa, whilst the APNR also extends into the Phalaborwa-Mopaneveld (SVmp 7) vegetation unit (Mucina and Rutherford 2006). The APNR and AFB fall within the Olifants River catchment, whilst the APNR is dissected by prominent non-perennial tributaries such as the Klaserie and Timbavati rivers (Marr *et al.* 2017). Many artificial waterholes exist in the APNR, meaning that water here is permanently available to elephants (Parker and Witkowski 1999, Henley 2014).

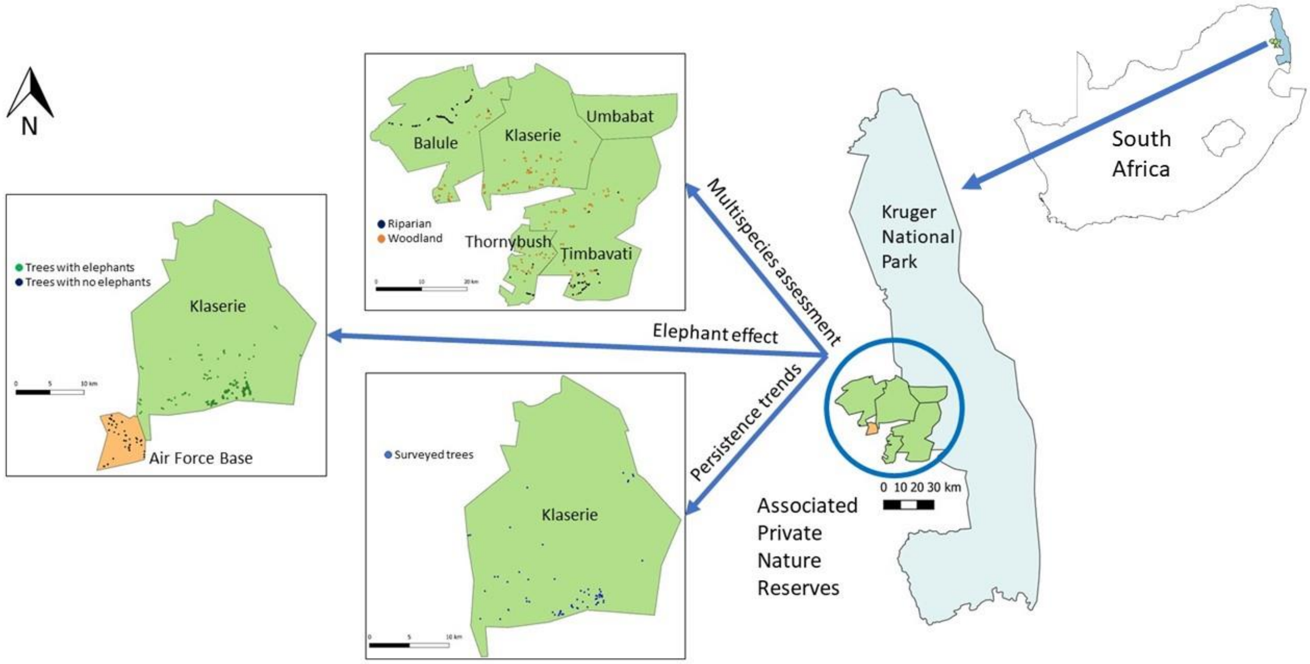

Figure 1. Location of the surveyed trees for each study objective in the Associated Private Natures Reserves (APNR) and Hoedspruit Air Force Base (AFB), bordering South Africa's Kruger National Park.

There are an estimated 220 breeding pairs of WbVs in the APNR (extracted from the APNR Annual Census Reports), with an additional 40-50 breeding pairs in AFB (L. Thompson, personal communication). The APNR's elephant population ranges between 2,000 and 3,000 individuals (Peel 2015), forming part of a metapopulation of over 30,000 individuals in the Great Limpopo Transfrontier Conservation Area (GLTFCA 2022).

Objective 1 (*multispecies assessment*) occurred across the entire APNR where a greater diversity of trees used by WbVs occurred than within any one reserve forming part of the collective whole; Objective 2 (*elephant effect*) occurred inside the Klaserie PNR and the AFB where comparisons in the presence and absence of elephants could be made for the longest period; and Objective 3 (*persistence trends*) occurred inside the Klaserie PNR as the monitoring in this protected area occurred for longer than any of the reserves within the APNR (Figure 1).

Field methods

Objective 1: multispecies assessment

Surveys were conducted across the APNR to investigate both the morphometric traits and elephant impact scores on tree species utilised by WbVs for nesting purposes (Figure 1). Individuals of all tree species that had contained active WbV nests in either 2019 or 2020 (n=266) were assessed across the Balule-, Klaserie-, Thornybush-, and Timbavati PNRs in October of the respective years, which is the end of the egg-laying period (Taylor *et al.* 2015; Figure 1). The locations of these trees were obtained and ground-truthed from the previous years' aerial surveys by APNR management, as well as through the historical database of the NGO *Elephants Alive*.

At each tree the following methodology was conducted: tree location was marked using a global positioning system (GPS) and tree species was identified; the tree's stem diameter at breast height (DBH, 1.3 m aboveground) (cm) was measured, whilst tree height (m) was measured using the *VolCalc* software (Barrett and Brown 2012). For large riparian trees with multi-stem diameters (example: *Ficus sycomorus* subsp. *sycomorus*), the diameter of the stem containing the nest was measured. Elephant impact on each tree was measured using published impact scoring practices (Table 1, (Walker 1976 (adapted), Helm and Witkowski 2013). An ethics waiver approval for this research was granted by the University of the Witwatersrand, Johannesburg (Waiver 18-01-2021-O).

Table 1. Scoring system for elephant impact on large trees (Walker 1976 (adapted), Helm and Witkowski 2013).

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

Objective 2: elephant effect

Surveys were conducted in the Klaserie PNR and the AFB to investigate the impact that elephants have on *S. nigrescens* trees, both with and without WbV nests (Figure 1). In October 2020, we surveyed 63 *S. nigrescens* in Klaserie PNR that had contained an active WbV nest in either the 2019 or 2020 surveys. Each tree had its morphometric measurements recorded (described in objective 1), and elephant impact scores were recorded (Table 1). These trees were termed 'Vulture trees (with elephants)'. We conducted the same assessments on the closest 1-4 *S. nigrescens* individuals within a radius of 100 m from the vulture nest tree, where one tree per cardinal direction point from the nest was measured where possible. The number of selected trees without vulture nests were limited by the number of available trees within the 100 m radius. As WbVs have previously been recorded nesting in trees >7 m in height (Johnson and Murn 2023), we selected trees ≥4 m in height as the lower limit for surveyed trees to eliminate saplings from the study (Watson *et al.* 2020). A total of 148 of these trees were recorded and were termed 'Control trees (with elephants)'.

In November 2022, permission was granted by the AFB to conduct morphometric assessments on the WbV nests within the base. Forty *S. nigrescens* with WbV nests were located and had their heights and DBHs measured (Figure 1) and were termed 'Vulture trees (no elephants)'. Using the same approach for surveying control trees in Klaserie PNR, we measured the morphometrics of 120 surrounding *S. nigrescens*, termed 'Control trees (no elephants)'.

Objective 3: persistence trends

To investigate how environmental co-variates have affected the persistence trends of WbV nests and the trees containing them, we selected 67 *S. nigrescens* trees that contained WbV nests in the Klaserie PNR in 2008 and conducted annual surveys on these trees and nests from 2008-2020 (Figure 1). Each tree had a single WbV nest in 2008. The surveys took place between August and October each year, with the following information recorded: tree height (m), DBH (cm), as well as elephant impact score (Table 1) and fire scar presence on the tree trunk. As tree persistence can also be negatively affected by the presence of termites (*Coptotermes* species) (Gould 1993) and shelf-bracket fungus (Hood 2006) within the tree, and positively affected by the presence of ants (*Crematogaster* species) as protection agents against herbivory (Palmer and Brody 2013), these agents' presences were recorded. Previous research has found that elephants tend to impact trees which are closer to surface water (Van Langevelde *et al.* 2017) and roads (Khosa *et al.* 2023). Therefore, we used the 'Nearest Euclidean Distance to Feature' analysis on ArcGIS to record each tree's distance to these surface layers. Lasty, after the surveys revealed a trend of nests falling after major windstorms, we recorded the maximum gust speed (km/h) for study site each year (South African Weather Service, unpublished data). The persistence of a nest was based on the structural intactness of the nest. A dilapidated nest consisted of the nest either missing from the tree, or signs of substantial nesting materials on the ground with only scattered remnants remaining within the tree's branches.

Data analyses

Statistical analyses were performed in R version 4.3.0 (R Development Core Team, 2012) and were considered significant at $p<0.05$. For the *multispecies assessment*: trees were grouped into 'Riparian' and 'Woodland' habitat categories, based on the vegetation zones into which they were recorded (Bamford *et al.* 2009, Table 1). As the data did not have a normal distribution, non-parametric tests were performed (Shapiro–Wilk test: $p<0.05$). The height, DBH and elephant impact score measurements were then pooled within the Riparian and Woodland groupings. Mann-Whitney U-tests were then used to test for significant differences between the height, DBH, and elephant impact scores between Riparian and Woodland trees.

For the *elephant effect*, we performed Kruskal-Wallis one-way analysis of variance tests, with Dunn's multiple comparison post-hoc test, to compare the differences in tree height and DBH of the four categories of both the control and vulture *S. nigrescens* trees that were surveyed with and without the presence of elephants. To calculate the variability of tree heights and DBH sizes used by vultures with and without the presence of elephants, we calculated the coefficient of variation of each of these four forementioned categories. A Mann-Whitney U-test was used to compare elephant impact scores between the Vulture trees (with elephants) and the Control trees (with elephants).

For the *persistence trends*: A Kaplan-Meier survival analysis (*survival* package, Allignol and Latouche 2022) was used to test for significant differences between the persistence proportions of WbV nests and the *S. nigrescens* trees they were found on from 2008-2020. The death of a tree and/or collapse of a nest was considered truncated (1), whilst tree and nest persistence were considered censored (0) for our analyses. Where significant differences occurred, the Holm-Sidak post-hoc method was applied (Holm 1979). Annual mortality rates of trees and nests were calculated as: mortality = $1-(1-\text{mortality}_i)^{1/\text{years}}$, where mortality_i refers to the overall mortality during the specified period of study, and years referred to the number of years since the study had commenced (Swemmer *et al.* 2023).

We then performed Cox proportional-hazard models (Cox model, *coxme* package, Therneau and Therneau 2015) independently on the trees and the nests to analyse how various co-variates have affected their persistence between 2008 and 2020. These multivariable models enable a group of co-variates to be used to measure time-to-event outcomes (Fisher and Lin 1999), and include i) a hazard (risk) function, ii) a time component, and iii) an event component (Kleinbaum and Klein 2012). The death of a tree or collapse of a nest were considered truncated (1) events, whilst nest and tree persistence were considered censored (0). As this test only focused on the persistence of the original nests, any nests that were rebuilt in subsequent years were not included in the Cox models. Both tree height and DBH were used as co-variates in the Cox models due to the low correlation score between them (Pearson's correlation: r=0.51). In addition, the following co-variates were used for both the tree and nest Cox models: distance to road (continuous), distance to water (continuous), fire scar presence (categorical), termite presence (categorical), shelf-bracket fungi presence (categorical), ant presence (categorical), previous elephant impact score (categorical), and maximum wind gust speed (continuous).

Stepwise backward selection was used to obtain the models' final versions, where we systematically eliminated the highest p-value from the model before repeating the modelling procedure. Final models were then confirmed through a forward selection process, which involved obtaining p-values through likelihood ratio tests of the full model with the selected co-variate versus the model without that co-variate, giving consistent regression parameter estimates (West *et al.* 2007).

Welch's t-tests were used to compare differences between the DBHs of living and dead trees, as well as differences of tree heights between trees with persisting nests and trees with fallen nests.

Results

Multispecies assessment

We recorded 266 WbV nests across 10 tree species in the APNR in 2019 and 2020 (Table 2). *S. nigrescens* was the most prolific species (n=148), followed by *Diospyros mespiliformis* (n=38). Six of the 10 tree species were classified as Riparian trees (n=102), whilst four species were Woodland trees (n=164) (Table 2).

Trees containing WbV nests had a height range of 7.4-22.8 m, with Riparian trees significantly taller (mean ±standard deviation: 15.25 ±3.4 m) than Woodland trees (11.96 ±1.53 m) ($U=2829.5$, $p<0.001$, Figure 2a). DBH sizes ranged from 32-204 cm, with the mean DBH of the Riparian trees (98.3 ±34.6 cm) significantly wider than those of the Woodland trees (61.2 ±13.9 cm) ($U=2172$, $p<0.001$, Figure 2b).

No elephant impact was found on 75 of the 266 surveyed trees (28.2%), including all the *Philenoptera violacea* and *Combretum imberbe* trees. Of the 191 trees (71.8%) with elephant impact, bark-stripping was the most common impact type (80.9%), followed by primary branch breakage (17.7%) and uprooting (1.4%). Of the bark-stripped trees, 55.6% had a bark-stripping score of >50%, and one individual tree (*S. nigrescens*) had died from bark-stripping. Elephant impact scores were significantly higher on the Woodland trees in comparison to the Riparian trees ($U=4861$, $p<0.001$, Figure 2c). Highest impact scores were recorded on *S. nigrescens,* and lowest impact scores recorded on *C. imberbe* and *P. violacea* (Table 2).

Table 2. Tree species recorded containing white-backed vultures (*Gyps africanus*) in the Associated Private Nature Reserves (APNR), South Africa, during the 2019 and 2020 surveys. Tree height, diameter at breast height, and elephant impact scores (mean ±standard deviation) are presented for each tree species.

Tree species	Number of trees with nests	Tree height	Stem diameter at breast height	Elephant impact score	Habitat category
Diospyros mespiliformis	38	15.9 ±3.1 m	101.1 ±35.8 cm	0.2 ±0.6	Riparian
Faidherbia albida	3	16.2 ±1.5 m	81.7 ±4.8 cm	1	
Ficus sycomorus subsp. *sycomorus*	24	17.3 ±2.8 m	121.4 ±35.9 cm	1.4 ±0.7	
Philenoptera violacea	7	12.1 ±1.8 m	64.6 ±12.6 cm	0	
Phyllogeiton discolor	4	16.9 ±2.2 m	93.4 ±24 cm	1 ±0.8	
Xanthocercis zambesiaca	2	18.9 ±3.8 m	117 ±3.1 cm	2 ±1.4	
Balanites maughamii	6	11.7 ±1.9 m	61 ±14.5 cm	0.8 ±0.4	Woodland
Combretum imberbe	2	11.8 ±1.3 m	62 ±21.2 cm	0	
Sclerocarya birrea subsp. *caffra*	8	12.8 ±1.7 m	77.9 ±18.1 cm	0.4 ±0.7	
Senegalia nigrescens	148	11.9 ±1.5 m	60.3 ±13.1 cm	1.9 ±1.4	

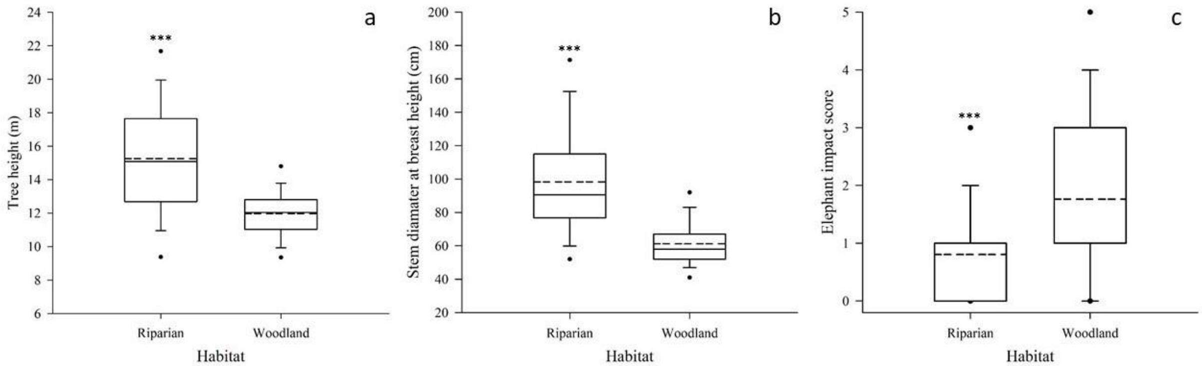

Figure 2. Comparison of a) tree height, b) stem diameter at breast height, and c) elephant impact scores of Riparian and Woodland trees containing white-backed vultures (*Gyps africanus*) nests in the Associated Private Nature Reserves (APNR), South Africa. Box plots are presented with the median (solid) and mean (dashed lines) values, as well as the 5th and 95th percentiles (black dots). Median lines for both Riparian and Woodland trees in Figure 2c =1. *** p<0.001

Elephant effect

WbV selected for larger *S. nigrescens* trees (height (Q=4.13, p<0.001) and DBH (Q=6.47, p<0.001)), in both Klaserie PNR and AFB, according to Dunn's multiple comparison tests (Figures 3a and b). In Klaserie PNR, the mean height of the vulture trees was 12 ±1.9 m, whilst the control trees' mean height was 11 ±1.4 m (Figure 3a). In AFB, the mean height of the vulture trees was 12.2 ±1.9 m in comparison to the control trees of 10.9 ±1.9 m (Figure 3a). The heights of the vulture trees in Klaserie PNR and AFB were not statistically different (Q=2.41, p=0.96, Figure 3a), however the coefficient of variation was lower for the trees with elephants (11.7%) versus trees without elephants (15.6%). A similar trend was observed for the control trees, where the trees with elephants had a smaller coefficient of variation (13.0%) in comparison to trees without elephants (17.1%).

WbV selected trees of similar DBH sizes (Q=2.42, p=0.94) in both Klaserie PNR (58.6 ±6 cm) and AFB (57.6 ±10.8 cm, Figure 3b). The coefficients of variation for DBH were similar for the vulture trees in Klaserie PNR (18.8%) and AFB (20%).

WbV nests occurred on trees with significantly less elephant impact in comparison to control trees in Klaserie PNR (U=3431, p<0.001, Figure 4). Of the vulture trees, 10.8% had not been impacted by elephants, whilst 12.3% had elephant impact scores of 4 or 5, signifying high levels of impact. Comparatively, every control tree had some form of elephant impact, whilst a large proportion (45.8%) of them had elephant impact scores of 4 or 5.

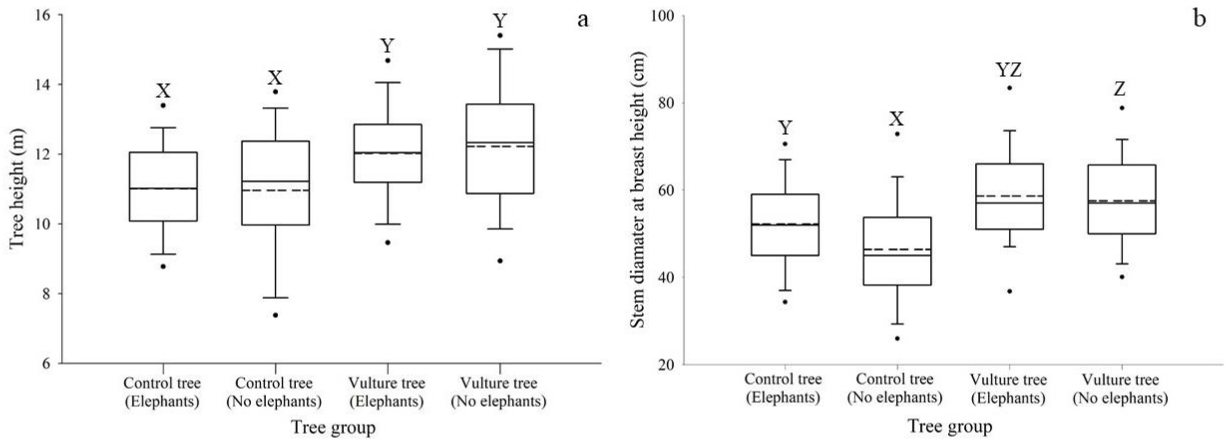

Figure 3. Comparison of *Senegalia nigrescens* a) height and b) stem diameter at breast height measurements for trees with and without white-backed vulture (*Gyps africanus*) nests in Klaserie Private Nature Reserve (with elephants) and the neighbouring Air Force Base Hoedspruit (no elephants), South Africa. Box plots are presented with the median (solid) and mean (dashed lines) values, as well as the 5th and 95th percentiles (black dots). Different letters indicate significant differences at $p<0.05$.

Persistence trends

Nest persistence was significantly lower in comparison to tree persistence (Log-rank test=52.13, d.f.=1, $p<0.001$, Figure 5). After 12 years, 51 of the 67 *S. nigrescens* trees (73.1%) that had originally held active WbV nests were still alive (Figure 5), in comparison to only 10 of the original 67 WbV nests (13.9%) recorded in those trees (Figure 5). Mean nest persistence was 4.1 ±2.2 years, whilst 15.9% of the 57 dilapidated nests were rebuilt by WbVs, at a median time of two years after the collapse of the nest, irrespective of the cause. Nest persistence declined annually at 15.2% in comparison to the trees at 2.5%. Substantial nest declines occurred within the 2010-11 and 2012-14 surveys, whilst tree numbers declined at a steady, albeit slower rate than nests between the 2010-14 surveys (Figure 5). Maximum wind gust speed ranged from 65.6-101.5 km/h across the study period. The average maximum gust speed during the large nest declines between 2012 and 2015 was 80.4 km/h, consistently higher than the median maximum gust wind speed for fallen nests (72 km/h). Of the dead trees, 78.6% died from bark-stripping, whilst uprooting constituted 14.3% of the deaths and main stem snapping 7.1%. For the period of 2016-19, no vulture tree within this survey died (Figure 5).

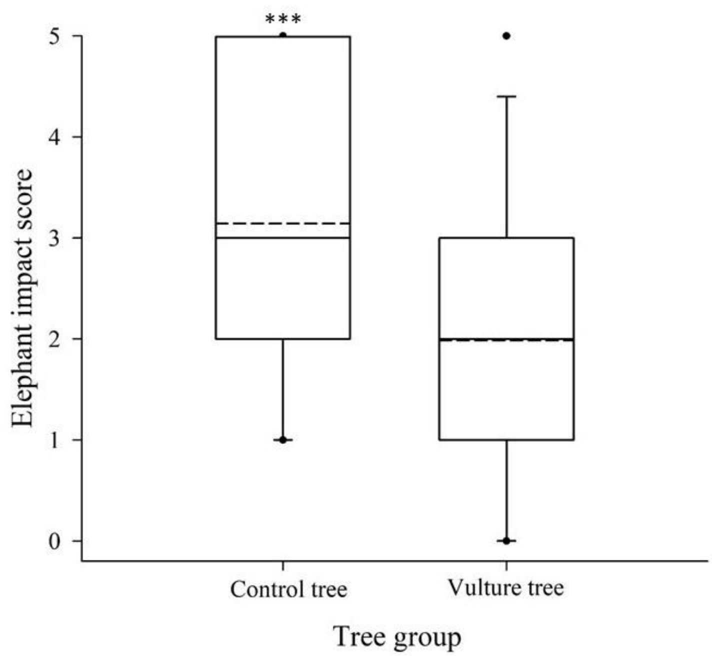

Figure 4. Comparison of elephant impact scores on *Senegalia nigrescens* trees with and without white-backed vulture (*Gyps africanus*) nests in Klaserie Private Nature Reserve, South Africa. Box plots are presented with the median (solid) and mean (dashed lines) values, as well as the 5th and 95th percentiles (black dots). *** p<0.001

According to the reduced tree persistence Cox model, DBH and maximum gust speed were the only co-variates which significantly influenced tree persistence, where an increase in DBH resulted in greater tree persistence, whilst increased wind gust speeds decreased tree persistence across the 12-year period (Table 3). The mean DBH of the dead trees during this study was 48.7

±11 cm, which was significantly smaller than the mean DBH of the surviving trees (62.3 ±11 cm) (t =4.5, p<0.001).

Nest persistence, according to the reduced Cox model, improved with an increase in tree height (Table 3), where mean tree height of the fallen nests (12.4 ±1.6 m) was significantly smaller than trees with persisting nests (14.1 ±1 m) (t =4.4, p<0.001). Nests were, however, vulnerable to high gusts of wind (Table 3).

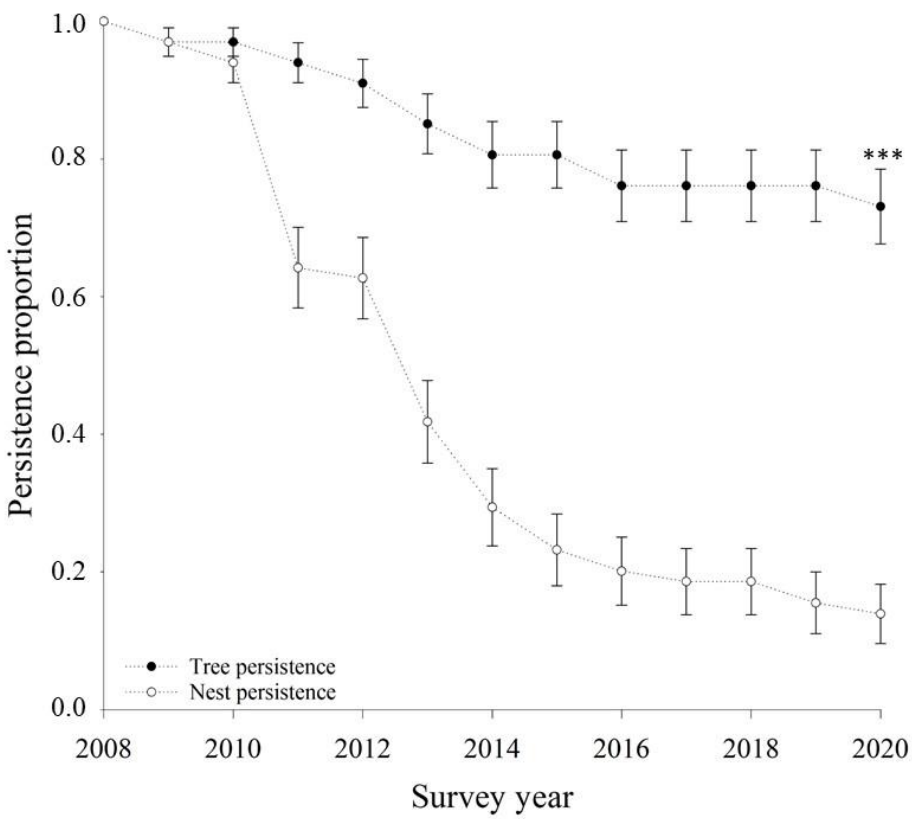

Figure 5. Comparison of the persistence proportions of *Senegalia nigrescens* and white-backed vulture (*Gyps africanus*) nests between 2008 and 2020 in Klaserie Private Nature Reserve, South Africa.
*** p<0.001

Table 3. The reduced Cox proportional-hazards models (with coefficients, hazard ratios, standard errors, and z- and p-values) with the significant co-variates affecting the persistence of *Senegalia nigrescens* trees and white-backed vulture (*Gyps africanus*) nests between 2008 and 2020 in Klaserie Private Nature Reserve, South Africa.

	Variable	Coefficient	Exp (Coefficient/ Hazard ratio)	Standard error	z-value	p-value
Tree persistence	Diameter at breast height (DBH) (cm)	-0.09	0.92	0.03	-3.37	$p < 0.001$
	Maximum wind gust speed (km/h)	0.09	1.09	0.03	3	$p < 0.01$
Nest persistence	Tree height (m)	-0.35	0.7	0.09	-3.72	$p < 0.001$
	Maximum wind gust speed (km/h)	0.03	1.03	0.02	2	$p < 0.05$

Discussion

WbVs face numerous continental and regional threats (Ogada *et al.* 2016), and understanding how elephants impact WbV nesting sites is important for the conservation and management of this critically endangered species (Rushworth *et al.* 2018).

We found that the riparian trees containing WbV nests had significantly taller heights, larger DBHs, and lower elephant impact scores in comparison to woodland trees. The capability of elephants to impact the structure of large trees signifies a potential threat to the persistence of trees selected by WbVs, although this threat may differ depending on the selected size and species of tree by the WbVs (Shannon *et al.* 2008). Whilst concerns exist over elephant impact on riparian vegetation in southern Africa's savanna systems (Teren *et al.,* 2018), our results show that the large trees containing WBV nests do not appear vulnerable to being directly killed by elephants. Rather, these trees may be more at risk from collapsing due to the effects of extreme flood events (Turner *et al.* 2022) or water stress from reduced water flow in the soil (Swemmer *et al.* 2023).

Furthermore, riparian trees' saplings can be subjected to intense herbivory pressures by herbivores such as impala (*Aepyceros melampus*), causing 'bottleneck' effects in the size class demographics (Moe *et al.* 2009, Turner *et al.* 2022). Excessive elephant impact to smaller adult riparian trees may further enhance this ‘bottleneck’ effect (Teren *et al.* 2018), and amplify the importance of the largest trees for WbV nesting sites. Encouragingly though, our results suggest that WbVs make use of a large range of tree heights (7.4-22.8 m) and DBHs (32-204 cm), suggesting a degree of flexibility in tree preferences, as long as nesting structures can be supported by a structurally robust and rounded tree canopy (Ogada *et al.* 2008). Smaller tree heights may, however, put WbV eggs and chicks at risk to predation (Wolter and Howard 2019), and as our study only focused on nest persistence and not breeding success, we cannot determine this effect.

Senegalia nigrescens, the most abundant tree species with WbV nests, also had one of the higher elephant impact scores. *Senegalia nigrescens* are often the tallest trees in the woodland habitat and have been recorded as the preferred tree species for WbV nests in various woodland habitats in South Africa (Kemp and Kemp 1975, Rushworth *et al.* 2018). As a favoured foraging tree species of elephants though, there exists the potential for elephants to have an adverse effect on the availability of large adult *S. nigrescens* (Cook *et al.* 2023). Our results however suggest that, given the small number of breeding pairs of WbVs in the APNR versus the slow decline of the large *S. nigrescens* trees used by WbVs for nesting purposes, elephant impact is not yet directly affecting the breeding potential of WbVs at a significant level, whereby WbVs appear to be choosing the largest trees with the lowest impact scores.

We did note though that there was less variation in tree heights selected by WbVs in Klaserie PNR (with elephants) versus the AFB (no elephants). This indicates that elephants could be having a ‘trimming’ effect on the tree height classes available to WbVs, whereby the range of tree height classes are being reduced as vulnerable height classes are targeted by elephants. Although this may not currently affect the availability of suitable nesting trees for WbVs, recruitment of new trees into suitable height classes may be a concern. Whilst a healthy rate of recruitment for *S. nigrescens* exists in Klaserie PNR (Vogel *et al.* 2014), individuals that are <11 m in height are particularly vulnerable to being pushed over by elephants (Shannon *et al.* 2008), or being killed by intense fires before they can escape the fire trap zone of 1 m – 3 m (Levick and Asner 2013). Monitoring of tree height demographics for important WbV nesting tree species is therefore necessary to understand where missing size classes are occurring.

Our results suggest that strong gusts of wind may be a primary cause of WbV nest collapse in the APNR, and a contributor to tree collapse. Previous research on raptors in the Mediterranean (Martínez *et al.* 2013) and vultures in West Africa (Daboné *et al.* 2019) have illustrated how strong winds can be a major cause of continued nest collapse, and personal observations in the APNR have revealed that >20% of surveyed nests can collapse in a single year after storms, usually collapsing along with the supporting secondary branches (unpublished data). Whilst rebuilding (15.9% in our study) or abandoning nests is not uncommon among WBVs (Chomba and M'Simuko 2013), the projected increase of wind speeds in the north eastern regions of South Africa because of climate change may be a potential concern for future WbV breeding success (Herbst and Rautenbach 2015). Major windstorms have also been responsible for up to 11% of tree mortality in research sites in the Kruger National Park (Turner *et al.* 2022). As WbVs are nesting in the tallest *S. nigrescens* trees, these older trees are also more likely to have been affected by progressive senescence, and therefore are more at risk to wind-related toppling (Owen-Smith *et al.* 2019).

Conclusions

We present results from surveys in South Africa's APNR to investigate the impact that elephants are having on trees nested in by critically endangered WbVs. We show that WbVs make use of a range of tree species and tree size classes in both riparian and woodland habitats, which in turn vary in their vulnerability to elephant impact. Focusing on *S. nigrescens*, the most abundant tree species containing WbV nests, our results suggest that the large trees nested in by WbVs are most at threat to bark-stripping by elephants but are mostly too large to be toppled or stem snapped. We also highlight the impact that strong gusts of wind can have on nest persistence in trees. Our results highlight that although elephants do impact certain species of trees nested in by WbVs, elephants do not appear to be having a major impact on the decline of large trees, with other environmental factors contributing to decreasing the persistence rates of both the WbV nests and the trees in which they nest.

Management recommendations

Due to the numerous waterholes available to elephants in the APNR (Parker and Witkowski 1999), there is concern that elephant impact on the environment is becoming homogenised (Linden *et al.* 2023). Whilst our results do not indicate that elephants are a direct threat to the large individual trees in which WbVs nest, recent trends do indicate a general decline in overall large tree ($\geq$5 m height) availability due to a combination of elephant- and fire- impact, as well as potential water stress from the most recent drought (Cook *et al.* 2023), as well as the replacement of size classes by smaller trees (Helm *et al.* 2011). Bark-stripping is the most common elephant impact type observed on trees used by WbVs for nesting, as the sizes of the trees may be too large for elephants to uproot or stem snap (Turner *et al.* 2022). Bark-stripping can leave trees vulnerable to insect and fungal infestations (Vogel *et al.* 2014, Wigley *et al.* 2019), as well as desiccation from fires (Helm *et al.* 2011), which negatively affects tree persistence. To prevent bark-stripping, recent research has shown that wire-netting, which involves wrapping chicken-mesh around a tree's main stem, can be highly effective by improving the persistence of trees with a DBH of >40 cm by reducing bark-stripping (Cook *et al.* 2023). As most WbV trees have a mean DBH of >60 cm, wire-netting may be a highly effective method for protecting these trees.

In terms of scale, our results come from the APNR, where water is readily available to elephants. The APNR however, is part of a larger open system with the Great Limpopo Transfrontier Conservation Area, where elephants can move freely across resource and safety gradients (Smit *et al.* 2020). Elephant impact may be more intense on trees selected by WbVs in small fenced-off PAs, where the spatial and temporal patterns of elephant effects on the environment are more difficult to regulate (Rushworth *et al.* 2018, Seloana *et al.* 2018).

Lastly, whilst our study focused on elephant impact to trees in which WbVs nest, it is imperative that conservation efforts are also focused on the factors that negatively affect adult WbV survival and breeding success, as this is critical for the survival of a long-lived bird species (Bamford *et al.* 2009, Monadjem *et al.* 2013). During our study period (2008-2020), a minimum of 803 WbVs died from either poisoning or powerline-related mortalities in South Africa's Lowveld (low altitude savanna) region alone, which includes the APNR (the Endangered Wildlife Trust and Eskom (South Africa's power utility), unpublished data). As a species which travels long distances across multiple countries and landscapes (Monadjem *et al.*

2013, Phipps *et al.* 2013), an interdisciplinary approach that promotes adult WbV survival and the protection/availability of breeding sites, is required to protect and increase the numbers of WbVs in South Africa (Gore *et al.* 2020, Thompson and Blackmore 2020).

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Research article

Protecting the resource: an assessment of mitigation methods used to protect large trees from African elephant impact in a savanna system

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African elephants *Loxodonta africana* can alter the structural components of savanna ecosystems, often through the reduction of the large tree ($\geq$ 5 m height) cover component. Elephant impact can be amplified in small, protected areas, or areas where water is readily available to elephants. One management option is to protect large trees directly using applied mitigation methods to limit elephant impact. In this paper, we assessed and compared the effectiveness and logistical requirements of four mitigation methods that have been applied to protect large trees from elephant impact in South Africa's Greater Kruger National Park – namely African honeybees *Apis mellifera scutellata* in beehives; creosote oil in glass jars, concrete pyramids arranged in circles around trees, as well as wire-netting the trees' main stems. For each method, elephant impact levels and tree mortality rates were measured over a 2–5-year period depending on the method in use. Sample sizes ranged from 43 to 59 trees per mitigation method, with a comparable control, which was a tree of the same species and morphological dimensions but lacking any mitigation application. Beehives were the most effective method at reducing tree loss, significantly reducing tree mortality from 34% (6.8%/year) in control trees to only 10% (2% year^{-1}) over the five-year experimental period. However, beehives were the most expensive method to apply to a tree, although this cost can be compensated through honey sales. Concrete pyramids reduced tree loss when the combined pyramid radius was > 1.5 m in length, whilst wire-netting was effective against bark-stripping by elephants but was still vulnerable to heavier forms of impact such as uprooting and stem snapping. Creosote jars did not prevent elephants from impacting treated trees. Our results provide managers with a toolkit for protecting large trees against elephant impact, commenting on both the efficacy and the logistical constraints for each method.

Keywords: beehives, elephant impact, human–elephant conflict, mitigation measures, tree protection, wire netting

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Introduction

The impact that elephants have on their environment is a contentious subject (Owen-Smith et al. 2006, Edkins et al. 2008, Scheiter and Higgins 2012), as elephants can modify the structural components of their environment, which can both increase and decrease species biodiversity (Pringle et al. 2008, Parker 2019). One such concern which arises from elephant impact is the loss of large trees (≥ 5 m in height, Shannon et al. 2008).

Large trees provide important ecological benefits to savanna ecosystems (Belsky and Canham 1994), creating a cooler, wetter microclimate underneath the canopy layer (Joseph et al. 2018), which provides habitat for more shade-tolerant plant species (Ludwig et al. 2004, Maponga et al. 2021). The root systems of large trees transport nutrients upwards from deeper soil layers, eventually dispersing these nutrients on the soil surface in the form of litter (Ward et al. 2018). This in turn can lead to more nutritious grasses growing underneath the canopy, which attracts grazing herbivores (Treydte et al. 2008). Large trees also serve important habitat functions within ecosystems due to their horizontal and vertical structuring, creating spatial heterogeneity (Dean et al. 1999, Pringle et al. 2016). For tree-nesting fauna species, these trees are important for landscape connectivity (Monadjem and Garcelon 2005), providing a 'life-boating' function for species which would otherwise not exist in that ecosystem (Franklin et al. 1997).

The decline of large trees due to elephant impact is an extensively studied field across the African continent (Leuthold 1977, Gandiwa et al. 2011, Teren et al. 2018, Coetsee et al. 2023, Khosa et al. 2023), and various management strategies have been applied to limit or redistribute the effects of elephants by compelling the elephants to move to different parts of the landscapes both seasonally and temporally (reviewed by Henley and Cook 2019). Elephant impact on large trees can differ in both type and severity, with the main impact-types being bark-stripping, branch breakage, main stem snapping, and uprooting (Walker 1976). Elevated levels of any of all these impact-types can lead to tree mortality (Gadd 2002, Das et al. 2022).

There also exists a human-centric element of aesthetic value of a healthy and functioning ecosystem, and this human perception of what constitutes a healthy ecosystem is often challenged by fallen trees (Edge et al. 2017). Conservation decision-makers are placed under pressure to manage the ecosystem accordingly with stakeholder views, and thus a mild form of human–elephant conflict (HEC) exists regarding elephant impact on large trees (Henley and Cook 2019).

In previous strategies aimed at reducing elephant impact on the environment, elephant numbers have also been decreased by means of culling entire herds of elephants (Whyte et al. 1998), or translocating elephants to other protected areas (PAs) (Grobler et al. 2008). However, modern management practices have moved away from directly managing elephant numbers, towards managing their effects on the ecosystem (Ferreira et al. 2011). In large and open systems, elephant impact on large trees has been managed through environmental manipulation strategies acting at a landscape level, such as by the closure of artificial waterholes (Purdon and Van Aarde 2017). Limiting the availability of waterholes can help create a gradient of varying elephant impact levels on trees, where trees closer to the remaining waterholes are expected to receive higher levels of impact in comparison to trees further away from a waterhole (Gaylard et al. 2003, Van Langevelde et al. 2017).

However, in small PAs, or PAs with an abundance of water, it can be difficult to manage elephant impact both spatially and temporally to create a heterogenic spatial and temporal distribution of elephant impact (Ferreira et al. 2017, Abraham et al. 2021). For these PAs, directly protecting the tree from elephants by using mitigation methods is a management option (Henley and Cook 2019). This targeted strategy gives decision-makers the choice to directly select which individual trees require protection, and then to apply a suitable mitigation method. However, whilst a variety of mitigation methods have been implemented to protect large trees from elephant impact, only a small number of scientific studies have been conducted to test the efficacy of some of these methods (Derham et al. 2016, Cook et al. 2018). Further studies are thus required to assess the various tree protection methods available to decision-makers, to review and compare the efficacy and logistics involved with the proposed methods.

South Africa's Associated Private Nature Reserves (APNR) within the Greater Kruger National Park (Greater KNP) provides an ideal experimental site to compare mitigation method efficacy and logistics, as it is a landscape where water is readily available to elephants (Linden et al. 2022). Both repellent and barrier-forming methods have been used in the APNR to protect large trees from elephant impact. Repellent methods serve to lessen the time that an elephant spends around a tree, thereby reducing the probability of impact (O'Connor et al. 2007). Repellent methods include the hanging of active beehives from trees' branches (termed 'beehives'), as well as glass jars containing creosote oil attached to the main stems of trees (termed 'creosote jars'). Barrier-forming methods serve to create an obstacle between the elephant and the tree. These include the placement of concrete pyramids (base length of 20 cm and height of 20 cm) in circles around the main stem of the tree (termed 'pyramids'), as well as placing chicken-mesh wire around a tree's main stem to prevent bark-stripping (termed 'wire-netting').

In this paper, we review these four mitigation methods which have been used to protect large trees from elephant impact in the savanna system of the APNR. Our objectives were 1) to assess the effectiveness of each mitigation method against various elephant impact-types; 2) to assess the survival rates of trees with each mitigation method in comparison to control trees; and 3) to evaluate the annual costs and logistic requirements for maintaining each mitigation method.

Material and methods

Study site and tree species

The study was conducted in the APNR, a privately-owned PA sharing an open boundary with the Greater KNP in South Africa's north-eastern region (24°04–24°55S; 30°82′–31°48′E, Fig. 1). The APNR is comprised of smaller PAs, of which three of these were used for testing mitigation methods, namely Ingwelala Private Nature Reserve (Ingwelala), Jejane Private Nature Reserve (Jejane), and N'tsiri Private Nature Reserve (N'tsiri) (Fig. 1). The APNR is located within the broad Savanna Biome of South Africa, with Ingwelala and N'tsiri occurring within the *Combretum*/*Colophospermum mopane* woodland vegetation unit, whilst Jejane is within the mixed *Combretum*/*Terminalia sericea* woodland vegetation unit (Mucina and Rutherford 2006). The APNR falls within the 300–500 m altitude range, with a mean annual temperature high of 22°C (Greyling 2004, Peel et al. 2007).

All four mitigation methods were assessed on adult *Sclerocarya birrea* A. Rich. trees (marula). *Sclerocarya birrea* is a deciduous keystone species, with both ecologic value and economic uses (Shackleton et al. 2002). Listed as a protected tree species in South Africa (Shackleton and Shackleton 2005), it is also a highly sort after tree species by African elephants (Jacobs and Biggs 2002, Helm and Witkowski 2013). Elevated levels of elephant impact can lead to the decline of adult *S. birrea* numbers in PAs (Cook et al. 2017), and elephants have been found to select for *S. birrea* above many other savanna tree species, especially by bull elephants which are known to impact trees more severely (Greyling 2004, Abraham et al. 2021). *Sclerocarya birrea* is therefore an ideal large tree species on which to assess elephant mitigation methods, as it is a proven important food source to elephants (Greyling 2004, Shannon et al. 2008).

At all three study sites, control trees were selected at a minimum distance of > 5 m from a mitigation tree. This was specifically done to reduce the probability of a tree with a beehive (repellent method) reducing the likelihood of a nearby control tree receiving elephant impact, as elephants have been found to approach active beehives within 3–5 m before being deterred (King et al. 2017, Cook et al. 2018). This distance was then standardised for the four mitigation methods.

Mitigation method descriptions and layout

Beehives

Beehives have been used as a mitigation method for promoting human–elephant co-existence in both Africa (King et al. 2017) and Asia (van de Water 2020), where the honeybees inside of beehives protect crop fields against elephant crop raiding events. Elephants are sensitive to the stings of honeybees around their ears, eyes, and inside of their trunks (Vollrath and Douglas-Hamilton 2002). Elephants also display a fearful retreating response to the sounds of swarming honeybees (King et al. 2018), as well as honeybee alarm pheromones (Wright et al. 2018).

Between November 2015 and November 2020, 50 *S. birrea* trees containing beehives with the *Apis mellifera scutellata* subspecies were monitored for elephant impact in Jejane, alongside 50 *S. birrea* control trees (Fig. 1, Supporting information). Two beehives were hung on the opposite sides of the main stem from the extended branches of each tree (Cook et al. 2018, Supporting information). Beehives were hung 2 m above the ground, roughly at the eye-level for an adult elephant (Vollrath and Douglas-Hamilton 2002) and

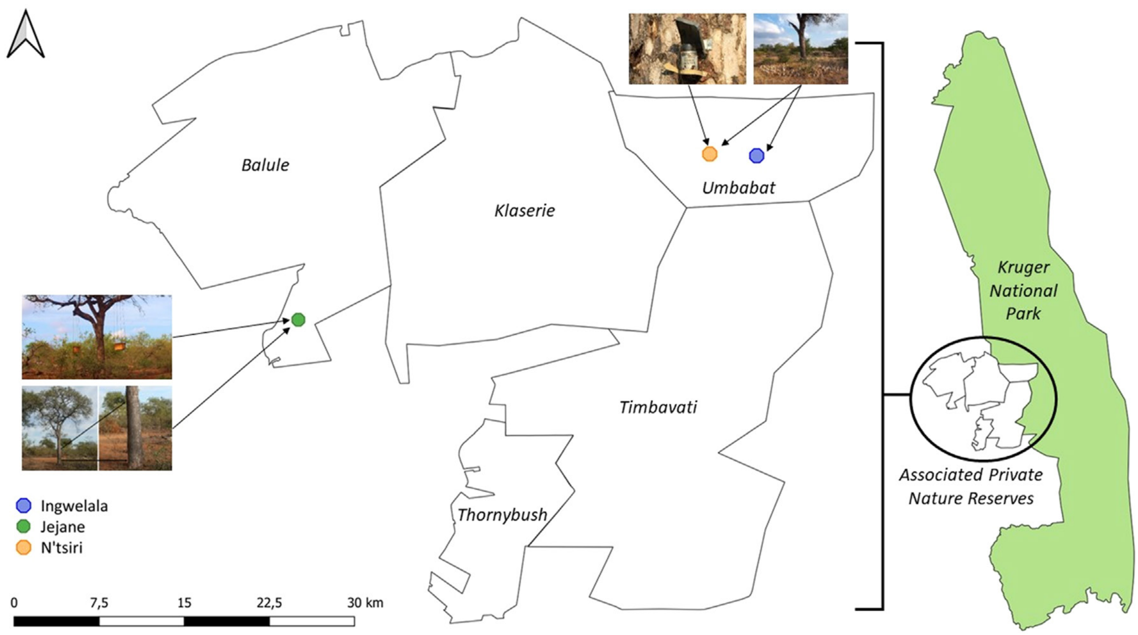


Figure 1. Location of the three tree study sites within the Associated Private Nature Reserves (APNR), South Africa.

were connected to nylon ropes. Plantex glue was spread along the ropes to prevent ants from entering the beehives. Beehive occupancy was assessed monthly. During May – September of each year, the driest months of the year, the beehives were given artificial pollen and nectar to minimize absconding events. Beehives that went inactive during the study period were left hanging in the trees to assess how the elephants responded to the presence of the vacated beehives alone after the colony had absconded.

Creosote oil in jars

Private landowners deployed the creosote method, with Elephants Alive asked to monitor the effectiveness of the method after its implementation. This method is based on anecdotal information that the smell of creosote is unappealing to elephants, and thus can serve as a repellent method to protect large trees from elephant impact. Creosote is a residue created by the distillation of coal-tar (Choudhary et al. 2002). It has a thick and oily composition, is highly flammable, and does not easily dissolve in water (Van Zyl 2013). Furthermore, creosote has carcinogenic properties due to presence of polycyclic aromatic hydrocarbons and phenolic compounds (Jurys et al. 2013). To our knowledge, no previous scientific studies have assessed whether creosote is an effective elephant mitigation method.

Between January 2018 and December 2019, 67 *S. birrea* trees containing creosote jars were monitored for elephant impact in N'tsiri (Fig. 1, Supporting information). This mitigation project was set up by N'tsiri management. Due to the limited availability of control *S. birrea* trees within the study site, a total of 59 were located and monitored. The following set up was applied to a creosote tree: a 300 ml glass jar was filled with creosote oil (*Powafix* brand). The jar was attached to the tree's main stem by hammering two nails into a tin strip around the jar, 1.5 m above the ground (Supporting information). A second tin roof-strip was placed above the jar to prevent rainfall from filling up the jar (Supporting information). Trees containing creosote were only assessed for a period of two years due to the respective management structure removing all the jars by the end of 2019.

Pyramids

Concrete pyramids, placed in rings around a tree's main stem, have been used to create a barrier between the tree and elephants (SANParks 2012). This method is a modification of the use of natural rocks to create a barrier between elephants and a desired resource to promote human–elephant co-existence (Fernando et al. 2008). However, to our knowledge, there have been no scientific studies performed to quantify the effectiveness of concrete pyramids as a mitigation method to protect trees against elephant impact.

Between January 2018 and December 2020, 43 *S. birrea* trees, encircled by rings of concrete pyramids extending away from the trees' main stems, were monitored for elephant impact at Ingwelala and N'tsiri (Fig. 1, Supporting information). This mitigation method project was set up by the management of Ingwelala and N'tsiri. An additional 59 *S. birrea* were used as control trees. All pyramid base lengths were 20 cm, and 20 cm in height, with each pyramid having a surface area of 400 cm^2, and approximate mass of 3 kg. Pyramids were placed next to one another in rings around each tree's main stem. A distance space of 0.5 m was left between the tree's main stem and the first circle of pyramids (inner gap, Fig. 2). However, the pyramid radius (i.e. the distance barrier created between an elephant and the inner gap, Fig 2) varied between individual trees (range: 0.56–2.5 m).

Due to the variation in pyramid arrangement around each tree, we calculated the mean surface area covered by the pyramids around each tree by firstly measuring the total radius length of the pyramids (tree stem to outer pyramid, Fig. 2) across eight cardinal direction points around the tree and averaging this measurement (mean total radius). We then used the following formulae to calculate the pyramid surface area (m^2) around each tree:

$$\text{Full surface area of pyramids and inner gap around tree}\,(A) = (\pi)(\text{mean total radius})^2$$

$$\text{Inner surface area}\,(B) = (\pi)(\text{inner gap radius})^2$$

$$\text{Pyramid surface area}\,(m^2) = A - B$$

Wire-netting

Wire-netting involves wrapping chicken-mesh around a tree's main stem to protect it from bark-stripping by elephants by creating a barrier around the stem (Derham et at. 2016). Wire-netting has been found to prolong the survival rates of large trees (Derham et al. 2016), as trees are less likely to die from the aftermath effects of bark-stripping such as insect infestation (Wigley et al. 2019) and desiccation after fires (Das et al. 2022). However, these trees are still vulnerable to

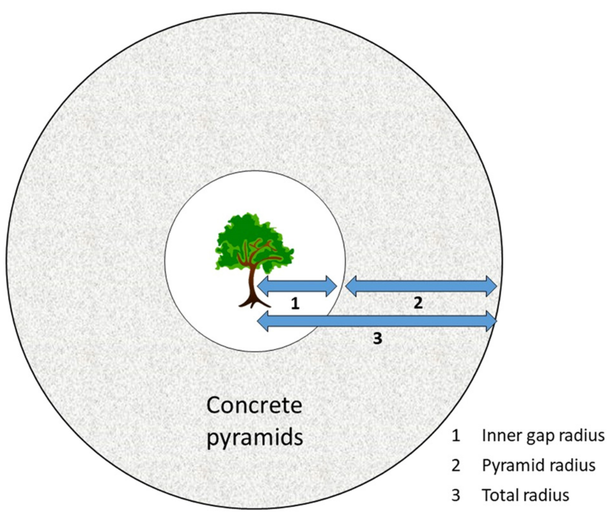


Figure 2. Illustration of the measurements taken for each pyramid tree in the Associated Private Nature Reserves (APNR).

heavier forms of elephant impact such as stem snapping and uprooting (Henley 2013, Cook et al. 2018).

Between November 2015 and November 2020, 50 wire-netted *S. birrea* trees were monitored for elephant impact in Jejane, alongside 50 *S. birrea* control trees (Fig. 1, Supporting information). This experimental research project was set up by Elephants Alive NPC as part of a MSc dissertation, where 1.8 m of 2 mm chicken mesh wire was wrapped around the main stem of large trees (Cook et al. 2018). The chicken mesh was placed 0.5 m above the ground, stretching up to 2.3 m in total height. The chicken mesh was wrapped around the tree twice to provide the tree with a double layer of protection, with a 50 cm overlap to accommodate any expansion of the tree's main stem. Five galvanised U-shaped nails were placed down the overlapped section to secure the chicken mesh to the tree. Where the chicken mesh covered holes/groves along the main stem, a hole was cut in the mesh to ensure no small animals would be trapped underneath the mesh.

Field assessments

Baseline field assessments were first conducted on all selected *S. birrea* trees with the following data being recorded: stem diameter at breast height (DBH) (cm), and tree height (m) using the *VolCalc* software program for measuring tree morphometrics (Barrett and Brown 2012). Elephant impact scoring methods, as developed by Walker (1976) and modified by Greyling (2004), were used to assess elephant impact for the following impact-types: bark-stripping, primary branch breakage, secondary branch breakage, main stem snapping, and uprooting (Table 1). Trees which contained fruit in the canopy, or had fruit kernels underneath the canopy, were recorded as female trees, whilst those large enough to be reproductively mature but without fruit or kernels were recorded as male trees (Helm and Witkowski 2012). Following the baseline assessment, each tree was assessed on an annual basis, where the same impact scores were re-assessed to evaluate whether the scores had increased following additional elephant impact, as well as to assess the survival status (alive/dead) of each tree.

The resilience of each mitigation method was also assessed. This included the following per mitigation method – 1) beehives: whether the tree's beehive was active or not; 2) creosote: whether the jar was still attached to the tree's main stem, or had been broken and spilt onto both the tree and the soil; 3) pyramids: whether the pyramids were arranged in tight formation around the tree, or had been shifted by elephants to reach the tree; and 4) wire-netting: whether the wire-netting was still in a rigid formation around the tree's main stem, or had been torn off by an animal or split by the growth of the tree's main stem.

Financial costings

Financial data for the set up and maintenance of the beehives and wire-netting were provided by Elephants Alive. For the beehives, this included the costs of the beehives, beehive

Table 1. Elephant impact scoring system for impact on large trees, as defined by Walker (1976) and modified by Greyling (2004).

Impact-type	Impact-type severity classes									
	1	2	3	4	5	6	7	8	9	10
Bark-stripping	No impact	< 1%	1–4%	5–10%	11–25%	26–50%	51–75%	76–90%	91–99%	100%
Primary branch breakage	No impact	> 0–25%	26–50%	51–99%	100%					
Uprooting	No impact	Tree alive, roots in ground, just leaning over (> 0–25%)	Tree pushed onto ground but is alive and has all roots in ground (26–50%)	Tree alive but has half of the roots in the ground and half of the roots exposed in the air (50–99%)	Tree has been uprooted (all the tree's roots are in the air) (100%)					
Main stem snapping	No impact	Main stem has been snapped but is in a re-coppicing state (> 0–25%)	Crown of tree is still attached to the main stem and the tree is still alive (26–99%)	Tree is still alive but not in a re-coppicing state (50–99%)	Tree has subsequently died from main stem breakage (100%)					
Secondary branch breakage	No impact since baseline assessment	New impact since baseline assessment								

hanging material, purchasing of a live *A. m. scutellata* colony, a bee suit with gloves and boots, *Plantex* glue, as well as artificial nectar and pollen to feed the bees during the winter. As beehives can be used for honey production, financial income data was provided by Elephants Alive for potential income per beehive. For wire-netting, financial data included the purchasing of chicken mesh and U-shaped nails. N'tsiri kindly provided financial data for the set up and maintenance of the creosote jars and the pyramids. For the creosote jars, this included the purchasing of creosote oil, a glass jar, tin material, as well as nails. For the pyramids, costs included the concrete and the mould to build each pyramid. All financial data was recorded in US Dollars (exchange rate: 1 ZAR to $18) (Exchange Rates UK 2023) and calculated over one- and five-year time periods per mitigation method. Cost of travel to set up the experimental site and monitoring were not included as the distances varied between sites.

Statistical analyses

All statistical analyses were conducted using R ver. 4.2.1 (www.r-project.org), with a significance level of $p < 0.05$. We constructed four classification trees (CT), based on conditional inference, to understand how different environmental variables influenced the probability of tree survival for each mitigation method ('party' package, Hothorn et al. 2006). Classification trees were constructed with tree survival (binomial) as the dependent variable on the following independent variables: presence of a mitigation method (categorical), tree sex (categorical), DBH (continuous), and tree height (continuous).

We used Fisher's exact test to investigate whether there was a significant difference between the proportion of dead mitigated and control trees for each mitigation method. Multiple logistic regression models were used to test for the significance of treatment, tree height, and tree diameter at breast height as predictor variables of tree mortality for each mitigation method. Whilst a positive correlation exists between tree height and tree diameter at breast height, it was weak for all four mitigation methods (Beehives: $r = 0.38$; Creosote: $r = 0.62$; Pyramids: $r = 0.48$; Wire-netting: $r = 0.41$) and so both factors were used for the multiple regression models.

We performed Kaplan-Meier log-rank survival analyses ('survival' package, Therneau 2023) to test for significant differences between the survival probabilities of the mitigated and control trees for each mitigation method. We did not run survival analyses between the mitigation methods due to the variation in time frames at each study site and locality, which was beyond the control of our study (Table 1). We were therefore interested in comparisons between each mitigation method its control counterparts, and not between sites and mitigation methods. For the survival analyses, tree death was considered truncated (1), whilst a surviving tree was considered censored (0) (Therneau 2023).

Due to non-normality of the elephant impact-type scores, Wilcoxon signed-rank tests were used to test for significant changes in median impact scores (baseline and final assessment) for each elephant impact-type per mitigation method (Table 1). For pyramids specifically, we also performed a Welch's t-test to assess whether there was a significant difference between the mean pyramid radius (Fig. 2) of the pyramid-treated trees which were alive and dead. We then ran a correlation between the pyramid radius of the living trees with pyramids and the pyramid surface area of surviving pyramid trees to calculate the 'ideal' number of pyramids required to protect a tree.

Results

Beehives

Beehive mean annual occupancy ranged from 3.5 to 100% throughout the five-year study duration, with the number of active beehives decreasing over the years due to factors such as ant invasions, lack of forage availability, and intense winds (Fig. 3). The large reduction in the number of active beehives between 2017 (21.9% occupancy) and 2018 (3.5% occupancy) was due to Elephants Alive removing active beehive colonies to a new site with a greater abundance of floral resources before the 2018 dry season. This was done to prevent colonies from rapidly absconding from their beehives. These active beehives were then replaced with inactive beehives. The increase in active beehives from 2018–2020 were from the natural colonisation of beehives by wild African honeybee swarms.

The presence of beehives in trees significantly decreased the likelihood of tree mortality (Fisher's exact test: $p = 0.007$), and according to the CT analysis, the presence of a beehive in a tree was the only significant variable affecting tree mortality probability at Jejane ($p < 0.05$). After five years, 10% of the beehive trees had died, at an annual tree mortality rate of only 2% per year (Supporting information). This was 3.4 times less in comparison to the control trees (Supporting information). Secondary branch breakage was the most common elephant impact on beehive trees, whilst control trees had significant increases in the impact scores of all impact-types except for uprooting (Supporting information). According to the multiple regression analysis, tree mortality probability was significantly decreased with both the presence of beehives (Z = 2.25, $p < 0.05$) and an increase in tree height (Z = 2.72, $p < 0.001$) (Supporting information). Beehives also significantly improved the survival probabilities of trees across the five-year study period (Log-Rank test = 7.675, df = 1, $p < 0.05$; Fig. 4a).

Whilst no active beehive was ever tampered with by elephants during the study, we did find that 14 inactive beehives were opened or pulled down by elephants in the final two years of the five-year study (Fig. 5a). A further two beehives fell and broke after a major windstorm in 2019. Financially, beehives were the most expensive method to set up and maintain per tree ($170), with the highest maintenance costs occurring during the dry months when artificial feeding was required, as natural forage availability for the honeybees was low (Table 2). Beehive costs could range as high as $280 if larger, higher quality beehives were required for honey production (Elephants Alive pers. comm.), with Elephants Alive recording an annual

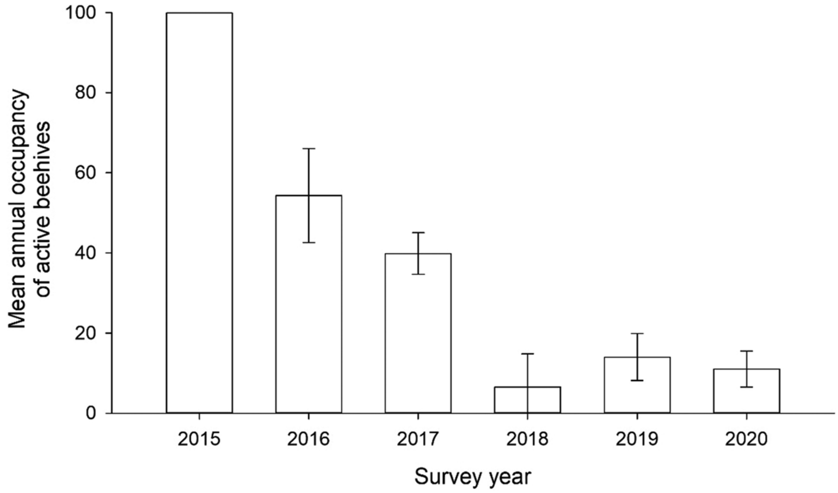


Figure 3. The annual mean number of active beehives (percentage (%) ± monthly standard deviation) in the study site within Jejane Private Nature Reserve.

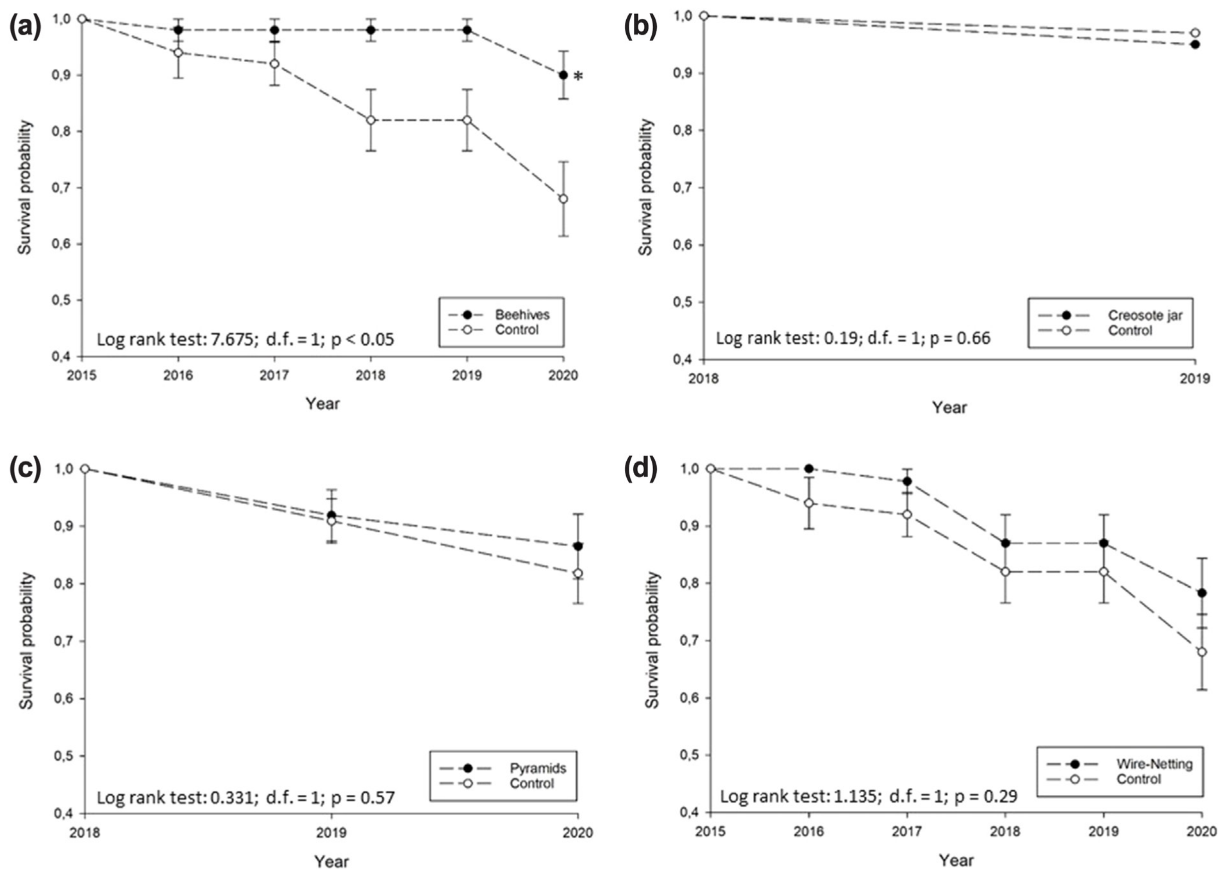


Figure 4. Survival probability (probability ± SE bars) of (a) *Sclerocarya birrea* trees protected by beehives (2015–2020), (b) creosote (2018–2019), (c) pyramids (2018–2020) and (d) wire-netting (2015–2020), alongside their control counterparts, in the Associated Private Nature Reserves (APNR), South Africa. Asterix symbol represents a significant difference ($p < 0.05$) in survival probabilities between the treatment and its respective control by the end of the trial.

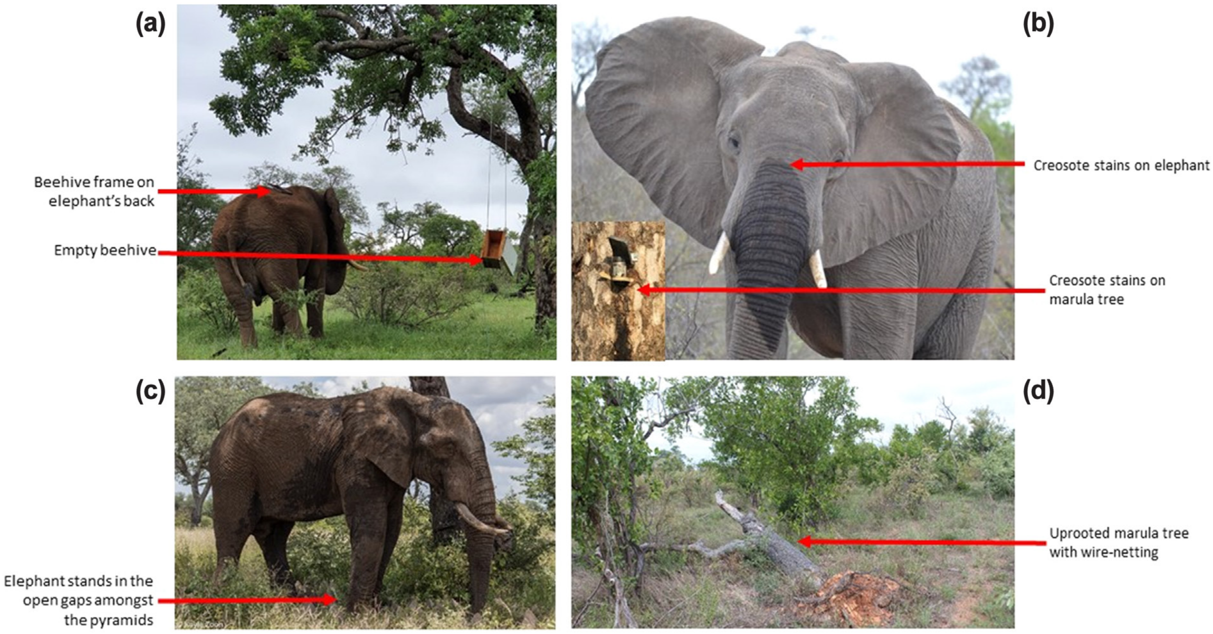


Figure 5. Examples of when (a) beehives, (b) creosote tins, (c) pyramids and (d) wire-netting are not effective against mitigating elephant impact on large tree species.

income of $78 per beehive for the duration of this study through the production and sales of honey, and hence potentially recouping the original outlay in five years.

Creosote jars

The presence of creosote jars did not significantly influence the likelihood of tree mortality in comparison to control trees (Fisher's exact test: $p = 0.84$). The CT analysis did not find any significant variables to explain tree mortality between creosote and control trees, whilst the multiple regression did not find either the presence of a creosote jar in a tree, nor height, to significantly influence tree survival probabilities (Supporting information).

Bark-stripping was the most common elephant-impact type recorded on both the creosote and control trees, with significant increases in the impact scores for both creosote and control trees over time (Supporting information). Creosote trees also had a slightly higher annual mortality rate in comparison to control trees (Supporting information), although there was no significant difference between the survival probabilities of control and creosote trees (Log-Rank test = 0.019, df = 1, $p = 0.66$; Fig. 4b).

After one year of study, 17 (25%) of the 67 creosote trees were broken by animals or potentially high gusts of wind. We observed elephants with creosote stains on their bodies, whilst creosote spillage was also seen on the trees' main stems (Fig. 5b). Financially, creosote jars were the cheapest mitigation method to set up and maintain per tree (Table 2), however, costs would increase if the glass jars were continuously broken by elephants, as observed after the one-year study.

Pyramids

The presence of pyramids around a tree's main stem did not significantly affect the tree's likelihood of mortality over the two-year study (Fisher's exact test: $p = 0.98$). There were significant increases to the bark-stripping scores on both the pyramid and the control trees over time, as the elephants were still able to reach the trees' main stems from the outskirts of the pyramids. However, heavier impact-types such as main stem snapping and uprooting tended to be more prevalent on control trees, although this difference was not significant (Supporting information). Neither the CT nor the multiple regression analyses found the presence of pyramids, nor tree height, were significant factors affecting tree mortality (Supporting information), and the survival analyses found that there was no significant difference between the survival probabilities of control and pyramid trees (Log-Rank test = 0.331, df = 1, $p = 0.57$; Fig. 4c).

However, we found that pyramid trees which were still alive had a mean pyramid radius and standard deviation of 148 ± 25 cm, which was significantly longer than those of dead pyramid trees (129 ± 9 cm; $t_{(38)} = 3.773$, $p < 0.001$). This equated to a mean pyramid surface area of 14.36 m^2 around a tree, and thereby 109 pyramids required per tree (if pyramids are 400 cm^2 at the base). Combined with the 50 cm gap between the tree and the first ring of pyramids, this results in a distance barrier of almost 2 m required between the elephant and the tree's main stem. However, even if the distance barrier was achieved, the pyramids were still required to be packed tightly, or else the elephants were able to push pyramids aside or stand in gaps amongst the pyramids (Fig. 5c). According to the financial analysis, pyramids were

Table 2. Cost–benefit analysis of each of the four mitigation methods used to protect *Sclerocarya birrea* trees from elephant impact in the Associated Private Nature Reserves (APNR), South Africa.

	Cost items	Predicted annual cost per tree	Predicted five-year cost per tree	Advantages	Disadvantages	Logistical notes
Beehives	Beehive (wooden)	$50	$50	Highly effective against all forms of elephant impact	Bee colony may abscond, after which a new colony may need to be purchased if no wild bee swarm is caught	Recommended small-scale usage in comparison to other mitigation methods
	Beehive colony	$35	$35			
	Nylon rope	$2	$5	Both active and inactive beehives can be used together to increase the number of protected trees	Fires around beehives may lead to the colony absconding	A trained beekeeper should conduct beehive installation and maintenance. Additional costs may occur if a full bee suit and gumboots are required ($130)
	Plantex glue[1]	$3	$15			
	Artificial pollen[2]	$45	$135	Beehive expenses can be supplemented through the sale of honey and other bee-related products	Beehives need continual maintenance, particularly when forage resources are low (seasonal effect)	Reapplication of Plantex glue once a year, and potentially more following heavy rains
	Artificial nectar[3]	$35	$110		Beehives do not protect neighbouring trees outside a 5m radius	Artificial pollen and nectar annual usage may vary, depending on rainfall and flower availability
	Total	**$170**	**$350**		This is the most expensive method of the four mitigation methods to implement	African honeybees can be aggressive pollinators and may exclude other pollinator species (Martins 2004)

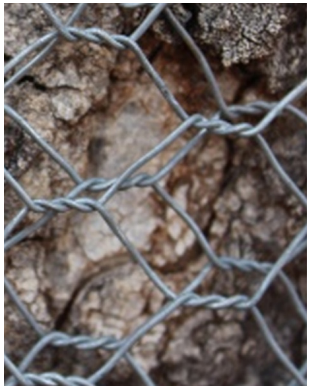
(Continued)

Table 2. Continued.

	Cost items	Predicted annual cost per tree	Predicted five-year cost per tree	Advantages	Disadvantages	Logistical notes
Creosote jars	Creosote oil[4]	$1	$5	Cheapest of the four mitigation methods	Elephants have been observed breaking creosote jars, leaving glass on the ground and creosote stains on both the elephants and the trees	Jars need a tin roof over the top to prevent the creosote oil from flowing out during rains
	Glass jar (300 ml)	$1	$1			
	Tin strips	$2	$10	Method is not affected by seasonal environmental changes	Creosote stains on trees lasts longer than two years (personal observations)	Spillage of creosote oil into the soil should be reported to reserve management
	Total	**$4**	**$16**		Creosote oil is an environmental pollutant and has carcinogenic properties	Our results recommend that this method is not suitable for tree-protection purposes
Concrete pyramids	Concrete pyramids (x109 minimum)	$35	$35	Minimal maintenance required once pyramids have been correctly arranged around the tree	Labour intensive to set up, which may limit the scale of usage of this method	Pyramids need to be tightly arranged to prevent elephants from stepping between pyramids and should be monitored thereafter
				Pyramids can last > 10 years once arranged (personal observations)	If pyramids are not arranged tightly and the radius is too short, elephants can still reach the main stem of a tree	
	Total	**$35**	**$35**	Method is not affected by seasonal environmental changes	If gaps between pyramids exist, elephants can move pyramids around with their feet	Pyramids can be replaced by natural rocks, however, the effect of the removal of many rocks on native fauna requires investigation

(Continued)

Table 2. Continued.

	Cost items	Predicted annual cost per tree	Predicted five-year cost per tree	Advantages	Disadvantages	Logistical notes
Wire-netting	1.8 m of 13 mm chicken mesh	`	S26	Wire-netting is relatively cheap and easy to place around a tree's main stem	Wire-netting loses its effectiveness on smaller trees which are more vulnerable to stem snapping and uprooting	Calculated on an average tree stem diameter of 40 cm
	U-shaped nails (25 mm)[5]		$2	Potential large-scale application due to price and relative effectiveness	Wire-netting may need replacement after 4–5 years	Ensure that there is a finger's gap between the chicken mesh and the main stem so that the mesh is not too tight
	Total	**$14**	**$28**	Method is not affected by seasonal environmental changes	Wire netting could prove challenging for multi-stemmed trees	Chicken mesh may need to be replaced after 4–5 years, using small chicken mesh (e.g. 13 mm diameter) to prevent elephants from ripping off the mesh with their tusks together with other factors that influence general deterioration (rust as an example) and structural integrity of the mesh around the tree (Cook et al. 2023)

[1]Calculated from the purchase of 20 kg of Plantex glue ($35); [2]Calculated from the purchase of 10 kg of artificial pollen; [3]Calculated from the purchase of 10 kg of artificial nectar; [4]Calculated from the purchase of five litres of creosote tar oil; [5]Calculated from the purchase of 100 U-shaped nails.

the second most expensive mitigation method to implement per tree (Table 2).

Wire-netting

The presence of wire-netting did not significantly influence a tree's likelihood of mortality during the five-year study period (Fisher's exact test: $p = 0.9$). The most frequent elephant impact-types on wire-netted trees were secondary branch breakage, > main stem snapping and > primary branch breakage, all of which had significant increases in their impact scores (Supporting information). Wire-netting was, however, particularly effective against bark-stripping, with only 4% of the wire-netted trees being bark-stripped across five years in comparison to 32% of the control trees. Impact scores significantly increased for all impact-types on control trees, apart from uprooting (Supporting information).

Tree height was the only significant variable influencing wire-netted tree survival according to both the CT ($p < 0.05$) and the multiple regression analyses ($Z = 1.99$, $p < 0.05$; Supporting information). The CT analysis found that trees > 7.81 m in height had a significantly higher survival probability in comparison to trees lower than this height ($p < 0.05$). Wire-netted trees had a higher probability of survival in comparison to control trees across the five-year study (0.78 vs 0.68 respectively), though this was not significant according to the survival analyses (Log-Rank test = 1.135, df = 1, $p = 0.29$; Fig. 4d). Wire-netted trees were still vulnerable to more severe elephant impact-types such as main stem snapping and uprooting (Fig. 5d). Financially, wire-netting was the second least expensive mitigation to implement, with small cost variations being based on the size of the tree's main stem diameter, as well as the potential need for replacement of the chicken-mesh 4–5 years after deployment (Table 2).

Discussion

Mitigation method efficacy and logistics

Beehives

Beehives proved to be the most effective mitigation method at protecting large *S. birrea* trees from elephant impact in the APNR, however, this was also the most expensive method to implement. The effectiveness of *A. m. scutellata* as an elephant deterrent is well documented (King et al. 2017), and to our knowledge, this is the longest known study to assess the effectiveness of beehives at protecting large trees from elephant impact (Vollrath and Douglas-Hamilton 2002, Ngama et al. 2016, Cook et al. 2018).

Considering that the mean occupancy level for the beehive site was 26.4%, and only 10% of the trees with beehive died from elephant impact over a five-year period, our results also suggest that inactive beehives can serve as elephant deterrents, at least when with the presence of active beehives. However, our results suggest that this deterrent effect may decline once elephants learn that an empty beehive box is not a threat, and so the temporal period of the deterrent effect on elephants may be limited if not accompanied by active beehives to reinforce the stimuli. The encouraging effectiveness of beehives, particularly active beehives, at protecting large trees against elephant impact supports its usage.

Bark-stripping was prevented altogether on the trees with beehives (Supporting information), with our results suggesting that elephants may avoid standing around the main stem of a tree with a beehive, preferring instead to feed on the smaller branches further away from the beehives where they may feel safer. This is important as *S. birrea* can usually withstand branch breakage if < 75% of the branches are broken, and smaller branches can always regrow (Jacobs and Biggs 2002). We suggest that beehives may play a crucial role in preventing heavier impact from elephants to large trees, thus improving tree survival rates.

The results of Elephants Alive's honey sales show that the financial costs of setting up a beehive in a tree could be recuperated five years from project setup. A high selling price may be set for this natural, (organic) conservation-orientated honey. For this study, the costs of all the beehives were sponsored by donors 'adopting' a hive. Projects run by charities therefore have the potential to offset costs.

However, both the logistical (Table 2) and potential environmental concerns (Martins 2004) surrounding the large-scale application of beehives limits this method to a small scale where the beehives can be actively managed. Furthermore, the predicted 2023 El Niño for southern Africa would also increase the difficulty of expanding the beehive project due to lower-than-expected rainfall (ECERA 2023). Conservation managers may wish to invest in a small number of beehives which may be highly effective at protecting selected ecologically or aesthetically important individual trees. Alternatively, beehives could also be moved around a PA periodically during the wet season to increase the impact of the beehives, if the distance moved is greater than 1.5 km from the original tree to prevent the honeybees from flying back to their original tree (Free 1958).

Creosote jars

Creosote jars were the least expensive method to implement, however, they were ineffective at protecting trees from elephant impact and were the only tested method to have a lower survival rate in comparison to their control trees. In Zimbabwe, creosote oil has been assessed as an olfactory deterrent for elephants as part of a 'virtual fence dynamic', where the repellent smell of the creosote oil has shown potential for deterring elephants from crop raiding (La Grange et al. 2022). This effect though, may have been heightened as elephants undertaking crop raiding activities typically have elevated stress levels in comparison to when in the safety of a protected area (Ahlering et al. 2011, Hunninck et al. 2017), and may therefore be more likely to be deterred by unfamiliar stimuli.

Our data suggests that elephants in our study were not deterred by the smell of creosote, and any potential suspicion or fear of the smell was disregarded by the elephants soon after application. This study was the shortest in duration of the four mitigation methods, resulting in only a small number of recorded dead creosote and control trees on which to draw conclusions. However, with 25% of the monitored trees having had their creosote jars broken within the first year of the study, our results suggest that there was no olfactory deterrent. Given the environmental concerns of spilt creosote oil in protected areas (Van Zyl 2013), as well as the lack of supporting evidence that creosote can protect trees from elephant impact, we recommend that this method is not applied to protect trees. Importantly, the study site where our assessments took place immediately removed the creosote jars following the completion of our assessments.

Pyramids

To our knowledge, this was the first study to focus on pyramids as a mitigation method for tree protection against elephant impact, and our results suggest that this method can be effective, but only when the correct distance barrier is created between the elephant and the tree's main stem. We found a large variation in the pyramid radius and stacking formation around the assessed trees, making the overall survival rates of trees with pyramids difficult to assess.

However, this method has been listed as a potential tree protection method by the South African National Parks (SANParks 2012), and if implemented correctly, may be an effective tree protection method. If correctly arranged around a tree, pyramids can prevent elephants from getting sufficiently close to push the tree over, thus restricting elephants to feeding off branches, similar to what was observed with the beehives, and hence generally reduce tree mortality (Jacobs and Biggs 2002). Pyramids should, however, be occasionally monitored to ensure that they have not been re-arranged by elephants. Pyramids or sharp rocks are recommended as a method to reduce other forms of HEC in both Africa and Asia, although the implementation of the method has been described as both time-consuming and labour-intensive (Osei-Owusu 2018). This may limit the scale at which this method can be used for tree protection. However, as the method requires little maintenance after implementation, it can still be an effective method for protecting selected large trees within a protected area, pending the financial and logistical resources of a protected area.

Wire-netting

Wire-netting was both the second most effective mitigation method for prolonging trees survival and to implement. Previous studies have illustrated that wire-netting can be effective at protecting trees from bark-stripping, and thereby potentially improving tree survival (Henley 2013, Derham et al. 2016). Our results, however, suggest that wire-netting loses its effectiveness for smaller trees, particularly in the 5–8 m height category, as these trees are still vulnerable to heavier elephant impact-types such as uprooting and stem snapping (Helm et al. 2009).

Recent research has shown that wire-netting is most effective on trees with a DBH of ≥ 40 cm (Cook et al. 2023a). Wire-netting is not a fear-based or repellent method, and elephants are still capable of walking up to the tree and pushing them over. Therefore, given the relatively low financial costs involved with wire-netting trees, it can be a highly effective method if used for larger trees that elephants cannot push over, thereby minimising bark-stripping by elephants and eventual tree death through desiccation (Jones et al. 2022), insect invasion (Wigley et al. 2019), and vulnerability to fire (Das et al. 2022).

The low financial costs also make this method attractive for a larger scale of implementation in comparison to beehives and pyramids. Importantly though, wire-netting still requires maintenance/replacement over time, of which failure to do will lead to a decrease in the wire-netting's effectiveness (Cook et al. 2023a). We also suggest that the smaller chicken-mesh (13 mm), double-wrapped around the tree, is effective as elephants do not appear to be able to place their tusks within the mesh's holes to rip it off the tree.

Combining methods and future research directions

Whilst we have focused on the effectiveness of each mitigation method as a stand-alone method, there is a potential to combine methods to increase tree protection. An integrated management approach, whereby mitigation methods complement one another, could prove highly effective at increasing tree survival.

We also suggest that methods may require further refinement to improve their efficiency. For pyramids, our results have suggested that arranging pyramids tightly together and ensuring a ≥ 2 m distance between an elephant and the tree's main stem would be the most effective implementation of that method. For beehives, the use of more expensive but longer lasting beehives may improve occupancy levels. And for wire-netting, the use of stronger wire, albeit of the same dimensions, may reduce the need to replace wire-netting every 4–5 years.

There is also the potential to test and integrate new mitigation methods which have been used for other HEC scenarios, such as honeybee alarm pheromones (Wright et al. 2018), honeybee buzzing sounds (King et al. 2007), chili paste/oil (Osborn and Rasmussen 1995), reflective metal strips (Corde 2022), and 'smelly' elephant repellent (Tiller et al. 2022). Importantly, as we have demonstrated in our field trials, mitigation methods for tree protection require basic experimental design to ensure that accurate assessments are made for method effectiveness, else method success may be inaccurately concluded against no comparison.

Future research into stakeholder perceptions regarding the use of mitigation methods for large tree protection should also be considered. Support for various elephant management strategies, such as the use of tree protection methods, may differ amongst stakeholder groups (Edge et al. 2017), and hence these views will need to be considered when contemplating using tree protection methods. Furthermore, careful consideration should also be taken regarding which tree species and size classes may require protection.

Mitigation methods may be most appropriate for tree species that are both highly selected for by elephants and have poor recruitment rates, which makes the surviving adult trees important seed banks for future generations (for example, *Adansonia digitata* (Venter and Witkowski 2010) and *S. birrea* (Helm and Witkowski 2012)). Managers may also want to protect large trees that provide important nesting sites for birds of conservation concern, such as the white-backed vulture (*Gyps africanus,* Vogel et al. 2014) and the southern ground hornbill (*Bucorvus leadbeateri*, Kemp and Begg 1996). Questionnaire surveys can also be performed to help assess about which trees managers and landowners are most concerned, and where efforts for mitigating purposes should be conducted (Henley 2013).

Conclusion

We have presented the results of field experiments to test the efficacy of four mitigation methods for large tree protection against elephant impact. Whilst disagreement exists over the management strategies surrounding managing elephant impact on large trees, we have provided results on both the effectiveness and logistical constraints of these four mitigation methods to provide conservation mangers with a scientifically assessed 'toolbox'. These tree protection methods should always be viewed as a small-scale solution for protecting large trees from elephant impact, and most applicable to small, protected areas, or where water is readily available to elephants and so elephant impact cannot be managed on a spatial scale (Henley and Cook 2019).

We encourage conservation managers to decide carefully on which methods are both ecologically and economically suited for both their protected areas and their elephant management plans, whilst understanding that method effectiveness may range across various protected areas. These methods can 1) aid in prolonging the survival of large trees in the presence of elephants, 2) protect important habitats of tree-dependent species (Rushworth et al. 2018), 3) ensure that the ecological value of large trees within savanna ecosystems is conserved (Belsky and Canham 1994), 4) ensure that sufficient reproductively adult trees of particular species, is available as potential seedbanks to repopulate the surrounding landscape (Helm et al. 2011), and 5) help reduce disagreements over management decisions related to elephant impact on large trees (Henley and Cook 2019).

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Author contributions

Robin M. Cook: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Writing – original draft (lead); Writing – review and editing (supporting). **Edward T. F. Witkowski**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (equal); Writing – review and editing (equal). **Michelle D. Henley**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Writing – review and editing (equal).

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Data are available from the Dryad Digital Repository: https://doi.org/doi:10.5061/dryad.h18931zsf (Cook et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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Supplementary material of Chapter 5

Table S1. Images of the four mitigation methods for tree protection assessed, together with time periods, study sites and vegetation units (Mucina and Rutherford 2006), within the Associated Private Nature Reserves (APNR), South Africa.

Mitigation method	Image	Time frame	Study site location	Vegetation unit)	Vegetation unit description
Beehives		2015-2020	Jejane Private Nature Reserve (Balule)	SVI 3: Granite Lowveld	Mixed *Combretum*/*Terminalia sericea* Woodland
Creosote jars		2018-2019	N’tsiri Private Nature Reserve (Umbabat)	SVmp 7: Phalaborwa-Timbavati mopaneveld	*Combretum*/*Colophospermum mopane* Woodland
Pyramids		2018-2020	Ingwelala Game Reserve (Umbabat); N’tsiri Private Nature Reserve (Umbabat)	SVmp 7: Phalaborwa-Timbavati mopaneveld	*Combretum* /*Colophospermum mopane* Woodland
Wire-netting		2015-2020	Jejane Private Nature Reserve (Balule)	SVI 3: Granite Lowveld	Mixed *Combretum* /*Terminalia sericea* Woodland

Table S2. Elephant impact scores (baseline (2015) and final assessment (2020)) per impact type on treatment and control *Sclerocarya birrea* trees per mitigation method. Asterix symbols represent levels of significant increases, from the baseline (pre-treatment) level, according to the Wilcoxon-signed rank tests. Number of trees assessed per mitigation method shown in brackets. Hashtag symbols represent significant differences in survival rates between treatment and control trees according to the Kaplan-Meier log-rank survival analyses.

	Beehives																			
	Bark-stripping				Primary branch breakage				Secondary branch breakage				Main stem snapping				Uprooting			
	Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control	
	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020
Mean impact score	1.98	1.98	1.56	2	1.42	1.44	1.24	1.94	1	1.32	1	1.42	1	1.16	1	1.54	1	1.24	1	1.4
Standard deviation	1.76	1.76	1.3	1.5	0.81	0.81	0.56	1.4	0	0.47	0	0.5	0	0.79	0	1.33	0	0.96	0	1.21
Significance	NS		***		NS		***		***		***		NS		**		NS		NS	
Annual tree mortality rate	Treatment = 2%#										Control = 6.8%#									

	Creosote																			
	Bark-stripping				Primary branch breakage				Secondary branch breakage				Main stem snapping				Uprooting			
	Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control	
	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
Mean impact score	3.95	4.63	4.76	5.23	1.89	1.93	1.44	1.46	1	1.07	1.08	1.12	1	1.07	1	1.56	1	1.07	1	1
Standard deviation	2.59	2.72	2.97	2.9	1.11	1.13	0.73	0.73	0	0.25	0.28	0.33	0	0.52	0	1.38	0	0.52	0	0
Significance	***		***		NS		NS		NS		NS		NS		NS		NS		NS	
Annual tree mortality rate	Treatment = 6%										Control = 5.1%									

	Pyramids																			
	Bark-stripping				Primary bark stripping				Secondary branch breakage				Main stem snapping				Uprooting			
	Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control	
	2018	2020	2018	2020	2018	2020	2018	2020	2018	2020	2018	2020	2018	2020	2018	2020	2018	2020	2018	2020
Mean impact score	3.4	4.28	4.76	5.53	1.32	1.36	1.44	1.49	1	1.28	1	1.13	1	1.32	1	1.68	1	1	1	1.07
Standard deviation	2.2	2.2	2.97	2.97	0.48	0.49	0.73	0.86	0	0.46	0	0.34	0	1.11	0	1.51	0	0	0	0.52
Significance	***		***		NS		NS		NS		NS		NS		NS		NS		NS	
Annual tree mortality	Treatment = 5.8%										Control = 5.95%									

	Wire-netting																			
	Bark-stripping				Primary branch breakage				Secondary branch breakage				Main stem snapping				Uprooting			
	Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control		Treatment		Control	
	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020	2015	2020
Mean impact score	1.72	1.8	1.56	2	1.58	1.82	1.24	1.94	1	1.56	1	1.42	1	1.74	1	1.74	1	1.38	1	1.4
Standard deviation	1.31	1.34	1.3	1.5	0.97	1.08	0.56	1.4	0	0.5	0	0.5	0	1.55	0	1.55	0	1.16	0	1.21
Significance	NS		***		**		***		***		***		**		**		NS		NS	
Annual tree mortality	Treatment = 5.2%										Control = 6.8%									

* $p < 0.05$; ** $p < 0.01$; ***$p < 0.001$; # $p < 0.05$

Table S3. Results of the multiple regression analyses to test for tree mortality as a response to mitigation method presence and tree height.

Mitigation method	Variable	Coefficient	Standard error	Wald statistic	P-Value
Beehives	Constant	4.5	2.13	5.28	< 0.05
	Mitigation method	-1.32	0.59	5.05	< 0.05
	Tree height	-0.7	0.28	7.41	< 0.001
	Tree stem diameter	-0.02	0.04	0.29	0.59
Creosote jars	Constant	-2.55	2.87	0.79	0.37
	Mitigation method	-0.43	0.86	0.25	0.62
	Tree height	0.03	0.25	0.02	0.9
	Tree stem diameter	0.08	0.04	0.06	0.06
Pyramids	Constant	-0.38	2.55	0.02	0.88
	Mitigation method	-1.3	1.15	1.27	0.26
	Tree height	-0.11	0.23	0.22	0.64
	Tree stem diameter	0.01	0.04	0.15	0.7
Wire-netting	Constant	3.22	1.94	2.74	< 0.05
	Mitigation method	-0.09	0.55	0.03	0.94
	Tree height	-0.5	0.25	3.96	< 0.05
	Tree stem diameter	-0.01	0.04	0.05	0.82

CHAPTER 6:

SYNTHESIS & CONCLUSION

General overview

African elephants (*Loxodonta africana*), as ecosystem engineers, have the capability to alter the structural landscape (Owen-Smith 1988). Concerns about the impact that increasing African elephant populations are having on large trees (≥5 m in height; Shannon *et al.* 2008) in protected areas in southern Africa, and particularly in South Africa, have conservation managers seeking novel management strategies that will help reduce these impact levels (Owen-Smith *et al.* 2006, Ferreira *et al.* 2017, Van Langevelde *et al.* 2017). Large trees provide important ecosystem services to savanna systems (Treydte *et al.* 2008, Joseph *et al.* 2018), and a large-scale loss of large trees and environmental homogenisation of the landscape could negatively impact a protected area's biodiversity (Helm *et al.* 2009, Rushworth *et al.* 2018).

Historically, culling was practiced across protected areas in Africa to reduce elephant numbers to a 'manageable' level (Whyte *et al.* 1998, Child 2004). However, culling as a sole-strategy to reduce elephant impact has been challenged by the scientific community (Owen-Smith *et al.* 2006, Dickson and Adams 2009), as well as animal welfare groups (IFAW 2005). International animal welfare groups, for example, have played significant roles in challenging the policies and plannings of the culling of Cape fur seals (*Arctocephalus pusillus*) in Namibia (Authority (EFSA) 2007) and non-native predators in New Zealand after the successful culling of cats on Marion Island, South Africa (Souther 2016). For elephant management, this has led to a new paradigm shift in elephant management focussing on managing elephant impact in a spatial and temporal manner (Ferreira *et al.* 2017, Robson and Van Aarde 2018). Here, conservation managers aim to redistribute elephant densities through the removal of artificial waterholes (Purdon and Van Aarde 2017) or the creation of elephant corridors that connect protected areas (Douglas-Hamilton *et al.* 2005). However, this management approach is not always possible in protected areas that either have an excess number of artificial waterholes (Linden *et al.* 2023), are too small for varying elephant spatial and temporal distributions to occur (Thompson *et al.* 2022), or in large and open systems where elephants may still be spatially confined once certain densities have been reached (MacFadyen *et al.* 2019, Louw *et al.* 2021). By adopting strategies that focus on mitigating the impact of elephants on large trees at a local scale, conservation managers can protect iconic trees in a targeted way. This spatially explicit approach not only preserves the key landscape features valued by stakeholders, but also ensures the availability of seedbanks for repopulating surrounding areas and provides conservation managers with a 'tool' in a 'toolbox' of appliable management strategies.

Moreover, stakeholder values need to be considered before elephant management strategies are applied, as an elephant management plan that is not aligned with its stakeholder values can result in a loss of financial income and protected area sustainability (Sutton and Taylor 2019). The integration of stakeholder values into conservation practice is summarised in the conceptual framework of this PhD thesis (Figure 1).

Furthermore, the strategy of 'adaptive management' is being applied in protected areas such as South Africa's Kruger National Park (KNP), whereby management strategies are followed by a monitoring process, a scientific review, and potential alterations (Gaylard and Ferreira 2011). Research into all management strategies aimed at reducing elephant impact to large trees at varying spatial scales is thus a necessity for conservation managers (Henley and Cook 2019).

Balancing elephant management strategies and stakeholder values

Elephant management strategies, particularly in South Africa, have moved away from a system where decisions were mostly internally-controlled and scrutinised, to one where a wide range of both internal and external stakeholders are able to engage in the decision-making process (Carruthers *et al.* 2008, Selier *et al.* 2023). However, a combination of internal and external stakeholders can produce a wide range of societal values, which need to be evaluated and integrated into a management strategy that promotes societal values alongside sound-conservation principles (Christie *et al.* 2022). As the variety of elephant management strategies available may vary in terms of how they may affect elephant population as a whole (APNR) (Henley and Cook 2019, GLTFCA 2022), an understanding of the social values surrounding large tree and elephant population dynamics, as well as proposed management strategies, would aid in conservation decisions that incorporate and promote the values of the relevant stakeholders. I present the Associated Private Nature

Reserves (APNR) as a case study; however, the process of stakeholder engagement is widely applicable.

The findings from Chapter 2 suggest that whilst stakeholders generally support the idea of a healthy functioning ecosystem, composed of both large trees and elephants, there is non-agreement as to whether directly controlling elephant numbers is the right conservation strategy (Figure 1). There is also non-agreement as to which strategy is best suited for the APNR, as it forms part of an open system with the KNP. Long-serving stakeholders (in terms years of residency) and older stakeholders (in terms of age) were more inclined to support the lethal management of elephants, whilst younger or newer stakeholders were more supportive of non-lethal strategies such as waterhole closures, contraception, and tree protection methods. Similar findings were observed in Edge *et al.* (2017), who found that APNR residents (internal stakeholders) were more likely to support intrusive management strategies in comparison to external stakeholders. However, the general trend in these value differences across generations probes further questions as to whether this is due to societal-intergeneration shifts in conservation values, or differences in exposure to new scientific approaches for managing elephant impact (Manfredo *et al.* 2009). Further research into the reasons behind stakeholder values surrounding the lethal and nonlethal management of elephant populations may bring about improved clarity surrounding the continued elephant management debates (see Van de Water *et al.* 2022).

Chapter 2 did not directly focus on the financial costs of the four elephant management strategies, however, the concerns surrounding the financial costs were brought up in various stakeholder responses to the questionnaire. Understanding how the financial costs of each elephant management strategy influences the stakeholders' perceptions and values will be of benefit to decision-making processes surrounding elephant management (Graeber 2001).

Furthermore, the electronic format of Chapter 2's questionnaire excluded any stakeholders who did not have access to a computer device with internet, or who may have been unable to complete the questionnaire due to a language barrier. Very little is known about the values of elephants and their interactions with large trees among many native, non-English communities living both around and within protected areas such as the KNP and APNR. Whilst this was beyond the scope of the PhD thesis, a study on these values of the surrounding communities will provide a more complete understanding on the consensus and non-agreement of stakeholder values.

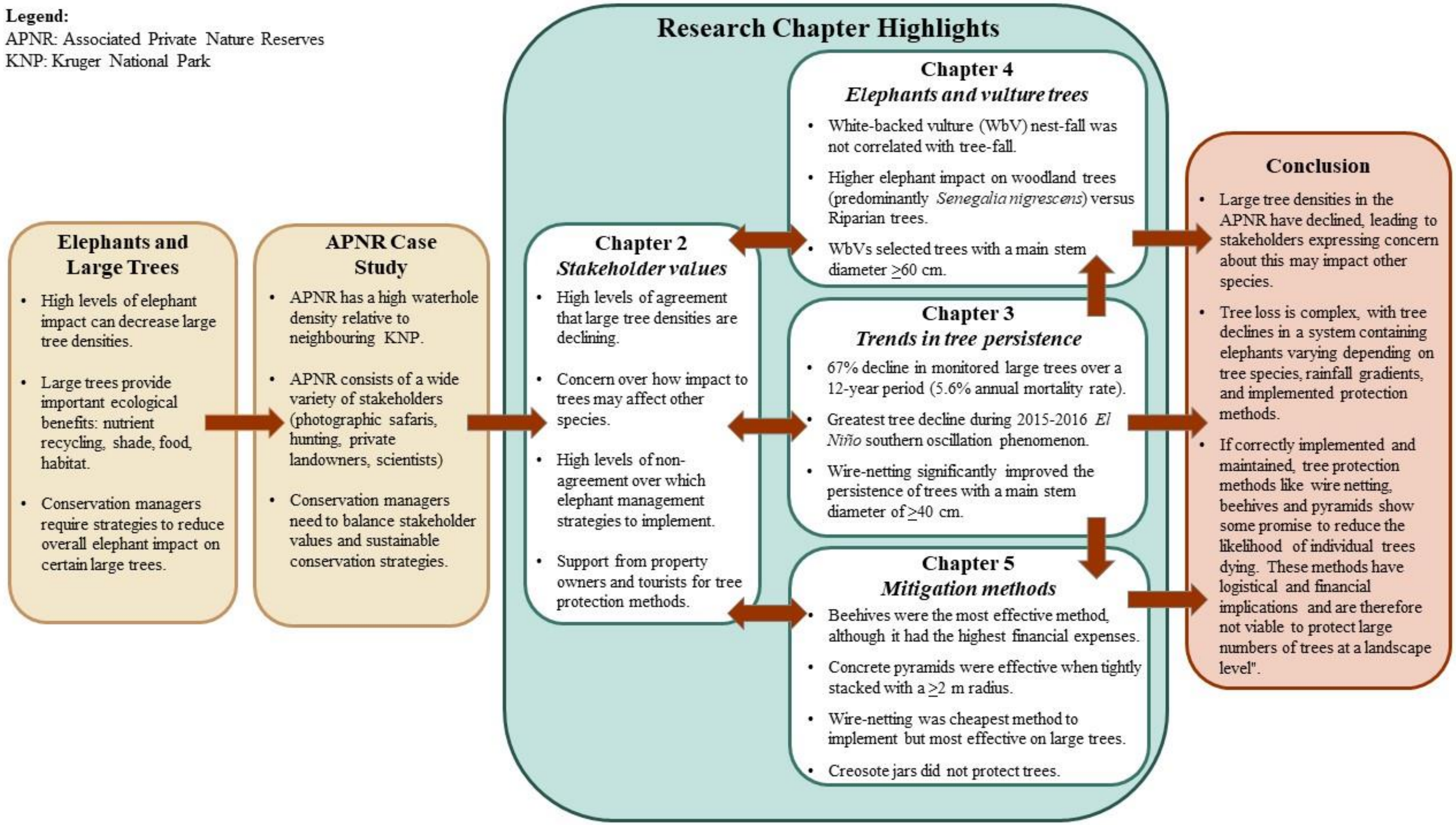

Figure 1. Conceptual summary of the PhD thesis, illustrating the linkages between the research chapters and the thesis conclusions.

Continued decline of large trees in the APNR and wire-netting effectiveness

The interactions of herbivory, fire, and rainfall patterns have considerable effects on the structure of savanna systems and persistence rates of large trees (Smit and Coetsee 2019, Das *et al.* 2022). Research by Trotter *et al.* (2022) and Coetsee *et al.* (2023) has shown that the 2015–2016 *El Niño* southern oscillation phenomenon, which brought about a significant decrease in mean annual rainfall to South Africa's lowveld savanna system, greatly reduced large tree densities, with a die-back of certain tree species (e.g. *Combretum imberbe* and *Ficus sycamorus*) occurring two-three years after the drought (Smit and Bond 2020). Furthermore, the termination of large herbivore culling has also pushed the KNP (and APNR) system from being primary shaped by fire dynamics, to one where herbivores are an increasingly important driver of the savanna structure and fire patterns (Smit and Archibald 2019).

The findings from Chapter 3 (Cook *et al.* 2023a) showed that the monitored trees of three species in the APNR have declined by 67% over a 12-year period (range: 35%-74% across sites), with the largest declines occurring during the 2015–2016 *El Niño* southern oscillation phenomenon (Figure 1). Smit *et al.* (2020) suggested that there was a movement of elephants out of KNP into APNR during the same *El Niño* time frame, which may have been due to the high waterhole density within the APNR versus the KNP, and thus contributed to the increased levels of monitored tree mortality during this period. High mortality also occurred on trees with a previous history of fire damage and elephant impact. The decline of large trees in the APNR was higher than what has been recorded by Das *et al.* (2022) in the KNP between 2006-2018 (48%), which may be explained by a number of factors. Firstly, two fires of high intensity affected two of the study sites within the APNR, causing high tree mortality rates regardless of elephant presence. Trees that have had previous elephant impact are rendered more vulnerable to fire damage and subsequent mortality (Jacobs and Biggs 2001, Helm, Wilson, *et al.* 2011, Das *et al.* 2022). Furthermore, as these are two long-term monitoring sites, we did not choose alternative sites for the study. Secondly, the high waterhole density in the APNR, versus that of the KNP, may be homogenising the APNR landscape in terms of elephant impact. This is because most regions of the APNR effectively fall within a few kilometres of surface water (Henley 2014, Peel 2015, Smit *et al.* 2020, Linden *et al.* 2023).

This high waterhole density, and the implications of the increased elephant impact on large trees, have been highlighted in several scientific reports and publications (Grossman 2010, Henley 2013, Cook *et al.* 2017, Linden *et al.* 2023). This may be suggested by a comparison study of tree mortality rates in comparison to a 12-year study by Das *et al.* (2022) in the KNP (Table 1)

Table 1. Comparison of the annual mortality rates of three species of trees recorded in South Africa's Associated Private Nature Reserves (APNR) (2008-2020) and the Kruger National Park (KNP) (2006-2018).

Tree species	Cook *et al.* (2023) – Associated Private Nature Reserves	Das *et al*. (2022) – Kruger National Park
Lannea schweinfurthii	5.7%	2.75%
Sclerocarya birrea	5.9%	1.5%
Senegalia nigrescens	4.9%	1.2%

Chapter 3 also highlighted the effectiveness of wire-netting for prolonging tree survival but importantly also showed how a lack of maintenance can decrease wire-netting's effectiveness (Cook *et al.* 2023a). This 12-year assessment was able to show that if wire-netting is not maintained after a 4-year period, the chicken-mesh can either fall off the tree in a rusted state or be ripped apart over time by tree growth or by elephants. Failure to maintain elephant mitigation methods is a common cause of mitigation method failure (Kamdar *et al.* 2022) and Chapter 3 highlights that maintenance is key when mitigating against elephant impact.

Chapter 3 also found that whilst wire-netting improved the overall persistence rates of trees, it was most effective on trees with a stem diameter of ≥40 cm, as smaller trees are more likely to be stem snapped or pushed over by elephants. Different strategies will thus be required for protecting smaller tree individuals to allow them to grow into a large tree cohort. These may include selected elephant-exclusion zones (Western and Maitumo 2004), or the artificial propagation of favoured tree species in a refugia location (Scholtz 2007), or altering fire burning frequencies and intensities which may lead to the loss of smaller trees (Helm, Wilson, et al. 2011).

The results of this chapter would have been strengthened with a comparison of a neighbouring site that did not contain elephants, to differentiate the impact that the 2015–2016 *El Niño* southern oscillation phenomenon had on tree mortality with and without elephants. This research would then compliment previous research done by Coetsee *et al.* (2023) inside of outside of the KNP to illustrate tree mortality during a drought, even in the absence of elephants. Long-term studies that focus on elephant impact across gradients of elephant densities (including no elephants) will help provide further information regarding how elephants and their densities influence tree persistence across changing climatic conditions.

Lastly, the sustainability mitigation methods applied within the human-wildlife context require the affected stakeholders to have access to both physical resources to implement the methods and financial resources to maintain these methods (Catalano *et al.* 2019, Tshewang *et al.* 2021). Osborn and Parker (2003) suggest that the failure of human wildlife conflict mitigation methods is often due to associated high financial costs, or a lack of human resources for method maintenance, or lack of belief in the effectiveness of methods. Chapter 5 in this thesis highlighted the varying costs and logistical requirements associated with each assessed tree protection method, as well as the raw materials required to implement each method. Chapter 2 suggested that if the mitigation method (in this case wire-netting) was not maintained, then its effectiveness as a tree protection method decreased. Indeed, this may apply to other methods where conservation managers or the individual landowners may be able to financially implement tree protection methods, but if human resources not available to monitor and maintain these methods, then problems may arise with the sustainability of the methods' effectiveness. Mitigation method ownership should also be discussed prior to implementation, as a lack of ownership entitlement can lead to the failure of mitigation measures (Sitati and Walpole 2006). In the context of the APNR, it is important that conservation managers and landowners discuss who is responsible for the implementation and maintenance of tree protection methods to ensure that the methods will not dilapidate overtime.

Persistence of large trees containing white-backed vulture nests in the APNR

The worrying decline of white-backed vulture (WbV, *Gyps africanus*) numbers places significant pressure on the protected areas in which these birds nest (Ogada *et al.* 2016).

WbVs have been listed as 'Critically Endangered' according to the International Union for Conservation and Nature's Red List of Endangered Species (Birdlife International 2021), with mass poisonings and powerline collisions having the greatest negative effect on the survival of the WbV population in the lowveld savanna (Monadjem *et al.* 2013). However, the ability of elephants to transform the density and structure of large trees has led to concerns over how this impact can affect WbVs, which are reliant on large trees as nesting sites (Rushworth *et al.* 2018). These concerns may be heightened in the APNR with its relatively high tree mortality (Chapter 3). Furthermore, Chapter 2 of this PhD found that 76% of the stakeholder participants agreed that pushed over large trees can decrease nesting site availability for birds.

However, in contrast to stakeholder views of Chapter 2, the findings from Chapter 4 illustrate that elephant impact to trees containing around 220 breeding pairs of WbVs across 10 tree species is currently not a major threat to the regional WbV population. Elephant impact on the trees nested in by WbVs is highly variable across tree species, with impact on woodland trees (dominated by *S. nigrescens*) being significantly higher in comparison to riparian trees (Figure 1). Chapter 4 also found that no direct correlation existed between tree fall and nest fall when focusing on *S. nigrescens* trees containing WbV nests across a 12-year period. However, elephants do appear to be having a 'trimming' effect on the tree height classes available to WbVs. Furthermore, as found in Chapter 3, adult *S. nigrescens* in the APNR are declining, and a healthy recruitment rate that ensures the persistence of the *S. nigrescens* population will be necessary to counter the loss of adult trees (and potential WbV nesting sites). To date, no in-depth tree demographic studies have taken place in the APNR, such as those performed by Helm and Witkowski (2012) on *S. birrea* across the KNP, barring a smaller-scale assessment on *S. nigrescens* recruitment rates by Vogel *et al.* (2014). Such a study will help conservation managers understand the population trends of trees of concern and help identify where recruitment bottlenecks may be taking place within populations. Conservation managers can then identify which environmental factors may be causing these bottleneck effects and how management actions can reduce these effects.

Chapter 4 has also found that WbVs appear to nest in trees with a stem diameter of $\geq$60 cm. This is a significant finding as Chapter 3 showed that wire-netting can be highly effective for trees with a stem diameter $\geq$40 cm. Wire-netting can therefore provide conservation managers with a practical strategy of reducing bark-stripping to trees nested in by WbVs, as bark-stripping was the most numerous impact type recorded on the trees containing WbV nests in Chapter 4.

A study on the changes in the nesting distributions of WbVs within a protected area, relative to elephant impact and tree mortality, will also aid in further understanding the dynamics of this complex relationship. Modelling whether zones of high elephant impact on large trees causes a shift in the distribution of WbV nests will support conservation management planning, and further highlight the importance of protecting the individual large trees nested in by WbVs. This can be done with long-term data on the WbV nest sites and elephant impact and would strengthen the results found in Chapter 4.

The methodology applied in Chapter 4 will also be useful for monitoring trends in other vulture and raptor species in protected areas containing elephants. As raptor numbers continue to decline across Africa (Shaw *et al.* 2024), the importance of protected areas as breeding sites will further increase. Research by Vogel *et al.* (2014) has shown that trends in raptor nest persistence in large trees differ to those of vultures, as raptors often nest further down the tree, nesting on larger and stronger branches. An understanding about the tree requirements of obligate tree-nesting raptors and vultures, as well as how elephant impact affects nest and tree persistence, will aid in the conservation efforts to ensure tree availability for both vulture- and raptor-species.

Tree protection methods as a tool for improving large tree persistence

Tree protection methods provide conservation managers with a practical (albeit small-scale) strategy for reducing elephant impact on selected large trees. However, whilst tree protection methods have been mentioned in management plans (Pienaar 2012, Enterprises University of Pretoria 2022) and scientific reviews (Rushworth *et al.* 2018, Henley and Cook 2019), only wire-netting and beehives have had any scientific analyses carried out in the published literature prior to this PhD (Derham *et al.* 2016, Cook *et al.* 2018). Chapter 5 (Cook *et al.* 2023b) provided the first in-depth comparative analysis among four tree protection methods (beehives, creosote jars, concrete pyramids, and wire-netting), providing data on both the efficacy as well as the practical constraints of these methods (Figure 1).

Importantly, Chapter 5's findings provide evidence that using creosote jars is not effective for tree protection and should be discouraged due to the potential environmental harm caused by creosote spillage (Van Zyl 2013). This method had gained popularity among some APNR stakeholders back in 2017-2018 prior to any scientific assessment on its efficacy. Chapter 5 contextualises the efficacy of each method versus its practicality (Figure 2). Beehives for example provide excellent protection to individual trees but are expensive and require high maintenance, especially in low rainfall periods. Concrete pyramids alternatively can significantly improve tree persistency, but the pyramids must be packed tight and create a minimum radius of $\geq$2 m away from the tree's main stem. Chapter 5's wire-netting results supported those found earlier in Chapter 3, in that the size of the tree is a significant determinant as to effectiveness of wire-netting for improving tree persistence.

Chapter 2's findings show that 77% of stakeholder respondents to the questionnaire believe that tree protection methods should be used in the APNR, with only 16% stating that they did not like seeing protection methods in trees. Tree protection methods were also highly supported by property owners (Chapter 2), who are usually the main implementers of this strategy (personal observation). It is therefore important that the results of Chapter 5 are made widely available to ensure that mitigation methods are correctly implemented and maintained for maximum sustainable success.

Building on from this research, an investigation into combining elephant deterrent methods may be beneficial for creating new tree protection methods. Additional methods to repel elephants from resources have included the use of chilies (Chang'a *et al.* 2016), 'smelly-elephant repellent' (Tiller *et al.* 2022) and even human sounds (Zanette *et al.* 2023). Exploring how these methods, among others, can be implemented for tree protection will help expand the 'toolbox' of tree protection methods available, allowing for a diversity of useable methods operating at different spatial scales under this elephant management strategy.

The lessons learnt from the evaluation of the tree protection methods in this thesis can also be applied to the broader field of human-elephant conflict. Whilst the use of beehives as an elephant deterrent method is well published (e.g. King *et al.* 2017, 2018), the research in Chapter 5 provides an important perspective regarding the supplementation of honeybees with feeding resources during seasons of low resource availability. This is particularly important for any conflict mitigation projects that may be using beehives in areas of low resource availability for the honeybees. Chapter 5's results also show that for distance barriers in the form of rocks (or in this case concrete pyramids), the actual distance created between the elephant and its intended resource is a vital component for the method's effectiveness. Conflict between humans and elephants can arise when elephants are attracted to water pipes for example (Thouless 1994), and thus ensuring that barriers are the correct radius around a resource is necessary to ensure that elephants are kept at bay and to decrease the levels of human-elephant conflict.

Implementing tree protection methods in the broader sphere of elephant management

Evidence suggests that elephant populations are most stable in either large protected areas or small interconnected protected areas that allow for elephants to roam across varied spatial and seasonal gradients (Huang *et al.* 2024). Elephants in the Great Limpopo Transfrontier Conservation Area (GLTFCA) show continual movements across international borders, highlighting the need to create safe movement passages for elephants to redistribute from South Africa's KNP into neighbouring cross-border protected areas (Cook *et al.* 2015, Appendix 1: Henley *et al.* 2023). These movements would help create a more vast spatial and temporal distribution of elephant impact, thereby promoting a more heterogeneous system (Ferreira *et al.* 2017), particularly as the elephant population is continually growing within the GLTFCA (GLTFCA 2022).

However, whether elephants are i) redistributing themselves over expanded protected areas; ii) concentrated in protected areas such as the APNR where water is readily available; or iii) are confined to small, protected areas; tree protection methods can still serve an important role by protecting iconic tree species within a landscape. Several decision making processes will influence the success of each tree protection method though, which will be briefly discussed below (Figure 2).

<u>Cause of implementation of tree protection methods (Sections 1 and 4)</u>

Conservation managers will need to decipher what is bringing about the original need to implement tree protection methods. This can include i) an over-abundance of artificial waterholes leading to elephants increasing their time spent in the area (Chapter 3, Cook *et al.* 2023b); ii) the protected area is too small to manipulate elephants' spatial and temporal movements (Thompson *et al.* 2022); iii) there are a select few iconic trees that require protection either due to aesthetic (Edge *et al.* 2017) or ecologic purposes (e.g. habitat creation, Chapter 4); additional financial income (e.g. honey production if beehive implementation and production is carried out at a large scale and in favourable environmental conditions, as discussed in Chapter 5); or stakeholders are concerned about elephants impacting trees and are trying to alleviate the impact on certain species (Chapter 2).

<u>The weight of stakeholders' values (Figure 2, Sections 1-4)</u>

The inclusion of stakeholders values in conservation decision making processes is important for reducing internal conflicts surrounding management decisions (Young *et al.* 2010), providing greater legitimacy for these decisions (Svarstad *et al.* 2006), and promoting a demographic process for decision making (Webler and Renn 1995). However, (Law *et al.* 2018) states that equity surrounding stakeholders' values should be explicit within the problem context and with respect to predetermined objectives. This means that the value of stakeholder groups can vary depending on the issue of concern. In India for example, Nayak and Swain (2022) suggest that stakeholder values surrounding elephant management decisions can be influenced by how impacted (positively or negatively) a stakeholder is by the decision. Should those most impacted on by a conservation problem and its pending decision have the greater say? In the APNR, it may be argued that qualified conservation managers who must carry out important elephant management decisions should have their values highly weighted in the decision-making process. However, landowners and hospitality stakeholders may feel that their values should be highly weighted as their livelihoods could be impacted by these decisions (e.g. if the closure of waterholes or the culling of elephants potentially negatively affect tourism). Importantly, these decisions require discussions across stakeholder groups, where concerns can be raised and discussed in a transparent manner to promote legitimacy surrounding the decision (Svarstad *et al.* 2006, Nayak and Swain 2022).

<u>Tree size morphometrics and species (specifically wire-netting) (Figure 2, Section 3.1)</u>

The findings of Chapters 3 and 5 show that wire-netting is most effective on large trees (main stem diameter ≥40 cm). Wire-netting should thus not be used for smaller trees that are more likely to be toppled or snapped by elephants. Furthermore, wire-netting is designed to minimise bark-stripping by elephants and should therefore be applied to trees that are most at risk to being bark-stripped, for example *Sclerocarya birrea* and *Senegalia nigrescens* (Helm *et al.* 2009, Vogel *et al.* 2014). Personal observations in the APNR of wire-netting on tree species that are not vulnerable to being bark-stripped by elephants, such as *Combretum imberbe*, could, for example, represent a misuse of financial resources, as the wire-netting will be protecting against an elephant impact type (bark-stripping) which does not usually occur on these species of trees.

Climate, habitat-type, and competition (specifically beehives) (Figure 2, Section 4.2)

African honeybees (*Apis mellifera scutellata*) are most efficient in wetter climates that support a wide range of floral species for honeybees to utilise (Johannsmeier 2001). Results from Cook *et al.* (2018) for example, show the high costs associated with providing honeybee colonies with supplementary feed that can only be mitigated through the commencement of large-scale honey production activities. Recent research by Ndlovu *et al.* (2023) though has provided a baseline summary of the species of pollen contained in the honey of honeybees within the lowveld savanna landscape (Appendix 2). This baseline could aid conservation managers in deciding whether they have the correct floral species for the implementation of the beehive mitigation method in the lowveld savanna. Conservation managers also need to be aware of interspecies competition. Research by Thornley *et al.* (2024) has shown that honeybee competition with ants (*Camponotus* and *Crematogaster* spp.) at feeding stations may decrease effectiveness of honeybees in resource-limited periods (Appendix 3). Furthermore, there are also concerns over the impact that high densities of honeybees may have on other indigenous pollinator-species (Martins 2004, De Morney and Moolman-Van der Vyver 2022). This method should therefore be implemented with caution in mind, and it would be recommended to sample and compare the pollinator biodiversity, both before and after the implementation of this method, to evaluate whether the presence of African honeybees in the beehives are impacting other pollinators (King, Serem, *et al.* 2018).

Scale of implementation and limitations (Figure 2, Sections 3 and 4)

Chapter 2's findings showed that one of the major concerns stakeholders had about tree protection methods were the financial costs and general practicality of implementing the methods. However, these will differ across each method (Chapter 5), whereby an expensive and highly labour-intensive method such as beehives will limit its usage-scale (even if highly effective), as will the application of the labour-intensive concrete pyramid method. Wire-netting, being cheaper and requiring less maintenance, may therefore me more practical over a greater number of trees in comparison to more expensive or labour-intensive methods such as pyramids and beehives (even if the overall results may be less effective than other methods). All three methods will still require maintenance over time, and it is important that conservation managers understand the reoccurring financial costs and practicality of each method to calculate the practical scale for method implementation and would not logistically be viewed as a landscape approach towards limiting elephant impact on large trees (Henley and Cook 2019).

Whilst tree protection methods may be a viable option for conservation managers to slow down the mortality rate of large trees, these methods alone are not a viable option for ensuring the persistence of large tree populations if other management interventions are not carried out at larger scales to reduce elephant densities in areas of concern (Pienaar 2012, Henley *et al.* 2023). Management interventions will need to assess where 'bottleneck' effects may be occurring within a particular tree species' population demographics before identifying appropriate interventions which may address the 'bottleneck' within the population (Helm and Witkowski 2012, Henley and Cook 2019). These interventions may focus on addressing concerns surrounding seed predation (Helm, Scott, *et al.* 2011), seedling recruitment into adult trees from herbivory or fire (Moe *et al.* 2009, Helm, Wilson, *et al.* 2011), or the loss of adult trees from elephant impact and other environmental external agents (Das *et al.* 2022, Cook *et al.* 2023a).

Interventions to reduce herbivory levels on large tree populations (both from elephants and other herbivores) and allow for smaller trees to recruit into large adults may include herbivore exclusion plots (Western and Maitumo 2004) or the artificial propagation of seeds into seedlings that are protected from both fire and herbivory (Scholtz 2007). As previously discussed, the closure of waterholes can help manipulate the temporal and spatial movements of elephants and their subsequent impact (MacFadyen *et al.* 2019), whilst it remains to be seen if inducing a 'fear' aspect into elephant populations through human disturbances will reduce the time spent in sensitive vegetation zones and have the desired effect of allowing smaller trees to be recruited into adult size classes (Cromsigt *et al.* 2013).

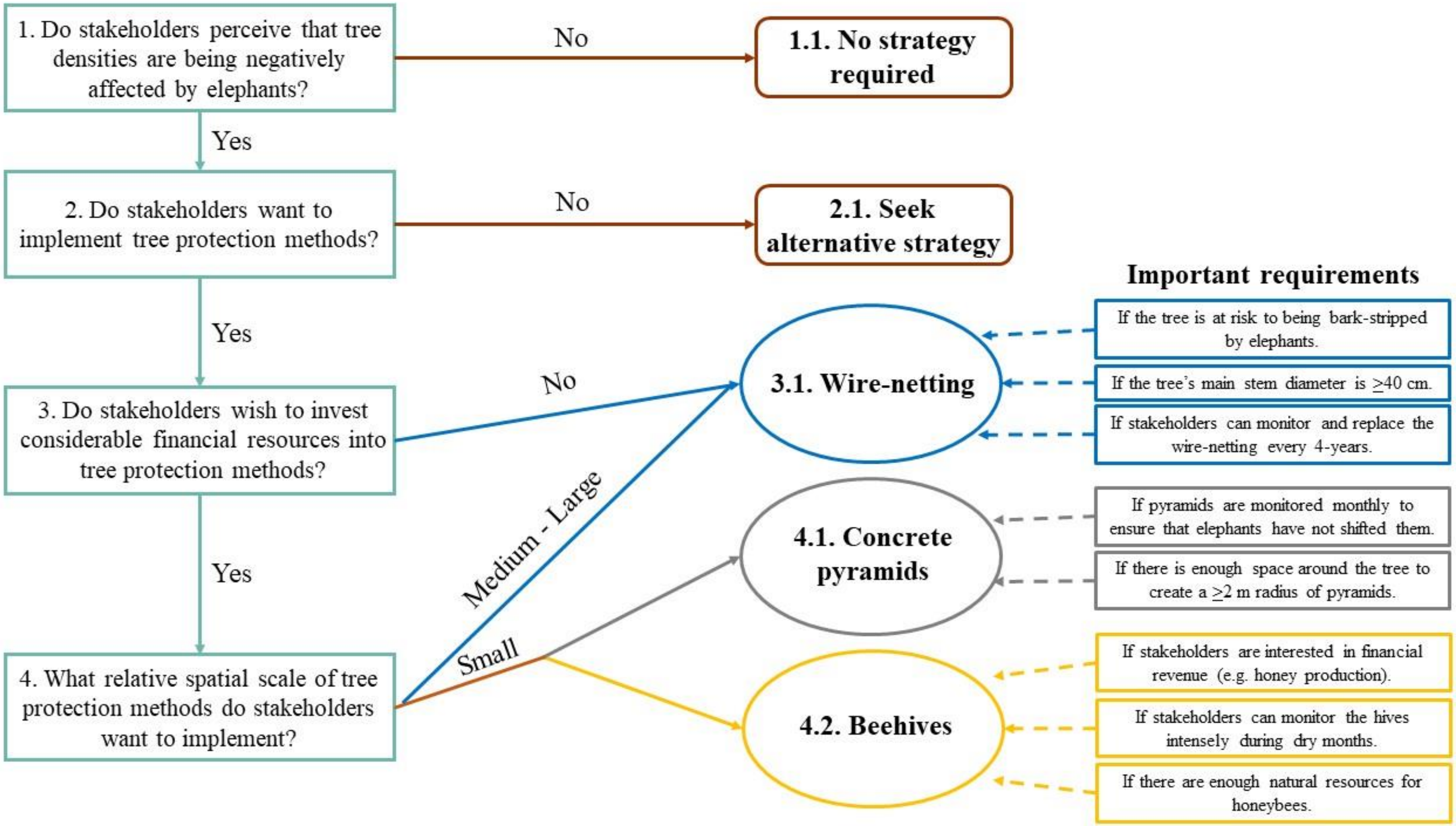

Figure 2. Conceptual decision diagram of a decision-making process for selecting either beehives, concrete pyramids, or wire-netting as tree protection methods as a part of an elephant management strategy to protect large trees from elephant impact.

Conclusion

The research in this thesis aims to contribute towards the greater understanding of elephant-tree ecology and interactions in a semi-arid savanna system containing a high number of artificial waterholes. It also addresses how stakeholder values can vary in terms of decision-making processes surrounding elephant management. Elephant impact on large trees is complex and non-uniform, with tree elephant impact levels varying across different tree species, tree size classes and rainfall gradients. These complexities will therefore determine how the impact of elephants will affect other species (e.g. white-backed vultures) and when management interventions may be required. Whilst tree protection methods may not influence the large-scale spatial and temporal movements and impacts of elephants, they provide an array of stakeholders with the ability to protect tree species across their protected areas on a smaller scale. Importantly though, the correct implementation and maintenance of these methods is required to ensure that the trees are correctly protected. These methods can therefore be implemented within an elephant management plan as a 'tool' in a 'toolbox' of available elephant management strategies.

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Appendix 1:

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Article

A Phased Approach to Increase Human Tolerance in Elephant Corridors to Link Protected Areas in Southern Mozambique

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Abstract: Pathfinding elephants are moving through human dominated landscapes, often across international boundaries, thereby playing a vital role in connecting protected areas. Their movements are a call to action to not only understand their spatial requirements but to urgently work towards innovative ways to make people's livelihoods compatible with conservation outcomes so that coexistence and connected landscapes can prevail. We discuss the first three phases of a long-term strategy to conserve elephant corridors whilst incorporating the socio-economic needs of the people that share the landscape with them. We present a comprehensive satellite-tracking history of elephants across two transfrontier conservation areas (TFCA), represented by Great Limpopo- and Lubombo TFCAs and involving four countries (South Africa, Zimbabwe, Mozambique and Eswatini) to flag where linking corridors exist. We use innovative cafeteria-style experiments to understand which elephant-unpalatable plants would offer lucrative alternative income streams to farmers living in human–elephant-conflict hotspots. The most suitable unpalatable plants are chosen based not only on whether they are unpalatable to elephants, but also on their life history traits and growth prerequisites. We consider a combination of potential economic values (food, essential oil, medicinal and bee fodder value) to ensure that selected plants would accommodate changing economic markets. Lastly, we highlight the importance of combining food security measures with ensuring people's safety by means of deploying rapid-response units. By implementing these three phases as part of a longer-term strategy, we draw closer to ensuring the protection of bioregions to achieve biodiversity objectives at a landscape scale.

Keywords: elephant movements; corridors; elephant unpalatable plants; human safety; coexistence

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1. Introduction

On a continental scale, primarily because of the illegal trade in ivory, elephants have recently been listed as Endangered by the IUCN Red List of Threatened Species™ [1]. Thirty years ago, the southern African states had a little over 20% of Africa's continental elephant population [2]. Today, these southern states have become the last stronghold of the African elephant as they hold over half of the continental population due to excessive poaching in Central and East Africa. Of the remaining elephants, 76% of elephants are found in populations spread over more than one national border [3], as with the meta-population of elephants we discuss here who share borders between Mozambique, Zimbabwe, South Africa and Eswatini. Each of these countries have Protected Areas (PAs) with varying densities of elephants. Mozambique and Eswatini have relatively low densities of elephants [4] compared to the neighbouring expanding populations of the Kruger National Park (KNP) in South Africa and Gonarezhou National Park (GNP) in Zimbabwe. As 54.7% of elephants' current range is outside of reserves [5] and elephants are known to move back to areas where they once occurred [6], elephant movement outside of PAs and across human-dominated landscapes is to be expected.

Human–Elephant Conflict (HEC) is rapidly increasing as elephants are being compressed within their natural range alongside burgeoning human populations, resulting in damage, economic losses, injuries and death of people and elephants [7,8]. Crop raiding by elephants represents a common form of HEC and could be driven by a lack of micro-minerals that are not available within the PAs when resources are limited such as during the dry season [9,10], although elephants are known to feed on cultivated crops even when sufficient natural forage is available, due to their high nutritional value, low natural defences and ease of access [11,12]. Irrespective of the drivers of crop-raiding in elephants, HEC represents a problem that poses serious challenges to wildlife managers, local communities, and elephants alike, and as elephants are highly adaptable and intelligent, finding sustainable mitigation solutions can prove difficult [6,13]. Hard barriers such as electric fencing often threaten connected landscapes if not strategically placed around local cluster crops and can prove to be expensive and ineffective if not maintained once elephants learn to breach them [14,15]. Furthermore, labour-intensive methods such as beehive fences or actively repelling elephant incursions using chilli smoke or noise aversion are not practical on a large scale [16]. Novel approaches are thus required to decrease HEC and increase human tolerance towards elephants within defined elephant corridors. One such approach is the growing of alternative crops that are not only unpalatable to elephants, but which can provide a source of alternative income [17]. Previous studies have shown that plants that contain higher amounts of secondary plant products were less attractive to elephants than maize [18].

On an ecological scale and beyond the local scale of crops that require protection within corridor zones, PAs are becoming islands in a sea of human development and over time this will have irreparable biodiversity implications [19,20]. The IUCN's Guidelines for Conserving Connectivity through Ecological Networks and Corridors outlines the importance of connected ecosystems to enable essential ecological functions such as migration, hydrology, nutrient cycling, pollination, seed dispersal, food security, climate resilience and disease resistance [21]. Connecting PAs across political borders, alongside building more sustainable, rural economies with communities that live in and around corridors delineated by elephant movements, is of prime importance [22]. To do so requires an understanding of the linkages between PAs that are being forged by collared, trailblazing elephants. Thereafter, people's financial assets (food crops) require protection, or people need to be equipped with the tools to offset any seasonal crop losses with alternative income streams to increase tolerance [23]. As safety ranks second on Maslov's hierarchy of needs after the psychological need for food as one of the survival prerequisites, human safety against marauding elephants needs to be addressed where people and elephants coexist [24]. Therefore, to contribute towards the ecological processes that propagate the coexistence of elephants, their habitat, and people, we present a phased approach of a long-term strategy developed for southern Mozambique, aimed at promoting coexistence between people and elephants while ensuring that landscape connectivity is maintained. Firstly, we discuss the use of satellite tracking of elephants to identify corridors linking PAs. Secondly, we make use of a cafeteria-type experiment involving semi-habituated free-roaming elephants to determine which literature-based elephant-unpalatable plants and those with commercial, medicinal and/or bee fodder value as potential alternative revenue streams are avoided by elephants. During the experimental setup, we also tested several crops planted by people in potential corridors and known to be palatable to elephants.

Lastly, we evaluate ways to ensure human safety as a priority once elephant tracking data have revealed potential conflict hotspots.

2. Material and Methods

2.1. Phase 1–Satellite Tracking Elephants

Study Site

Our study site is defined by the movements of the global positioning points of satellite-collared elephants. The Great Limpopo Transfrontier Conservation Area (GLTFCA) is located across the international boundaries of South Africa, Mozambique and Zimbabwe. It encompasses an area of around 100,000 km^2, incorporating the KNP (South Africa), Banine, Limpopo and Zinave National Parks (Mozambique), Gonarezhou National Park (Zimbabwe), as well as other smaller PAs. Midday temperatures range between 20 and 30 °C, with a predominantly summer mean annual rainfall of 500 mm [25]. This Transfrontier Conservation Area is linked to the Lubombo TFCA (LTFCA), which includes Maputo Special Reserve (Mozambique), Hlane Royal National Park (Eswatini), Tembe Elephant Park (South Africa), as well as other smaller PAs (Figure 1). The LTFCA encompasses an area of around 4195 km^2, with a mean annual rainfall of 500–800 mm and midday temperature ranges of 20–28 °C [26].

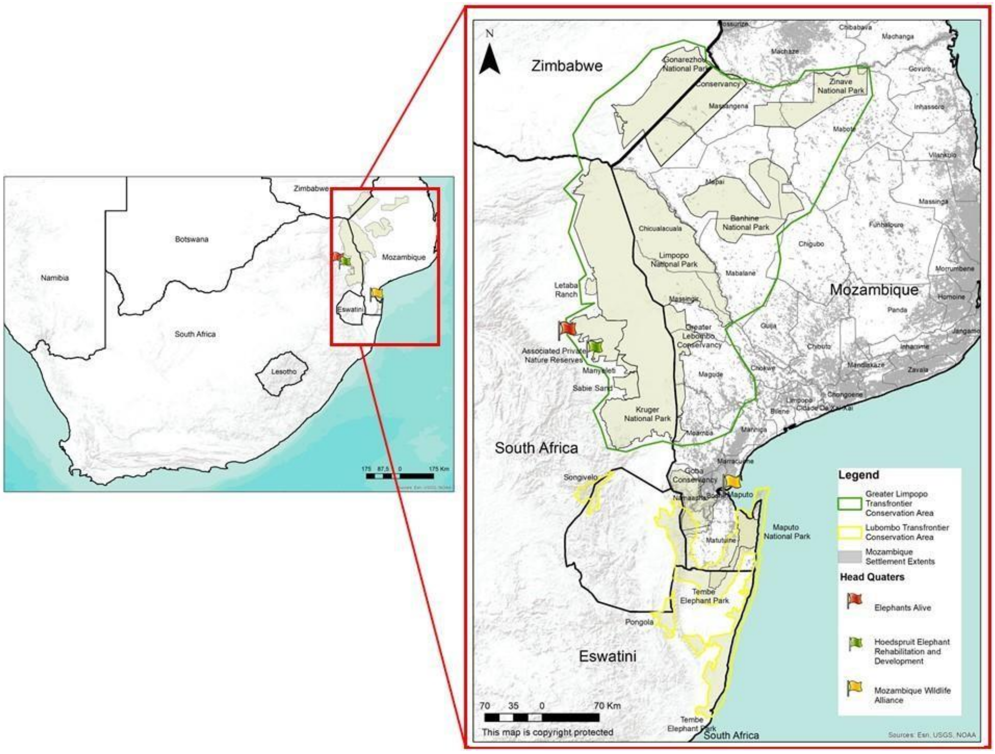

Figure 1. Maps showing the location of the main headquarters in South Africa and Mozambique. The red square depicts the study site as defined by the elephants' movements. The enlarged map shows a more detailed representation of the protected areas and Mozambican districts within the study site. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022).

Elephants Alive (a South African based NGO) first started collaring elephants in 1998 following the standard operational procedures by the South African National Parks Animal Use and Care Committee [27], using collars sourced from AWT (African Wildlife Tracking, Pretoria, South Africa) and Savannah Tracking (Nairobi, Kenya). All GPS fixes and associated information are kept in a central database managed and curated by Elephants Alive using Ecoscope analytical tools https://ecoscope.io (accessed on 1 July 2022) and an Earth Ranger platform https://www.earthranger.com (accessed on 1 February 2019). Erroneous GPS fixes were filtered out based on a biologically defined upper movement limit of 7 km/h [28]. All spatial data were projected to the Universal Transverse Mercator (UTM) WGS1984 reference system (Zone 36S). In total 140 elephants have been collared from 1998–2022 (Figure 2).

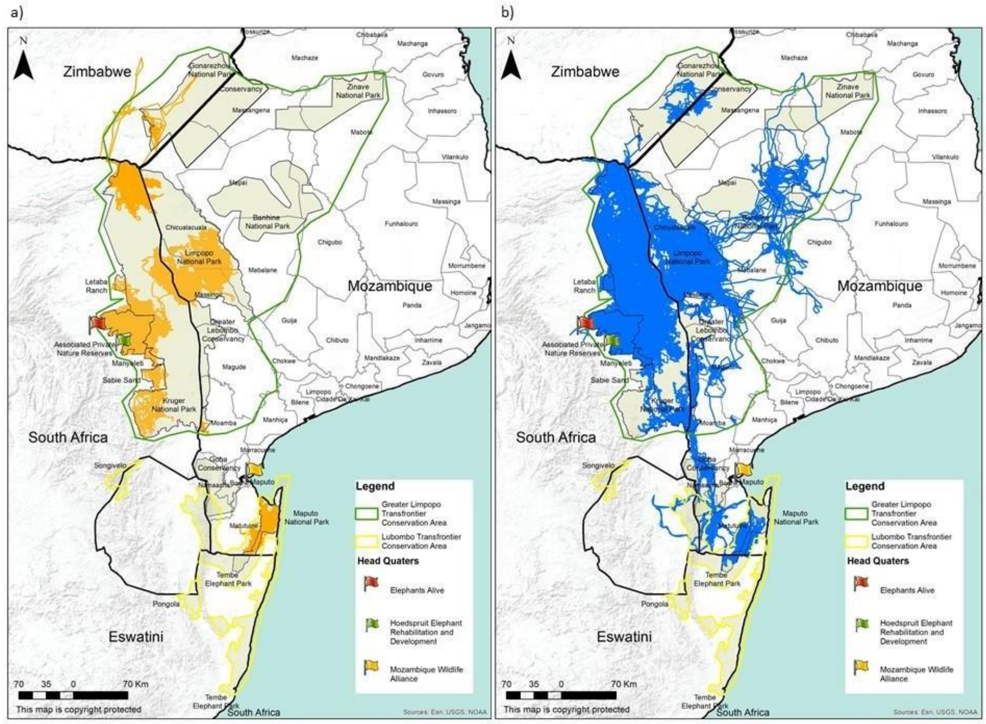

Figure 2. The transboundary movements of elephants between South Africa, Mozambique and Zimbabwe. A total of 38 cows from family units have been collared over time with the first cows (**a**) collared in 2004 in the Associated Private Nature Reserves (APNR) to the west of the Kruger National Park (KNP). In 2008–2012 elephant cows were collared in the Makuleke Concession in the northern regions of the KNP. In 2016–2021 cows were collared in Limpopo National Park (LNP) and in 2019–2022 in Maputo Special Reserve in Mozambique. The first two cows were collared outside of protected areas (PAs) in 2022. Of the 102 bulls collared over time, the first (**b**) bulls were collared in 1998 in the APNR, with seven bulls collared on the eastern border of the KNP in 2006. Bulls were also collared from 2008–2012 in northern KNP. The first bulls were collared in LNP in 2016–2021 and in Banhine National Park in 2019. The first bull was collared outside of PAs in Mozambique in 2018. In total 140 elephants have been collared over time, not including any recollaring events. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022).

Within PAs, Elephants Alive first collared elephants in the Associated Private Nature Reserves (APNR) in 1998, on the western boundary of the KNP [29,30] (Figure S1), where to date 18 female and 55 male elephants have been collared of which 37 elephants were recollared to ensure a long-term tracking dataset. We set out to investigate the extent of transboundary movements as amalgamated private conservation areas planned to expand over time. In December 2002 sections of the fence that separated the KNP in South Africa from Limpopo National Park (LNP) in Mozambique were removed [31]. Within the KNP, seven bulls were collared in 2006 on the eastern border with Mozambique to see if they were utilizing LNP to which they had access since sections of the dividing fences were removed (Figure S2). Between 2008 and 2012 we collared 12 and recollared nine elephants in the Makuleke Community of northern KNP to determine whether they were using the Sengwe corridor linking KNP with GNP in Zimbabwe (Figure S3). Collaring elephants within Mozambique's PAs started in 2016 with six female and 13 male elephants collared in LNP from 2016–2021 to further understand cross-border movements (Figure S4). From 2018–2022, we collared a total of 22 elephants outside of PAs of which two were females within a family unit (Figure S5). In 2019 we collared the first bull in Banhine National Park which has a very low density of elephants (Figure S4—individual tracks depicted in black). From 2019–2022 six females were collared in Maputo Special Reserve (Figure S6).

Using elephants as the landscape planners for connectivity over national boundaries, we have identified several corridors in which the knowledge gained from the cafeteria experiments of phase 2 of this study will be applied. Ensuring human safety was phase 3, already commenced in 2021 and applied over the larger landscape with elephant movements enabling us to understand where our efforts can be concentrated across southern Mozambique (Figure S1–6).

2.2. Phase 2 – Cafeteria Experiments

2.2.1. Study Site

Cafeteria experiments took place at the Hoedspruit Elephant Rehabilitation and Development (HERD) orphanage in Kapama Private Game Reserve (Kapama) (24.420343° S; 31.100546° E). The HERD orphanage was built in 2019 and serves as a sanctuary for orphaned African elephants (Figure 1). HERD currently has 16 semi-habituated elephants of which two bulls were made available for the cafeteria experiments, namely Sebakwe (age 37 years) and Somopane (age 35 years) [32]. The HERD orphanage offers elephant interactions in the mornings to tourists, where elephants are fed a combination of peanuts and oranges, after which they are free roaming, feeding on natural vegetation throughout the day.

2.2.2. Plant Type Selection and Harvesting Criteria

Eighteen plant or crop types were chosen for the cafeteria experiments, the majority of which have a high essential oil potential (African blue bush (*Ocimum americanum* L.), Cape gold (*Helichrysum splendidum* Thunb.), Cape snowbush (*Ericephalus africanus* L.), borage (*Borago officinalis* L.), bulbine (*Bulbine frutescens* L.), fever tea (*Lippia javanica* Burm. f.), geranium (*Pelargonium graveolens* L'Heritier), lavender (*Lavandula x intermedia* L.), lemon grass (*Cymbopogon* L.) and worm wood (*Artemisia afra* Jacq.)). The selection of plant types included common food crops cultivated by subsistence farmers in Mozambique (cassava (*Manihot esculenta* Crantz.) and corn (*Zea mays* convar. *Saccharate* var. *rugosa* L.)), unpalatable crops already described in the literature (bird's eye chilli (*Capsicum frutescens* L.), garlic (*Allium sativum* L.), ginger (*Zingiver officinale* Roscoe) and sunflower (*Helianthus annus* L.)), a potential aromatic herb not yet tested (rosemary (*Rosmarinus officinalis*)) and a commercial crop native to Mozambique and used extensively within the tea industry (hibiscus (*Hibiscus sabdariffa* L.) [33].

Of the plant or crop types selected for their essential oil content and thus a potential alternative crop due to their unpalatability, many also have a multi-purpose value such as medicinal and high bee fodder values (pollen and nectar). Therefore, the cafeteria-style experiments were used to determine if plants with a known high essential oil, medicinal use or other commercial value were also unpalatable to elephants. As beehive fences have already proven to represent effective barriers to food crops throughout Africa and Asia [34,35], knowing which plants represent good bee fodder would help ensure that subsistence farmers have viable bee swarms not only to protect their crops, but also to pollinate all their agricultural products [36]. Each food type was rated on a 4-point scale according to different categories, with ′1′ representing a good plant choice within a high HEC area, whilst ‘4′ meant that the plant would not be suitable for several reasons, including requiring considerable protection to prevent HEC (Table 1).

We grew 15 of the plant types at the Elephants Alive HQ (Figure 1) to ensure a fresh supply during experimentation. As the fruit bodies of cassava, corn and garlic were less susceptible to wilting and rapid degradation, they were ordered and transported from elsewhere. All 18 plant types were prepared and packaged in the morning before sunrise and kept in a cooler box until just before experimentation. As we were focussed on comparative selectivity between crop types, and not intake rates, only small portions, of equal weight and irrespective of the structural diversity between plant types, were used. For all the plant types presented, with the exception of corn, cassava, garlic and ginger due to availability, the whole fresh plant was presented to try and represent what crop-raiding elephants might encounter. This also ensured that the elephants could move through the experimental site quickly, assessing the diversity on offer, before becoming bored or satiated after feeding at only a few experimental troughs.

Table 1. The 4-point scoring of each of the chosen plant or crop types according to border life cycle characteristics (B), growth requirements (G), their potential economic value based on the literature (E) and their palatability following the cafeteria experiments (P). The reasoning behind the scores is explained under the motivation.

Categories	Score	Motivation
Broader life cycle characteristics	B	
Indigenous & perennial	1	Indigenous plants would be more resistant to pests and if perennial, less labour intensive to farm
Indigenous & annual	2	Indigenous plants would be more resistant to pests and if annual, more labour intensive to farm
Exotic & perennial	3	Non-native species are usually very susceptible to pests and if perennial, less labour intensive to farm
Exotic & annual	4	Non-native species are usually very susceptible to pests and if annual, more labour intensive to farm
Growth requirements	G	
Low rainfall dependent, any soil type & drought tolerant	1	Well adapted to arid regions, doesn't require rich soils and can withstand droughts
Medium rainfall dependent, nutrient rich/any soil type & drought tolerant	2	Adapted to medium rainfall, may or may not depend on particular soil types but still drought resistant
Medium rainfall dependent, nutrient rich/any soil type & drought intolerant	3	Adapted to medium rainfall, may or may not depend on particular soil types but not drought resistant
High rainfall dependent, nutrient rich/any soil type & drought intolerant	4	Requires high rainfall, may or may not depend on a particular soil type and not drought resistant
Economic value	E	
Has food-, essential oil-, medicinal- and bee fodder value	1	A very versatile plant type that has a very wide market value with the processing thereof adaptable to the demand
Has only three of the four potential value types	2	A versatile plant type that can adapt to different market demands
Has only two of the four potential value types	3	A plant type that has economic value, but which is limited in terms of what markets it can serve
Has only one of the four potential value types	4	A plant type that is specialised to only serve one market type
Palatability	P	
Was not eaten/ignored by elephants/spat out after tasting	1	Strongly avoided
Mostly played with the plants and didn't consume them	2	Avoided
Showed some interest and ate parts of the plant but played with other parts	3	Edible
Readily consumed all plant parts each time	4	Favoured

2.2.3. Cafeteria Experiments

The cafeteria experiments were run from 24 August–8 September 2022 and were approved by the Animal Ethics Screening Committee of the University of Witwatersrand, Johannesburg (AESC 2022/02/04/B). During this period, five experimental days of both morning and afternoon experimental sessions were carried out. For each experimental session, two cafeteria experiments were completed (one per elephant). Due to logistical constraints regarding the location of the semi-habituated elephant herd throughout the day, two separate experimental sites were used to accommodate the morning and afternoon feeding sessions. Morning sessions began at 9:30 am and afternoon sessions began at 3:15 pm. Wind and temperature measurements were recorded at the start of each feeding session.

The following methodology was carried out per cafeteria experiment (Figure 3): 18 rubber feeding troughs were placed 2 m apart in a semi-circular fashion. Each trough had 50 g of a randomly selected plant or crop type placed inside of it. The random plant type order ensured that no plant type would be favoured by the elephants based on its location throughout the cafeteria-style experimentation. Plant type order, however, remained constant for both elephants within an experimental session as they happened consecutively. Two video cameras were placed on opposite ends of the cafeteria site to record the full experiment. To begin the experiment, the elephant was brought to the same first feeding trough by its handler. Thereafter the handler removed himself from the experiment to avoid further influence. Upon reaching trough one, the elephant would have five minutes to feed throughout the whole cafeteria-style experiment without guidance. As soon as the experimental time was up, recording ceased, the handler guided the elephant away and the experimental session for that particular elephant ended. All remaining food items were removed from the trough and placed in corresponding bags. The same experimental setup was then prepared before the next elephant entered the site. For each trough, we recorded whether the elephant smelt, consumed, played with, or ignored the plant type. For consumed crops, the remaining crop materials were reweighed to calculate the quantity of each food type consumed of the original 50 g.

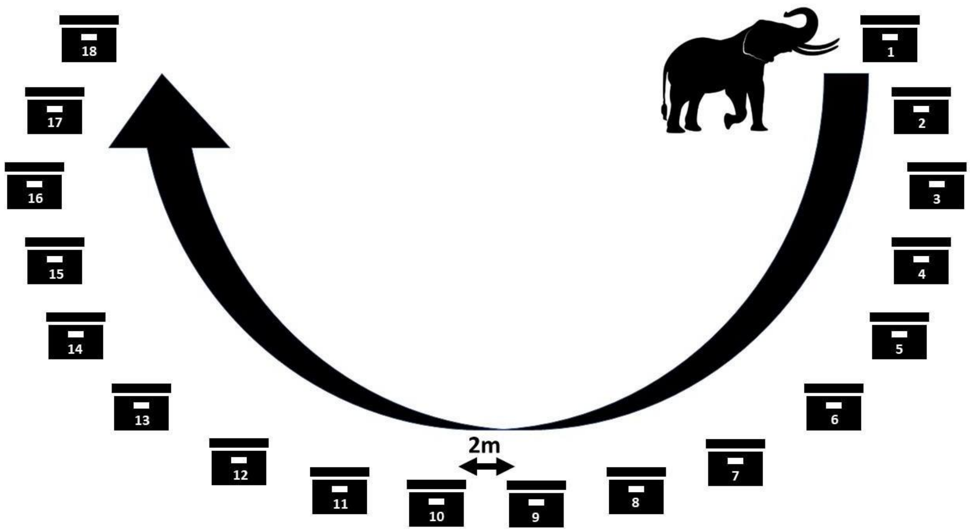

Figure 3. Diagrammatic view of a cafeteria experiment. Elephants were brought to the first feeding trough, after which they were left alone for five minutes to explore the eighteen feeding troughs. Each trough had 50 g of a randomly selected crop or plant type placed inside of it.

2.2.4. Data Analyses

All analyses were performed using R version 4.2.1 (R Development Core Team 2012). All tests were two-tailed and were considered significant at $p < 0.05$. Parametric tests were conducted where data fitted the relevant assumptions of normality and homogeneity of variance; otherwise, non-parametric equivalents were used.

We used a classification tree (CT) approach, based on conditional inference [37], to explore the predicting factor effects of crop type, elephant individual, session time (morning/afternoon), temperature and wind speed on crop consumption probability. The conditional inference approach avoids bias towards predicting factors, whilst allowing for data to be partitioned into multiple categories [38]. CTs were constructed using the party package [37].

We calculated Ivlev's electivity index as a measure for utilisation of food, which when consumed in larger proportion were considered preferred [39]:

$$E = ri - pi/ri + pi$$

where r is the proportion of the plant or crop type utilized and p the proportion of the plant available per session.

We developed a Generalised Linear Mixed Model following a Gaussian distribution to investigate if elephant selection of plant or crop types was influenced by the time of day, wind and temperature. Electivity was thus used as the response variable in relation to the crop type (categorical), speed of the wind (continuous), temperature (continuous) and time of day the session occurred (categorical), as covariates included as fixed effects. The elephant identity (categorical) was included as a random variable as was the session's number (categorical), accounting for repeated measures for each crop type and individual. Akaike Information Criterion (AIC) ranking was used to select our minimal model [40] (package: MuMIn, [41]). The p-values of the variables' effects were obtained using likelihood ratio tests of the full model with and without the effect in question to provide reliable estimates for regression parameters [42]. Where significance was found, post-hoc Tukey's tests were run using the 'emmeans' package [43] to compare means. Checks revealed no overdispersion (conducted by evaluating if the dispersion parameter (residual deviance/df) was between 0 and 1 [44]).

2.3. Phase 3 – Ensuring Human Safety

The mobilisation of the first Rapid Response Unit (RRU) in Mozambique in June 2021 consisted of two trained people on a motorbike together with a backup vehicle. Toolkits for mitigating human–wildlife conflict (HWC) consisted of the following: firecrackers, foghorns, vuvuzelas, paintball guns with chilli pellets, double shot launchers (15 mm) and danger tape. The Mozambique Wildlife Alliance (MWA) strategically operated the RRU and ensured their day-to-day running with strategic and financial support from Elephants Alive via our existing donor base. The RRU covered 15,480 km since being in operation (June 2021–June 2022) and responded to both reported HEC incidents as well as pre-empted incidents based on predicting elephant crop raids from elephant tracking histories. The reported incidents were obtained by phoning 21 districts every two weeks and working closely with Servico Distrital de Actividades Economicas (SDAE), which have been mandated by the Administração Nacional das Áreas de Conservação (ANAC) to deal with HWC in Mozambique. The RRU's scope of work is aimed not only at deterring elephants from potential crop-raiding at night, but also at spending considerable time educating the community about how to behave around elephants pre-and post-incursion events. Although most HEC incidents were mitigated within identified elephant corridor regions, HEC in Mozambique with its unfenced PAs is not restricted to corridors flagged by collared elephants but occurs widely throughout southern Mozambique (Figure 4).

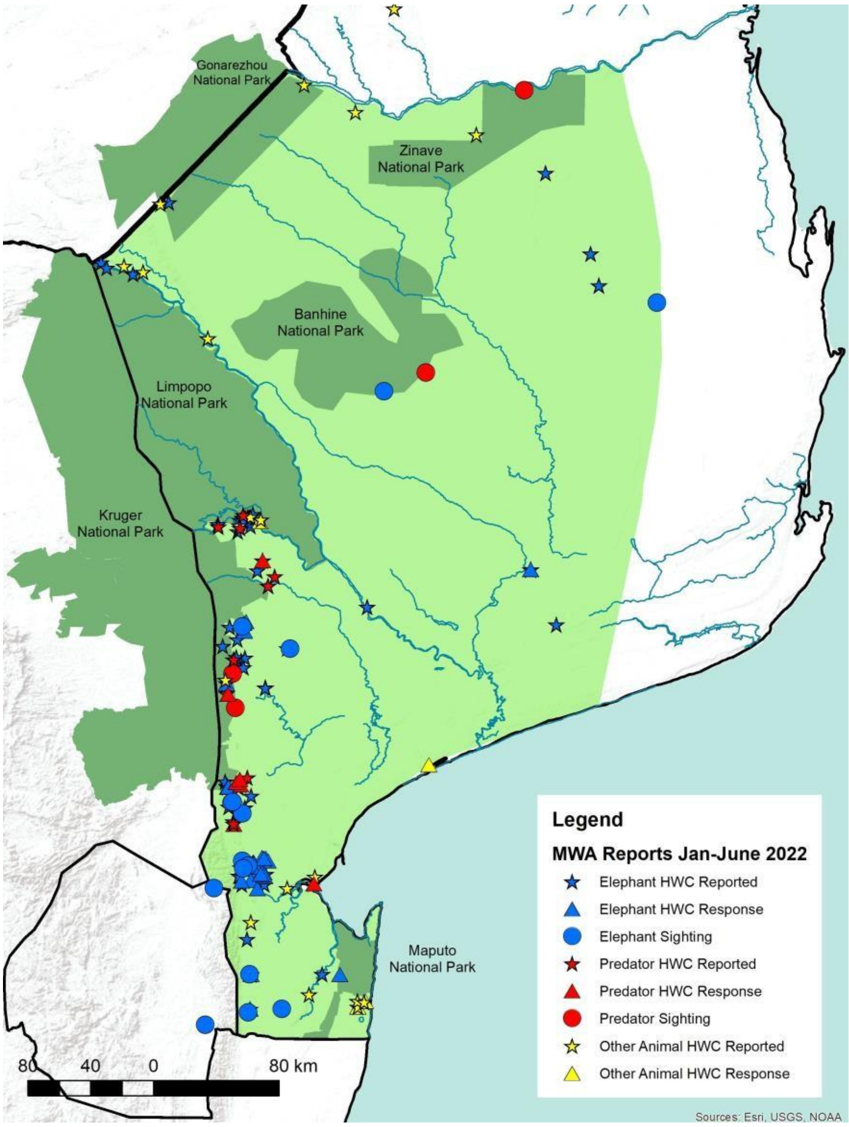

Figure 4. Human–wildlife conflict (HWC) events for a six-month period indicating that most conflict events are occurring within the corridor regions flagged by the satellite-collared animals moving between PAs.

3. Results

3.1. Phase 1 – Satellite Tracking Elephants

After 24 years of tracking elephant movements in relation to expanding conservation areas using satellite collars, we have amassed over two million data points. Of the two million data points through time, 9.5% are found outside of PAs. These related to 37 elephants having moved outside of PAs over time. Within South Africa (the APNR–KNP complex), seven elephants have moved outside of the PAs to the west and south. Seven elephants have moved out of KNP in South Africa into Mozambique, and two moved from northern KNP into Zimbabwe and back. Furthermore, six elephants have moved from southern KNP across southern Mozambique of which one entered Tembe National Park in South Africa and then proceeded to Eswatini with another bull. The other collared bull returned to the KNP and later Mozambique while the bull in Eswatini has remained trapped within an enclosure of 4.13 km^2 for almost a year (Figure S1–S6). The accurate delineation of the corridors used by elephants as well as the use of elephant tracking data to predict crop-raiding events forms part of larger study by Elephants Alive with publication of the results underway.

3.2. Phase 2 – Cafeteria Experiments

The analysis of the cafeteria experiments produced a CT of two inner nodes and three terminal nodes, with a 77.4% prediction success value. The results indicated that plant or crop type (p < 0.001), followed by session time (p < 0.05), were significantly associated with plant consumption probabilities (Figure 5). The CT divided the 18 plant types into 10 palatables and eight unpalatables (Figure 5) with varying degrees of selectivity (Figure 6), whilst further dividing the palatables into increased consumption probability in the afternoon sessions in comparison to the mornings (Figure S6).

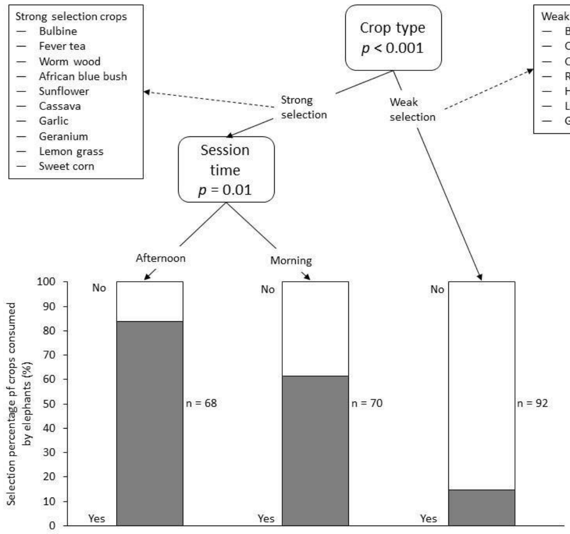

Figure 5. Results of the classification tree analysis representing the selection percentage of plant or crop types consumed by elephants in the cafeteria experiments.

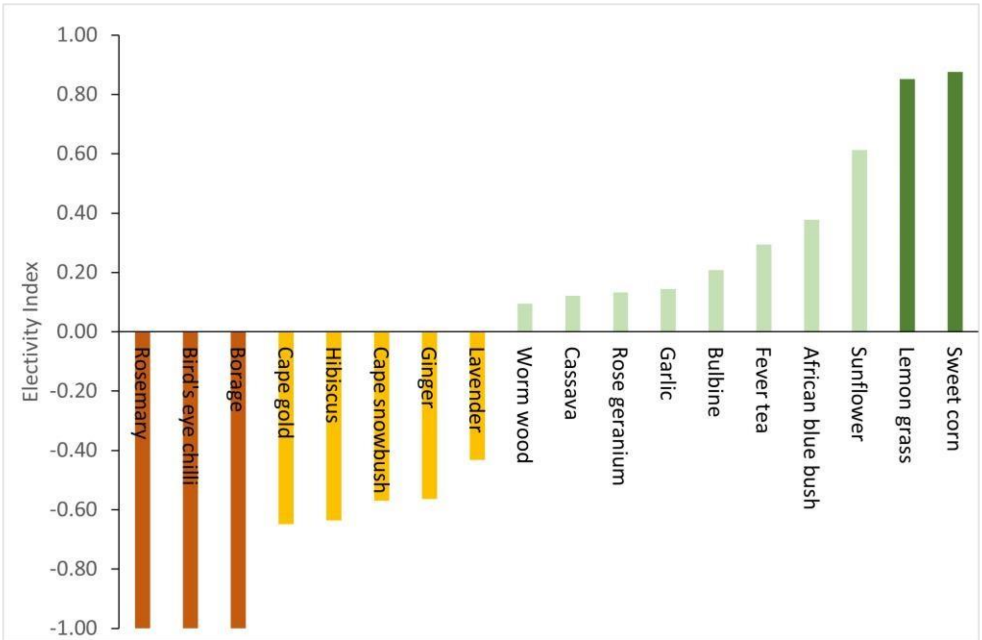

Figure 6. The Electivity Index in ascending order as calculated across all sessions for both elephants combined.

Electivity indices were significantly influenced by crop type (GLMM χ^2_{17} = 135.08, p < 0.0001, Figure 6, Table S1) and if the session took place in the morning or afternoon (GLMM χ^2_1 = 16.49, p < 0.0001, Figure S2, Table S1). Tukey's post-hoc testing with 95% confidence intervals when averaged over time of the session (see Table S1) showed that sweet corn (E_{mean} = 0.82 ± 0.30) and lemon grass (E_{mean} = 0.88 ± 0.28) were significantly preferred whereas borage (E_{mean} = −1.00 ± 0.29), bird's eye chilli (E_{mean} = −1.00 ± 0.29) and rosemary (E_{mean} = −0.99 ± 0.287) significantly avoided. Furthermore, significantly higher electivity indices were observed during the afternoon sessions (E_{mean} = 0.14 ± 0.22) compared to the morning sessions (E_{mean} = −0.38 ± 0.22). Moreover, there was no significant effect of wind (p = 0.25) nor temperature (p = 0.12) on the electivity index. Lastly, Elephant ID had a significant effect (GLMM χ^2_{17} = 13.268, p = 0.0003, Table S1), with Sebakwe selecting more crop types (E_{mean} = 0.09 ± 0.08) compared to Somopane (E_{mean} = −0.27 ± 0.09), but this only explained 14% of the variance. The number of the session did not have an effect on the electivity indices (GLMM χ^2_{17} = 1.16, p = 0.28, Table S1).

The growth traits, economic value and palatability of each plant were categorised according to the four-point scale mentioned earlier (Table 2). We then summed the scores per plant and rated them as (1) highly favourable to propagate in elephant corridors (the lowest overall score, i.e., 6), (2) favourable to propagate as an income-generating soft barrier (scores between 7 and 10), (3) not favourable to propagate as they were edible to the semi-habituated elephants, with the exception of ginger whose growth characteristics would not make it suitable given potential climatic effects (scores ranged from 11–15) and (4) only suitable as a food crop in need of protection from elephants (score above 16). Using these scores, a final list of potential alternative crops was generated to compare with what is available in the literature based on the crop's palatability, essential oil potential, medicinal and bee value (Table 3).

Table 2. The 18 plant types that were included in the cafeteria-type experiments. Their broad life cycle characteristics (B) were scored, while their growth requirements (G) and their economic value (E) were based on information available in the literature. Their palatability scoring was derived from the electivity indices of the elephants during the cafeteria experimental setup (P). The score for each category was based on the reasoning explained in Table 1. The colours under the economic value correspond with those of Figure 6 with rust representing the strongly avoided plants, yellow those that were avoided, light green those that were edible and dark green those that were favoured.

Crop	Latin Name	Origin	Native to Southern Africa	Life Cycle	Growing Condition		Drought Tolerant	Economic Value				Palatability to Elephants	Scoring				
					Rainfall	Soils		Food	Oil	Med	Bee		B	G	E	P	O
Borage	*Borago officinalis*	Middle East	No	Annual	Low	Any	Yes				N *	Strongly avoid	4	1	1	1	7
Bird's eye chilli	*Capsicum frutescens*	Africa & southeast Asia	Yes	Perennial	Medium	Any	Yes					Strongly avoid	1	2	2	1	6
Rosemary	*Rosmarinus officinalis*	Mediterranean region	No	Perennial	Low	Any	Yes				N	Strongly avoid	3	1	1	1	6
Cape gold	*Helichrysum splendidum*	Africa & Ethiopia	Yes	Perennial	Low	Any	Yes				P *	Avoid	1	1	2	2	6
Cape snowbush	*Eriocephalus africanus*	South Africa	No	Perennial	Low	Any	Yes				N	Avoid	3	1	2	2	8
Ginger	*Zingiber officinale*	Southeast Asia, India & China	No	Annual	High	Nutrient rich	No					Avoid	4	4	2	2	12
Hibiscus	*Hibiscus sabdariffa*	Africa	Yes	Perennial	Medium	Any	No				N	Avoid	1	3	1	2	7
Lavender	*Lavandula x intermedia*	France	No	Perennial	Low	Any	Yes				N	Avoid	3	1	2	2	8
Bulbine	*Bulbine frutescens*	South Africa	Yes	Perennial	Low	Any	Yes		Gel		P	Edible	1	1	2	3	7
Cassava	*Manihot esculenta*	South America	No	Perennial	Medium	Any	Yes				N	Edible	3	2	3	3	11
Fever tea	*Lippia javanica*	South Africa	Yes	Perennial	Low	Any	Yes				N	Edible	1	1	2	3	7
Garlic	*Allium sativum*	Middle Asia	No	Annual	Medium	Nutrient rich	Yes					Edible	4	2	2	3	11
Geranium	*Pelargonium graveolens*	South Africa	No	Perennial	Medium	Nutrient rich	No					Edible	3	3	3	3	12
African blue bush	*Ocimum americanum*	Africa, India & southeast Asia	Yes	Perennial	Medium	Nutrient rich	No				N	Edible	1	3	1	3	8
Worm wood	*Artemisia afra*	Africa & Ethiopia	Yes	Perennial	Low	Any	Yes				P	Edible	1	1	2	3	7
Sunflower	*Helianthus*	North America	No	Annual	Low	Any	Yes		Food		P	Favour	4	1	1	3	9
Lemon grass	*Cymbopogon*	Southeast Asia	No	Perennial	High	Nutrient rich	No					Favour	3	4	2	4	13
Sweet corn	*Zea mays convar. saccharata* var. *rugosa*	South America	No	Annual	High	Nutrient rich	No					Favour	4	4	4	4	16

* A pollen index (P) refers to the availability of pollen on a given beeplant, ranging from 0 (no pollen available) to 3 (major pollen source) [45]. The nectar (N) or 'sugar' value of a beeplant refers to the number of milligrams of sugar available per flower over a 24 h period [46].

Table 3. The final recommendation for the 18 crops tested in terms of their palatability. The scores were obtained from several factors and not their palatability to elephants alone. Overall scores refer to crops that will be very suitable to test due to their unpalatability to elephants, their growing requirements as well as their versatile economic value (score below 7). Some crops may be unpalatable or edible, but they would be suitable for propagation and have high market values (score 7–10). Others were all edible to the elephants except for ginger so they would be at risk of crop damage (score above 10).

Type	Overall Score	Literature Description	Reference
Bird's eye chilli	6	Unpalatable	[b] [45], [a] [47]
Cape gold	6	Unknown	[o] [48], [m] [49], [b] [45]
Cape snowbush	6	Unknown	[o] [50], [m] [51], [b] [45]
Rosemary	6	Unknown	[o] [48], [m] [52], [b] [45]
Borage	7	Unknown	[o, m] [53], [b] [45]
Bulbine	7	Unknown	[o, m] [54], [b] [45]
Fever tea	7	Unknown	[o] [48], [m] [50], [b] [45]
Hibiscus	7	Unknown	[m] [55], [b] [45]
Worm wood	7	Unknown	[o] [48], [m] [56], [b] [45]
African blue bush	8	Unknown	[o] [57], [m] [58], [b] [45]
Lavender	8	Unknown	[o] [48], [m] [59], [b] [45]
Sunflower	9	Unpalatable	[o] [60], [b] [45], [a] [61]
Cassava	11	Palatable	[b] [45], [a] [62]
Garlic	11	Unpalatable	[o] [48], [a] [17]
Geranium	12	Unknown	[o] [48], [m] [63]
Ginger	12	Unpalatable	[o] [48], [a] [17]
Lemon grass	13	Unpalatable	[o] [48], [m] [64], [a] [17]
Sweet corn	16	Palatable	[a] [62]

o—oil property, m—medicinal property, b—bee food property, a—attractiveness to elephants.

3.3. *Phase 3—Ensuring Human Safety*

The reach of the RRU involves three districts (Namaacha, Moamba and Matutuine), which have all been identified as high-HWC areas (Figure 1). A total of 270 conflict events have been reported in the past year of which 65% of all HWC incidents involved elephants. A seasonal effect is apparent in elephant crop-raiding events with the highest frequency of events occurring in the early dry season. Despite the near doubling of conflict reports in the second half of the study year, there has been a concurrent 34% decline in actual conflict events that the RRU needed to try and deal with over the same period. The efficacy of the RRU has also increased over time as unsuccessful mitigation events led by the RRU have decreased from 64% in the first half of the year to 36% in the second half of the study year. Overall, the RRU has mitigated 76% of all HWC conflict events (Table 4). They have also played a considerable role in pre-emptive mitigation through educational workshops. In 16 training sessions they have trained 178 people in the last year, delivering 37 toolboxes to trained community members. The RRU has empowered community members to deal with conflict themselves by delivering deterrence equipment after training or teaching them to manufacture their own means of mitigation such as chilli bricks. The RRU has recorded 725 units of deterrence equipment used by themselves while in total 4685 units of equipment have been delivered to the communities.

Table 4. The metrics of the RRU in operation within southern Mozambique over a 12-month period with the proportional difference in the categories over time and as divided int6 two six-month periods to evaluate the progress made to date in terms of mitigating HEC.

Description	1st 6 mon.	2nd 6 mon.	1 Year	Prop. diff. between Periods
Number of conflict cases	91	179	270	34% vs. 66%
Conflict cases involving elephants	54	121	175	31% vs. 69%
Conflict cases involving predators and other ungulates	37	58	95	39% vs. 61%
Number of responses by the RRU	82	39	121	68% vs. 32%
Number of successful chases	64	28	92	70% vs. 30%
Number of unsuccessful chases	18	10	28	64% vs. 36%

4. Discussion

Bioregions represent areas of land or water where the geographical distribution of biophysical attributes, ecological systems and human communities define the area [65]. They redefine the scale at which biodiversity can be protected and often involve a network of transfrontier conservation areas that necessitate collaboration between states, the private sector, and communities [66]. Elephants have large spatial requirements driven by a need to access resources over vast areas, causing a substantial proportion of elephants to be distributed across more than one national border [3,28]. Connecting PAs across political borders, whilst building more sustainable, rural economies in collaboration with communities that live in and around corridors delineated by elephant movements, becomes a critical long-term solution to achieving biodiversity outcomes. However, where elephants and people intersect, increased HEC and retaliation killings of corridor-moving elephants could terminate landscape connectivity [67]. Insight into elephant movements outside of PAs thus helps place localized HEC incidents within a larger perspective, assisting with predicting when and for how long HEC incidents in particular areas along the length of mapped corridor zones can be expected. This enables us to formulate both reactive short-term mitigation strategies whilst working towards longer, proactive mitigation strategies to decrease HEC. We discuss the first three phases of a long-term transnational community-based approach to protect African elephants and their habitat through a unique multidimensional and integrated approach of community engagement, knowledge creation and practical conservation action.

Elephants moving beyond PAs with satellite tracking devices become important landscape planners for bioregions. Mapping potential corridors with the elephants as the intelligence agents represents the first step to understanding landscape connectivity. These movements occur under the cover of darkness due to the risky human-dominated landscapes they need to cross [68]. Although our elephant tracking history revealed only 9.5% of data recordings have occurred outside of PAs, this can be explained by a long initial history of recording elephant movements within fortified PAs within South Africa. When considering only the PAs in neighbouring Mozambique, we found that 28% of movements were outside of PAs, which was closer to the findings of [5] where more than half of elephant movements over largely unfenced PAs across Africa were outside of PAs. The tracking data have shown us that Transfrontier Conservation Areas (TFCAs), where the management of PAs considers neighbouring PAs across international boundaries [69], are too small for elephants. We show that both the GLTFCA and LTFCA have been linked by trailblazing bulls with this connectivity involving two South African national parks (KNP and Tembe Elephant Park) and five PAs within Eswatini (Big Bend Conservancy, Hlane Royal National Park, Mkhaya Game Reserve, Mlawula Nature Reserve and Panata Ranch) over an international border and across three political borders (South Africa, Eswatini and Mozambique). The next step will be to model the occurrence of elephant locations versus suitable habitat (see [70]). This is being carried out in a follow up study (Bedetti et al. in prep.).

Although HEC is widespread throughout southern Mozambique, most conflict is occurring in the corridor regions linking PAs (Figure 4, Figure S5). The satellite tracking enables mitigation efforts to be concentrated in HEC hotspot regions instead of diluting manpower and resources across the whole region. Training workshops by the RRU can then also be focussed on strategic areas.

The cafeteria-style experiments proved to be effective in evaluating several plants that have never been tested in terms of their palatability to elephants. Experiments such as these can assist in saving time and resources and avoid demoralizing poverty-stricken community members that often must share the landscape with crop-raiding elephants. The experiments, as a precursor to planting alternative crops with a market value in the corridor regions, delivered some interesting results. Herbs such as borage and rosemary with medicinal and aromatic properties, respectively, were strongly avoided together with bird's eye chilli. Elephants' avoidance of antifeedants such as capsaicin found in chillies is well-documented [71]. Their avoidance of medicinal or aromatic plants may be due to it being energetically costly to detoxify the secondary compounds [17,18], despite having well-developed salivary glands with proteins efficient at neutralizing tannins [72]. As most crop raiding occurs at night [73], it would follow that the elephants have a short window in which they need to optimize their foraging to obtain as much protein and micro-minerals as possible to make up for deficits elsewhere [9]. We found that lemon grass and sunflowers, presented as whole fresh plants to the elephants, were highly sought after by the elephants. The results require further investigation as both these plant types have been described as unpalatable to both Asian and African elephants alike [17,18]. As lemon grass needs high rainfall and soil nutrients, as well as being drought intolerant, we rated it as the second-least-suitable plant to propagate in corridor regions linking GLTFCA and LTFCA. Our results also showed that it would be preferable to plant cassava as a staple compared to any corn variant which was highly favoured by the elephants. According to the overall scoring system, four food types, with only one of them tested before on elephants, proved best suited for the proposed corridor region (bird's eye chilli, Cape gold, Cape snowbush and rosemary). The latter three plant types have been used in producing essential oil and hold great promise. The global market for essential oils continues to reflect a strong upward trend, having increased by an average of 15% from 2018 to 2019. Global production is estimated to be more than 150,000 t, valued at USD6.5bn and projected to rise at a compound annual growth rate of 8.4% to 11.8% (valued at USD15.8bn) by 2024–2025 [74].

The overall scoring system, which combined the lifecycle traits of the plants, together with the growth requisites, their combined economic value (food, essential oil, medicinal and bee fodder value) and their palatability to elephants, proved to be a novel way in which a more holistic approach can be taken towards encouraging community members to try to offset their loses by growing alternative crops with a market value. Following this approach, more plant types can be chosen and tested according to the climatic conditions of the proposed areas in which they may be propagated. Following cafeteria trials, market research is needed [71], as well as yields to sufficiently equip communities with the right produce that will achieve the desired outcome of increasing tolerance in as short a time as possible.

Knowledge gained through trials such as these open the doors to two possible scales at which land-use planning can take place. At a more local scale a combination of hard barriers, such as electric fences, around small cluster farms that do not prohibit the movement of elephants can be used. Within these hard boundaries, highly palatable crops are secured. Outside of these areas, income-generating barriers (unpalatable crops with a market value), pollinated by the bees occupying beehive fences, not only add to the protection of the palatable crops but also diversify the income of the farmers [34]. Softer barriers other than electric fences can also be implemented, such as beehive fences together with intercropping, to lower HEC [34,47]. New research in the field of melissopalynology has revealed how pollen grains stored in the bees' honey, can be used as an indicator for bee foraging behaviour. This technique, when combined with vegetation surveys, can therefore be used to identify the diversity of plants available to bees within a given area, as well as the distances that bees are willing to travel to forage [75], and could become a valuable tool to assess the general health and biodiversity objectives of the corridor regions. Thus, strategic use of beehive fences at a local scale would not only offer a second barrier next to unpalatable crops, but they would also function as alternative income streams—the bees would pollinate the produce and could be strategically used as biodiversity indicators. At a much larger scale, in crop-raiding hotspots identified through tracking data and reported information via RRUs, farmers can be encouraged to only farm with viable unpalatable crops with high market values and yields. With the sale of these 'elephant-friendly products', staple food sources could be bought where the conflict risk is low [76]. Irrespective of the scale at which HEC mitigation is being offered, assistance should be offered to communities to encourage a switch to income-generating softer barriers where needed by either implementing buy-back schemes or helping with transport to obtain elephant-palatable staples that may be grown outside of conflict areas.

The income-generating soft barriers being proposed here represent a longer-term, more proactive strategy to decrease conflict over time. However, this should not distract from the need for a short-term reactive RRU to ensure human safety. After a 12-month assessment of the RRU, the overall HWC and HEC reports had doubled in the second half of the one-year study period, which can be attributed to a greater awareness in reporting due to the presence of the RRU operating on the landscape. Changing weather patterns could also be driving elephants to range over larger areas as elephants are known to expand their range during the wet season [77,78]. As elephants become accustomed to breaking out of formerly fortified areas, such as the south of KNP, more elephants are expected to follow the trailblazing individuals over time [67,79]. Nevertheless, the RRU experienced a decline in actual conflict events and concurrently became more successful and experienced at mitigating over time. As the RRU also educated and empowered the communities they were protecting, the farmers readily took on the responsibility to ensure their own safety after training in the mitigation techniques. We propose that the initial strategy to address HEC at landscape scale along the length of an elephant corridor would involve satellite tracking of elephants over time and having RRUs run concurrently with getting farmers in high-conflict areas to adopt alternative crops with a high market value.

5. Conclusions

This work will contribute to the ecological processes that propagate the coexistence of elephants, their habitat, and people. If elephants are to survive, we need scientific knowledge and an intimate understanding of their movements and spatial requirements in combination with understanding the socio-economic needs of the people that share the landscape with elephants. This is particularly necessary where vital corridors have been identified and within which we can strive towards innovative ways to make people's livelihoods compatible with conservation outcomes.

The three phases presented here form part of a longer-term strategy to increase the tolerance of people that occupy the corridor areas. By understanding elephants' movements and ensuring food security and human safety, farmers' tolerance will increase. Social surveys, after earmarking suitable unpalatable crops through cafeteria-style experiments and conducting the necessary research on market values and yields, then need to be conducted before the implementation of alternative crops that have never been propagated before so that changes in farmers' attitudes can be monitored over time. Once softer income-generating barriers such as elephant-unpalatable crops with a market value, potentially combined with beehive fences, start offering lucrative alternative income, thereby offsetting any potential losses or supplementing existing income, people will realise that living with wildlife can be a bonus and not a burden.

Elephants moving across human-dominated landscapes depend on places where they can hide from people during the day, and these are often characterized by vegetation of a specific height and stem density (unpublished data, Elephants Alive). Thus, creating vegetation 'stepping stones' [80] functioning as a mosaic of woodlots over time should be implemented as additional income both locally and internationally as part of a carbon credit system, because elephants play an important role in combatting global climate change [81,82]. Elephants moving along corridors also represent crucial seed-dispersing agents in the larger landscape [83]. Established corridors thus offer valuable employment opportunities in the long term either to women as a part of spatially explicit tree planting schemes or to both men and women in terms of patrolling corridors to ensure the safety of both wildlife and people [84]. Within an integrated and holistic approach of TFCAs linked by functioning corridors, bioregions and biosphere will be realized.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15010085/s1, Figure S1: Map showing the accumulated data of 55 male (blue) and 18 female (orange) elephant in the APNR from 1998 to 2022. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022); Figure S2: Map showing the accumulated data of seven male elephants collared in Eastern Kruger from 2006 to 2010. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022); Figure S3: Map showing the accumulated data of six male (blue) and six female (orange) elephant collared in the Northern Kruger (Pafuri) from 2008 to 2015. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022); Figure S4: Map showing the accumulated data of 13 male (blue) and six female (orange) elephants collared in the LNP from 2016 to 2022. The black trajectory is from the one elephant male that was collared in Banhine in 2019. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022); Figure S5: Map showing the accumulated data of 20 male (blue) and two female (orange) elephants outside the protected areas from 2018 to 2022. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022); Figure S6: Map showing the accumulated data of six female (orange) elephants collared within Maputo National Park from 2018 to 2022. The headquarters of the three collaborating entities are shown, with Elephants Alive (red flag) and Hoedspruit Elephant Rehabilitation and Development (green flag) based in South Africa while the Mozambique Wildlife Alliance (yellow flag) is based in Mozambique. The various protected areas that form part of two Transfrontier Conservation Areas (TFCAs) are outlined in green for Great Limpopo Transfrontier Conservation Area and yellow for Lubombo Transfrontier Conservation Area. The Peace Park Foundation formulated the concept of TFCAs. (human settlement layers source: https://wopr.worldpop.org/?MOZ/Population (accessed on 11 October 2022); Figure S7: The electivity indices calculated per elephant during the morning sessions (a) and afternoon sessions (b); Table S1: Output from the General Linear Mixed Model investigating the electivity index in relation to the different crops for two semi-habituated elephant bulls. Significant fixed terms shown in bold; variance (±SD) reported for random terms (in italics); Table S2: Post-hoc pairwise contrasts for significant interaction terms from the generalised linear mixed model presented in Table S1. Results are averaged over the levels of morning and afternoon session.

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APPENDIX 2:

PALYNOLOGY
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Melissopalynological investigations of seasonal honey samples from the Greater Kruger National Park, Savanna biome of South Africa

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ABSTRACT
In melissopalynological studies, the investigation of pollen composition in honey samples reveals the geographical and botanical origin of the samples and links them to the regional climatic conditions. Honeybees (*Apis mellifera*), collect pollen and nectar for their nutritional requirements based on the seasonal availability of surrounding flora. In this study, pollen content in honey was temporarily investigated for seasonal differences of the bee foraged plants. A melissopalynological investigation was applied to honey samples harvested from 13 beehives located in the Greater Kruger National Park, South Africa. Multivariate statistics (NMDS and Rarefaction curves) were used to show spatial and temporal clustering of the samples. The melissopalynological data were then compared to the species' flowering season and a botanical survey of the surrounding area. The turnover in pollen composition for different seasons signifies seasonal variation in pollen types. For example, during summer, bees foraged from fewer floral sources. The highest species richness was observed during winter, suggesting a higher dependence on a diversity of floral resources during the driest months. Various seasonal pollen spectra were characterised by a pollen turnover from numerous species, including *Combretum* type, *Sclerocarya birrea*, Poaceae, *Harpephyllum caffrum* and *Lannea schweinfurthii* but also neophytes such as *Medicago sativa*. Therefore, honey samples from the Lowveld region in South Africa reflected the seasonal patterns of the surrounding flora although pollen from taxa such as *Combretum* spp. (average 56%) and *Sclerocarya birrea* (average 14%) were continuously sought after by bees throughout the year.

KEYWORDS
Melissopalynology; *Apis mellifera*; honey; seasonality; bee plants; Savanna; South Africa

1. Introduction

Honeybees (*Apis mellifera*) are important pollinators in many ecosystems (Axelrod 1960; Bawa 1990; Greenleaf et al. 2007) and they collect nectar to make honey within 1-3 weeks (Reinhardt 1939). In addition to nectar, pollen is intentionally collected to meet the bees' nutritional needs (Ghosh et al. 2020). Consequently, pollen can also be unintentionally collected if the bees become dusted with pollen that is not brushed off before they return to the hive or move on to another plant source (Westerkamp 1996). Therefore, pollen spectra in honey are unique to the region where the nectar and pollen are collected by bees (Igbe and Obasanmi 2014). Melissopalynology, the study of pollen in honey (Dustmann and Von Der Ohe 1993; Ponnuchamy et al. 2014; Johannsmeier 2016), uncovers the plant diversity within honey samples, and this is necessary for the authentication of honey (Ndlovu et al. 2021), influencing its economic value and food quality (Guelpa et al. 2017). Apart from using melissopalynology as an authentication tool, the method can also help beekeepers to relocate their beehives closer to favoured important bee plants during winter for example, *Aloe greatheadii var davyana* (Schönland) Glen & D.S.Hardy (Fletcher and Johannsmeier 1978; Human and Nicolson 2006; Human and Nicolson 2008; Johannsmeier 2016).

South Africa has a tremendously high biodiversity with >30,000 plant species, and it is floristically the third most diverse country worldwide (Wilhelm-Rechmann and Cowling 2013; Bux et al. 2021). The second richest species diversity region is the Mixed Bushveld bioregion within the Savanna biome, following the Fynbos biome which has the highest species diversity in the country (Johannsmeier 2016). Surprisingly, despite the vast potential of nectar and pollen-producing plants as indicated by the rich biodiversity of the Savanna biome (Johannsmeier 2016; Guelpa et al. 2017), South Africa's commercial honey production is negligible compared to other African countries such as Kenya and Tanzania (Guelpa et al. 2017) while the country's honey

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investigation information is scarce compared to Ghana and Niger (Onyango 2009; Esterhuzen 2020.

Understanding the foraging behaviour of honeybees in distinct ecosystems such as the Savanna biome, is crucial and can be done by the evaluation of honey using melissopalynology. Honeybees are generalist pollinators, although different colonies can have specific plant preferences (Grüter et al. 2011; Garibaldi et al. 2013; Hausmann et al. 2016). Food preferences are influenced by the availability and diversity of plants in the surrounding area (Grüter et al. 2011). Plants are foraged depending on the rewards they have to offer, including nutritional value (corresponding to the crude protein contained in pollen, Johannsmeier 2016) and the attractiveness of its flowers (Baude et al. 2011). The nutritional reward, rather than the distance between the plant species, is regarded as the most important determinant for forage selectivity in honeybees (Grüter and Ratnieks 2011). Additionally, bee plant seasonality is also an influential component, where variations in pollen density over time may be attributed to changes in density and richness of plant species that are foraged by bees across seasons (Aswini 2013).

This melissopalynological study aimed to investigate the influence of seasonality on bee foraging behaviour from the pollen contained in the honey from the Savanna biome of the Greater Kruger National Park (GKNP, stretches out from the Kruger National Park (KNP)), in order to develop a baseline pollen spectrum across seasons and to determine favoured bee plants. Since the GKNP largely constitutes a natural environment with little human disturbances within the Savanna biome, it has been selected as a good representation of a natural source of raw honey. The objective of the study was to identify which specific pollen types were preferred by bees and how the frequency changes with the seasons. Therefore, a botanical survey based on a resource selection method was conducted to compare the proportion of selected plant resources to their availability in the vicinity of the sample site. This was a first attempt for South Africa to collect honey pollen spectra across the seasons and to correlate the findings to the flowering times of the surrounding plant species in the vicinity of the beehives.

2. Materials and methods

2.1. Study site location and description

The melissopalynological investigation was conducted on honey samples harvested and supplied by the South African Non-Government Organization (NGO) *Elephants Alive* (https://elephantsalive.org/). Across four seasons collected from five different months (sample dates: summer months: 10th December 2019 and 15th January 2020, autumn month: 19th March 2020, winter month: 1st July 2020, and spring month: 26th October 2020) from 13 hives throughout the year (38 samples). December and January samples were sampled in addition to the proposed three harvest seasons (autumn, winter, and spring) and they were specifically harvested from only a single hive with a strong swarm (H1: Monokane Hive), therefore the summer results were tentative. The tree (*Sclerocarya birrea* A.Rich. Hochst) hung beehives were located west of the Associated Private Nature Reserves (APNR) (coordinate, Supplementary material, Figure S1) within the Lowveld bioregion (VI) (Mucina et al. 2006) of the GKNP in the Savanna biome (Figure 1). Approximately 383.50 m west of the vicinity of the hives (specifically Hive 9 and Hive 8 which are furthest west of all the hives) is a lucerne (*Medicago sativa* L. Sullivan, Janet) field. Further away from the hives, approximately 920 m to the West, is the Olifants River, which drains the region.

The savanna biome is characterised by seasonal rainfall (dry winters and wet summers) and a (sub)tropical thermal regime with low frost incidences (Rutherford et al. 2006). The area belongs to hot semi-arid climates (BSh: arid, steppe, hot arid) (Conradie 2012). The study was conducted in the Lowveld bioregion (VI) of the savanna biome within a frost-free region and the vegetation type is classified as Granite Lowveld (SVl 3) (Figure 1, Rutherford et al. 2006). The Granite Lowveld receives a mean annual rainfall of 400 mm to 600 mm and mean monthly maximum and minimum temperatures of 39.5 °C and —0.1 °C for January (summer month) and June (winter month) respectively (Mucina et al. 2006). Therefore, the study data represented the summer (wet and hot) season: December and January harvests, autumn (semi-dry) season: March harvest, winter (dry) season: July harvest, and the spring (semi-wet and semi-hot) season: October harvest. The vegetation and landscape around the beehives are characterised by woodlands on deep sandy uplands and the vegetation is characterised by tall shrubs and a few trees for example, *Combretum zeyheri* Sond., *Terminalia sericea* Burch. ex DC. and *Capiculatum* taxa along with ground layers consisting of *Poponarthria squarrosa* (Roem. & Schult.) Pilg., *Eragrostis rigidior* Pilg. and *Tricholaena monachne* (Trin.) Stapf & C.E.Hubb. (Mucina et al. 2006).

2.2. Botanical survey in the vicinity of the hives

A botanical survey conducted on the 12 October 2021, served to examine the surrounding vegetation to evaluate the degree of similarity between the contemporary vegetation and the pollen which was collected by the bees. The focus was on several specific species that were commonly (including very frequent, frequent, and isolated pollen) found in pollen samples (> 1% average abundance). Selected plants with a high relative abundance of associated pollen in the honey samples were identified along two 250 m transects from North to South and from West to East across the centre of the location of all the beehives (adapted from Tabares et al. 2021), since the hives where all within 150 m range of each other.

2.3. Melissopalynological sample processing

(A) Honey samples (10 g each) were processed using the melissopalynological standard procedure based on acetolysis. One *Lycopodium* spore tablet (Batch number 1031) with a known number of spores (12,000) was dissolved in hydrochloric acid (HCl) to calculate the pollen concentration (Queiroz and Mateus 1998). (B) The acetolysis solution was

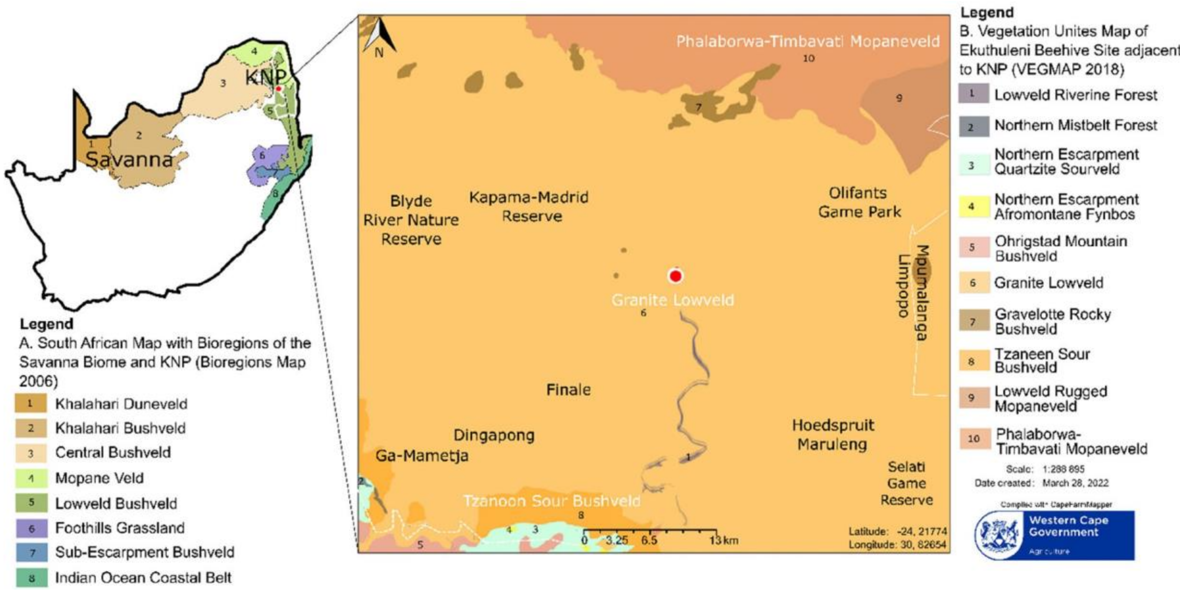

Figure 1. South African map with bioregions of the Savanna biome (A) and a vegetation unit map surrounding the study site (B) adapted from Mucina *et al.* (2006) using the Geographic Information System (GIS) Esri tool (CapeFarmMapper (CFM) 2.6.2 – Elsenburg). The study site/Ekuthuleni Beehive site in the Associated Private Nature Reserve is indicated as a red dot within the Greater Kruger National Park (KNP, white outline in Figure 1A).

prepared by adding 1 ml of sulphuric acid (H_2SO_4) to 9 ml of acetic anhydride ($(CH_3\ CO)_2O$) (Louveaux et al. 1978). (C) Then the residue was mounted on glass microscope slides using drops of glycerine gelatine. Surplus residues were archived in Eppendorf tubes at ESI (Evolutionary Studies Institute, University of Witwatersrand).

2.4. Microscopic analysis

The slides were analysed with a Zeiss Axioscope 5 light microscope with a magnification of 4000x. Pollen grains were photographed with an Olympus 2L04386 camera using image analysis software. Identification was supported by a modern pollen reference collection housed at ESI, online guides (Master Reference Collection from The Global Pollen Project at https://globalpollenproject.org/Taxon), and references (Bonnefille and Riollet 1980; Scott 1982; Gosling et al. 2013). Thirty-eight honey samples were counted to a pollen sum target of 300 then adjusted to 600 where possible (mean of 333, range of 622, minimum 26 and a maximum of 648 pollen) per sample. The pollen sum was affected by limited honey production, subsequently affecting the quantity (<10 g) harvested. The data was statistically analysed and depicted in several pie charts using R software (R 4.1.2) to display the relative abundance of different pollen taxa between seasons and samples (Adeonipekun 2012; Song et al. 2012; Sauliene et al. 2015; Brodschneider et al. 2019).

Pollen frequency classes were used to classify pollen types into categories according to their abundance throughout all seasons combined. Firstly being very frequent pollen (>45%), frequent pollen (16–45%), isolated pollen (4–15%), rare pollen (<3%) (Louveaux et al. 1978) and finally extremely rare pollen (<1%). Additionally, honey pollen concentration (Pcon) values were used to allocate the honey samples into one of the five different categories following Louveaux et al. (1978) (Supplementary material, Table S2). The pollen concentration value was calculated using a *Lycopodium* spore tablet (Queiroz and Mateus 1998). The following formula was used to calculate the pollen concentration value (number of pollen/10 g honey) (Equation (1), Queiroz and Mateus 1998):

$$\text{Pcon} = \frac{\textit{Lycopodium}\ \text{spores added}}{\textit{Lycopodium}\ \text{spores counted}} \times \frac{\text{pollen counted}}{\text{10g (mass of honey)}} \qquad (1)$$

2.5. Statistical analysis

The honey samples were analysed using multivariate analysis with the aim of identifying the variance across different pollen species within the samples. This was performed in R (R 4.1.2) with functions from the vegan package (version 2.6-2) for multivariate analysis (Dixon 2003; Oksanen et al. 2015). The results were graphically displayed using a non-metric multidimensional scaling (NMDS) ordination method (Dixon 2003; Oksanen et al. 2007). According to the Bray-Curtis distance matrix, the NMDS attempts to represent as closely as possible the pairwise dissimilarity between the honey sample groups (Dixon 2003). The closer the species plot on the dimensional space to the sample groups/season, the more abundant the species is within that specific sample. Therefore, the results indicate if there is any correlation between seasons and the plants the bees prefer.

Rarefaction curve (95% Confidence Intervals (CI)) graphs were also generated to display the species diversity (according to Shannon's diversity indices) and species richness of all the seasons. These metrics were calculated using the iNEXT package in R. The Chao1 estimator was used to extrapolate species richness while the Chao-Jost estimator was used to extrapolate the samples' diversity (Hsieh et al. 2016).

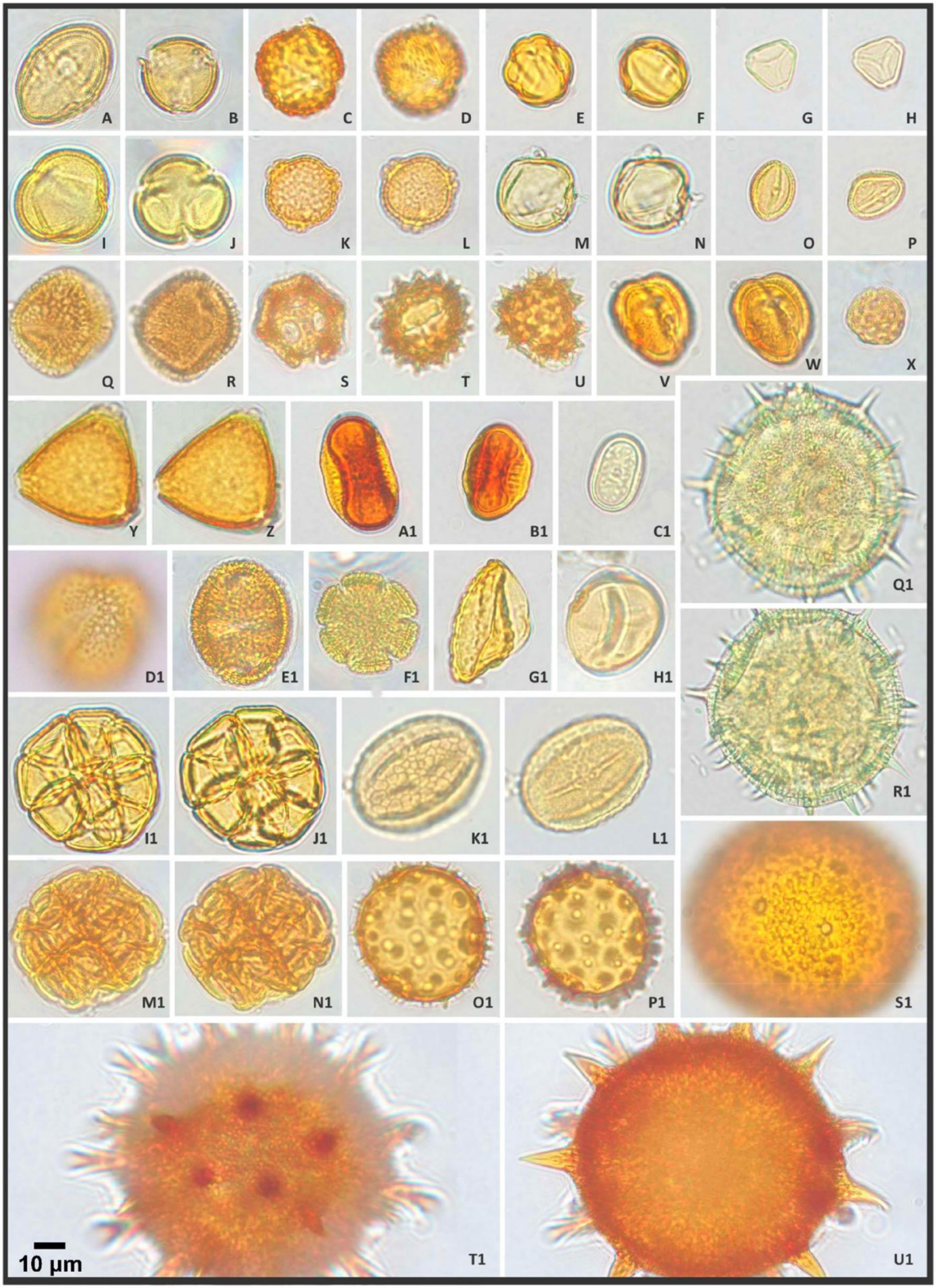

Plate 1. Photo plate of various pollen types found in honey samples from the Lowveld bioregion of the Savanna biome, South Africa. (A, B) *Medicago sativa*, (C, D) *Sclerocarya birrea*, (E, F) *Combretum* type, (G, H) Myrtaceae (*Eugenia* type), (I, J) *Euphorbia* type, (K, L) *Commiphora* type, (M, N) *Lannea* type, (O, P) *Harpephyllum caffrum*, (Q, R) *Peltophorum africanum*, (S) *Alternanthera* type, (T, U) Tubuliflorae, (V, W) *Gerbera* type, (X) Amaranthaceae, (Y, Z) *Protea/Faurea* type, (A1, B1) *Justicia flava*, (C1) *Justica decurrens*, (D1) *Salix* type, (E1, F1) *Plectranthus* type, (G1) *Dichrostachys* type, (H1) Poaceae, (I1, J1) *Senegalia* type, (K1, L1) *Grewia* type, (M1, N1) *Vachellia* type, (O1, P1) *Dombeya*, (Q1, R1) *Hibiscus* type, (S1) *Phaeoptilum spinosum* and (T1, U1) *Hibiscus* type.

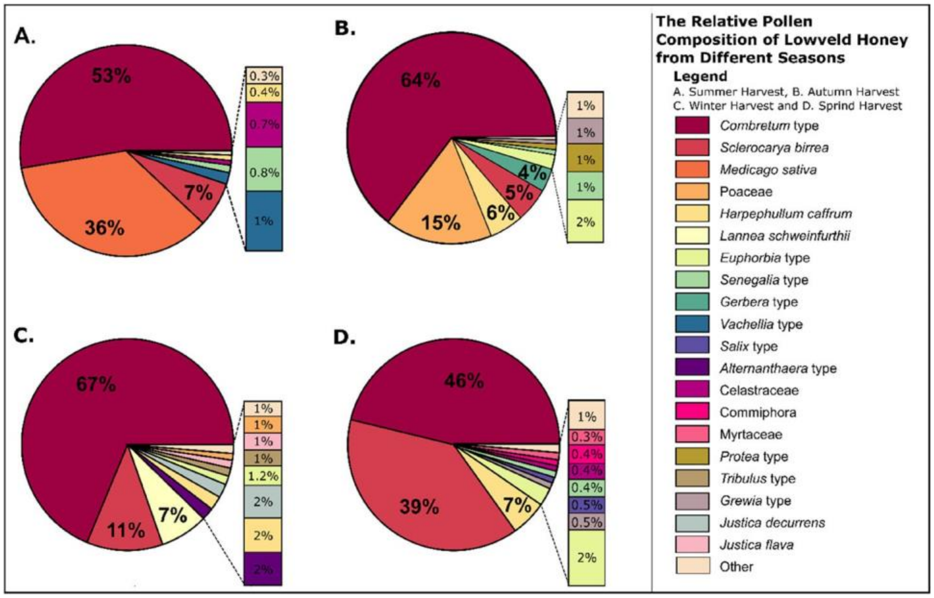

Figure 2. Pie chart plot displaying the pollen type percentage composition present in four different seasons from honey samples in the Lowveld bioregion of the Savanna biome, South Africa. (A) Summer (January and December) honey samples, other represents *Tribulus* type. (B) Autumn (March) honey samples, other represents: *Vachellia* type, *Helianthus* type, *Podocarpus/Afrocarpus*, *Plectranthus*, *Myriophyllum* type and Cyperaceae. (C) Winter (July) honey samples, other represents: *Vachellia* type, Poaceae, *Protea/Faurea*, *Helianthus* type, *Ambrosia artemisiifolia*, Tubuliflorae, *Myriophyllum* type, *Gerbera* type, *Dichrostachys* type, Celastraceae, *Grewia* type and *Peltophorum africanum*. (D) Spring (October), other represents: *Vachellia* type, Poaceae, *Triumfetta* type, *Lannea* type and *Plectranthus* type.

3. Results

In total, 32 pollen types from 20 plant families were identified (Plate 1, Supplementary material, Table S3). Pollen grains totalled 13,053 were counted across 38 samples from 13 different beehives harvested throughout four different honey seasons. The mean pollen concentration of the honey samples was 50,080 pollen grains per 10 g of honey, which classified the honey as Category 2, representing honey samples produced from floral sources (extended definitions and category of pollen concentration values [Supplementary material, Table S2]). Furthermore, pollen 'type' is named after a taxon or group of taxa, that produce similar or identical pollen, while 'taxon' would be used as a referral to a plant taxonomical name (Joosten and De Klerk 2002; De Klerk and Joosten 2007). Additionally, Table S3 (Supplementary material) represents all the pollen types raw counts and percentage values for each harvest from the honey samples, along with their flowering periods and bee plant values.

3.1. Relative pollen composition of Lowveld honey

The abundance of *Combretum* type (average 56%) classified the species as a 'very frequent pollen type' (Louveaux et al. 1978), since it was highly abundant in most samples (>46%), except in January (7.99%), (Figure 2, Supplementary material, Table S3). Based on the honey sample average the Anacardiaceae family species where the second most abundant species with *Sclerocarya birrea* (average 14%, most abundant in October samples by 39.95%) being classified as a 'frequent pollen type'. Followed by *Harpephyllum caffrum* (most abundant in October samples by 7.09%) and *Lannea* type (most abundant in July sample by 7.10%) which are classified as 'isolated pollen types' based on sample average (Figure 2, Supplementary material, Table S3).

Several additional rare pollen types were continually common in various harvest months. They include *Senegalia* type (abundant in March samples by 0.97%), *Vachellia* type (abundant in January samples by 2.56%), *Euphorbia* type (abundant in October samples by 2.43%) and Poaceae (abundant in March samples by 15.12%). Generally, the pollen spectra and predominant pollen taxa varied over different seasons (Supplementary material, Table S3, Figure 2).

3.2. Honey seasonal comparison

How pollen diversity and composition corresponded to seasonal changes, was represented by the results of the Non-Metric Multidimensional Scaling (NMDS) ordination method (Figure 3). The stress value of 0.0875 indicated a satisfying significance of the assumed heterogeneity (variation) of the different seasonal harvests (Figure 3). Combretaceae (*Combretum* type), *Euphorbia* type, *Peltophorum africanum*, *Senegalia* type, *Vachellia* type, *Harpephyllum caffrum*, *Grewia* type, *Plectranthus* type and *Commiphora* type clustered within the March, July and October samples (coloured polygons). Poaceae, Cyperaceae, *Gerbera* type, Tubuliflorae and Myrtaceae were clustered at a further distance from all other taxa within the autumn (March) samples (Figure 3).

The hives (honey samples) were spread throughout the NMDS plot with varying distances between them. The colour-coded polygons (coded according to their relevant seasonal harvest) showed an overlap of the sample groups throughout the dimensional space (Figure 3). The summer samples (December H1 and January H1) did not have polygon shapes grouping them since the samples were few compared to the other seasons (March, July and October); however, the two samples interestingly overlapped with other seasons (March and July) (Figure 3).

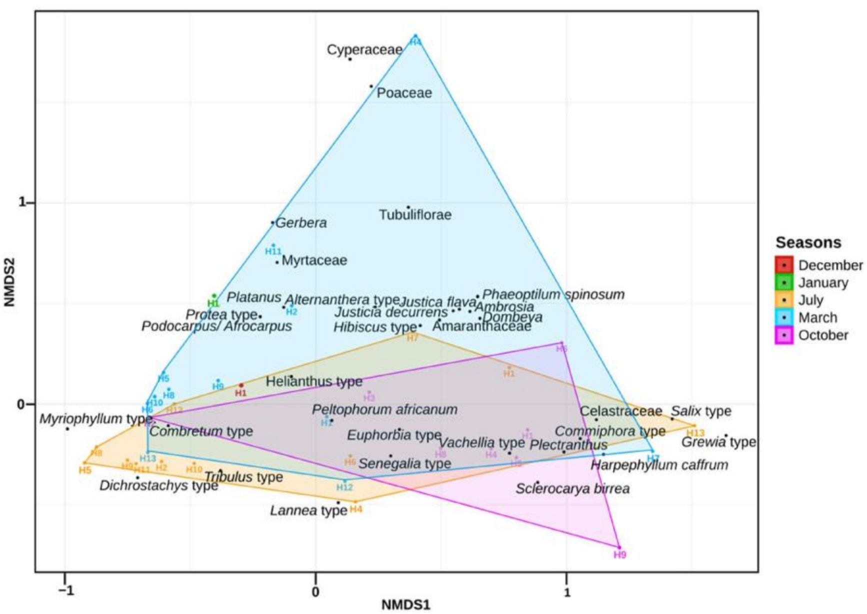

Figure 3. Non-metric multidimensional scaling (NMDS) plot displaying the Bray-Curtis distance between five honey seasonal samples collected all year from different hives of the APNR location within the GKNP. The coloured dots represent the different hives corresponding to their seasons and the black dots represent different pollen taxa. The coloured polygon shapes group all the hives according to seasonality. Seasonality is displayed as December and January (summer), July (winter), March (autumn) and October (spring).

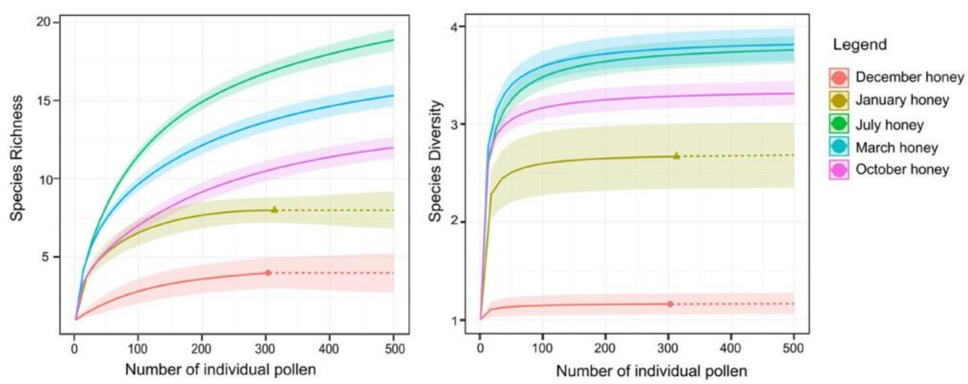

Figure 4. Rarefaction curves (95% CI) displaying differences in richness and diversity between all honey seasons (hives averaged for each season) collected throughout the year. The left figure (q=0) is comparing the sites in terms of the Species Richness index, the right figure (q= 1) is comparing the sites in terms of the Shannon diversity index.

3.3. Pollen type species richness and diversity

According to the rarefaction curves (95% CI), the summer season had the lowest average species richness (January was 8.00 ± 0.53 and December was 4.00 ± 0.54) and Shannon's diversity (January was 2.60 ± 0.19 and December was 1.10 ± 0.05) compared to the March, July and October months subsequently (Figure 4). The July (winter) month had the highest average species richness (18.00 ± 1.32) and second-highest average species diversity (3.60 ± 0.08) after March (autumn) (3.70 ± 0.07) (Figure 4). The other months, such as March (15 ± 1.32) and October (12.50 ± 0.41), had a higher species richness than the summer samples and lower species richness than most July samples (Figure 4). Furthermore, the species diversity of both March (3.70 ± 0.08) and October (3.20 ± 0.06) was higher than most summer samples and lower than most winter samples (Figure 4). Apart from the varying species diversity observed from different honey seasons, the pollen diversity varied considerably according to the Shannon Wiener diversity indices amongst hives that were within a 150 m range of each other (Figure 5).

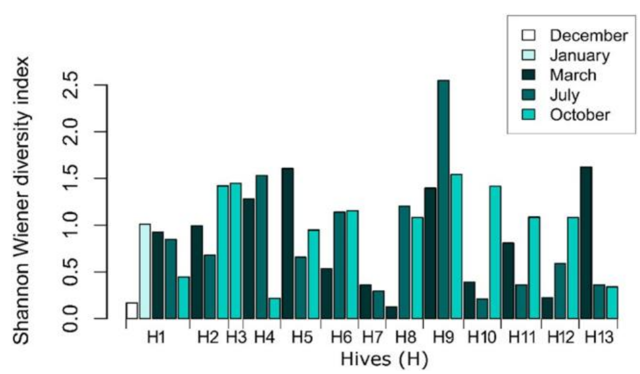

Figure 5. Shannon Wiener diversity indices displayed on a histogram for all hives from different harvest seasons (December 2020 to October 2021).

3.4. Botanical survey

The frequency of the species surveyed was represented as percentages with *Senegalia nigrescens* (Oliv.) P.J.H.Hurter (54%), *Sclerocarya birrea* (A.Rich.) Hochst (19%) and *Euphorbia* taxa (13%) being the most dominant species found on the

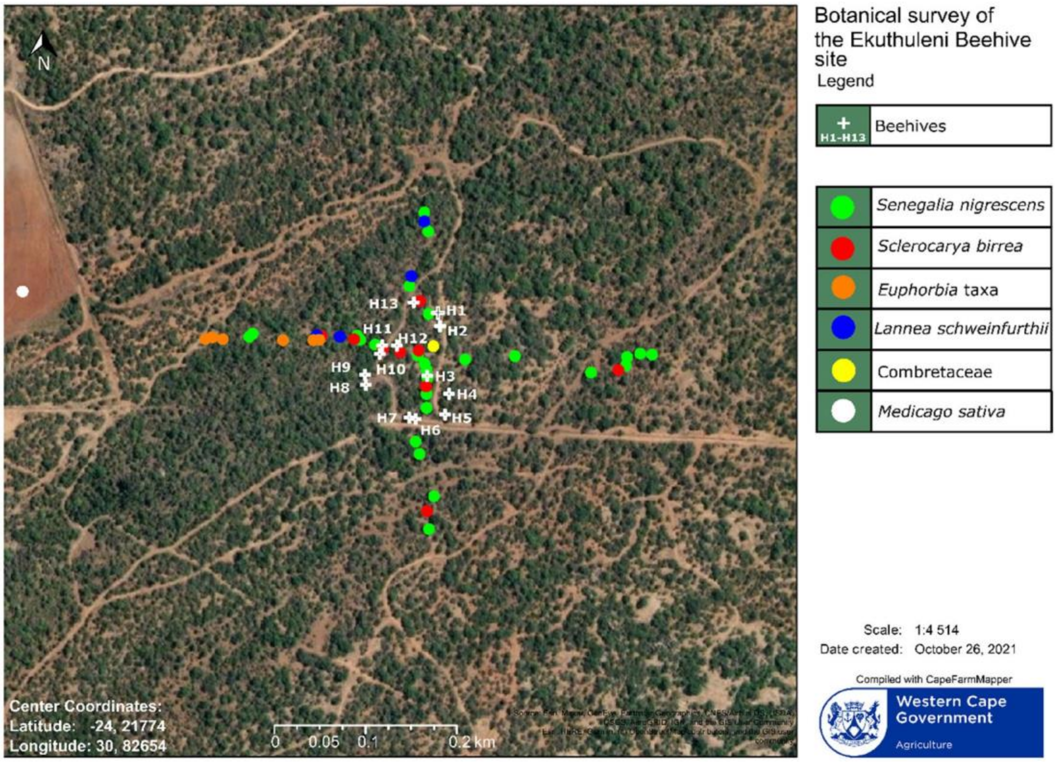

Figure 6. Species plot of plants identified from the botanical survey conducted in the Lowveld bioregions, Savanna biome of South Africa. Displayed using the (GIS) Esri tool (CapeFarmMapper (CFM) 2.6.2 – Elsenburg).

transect, while *Lannea schweinfurthii* (Engl.) Engl. (2%) and Combretaceae (2%) were the least abundant species of those commonly found in honey samples (>1%) (Figure 6). As well as the presence of numerous individuals of Poaceae and *Grewia* taxa which were growing within a metre of every beehive tree. Approximately 383.50 m west from hive 9 was a lucerne field (*Medicago sativa* L. Sullivan, Janet) (pollen contribution: 2%), and approximately 773.70 m further west were *Vachellia xanthophloea* (Benth.) P.J.H.Hurter trees (pollen contribution: 2%). These plant species were further from the 250 m long transects surveyed but were in the surrounding area.

4. Discussion

4.1. Melissopalynological investigation

The honey pollen spectra were characterised by Combretaceae (*Combretum* type), Poaceae, *Harpephyllum caffrum*, *Sclerocarya birrea*, *Gerbera* type, *Lannea* type, *Euphorbia* type, *Senegalia* type, *Vachellia* type and *Peltophorum africanum*. According to Johannsmeier (2016), the known bee plants of the Lowveld bioregion include *Combretum* taxa, *Senegalia mellifera* (Vahl) Seigel & Ebinger, *Sclerocarya birrea* (A.Rich.) Hochst., *Vachellia tortilis* (Forssk.) Gallaso & Banfi as well as *Grewia* taxa and *Dichrostachys cinerea* (L.) Wight & Arn., which were not dominant species, but minor pollen types found in the total honey sampled.

Based on the percentages of each pollen type in all the honey samples, *Combretum* type was the only frequent pollen type found in most honey samples (December, March, July and October). The high abundance of *Combretum* taxa (56% all year) from honey samples relative to its low (2%) abundance in the immediate surrounding vegetation (Figure 6) signifies how highly favoured and sought-after the tree was by bees of the Lowveld. In this study, *Combretum* type can thus be considered as both preferred and principal forage plants to bees as it was foraged on by bees in the greatest quantities in relation to its abundance (Petrides 1975). Similar results were observed in the Savanna biome from Ghana and Gaya, southern Niger, where a melissopalynological study was conducted over a time span of two years, and pollen of *Combretum* type was one of the dominant species forged by bees (Schulz and Lueke 1994; Letsyo and Ameka 2019).

However, the favourability of *Combretum* type can be contested on the observations that the species produces a relatively large pollen sum and nectar (N0-3, P0-3) (Johannsmeier 2016), especially since it has attractive brightly coloured (white, yellow or cream) flowers (Schulz and Lueke 1994). Additionally, bees perform buzz pollination on *Combretum* taxa flowers by opening the anthers with the help of vibrations, resulting in a heavy pollen load that can be collected by bees or fall to the surface (Proenc¸a 1992; Schulz and Lueke 1994). These factors can increase the amount of pollen collected by the bees and amplify the bee's inability to dust off all the pollen stuck to it (Westerkamp 1996).

The second most dominant/frequent pollen type was *Sclerocarya birrea*, with a 14% average pollen presence in the honey samples throughout the year. The pollen type was most abundant in the spring (October) harvests with 39.95% (Figure 3), despite not being recorded by any melissopalynological study known to the present authors. *Sclerocarya birrea* (A.Rich.) Hochst. was found to be the third most abundant plant species within a 250 m radius of the beehives (54%), making it a widely available food source in the Lowveld for the bees. The tree is mainly pollinated by honeybees and its production of sticky pollen and prolific secretion of nectar is one of the main reasons it is highly favoured by bees (Hall et al. 2002; Msukwa et al. 2019).

Underestimated bee plants of the Savanna biome that are important minor/rare pollen types include Poaceae (3%), *Harpephyllum caffrum* (3%) and *Lannea* type (1.5%) which might be *Lannea schweinfurthii* (Engl.) Engl. (Supplementary material, Table S3, Figure 3). *Lannea* type has been described as a major source for both nectar and pollen in other Savanna sites in Ghana and Gaya (south Niger) (Schulz and Lueke 1994; Letsyo and Ameka 2019). *Harpephyllum caffrum* (N0-1, P0-1) was absent within the surveyed beehive location and has not been recorded in any Savanna melissopalynology studies, apart from a single bee visitation sitting in the southwestern Cape (Johannsmeier 2016). Lastly, Poaceae tends to be present in honey samples during the dry seasons (Aina and Owonibi 2011; Adeonipekun 2012) and grass species are highly abundant in the Savanna vegetation (Ige and Modupe 2010; Adeonipekun 2012). Our study found that the bees foraged Poaceae family plants mostly during autumn (15.12%) even though the plants typically flower from summer to winter (December to June) (Russell et al. 1990; van Ginkel and Cilliers 2020) and therefore, we propose that in summer there might be more favourable plants flowering (e.g. *Combretum* taxa and *Medicago sativa* L. Sullivan, Janet) that are sought-out despite not being in the immediate vicinity of the beehives (Supplementary material, Table S3, Figure 3).

4.2. Seasonality in honey samples and bee foraging behaviour

The species diversity and richness of all seasons vary over time, suggesting that the pollen spectra of honey vary seasonally, but the important bee plant species of the region are generally represented all year. These include *Combretum* type, *Senegalia* type, *Vachellia* type and *Sclerocarya birrea* hence they plotted were the seasons overlap in the NMDS (Figure 3). The highest average species diversity was observed in the spring harvest, whilst the winter season had the widest species diversity across its samples (Figure 4, Supplementary material, Figure S4). These seasonal findings imply that bees forage from more floral sources in drier, cool seasons compared to the warmer, wetter seasons (Aswini 2013; Danner et al. 2017; Laura and Cynthia 2018) due to environmental stress (resource depletion). Hence the winter season reflected the highest average pollen species richness throughout the year (Figure 4).

Even though seasonality affects the density and richness of pollen found in honey (Aswini 2013; Laura and Cynthia 2018), bees forage from similar sources in all hives, but each hive has its unique pollen spectra (Supplementary material, Table S3). Therefore, foraging economics and strategies might be responsible for the varying pollen diversity in different hive (Núñez 1982; Carvalheiro et al. 2011), because foraging distances vary depending on landscape structure, resource availability, and seasonal changes (Visscher and Seeley 1982; Steffan-Dewenter and Kuhn 2003; Danner et al. 2016). Conclusively; however, the nutritional needs of honeybees as reflected by the bee plant values (Johannsmeier 2016), are more important than the relative distance of the bee plants that are seasonally selected for their provided nutrient (Grüter and Ratnieks 2011).

For future studies, seasonal patterns can be accurately investigated by the extraction of nectar directly from the bee's stomach (Bryant and Jones 2001, Christian Pirk, personal communication, 21 April 2021). This will correct for the observed overlap between different seasons (Supplementary material, Table S3, Reinhardt 1939, Christian Pirk, personal communication, 21 April 2021) and eliminate external pollen deposited by other forms of transportation apart from insect pollination. Therefore, eliminating the possible over representation of taxa such as Poaceae, which is both insect and wind-pollinated (Kosina and Florek 2011) and have contributed to the honey pollen data through various transportation pathways (Bryant and Jones 2001). Furthermore, a detailed botanical survey, meteorological investigation, and landscape survey particular to the Lowveld would assist in the understanding of other factors that may contribute to the variability of pollen indices (Danner et al. 2017; Lau et al. 2019).

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Disclosure statement

The authors declare no competing interests.

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WILEY

RESEARCH NOTE

Conservation Science and Practice
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Interspecific competition between ants and African honeybees (*Apis mellifera scutellata*) may undermine the effectiveness of elephant beehive–deterrents in Africa

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Abstract

Beehive deterrents are commonly used to mitigate human–elephant conflict and protect woody vegetation. To ensure hive activity, reduce abscondment risks, and maintain deterrent effectiveness, resident bee colonies require supplementary feeding during periods of low resource availability. However, our study found that ants frequently consume the supplementary feed in open feeders intended for bees. *Anoplolepis custodiens* was the most numerically dominant species that excluded bees from the feeders, followed by *Camponotus* and *Crematogaster* spp. With higher ant abundance, the predicted probability of zero bees being present at feeders increased up to 82%. This competition may undermine the efficacy of beehive deterrents as a conflict mitigation tool. We developed a simple and effective ant exclusion method that raised the overall predicted probability of bees' presence at supplementary feeding stations from 32% to 68%. Our findings suggest that innovative solutions to exclude ants from supplementary feed may improve the implementation and success of this conflict mitigation method across Africa.

Catherine L. Parr and Michelle Henley shared equal senior authorship.

KEYWOR DS

Apidae, beehive deterrents, conflict mitigation, elephants management, Formicidae, human–wildlife conflict, insect ecology, *Loxodonta africana*

1 | INTRODUCTION

Conservation stakeholders in South Africa are concerned that high African elephant populations (*Loxodonta africana*) lead to the expiration of large/iconic trees and, subsequently, the homogenization of savanna woody structure and diversity (O'Connor et al., 2007). Likewise, crop raiding by elephants across Africa severely undermines conservation efforts, causing human–wildlife conflict, and compromising people's livelihoods (Vogel et al., 2020). To overcome these challenges, hives of African honeybees (*Apis mellifera scutellata*; hereafter, bees) have been lauded as an effective and ethical way of mitigating these tensions. Bees have been shown to be an effective elephant deterrent, reducing damage to large and iconic trees [e.g., Marula trees (*Sclerocarya birrea*)] and significantly reducing elephant crop raiding (—80%) in East Africa (Cook et al., 2018; King et al., 2017). This has led to the widespread adoption of this conservation tool across Africa over the last 8 years, and ensuring this elephant deterrent is effective is of significant interest to conservation practitioners, protected area authorities, and local communities (King, 2020).

While beehives have been shown to be an effective elephant deterrent, Cook et al. (2018) raised the point that supplementary feeding (a mixture of sugar water and nectar/pollen substitute) must be provided in the dry seasons or during drought periods to maintain beehive occupation and activity when key resources (e.g., water, nectar, and pollen) are scarce (Caron, 2021). Supplementary feeding mitigates the physiological constraints, such as temperature extremes and food/water scarcity, that reduce hive activity by increasing the risk of desiccation, starvation, and heat stress for bees (Abou-Shaara et al., 2017; Tan et al., 2012). Beehive activity during the dry season is crucial as elephant impact on woody vegetation and human–wildlife conflict is at its highest (Greyling, 2004; Loarie et al., 2009). Supplementary feeding is one of the essential tools used to maintain hive activity and mitigate elephant impact on woody vegetation and human–elephant conflict. However, observations of open feeding stations (e.g., feeding not directly in the hive) have revealed potentially concerning competition between ants and bees for the supplementary feed (R. Cook, *personal observation*, and K. Bunney, *unpublished data*).

Interspecific competition through behavioral aggression (e.g., biting, swarming, etc.) for resources, territory, and defense, is a cornerstone of ant, and bee (though to a lesser extent) ecology in African savannas (Hölldobler & Wilson, 1990; Parr, 2008; Rudolph & Palmer, 2013). Niche partitioning, distinct foraging behavior, and space requirements usually reduce interspecific competition between these two taxa under normal conditions, reducing the risk of interspecific interactions (Barônio & Del-Claro, 2018). However, the provision of sugar and nectar during the dry season may result in the artificial modification of species niche spaces and may therefore result in direct competition between ants and bees for supplementary feed during a resource-limited period. Consequently, it is necessary to understand whether interspecific competition for supplementary feed could reduce bee access to supplementary feed and undermine their conservation value.

The extent to which interspecific competition with ants and temperature may undermine the ability of the bees to access supplementary feed during the dry season is currently unknown. Accordingly, we aimed to investigate: (1) what level of ant abundance would reduce the probability of bee abundance at the feeders, (2) whether excluding ants from the bee feeders would increase the probability of bee abundance at the feeders, (3) if air temperature influenced bee abundance. We predicted that (1) interspecific competition between ants and bees will result in reduced bee abundance at the feeding stations due to the bees' naturally less aggressive behavior compared with ants, (2) excluding ants from the feeders will substantially increase the probability of bee abundance at the feeders, and (3) lower air temperatures will limit bee abundance at the feeders.

2 | METHODS

2.1 | Study site

Data were collected at Ndabushi Bushveld Retreat (hereafter referred to as Ndabushi), a small (14 hectare) property located in the lower bushveld of the Greater Kruger National Park, Limpopo Province, South Africa ($24^{\circ}20^{0}26.4^{00}$ S, 31° $09^{0}18.3^{00}$ E). Ndabushi has a hot and semi-arid climate, with a dry (18.8°C on average, April–September) and wet season (24.1°C, average, October–March). The mean annual rainfall is 500 mm per annum. Ndabushi falls within the Granite Lowveld vegetation unit (SVI 3) in the Savanna biome (Mucina & Rutherford, 2006). The site has a limited number of meso-herbivores (e.g., Nyala, *Tragelaphus angasii*), but no mega-herbivores are present.

2.2 | Supplementary feeding and beehive placement

All data were collected in a one-hectare site dominated by knobthorn [*Senegalia* (*Acacia*) *nigrescens*] savanna woodland. We suspended four active hives from knobthorn trees at a height of 1.5–2 m from the ground (Cook et al., 2018), after ensuring all hives were healthy and active. Feeders were attached to four different knobthorn trees that were >5 m apart, and within 15 m of trees containing active beehives. The supplementary feed is a mixture of sugar, nectar, and water, following the described methods by Cook et al. (2018). Feeders consisted of 2–3 metal containers, filled with the sugar solution, attached to a wooden plank, covered in wire-mesh [to prevent mammals such as primates (etc.) from accessing the feed], and secured to a tree trunk. These feeders are "open feeders" for example, not directly placed within the hive, and so are accessible to most invertebrates in the system. The containers were filled with sticks to prevent the bees from drowning. The feeders were re-filled every 2–3 days (depending on logistical constraints) from June 7 to 30, 2019. There was a gap of 2 days between the first feeding and the start of data collection to allow both bees and ants adequate time to locate this new resource. Bees are known to travel up to 9.5 km from their hive in search of food and water (Beekman & Ratnieks, 2000), and so we assumed that all hives had equal access to all feeders.

2.3 | Ant species

Ant ground abundance and genus were recorded using six pitfall traps filled with 80% ethanol solution, 1 m from the base of each tree containing a supplementary feeding station (24 in total). Pitfall traps were in place for 5 days, both before supplementary feeding was started and for 5 days before ants were excluded from the feeders (Parr et al., 2004). These specimens were then counted and identified to the morpho species level.

2.4 | Ant–bee abundance

Data were collected for three observation periods per day between 07 h 30 min and 17 h 30 min. Ants and bees were observed on the feeders in the trees and on the ground directly below the feeder, where supplementary sugar feed dripped into small puddles [roughly 30 cm^2, referred to collectively as the feeder, except when discussing Ant Exclusion (see below)]. Bee abundance was categorized as the number of bees that were present at the feeders (0, 1–20, and >20 individuals). Ant abundance was recorded as the percentage of the feeder surface area that was covered by ants from 0%, 1%–25%, 25%–50% to 51%–100%. We used percent cover as a proxy for abundance, as ants were too numerous to be counted individually. As temperature is known to influence ant and bee activity (Abou-Shaara et al., 2017; Hölldobler & Wilson, 1990), we recorded air temperature using a hand-held Kestrel® weather station (Kestrel Meters, Boothwyn, PA).

2.5 | Ant exclusion

From June 29, 2019 to July 02, 2019, ants were excluded from the four trees containing feeders to determine bee access to supplementary feed in the absence of ants. Prior to the exclusion, ants were flushed from the tree trunk and feeders using warm water. Once each tree and feeder were free of ants, we applied a 7-cm wide layer of engine grease to the entire circumference of the tree trunk, 30 cm above the base of each tree, to prevent ants from gaining access to the feeders. Ants still had access to supplementary feed that dripped on the ground, and so these observations were recorded separately. We then recorded ant–bee abundance at the feeders in the same manner as described above to record the effect that the exclusion of ants had on bee abundance at the feeders.

2.6 | Statistical analysis

2.6.1 | Ant–bee abundance

To determine which factors influenced the predicted probability of varying bee abundances at the feeders, we used a multinomial logistic regression (Qian et al., 2012), implemented in the package *nnet* in *R* 3.5.2 (R Foundation for Statistical Computing, 2021; Venables & Ripley, 2002, section 7.3). See Agresti (2002, section 7.1), Burnham and Anderson (2002), and Thornley et al. (2020) for more detailed descriptions of this modeling approach. Our model attempted to estimate the predicted probability of bee abundance at the feeding stations, as a function of ant abundance, air temperature, squared air temperature, whether observations were in trees or on the ground, and if observation were recorded during our exclusion treatment or not. We included the interaction between ant exclusion and ground/tree observation to address the caveat that ants could not be excluded from supplementary feed on the ground during our exclusion experiment. By including this interaction term, we account for changes in bee abundance based on the manipulation of ant abundance (or lack of) that result from ant exclusion, and where bees and ants were recorded feeding during the exclusion experiment.

We both air temperature and squared temperature as an explanatory variables to allow for the possibility of a quadratic relationship, i.e., an optimum temperature within our temperature range. The ground temperature and temperature of the feeder was not included in the model, as it was co-linear with air temperature ($r(490) = 0.71$; Dormann et al., 2013), and air temperature more likely to directly drive bee abundance (Abou-Shaara et al., 2017). We fitted a saturated model including all the outlined predictors and used the *dredge* function in the *MuMIn* package (Bartoń, 2022) to select the best-fitting model based on the models AICc, and extracted the predicted probability of ant abundance from our best-fitting model. Figures were created using the *ggplot* package using the predicted probabilities extracted from our model outputs produced using the *nnet* package (Wickham, 2022).

3 | RESULTS

3.1 | Best fitting model for bee abundance

Bee abundance at the feeders was influenced by ant abundance, squared air temperature, and ant exclusion, with an interaction between ant abundance being recorded on the ground or in the tree (during the exclusion part of the experiment only). No other model was considered as the delta value >2 (Symonds & Moussalli, 2011; Table A1).

3.2 | Ant species

During our study, *Anoplolepis* spp. ants were the most numerically dominant species, which increases substantially in numbers once feeding was commenced. On the feeders, we noted that arboreal ants from the genus *Camponotus* and *Crematogaster* were also consistently recorded, but due to their arboreal ecology, they were not recorded in the ground feeders in significant numbers (Table A2).

3.3 | Ant abundance

Ant abundance substantially reduced bee abundance at the feeders (Figure 1). The most adverse effect on bees was at 51%–100% ant abundance, where bees had an 82% probability of being entirely absent from the feeders and only a 1% probability of high abundance (>20 bees; Figure 1). Low levels of ant abundance (1%–25%) were sufficient to decrease the probability of high bee abundance from 36% to 27%, but low ant abundance did not adversely affect the probability of low bee abundances (e.g., 1–20 bees, Figure 1). High bee abundance decreased consistently in probability when ant abundance ≥26% (Figure 1).

3.4 | Ant exclusion

Our method of ant exclusion was effective at preventing ants access to feed placed in trees, which facilitated consistently higher bee abundances (Figure 2). When ants were excluded from tree feeders, the probability of high bee abundance (>20 bees) increased from 6% to 16% and low bee abundance (1–20) from 25% to 77% (Figure 2). The probability of zero bees declined dramatically from 68% to 8% when ants were excluded from tree feeders (Figure 2).

The exclusion of ants from tree feeders did not inhibit ants from accessing the supplementary feed that drips onto the ground, where high ant abundances continued to dominate the supplementary feed, excluding bees in the process (probability of zero bees on the ground during the exclusion trial increased from 72% to 85%, and the predicted probability of >20 bees was only 0.1%; Figure 2).

3.5 | Bee abundance and temperature

Air temperature affected bee abundance independently of our other predictor variables (e.g., the effect of

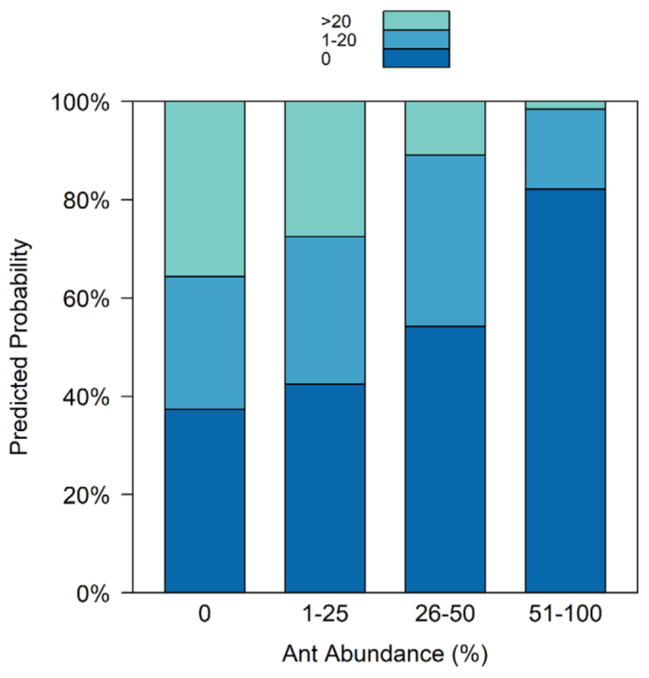

FIGURE 1 Predicted probability (%) of our three bee abundance categories (0, 1–20, and >20) occurring at the feeders with increasing ant abundance (increasing percentage of the feeders covered in ants).

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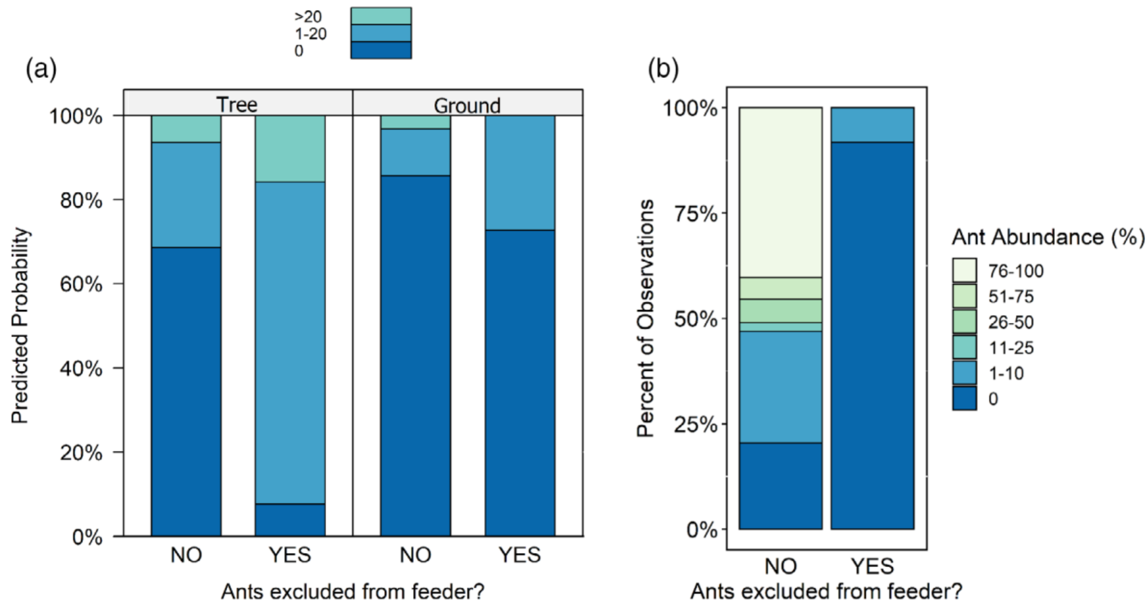

FIGURE 2 (a) Predicted probability (%) of our 3 bee abundance categories (0, 1–20, and >20) relative to whether ants were excluded from tree feeders, or the ground (where interspecific competition with ants was still present) during the exclusion experiment. (b) The percent of ant abundance categories recorded at the feeders, in the trees, before ($n = 190$) and during ($n = 49$) during ant exclusion.

temperature was not influenced by ant abundance). Air temperatures between 17 and 24°C predicted the greatest probability of high bee abundance (6%–8%, respectively), lower bee abundance was most probable at 24°C (25%), and temperature extremes (e.g., <10°C and >37°C) were the most likely to result in zero bees at the feeders. Ground temperature did not affect bee or ant abundance.

4 | DISCUSSION

Our study demonstrated that ants can have a substantial impact on bee abundance through the competitive exclusion of bees from open supplementary feeding stations. Ants, therefore, may have a significant effect on the effectiveness of beehives as elephant deterrents during the dry season. Ant presence alone does not prevent bees' access to supplementary feed; however, ants leverage numerical dominance and behavioral aggression to exclude bees from supplementary feed severely reducing the probability of bees utilizing this resource. Our study demonstrates an easy-to-use method of ant exclusion, that is effective at inhibiting ant access, and facilitating high bee abundance, at the feeders during resource-limited periods.

Behavioral aggression by ants is common in African savanna systems, where the defense of spatially and temporally limited resources is necessary to ensure colony fitness, growth, and reproduction (Parr, 2008; Parr et al., 2005). Supplementary feeding provides a highly nutritious resource during a severely resource-limited time of year. Consequently, the utilization and robust defense of such a resource by ants should be expected, as it removes resource scarcity as a limiting factor of ant colony fitness, growth, and expansion (Bishop et al., 2014). However, the spatial and temporal limitations constraining colonies of ants during the dry season also apply to bee colonies (Klein et al., 2019). Supplementary feed is provided to mitigate the possibility of bees absconding from their hives, as well as to maximize the effectiveness of the beehive deterrent action during the dry season when elephant impact on Marula trees, and crop raiding elsewhere, is at its highest (Cook et al., 2018; Cook & Henley, 2019). High levels of ant utilization of supplementary feed may seriously undermine the effectiveness of supplementary feed by causing resource scarcity to persist as a limiting factor of bee abundance and beehive activity in the dry season (Kuboja et al., 2020). This may reduce hive activity, increasing the risk of beehive abscondment, and the habituation of elephants to empty or low-activity hives—further undermining the deterrent's effectiveness. To improve our understanding of inter-specific competition and its implications, further research is needed that assesses the exact size, and population structure of beehives to understand exactly how hive health and activity is affected by interspecific competition, and the abundance threshold where bee activity becomes an ineffective deterrent. Currently, it is unclear what proportion of the bees diet is made up of supplementary feed in comparison to wild food alternatives (e.g., pollen from flowers), although both should be quite low considering the time of year. However, this should be investigated to ascertain the importance of supplementary feed for bees at this time of year. Furthermore, the provisioning of supplementary feed may give domesticated bees a competitive advantage by increasing their fitness and ability to compete with their wild counterparts and other pollinators. This is because domesticated bees could increase disease exchange where individuals interact at supplementary feeders or on flowers, competition for resources in the wet season (e.g., floral resources), and indirect effects through changes in the plant community could all reduce wild pollinator fitness and success (Mallinger et al., 2017). Where these beehive deterrents and supplementary feeders are broadly used across the landscape, biodiversity trade-offs (e.g., mitigating elephant tree damage vs. effects on wild pollinators) of using this method should be investigated further.

During our study, *Anoplolepis custodiens* was overwhelmingly the most common ant species (Table A2). *Anoplolepis custodiens* is notoriously aggressive, and specializes in the consumption and exploitation of sugar-based carbohydrates, making the supplementary feed an ideal resource (Mothapo & Wossler, 2017; Wittman et al., 2018). Other ants, particularly the arboreal *Crematogaster* spp., were also observed competing with bees for access to the supplementary feed but did not recruit conspecifics to feeders in substantial numbers, like *Anoplolepis* ants. However, these species still exhibited significant behavioral aggression (e.g., biting and charging toward bees) that inhibited bee access to supplementary feed (*personal observation*). The intense numerical dominance and interspecific aggression by *Anoplolepis* and other ant species resulted in a high level of competitive exclusion of bees (42%–82%, Figure 1) throughout the first phase of our study. However, we did not collect the data needed to analyze ant species effects separately—which would be advisable for future research. Furthermore, ant community composition and structure change along rainfall, temperature, vegetation, and topographic gradients (Parr et al., 2004), and so interspecific competition and aggression between bees and ants may vary in intensity depending on the location. Invertebrate surveys (e.g., pitfall traps) would thus be advisable before employing the beehive deterrent to gauge the potential for interspecific competition. This being said, highly aggressive and competitive ant species are present throughout southern, eastern, and central Africa (Fisher & Bolton, 2019), and so ant–bee competition may be a persistent challenge to the effectiveness of the beehive deterrents without sufficient intervention. However, due to the limited sample size in our experiment (one field site), further research would be required to ascertain the scale of this issue beyond the specific ecological context (e.g., a greater range of rainfall, temperatures, etc.) of our experiment and personal observations.

We have demonstrated a method of ant exclusion from open feeding stations that is simple, economical, and dramatically increases bee abundance at feeders by eliminating interspecific competition between bees and ants within trees. The effective exclusion of ants from tree feeders facilitated substantially greater access for bees to the supplementary feed. For example, the probability of no bees at the tree feeders decreased from 52% to 7% when ants were excluded from the trees. However, extreme aggression and the competitive exclusion of bees by ants persisted on the ground, where ant exclusion was not possible. Therefore, the redesign of the feeders, in addition to the exclusion of ants, would be advisable to ensure the most effective and economical delivery of supplementary feed to bees. Cook et al. (2018) originally estimated a minimum running cost of \$900 per year to provide supplementary feed to 50 occupied beehives during the South African dry season (March–August). To put our results into context, we assume the same cost of beehive maintenance and feeding given by Cook et al. (2018) and if ant/bee abundance correlates to the amount of food consumed by each species. An 82% predicted probability of 51%–100% ant abundance at the feeders throughout the dry season could result in \$738 per year being wasted on supplementary feed being consumed by ants across 50 beehives. Furthermore, beehive deterrents could potentially have an added cost of \$27.75 per beehive to replace bee colonies that abscond because of resource scarcity caused by the usurpation of supplementary feed. The potential for beehive abscondment directly because of interspecific competition with ants, however, warrants further investigation.

We have shown that interspecific competition for supplementary feed can be prevented through the application of engine grease to tree trunks, which substantially increased bee access to the supplementary feeding stations while costing as little as \$2–\$6 per tree, per year, to apply and maintain an 8–10 cm layer of engine grease or Plantex® (the minimum required to be effective). However, it would be advisable to investigate the feasibility of feeding the beehive colonies directly (e.g., through feeding ramps situated at the entrance of each beehive) to further reduce the potential for interspecific competition and reduce project costs. The use of engine grease was purely for our experimental assay, and due to environmental concerns related to the toxicity of engine grease, we strongly recommend against its wider use to deter ants. As a direct substitute, organic alternatives, such as Plantex® glue or mint, chalk, vinegar solutions, should be used because they are less environmentally hazardous. However, these alternatives were not available at the time of our experiment. During our experiment, small nontarget animals such as those from Diptera and Hymenoptera were caught in the grease, but these instances were minimal (R. Thornley, *personal observation*). To reduce the risk feeders could also be attached to wooden or metal poles that can be removed when not in use, reducing the long-term exposure of the environment and nontarget animals to any glue or other deterrents used. With the addition of Plantex® glue or other substances on the ropes of each individual beehive to prevent ant invasions (Cook et al., 2018), feeding stations will hopefully remain isolated from ant invasions, increasing the availability and effectiveness of open supplementary feeding for bees.

Lastly, ambient air temperature is an important predictor of bee abundance at the feeders. High abundances of bees (>20) were most likely around 18–26°C, which is consistent with the honeybees' optimum temperature range (e.g., temperature with maximum activity with minimal water loss) of 20°C (e.g., Abou-Shaara et al., 2017; Tan et al., 2012). Fewer bees are likely to be present at the feeders during low or high temperatures, as bees remain at their hives to maintain beehive temperature to an optimum of 36–37°C (e.g., through fanning; Peters et al., 2019). Ensuring that beehives and supplementary feeders are placed in a location with adequate shade to prevent exposure to extreme heat and desiccation will help facilitate higher bee activity and greater use of supplementary feed.

Our findings suggest that ant–bee competition may be a major threat to the sustainability of the beehive mitigation method for tree protection and human–elephant conflict. Innovative methods that exclude ant competition from supplementary feed are required to ensure that beehive occupancy levels remain high when resources are limited and elephant impact increases.

AUTHOR CONTRIBUTIONS

Conceptualization: Reece Thornley, Catherine L. Parr, Michelle Henley, Robin Cook. Data collection: Reece Thornley, Robin Cook. Data analysis: Reece Thornley, Matthew Spencer, Catherine L. Parr. Writing and reviewing of manuscript: Reece Thornley, Robin Cook, Matthew Spencer, Catherine L. Parr, Michelle Henley.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Please contact the corresponding author for data access requests.

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APPENDIX

TABLE A1 Model output for a multinomial logistic regression models.

(Intercept)	Air temperature	Ant abundance	Exclusion treatment: ground or feed	df	logLik	AICc	Delta	Weight
+	+	+	+	16	−282.928	599.0011	0	0.793532
+	—	+	+	14	−286.407	601.6938	2.692692	0.206468
+	+	—	+	10	−309.448	639.3527	40.35156	1.37E−09
+	+	+	—	10	−311.295	643.0476	44.04651	2.16E−10
+	—	—	+	8	−316.846	649.9899	50.98882	6.72E−12
+	—	+	—	8	−319.756	655.8091	56.80804	3.66E−13
+	+	—	—	4	−369.325	746.732	147.7309	6.61E−33
+	—	—	—	2	−377.571	759.1656	160.1645	1.32E−35

Note: + indicates where the model term was included, and — indicates where model term was excluded from the model selection process.

TABLE A2 Ant genus abundance in relation to feeder number and treatment.

During/before	Feeder (tree)	*Genus name*	Abundance
Before	Control	*Anoplolepis*	36
Before	Control	*Crematogaster*	1
Before	Control	*Monomorium*	2
Before	Control	*Pheidole*	1
Before	Control	Total	40
Before	Feeder 1	*Anoplolepis*	32
Before	Feeder 1	*Crematograster*	2
Before	Feeder 1	*Monomorium*	1
Before	Feeder 1	*Pheidole*	2
Before	Feeder 1	*Tetraponera*	1
Before	Feeder 1	Total	38
Before	Feeder 2	*Anoplolepis*	12
Before	Feeder 2	*Monomorium*	13
Before	Feeder 2	*Ocymyrmex*	3
Before	Feeder 2	*Pheidole*	6
Before	Feeder 2	*Technomyrmex*	2
Before	Feeder 2	*Tetramorium*	2
Before	Feeder 2	Total	37
Before	Feeder 3	*Anoplolepis*	578
Before	Feeder 3	*Crematogaster*	1
Before	Feeder 3	*Monomorium*	29
Before	Feeder 3	*Ocymyrmex*	1
Before	Feeder 3	*Pheidole*	13
Before	Feeder 3	*Polyrhachis*	2
Before	Feeder 3	*Technomyrmex*	1
Before	Feeder 3	*Tetramorium*	19
Before	Feeder 3	Total	644

(Continues)

TABLE A2 (Continued)

During/before	Feeder (tree)	*Genus name*	Abundance
Before	Feeder 4	*Anoplolepis*	7
Before	Feeder 4	*Camponotus*	3
Before	Feeder 4	*Crematogaster*	1
Before	Feeder 4	*Monomorium*	1
Before	Feeder 4	*Pheidole*	4
Before	Feeder 4	*Tetramorium*	5
Before	Feeder 4	Total	21
During	Control	*Crematograster*	3
During	Control	*Monomorium*	9
During	Control	*Ocymyrmex*	1
During	Control	*Pheidole*	3
During	Control	*Technomyrmex*	2
During	Control	Total	18
During	Feeder 1	*Anoplolepis*	40
During	Feeder 1	*Camponotus*	2
During	Feeder 1	*Crematograster*	1
During	Feeder 1	*Monomorium*	32
During	Feeder 1	*Pheidole*	28
During	Feeder 1	*Polyrhachis*	1
During	Feeder 1	*Tapinoma*	2
During	Feeder 1	*Technomyrmex*	38
During	Feeder 1	*Tetramorium*	28
During	Feeder 1	Total	172
During	Feeder 2	*Anoplolepis*	16
During	Feeder 2	*Bothroponera*	4
During	Feeder 2	*Camponotus*	2
During	Feeder 2	*Monomorium*	10
During	Feeder 2	*Myrmicaria*	1
During	Feeder 2	*Ocymyrmex*	13
During	Feeder 2	*Opthalmopone*	4
During	Feeder 2	*Pheidole*	30
During	Feeder 2	*Polyrhachis*	2
During	Feeder 2	*Technomyrmex*	13
During	Feeder 2	*Tetramorium*	5
During	Feeder 2	Total	100
During	Feeder 3	*Anoplolepis*	4837
During	Feeder 3	Total	4837
During	Feeder 4	*Anoplolepis*	9903
During	Feeder 4	Total	9903

Note: Ants were recorded using six pitfall traps filled with 80% ethanol solution, 1 m from the base of each tree containing a supplementary feeding station. Pitfall traps were in place for 5 days, both before supplementary feeding was started and during.

Popular articles

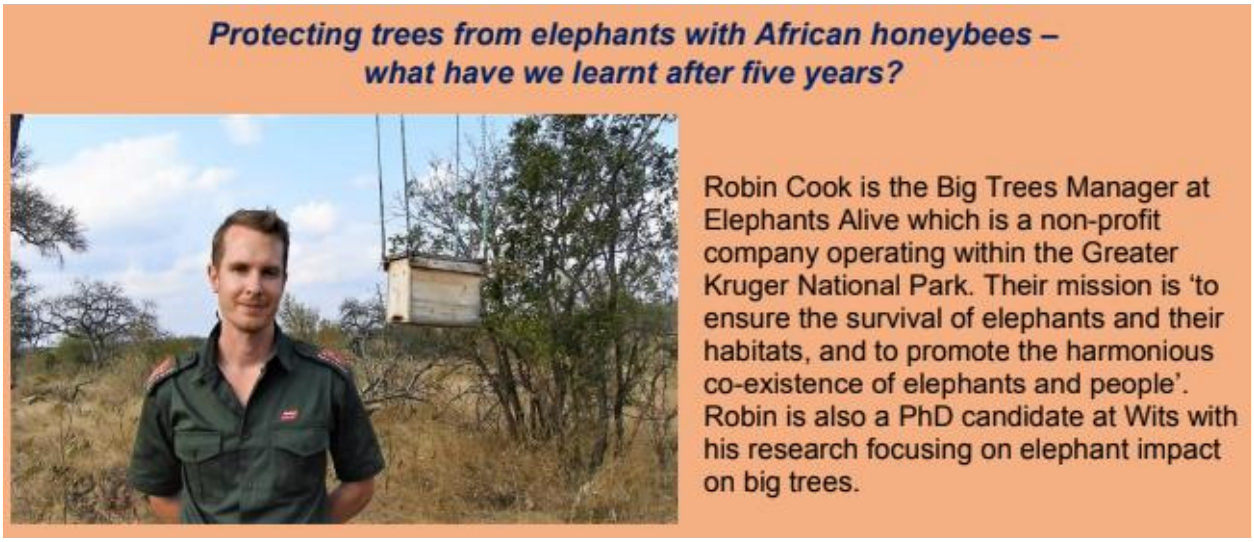
The following popular articles/online presentations were produced to support the findings of the PhD and aided in allowing a broader audience to access the information:

1. **Celebrating Five Years of Protecting Trees with Bees**. May 2021. Written by Robin Cook. Published on Elephants Alive's website. https://elephantsalive.org/celebrating-five-years-of-protecting-trees-with-bees/

2. **Elephants, Bees and Trees.** July 2021. Online presentation by Robin Cook. Platform: What Does The Giraffe Say Media.

3. **Elephants, Bees and Trees**. August 2021. Online presentation by Robin Cook. Platform: South African National Parks Honorary Rangers.

4. **Protecting trees from elephants with African honeybees – what have we learnt after five years?** September 2021. Written by Laura Knight. Published in the University of the Third Age – False Bay September 2021 Newsletter.



5. **The Marula Tree.** July 2022. Written by Kayleigh-Rose Humphries. Published on Elephant Plains' Website. https://elephantplains.co.za/big-5-blog/2022/07/the-marula-tree/

Beehive hanging from a Marula Tree
Photo by Robin Cook, Elephants Alive

6. **Battle of the titans: Africa's largest land mammal vs Africa's large trees.** July 2023. Written by Dr. Evelyn Poole. Published on Elephants Alive's website. https://elephantsalive.org/battle-of-the-titans-africas-largest-land-mammal-vs-africas-large-trees

Battle of the titans: Africa's largest land mammal vs Africa's large trees

An elephant pushing down a large tree to reach the canopy leaves. By Michael Lorentz

7. **Celebrating 16 years of Vulture Tree Surveys.** October 2023. Written by Robin Cook. Published on Elephants Alive's LinkedIn. https://www.linkedin.com/pulse/celebrating-16-years-vulture-tree-surveys-elephants-alive/?trk=organization_guest_main-feed-card_feed-article-content

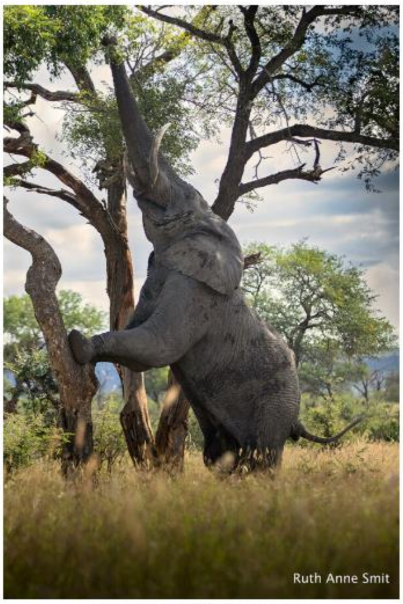
Can we keep them safe? A white backed vulture on its next in the Klaserie Private Nature Reserve. ©Ambersunny

Celebrating 16 years of Vulture Tree Surveys

Elephants Alive
829 followers

8. **Cutting corners when protecting trees? Not a great idea.** Written by Dr. Evelyn Poole. Published on Elephants Alive's website. https://elephantsalive.org/cutting-corners-when-protecting-trees-not-a-great-idea/

Cutting corners when protecting trees? Not a great idea ...



An elephant reaches for higher branches. Credit Ruth Smith

9. **Net win – saving Africa's trees from elephants.** November 2023. Written by Dr. Evelyn Poole and Robin Cook. Published on Africa Geographic's website. https://africageographic.com/stories/net-win-saving-africas-trees-from-elephants/

Net win – saving Africa's trees from elephants

Posted on November 7, 2023 by Evelyn Poole and Robin Cook, Elephants Alive in the DECODING SCIENCE post series.

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10. **Celebrating 15 years of vulture tree surveys.** February 2024. Written by Robin Cook. Published in Klaserie Chronicle magazine.

CONSERVATION

Celebrating 15 years

of vulture tree surveys

Words Robin Cook | Photos Elephants Alive

One can only wonder if, back in 2008, when Dr Michelle Henley conducted her first survey on trees containing vulture nests in the Klaserie Private Nature Reserve (KPNR) and continued with them until 2017, she had any idea that over the next 15 years of annual surveys, it would spread into five private nature reserves bordering the Kruger National Park, and include the Hoedspruit Airforce Base?

The study has figuratively "taken on wings" of its own, producing many reports over the years plus one scientific paper, and currently forming a chapter of a PhD thesis. From analysing the survival rates of vulture nests and trees, understanding which tree species are most vulnerable to elephant impact, and investigating which morphometrics makes a tree most suitable to vultures, the study continues to expand.

One of the first significant findings, based on continuously surveying the same trees and vulture nests, was that there is no correlation between an individual tree and nest survival. White-backed vulture nests, for example, are dilapidated regularly due to strong winds or the die-back of the upper branches supporting the nest.

In 2021, for example, the Greater Kruger National Park region experienced exceptionally high gusts of winds, resulting in a quarter of the nests surveyed during the previous year collapsing to the ground. Nests may also be abandoned, sometimes, unfortunately, due to the adult birds dying in poisoning events or electrocutions. Poisoning events can remove many adult birds from a population in a single event, resulting in fewer birds capable of building nests during the following years.

In 2018, the study expanded to cover large trees along the banks of the Olifants River. Here, the increased sample size of riverine trees containing vulture nests meant Dr Henley could statistically assess whether these large trees were indeed vulnerable to elephant impact. After just over four years, no riverine tree in the study has yet fallen. This is certainly good news when considering these trees are important breeding sites for the Hooded vulture.

This year, one of the knob thorn trees containing a vulture nest fell after a large fire swept over areas of the Timbavati and Thornybush Private Nature Reserves. The tree, which had previously been bark-stripped by elephants, was burnt through at the main stem and collapsed. This highlights how the combined natural forces of elephants and fire can influence tree survival. It was a relief, though, that all the other trees containing vulture nests in the area survived the fire. The vulture tree survey continuously reveals the complexity of ecological systems. Vulture nest vulnerability (with regards to elephant impact) depends on where the trees occur, which species of tree is in question, and the size of the tree. Furthermore, adult bird survival is critical when assessing population persistence, and the impact that poisonings and electrocutions have on vultures must be considered when assessing vulture population dynamics.

Thank you to the management of the Associated Private Nature Reserves and the Hoedspruit Airforce Base for allowing these studies to be conducted on their properties – as well as thanks to the volunteers who help with the fieldwork each year. It's with great pride that the 15-year milestone has been reached. ■

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