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Effects of elephants on seed dispersal and germination of *Balanites maughamii* in an East African dry coastal forest

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ABSTRACT

Elephants play a significant role in shaping tropical ecosystems. They influence the dispersal and regeneration of various plant species and thus shape plant and animal communities. In this study, we investigate seed predation rates by the African elephant on the torchwood forest tree (*Balanites maughamii*) in a part of the Arabuko Sokoke dry coastal forest in southern Kenya. We test for effects on the germination and seedling growth rates in *ex situ* experiments and consider the role of passing through the elephant gut and the effect of elephant dung on germination. Seed predation rates were highest close to parent trees. Seeds that passed through elephant guts had the highest germination and growth rates. Seeds enclosed by dung did not show higher rates of germination than seeds without dung. In general, our results underline the important role of elephants for seed dispersal and germination of *B. maughamii* in tropical forest ecosystems.

Keywords: seed predation; seed dispersal; germination; growth rate; Arabuko Sokoke Forest; Kenya

INTRODUCTION

A central goal of community ecology is to understand the processes that generate and maintain diversity and enhance coexistence of a large number of species in a confined space (Levine and HilleRisLambers 2009, Gerz *et al.* 2018). In this respect, an important mechanism is disturbance. Disturbance by large animals creates numerous ecological niches, which can then be colonized by organisms across all trophic levels (Dornelas 2010, Hall *et al.* 2012). Mega-herbivores, such as elephants, can play a central role here as disturbers and important ecosystem engineers (Theuerkauf *et al.* 2000, Coverdale *et al.* 2016) that contribute to the maintenance of plant and animal diversity in savannah and forest habitats (Pringle 2008). Long-distance dispersal by elephants is particularly important in shaping plant communities, maintaining genetic diversity, and promoting forest regeneration (Poulsen *et al.* 2021).

Elephants are known to shape ecosystems as browsers, with trampling, uprooting, pollarding, and debarking. Thus, the presence of elephants can cause severe disturbance of ecosystems (White *et al.* 1993, Theuerkauf *et al.* 2000). Similar to the African savannahs, elephants can also play a central role in tropical forest ecosystems, where a considerable number of different plant (and animal species) coexist in a limited space (e.g. 300 tree species found per hectare; Wright 2002, Silvertown 2004). Elephants can create forest gaps when occurring in high densities. They are known even to convert a primary forest into a secondary forest state (Western 1989). Elephants might also act as important seed dispersers (Campos-Arceiz and Blake 2011, Bunney *et al.* 2017, Poulsen *et al.* 2021, Tan *et al.* 2021). Some tree species rely completely on seed ingestion and subsequent dispersal by elephants, such as the Ugobandlovu or torchwood tree (*Balanites maughami*), a common deciduous tree in Eastern African dry forests (Midgley *et al.* 2015). The temporal dynamics of seed dispersal exert a strong influence on germination success, primarily owing to the varying environmental conditions encountered by seeds (de Souza *et al.* 2022). The foraging behaviour of elephants, characterized by their ability to recall fruiting phenology and target specific trees, contributes significantly to effective seed dispersal (Poulsen *et al.* 2021).

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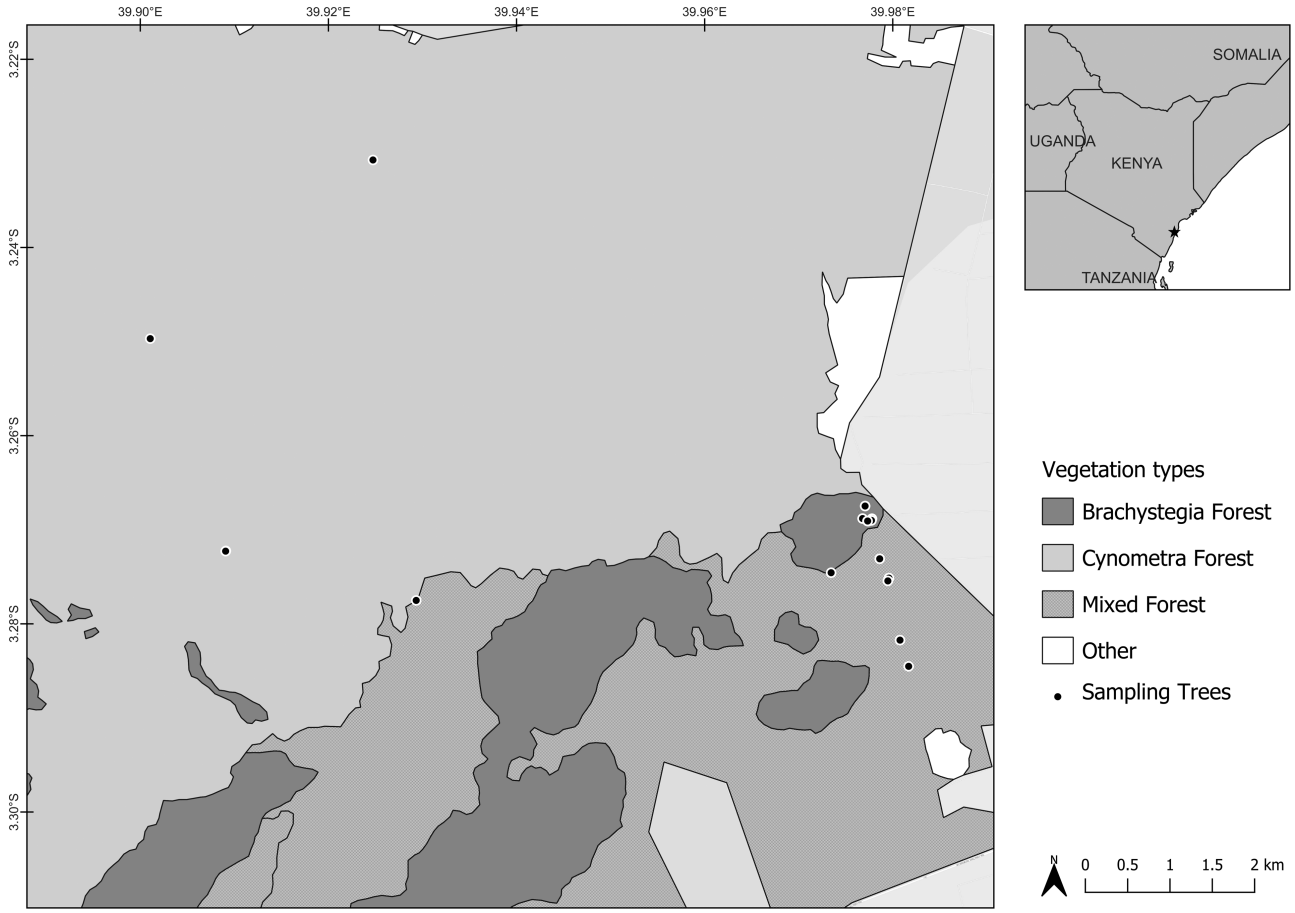


Figure 1. The Arabuko Sokoke Forest in southern Kenya (marked with a star in the small inset map) and the sampling area with the different forest types: *Brachystegia* forest, *Cynometra* forest, mixed forest, and other vegetation types. Dots represent the trees for sampling.

A number of studies have dealt with the diversity effects of elephants as seed dispersers (Hawthorne and Parren 2000, Blake *et al.* 2009, Inogwabini *et al.* 2013), the spatial distribution of transported seeds (Yumoto *et al.* 1995, Babweteera *et al.* 2007, Blake and Maisels 2023), and the movement behaviour of elephants (Vanleeuwé *et al.* 1998). Less known is the efficiency of elephant seed dispersal. The Janzen–Connell hypothesis states that density-dependent seed predation increases tree recruitment distant from the host tree and stabilizes tropical forest tree diversity (Janzen 1970). However, seed dispersal by elephants and the effect of dung on the germination did not unequivocally confirm this model (Tan *et al.* 2021).

In this study, we conducted *in situ* observations on fruit predation rates on the tree species *B. maughami* by elephants depending on the distance to the respective parent tree in the Arabuko Sokoke Forest in southern Kenya. We also analysed seed germination and seedling growth rates of *B. maughami*. This forest is known for a high elephant density, estimated to reach ~215 individuals in total (~0.5 elephants/km^2) (Kinyanjui 2020). The Arabuko Sokoke Forest still represents intact dry coastal forest (Loarie *et al.* 2009, Otieno *et al.* 2014). Based on the results obtained from our observations and experiments, we will answer the following research questions:

(1) Do predation rates on *B. maughami* seeds by elephants depend on the distance to the parent tree?
(2) Does elephant predation of *B. maughami* seeds by elephants positively impact their germination and growth rates?
(3) Does elephant faeces affect the germination and growth rates of *B. maughami* seedlings?

MATERIALS AND METHODS

Study area

We conducted this study in the East African dry coastal Arabuko Sokoke Forest in southern Kenya (Fig. 1). This forest remnant covers an area of 420 km^2 (Arabuko-Sokoke Forest Management Team 2002) and is located northeast of the city Mombasa. The region is characterized by bimodal rainfalls (long rains from April to September and short rains from October to December) (Otieno *et al.* 2014) and with mean temperatures of 29°C (Muriithi 2001). The Arabuko Sokoke Forest consist of three forest types that grow on different soil types (Fig. 1): mixed forest grows on red soils and comprises dense vegetation; *Brachystegia* forest grows on white sand; and *Cynometra* forest grows on red soils (Ochien *et al.* 2017). The Arabuko Sokoke Forest represents a high plant and animal diversity, including the African elephant, *Loxodonta africana* (Banks *et al.* 2010).

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Elephant individuals are usually distributed homogeneously across the forest, but can accumulate in the northwest of the forest during the dry season (Kinyanjui 2020). The tree species *Balanites maughamii* grows mainly in mixed and *Brachystegia* forest, but also, in lower densities, in *Cynometra* forest. The tree produces bitter-sweet and edible fruits containing extremely hard seeds that constitute >50% of the fruit volume.

Seed predation

To answer our first question, we selected 21 *B. maughamii* trees and collected ripe fruits. We then placed these fruits in piles (10 fruits per pile) every 20 m, up to a total distance of 200 m from the *B. maughamii* host tree. Pile deposition lines did not overlap and did not run directly along other *B. maughamii* trees. We controlled these piles weekly, from October 2018 until June 2019 (36 weeks in total). During each visit, we recorded the following details: number of fruits missing, bite marks on fruits, cracked fruits, and scratches on fruits. Fruits that had been removed were not replaced. The animal species that removed (or destroyed) the fruits were identified from bite marks, footprints, or dung (from larger animals, such as elephants and antelopes) and faecal pellets (from smaller vertebrates). Additional observations were the stripping of branches on the tree/s where the experiments were set. Observations were highly based on knowledge of the staging areas for the elephants. Nine of the parent trees were located in the mixed forest, eight trees in *Brachystegia*, and four trees in the *Cynometra* forest. For each single parent tree, we assessed canopy area classes according to Silva *et al.* (2011). The complete set of raw data is contained in Supporting Information, Table S1 of Appendix S1.

Germination and growth rates

To answer our second question, we collected 224 seeds from ripe fruits of *B. maughamii* and 224 seeds from fresh (<1-week-old) elephant dung. We established the following treatments: (i) seed germination from elephant dung after gut passage planted with elephant dung ($N = 112$); (ii) seed germination from elephant dung after gut passage planted without elephant dung ($N = 112$); (iii) seeds from parent trees planted with elephant dung (therefore without gut passage; $N = 112$); and (iv) seeds from parent trees planted without elephant dung (and without gut passage; $N = 112$). Seeds were cultivated according to the recommendations of the International Centre for Research in Agroforestry and Kenya Forest Research Institute Tree Nursery Training Manual (Oballa *et al.* 2017), monitored daily in the first month and once a week for the next 2 months. At each visit, we measured seedling height and the number of leaves. The raw data are given in .Supporting Information, Table A2 of Appendix A.

Statistics

With respect to our first question and the fruit predation experiment, we used generalized linear models with a Poisson error structure and linear link function to relate numbers of removed fruits (count data) to the forest type, duration of the fruiting period, and canopy diameter class as categorical variables, and distance from the host tree as a metric predictor.

To compare the importance of gut passage and dung, we used factorial general linear models, with final plant height and the number of leaves as the response and with gut passage (yes/no), dung presence (yes/no), and season (dry/wet) as categorical predictors. Contingency table analyses served to assess the difference in numbers of germinating seeds between the four experimental variants.

To answer our second and third questions regarding the role of gut passage and dung, we fitted the classical von Bertalanffy growth model to the plant growth experiment:

$$Y = Y_{\infty}\left[1 - e^{-k(t-t_0)}\right] \quad (1)$$

where Y_{∞} denotes the maximum value of variable Y, k is the growth rate coefficient, and t_0 is the beginning of the growth process. The coefficient k quantifies the rate at which the growth process reaches an asymptote, and low k values indicate constant exponential growth in time. Given that model parameters depend on the time of growing, we considered only plants that germinated within the first 3 days of exposure and were alive at the end of the experiment. They therefore grew for ≥90 days (in total, 32 plants). Each growth curve consisted of 38 single data points. The von Bertalanffy model fitted well, and all 32 single growth functions explained more than $r^2 = 85\%$ of variance (mean $r^2 = 0.97$) in height increase and the number of leaves. For final plant height and for the final number of leaves, we used general linear models with ln-transformed values of k to assess whether growth patterns varied between seasons and dung availability. Final plant height or number of leaves served as metric covariates in the models.

RESULTS

Regarding our first question, the number of fruits removed by elephants was significantly [$P(F) < .001$; Table 1] higher in the mixed and *Brachystegia* forests than in the two other forest types (Fig. 2A). The number of fruits removed declined significantly with the length of the fruiting period (Fig. 2B; Table 1) and with increasing distance from the parent tree [Fig. 2C; $P(F) < .001$; Table 1].

Regarding the second question, we found that during the wet season *B. maughamii* fruits germinated only after elephant gut passage (Table 2). In the dry season, 18 of 224 fruits (8.0%) germinated with elephant dung only, 9 without gut passage and dung (4.0%), and 152 (67.9%) germinated after gut passage (Table 2). Dung and gut passage accelerated germination by >1 week (Table 2). The nine plants that germinated without dung availability and gut passage were comparatively small and had fewer leaves, despite longer growth times (Table 2). The

Table 1. Main effects generalized linear model (Poisson error structure, linear link function) for numbers of removed *Balanites maughamii* fruits as the response variable ($N = 190$).

Predictor	d.f.	Wald value	*P*-value
Intercept	1	14.96	<.001
Forest type	3	76.38	<.001
Fruiting period	8	32.574	<.001
Canopy diameter	4	49.601	<.001
Distance	1	8.48	.004

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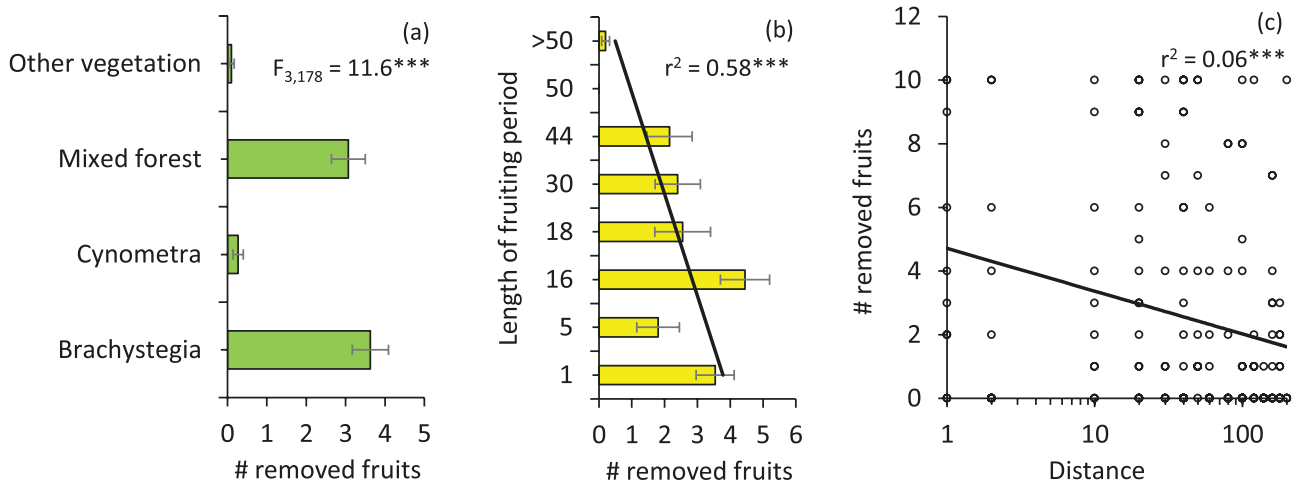


Figure 2. Summary of the results of the fruit removal experiment. A, B, differences in the mean number of fruits removed between habitat types (A) and the length of the fruiting period (in days) at the 190 experimental sites. C, total numbers of fruits removed across all sites depending on the distance from *Balanites maughamii* trees. Error bars denote standard errors.

final height of plants did not differ significantly with respect to gut passage and dung presence (Table 3). In turn, final leaf numbers were significantly higher after gut passage and in the presence of dung (Tables 2 and 3).

Finally, we found an indication that plant growth differed between seasons and was influenced by the presence of dung (this analysis could only be done with plants after gut passage). Asymptotic (von Bertalanffy) growth was associated with gut passage and dung in the wet season, but not in the dry season (Fig. 3). The seasonal differences were most pronounced for leaf numbers when including final plant size as a covariate. (Table 4). In the dry season, the combination of gut passage and dung caused constant exponential plant growth throughout the observation time, whereas in the wet season it resulted in more asymptotic growth and limited final plant size.

DISCUSSION

Seed predation

In line with previous studies in savannahs, our forest data also show that seed predation rates are highest close to *B. maughamii* parent trees (Chapman and Chapman 1996, Matthesius *et al.* 2011). Predation rates decreased with increasing canopy diameter. An explanation might be that canopy diameter is positively correlated with fruit production (Camarero *et al.* 2010, Venter and Witkowski 2011) and that predators might quickly become satiated (see Espelta *et al.* 2017). Our findings indicate highest fruit predation in the *Brachystegia* and mixed forests compared with the *Cynometra* forest or other vegetation forest types. Higher predation rates might be related to the vegetation structure. *Brachystegia* and mixed forests have a more open understorey compared with the dense *Cynometra* forest (Otieno *et al.* 2014). Previous studies have already shown that such more accessible vegetation supports the presence of seed dispersers (including elephants) and thus increases fruit predation rates (Chimera and Drake 2011).

Elephants appeared to be important dispersers of *B. maughamii* seeds across the Arabuko Sokoke Forest. We found many *B. maughamii* seeds in elephant dung, and the perception of these fruits seems to be based largely on their scent, to which elephants are strongly attracted. Elephants have poor eyesight but have an excellent sense of smell (Midgley *et al.* 2015). Furthermore, the highly camouflaged fruits drop on the ground early in development, which would indicate that they are not presented to dispersers in the canopy. Other studies have also shown that various plant species produce large, dull-coloured fruits that might prevent predation by antelopes, rodents, birds, or monkeys, but will be eaten by mega-herbivores, resulting in only limited damage and excellent dispersal (Gautier-Hion *et al.* 1985, Yumoto *et al.* 1995). Our findings and prior observations underline that elephants (and other mammals) are very important seed dispersers in forests, and thus significantly shape the tree diversity, in addition to the understorey vegetation structure (cf. Berzaghi *et al.* 2023). Investigation of the diet of elephants indicates that they feed on selected trees and avoid shrubs, herbs, and grass (Struhsaker *et al.* 1996, Theuerkauf *et al.* 2000). They prefer shade-tolerant to light-tolerant plant species (Theuerkauf *et al.* 2000).

Germination and growth rates

Successful seed germination would require the embryo to access water and oxygen. Thick seed coats delay germination, whereas removed or damaged endocarps might allow for faster germination (Midgley *et al.* 2015). This happens when elephants chew the fruits by a downward and backward motion across the enamel plates. This removes the fleshy part of the *B. maughamii* fruits, as confirmed by the seeds collected from the elephant dung. It is unlikely that other mega-herbivores (within our study region,

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Table 2. Basic information on the *Balanites maughamii* germination experiment, including data on the numbers of exposed and germinated plants, the duration of exposure, the number of germinated plants that died before the end of the experiment, the earliest germination day, and the final plant height and number of leaves. Data are for the wet season 2018 and dry season 2019.

Season	Variable	Gut passage and dung	Gut passage only	Dung only	No gut passage, no dung
Wet	Plants exposed (*N*)	30	30	30	30
	Period of exposure (days)	99	99	99	99
	Plants germinating (*N*)	27	27	0	0
	Plants dying (*N*)	4	6		
	Earliest germination (days)	1	1		
	Final plant height (cm)	6 (3.0;8.6)	5.9 (2.6;9)		
	Final leaves (*N*)	39 (22.0;50.8)	46 (22.0;66)		
Dry	Plants exposed (*N*)	112	112	112	112
	Period of exposure (days)	93	119	95	125
	Plants germinating (*N*)	77	75	18	9
	Plants dying (*N*)	1	1	1	0
	Earliest germination (days)	3	11	18	80
	Final plant height (cm)	3.1 (1.7;6.2)	6.1 (2.7;12.2)	4.6 (2.0;7.7)	2.9 (1.7;5.1)
	Final leaves (*N*)	23 (9;38)	38 (17;72)	33 (16;53)	15 (7;25)

Table 3. General linear model, with final plant height and final number of leaves as the response and with gut passage, dung, and season as categorical predictors. Given are degrees of freedom (d.f.), partial η^2 values, and parametric probabilities. Only plants alive at the end of the experiment are included.

Predictor	d.f.	Partial η^2	*P*-value
Plant height			
Intercept	1	0.29	<.001
Gut passage	1	0.01	.24
Dung	1	0.01	.39
Dung × gut passage	1	0.01	.18
Season	1	0.04	<.01
r^2 (model)	224	0.06	<.01
Number of leaves			
Intercept	1	0.55	<.001
Gut passage	1	0.06	.02
Dung	1	0.03	.02
Dung × gut passage	1	0.05	<.001
Season	1	0.03	.02
r^2 (model)	224	0.09	.001

Table 4. General linear model with von Bertalanffy height growth rate coefficient, *k*, and the number of leaves as the response and with dung and season as categorical predictors and plant height (number of leaves) as metric predictors. Given are degrees of freedom (d.f.), partial η^2 values, and parametric probabilities. Only the 32 plants that germinated within the first 3 days and were alive at the end of the experiments are included.

Predictor	d.f.	Partial η^2	*P*-value
Height growth parameter			
Intercept	1	0.23	.01
Dung	1	0.14	.05
Season	1	0.04	.28
Plant height	1	0.39	.03
r^2 (model)	32	0.15	.20
Leaf increase parameter			
Intercept	1	0.42	<.001
Dung	1	0.07	.17
Season	1	0.16	.03
Number of leaves	1	0.05	.25
r^2 (model)	32	0.34	.01

only buffaloes or rhinoceroses) would be powerful enough to increase the germination of *B. maughamii* in this way (Midgley *et al.* 2015, Gordon *et al.* 2023).

In line with this prediction, we found that gut passage reduced germination latency from 96 to 47 days and increased the germination rate from 11% to 74%. These findings are in congruence with other studies showing that gut passage positively impacts germination and growth rates of plant seeds (Traveset *et al.* 2007, Poulsen *et al.* 2021). Seed fruit pulp often consists of germination inhibitors that can block biochemical pathways to prevent seeds from sprouting (Meyer and Witmer 1998). This guarantees that the seeds do not sprout when attached to the adult parent tree (Samuels and Levey 2005).

We also found seasonal differences in the effect of dung on germination. Elephant dung accelerated germination and plant development only in the wet season. This finding extends results from other studies showing that faecal material enhances seed sprouting (Traveset *et al.* 2007). Apart from promoting the growth of seedlings, frugivore manure can also contain toxic compounds that might impact seedlings negatively, such as phenolic compounds and fatty acids (Cosyns *et al.* 2005), in addition to fungi and bacteria (Meyer and Witmer 1998).

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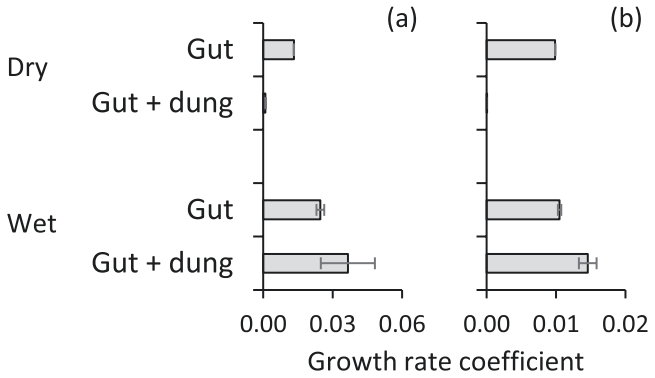


Figure 3. Average growth rate coefficient of plant height (A) and number of leaves (B) from the wet season and the dry season that germinated after gut passage, either with or without dung. Error bars denote standard errors.

CONCLUSION

In conclusion, in this study we have combined *in situ* observations and *ex situ* experiments to investigate the relevance of elephants for the distribution and germination of *B. maughamii*, a typical East African forest tree. We found that elephants in the East African Arabuko Sokoke coastal forest frequently eat seedlings of *B. maughamii* and subsequently excrete them as part of the faeces, hence distributing them in the forest. Elephants appear to be very important seed dispersers and support the regeneration of *B. maughamii*.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABLITY

All raw data used in this study are contained in the supplementary file Appendix A.

REFERENCES

Arabuko-Sokoke Forest Management Team. Arabuko-Sokoke Strategic Forest Management Plan 2002-2027. *Report* 2002;1–53. https://friendsarabukosokoke.org/wp-content/uploads/2021/08/Arabuko-Sokoke-Forest-Strategic-Management-Plan-2002-2027.pdf

Babweteera F, Savill P, Brown N. *Balanites wilsoniana*: regeneration with and without elephants. *Biological Conservation* 2007;**134**:40–7. https://doi.org/10.1016/j.biocon.2006.08.002

Banks JE, Jackson C, Hannon LM *et al.* The cascading effects of elephant presence/absence on arthropods and an Afrotropical thrush in Arabuko-Sokoke Forest, Kenya. *African Journal of Ecology* 2010;**48**:1030–8. https://doi.org/10.1111/j.1365-2028.2010.01211.x

Berzaghi F, Bretagnolle F, Durand-Bessart C *et al.* Megaherbivores modify forest structure and increase carbon stocks through multiple pathways. *Proceedings of the National Academy of Sciences of the United States of America* 2023;**120**:e2201832120. https://doi.org/10.1073/pnas.2201832120

Blake S, Deem SL, Mossimbo E *et al.* Forest elephants: tree planters of the Congo. *Biotropica* 2009;**41**:459–68. https://doi.org/10.1111/j.1744-7429.2009.00512.x

Blake S, Maisels F. 2023. Forest elephant movements in Central Africa: megafauna need megaspaces. In: Reyna-Hurtado R, Chapman CA, Melletti M (eds), *Movement Ecology of Afrotropical Forest Mammals*. Springer International, 27–58. https://doi.org/10.1007/978-3-031-27030-7_3

Bunney K, Bond WJ, Henley M. Seed dispersal kernel of the largest surviving megaherbivore—the African savanna elephant. *Biotropica* 2017;**49**:395–401. https://doi.org/10.1111/btp.12423

Camarero JJ, Albuixech J, López-Lozano R *et al.* An increase in canopy cover leads to masting in *Quercus ilex*. *Trees* 2010;**24**:909–18. https://doi.org/10.1007/s00468-010-0462-5

Campos-Arceiz A, Blake S. Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecologica* 2011;**37**:542–53. https://doi.org/10.1016/j.actao.2011.01.014

Chapman CA, Chapman LJ. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 1996;**12**:491–504. https://doi.org/10.1017/s026646740000972x

Chimera CG, Drake DR. Could poor seed dispersal contribute to predation by introduced rodents in a Hawaiian dry forest? *Biological Invasions* 2011;**13**:1029–42. https://doi.org/10.1007/s10530-010-9887-4

Cosyns E, Delporte A, Lens L *et al.* Germination success of temperate grassland species after passage through ungulate and rabbit guts. *Journal of Ecology* 2005;**93**:353–61. https://doi.org/10.1111/j.0022-0477.2005.00982.x

Coverdale TC, Kartzinel TR, Grabowski KL *et al.* Elephants in the understory: opposing direct and indirect effects of consumption and ecosystem engineering by megaherbivores. *Ecology* 2016;**97**:3219–30. https://doi.org/10.1002/ecy.1557

de Souza AC, Donohue K, de Mattos EA. The effect of seed-dispersal timing on seedling recruitment is modulated by environmental conditions that vary across altitude in a threatened palm. *Annals of Botany* 2022;**129**:839–56. https://doi.org/10.1093/aob/mcac038

Dornelas M. Disturbance and change in biodiversity. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 2010;**365**:3719–27. https://doi.org/10.1098/rstb.2010.0295

Espelta JM, Arias-LeClaire H, Fernández-Martínez M *et al.* Beyond predator satiation: masting but also the effects of rainfall stochasticity on weevils drive acorn predation. *Ecosphere* 2017;**8**:e01836.

Gautier-Hion A, Duplantier J-M, Quris R *et al.* Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 1985;**65**:324–37. https://doi.org/10.1007/BF00378906

Gerz M, Guillermo Bueno C, Ozinga WA *et al.* Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. *Journal of Ecology* 2018;**106**:254–64.

Gordon CE, Greve M, Henley M *et al.* Elephant rewilding affects landscape openness and fauna habitat across a 92-year period. *Ecological Applications* 2023;**33**:e2810. https://doi.org/10.1002/eap.2810

Hall AR, Miller AD, Leggett HC *et al.* Diversity–disturbance relationships: frequency and intensity interact. *Biology Letters* 2012;**8**:768–71. https://doi.org/10.1098/rsbl.2012.0282

Hawthorne WD, Parren MPE. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *Journal of Tropical Ecology* 2000;**16**:133–50. https://doi.org/10.1017/s0266467400001310

Inogwabini B-I, Ngama-Nkosi M, Wema-Wema L *et al.* Elephant effect on forest physical structure and plant species composition in Salonga and Lac Tumba, Democratic Republic of Congo. *Pachyderm* 2013;**53**:28–37. https://doi.org/10.69649/pachyderm.v53i.321

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Janzen DH. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 1970;**104**:501–28. https://doi.org/10.1086/282687

Kinyanjui PW. *Effects of African Elephant (Loxodonta africana) Population on Vegetation Around Water Points in Arabuko Sokoke Forest*. Kilifi County, Kenya: Kenyatta University, 2020.

Levine JM, HilleRisLambers J. The importance of niches for the maintenance of species diversity. *Nature* 2009;**461**:254–7. https://doi.org/10.1038/nature08251

Loarie SR, Aarde RJV, Pimm SL. Fences and artificial water affect African savannah elephant movement patterns. *Biological Conservation* 2009;**142**:3086–98. https://doi.org/10.1016/j.biocon.2009.08.008

Matthesius A, Chapman H, Kelly D. Testing for Janzen–Connell effects in a West African montane forest. *Biotropica* 2011;**43**:77–83. https://doi.org/10.1111/j.1744-7429.2010.00664.x

Meyer GA, Witmer MC. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *The American Midland Naturalist* 1998;**140**:129–39. https://doi.org/10.1674/0003-0031(1998)140[0129:iospbf]2.0.co;2

Midgley JJ, Kruger LM, Viljoen S *et al.* Fruit and seed traits of the elephant-dispersed African savanna plant *Balanites maughamii*. *Journal of Tropical Ecology* 2015;**31**:557–61. https://doi.org/10.1017/s0266467415000437

Muriithi K. Biodiversity and conservation in the Arabuko Sokoke Forest, Kenya. *Biodiversity and Conservation* 2001;**2**:1437–1450.

Oballa P, Mengich E, Nyambati R. *Training manual for tree nursery operations: KFS, Counties, NGOs, CBOs and farmers*, 2017.

Otieno NE, Ngala D, Mwalimu A. Spatial response of the globally-endangered Sokoke Pipit (*Anthus sokokensis* van Someren, 1921) to habitat degradation in an Eastern Arc Coastal forest. *F1000Res* 2014;**3**:59. https://doi.org/10.12688/f1000research.3-59.v2

Poulsen JR, Beirne C, Rundel C *et al.* Long distance seed dispersal by forest elephants. *Frontiers in Ecology and Evolution* 2021;**9**:789264. https://doi.org/10.3389/fevo.2021.789264

Pringle RM. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* 2008;**89**:26–33. https://doi.org/10.1890/07-0776.1

Samuels IA, Levey DJ. Effects of gut passage on seed germination: do experiments answer the questions they ask? *Functional Ecology* 2005;**19**:365–8.https://doi.org/10.1111/j.1365-2435.2005.00973.x

Silva GL, Lima HV, Campanha MM *et al.* Soil physical quality of luvisols under agroforestry, natural vegetation and conventional crop management systems in the Brazilian semi-arid region. *Geoderma* 2011;**167–168**:61–70. https://doi.org/10.1016/j.geoderma.2011.09.009

Silvertown J. Plant coexistence and the niche. *Trends in Ecology & Evolution* 2004;**19**:605–11. https://doi.org/10.1016/j.tree.2004.09.003

Struhsaker TT, Lwanga JS, Kasenene JM. Elephants, selective logging and forest regeneration in the Kibale forest, Uganda. *Journal of Tropical Ecology* 1996;**12**:45–64. https://doi.org/10.1017/s0266467400009305

Tan WH, Hii A, Solana-Mena A *et al.* Long-term monitoring of seed dispersal by Asian elephants in a Sundaland rainforest. *Biotropica* 2021;**53**:453–65. https://doi.org/10.1111/btp.12889

Theuerkauf J, Waitkuwait WE, Guiro Y *et al.* Diet of forest elephants and their role in seed dispersal in the Bossematié Forest Reserve, Ivory Coast. *Mammalia* 2000;**64**:447–60. https://doi.org/10.1515/mamm.2000.64.4.447

Traveset A, Robertson AW, Rodríguez-Pérez J. A review on the role of endozoochory in seed germination. In: Dennis AJ, Schupp EW, Green RJ *et al.* (eds), *Seed Dispersal: Theory and Its Application in a Changing World*, 1st edn. 2007, 78–103. http://www.cabidigitallibrary.org/doi/10.1079/9781845931650.0078

Vanleeuwé H, Gautier-Hion A. Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantaceae forests. *African Journal of Ecology* 1998;**36**:174–82. https://doi.org/10.1046/j.1365-2028.1998.00123.x

Venter SM, Witkowski ETF. Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa. *Forest Ecology and Management* 2011;**261**:630–9.

Western D. The ecological role of elephants in Africa. *Pachyderm* 1989;**12**:42–5. https://doi.org/10.69649/pachyderm.v12i1.692

White LJT, Tutin CEG, Fernandez M. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology* 1993;**31**:181–99. https://doi.org/10.1111/j.1365-2028.1993.tb00532.x

Wright JS. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 2002;**130**:1–14. https://doi.org/10.1007/s004420100809

Yumoto T, Maruhashi T, Yamagiwa J *et al.* Seed-dispersal by elephants in a tropical rain forest in Kahuzi-Biega National Park, Zaire. *Biotropica* 1995;**27**:526–30. https://doi.org/10.2307/2388968

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