The effect of insects on elephant-induced tree damage within a small, fenced reserve in South Africa

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Abstract
African savanna elephants (Loxodonta africana) have been recognised as ecosystem engineers, where their feeding habits have been shown to alter landscapes. Within small, fenced reserves, studies exploring elephant damage on trees and their recovery have overlooked secondary damages that could be contributing to tree mortality. The aim of this study is to assess the significance of both elephant damage and secondary damage, and the subsequent tree recovery. We identified secondary damage as insects and considered wood borers and termites in this study. This was conducted in the small fenced Karongwe Private Game Reserve, South Africa. We analysed the level of damage, recovery and insect presence using vegetation transects, where all trees ≥2 m in height were surveyed (n = 1278 trees). Forty tree species were recorded, with 5 species accounting for 77% of the data set and used for further analysis. Termites were found to be more likely to colonise damaged trees without signs of recovery. However, wood borers were more likely to colonise damaged trees showing signs of recovery. Termites and wood borer presence on damaged trees was not dependent on tree height. We suggest carefully considering management approaches for elephant-induced termite and wood borer damage on trees.

Key words
elephant density, Karongwe Game Reserve, Loxodonta africana, termite damage, tree damage, tree recovery, wood borer damage

Résumé
Les éléphants de la savane africaine (Loxodonta africana) sont perçus comme les ingénieurs de l’écosystème, car il a été démontré que leurs habitudes alimentaires modifient les paysages. Dans les petites réserves clôturées, les études portant sur les dommages causés par les éléphants aux arbres et leur rétablissement ont jusqu’à maintenant négligé les dommages secondaires qui pourraient contribuer à la mortalité des arbres. L’objectif de cette étude est d’évaluer l’importance relative des dommages directs causés par les éléphants et les dommages secondaires ainsi que le rétablissement ultérieur des arbres. Nous avons identifié les dommages secondaires...
African savanna elephants (Loxodonta africana) are known to be capable of altering landscapes by reducing plant biomass and changing species composition (White & Goodman, 2009). Their ability to structurally modify vegetation has resulted in several studies on savanna trees, the damages elephants can inflict to them (Asner et al., 2016; Ben-Shahar, 1998; Gandiwa et al., 2011), and the subsequent impact on this may have on other tree species (Hrabar & Du Toit, 2014; Joseph et al., 2018; Kerley & Landman, 2006). The direct impact elephants have on vegetation is a particular concern in areas of high elephant density (Bounja & Midgley, 2009), such as fenced reserves, where increased damage can decrease savanna vegetation heterogeneity (Pringle, 2008). To date, literature has largely focussed on elephant damage with regards to the abundance of large trees, due to their significant environmental and economic value (Shannon et al., 2008). Types of damages caused by elephants include breaking branches and stems (Nasseri et al., 2011), as well as debarking (Calenge et al., 2002). Debarking has been shown to increase tree susceptibility to other associated damages, such as disease infection (for example, heart rot of the stem and branches) (Helm et al., 2011; Shannon et al., 2011; White & Goodman, 2009). Tree damage can also enhance tree susceptibility to termites (Coptotermes species), wood borers (Cerambycidae species) or other insects, which may shorten trees’ lifespan (Hatcher, 1995).

Termites can indeed penetrate trees through fractures in the bark (Gould et al., 1993; N’Dri et al., 2011) and establish secondary nests inside the tree’s cavities (Harris, 1968), increasing tree susceptibility to insect colonisations. This happens more frequently when bark is removed by animals such as elephants or porcupines (Hystrix africa-eastra); (Helm et al., 2011). Termites seem to prefer older, stressed trees with low water content and gaps within the bark (Cowie et al., 1989; Gould et al., 1993; Werner et al., 2008). Within the Kruger National Park (South Africa), termites have been shown to prevent regrowth of marula trees (Sclerocarya birrea) (Coetzee et al., 1979) and affect tree survival (Cook & Henley, 2019). Additionally, termite presence can result in trees being hollowed out from the inside, which may exacerbate vulnerability to elephant’s and other animals’ damage (Werner et al., 2008).

Wood borer damage to trees is characterised by the boring activity of larvae and adult beetles in the stems and branches of damaged or stressed hosts (Halperin & Geis, 1999; Liu et al., 2003; Nair, 2007; Peters et al., 2002). Adult mortality of marula trees has been suggested to be attributed to rapid invasion by wood borers after bark stripping occurs and the sapwood is exposed (Coetzee et al., 1979; Guy, 1989; Helm et al., 2011; Jacobs & Biggs, 2002). Structural damage caused by elephants and other herbivores enables wood borers to substantially weaken the stem (Coetzee et al., 1979), exacerbating the original damage by reducing the trees’ ability to recover (Guy, 1989). Recently, Vogel et al. (2014) found that the presence of insects on large, older trees with high elephant impact was negatively related to knob thorn trees’ (Sengilia nigrescens) survival, indicating elephant impact could indeed be indirectly facilitating insect attack and shortening the trees lifespan.

The interactive effects of multiple disturbances on different woody savanna species, such as the subsequent impact of insects on trees damaged by megaherbivores, are currently not completely understood (Holdo, 2007; Midgley et al., 2010). Increasing elephant densities in fenced reserves (Shannon et al., 2008; Skarpe et al., 2004) and the decreasing numbers of large trees (Ben-Shahar, 1993; Eckhardt et al., 2000; Moncief, et al., 2008) have resulted in a need for improved knowledge of how elephants and other subsequent disturbances can result in tree death (Holdo, 2005). Tree species are faced with several biotic constraints such as insects (Hakeem et al., 2012; Wargo, 1996), and this secondary damage partnered with the lack of tree recovery has been overlooked in many studies focussed on elephant damage. This paper aims to address this knowledge gap, by investigating how insect presence relates to tree damage and affects tree recovery. While doing so, this contribution will test the following hypotheses:
1. Insects are more likely to colonise trees damaged by elephants than trees not damaged by elephants.
2. Insects are more likely to colonise taller trees damaged by elephants than shorter trees.
3. Insects are less likely to colonise damaged trees exhibit signs of recovery.

2 | METHOD

2.1 | Study site

The study was carried out in Karongwe Private Game Reserve (KPGR), a 7960-hectare fenced private reserve in the Limpopo province of South Africa (centred on 30.60°E 24.23°N). The reserve consists of two savanna vegetation types: Granite Lowveld and Tzaneen Sour Bushveld (Mucina & Rutherford, 2006). Daily mean ambient air temperatures range from 5 to 17°C in winter (June to August) to 17–28°C in summer (December to February). The elevation range is 489–520 m above mean sea level (Lehmann et al., 2008).

The reserve originally consisted of 10 individual private farmlands, but division fences were removed in 1998 and a Reserve was established. KPGR is bordered by public roads, which are as close as 50 m from the fence line. The western fence line (19.1 km) runs along the paved R36 route, while gravel roads run parallel along the eastern (14.5 km) and northern (11.9 km) fence lines.

Elephants (seven individuals) were translocated to KPGR in 1999 from Kapama Game Reserve and Maggudu, Kwaza-Zulu Natal. Since 2011 the elephant population has consisted of one stable family unit of adult females, both male and female subadults and juveniles. There are also two bulls present on this reserve. Owen-Smith et al. (2006) suggest that an effective elephant population density is 0.28 km², based upon which KGPR could support 22.28 elephants. KGPR currently supports 20 elephants.

2.2 | Data collection

Vegetation data were collected in June – October 2019, with 84, 10 x 100 m transects to represent the vegetation type across the reserve. A navigation-grade GNSS (Garmin™ GPSMap® 60CSX) was used to acquire co-ordinate pairs at the start of each transect. Every tree of height ≥2 m and diameter breast height (DBH) of ≥10 cm was sampled for elephant damage and recovery (Coetzee et al., 1979; Staub et al., 2013). When a tree met the necessary requirements, the following parameters were recorded:

1. Species, height (m), DBH (cm).
2. Elephant damage type (Table 1).
3. Tree recovery type (Table 1).
4. Insect presence: Termites, Wood borers.

### TABLE 1 Scale used to record elephant browsing damage and recovery levels on tree species after Walker (1976)

| Variable          | Observation                  |
|-------------------|------------------------------|
| Damage            | Branches broken              |
|                   | Condition of the tree: Alive/Dead |
|                   | Main stem broken             |
|                   | Main trunk debarked          |
|                   | Pushed over                  |
| Recovery          | Presence of coppicing        |
|                   | Bark regrowth                |
|                   | Presence of sprouting        |

Tree damages were derived from the Walker damage scale (Walker, 1976) (Table 1) to determine the types of elephant damage on each tree during data collection. Elephant damage on trees is easily distinguished from that of other browsers due to their foraging behaviours (Jachmann & Bell, 1985). Damages were recorded according to the methods used by Jacobs and Biggs (2002). The types of recovery were also recorded for each tree based on the types of recovery identified by Gadd (2002) (Table 1). All trees sampled were recorded using a binary scoring system for each parameter.

2.3 | Data analysis

A total of 1278 trees were used in our analysis, on the five most abundant tree species: knobthorn (S. nigrescens; 382), marula (S. birea; 175), velvet corkwood (Commiphora mollis; 179), red bush willow (Combretum apiculatum; 493), and leadwood (Combretum imberbe; 49).

Data exploration was carried out following the protocol described in Zuur et al. (2010). Generalised linear mixed effect models (GLMM; binomial distribution) were used to model the likelihood of a given insect type to be found on any given tree, as a function of the height of the tree, the level of tree damage, and the two-way interactions between covariates (all fixed effects). We also used GLMM to model the likelihood of a given insect type to be found on any damaged tree, as a function of the height of the tree, whether the damaged tree showed any signs of recovery, and the two-way interactions between covariates (all fixed effects). In all cases, transect identity was modelled as a random effect. Identified damage and recovery types were classified into ‘DamageScore’ (0–5, depending on the number of types of damages identified) and ‘RecoveryScore’ (0–3, depending on the number of types of recovery identified) for each observed tree (Table 1). We tested the model structure by adding the independent variables and then tested the main effects plus the interactions; the best models were used for further inference. All models were built in R using the ‘lme4’ package (Pinheiro & Bates, 2000; R Core Team, 2014).

Model assumptions were verified by plotting residuals for spatial dependency. We determined that the random effect approach was sufficient for spatial dependency by conducting Moran’s I test on all models (Getis, 2008). Results confirm that spatial autocorrelation is
absent in the residuals of all models, and inference was taken from the best performing models (Moran’s I for all models < 0.02; p-value < 0.05 for all models).

3 | RESULTS

Termites were more likely to be found on more damaged trees, (p = 0.02); however, tree height was less important as the score damage increased (p = 0.01; Table 2).

The likelihood of finding wood borers on trees, on the other hand, was not impacted by tree height or damage score (all p > 0.05; Table 2).

We also found that recovery was significantly linked to wood borers presence: the higher the recovery score, the greater the chance of finding wood borers on damaged trees (p = 0.03). However, the likelihood of finding termites on damaged trees was not related to the tree’s recovery score (p > 0.05). Both termite and wood borer presence was not affected by tree height of damaged trees (p > 0.05; Table 2).

4 | DISCUSSION

Our results show that (a) termites are more likely to colonise damaged trees; (b) wood borers are more likely to colonise damaged trees that are showing signs of recovery, and that (c) insect presence on damaged trees did not depend on tree height.

Studies to date that have considered elephant damage on trees have overlooked the impact of insects. We show here that termites colonising damaged trees should be regarded as a significant contributor to secondary damage. We also found that the effect of tree height was not related to insect presence, suggesting that insects do not colonise tall trees. This raises concerns, as management efforts to date on trees have focussed on large trees as they are considered the most susceptible to elephant damage (Jacobs & Biggs, 2002; Helm et al., 2009; Helm & Witkowski, 2012; Cook et al., 2017). Howes et al. (2020) determined that tree damage by elephants in an enclosed reserve was non-lethal to trees, and that taller trees were less likely to suffer from elephant damage. However, once elephant damage on trees has occurred, it was not known how the level of insect damage impacts tree mortality. We have shown here that termite presence on damaged trees could be leading to increased mortality if the tree is unable to recover from elephant damage, as they were more likely to be found on damaged trees that did not show any signs of recovery. In addition, the trees inability to recover from elephant damage could be the trigger to termite colonisation.

It could also be conceivable that debarking may not be the main driver for subsequent insect damage. Debarking has been shown to increase tree susceptibility to other damages including fires (Ihwagi et al., 2010) and diseases and has shown to be attributed to cause direct mortality (White & Goodman, 2009). This method of elephant feeding has also been shown to make the tree more susceptible to termites, wood borers and other insect activity and ultimately, shortening the trees lifespan (Hatcher, 1995). However, our results show that termites are more likely to colonise trees that have a greater number of damages. Added to this, our results showed that wood borer presence was likely to be found on trees that exhibited signs of recovery, suggesting that even trees showing signs of recovery may encounter further damage from insects. We suggest mitigation methods should focus on the most susceptible trees that show high levels of damage, that are likely to incur further damages from termites and consider wood borers presence on trees with recovery.

We stress that our study does not indicate the removal and prevention of insects at this stage. We are suggesting that more focus should be directed towards secondary impacts of damage, as opposed to just considering elephant damage on its own in relation to tree mortality. Additionally, elephant feeding habits result in greater availability of food for termites and woodborers (Holdo & McDowell, 2004). In fact, within fenced reserves that limit wildlife migration between reserves, high densities of termite mounds are important to conservation as they are able to sustain wildlife population by

| Variable | Fixed effects | GLM coefficient (estimate) | SE | Z value | p value |
|----------|---------------|----------------------------|----|---------|---------|
| Wood borer | Height, RecoveryScore | -0.04, 0.35 | 0.05, 0.17 | -0.66, 2.16 | 0.49, 0.03 |
| Termite | Height, RecoveryScore | -0.13, -0.68 | 0.11, 0.76 | -1.21, -0.89 | 0.23, 0.37 |
| Wood borer | Height, DamageScore | 0.09 | 0.10 | 0.86 | 0.39 |
| Termite | Height, DamageScore | -0.07 | 0.06 | -1.25 | 0.21 |

Bold indicates Significant values (0.03, 0.01, 0.02)
sustaining nutritious forage availability across seasons. This can be crucial during the dry season when forage is limited (Davies et al., 2016). Studies have also suggested that within fenced reserves, elephants show feeding preferences to browsing over grazing, which only enhances the need for termites as mounds (Jouquet et al., 2011). Few tree species such as C. apiculatum and Combretum mopane grow on termite mounds, where other species have been found in proximity to mounds such as Sclerocarya birrea (Davies et al., 2016). Trees species within proximity to termite mounds within savanna environments benefit as termite mounds can aid tree growth due their increased soil fertility as well as water availability. There have been studies on the relationship between termite mounds and herbivore feeding patterns (Muvengwi et al., 2013; Okullo & Moe, 2012; Van der Plas et al., 2013). A recent study focussed on the influence of mound size on vegetation diversity, finding that elephant damage to mound associated vegetation reduced the microclimate effects provided by vegetation (Joseph et al., 2013). However, termite mounds have been shown to provide both refugia and high-quality forage for a range of herbivore species (Fleming & Loveridge, 2003; Grant & Scholes, 2006; Mobaek et al., 2005). Therefore, we acknowledge that termite mounds are essential for biodiversity and providing ecosystem services.

Further studies are therefore needed to determine the level of mitigation required to suppress elephant-induced damages and the subsequent impacts of insects on susceptible trees. This way, we will be able to determine the best approach to maintain sufficient vegetation for elephant feeding. Some tree species are not impacted highly by feeding and can persist through time, however further damage by insects can cause an increased severity of damage and limit the ability of a tree to recover. Conservation efforts should focus on trees that are unable to recover and are susceptible to elephant and insect damage.

We attempted to address some of the explanatory factors of elephant damage and the impact of insects; however, there are limitations to this study. We only considered termite and wood borer presence in our analysis. Our study is constrained both temporally and spatially, as we only collected data over 3 months in one area. If tree damage was recent, then there may have not been enough time to show levels of recovery or subsequent insect activity. We recommend that studies using our approach consider a larger temporal range as well as considering other insect species. It may also be informative to further studies to identify the density and size of termite mounds and their spatial distribution, associated with damaged trees in a fenced reserve, as termite mounds themselves play a part in the spatial heterogeneity of the landscape.

Our study has provided fresh insight regarding insect presence in trees damaged by a high density of elephants within a fenced reserve, and their subsequent recovery. There remains a need to determine how insects directly impact further damage to trees, and their subsequent recovery, in the longer-term. Therefore, we suggest carefully considering management approaches for elephant-induced insect damage on trees. We acknowledge the importance of insects for many ecological processes and other species that live within fenced reserves. We have shown that even damaged trees that exhibit recovery have wood borer presence, which is a concern when considering the level of damage in a fenced reserve. As reserves vary in elephant density and the spatial distribution of termite mounds and therefore termite induced damages, it is essential that we determine how to manage the secondary effects of elephant damage so that vegetation can be maintained.

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CONFLICT OF INTEREST
The authors declare no competing interests.

AUTHOR CONTRIBUTIONS
K.T. conceived the study. K.G. performed data collection. N.P. provided critical analysis and discussion. K.T. performed data analysis. K.T. wrote the manuscript with support of N.P., G.E. and A.F. All authors edited and approved the content.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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