



Baobab fruiting is driven by scale-dependent mediation of plant size and landscape features

Macy A. Krishnamoorthy · Paul W. Webala · Tigga Kingston

Received: 31 December 2020 / Accepted: 14 March 2022
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

Abstract

Context Both plant size and distribution of plants and resources across landscapes are known to influence pollinator behavior and resulting plant reproductive success. However, the relative influence of these intrinsic and extrinsic factors is unknown.

Objectives We evaluated the relative contribution of individual plant size and landscape variables to reproductive success in bat-pollinated baobabs (*Adansonia digitata*) and determined if the interaction is scale-dependent.

Methods We recorded fruit number per baobab of 741 baobab in south-central Kenya and measured size metrics of individuals. We georeferenced baobabs and relevant resources across 10 km² to generate landscape variables. Conditional inference forests

determined scale-specific responses over 20 buffer distances (50-m to 1000-m) around baobabs and identified relative variable importance. We modeled presence of fruit, as not all trees produce fruit. For fruiting baobabs, we modeled whether there were few or many fruits.

Results Conditional inference forests were significant at 50-m to 600-m buffer distances. Individual characteristics of baobabs were the primary drivers of fruit presence, with larger trees more likely to fruit. Fruit presence was modified by baobab height and landscape variables. Land use primarily drove baobab fruit production category, which was modified by baobab size and other landscape variables. The importance of distance to and density of alternate food resources changed with scale.

Conclusions Individual characteristics and landscape variables both influence reproductive success in the bat-pollinated baobab system, and relative variable importance was scale-dependent. The pollinator landscape is complex and scale-dependent, encompassing not only the distribution of the baobab population but also attractants (pawpaws) and distractants (figs) that further influence reproductive success.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-022-01435-7>.

M. A. Krishnamoorthy (✉)
Department of Biological Sciences and Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409-3131, USA
e-mail: macy.krishnamoorthy@ttu.edu

P. W. Webala
Department of Forestry and Wildlife Management, Maasai Mara University, Narok, Kenya

T. Kingston
Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131, USA

Keywords Baobab · Bat pollination · Individual traits · Landscape context · Pollination · Reproductive success

Introduction

Many factors influence plant reproductive success including size and age of the plant (Wickens and Lowe 2008; Angoh 2016), soil characteristics (Assogbadjo et al. 2005; Neil and Wu 2006; Kermack and Rauschert 2019), and successful pollination. For example, as girth at breast height (GBH) increases in ebony trees (*Diospyros* species), so does the proportion of flowers that set fruit successfully (Somanathan and Borges 2000). The relationship between GBH and fruit production occurs in many plant species, presumably reflecting greater allocation of resources to reproduction rather than growth in more mature trees (Chapman et al. 1992; Somanathan and Borges 2000; Snook et al. 2005). Increases in other measures of plant size, such as root mass in Texas Dutchman's pipe (*Aristolochia reticulata*), increase seed production (Rausher and Feeny 1980), likely because they increase the acquisition of resources needed for reproduction.

In the case of plants reliant on cross-pollination from animal pollinators, pollinator movement becomes important. Not only must plants attract pollinators, but pollinators need to bear pollen to or from conspecifics distributed across the landscape. Consequently, reproductive success arises from an interaction of individual plant characteristics that attract pollinators and support reproductive success (e.g., plant size, flower height, number of flowers produced, flower structure) and the positioning of the plant in a plant-pollinator network. For example, taller plants attract more pollinators (Dickson and Petit 2006; Dudash et al. 2011) and increase connectivity of plant-pollinator networks (Dupont et al. 2011, 2014), which can be important for successful pollination (Ghazoul 2005). Similarly, the more flowers produced, another characteristic of individual plants, the more frequent the visits by pollinators in a savanna shrub species (*Palicourea rigida*; Justino et al. 2012) and fruit set in thistles (Dupont et al. 2011, 2014) in part due to the structure of the pollination network.

Plant-pollinator networks are also determined by the spatial arrangement of conspecifics within the population, most notably the distance to and density of neighbors. Within plant populations, pollinator visits increase as distance to nearest neighbor of thistles decreases (Dupont et al. 2011) and as distance to patch center in clustered thistle populations decreases

(Dupont et al. 2014). Pollinator visits become more efficient at less dense spatial configurations of artificial flowers (Pasquaretta et al. 2017). Further, pollinator visits occurring over larger distances are more effective in *P. rigida* (Maruyama et al. 2016). Density of conspecifics surrounding an individual plant has been found to have contrasting effects. Bosch and Waser (2001) found that Nuttall's larkspur (*Delphinium nuttallianum*) in sparse arrays of multiple individuals received higher pollen loads from hummingbird and bee pollinators. Intraspecific competition for pollinator visitation leads to negative relationships between reproductive success and number of flowers in a South African iris (*Lapeirousia oreogena*; Johnson et al. 2012) and large population size in three shrub species (*Asclepias curassavica*, *Gomphocarpus fruticosus*, *Gomphocarpus physocarpus*; Ward et al. 2013). Contrastingly, Jones and Comita (2008) found a positive density-dependent relationship between density of self-incompatible *Jacaranda* trees and fruit set.

Pollinators must navigate complex landscapes, so their movement is further influenced by the density and distribution of key resources, including other food sources, water, and shelter. Alternate food resources may increase efficiency of pollination services for focal plant species by attracting pollinators to the area, and even subsidizing and bolstering populations, as with some frugivorous bat species (Fukuda et al. 2009; Aziz et al. 2016). Other foods may act as distractants, waylaying pollinators and reducing visitation rates (Circe's Principle; Lander et al. 2011). Proximity to water can also influence where pollinators forage (Kasangaki 2018) or where animals choose shelter (Li and Wilkins 2015). For a plant dependent on pollinator visitation, proximity to other resources could thus be detrimental or beneficial to the focal plant species. This is especially true when plants depend on generalist pollinators or species that are facultatively nectarivorous (e.g., members of the plant-visiting bat family Pteropodidae Marshall 1983; Singaravelan and Marimuthu 2004; Southerton et al. 2004) or rodents (Johnson et al. 2001; Kleizen et al. 2008; Wester et al. 2009)).

Land use can influence plant reproductive success through resources available for reproduction and pollinator movement. Fruit production is often greater in human-modified landscapes due to additional resources provided to plants, including in baobabs

(*Adansonia digitata*; Venter and Witkowski 2011) and in bat-pollinated columnar cactus (*Stenocereus stellatus*; Arias-Cóyotl et al. 2006). Venter and Witkowski (2011) suggested that fruit production is greater in human-modified landscapes due to crop irrigation. Similarly, arid agricultural lands rehabilitated with native plants have been found to have altered hydrology patterns and high nutrient availability (Baer et al. 2009). This boost in resources may alone support greater fruit production, but it can also increase flower production and even plant population density, attracting more pollinators to the area and further increasing reproductive success (Arias-Cóyotl et al. 2006). Proximity to natural habitats also promotes pollination in non-natural areas (Cranmer et al. 2012; Joshi et al. 2016), indicating the importance of the attractant and subsidy effects.

Scale is an important issue in landscape and pollination biology, as interactions between plants and pollinators occur over different scales. The spatial scale at which pollinators operate is dependent on several factors, including the flight and visual capabilities of the pollinator, their dependence on alternate food resources, or dependence on the pollinated species (Ghazoul 2005). Interactions between pollinator and plant may be determined by individual plant characteristics, land use, and the spatial distribution of conspecifics and resources, but the proportional contribution of these determinants may vary across landscape. For example, Schüepp et al. (2013) found that at landscape (100-m to 350-m or 500-m) scales, isolation of cherry trees within the conspecific population decreased both pollination success and pollinator visitation. Additionally, they found that the amount of pollinator habitat surrounding the cherry tree increased pollinator visitation. At local scales (50-m), the greater the heterospecific flower density (flowers on another shrub species) surrounding the cherry tree, the lower the pollination success of the cherry tree.

To address the relative contribution of individual and spatial characteristics to reproductive success and how reproductive success varies with landscape scale, we studied the bat-baobab system in south-central Kenya. There are eight species of baobab in the genus *Adansonia*, though only *Adansonia digitata* occurs on mainland Africa. Baobabs (hereafter, all mentions of ‘baobab’ refer to *A. digitata*) are large, long-lived trees that span mainland Africa

in arid and semi-arid environments (Gebauer et al. 2016). Trees reach up to 5 m diameter at breast height (Fig. 1A) and, from radiocarbon dating, can live for 1400–1500 years (Patrut et al. 2007; Venter and Witkowski 2010). Most baobabs flower across a four- to six-week period, opening between 10 and 50 flowers each night (Fig. 1B), and flowers are no longer viable by the morning after they open (Baum 1995; Venter and Witkowski 2011). Mature baobab fruits (Fig. 1C) contain many seeds inside a dry, hard shell and are classified as aggregate fruits (Baum 1995). Immature fruits have a softer, green exterior (Fig. 1D). The hard shells of mature fruits are relatively difficult to open and the fruit is not eaten by bats, but dispersed by a variety of larger terrestrial mammals, including baboons, ungulates, elephants, and humans (Wickens and Lowe 2008; Gebauer et al. 2016). Baobabs are economically important to many communities across sub-Saharan Africa, providing nutrition and a source of income to local people (Sidibe and Williams 2002; Venter and Witkowski 2013; Gebauer et al. 2016). Reproductive success varies among baobab individuals in populations, with individual baobabs termed poor producers (few fruit) or producers (many fruit; Venter and Witkowski 2011; Venter et al. 2017).

Baobabs are self-incompatible, requiring cross-pollination (Venter et al. 2017), and are primarily pollinated by bats of the family Pteropodidae (van der Pijl 1937; Baker 1961; Start 1972; Djossa et al. 2015, but see Taylor et al. 2020; Karimi et al. 2021). In Kenya, the pollinators include Rousette fruit bats (*Rousettus aegyptiacus*), epauletted fruit bats (*Epomophorus* species; Fig. 1E), and straw-colored fruit bats (*Eidolon helvum*; Patterson and Webala 2012). The bat-baobab system offers a unique perspective on plant–pollinator systems because the bat pollinators are primarily frugivorous (Patterson and Webala 2012). Due to the seasonal flowering and nutritional content of nectar, bat pollinators in this landscape are generally not able to rely solely on nectar sources for survival, so must use other food sources. Fruit bats only visit baobabs for the nectar and pollen resources flowers provide, do not consume immature or mature baobab fruit, and rely on other species in the landscape for fruit. Fruit bats in the area consume primarily figs (*Ficus* species) but also take advantage of cultivated pawpaw (*Carica papaya*) trees year-round (Webala et al. 2014; Olu-bode et al. 2016). These fruits could function as

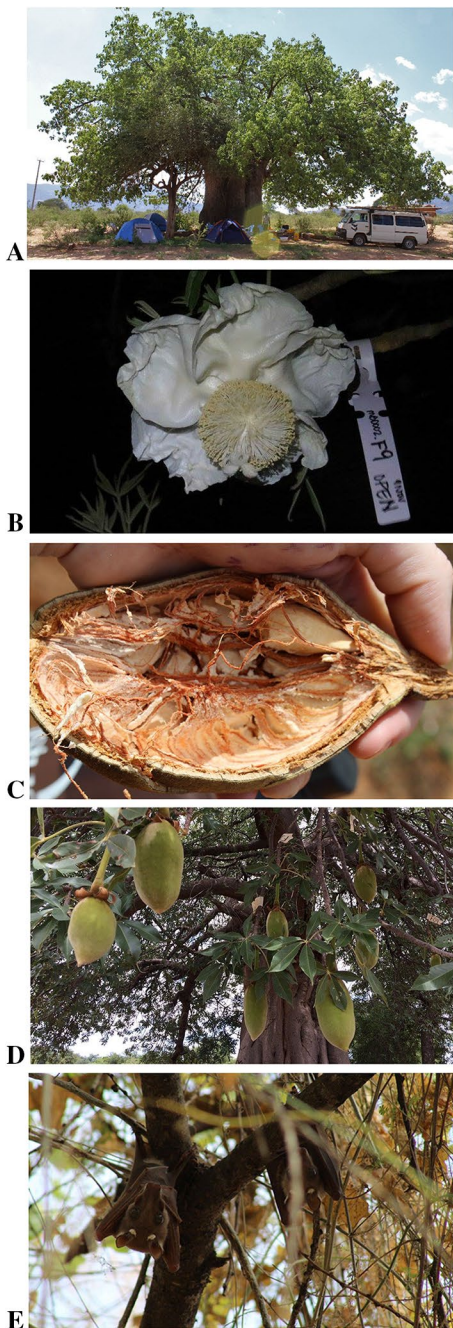


Fig. 1 Plate of pictures showing **A** baobab tree (*Adansonia digitata*) with van and tents for scale, **B** opened baobab flower, **C** a small, mature fruit opened to show pulp covered seeds inside, **D** immature fruit hanging on baobab tree, and **E** potential bat pollinators (*Epomophorus* species) hanging in trees in Kenya

attractants, subsidizing bats in the area, or as distractants. Figs have more complete nutritional value than do baobab flowers (e.g., nectar and pollen; Baker and Baker 1975; Baker 1977; Batista et al. 2016), suggesting that they may act as distractants to baobabs.

The objectives of our study were twofold. First, we sought to determine the relative contribution of individual tree characteristics and landscape context, in the context of pollinator landscapes, to baobab reproductive success. We built models around two measures of reproductive success—the absence or presence of fruit on a baobab and, if a baobab produced fruit, the fruit production category of the baobab (few or many fruit). Tree height and GBH were our measures of individual characteristics. Baobabs with large GBH may have resources to allocate to reproduction and be better at securing water and soil nutrients due to larger root networks. Alternatively, tall trees may be more visible to bat pollinators as they are notably taller than surrounding bush (Fenner 1982), so may be identifiable to fruit bats relying on vision (Fleming et al. 2009). In addition, tall trees (i.e., greater GBH and height) are more likely to produce fruit (presence/absence models) and produce more fruit (few/many models), than shorter trees due to resource acquisition (West et al. 2009).

Our measures of spatial and landscape context were baobab densities, distances to conspecifics, other food sources and water, and recorded land use patterns in the area. Plant-visiting bats are known to travel over large distances (e.g., *Epomophorus wahlbergi* over 4–14 km; Bonaccorso et al. 2014) and commonly adopt foraging strategies that align with predictions from optimal foraging theory (Charnov 1976; Pyke et al. 1977; Calderón-Capote et al. 2020; Walter et al. 2020) so landscape variables (e.g., density of food resources) are likely to influence foraging decisions. For example, it may be energetically profitable to travel a long distance to an area where food is available at high density, whereas energetic costs may not exceed gains if only a single tree with food is available at a distant destination. In contrast, local foraging decisions (e.g., moving from one tree to another within a patch) is thought to be influenced by the distances to the next nearest resource. We predicted that reproductive success would be greatest in focal trees surrounded by conspecifics (small distances to conspecifics and high baobab densities). We hypothesized that pawpaw and figs would function as

distractants, because they are large (pawpaw), abundant (figs), and of high nutritional value, reducing reproductive success of focal baobab trees nearby. Disturbed land uses have been demonstrated to provide additional water or fertilizer, or bolster fruit bat populations with additional food resources. We, therefore, predicted that baobabs on disturbed lands (e.g., homesteads or farms) produce more fruit than baobabs on undisturbed lands (e.g., bush).

Our second objective was to determine if relative variable importance was scale-dependent. We hypothesized that the relative contribution of individual characteristics and landscape variables would be scale-dependent, with landscape variables (e.g., density metrics) being more important at larger scales and individual plant characteristics dominating responses at local scales. Individual characteristics should be dominant at local (i.e., small) scales as these should reflect ability of plants to access resources (soil nutrients and water) and maturity of the tree. At larger scales, landscape variables influencing pollinator movements start to determine tree-level visitation rates, and should make greater contributions to reproductive success. We anticipated maturity thresholds to be influential in a tree's ability to produce fruit, so expected that fruit presence would be primarily a function of GBH and tree height, with limited landscape influence. In contrast, we expected fruit production category models to be more influenced by a larger relative contribution of landscape.

Methods

Study site

The study was conducted at the Nuu Hills, Mwingi Central Sub-County of Kitui County, south-central Kenya (Fig. 2). This area was selected because of the high baobab population, and because it is known to support fruit bat populations. Kitui County is categorized as arid and semi-arid (Orindi et al. 2007), with 200–600 mm of rain annually (Burgess et al. 2004), falling in two seasons. 'Long' rains occur between March and May while 'short' rains fall between October and December, with short rains sustaining crop production (Cassim and Juma 2018). Baobabs flower primarily during short rains and do not produce flowers year-round, and so they provide a seasonally

flowering resource for bats. The bounded study area spanned approximately 10 km², primarily comprising the Northern *Acacia-Commiphora* Bushlands and Thickets ecoregion (Burgess et al. 2004). People live throughout the landscape on small, primarily agrarian homesteads. Land is either grazed by cattle or cleared for agriculture, leaving only large trees that are too difficult or valuable to cut down (oftentimes baobabs).

Fieldwork took place from December 2017 through January 2018, estimating fruit production from one season. During this time, the seasonal Uva River running through the study site was completely dry (Fig. 2), but it has water during long rains. Baobabs were primarily maturing fruit and only a handful (50 of 741 trees surveyed) were flowering during this time. Figs and pawpaw are common in the study landscape and fruit asynchronously so are potential food sources for bats year round (Olubode et al. 2016). Figs are especially prominent along waterways (Njoroge et al. 2010), and pawpaw is grown in gardens. Both are consumed by Kenyan fruit bats (Webala et al. 2014). Although mango trees are present and bats are known to eat mangoes in the study area, mango trees are not in fruit when baobabs are flowering, so were not included in the study. Figs and pawpaws were included, along with conspecific baobabs, in measures of density and nearest neighbor as alternate fruiting resources that could act either as a distractant for a bat pollinator (Lander et al. 2011), or a subsidy/attractant (Oro et al. 2013). There were three identifiable water sources: a dammed pond, the Uva river, and a small pond near the main road that connects Mwingi and Nuu. All baobabs, figs, pawpaws and water sources were located while in the field, georeferenced, and imported into ArcMap version 10.3 (Environmental Systems Resource Institute 2014). The overall shape of the study area where trees were georeferenced was dictated by baobab density and permission to access land.

Tree variables

Reproductive success of baobabs was measured as the number of developing or mature fruit on each baobab. After pollination, baobab fruit takes approximately six months to mature (Sidibe and Williams 2002). During maturation, the fruit has a fuzzy, green coat on the outside. Once mature, the fruit is dry and

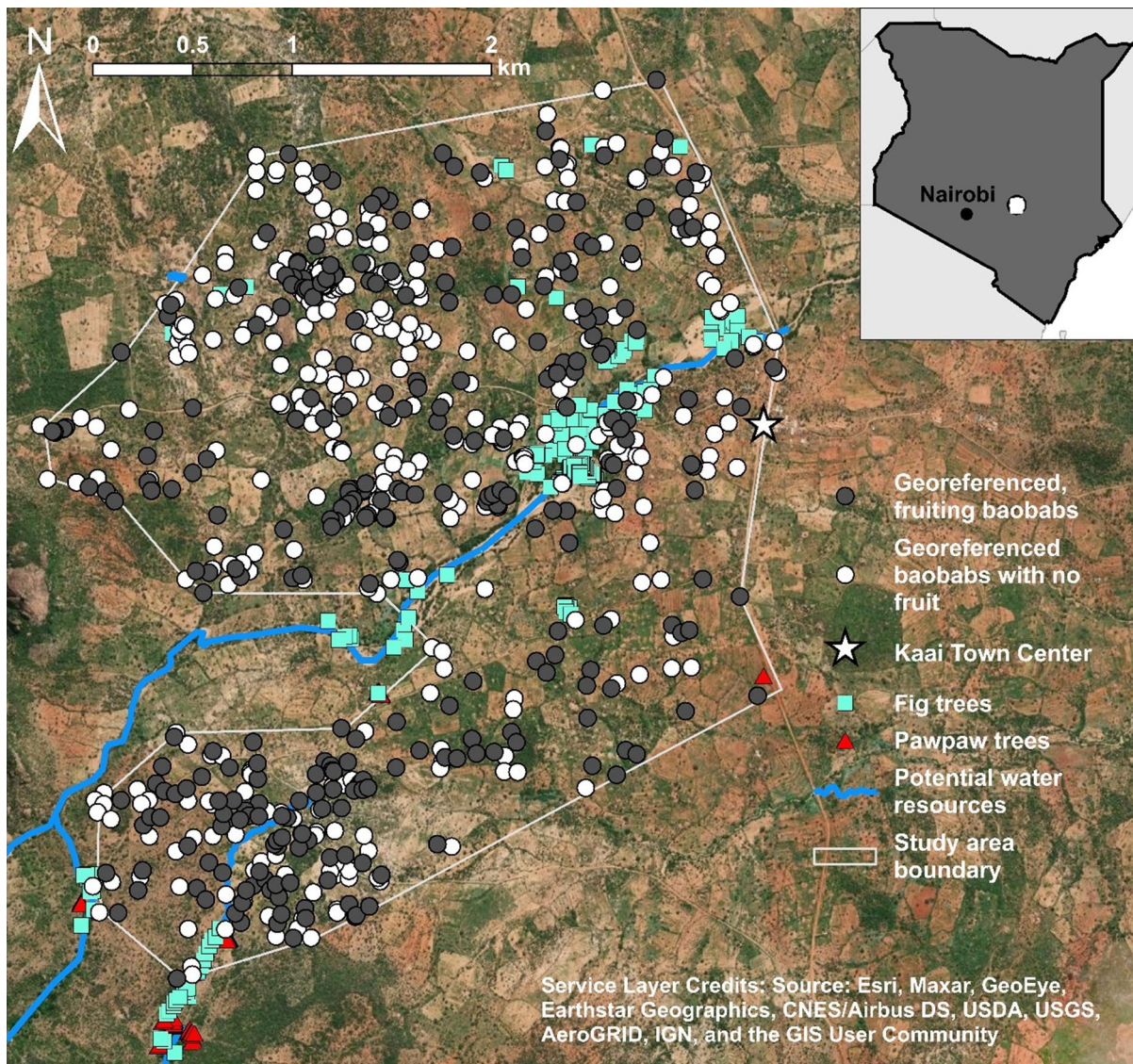


Fig. 2 Study area and location in Kenya (white rectangle in inset)

becomes brown, and can be up to 20 cm by 10 cm in size (Venter and Witkowski 2011) and easily visible on the tree (Fig. 1C, D). Whole fruit that is no longer developing and would not mature may still be attached to branches, but usually has a small or shriveled appearance, suggesting seed and fruit abortion. Only mature or developing fruit were counted. We counted fruit by dividing the tree at the trunk into four sections by cardinal directions, counting fruit in each section with the naked eye, and summing the four totals.

Individual properties of the baobab included the georeferenced coordinates to ± 4 m, the height of the tree, and girth (circumference) at breast height (GBH). Height of each baobab was calculated from readings of a SUUNTO PM-5/360 PC Clinometer at 20 m from trunk of each tree. We focused on circumference because mature baobabs have asymmetrical trunks and uneven surfaces, and we used a flexible 50-m tape to take the GBH measure (Wickens and Lowe 2008). All trees that could not have GBH measured (fallen over, but still alive) or had a GBH

less than 1.27 m were excluded from analysis. Venter and Witkowski (2010) categorized juvenile baobabs generally as having < 1.0 m diameter at breast height (~3.14 m GBH) with few individuals producing fruit. In this study, we found that baobabs with at least 1.27 m GBH were capable of producing fruit. Though previous studies of baobabs have reported that there is no clear relationship between GBH and fruit production (Killmann et al. 2003; Venter and Witkowski 2011), Killmann et al. (2003) suggested that other drivers of inter-individual variation in fruit production (e.g., soil characteristics and land use) may have masked this relationship. However, our methodology can accommodate correlated factors and is able to elucidate the relationship between GBH and fruit production.

Landscape variables

Our study predicted that reproductive success was in part attributable to the density of conspecifics in the area surrounding each baobab. Baobabs on the edge of the study area may not have complete spatial information available; for example, density counts may be incomplete as conspecifics or other asynchronous fruiting trees were outside the bounds of the study area. To account for this, we buffered each baobab in ArcGIS, using increments of 50 m, from 50 to 1000 m. Only baobabs that had 99.9% of the area of the buffer within the bounds of study area were used in the analysis resulting in subsets of the total number of baobabs. Each buffer distance was included in the data analyses. Buffer distances are our measures of different scales in the study, where smaller scales refer to smaller buffering distances and larger scales refer to larger buffering distances.

We categorized land-use types immediately surrounding each tree in the field as cleared area (homestead or other land cleared by humans for their use, not including farmland), farm (areas of land cleared specifically for crop-growing), rocky area (naturally-occurring rocky outcrop, which tend to be cleared of brush), bush areas ('natural' areas that have not been cleared of brush, so have low, bush-like trees (*Acacia-Commiphora*), but may be utilized for grazing livestock), road (trees occurring near non-paved roadways or walkways, which may border other land-use types), and school (space cleared of vegetation adjacent to school for human use). In ArcGIS, we measured

distances to nearest baobab, fig, pawpaw and water, and counted number of baobabs, pawpaw, or figs within the various buffers surrounding the focal baobab to give density measures. For distance to nearest conspecific and density of surrounding baobabs, we used all baobabs (fruiting and non-fruiting) as the potential nearest neighbor or in the count for density. Each water source was identified from ground-truthed aerial images in ArcMap version 10.3 (Environmental Systems Resource Institute 2014).

Bat captures

To confirm presence of fruit bat species in the study area, we conducted five nights of opportunistic mist-net surveys at dammed water sources, a mango grove, and at one baobab. From one to four mist-nets or canopy nets were set up over water sources or along potential fly-ways around baobab or mango trees (as the latter were fruiting and ripe at this time). Nets were open for approximately two and a half hours each night from 18:30 to 21:00 and checked every 15 to 30 min. Species were identified following Patterson and Webala (2012). Procedures involving bat capture and handling followed guidelines established by the American Society of Mammalogists (Sikes 2016) and were approved by the Texas Tech University Institutional Animal Care and Use Committee (Protocol 16100-10).

Data analyses

Conditional inference forests (CIFs) were used to identify the relative importance of individual and landscape characteristics to baobab reproductive success. CIFs combine Breiman's random forests (Breiman 2001) that use recursive bagging of observations, and conditional inference trees, which consist of a series of nonparametric tests, capable of handling many predictor variables, including correlated variables, and so are ideal for our dataset (Hothorn et al. 2006b). For example, in our dataset, GBH and height of baobabs are closely related according to Pearson's product-moment correlation ($t=26.374$, $df=587$, $p<2.2\times 10^{-16}$), but both were retained because baobabs do not always exhibit proportional growth in height and GBH throughout their lifetime (Wickens and Lowe 2008). Due to conditional inference trees flexibility in handling many types of data (e.g.,

categorical, continuous, ordinal), and non-normal data, CIFs and related techniques such as conditional inference trees and random forests are increasingly used to analyze ecological data (Collins et al. 2018; Liao et al. 2018; Phelps and Kingston 2018).

Two models were constructed for analyses, and all methods repeated with each model. Using the count of total number of fruit on each baobab tree, we calculated two response metrics: (i) the capability to produce fruit (presence or absence); and ii) if baobabs fruited, the fruit production category ('few' or 'many'). Categories in (ii) were determined by quantile binning, using the base quantile function in R, performed on each buffer distance dataset. The structure of the number of baobab fruit per tree was found to be non-normal using Shapiro-Wilks normality tests (all baobabs, $W=0.55383$, $p<2.2\times 10^{-16}$, fruiting baobabs only, $W=0.77054$, $p<2.2\times 10^{-16}$), but CIFs are able to utilize non-parametric data.

Two statistical models were created for each buffer-distance dataset, one for each response variable (presence/absence of fruit and few/many fruit). The independent variables are those described above. We constructed conditional inference forests of 500 iterations of CIFs for each buffer-distance dataset, specifying that all 10 independent variables were to be tried at each split. To avoid having forests of trees with many, sometimes non-significant splits in our independent variables, we limited splits to three levels before final nodes (maximum depth), and required final nodes to have a minimum of 10 baobabs.

All analyses were run using RStudio (RStudio 1.3.1073, <https://www.rstudio.com/>) with R version 3.6.1, and *party* (Hothorn et al. 2006a), specifically using the function *cforest* (Hothorn et al. 2006b; Strobl et al. 2007, 2008) to construct conditional inference forests with parameters in the above paragraph and to determine relative variable importance for each model. Relative variable importance is a count of the times each independent variable was used in splits for each tree within a forest. The package *partykit* (Hothorn and Zeileis 2015) was used to visualize individual conditional inference trees comprising the forests to assess the direction of influence for land-use types. Confusion matrices from *caret* (Kuhn et al. 2019) were used to assess accuracy and agreement of conditional inference forest models and function *hetcor* from *polycor* (Fox 2019) was used to

determine the relationship between independent variables and response variables.

Results

A total of 741 baobabs were georeferenced within the study area. Of those, 301 baobabs produced at least 1 fruit (range of fruit per baobab: 1–1293). Descriptive statistics for all buffer distance datasets are included in Table 1, including the number of baobabs retained (i.e., those baobabs with 99.9% of the buffer within the bounds of the study area). The buffer-distances are representative of different scales tested in the study. In addition, we georeferenced 211 fig trees and 72 pawpaw trees.

We captured one individual each of two bat species known to visit baobab trees. One adult female *Epomophorus wahlbergi* was caught at the water dam near a mango grove (01.02125° N 038.32526° E), in a mist-net set. Species identification was determined by the presence of a single post-dental ridge where other *Epomophorus* species have two (Patterson and Webala 2012). The second Pteropodid captured was an adult male *Rousettus aegyptiacus*, caught in a canopy net set in a fly-way between mango trees (01.02769° N, 038.32901° E). In addition to mist-net captures, we were alerted by a landowner of fruit bats roosting in the bush on his land. Based on pelage (fur), specifically the tufts of white fur by ears, we determined them to be an *Epomophorus* species (Fig. 1E).

From the CIFs modeling presence or absence of fruit, significant models were obtained at buffer distances from 50 to 450-m. For these buffers, accuracy of the models was significantly better than the no-information rate (Table 2) and ranged from 0.645 (64.5%) to 0.701 (70.1%). The Kappa statistics, used as a measure of agreement between the model and predicted values, for significant models ranged between 0.298 and 0.407 (Table 2). GBH, total height of the baobab, and distance to nearest pawpaw tree were the most used variables in CIFs when compared to other variables. In all buffer-distance models, GBH was always the most important variable in determining the presence/absence of fruit on baobabs fruited (Fig. 3). The second-most important variable switches between total height and distance to nearest pawpaw depending on the buffer distance (Fig. 3A).

Table 1 Descriptive parameters (mean ± first standard deviation) of the response variable (number of fruit per baobab) and variables included within the conditional inference forest models for all buffer datasets. Summary statistics are also included for all georeferenced baobabs (those with and without fruit)

Buffer distance of dataset	No. of baobabs in dataset	No. of fruit per baobab tree	Height of baobabs (m)	Girth at breast height of baobabs (m)	Distance to water (m)	Distance to nearest baobab (m)	Distance to nearest fig tree (m)	Distance to nearest pawpaw tree (m)	No. of baobabs within buffer	No. of fig trees within buffer	No. of pawpaw trees within buffer
All georeferenced baobabs	741	70 ± 159	13 ± 5	4 ± 3	NA	NA	NA	NA	NA	NA	NA
50 m	589	83 ± 172	14 ± 5	5 ± 3	500 ± 303	46 ± 40	409 ± 210	974 ± 612	4 ± 6	0 ± 1	0 ± 0
100 m	557	83 ± 173	14 ± 5	5 ± 3	504 ± 303	46 ± 41	405 ± 208	976 ± 612	10 ± 15	0 ± 2	0 ± 1
150 m	530	84 ± 169	14 ± 5	5 ± 3	506 ± 303	46 ± 41	402 ± 205	978 ± 613	16 ± 21	1 ± 4	0 ± 1
200 m	493	84 ± 168	14 ± 5	5 ± 3	512 ± 305	46 ± 41	400 ± 202	978 ± 606	23 ± 24	2 ± 7	0 ± 1
250 m	459	82 ± 165	13 ± 5	5 ± 3	525 ± 305	44 ± 40	401 ± 200	990 ± 606	30 ± 27	4 ± 11	0 ± 1
300 m	421	82 ± 167	13 ± 4	5 ± 3	539 ± 305	43 ± 40	401 ± 198	1002 ± 598	39 ± 29	6 ± 16	0 ± 1
350 m	386	71 ± 145	13 ± 4	5 ± 3	557 ± 299	41 ± 40	398 ± 198	1027 ± 594	50 ± 32	10 ± 22	0 ± 1
400 m	360	68 ± 141	13 ± 4	5 ± 3	557 ± 298	42 ± 40	390 ± 199	1048 ± 596	62 ± 35	13 ± 28	0 ± 1
450 m	321	66 ± 139	13 ± 5	4 ± 3	577 ± 285	40 ± 38	380 ± 201	1085 ± 572	74 ± 38	19 ± 34	0 ± 1
500 m	285	63 ± 142	13 ± 5	4 ± 3	588 ± 283	39 ± 37	369 ± 205	1104 ± 555	87 ± 41	25 ± 40	0 ± 1
550 m	252	55 ± 134	13 ± 5	4 ± 3	598 ± 289	39 ± 38	364 ± 213	1105 ± 549	101 ± 43	32 ± 45	0 ± 1
600 m	224	56 ± 136	13 ± 5	4 ± 3	595 ± 301	39 ± 34	363 ± 220	1052 ± 533	113 ± 44	40 ± 49	0 ± 1
650 m	182	59 ± 143	13 ± 5	5 ± 3	575 ± 317	41 ± 32	357 ± 240	947 ± 493	122 ± 44	50 ± 53	1 ± 1
700 m	157	65 ± 150	13 ± 5	5 ± 3	568 ± 334	40 ± 30	360 ± 254	909 ± 455	139 ± 45	59 ± 55	1 ± 1
750 m	135	61 ± 136	14 ± 5	5 ± 3	548 ± 332	42 ± 32	337 ± 254	872 ± 431	156 ± 49	69 ± 55	1 ± 1
800 m	116	59 ± 140	13 ± 5	4 ± 3	577 ± 326	41 ± 32	360 ± 259	920 ± 412	180 ± 52	71 ± 56	1 ± 1
850 m	92	59 ± 150	13 ± 5	4 ± 3	609 ± 306	41 ± 32	393 ± 261	974 ± 382	208 ± 51	73 ± 57	1 ± 1
900 m	76	55 ± 140	13 ± 5	4 ± 3	602 ± 303	39 ± 32	389 ± 260	964 ± 360	232 ± 50	83 ± 55	1 ± 1
950 m	55	50 ± 143	13 ± 5	4 ± 3	540 ± 306	38 ± 34	343 ± 247	878 ± 352	245 ± 54	103 ± 50	2 ± 1
1000 m	41	47 ± 140	13 ± 5	4 ± 3	500 ± 280	36 ± 33	299 ± 223	807 ± 282	260 ± 52	121 ± 33	2 ± 1

Total height has a positive relationship with fruiting, whereby fruiting baobabs are taller trees and non-fruiting baobabs are shorter trees. Distance to nearest pawpaw has a negative relationship across all buffers, suggesting that the closer a baobab is to a pawpaw tree, the more likely the baobab is to produce fruit. Distance to nearest pawpaw appears to follow a negative quadratic formula when plotted across significant buffer-distance models (Fig. 3B). The density metrics (number of baobab, fig or pawpaw trees within a buffer) had very low relative importance in the models of fruit presence or absence. The relative importance metrics across all buffer-distance models for determining presence or absence of fruits are provided in Fig. S1.

Significant models for the fruit production categories of baobabs were reported at buffer distances 50-m through 400-m and the 550-m models (Table 3, Fig. 4). The few fruit category ranged from 1 to 109 fruit, dependent on buffer distance, while the many fruit category ranged from 88.6 to 1293 fruit (Table 3). Accuracies for these buffer distances ranged from 0.587 (58.7%) to 0.703 (70.3%) and Kappa statistics estimating agreement between models and predicted variables ranged from 0.173 and 0.407 (Table 3). Across all significant buffer distances, land use is the most important variable determining fruit production category, generally followed by total height of the baobab (Fig. 4A). Total height consistently had a positive relationship with total number of fruit, so that taller baobabs are likely to produce more fruit (Fig. 4B). Land-use is a categorical variable, so we used the first 10 conditional inference trees of the forest for 200-m, 250-m, and 300-m buffer-distance models (where land-use importance was highest; Fig. 4A) to determine the relationship between land-use categories and fruit production category. Most fruit production is associated with cleared, farm, and road land-uses and less fruit production more associated with bush, rocky, and school land-uses (Fig. 5).

Foraging resources showed fewer contributions to the overall models but did exhibit scale-dependent influence on reproductive success of those trees that fruited. Although the relationship between distance to the next-nearest baobab and total number of fruit contributed little to the overall models, the nature of the relationship changed with buffer distance. From 50 to 250 m, there was a positive relationship between

nearest neighbor distance and fruit production, but from 300 to 550 m the relationship was negative. Number of pawpaw within the buffer distance also exhibited a scale-dependent relationship with fruit category, but only at the 550-m buffer appears to contribute importance to the model. The density of figs exhibited a negative relationship with fruit category from 150 through 400 m and a positive relationship at 550 m (but with a near-zero relative importance contribution to the model). To summarize, at the 550-m buffer distance, number of pawpaw within 550 m of baobab, distance to water, and GBH are as important as total height (Fig. 4A). Relative variable importance for all buffer distances for the fruit production CIFs are in Fig. S2.

Discussion

We sought to determine the relative contribution of individual tree characteristics and landscape context to reproductive success in baobab trees and evaluate whether contributions were scale dependent. We found that individual characteristics, specifically GBH and sometimes height, were the primary determinants of whether a tree produced fruit or not. Among trees that produced fruit, land-use type was the most important factor determining whether baobabs produced few or many fruit. Trees in human-modified land uses, especially farmland, tended to produce many fruit while baobabs in the less modified bush land use produced few fruit. Other parameters contributed to our models to a lesser, but often scale-dependent, extent. None of our models were significant at buffers beyond 500–600 m, suggesting the extent of landscape influence in this system.

Our findings suggest a maturity threshold for fruit production, below which trees do not produce fruit. Above threshold, size continues to influence production, but other factors, notably proximity to pawpaw trees, can mediate the relationships. Our findings agree with Venter and Witkowski (2011) where adult baobabs produce significantly more fruit than sub-adult baobabs and age classes are based on size of the baobab.

Although land-use type was the primary determinant of whether baobabs produced few or many fruit, reproductive success was further mediated by individual characteristics (primarily height, sometimes

Table 2 Metrics of conditional inference forests (CIF) for the presence or absence of fruit response variable

Buffer distance (m)	Accuracy of CIF model	95% confidence interval around accuracy	No-information Rate	p-value	Kappa
50	0.645	0.605–0.684	0.560	< 0.001	0.298
100	0.670	0.629–0.709	0.573	< 0.001	0.347
150	0.679	0.638–0.719	0.587	< 0.001	0.368
200	0.686	0.643–0.726	0.574	< 0.001	0.379
250	0.668	0.637–0.724	0.573	< 0.001	0.372
300	0.701	0.655–0.744	0.551	< 0.001	0.407
350	0.674	0.624–0.72	0.503	< 0.001	0.348
400	0.653	0.601–0.702	0.531	< 0.001	0.298
450	0.682	0.628–0.733	0.570	< 0.001	0.347
500	0.656	0.598–0.711	0.698	0.945	0.239
550	0.706	0.646–0.762	0.778	0.996	0.287
600	0.719	0.655–0.777	0.728	0.650	0.353
650	0.692	0.620–0.759	0.670	0.293	0.321
700	0.682	0.603–0.754	0.650	0.227	0.318
750	0.667	0.580–0.745	0.644	0.329	0.296
800	0.690	0.597–0.772	0.733	0.875	0.307
850	0.674	0.568–0.768	0.728	0.900	0.234
900	0.750	0.637–0.842	0.658	0.055	0.450
950	0.655	0.514–0.778	0.764	0.977	0.114
1000	0.659	0.494–0.799	0.927	1	–0.130

Accuracy of each model, along with the 95% confidence interval surrounding that accuracy, ranges from zero (no accuracy) to one (complete accuracy). No-information rate occurs when there is randomization between the independent variables and the response variable. Significant p-values are given in bold and indicate buffer size models that have an accuracy that is significantly better than the no-information rate. Kappa values indicate the amount of agreement between machine-based predictions of classification and true classification from the dataset. A Kappa of zero (or negative) indicates poor agreement while a Kappa of one indicates complete agreement

GBH), distance to nearest pawpaw, number of figs within buffer, and distance to nearest baobab. Moreover, moderation by these secondary characteristics was sometimes scale dependent. Proximity to, and density of pawpaw trees generally had a positive influence on reproductive success (so an attractant) at buffer distances to 500 m, but a negative influence at 550 m (distractant). Fig trees appear to be distractants to bats performing a pollinating duty—the closer a fig tree, or the more figs surrounding a baobab, the fewer fruit the baobab produced. Being nearer a conspecific negatively influenced fruit production at small scales (50-m through 300-m buffers), but was not relevant in models at larger scales.

Our models address determinants of reproductive success in a single fruiting season, but baobabs are long-lived trees. Work in South Africa suggests that individual baobab trees are consistent in their

reproductive output across years, with some trees producing few and others many fruits each year (Venter and Witkowski 2011), although South African populations of baobabs are unusual in continental Africa in that bats do not seem to act as pollinators (Taylor et al. 2020), and the difference in fruiting appears to be in part linked to flower morphology (Chetty et al. 2021). Further, floral volatiles indicate a shift away from bat pollination to hawkmoth pollination (Karimi et al. 2021). Future work could thus evaluate the validity of our models across years, and might expand to make and incorporate direct observations of pollinator visitation and frequency. Many of our predictions were based on optimal foraging theory, so it is important to consider monitoring pollinator movement through telemetry or GPS to test new hypotheses from this study (e.g., that pawpaw are attractants or distractants depending on scale and that figs are

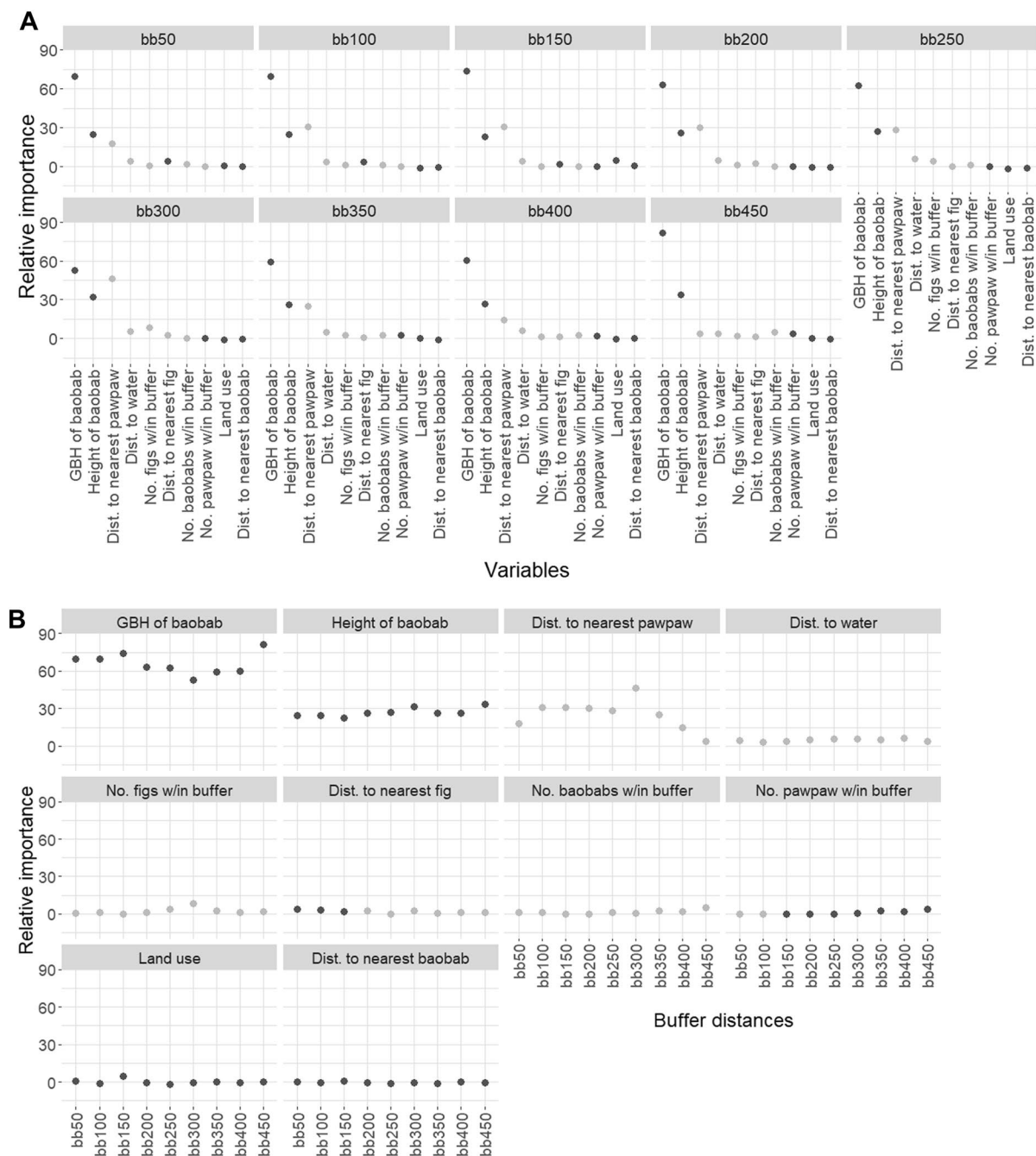


Fig. 3 Relative importance of independent variables in the significant fruit production capability (presence or absence of fruit) models. Data are aggregated by: **A** buffer size, where 'bb50' is the model based on the 50-m buffer and the notation is repeated for all buffers; and **B** variable. Grey dots indicate

that the independent variable has a negative relationship with the presence or absence of fruit while black dots indicate positive relationships. Models were only significant through to the 450-m buffer, relative importance of variables from the non-significant models at greater distances are available in Fig. S2

distractants). It would be beneficial to also consider flower morphology, as these features are known to differ among poor-producing and producing baobabs (Chetty et al. 2021) and soil characteristics, as it is known that increased composition of clay and crude silt increases fruit production (Assogbadjo et al. 2005).

Plant reproductive success as a result of animal-mediated pollination is known to be influenced by a multitude of factors. Pollinators exist in complex landscapes, so plants reliant on cross-pollination services are affected by resources surrounding them. Pollinators are also known to be influenced by

individual traits of the plant itself, so it is crucial to consider both sets of factors when evaluating drivers of reproductive success of plants. Moreover, pollinator landscapes are constantly changing, and pollinator declines worldwide leave the long-term survival of plant species in jeopardy as some 85% of plant species rely on pollinators, at least in some capacity (Ollerton et al. 2011). Securing pollination services requires integrative understanding through landscape, behavioral, community, and pollination ecology lenses (Betts et al. 2019).

Table 3 Metrics of conditional inference forests (CIF) for each buffer distance for the few and many fruit production response variable

Buffer distance (m)	Accuracy of CIF model	95% confidence interval around accuracy	No-information Rate	p-value	Kappa	Grouping for few fruit production (no. fruit)	Grouping for many fruit production (no. fruit)
50	0.628	0.568–0.686	0.569	0.028	0.258	1–105	106–1293
100	0.635	0.573–0.695	0.561	0.009	0.272	1–105	106–1293
150	0.654	0.591–0.714	0.568	0.003	0.309	1–109	110–954
200	0.659	0.594–0.721	0.553	0.001	0.319	1–106	107–954
250	0.703	0.636–0.764	0.541	0.000	0.407	1–109	110–954
300	0.662	0.590–0.728	0.537	0.000	0.323	1–108	109–954
350	0.607	0.529–0.682	0.500	0.003	0.214	1–105	106–892
400	0.587	0.504–0.666	0.507	0.030	0.173	1–105	106–892
450	0.592	0.503–0.678	0.523	0.067	0.185	1–106	107–892
500	0.620	0.522–0.712	0.546	0.073	0.241	1–108	109–892
550	0.628	0.517–0.730	0.523	0.033	0.256	1–88.5	88.6–843
600	0.525	0.410–0.638	0.525	0.545	0.050	1–71.5	71.6–843
650	0.591	0.463–0.711	0.515	0.134	0.182	1–71.5	71.6–843
700	0.574	0.441–0.700	0.525	0.261	0.148	1–96	97–843
750	0.509	0.371–0.647	0.582	0.890	0.021	1–68	69–812
800	0.422	0.277–0.579	0.511	0.910	–0.156	1–68	69–812
850	0.613	0.422–0.782	0.548	0.296	0.228	1–64	65–812
900	0.333	0.165–0.540	0.519	0.984	–0.335	1–64	65–812
950	0.000	0–0.206	0.500	1	–1	1–90	91–812
1000	0.182	0.023–0.518	0.636	1	–0.678	1–105	106–812

Accuracy of each model, along with the 95% confidence interval surrounding that accuracy, ranges from zero (no accuracy) to one (complete accuracy). No-information rate occurs when there is randomization between the independent variables and the response variable. Significant p-values given in bold and indicate buffer size models that have an accuracy that is significantly better than the no-information rate. Kappa values indicate the amount of agreement between machine-based predictions of classification and true classification from the dataset. A Kappa of zero (or negative) indicates poor agreement while a Kappa of one indicates complete agreement

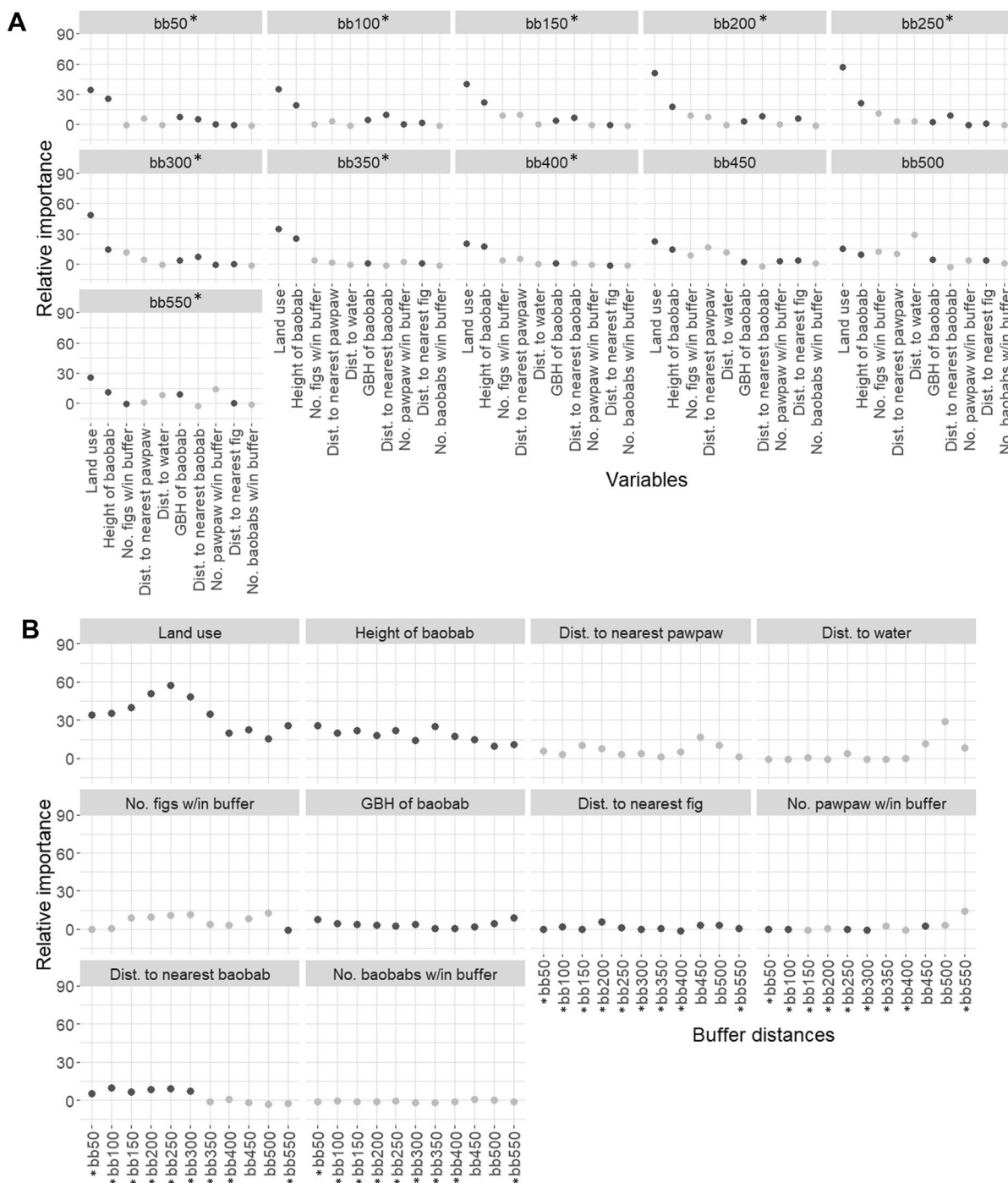


Fig. 4 Relative importance of all independent variables in the significant fruit production categories (few or many fruit) models. Data are aggregated by: **A** buffer size, where ‘bb50’ is the model based on the 50-m buffer, and the notation is repeated for all buffers; and **B** variable. The 450-m and 500-m buffered models are not significant, but are included as they fall inside the range of significant buffers (asterisks mark signifi-

cant buffer distances). Grey dots indicate that the independent variable had a negative relationship with total number of fruit while black dots indicate a positive relationship. Models were only significant through to the 550-m buffer, relative importance of variables from the non-significant models at greater distances are available in Fig. S2

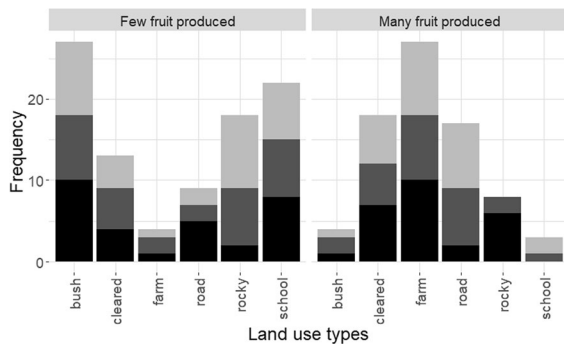


Fig. 5 Frequency of land-use categories where conditional inference forests (CIFs) determined splits between fruiting categories (few or many fruit). Contributions of frequency from 200-m model ($n = 10$ CIFs) are light grey, 250-m model ($n = 10$ CIFs) are dark grey, and 300-m model ($n = 10$ CIFs) are black

Acknowledgements We would like to thank our field assistant, Michael Bartonjo, and local host Daniel Ngei and his family for all their assistance. We are also grateful to Joseph Kavui, the local chief, for facilitating our research, and to all the landowners in the villages of Kaai, Kalesi, Kaluku South, Kandundu, Katithini, Kavui, Kawula, Kiwaani, Mutoleka, Ngieni East, Ngieni West, and Yungamaduu, who allowed us to sample baobabs or other fruiting trees on their land. Funding for this research was awarded by Bat Conservation International, the Association of Biologists at Texas Tech University, and the Department of Biological Sciences at Texas Tech University. PWW is grateful to Bruce D. Patterson, MacArthur Zoology/Mammals Curator of Mammals at the Field Museum of Natural History (Chicago, IL, USA), for supporting and facilitating his research activities in Kenya. Research was conducted under appropriate permits, obtained from the Kenyan National Commission for Science, Technology, and Innovation (NACOSTI/P/79660/20292).

Funding Funding provided by Bat Conservation International (US), Association of Biologists at Texas Tech University, and the Department of Biology at Texas Tech University (US)

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Angoh SYJ (2016) The birds, the bees and *Erica*: vulnerability of plant-pollinator communities in fragmented fynbos landscapes. University of Cape Town, Cape Town

Arias-Cóyotl E, Stoner KE, Casas A (2006) Effectiveness of bats as pollinators of *Stenocereus stellatus* (Cactaceae)

in wild, managed in situ, and cultivated populations in La Mixteca Baja, central Mexico. *Am J Bot* 93:1675–1683

Assogbadjo AE, Sinsin B, Codjia JTC, van Damme P (2005) Ecological diversity and pulp, seed and kernel production of the baobab (*Adansonia digitata*) in Benin. *Belg J Bot* 138:47–56

Aziz SA, Olival KJ, Bumrungsri S, Richards GC, Racey PA (2016) The conflict between Pteropodid bats and fruit growers: species, legislation and mitigation. In: Voigt CC, Kingston T (eds) *Bats in the Anthropocene: conservation of bats in a changing world*. Springer International Publishing, New York

Baer SG, Engle DM, Knops JMH, Langeland KA, Maxwell BD, Menalled FD, Symstad AJ (2009) Vulnerability of rehabilitated agricultural production systems to invasion by nontarget plant species. *Environ Manage* 43:189–196

Baker HG (1961) The adaptation of flowering plants to nocturnal and crepuscular pollinators. *Q Rev Biol* 36:64–73

Baker HG (1977) Non-sugar chemical constituents of nectar. *Apidologie* 8:349–356

Baker HG, Baker I (1975) Studies of nectar-constitution and pollinator-plant coevolution. In: Jones CE, Little RJ (eds) *Coevolution of animals and plants*. Van Nostrand-Reinhold, New York, pp 100–140

Batista CB, Reis NR, Rezende MI (2016) Nutritional content of bat-consumed fruits in a forest fragment in Southern Brazil. *Braz J Biol* 77:244–250

Baum D (1995) The comparative pollination and floral biology of baobabs (*Adansonia*—Bombaceae). *Ann Mo Bot Gard* 82:322–348

Betts MG, Hadley AS, Kormann U (2019) The landscape ecology of pollination. *Landsc Ecol* 34:961–966. <https://doi.org/10.1007/s10980-019-00845-4>

Bonaccorso FJ, Winkelmann JR, Todd CM, Miles AC (2014) Foraging movements of epauletted fruit bats (Pteropodidae) in relation to the distribution of sycamore figs (Moraceae) in Kruger National Park, South Africa. *Acta Chiropterol* 16:41–52

Bosch M, Waser NM (2001) Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. *Oecologia* 126:76–83

Breiman L (2001) Random forests. *Mach Learn* 45:5–32

Burgess N, D'Amico J, Underwood E, Olson D, Dinerstein E, Itoua I (2004) *Terrestrial ecoregions of Africa*. Island Press, Washington

Calderón-Capote MC, Dechmann DKN, Fahr J, Wikelski M, Kays R, O'Mara MT (2020) Foraging movements are density-independent among straw-coloured fruit bats. *R Soc Open Sci* 7:1–13

Cassim JZ, Juma GS (2018) Temporal analysis of drought in Mwingi sub-county of Kitui County in Kenya using the standardized precipitation index (SPI). *Clim Change* 4:728–733

Chapman CA, Chapman LJ, Wanhom R, Hunt K, Gebo D, Gardner L (1992) Estimators of fruit abundance of tropical trees. *Biotropica* 24:527–531

Charnov EL (1976) Optimal foraging theory: the marginal value theorem. *Theor Popul Biol* 9:129–136

Chetty A, Glennon KL, Venter SM, Cron GV, Witkowski ETF (2021) Reproductive ecology of the African baobab: floral

- features differ among individuals with different fruit production. For Ecol Manag 489:119077
- Collins BM, Lydersen JM, Everett RG, Stephens SL (2018) How does forest recovery following moderate-severity fire influence effects of subsequent wildfire in mixed-conifer forests? Fire Ecol 14:1–9
- Cranmer L, McCollin D, Ollerton J (2012) Landscape structure influences pollinator movements and directly affects plant reproductive success. Oikos 121:562–568
- Dickson CR, Petit S (2006) Effect of individual height and labellum colour on the pollination of *Caladenia* (syn. *Arachnorchis*) *behrii* (Orchidaceae) in the northern Adelaide region. South Austral Plant Syst Evol 262:65–74
- Djossa BA, Toni HC, Adekanmbi ID, Tognon FK, Sinsin BA (2015) Do flying foxes limit flower abortion in African baobab (*Adansonia digitata*)? Case study in Benin, West Africa. Fruits 70:281–287
- Dudash MR, Hassler C, Stevens PM, Fenster CB (2011) Experimental floral and inflorescence trait manipulations affect pollinator preference and function in a hummingbird-pollinated plant. Am J Bot 98:275–282
- Dupont YL, Trøjelsgaard K, Olesen JM (2011) Scaling down from species to individuals: a flower-visitation network between individual honeybees and thistle plants. Oikos 120:170–177
- Dupont YL, Trøjelsgaard K, Hagen M, Henrikson MV, Olesen JM, Pederson NME, Kissling WD (2014) Spatial structure of an individual-based plant–pollinator network. Oikos 123:1301–1310
- Environmental Systems Resource Institute (2014) ArcMap 10.3, Redlands, California: ESRI (Environmental Systems Resources Institute)
- Fenner M (1982) Aspects of the ecology of *Acacia-Commiphora* woodland near Kibwezi, Kenya. J East Africa Nat Hist Soc Natl Museum 175:1–11
- Fleming TH, Geiselman C, Kress WJ (2009) The evolution of bat pollination: a phylogenetic perspective. Ann Bot-London 104:1017–1043. <https://doi.org/10.1093/aob/mcp197>
- Fox J (2019) polycor: Polychoric and polyserial correlations, R package
- Fukuda D, Tisen OB, Momose K, Sakai S (2009) Bat diversity in the vegetation mosaic around a lowland dipterocarp forest of Borneo. Raffles B Zool 57:213–221
- Gebauer J, Adam YO, Cuní Sanchez A et al (2016) Africa's wooden elephant: the baobab tree (*Adansonia digitata* L.) in Sudan and Kenya: a review. Genet Resour Crop Ev 63:377–399
- Ghazoul J (2005) Pollen and seed dispersal among dispersed plants. Biol Rev Camb Philos 80:413–443
- Hothorn T, Zeileis A (2015) partykit: a modular toolkit for recursive partytioning in R. J Mach Learn Res 16:3905–3909
- Hothorn T, Bühmann P, Dudoit S, Molinaro A, Van Der Laan MJ (2006a) Survival ensembles. Biostatistics 7:355–373
- Hothorn T, Hornik K, Zeileis A (2006b) Unbiased recursive partitioning: a conditional inference framework. J Comput Graph Stat 15:651–674
- Johnson SD, Pauw A, Midgley J (2001) Rodent pollination in the African lily *Massonia depressa* (Hyacinthaceae). Am J Bot 88:1768–1773
- Johnson SD, Hollens H, Kuhlmann M (2012) Competition versus facilitation: conspecific effects on pollinator visitation and seed set in the iris *Lapeirousia oreogena*. Oikos 121:545–550
- Jones FA, Comita LS (2008) Neighbourhood density and genetic relatedness interact to determine fruit set and abortion rates in a continuous tropical tree population. Proc R Soc B 275:2759–2767. <https://doi.org/10.1098/rspb.2008.0894>
- Joshi NK, Otieno M, Rajotte EG, Fleischer SJ, Biddinger DJ (2016) Proximity to woodland and landscape structure drives pollinator visitation in apple orchard ecosystem. Front Ecol Environ 4:1–9
- Justino DG, Maruyama PK, Oliveira PE (2012) Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. J Ornithol 153:189–197
- Karimi N, Saghafi S, Keefover-Ring K, Venter SM, Ané C, Baum DA (2021) Evidence for hawkmoth pollination in the chiropterophilous African baobab (*Adansonia digitata*). Biotropica. <https://doi.org/10.1111/btp.13033>
- Kasangaki P (2018) Assessment of honeybee colony performance in the agro-ecological zones of Uganda. Current Investig Agric Current Res 1:1–6
- Kermack JP, Rauschert ESJ (2019) Soil characteristics drive *Ficaria verna* abundance and reproductive output. Invasion Plant Sci Mana 12:214–222
- Killmann W, Ndeckere F, Vantomme P, Walter S (2003) Developing inventory methodologies for non-wood forest products: lessons learned from an analysis of case studies in African countries. In: Proceedings of the IUFRO Division 5 Research Groups 5.11 and 5.12. United State Department of Agriculture, Portland, Oregon, pp 1–128
- Kleizen C, Midgley J, Johnson SD (2008) Pollination systems of *Colchicum* (Colchicaceae) in Southern Africa: evidence for rodent pollination. Ann Bot 102:747–755
- Kuhn M (2019) caret: classification and regression training
- Lander TA, Bebbler DP, Choy CTL, Harris SA, Boshier DH (2011) The Circe Principle explains how resource-rich land can waylay pollinators in fragmented landscapes. Curr Biol 21:1302–1307
- Li H, Wilkins KT (2015) Selection of building roosts by Mexican free-tailed bats (*Tadarida brasiliensis*) in an urban area. Acta Chiropterol 17:321–330
- Liao H, Sarver E, Krometis LAH (2018) Interactive effects of water quality, physical habitat, and watershed anthropogenic activities on stream ecosystem health. Water Res 130:69–78
- Marshall AG (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. Biol J Linn Soc 20:115–135
- Maruyama PK, Justino DG, Oliveira PE (2016) Does intraspecific behavioural variation of pollinator species influence pollination? A quantitative study with hummingbirds and a Neotropical shrub. Plant Biol 18:913–919
- Neil K, Wu J (2006) Effects of urbanization on plant flowering phenology: a review. Urban Ecoyst 9:243–257
- Njoroge GN, Kaibui IM, Njenga PK, Odhiambo PO (2010) Utilisation of priority traditional medicinal plants and local people's knowledge on their conservation status in arid lands of Kenya (Mwingi District). J Ethnobiol Ethnomed 6:1–8

- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326
- Olubode OO, Odeyemi OM, Olatokunbo Aiyelaagbe IO (2016) Influence of environmental factors and production practices on the growth and productivity of pawpaw (*Carica papaya* L.) in south western Nigeria—a review. *Fruits* 71:341–361
- Orindi VA, Nyong A, Herrero M (2007) Pastoral livelihood adaptation to drought and institutional interventions in Kenya. Occasional Paper of the Human Development Report Office
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* 16:1501–1514
- Pasquaretta C, Jeanson R, Andalo C, Chittka L, Lihoreau M (2017) Analysing plant–pollinator interactions with spatial movement networks. *Ecol Entomol* 42:4–17
- Patrut A, Von Reden KF, Lowy DA, Alberts AH, Pohlman JW, Wittmann R, Gerlach D, Xu L, Mitchell CS (2007) Radiocarbon dating of a very large African baobab. *Tree Physiol* 27:1569–1574
- Patterson BD, Webala PW (2012) Keys to the bats (Mammalia: Chiroptera) of East Africa. *Fieldiana Life Earth Sci* 6:1–60
- Phelps KL, Kingston T (2018) Environmental and biological context modulates the physiological stress response of bats to human disturbance. *Oecologia* 188:41–52
- Pyke GH, Pullman HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- Rausher MD, Feeny P (1980) Herbivory, plant density, and plant reproductive success: the effects of *Battus philenor* on *Aristolochia reticulata*. *Ecology* 61:905–917
- Schüepp C, Herzog F, Entling MH (2013) Disentangling multiple drivers of pollination in a landscape-scale experiment. *Proc R Soc B*. <https://doi.org/10.1098/rspb.2013.2667>
- Sidibe M, Williams JT (2002) Baobab. *Adansonia digitata*. International Centre for Underutilised Crops, Southampton
- Sikes R, Animal Care and Use Committee of the American Society of Mammalogists (2016) 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J Mammal* 97:663–688
- Singaravelan N, Marimuthu G (2004) Nectar feeding and pollen carrying from *Ceiba pentandra* by Pteropodid bats. *J Mammal* 85:1–7
- Snook LK, Cámara-Cabrales L, Kelty MJ (2005) Six years of fruit production by mahogany trees (*Swietenia macrophylla* King): patterns of variation and implications for sustainability. *For Ecol Manag* 206:221–235
- Somanathan H, Borges RM (2000) Influence of exploitation on population structure, spatial distribution and reproductive success of dioecious species in a fragmented cloud forest in India. *Biol Conserv* 94:243–256
- Southern SG, Birt P, Porter J, Ford HA (2004) Review of gene movement by bats and birds and its potential significance for eucalypt plantation forestry. *Aust For* 67:44–53
- Start AN (1972) Pollination of the baobab (*Adansonia digitata* L.) by the fruit bat *Rousettus aegyptiacus* E. Geoffrey E Afr Wildl J 10:71–72
- Strobl C, Boulesteix AL, Zeileis A, Hothorn T (2007) Bias in random forest variable importance measures: illustrations, sources and a solution. *BMC Bioinform*. <https://doi.org/10.1186/1471-2105-8-25>
- Strobl C, Boulesteix AL, Kneib T, Augustin T, Zeileis A (2008) Conditional variable importance for random forests. *BMC Bioinformatics* 9:1–11
- Taylor PJ, Vise C, Krishnamoorthy MA, Kingston T, Venter S (2020) Citizen science confirms the rarity of fruit bat pollination of baobab (*Adansonia digitata*) flowers in southern Africa. *Diversity* 12:1–19
- van der Pijl V (1937) Fledermäuse und blumen. *Flora* 31:1–40
- Venter SM, Witkowski ETF (2010) Baobab (*Adansonia digitata* L.) density, size-class distribution and population trends between four land-use types in northern Venda. *S Afr J Ecol Manag* 259:294–300
- Venter SM, Witkowski ETF (2011) Baobab (*Adansonia digitata* L.) fruit production in communal and conservation land-use types in Southern Africa. *For Ecol Manag* 261:630–639
- Venter SM, Witkowski ETF (2013) Fruits of our labour: contribution of commercial baobab (*Adansonia digitata* L.) fruit harvesting to the livelihoods of marginalized people in northern Venda, South Africa. *Agrofor Syst* 87:159–172
- Venter SM, Glennon KL, Witkowski ETF, Baum D, Cron GV, Tivakudze R, Karimi N (2017) Baobabs (*Adansonia digitata* L.) are self-incompatible and ‘male’ trees can produce fruit if hand-pollinated. *S Afr J Bot* 109:263–268
- Walter MH, Verdong A, Olmos V, Weiss CC, Vial LR, Putra A, Müller J, Tschapka M, Schnitzler HU (2020) Discrimination of small sugar concentration differences helps the nectar-feeding bat *Leptonycteris yerbabuenae* cover energetic demands. *J Exp Biol* 223:1–5
- Ward M, Johnson SD, Zalucki MP (2013) When bigger is not better: Intraspecific competition for pollination increases with population size in invasive milkweeds. *Oecologia* 171:883–891
- Webala PW, Musila S, Makau R (2014) Roost occupancy, roost site selection and diet of straw-coloured fruit bats (Pteropodidae: *Eidolon helvum*) in western Kenya: the need for continued public education. *Acta Chiropterol* 16:85–94
- West GB, Enquist BJ, Brown JH (2009) A general quantitative theory of forest structure and dynamics. *Proc Natl Acad Sci USA* 106:7040–7045. <https://doi.org/10.1073/pnas.0812294106>
- Wester P, Stanway R, Pauw A (2009) Mice pollinate the Pagoda Lily, *Whiteheadia bifolia* (Hyacinthaceae). First field observations with photographic documentation of rodent pollination in South Africa. *S Afr J Bot* 75:713–719
- Wickens GE, Lowe P (2008) The baobabs: Pachycauls of Africa, Madagascar, and Australia. Springer, New York