Check for updates

Received: 7 June 2021 | Revised: 23 December 2021 | Accepted: 24 February 2022

DOI: 10.1111/aje.13002

RESEARCH ARTICLE

African Journal of Ecology WILEY

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

Katie Elizabeth Thompson[1] | **Andrew Ford**[1] | **Genoveva Esteban**[1] | **Kayla Zoon**[2,3] | **Nathalie Pettorelli**[4]

[1]Faculty of Science and Technology, Department of Life and Environmental Sciences, Bournemouth University, Poole, UK

[2]Elephants Alive, Hoedspruit, South Africa

[3]Global Vision International, South African Wildlife Research Expedition, Ofcolaco, South Africa

[4]Institute of Zoology, Zoological Society of London, London, UK

Correspondence
Katie Elizabeth Thompson, Bournemouth University, Faculty of Science and Technology, Department of Life and Environmental Sciences, Poole, Dorset BH12 5BB, UK.
Email: thompsonk@bournemouth.ac.uk

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 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.

KEYWORDS
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

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2022 The Authors. *African Journal of Ecology* published by John Wiley & Sons Ltd.

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

comme étant dus aux insectes et dans le cadre de cette étude nous nous concentrons sur les xylophages et les termites. Cette étude a été menée dans la petite réserve privée clôturée de Karongwe, en Afrique du Sud. Nous avons analysé le niveau de dommages, la récupération et la présence d'insectes en utilisant des transects de végétation, où tous les arbres ≥2 m de hauteur ont été étudiés (n = 1278 arbres). Quarante espèces d'arbres ont été enregistrées, avec 5 espèces représentant 77% de l'ensemble des données et utilisées pour une analyse plus approfondie. On a constaté que les termites étaient plus susceptibles de coloniser les arbres endommagés qui ne présentent pas de signes de rétablissement. En revanche, les xylophages étaient plus susceptibles de coloniser les arbres endommagés présentant des signes de rétablissement. La présence de termites et de xylophages sur les arbres endommagés ne dépendait pas de la hauteur de l'arbre. Nous suggérons d'examiner attentivement les approches de gestion des dommages secondaires causés par les termites et les xylophages aux arbres endommagés par les éléphants.

1 | INTRODUCTION

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), woodborers (*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 africaeaustralis*) (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' (*Sengalia 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; Moncrieff 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:

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

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 km^2, 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 × 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. birrea*; 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

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 2 GLMM outputs of dependent (termites and wood borers) and independent variables (fixed effects) for both insects tested

Variable	Fixed effects	GLM coefficient (estimate)	SE	*Z* value	*p* value
Wood borer	Height+	−0.04	0.05	−0.66	0.49
	RecoveryScore	0.35	0.17	2.16	**0.03**
Termite	Height	−0.13	0.11	−1.21	0.23
	RecoveryScore	−0.68	0.76	−0.89	0.37
	Height: RecoveryScore	0.09	0.10	0.86	0.39
Wood borer	Height	0.08	0.06	1.39	0.10
	DamageScore	0.64	0.39	1.63	0.10
	Height: DamageScore	−0.07	0.06	−1.25	0.21
Termite	Height	0.09	0.07	1.29	0.19
	DamageScore	1.14	0.47	2.41	**0.02**
	Height: DamageScore	−0.17	0.07	−2.51	**0.01**

Bold indicates Significant values (0.03, 0.01, 0.02)

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 woodborers 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

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

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; Mobæk 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 supress 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.

ACKNOWLEDGEMENTS

The authors would like to thank the Global Vision International research team and the landowners of Karongwe Private Game Reserve (SA). NP is funded by Research England.

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.

ORCID

Katie Elizabeth Thompson https://orcid.org/0000-0002-9027-6718

REFERENCES

Asner, G. P., Vaughn, N., Smit, I. P., & Levick, S. (2016). Ecosystem-scale effects of megafauna in African savannas. *Ecography*, *39*(2), 240–252. https://doi.org/10.1111/ecog.01640

Ben-Shahar, R. (1993). Patterns of elephant damage to vegetation in northern Botswana. *Biological Conservation*, *65*(3), 249–256. https://doi.org/10.1016/0006-3207(93)90057-8

Ben-Shahar, R. (1998). Elephant density and impact on Kalahari woodland habitats. *Transactions of the Royal Society of South Africa*, *53*(2), 149–155. https://doi.org/10.1080/00359199809520383

Boundja, R. P., & Midgley, J. J. (2009). Patterns of elephant impact on woody plants in the Hluhluwe-Imfolozi park. *Kwazulu-Natal, South Africa, African Journal of Ecology*, *48*, 206–214.

Calenge, C., Maillard, D., Gaillard, J. M., Merlot, L., & Peltier, R. (2002). Elephant damage to trees of wooded savanna in Zakouma National Park, Chad. *Journal of Tropical Ecology*, *18*, 599–614. https://doi.org/10.1017/S0266467402002390

Coetzee, B., Engelbrecht, A., Joubert, S., & Retief, P. (1979). Elephant impact on *Sclerocarya caffra* trees in *Acacia nigrescens* tropical plains thornveld of the Kruger National Park. *Koedoe*, *22*(1), 39–60.

Cook, R. M., & Henley, M. D. (2019). Complexities associated with elephant impact on *Sclerocarya birrea* subsp. *caffra* in the Greater Kruger National Park. *South African Journal of Botany*, *121*, 543–548.

Cook, R., Witkowski, E., Helm, C., Henley, M., & Parrini, F. (2017). Recent exposure to African elephants after a century of exclusion: Rapid accumulation of marula tree impact and mortality, and poor regeneration. *Forest Ecology and Management*, *401*, 107–116. https://doi.org/10.1016/j.foreco.2017.07.006

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Cowie, R. H., Logan, J. W., & Wood, T. G. (1989). Termite (Isoptera) damage and control in tropical forestry with special reference to Africa and Indo-Malaysia: A review. *Bulletin of Entomological Research*, *79*(2), 173–184. https://doi.org/10.1017/S0007485300018150

Davies, A. B., Baldeck, C. A., & Asner, G. P. (2016). Termite mounds alter the spatial distribution of African savanna tree species. *Journal of Biogeography*, *43*(2), 301–313. https://doi.org/10.1111/jbi.12633

Eckhardt, H. C., Van Wilgen, B. W., & Biggs, H. C. (2000). Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, *38*(2), 108–115. https://doi.org/10.1046/j.1365-2028.2000.00217.x

Fleming, P. A., & Loveridge, J. P. (2003). Miombo woodland termite mounds: Resource islands for small vertebrates? *Journal of Zoology*, *259*(2), 161–168. https://doi.org/10.1017/S0952836902003084

Gadd, M. (2002). The impact of elephants on the marula tree *Sclerocarya birrea*. *African Journal of Ecology*, *40*(4), 328–336.

Gandiwa, E., Magwati, T., Zisadza, P., Chinuwo, T., & Tafangenyasha, C. (2011). The impact of African elephants on *Acacia tortilis* woodland in northern Gonarezhou National Park, Zimbabwe. *Journal of Arid Environments*, *75*(9), 809–814. https://doi.org/10.1016/j.jaridenv.2011.04.017

Getis, A. (2008). A history of the concept of spatial autocorrelation: A geographer's perspective. *Geographical Analysis*, *40*(3), 297–309. https://doi.org/10.1111/j.1538-4632.2008.00727.x

Gould, M. S., Lowe, A. J., & Clarke, G. P. (1993). The frequency of termite (Isoptera) damage to tree species in Namakutwa forest. *Tanzania*, *Sociobiology*, *23*, 189–198.

Grant, C. C., & Scholes, M. C. (2006). The importance of nutrient hotspots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, *130*(3), 426–437. https://doi.org/10.1016/j.biocon.2006.01.004

Guy, P. R. (1989). The influence of elephants and fire on a Brachystegia-Julbernardia woodland in Zimbabwe. *Journal of Tropical Ecology*, *5*, 215–226.

Hakeem, K. R., Chandna, R., Ahmad, P., Iqbal, M., & Ozturk, M. (2012). Relevance of proteomic investigations in plant abiotic stress physiology. *Omics: A Journal of Integrative Biology*, *16*(11), 621–635. https://doi.org/10.1089/omi.2012.0041

Halperin, J., & Geis, K. U. (1999). Lyctidae (Coleoptera) of Israel, their damage and its prevention. *Phytoparasitica*, *27*(4), 257–262. https://doi.org/10.1007/BF02981481

Harris, W. V. (1968). African termites of the genus Schedorhinotermes (Isoptera: Rhinotermitidae) and associated termitophiles (Lepidoptera: Tineidae). *Proceedings of the Royal Entomological Society of London*. *Series B*, *Taxonomy*, *37*(8), 103–113.

Hatcher, P. E. (1995). Three-way interactions between plant pathogenic fungi, herbivorous insects and their host plants. *Biological Reviews*, *70*(4), 639–694. https://doi.org/10.1111/j.1469-185X.1995.tb01655.x

Helm, C., Wilson, G., Midgley, J., Kruger, L., & Witkowski, E. T. F. (2011). Investigating the vulnerability of an African savanna tree (*Sclerocarya birrea* ssp. *caffra*) to fire and herbivory. *Austral Ecology*, *36*(8), 964–973.

Helm, C. V., & Witkowski, E. T. F. (2012). Characterising wide spatial variation in population size structure of a keystone African savanna tree. *Forest Ecology and Management*, *263*, 175–188. https://doi.org/10.1016/j.foreco.2011.09.024

Helm, C., Witkowski, E., Kruger, L., Hofmeyr, M., & Owen-Smith, N. (2009). Mortality and utilisation of *Sclerocarya birrea* subsp. *caffra* between 2001 and 2008 in the Kruger National Park, South Africa. *South African Journal of Botany*, *75*(3), 475–484.

Holdo, R. M. (2005). Stem mortality following fire in Kalahari sand vegetation: Effects of frost, prior damage, and tree neighbourhoods. *Plant Ecology*, *180*(1), 77–86. https://doi.org/10.1007/s11258-005-2796-4

Holdo, R. M. (2007). Elephants, fire, and frost can determine community structure and composition in Kalahari woodlands. *Ecological Applications*, *17*(2), 558–568. https://doi.org/10.1890/05-1990

Holdo, R. M., & McDowell, L. R. (2004). Termite mounds as nutrient–rich food patches for elephants. *Biotropica*, *36*(2), 231–239. https://doi.org/10.1111/j.1744-7429.2004.tb00314.x

Howes, B., Doughty, L., & Thompson, S. (2020). African elephant feeding preferences in a small South African fenced game reserve. *Journal for Nature Conservation*, *53*, 125700. https://doi.org/10.1016/j.jnc.2019.03.001

Hrabar, H., & Du Toit, J. T. (2014). Interactions between megaherbivores and microherbivores: Elephant browsing reduces host plant quality for caterpillars. *Ecosphere*, *5*(1), 1–6. https://doi.org/10.1890/ES13-00173.1

Ihwagi, F. W., Vollrath, F., Chira, R. M., Douglas-Hamilton, I., & Kironchi, G. (2010). The impact of elephants, *Loxodonta africana*, on woody vegetation through selective debarking in Samburu and Buffalo Springs National Reserves, Kenya. *African Journal of Ecology*, *48*(1), 87–95.

Jachmann, H., & Bell, R. H. V. (1985). Utilization by elephants of the Brachystegia woodlands of the Kasungu National Park, Malawi. *African Journal of Ecology*, *23*(4), 245–258.

Jacobs, O., & Biggs, R. (2002). The impact of the African elephant on marula trees in the Kruger National Park. *South African Journal of Wildlife Research-24-month Delayed Open Access*, *32*(1), 13–22.

Joseph, G. S., Seymour, C. L., Coetzee, B. W., Ndlovu, M., Deng, L., Fowler, K., Hagan, J., Brooks, B. J., Seminara, J. A., & Foord, S. H. (2018). Elephants, termites and mound thermoregulation in a progressively warmer world. *Landscape Ecology*, *33*(5), 731–742. https://doi.org/10.1007/s10980-018-0629-9

Joseph, G. S., Seymour, C. L., Cumming, G. S., Cumming, D. H., & Mahlangu, Z. (2013). Termite mounds as islands: Woody plant assemblages relative to termitarium size and soil properties. *Journal of Vegetation Science*, *24*(4), 702–711. https://doi.org/10.1111/j.1654-1103.2012.01489.x

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., & Bignell, D. (2011). Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, *47*(4), 215–222.

Kerley, G., & Landman, M. (2006). The impacts of elephants on biodiversity in the Eastern Cape Subtropical Thickets: Elephant conservation. *South African Journal of Science*, *102*(9–10), 395–402.

Liu, H., Bauer, L. S., & Gao, R. (2003). Exploratory survey for the emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), and its natural enemies in China. *Great Lakes Entomologist*, *36*, 191–204.

Lehmann, M. B., Funston, P. J., Owen, C. R., & Slotow, R. (2008). Home range utilisation and territorial behaviour of lions (Panthera leo) on Karongwe Game Reserve. *South Africa*. *PLoS One*, *3*(12), e3998.

Midgley, J. J., Lawes, M. J., & Chamaillé-Jammes, S. (2010). Savanna woody plant dynamics: The role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*, *58*(1), 1–11. https://doi.org/10.1071/BT09034

Mobæk, R., Narmo, A. K., & Moe, S. R. (2005). Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. *Journal of Zoology*, *267*(1), 97–102. https://doi.org/10.1017/S0952836905007272

Moncrieff, G. R., Kruger, L. M., & Midgley, J. J. (2008). Stem mortality of *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. *Journal of Tropical Ecology*, *24*(6), 655–662.

Mucina, L., & Rutherford, M. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute.

Muvengwi, J., Mbiba, M., & Nyenda, T. (2013). Termite mounds may not be foraging hotspots for mega-herbivores in a nutrient-rich matrix. *Journal of Tropical Ecology*, *29*, 551–558. https://doi.org/10.1017/S0266467413000564

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Nair, K. S. (2007). *Tropical forest insect pests: Ecology, impact, and management*. Cambridge University Press.

Nasseri, N. A., McBrayer, L. D., & Schulte, B. A. (2011). The impact of tree modification by African elephant (*Loxodonta africana*) on herpetofaunal species richness in northern Tanzania. *African Journal of Ecology*, *49*(2), 133–140. https://doi.org/10.1111/j.1365-2028.2010.01238.x

N'Dri, A. B., Gignoux, J., Konaté, S., Dembélé, A., & Aïdara, D. (2011). Origin of trunk damage in West African savanna trees: The interaction of fire and termites. *Journal of Tropical Ecology*, *27*, 269–278. https://doi.org/10.1017/S026646741000074X

Okullo, P., & Moe, S. R. (2012). Large herbivores maintain termite-caused differences in herbaceous species diversity patterns. *Ecology*, *93*(9), 2095–2103. https://doi.org/10.1890/11-2011.1

Owen-Smith, N., Slotow, R., Kerley, G., Van Aarde, R., & Page, B. (2006). A scientific perspective on the management of elephants in the Kruger National Park and elsewhere: Elephant conservation. *South African Journal of Science*, *102*(9), 389–394.

Peters, B. C., Creffield, J. W., & Eldridge, R. H. (2002). Lyctine (Coleoptera: Bostrichidae) pests of timber in Australia: A literature review and susceptibility testing protocol. *Australian Forestry*, *65*(2), 107–119. https://doi.org/10.1080/00049158.2002.10674861

Pinheiro, J., & Bates, D. (2000). Fitting linear mixed-effects models. In *Mixed-effects Models in S and S-PLUS* (pp. 133–199).

Pringle, R. M. (2008). Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology*, *89*(1), 26–33. https://doi.org/10.1890/07-0776.1

R Core Team (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Shannon, G., Druce, D., Page, B., Eckhardt, H., Grant, R., & Slotow, R. (2008). The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology*, 281–289. https://doi.org/10.1017/S0266467408004951

Shannon, G., Thaker, M., Vanak, A. T., Page, B. R., Grant, R., & Slotow, R. (2011). Relative impacts of elephant and fire on large trees in a savanna ecosystem. *Ecosystems*, *14*(8), 1372–1381. https://doi.org/10.1007/s10021-011-9485-z

Skarpe, C., Aarrestad, P. A., Andreassen, H. P., Dhillion, S. S., Dimakatso, T., du Toit, J. T., Halley, D. J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G., Modise, D., Moe, S. R., Mojaphoko, R., Mosugelo, D., Mptsumi, S., Neo-Mahupeleng, G., Ramotadima, M., … Wegge, P. (2004). The return of the giants: Ecological effects of an increasing elephant population. *AMBIO: A Journal of the Human Environment*, *33*(6), 276–282. https://doi.org/10.1579/0044-7447-33.6.276

Staub, C., Binford, M., & Stevens, F. (2013). Elephant herbivory in Majete wildlife reserve, Malawi. *African Journal of Ecology*, *51*(4), 536–543. https://doi.org/10.1111/aje.12064

Van der Plas, F., Howison, R., Reinders, J., Fokkema, W., & Olff, H. (2013). Functional traits of trees on and off termite mounds: Understanding the origin of biotically-driven heterogeneity in savannas. *Journal of Vegetation Science*, *24*(2), 227–238. https://doi.org/10.1111/j.1654-1103.2012.01459.x

Vogel, S. M., Henley, M. D., Rode, S. C., van de Vyver, D., Meares, K. F., Simmons, G., & de Boer, W. F. (2014). Elephant (*Loxodonta africana*) impact on trees used by nesting vultures and raptors in South Africa. *African Journal of Ecology*, *52*(4), 458–465.

Walker, S. H. (1976). An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research-24-month Delayed Open Access*, *6*(1), 1–32.

Wargo, P. M. (1996). Consequences of environmental stress on oak: Predisposition to pathogens. *Annales Des Sciences Forestières*, *53*(2-3), 359–368. https://doi.org/10.1051/forest:19960218

Werner, P. A., Prior, L. D., & Forner, J. (2008). Growth and survival of termite-piped *Eucalyptus tetrodonta* and *E. miniata* in northern Australia: Implications for harvest of trees for didgeridoos. *Forest Ecology and Management*, *256*, 328–334.

White, A. M., & Goodman, P. S. (2009). Differences in woody vegetation are unrelated to use by African elephants (*Loxodonta africana*) in Mkhuze Game Reserve, South Africa. *African Journal of Ecology*, *48*, 215–223.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

How to cite this article: Thompson, K. E., Ford, A., Esteban, G., Zoon, K., & Pettorelli, N. (2022). The effect of insects on elephant-induced tree damage within a small, fenced reserve in South Africa. *African Journal of Ecology*, *60*, 641–647. https://doi.org/10.1111/aje.13002

13652028, 2022, 3, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/aje.13002 by Bournemouth University, Wiley Online Library on [18/01/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License