

The historical distribution of megaherbivores does not determine the distribution of megafaunal fruit in southern Africa

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Large specialized fruit (megafaunal fruit) have evolved alongside megaherbivores to take advantage of their unparalleled seed dispersal service. Megaherbivores were widespread and abundant in the Pleistocene but due to multiple extinction events have been extirpated from all continents except Africa and small pockets of South East Asia. In Africa, we are in the unique position of being able to study megafaunal fruits where there are still areas with a largely intact megaherbivore community. The megafaunal fruits of the African forests have been examined but those of the African savannas have been largely overlooked. We use an operational definition of megafaunal fruit developed in the Neotropics to identify megafaunal fruit in the South African tree flora. Thirty-one species were identified as megafaunal fruit-bearers, representing only 3% of the tree flora. Megafaunal tree species are well represented in the families Mimosoideae, Arecaceae, Strychnaceae and Caesalpinoideae. We explored the factors underlying the distribution of these megafaunal tree species. We found that the historical distribution of megaherbivores in South Africa does not explain the distribution of these fruit. Megaherbivores have historically been found throughout South Africa while megafaunal fruit tree species occur almost exclusively in the northern tropical reaches of the country. Abiotic factors such as precipitation and temperature appear to best explain the distribution of megafaunal fruit species in the region. We conclude that megafaunal fruit are a tropical phenomenon and their tropical origins now limit their distribution.

ADDITIONAL KEYWORDS: abiotic environment – African savanna elephant – historical distribution – megaherbivores – megafauna – megafaunal fruit – savannas – seed dispersal – seed dispersal guilds – tropical biota.

INTRODUCTION

Large seed size confers better seedling competition for safe sites but generally comes at the cost of reduced dispersal ability (Ezoe, 1998). Megaherbivores were defined by Owen-Smith (1988) as mammals typically exceeding a body mass of 1000 kg. Dispersal by megaherbivores circumvents the dispersal/survivability trade-off in seed size as these animals can transport considerable seed loads over significant distances (Dudley, 2000; Guimarães *et al.*, 2008;

Sridhara *et al.*, 2016; Bunney *et al.*, 2017). Large fruits (megafaunal fruits) have evolved alongside large vertebrates to take advantage of these remarkable seed vectors.

Unfortunately, due to a series of extinction events at the end of the Pleistocene (50 000–10 000 years ago) the large vertebrate communities of Europe, non-tropical Asia, Australia and the Americas vanished almost in their entirety and with them the dispersal services they offered megafaunal fruit (Martin, 1984).

Megaherbivores were widespread and occurred at far higher densities in the Pleistocene but owing to a series of extinction events, from 50 000 to 1000 years ago, were lost from all continents and island groups

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with the exception of Africa and small pockets of South East Asia (Hansen & Galetti, 2009). Five genera of Africa's megafaunal community, *Loxodonta* (African elephant), *Ceratotherium* (white rhinoceros), *Diceros* (black rhinoceros), *Giraffa* (giraffe) and *Hippopotamus* (hippopotamus) remain, whereas two genera, *Elephas* (Asian elephant) and *Rhinoceros* (one-horned rhinoceros), survive in Asia (Owen-Smith 1988).

On all but these two continents, megafaunal fruit can now be considered 'overbuilt' (Barlow, 2000) – diaspores that owing to their large size and/or degree of mechanical and chemical protection are ill-fitted for effective dispersal by the extant frugivore communities. They are ecological anachronisms: fruits that evolved in the presence of megaherbivores but have remained long after their demise (Janzen & Martin, 1982; Barlow, 2000; Guimarães *et al.*, 2008). In Africa, we are in the unique position of being able to study megafaunal fruits in areas with an intact megaherbivore community. The megafaunal fruits of the Central and West African forests have been studied on a few occasions (Alexandre, 1978; Short, 1981; Feer, 1995; Blake, 2002) but those of the African savannas have been given limited attention (Dudley, 2000). African savannas possess some charismatic large-fruited trees. One such example is the African fan palm (*Borassus aethiopum*) that stands 20 m tall and produces scores of large (15 cm in diameter) hard, orange–brown fruit that contain just one to three very large seeds, each enclosed within a woody endocarp (Bayton, 2007). These fruit drop to the ground with a thud upon ripening and are a favoured food of elephants (Burt & Salisbury, 1929; Salako *et al.*, 2016). A second example is the very distinct evergreen sausage tree (*Kigelia africana*) with its wide spreading branches that has very large woody sausage-like fruits that hang down on long rope-like peduncles. These fruits can weigh up to 12 kg and can reach almost 1 m in length. They contain numerous seeds embedded within a mesh of fibrous pulp (Joffe, 2003). These fruits are consumed in large quantities by hippopotamus on the Luangwa River in Zambia at the end of the dry season when grass is in short supply (Ansell, 1965, in Namah *et al.*, 2019).

Janzen & Martin (1982) set out descriptive traits that characterize megafaunal fruits, including large seed and fruit size, seeds protected mechanically by a thick and hard endocarp, and fruit that fall to the ground on ripening. Guimarães *et al.* (2008) subsequently developed an operational definition that allows megafaunal fruit to be identified on the basis of physical characteristics of the fruit and seeds. To do this they examined numerous studies of African forest elephant diets (*Loxodonta cyclotis*; Alexandre, 1978; Short, 1981; Yumoto *et al.*, 1995). They observed

that fruits that are primarily consumed by elephants and remain intact in their dung fall into two distinct categories: the first are 4–10 cm in diameter with up to five large seeds while the second are fruits that are greater than 10 cm in diameter with numerous small seeds. Guimarães *et al.* (2008) used this definition to identify megafaunal fruit in the South America flora.

As limited work (with the exception of Dudley, 2000; Spanbauer & Adler, 2015; Bunney *et al.*, 2017) has been done on savanna megaherbivore fruit consumption and dispersal, we used the operational definition developed by Guimarães *et al.* (2008) to compile a first list of the megafaunal fruit tree species of South Africa. Given that this definition is based solely on fruits dispersed by forest elephants, it is likely that it is not sufficient to capture fruits that have evolved for dispersal by all megaherbivores both extant and extinct. For this reason, we made use of their definition but also examined the flora more widely looking at candidate megafaunal fruit to give a first appraisal of how well the operational definition fits in a savanna context.

Having identified the megafaunal fruit, we examine characteristics of these fruit and assess how they differ from other vertebrate-dispersed fruit. In addition, we examine the patterns underlying their distribution by considering two factors. The first is the historical distribution of their putative dispersers. Historical distribution data are based on records of megaherbivore skeletal remains, historical sightings, and written records left by early European travellers, naturalists and hunters. The second factor is the environmental conditions for the trees. Here, we explore the frequency and reach of megafaunal fruit across the South African biomes and along major environmental gradients such as precipitation and temperature. We examine these two factors to elucidate which best predicts where they occur.

MATERIAL AND METHODS

CLASSIFICATION OF MEGAFANAUNAL FRUIT

We constructed a comprehensive database of all South African trees species ($N = 1126$) from information obtained in Coates Palgrave (2002). Gaps were filled by information sourced from the South African National Biodiversity Institute's plant information website, the Royal Botanic Gardens Kew Seed Information Database (SID, 2019) and the JStor Global Plants database (2013), in addition to an extensive literature review (Supplementary Reference List A). We adhered to the Coates Palgrave (2002) definition of a tree (a woody perennial plant that typically possesses a single stem or trunk,

bearing lateral branches at some distance from the ground) and we included only those tree species that had a South African tree number (Tree Tags, 2019). The database includes information on the taxonomy, morphology and ecology of each tree species. Fruits were classified as either dry or fleshy, and their diameter, length and width were recorded. Fruit size was taken to be the diameter of berries and drupes while for pods the length was used. Fruit colour at maturity was recorded as brown, grey, green, yellow–orange, white, red, purple–black, or other, in a similar manner to Janson (1983) but with the addition of the colour grey. Seed data included number per fruit, size and colour. Seed mass estimates were sourced from the Royal Botanic Gardens Kew Seed Information Database (SID, 2019; and references therein – Supplementary Reference List A). The fruiting phenology of the trees was also recorded.

Guimarães *et al.*'s (2008) operational definition of megafaunal fruit was then applied across all 1126 tree species. Large fruit (≥ 4 cm in diameter) were tagged and separated into two types: Type 1 consisted of fleshy fruit 4–10 cm in diameter with up to five large seeds, while Type 2 was made up of either fleshy or dry indehiscent fruit greater than 10 cm in diameter with numerous small seeds. We modified Guimarães *et al.*'s Type 2 definition to include dry indehiscent pods in keeping with Janzen & Martin's (1982) initial description of the megafaunal fruit syndrome in the dry lowland forests of Costa Rica. An additional Type 1b category was also created for those fleshy fruit that were 3–4 cm in diameter but possessed three or fewer seeds (seed mass > 5 g).

Differences in the frequency of fruit colour across vertebrate-dispersed (small to medium) and megafaunal-dispersed (large) tree species were analysed by means of chi-squared tables (χ^2 test). The criterion for statistical significance was set at $\alpha = 0.05$ (95% confidence).

PATTERNS UNDERLYING THE DISTRIBUTION OF MEGAFAUNAL FRUIT TYPE (MFFT) SPECIES

Historical megaherbivore distributions

To establish the historical distribution of the five South African megaherbivores (African savanna elephant, giraffe, white rhinoceros, black rhinoceros and hippopotamus), a database was constructed collating records of skeletal remains, historical sightings, indigenous art, and written records left by early European travellers, naturalists and hunters. For the Northern, Western and Eastern Cape provinces, the volumes of Skead *et al.* (2007, 2011) were used and every note on historical megaherbivore sightings since 1497 was recorded and assigned to a quarter

degree grid square. For the remainder of the country, records were taken directly from maps produced by Boshoff *et al.* (2016). The possibility that skeletal remains might have been moved from elsewhere was disregarded.

Tree species distribution data

Digital distribution data for each tree species was obtained from the National Herbarium Pretoria Computerised Information System (PRECIS). This electronic database system is an index of plant specimen records from across South African herbaria. The tree species in our database ($N = 1126$) were represented by 273 595 individual location records of which megafaunal fruit comprised 2048.

Environmental correlation data

To obtain information on the vegetation type and biome for each tree species, the location data points were spatially joined to Mucina & Rutherford's (2006) vegetation map layer through the linking of shape files in ArcView (3.1). This resulted in comprehensive species lists across each of Mucina & Rutherford's (2006) vegetation types and biomes.

To explore environmental correlates, species distribution models were produced in Maxent v.3.3.3k (Phillips *et al.*, 2006) for all species for which there were five or more occurrence records. The parameters in Maxent were set to a maximum number of 500 iterations, a regularization multiplier of 1, auto features and a convergence threshold of 0.00001. Four climatic variables, obtained from Worldclim (www.worldclim.org; Hijmans *et al.*, 2005), were used as predictors in the models: annual mean temperature (AMT), precipitation in the wettest quarter (PWQ), mean temperature of the coldest month (MTCM) and annual precipitation (AP). These predictor variable maps were resampled from 10- to 15-min spatial resolution to match the resolution of the occurrence data. Separate masks were applied to the predictor variable maps for the species with fleshy fruits and for the species with dry fruits, which delimited the regions from which the background records used by Maxent could be drawn. To produce the mask for the species with fleshy fruits, we selected grid cells that contained at least one occurrence record of any of the fleshy fruited species. A similar approach was used to produce the mask for the dry fruited species.

The percentage contribution of the variables for each model was collated for all the species in order to determine the potential importance of these variables for limiting the distributions of these species.

RESULTS

THE MEGAFALFAUNAL FRUIT OF SOUTH AFRICA

Of the 1126 South African tree species, 31 were identified as having megafaunal fruit (Table 1). Thirteen species fitted Guimarães *et al.*'s (2008) definition of Type 1 fruit. This included fruit of two species, *Schinziophyton rautanenii* and *Sclerocarya birrea* (called Type 1b, Table 1), that are only 3–4 cm in their maximum length but have particularly hard and heavy seeds (12.5 and 5.4 g respectively). Eighteen species fitted the Type 2 definition; seven of these are fleshy while the remaining 11 are dry (Table 1). A number of fleshy fruited species ($N = 11$) that are 4–10 cm in maximum length were rejected as megafaunal fruit species because their fruit contained more than five seeds. They included (Supporting Information, Table S1) *Rothmannia capensis*, *Rothmannia fischeri*, *Strychnos madagascariensis*, *Gardenia cornuta*, *Monodora junodii* and *Solanum aculeastrum* with sizeable fruits that deserve further study.

The majority (54.8%) of species with megafaunal fruit are found in four families – Mimosoideae (seven, 22.6%), Areceae (four, 12.9%), Strychnaceae (three, 9.7%) and Caesalpinoideae (three, 9.7%). In terms of frequency, however, megafaunal fruit appear most often in Chrysobalanaceae (1/1, 100%), Bombacaceae (1/1, 100%), Arecaceae (4/6, 66.7%) and Balanitaceae (2/3, 66.7%). Among these families, the genera represented by the largest numbers of megafaunal fruit species are *Acacia* (Mimosoideae), *Strychnos* (Strychnaceae), *Hyphaene* (Arecaceae) and *Balanites* (Balanitaceae).

Fruit ranged in size over an order of magnitude, from 35 mm in *Sclerocarya birrea* to 450 mm (up to a maximum of 900 mm) in *Kigelia africana* (Table 1, Fig. 1). Mean seed size for Type 1 fruit is 34 mm whereas for Type 2 it is 13 mm. Seeds of Type 2 fruits are larger than one might have expected; *Strychnos pungens*, for example, has more than five seeds each over 3 g in mass (SID, 2019; Fig. 2). For those species with data available, the majority of forms are either drupes (38.5%) or leguminous pods (42.3%) while berries (19.2%) represent the least likely form. With regard to fruiting phenology, there is little difference between the megafaunal-dispersed trees and those dispersed by smaller vertebrates (Fig. 3). *Schinziophyton rautanenii* fruits for only one month of the year while three of the palms (*Raphia australis*, *Hyphaene coriacea* and *Hyphaene petersiana*) fruit all year round. Megafaunal fruit are predominantly brown (53.3%), yellow–orange (26.7%) or green (10%) (Figs 1, 4). This is in stark contrast ($\chi^2 = 265$, $P < 0.05$, d.f. = 2, Fig. 4) to smaller vertebrate-dispersed fruit that are for the most part purple–black (31.7%) or red (24.4%).

DISTRIBUTION OF MEGAFALFAUNAL FRUIT

Megafaunal fruit tree species occur almost exclusively in the northern half of the country, which falls into Africa's tropical climatic zone (Fig. 5). When separated into fleshy and dry fruit, unmistakable patterns emerge. The fleshy fruit hotspot is situated on the north-eastern border of South Africa and extends down the eastern coastline. In contrast, the dry fruit hotspot (Fig. 5) is located along the north central border of South Africa west of the fleshy fruit hotspot.

THE HISTORICAL DISTRIBUTION OF MEGAHERBIVORES

The historical distribution of megaherbivores in South Africa is indicated in Figure 6. It appears that elephants, black rhinoceros and hippopotamus have at one time or another occurred over much of South Africa. However, there is a clustering of historical elephant, black rhinoceros and hippopotamus occurrence along the east coast in the Albany Thicket and of elephants in the Indian Ocean Coastal Belt Biome (Fig. 6). This result should be treated with some caution as the available information is not systematic and distribution gaps may be the product of a lack of information and/or unreliable historical records. Analysis of Skead's record collection indicates that historical elephant herds were large – up to 450 animals being sighted in the Bushman's River region of the Eastern Cape.

DISTRIBUTION OF MEGAFALFAUNAL FRUIT TREE SPECIES ALONG MAJOR ENVIRONMENTAL GRADIENTS

Most megafaunal fruit species occur in the Savanna biome (Fig. 5) with 29 of the 31 tree species (93.5%). However, megafaunal fruit species generally represent a very small proportion of the dispersal spectra in all biomes (1–5%; Supporting Information, Table S2). Even in the Savanna biome megafaunal fruit dispersal only occurs in 3% (29 of 846) of tree species. This is in stark contrast to the 54% (460 of 846) of trees that rely on small to medium-sized vertebrates for the dispersal of their fruits (Table S2).

When split into dry and fleshy megafaunal fruit our model predicts that it is the minimum temperature in the coldest month (MTCM) that is most important factor limiting the distribution of dry-fruited species whereas annual precipitation (AP) is the important factor limiting the distribution of fleshy-fruited species (Fig. 7).

DISCUSSION

THE MEGAFALFAUNAL FRUIT OF SOUTH AFRICA AND THE PATTERNS UNDERLYING THEIR DISTRIBUTION

This study provides the first comprehensive list of megafaunal fruit tree species for South Africa and,

Table 1. The megafaunal fruit tree species of South Africa

Family	Megafaunal species/family	Mega-faunal type	Species	Fruit type	Size of fruit (mm)	Number of seeds	Size of the seed (mm)	Seed mass
Arecaceae	4 (6)	Type I	<i>Raphia australis</i>	Drupe	90	1	–	–
		Type I	<i>Hyphaene petersiana</i>	Drupe	50	1	50	21 500
		Type I	<i>Hyphaene coriacea</i>	Drupe	50	1	50	–
Balanitaceae	2(3)	Type I	<i>Borassus aethiopicum</i>	Berry	150	3	–	–
		Type I	<i>Balanites aegyptiaca</i>	Drupe	50	1	50	1150
		Type I	<i>Balanites maughamii</i>	Drupe	50	1	50	827
Boraginaceae	1(9)	Type I	<i>Cordia grandicalyx</i>	Drupe	40	1	–	–
Chrysobalanaceae	1(1)	Type I	<i>Parinari curatellifolia</i>	Drupe	50	1	27	3315
Papilionoideae	1(56)	Type I	<i>Cordyla africana</i>	Drupe	80	1–3	32	10 000
Sapotaceae	2(15)	Type I	<i>Mimusops zeyheri</i>	Berry	45	1	18	291
		Type I	<i>Vitellariopsis marginata</i>	Berry	50	1–2	25	–
Euphorbiaceae	1(75)	Type Ib	<i>Schinziophyton rautanenii</i>	Drupe	35	1	20	12 500
Anacardiaceae	1 (59)	Type Ib	<i>Sclerocarya birrea</i>	Drupe	35	2–3	15	5405
Rubiaceae	1 (89)	Type II	<i>Gardenia volkensii</i>	Drupe	100	Numerous	10	24
Strychnaceae	3 (10)	Type II	<i>Strychnos cocculoides</i>	Berry	100	Numerous	22	476
		Type II	<i>Strychnos spinosa</i>	Berry	120	Numerous	–	377
		Type II	<i>Strychnos pungens</i>	Berry	120	Numerous	27	3286
Bombacaceae	1(1)	Type II	<i>Adansonia digitata</i>	Berry	240	Numerous	10	478
Bignoniaceae	1(8)	Type II	<i>Kigelia africana</i>	Berry	675	125	10	125
Capparaceae	1(26)	Type II	<i>Cladostemon kirkkii</i>	Berry	220	Numerous	13	–
Mimosoideae	7(67)	Type II dry	<i>Faidherbia albida</i>	Pod	250	Numerous	11	110
		Type II dry	<i>Acacia erioloba</i>	Pod	130	18	14	251
		Type II dry	<i>Acacia sieberiana</i>	Pod	210	Numerous	12	129
		Type II dry	<i>Acacia nilotica</i>	Pod	125	Numerous	9	127
		Type II dry	<i>Acacia haematoxylon</i>	Pod	140	Numerous	11	500
		Type II dry	<i>Amblygonocarpus andongensis</i>	Pod	170	Numerous	–	–
Caesalpinoideae	3(33)	Type II dry	<i>Dichrostachys cinerea</i>	Pod	100	Numerous	6	26
		Type II dry	<i>Piliostigma thonningii</i>	Pod	220	Numerous	9	138
		Type II dry	<i>Tamarindus indica</i>	Pod	140	6–12	17	542
Papilionoideae	1(56)	Type II dry	<i>Cassia abbreviata</i>	Pod	900	Numerous	12	357
		Type II dry	<i>Swartzia madagascariensis</i>	Pod	300	Numerous	8	105

The fruit are separated into type according to Guimaraes *et al.* (2008). Type 1 consists of fleshy fruit 4–10 cm in diameter with up to five large seeds. A subset to Type 1 (b) was created for those fleshy fruit that were 3–4 cm in diameter but possess large seeds (seed mass > 5 g). Type 2 is made up of either fleshy or dry fruit greater than 10 cm in their length with numerous small seeds (where dry these fruit are also required to be indehiscent). Megafaunal species/family is the total number of identified and listed megafaunal species and (in parentheses) the total number of species per family. With regard to fruit and seed traits: fruit size is the maximum dimension (diameter or length); seed size and seed number were taken from the Jstor Plant Database (2013). Seed mass (g) is per seed and was taken from the Kew Seed Database (Royal Botanic Gardens Kew, 2019). Species name are as per Coates Palgrave (2002). The changes in the genus *Acacia*, with the exception of *Faidherbia*, are not recognized here.

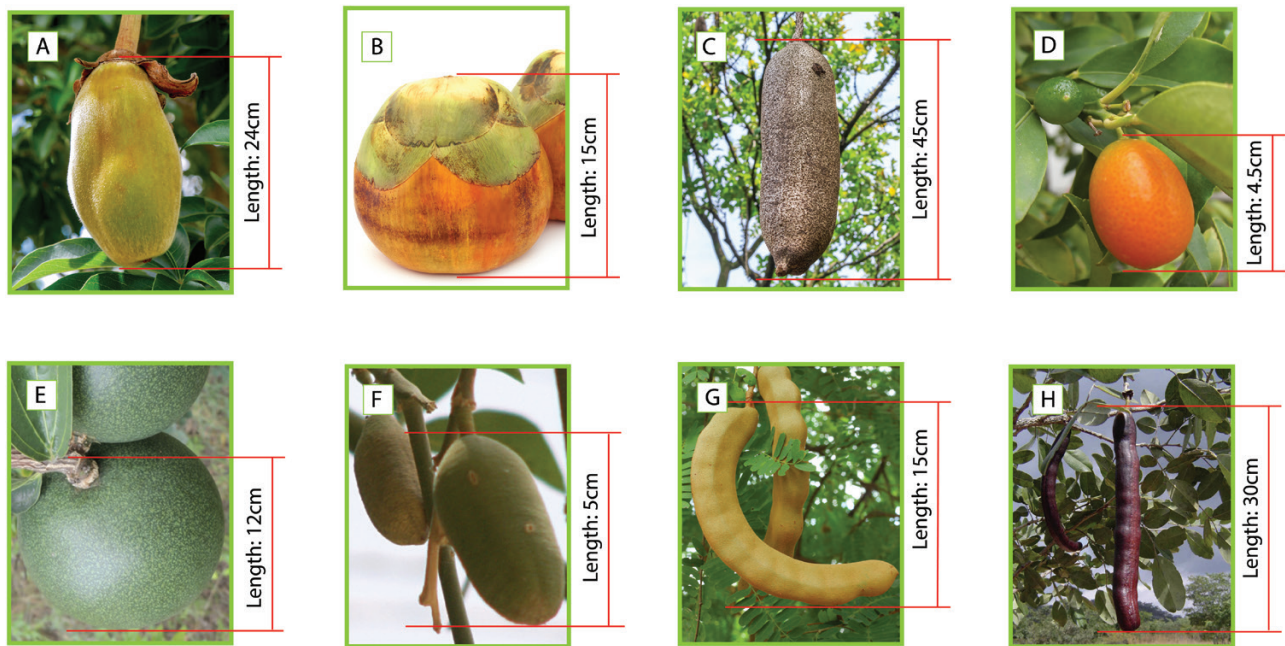


Figure 1. A selection of fleshy and dry fruited megafaunal species from South Africa depicting their size, shape and colour variability. A., *Adansonia digitata*, Bombacaceae; B, *Borassus aethiopum*, Arecaceae; C, *Kigelia africana*, Bignoniaceae; D, *Mimosops zeyheri*, Sapotaceae; E, *Strychnos spinosa*, Strychnaceae; F, *Balanites aegyptiaca*, Balanitaceae; G, *Tamarindus indica*, Caesalpinoideae; H, *Swartzia madagascariensis*, Papilionoideae. Fruit length is indicated.

indeed, for the African savanna landscape at large. Of the 1126 tree species found in South Africa, only 31 were identified as having megafaunal fruit. Thus, megafaunal fruit trees represent just 2.8% of the total tree dispersal spectra and 4% of the vertebrate-dispersed tree species. The paucity of megafaunal fruit tree species was unexpected, particularly relative to the Neotropics where Donatti *et al.* (2007) reported that 13% of the fleshy-fruited species in the lowland Atlantic rainforest ($N = 246$) and 30% of species in the Pantanal ($N = 147$ species) were considered to have once been dispersed by megaherbivores.

From a phylogenetic perspective, megafaunal fruit trees are restricted to a few angiosperm families, most frequently occurring in Chrysobalanaceae, Bombacaceae, Arecaceae and Balanitaceae. These and several other megafaunal fruit families are tropical in origin. Southern Africa's flora is in part derived from a tropical African forest flora but for the most part from an ancient southern African temperate flora (Linder & Verboom, 2015). The flora began to evolve in the early to mid-Tertiary (~65 Mya) at the southern edge of the tropics as Africa became increasingly drier. The fact that the majority of the megafaunal fruit tree species belong to tropical clades suggests that the abiotic conditions that characterize the Palaeotropics have to some extent underpinned the evolution of large fruit and seeds.

Further weight is given to this idea when one considers that there appears to be no correlation between the historical distribution of megaherbivores and that of megafaunal fruits. In the past – at one time or another – megaherbivores occurred over much of what is now South Africa, including the arid north-western parts. Elephants, for which the most data are available, appear to have been particularly common in the coastal and sub-coastal regions of the Eastern Cape and especially within the Albany Thicket Biome (Skead, 2007, 2011). Megafaunal fruit, in contrast, occur in their smallest numbers in the Albany Thicket and Desert Biome (Supporting Information, Table S2).

Megafaunal fruit tree species in South Africa occur in a narrow northerly band that runs along the edge of the tropics ($23^{\circ}26'16''S$) and then southwards along the eastern coastline. This region coincides with the savanna biome, which is the centre of distribution of megafaunal fruit tree species. The biome includes forest patches that are too small to be considered separately at the biome scale (as mapped by Mucina & Rutherford, 2006). Differences in the distribution of megafaunal fruit across closed forest vs. open sunlit savannas is therefore not evident in this study but warrants investigation. Within the savanna biome, fruit type varies from west to east along the precipitation gradient. The majority of the dry megafaunal fruits are found in the arid western savannas while fleshy

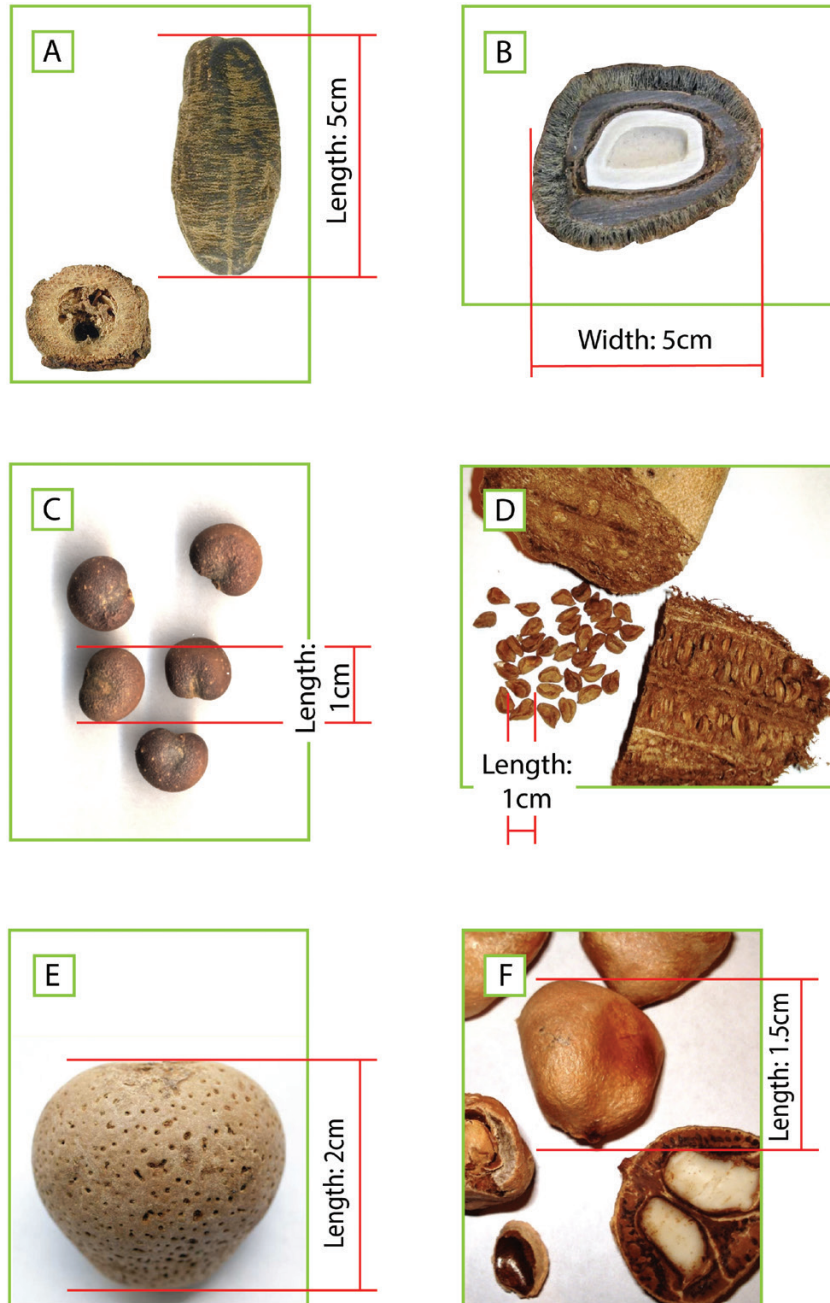


Figure 2. Examples of seeds of megafaunal fruits. A, *Balanites maughamii*; B, *Hyphaene coriacea*; C, *Adansonia digitata*; D, *Kigelia africana*; E, *Schinziophyton rautanenii*; F, *Sclerocarya birrea*.

megafaunal fruits predominate in the wetter eastern savannas extending southwards into the Indian Ocean Coastal Belt biome, a mosaic of savannas, grasslands and closed forests. These patterns further support the idea that the distribution of megafaunal fruit tree species in the region is determined more by climatic factors than by the presence of megaherbivores. Studies in more tropical regions north of South Africa

are needed to test whether megafaunal fruits are more common in lower latitudes.

HOW WELL DOES THE MFFT FRAMEWORK FIT?

MFFT species were identified by means of a framework developed by [Guimarães *et al.* \(2008\)](#) for analysing neotropical fruits and based on fruits consumed by

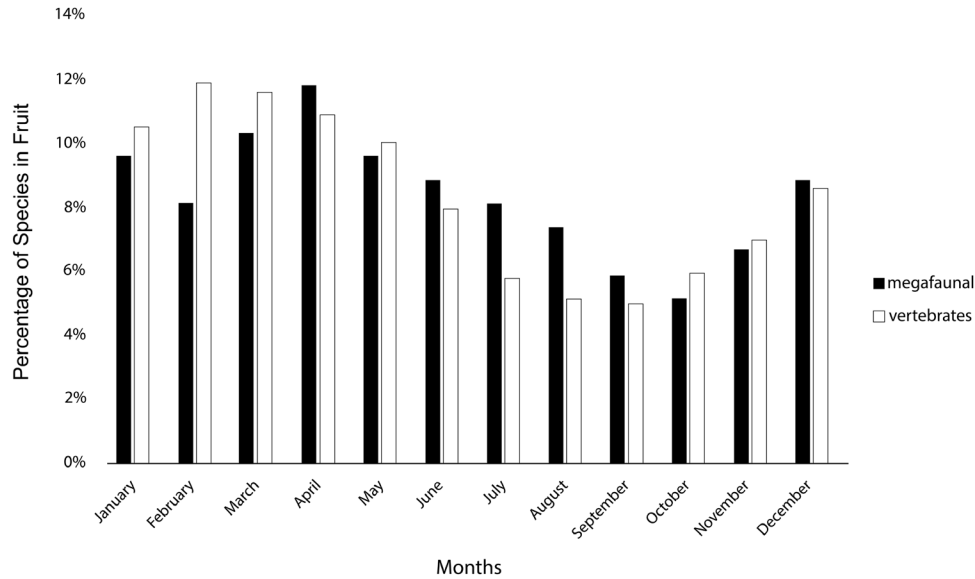


Figure 3. Fruiting phenology in smaller vertebrate-dispersed (black bars, $N = 536$) and megafaunal fruit trees (white bars, $N = 30$).

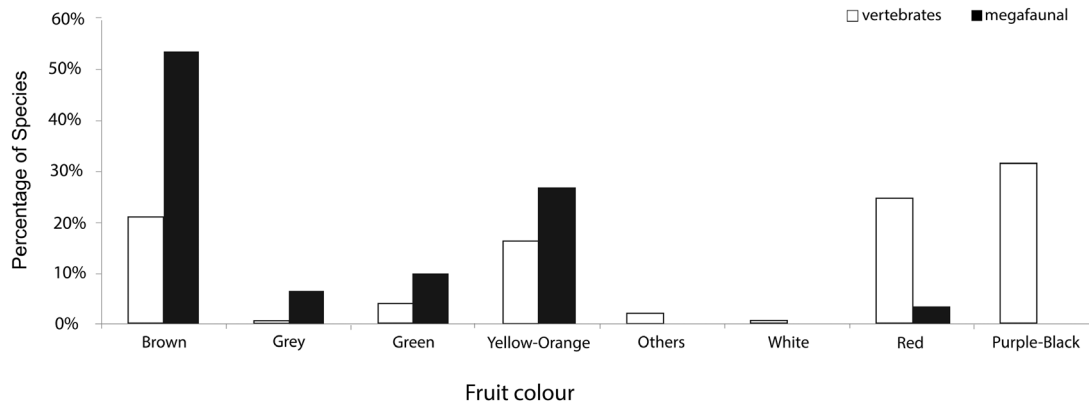


Figure 4. Fruit colour in both smaller vertebrate-dispersed (black bars, $N = 536$) and megafaunal fruits (white bars, $N = 30$). To explore the statistical difference between the two disperser classes, colour categories were combined into 'brown/grey/green', 'yellow–orange' and 'red/purple–black' as some contained cell expected values <5 ; 'other' and 'white' were excluded from the analysis. Colour categories are significantly different for the two disperser classes ($\chi^2 = 265$, $df = 2$, $P < 0.05$ or more). *Fruit colour data were missing for the megafaunal species *Ochna glauca*.

African forest elephants. This framework provided a useful set of starting criteria by which to identify megafaunal fruit tree species. MFFT species resembled those in African forests and in the Pantanal in South America in terms of their size and colour. The finding that megafaunal fruits in African savannas are dull coloured is not surprising as elephant, rhinoceros, hippopotamus and giraffe all have limited colour vision, seeing only in two colours (dichromatic) – blue and green (Jacobs, 2004).

The MFFT definition failed to account for the large (>10 cm in length) dry indehiscent pods that have unmistakably evolved alongside large vertebrates. We

modified the definition at the outset to include these pods (as Type 2b). Indeed, it was the dry indehiscent pods of *Cassia grandis* that first caught Janzen's attention when he explored the dry lowland forests of Costa Rica in the 1970s and upon these pods that the idea of the megafaunal syndrome was first developed.

In addition, there are at least 11 of the fruit species that did not fit the criteria, based on the number of seeds they contain, that are likely to be megafaunal fruit tree candidates. They include *Gardenia* species, which are thought to rely on elephants and buffalo for their dispersal, with hard endocarps that are difficult to crack open with a hammer (e.g. *Gardenia thunbergia*).

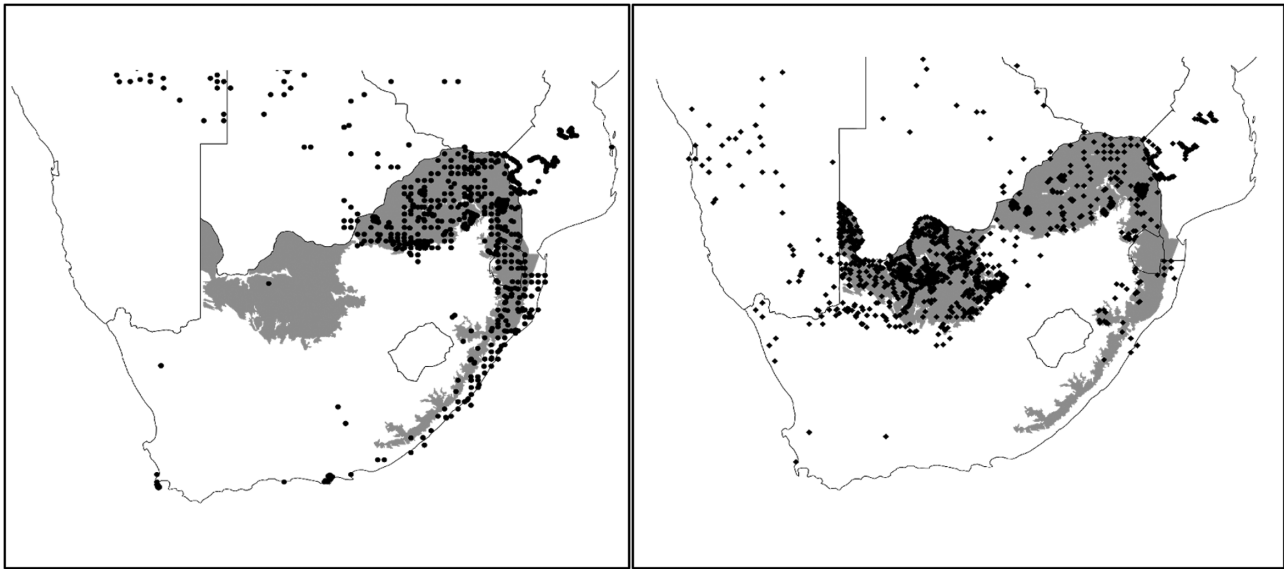


Figure 5. Distribution of fleshy (left) ($N = 20$) vs. dry (right) ($N = 11$) megafaunal fruit relative to the distribution of the Savanna biome (overlaid in grey). Distribution data were derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. The extent of the Savanna biome is given as per [Mucina & Rutherford \(2006\)](#).

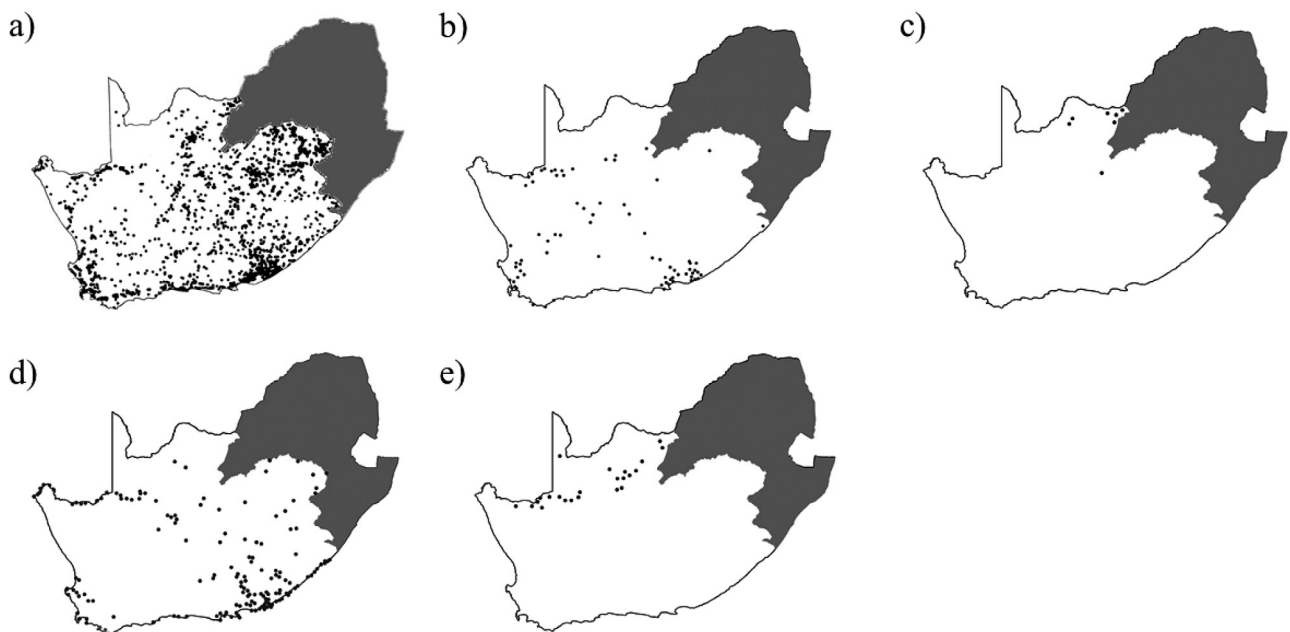


Figure 6. The historical distribution of (A) elephants, (B) black rhinoceros, (C) white rhinoceros, (D) hippopotamus and (E) giraffe in South Africa (adapted in part from [Boshoff *et al.*, 2016](#)). Occurrences include finds of skeletal remains, historical sightings and presence of indigenous art depicting elephants. The area in grey indicates where megaherbivore distribution records have not yet been collated.

From our study, we suggest that fruits greater than 4 cm that possess a hard exocarp or endocarp should be considered candidate megafaunal fruits. The dispersal of these fruits needs exploration. The MFFT framework requires more rigorous testing to ascertain its relevance in an African savanna context.

THE SERVICE MEGAHERBIVORES OFFER MFFT SPECIES

Owing to their size and behaviour, megaherbivores may form a unique functional group with regard to the dispersal service they offer MFFT species ([Sekar & Sukumar, 2013](#), [Sridhara *et al.*, 2016](#)). First,

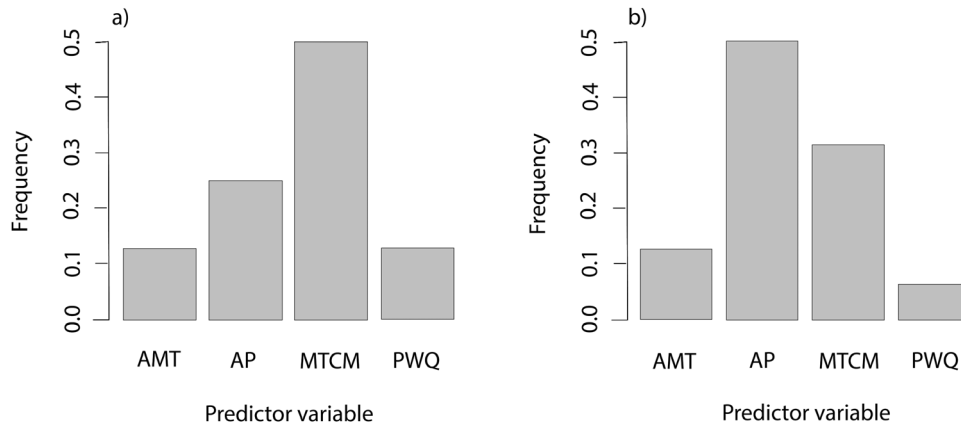


Figure 7. The relative frequency with which each of the variables had the highest rank in percentage contribution in the models for (A) dry fruited species and (B) fleshy fruited species. AMT = annual mean temperature; AP = annual precipitation; PWQ = precipitation in the wettest quarter and MTCM = mean temperature of the coldest month.

megaherbivores generally have large home-ranges and make long foraging treks with them (Owen-Smith, 1988). Elephants in the Kalahari Sands, for example, travel 20–50 km or more in daily foraging treks within home ranges of 900–3000 km (Conybeare, 1991). Within South Africa, we found that savanna elephants are capable of moving seeds in excess of 65 km from their parent tree (Bunney *et al.*, 2017). Furthermore, giraffe bulls are known to make long-distance movements, in excess of 50 km, between river systems (Fennessy, 2004, 2009). Even hippopotamus have been found to move up to 10 km away from their river territory in a single night (Estes, 1992). Second, megaherbivores have long seed retention times. Savanna elephants retain the seeds of megafaunal fruit for up to 96 h (Bunney *et al.*, 2017). It is likely that the white and black rhinoceros have especially long seed retention times given that the Indian one-horned rhinoceros (*Rhinoceros unicornis*) has a maximum gut passage time of 172 h (7 days; Dinerstein & Wemmer, 1988). Finally, megaherbivores have very large gape sizes. Elephants, for example, consume fruit up to 36 cm in diameter, whole (Yumoto *et al.*, 1995).

Unfortunately, very little work has been done on vertebrate seed dispersal in African savannas. What we know of African megaherbivore seed dispersal is based on a few studies (see Supporting Information, Table S3) from savannas across the continent. Of the MFFT species identified in this study, 16 (of 31, 52%) are known to be dispersed by elephants (Table S3). A particularly comprehensive study by Dudley (2000) in Hwange National Park, Zimbabwe, highlighted three of our MFFT species that are transported as seeds in vast quantities by savanna elephants. Dudley (2000) found one dung pile containing over 5000 *Acacia erioloba* seeds and another that contained nearly 400 *Schinziophyton rautanenii* seeds (2.8 kg worth in dry

weight and each approx. 2 cm in length; Table S3). In addition, Dudley (2000) found that on average one elephant in Hwange National Park is responsible for transporting approx. 3500 *Acacia erioloba* seeds, 500 *Schinziophyton rautanenii* seeds and 125 *Sclerocarya birrea* seeds per day.

Black rhinoceros, white rhinoceros and giraffes have a penchant for dry indehiscent fruit, consuming large quantities of *Acacia* pods (Hofman, 1973; Miller & Coe, 1993, 1994). Dry megafaunal fruit, although consumed by a suite of other vertebrates, might prove highly reliant on megafauna for escaping seed predators (Dinerstein & Wemmer, 1988; Fragoso, 1997). Most pods that are consumed after having fallen are typically highly infested by bruchids (Miller & Coe, 1993; Gonthier, 2009). Those that are consumed directly from the tree by megaherbivores showed low predation by bruchids in comparison and have markedly higher rates of germination (Miller & Coe, 1993). Hippopotamus and rhinoceros consume the fruit of the enigmatic sausage-tree *Kigelia africana* (Dierenfeld *et al.*, 1995; Gonthier, 2009).

THE ROLE OF PRIMATES IN MEGAFANAL FRUIT DISPERSAL IN AFRICAN SAVANNAS

Many of the megafaunal fruit identified in this study are undoubtedly also dispersed by animals other than elephants. The evolution and fate of MFFT species in Africa is likely to differ from those in the Americas as they have been moulded through evolutionary interactions with a divergent fauna. First, the presence of ground-dwelling primates sets Africa apart from the Americas. Human and non-human primates have coexisted with megafauna in the African landscape for millennia. The role that early hominins played in shaping the current distribution

of megafaunal fruit and the characteristics of the fruit themselves has not, as far as we are aware, been investigated. Seed dispersal by baboons, an extant African ground-dwelling savanna primate, has been extensively researched in the savanna–forest mosaics of West Africa (olive baboon – Kunz & Linsenmair, 2010); in the savannas of East Africa (yellow baboon – Dunbar & Dunbar, 1974; Barton *et al.*, 1993) and in the Namibian desert (chacma baboon – Hamilton, 1985). Very little is known about fruit selection by baboons in the South African savannas (Codron *et al.*, 2006). Studies in West and East Africa (Dunbar & Dunbar, 1974; Kunz & Linsenmair, 2010) found that a disproportionate number of the fruit species consumed by baboons were of medium or large size. In addition, they found that baboons fed on both fleshy and dry-fruited species according to their availability in the plant species pool. Finally, and of significance, they found that baboons tended to act as seed predators when fruit were dry, the seeds were large and, when baboons fed on the pulp of fleshy fruits with large seeds, the seeds were usually dropped rather than swallowed (Kunz & Linsenmair, 2010). Medium- and large-sized fruit with small to medium-sized seeds, on the other hand, were in most instances swallowed and effectively dispersed (Kunz & Linsenmair, 2010).

From these studies the dispersal service that baboons and by extension early hominins (Jolly, 2001) offer to megafaunal fruit is highly variable – baboons act as either effective dispersers or potent predators depending on the fruit species in question. We might therefore expect that the fate of megafaunal fruits in Africa is likely to differ from that in the Americas, if megaherbivores are lost from an area.

THE ROLE OF MESOFAUNA IN MEGAFANAL FRUIT DISPERSAL IN AFRICAN SAVANNAS

Another important difference between the palaeotropics and the neotropics lies in the diversity and abundance of the mesofauna. Approximately 60% of bovid genera (26 of 45) occur on the African continent (Gagnon & Chew, 2000). The body mass of African bovids ranges from the 2-kg royal antelope (*Neotragus moschatus*) to the African buffalo (*Syncerus caffer*), which weighs up to 900 kg (Nowak, 1991). The proportion of the bovid diet composed of fruit varies a great deal. Small bovids such as the duiker (Cephalophini), with the exception of *Sylvicapra*, are highly frugivorous. By contrast, larger species of bovid such as the eland (*Taurotragus*) and wildebeest (*Connochaetes*) have a diet composed of approximately 5% fruit. Although primarily grazers, wildebeest are very abundant and tend to dominate their ecosystems (Cumming, 1982; McNaughton & Georgiadis, 1986) so that the number of fruits they

consume, even though a small part of their diet, is likely to be appreciable.

Africa and America possess highly divergent functional seed disperser guilds. These distinct features of the fauna need to be taken into consideration when exploring the evolution of large fruit and when estimating the impact of mammal extirpation. There is clearly enormous scope for disperser studies in Africa that will help to both define and refine the distinctive role of megafauna in fruit dispersal and the consequences for plant species of extinction and extirpation of their dispersal partners.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. List of fleshy fruited species (4–10 cm in maximum length) that were rejected from the megafaunal list on the basis that their fruit contained more than five seeds.

Table S2. Megafaunal fruit tree species distributions across biomes. For comparative purposes, the numbers of smaller-vertebrate-dispersed species are also listed. For both the smaller-vertebrate-dispersed species and the megafauna-dispersed species the actual numbers of tree species are given with the percentage of the total number of species found in the biome in parentheses. The biomes are as mapped in [Mucina & Rutherford \(2006\)](#). Forests are generally too small to be mapped and tree species confined to forests are listed in the larger biomes containing forest patches.

Table S3. Megafaunal fruit tree species and the megafauna that are known to consume and disperse their seeds. The highlighted gaps indicate where there is no formal documentation of its consumption or dispersal by any of the five megaherbivore species present in the South African savanna (elephant, white rhinoceros, black rhinoceros, hippopotamus and giraffe) **Hyphaene petersiana* in the study by [Dudley \(2000\)](#) is referred to by its former name *H. benguellensis*.