Seed Dispersal in South African Trees:

with a focus on the megafaunal fruit and their dispersal agents

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Preface

I know the meaning of Plagarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

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CHAPTER 1

General Introduction

Seed dispersal is a key process. It is important in plant population biology because it influences the fate of seeds and the probability of recruitment, in plant biogeography since dispersal mode can influence the distribution range and rate of response to environmental change and habitat fragmentation, and in animal ecology since fruits can be an important dietary item (Wang and Smith, 2002). The majority of trees in the tropics (70 – 90%) and a large proportion of trees in temperate regions (up to 60%) rely on vertebrates for their dispersal (Howe and Smallwood, 1982; Fleming *et al.*, 1987, Willson, 1990). Vertebrate dispersers range in size from 5g mistletoe birds (*Dicaeidae*) to 7,500,000g elephants (*Elephantidae*). The range and distribution of frugivore sizes is not uniform across ecosystems or geographical regions (Mack, 1993). These differences, one might suspect would be mirrored in the range and distribution of fruit size. This is not the case; in South America where the largest frugivorous mammal is the tapir (300kg; Hansen and Galetti, 2009), there is a subset of fruit that are conspicuously large. The paradoxical existence of such large fruit in the lowlands of Costa Rica was first noted by Janzen. In collaboration with Pleistocene faunal expert Paul Martin they conjectured that these fruit were ecological anachronisms that had evolved in the presence of large terrestrial vertebrates (>1000kg - megafauna) but had remained long after their demise (Janzen and Martin, 1982).

The demise of these large vertebrates (megafauna) was brought about by a series of extinction events during, and at the end of, the Pleistocene from ~50 thousand to ~10 thousand years ago. The large vertebrate communities of Europe, non-tropical Asia, Australia and the Americas vanished in their entirety and with them the dispersal services they offered megafaunal fruit (Martin, 1984; Barlow, 2000). On these 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. Guimares *et al.* (2008) tested for the existence of these ‘overbuilt’ fruit in Brazil, by identifying fruit traits of African elephant fruit and mapping these traits onto a database of fruit traits over a broad selection of vegetation types. This approach identified 103 species matching elephant-dispersed African fruit. Megafaunal fruit species were found to be well represented in certain plant communities, such as the Pantanal - the world’s largest freshwater wetland - in which 30 per cent of fleshy-fruited tree species have fruit with megafaunal characteristics. Guimares *et al*. (2008) suggested that in the Pantanal, seasonal flooding acted as a surrogate for dispersal by megafauna. Trees with megafaunal fruit in Central and North America are typically restricted to lowlands and flood plains, reflecting their current reliance on gravity and water for the movement of their seeds (Janzen and Martin 1982; Barlow 2000). Donatti *et al.* (2007) noted that a disproportionate number of these megafaunal fruit tree species showed a high capacity for vegetative propagation or vigorous resprouting, were long-lived or were able to establish beneath the parent plant. It is probable that local populations persist largely as a result of these traits, while megafaunal fruit species that lacked them slipped into extinction (Johnson, 2009). Regrettably, the plant fossil record is largely incomplete and little is known of what has already been lost (Barlow, 2000). One exception is the large-fruited genus of *Maclura*, a wind-pollinated tree genus that is known from pollen samples to have been widespread during the Pleistocene and has since declined from several species to a single narrowly distributed survivor species, the Osage orange - *Maclura pomifera* (Barlow 2000). These findings suggest that, on many continents vegetation communities are in a process of long-term unwinding from a megafaunal-adapted to a 'megafaunal-naive' state (Johnson, 2009).

While the era of large vertebrates might have seen its end on most continents, Africa and small patches of tropical Asia remain the exception (Barlow, 2001). Five genera of Africa's megafaunal community (*Ceratotherium, Diceros, Giraffa, Hippopotamus*, and *Loxodonta)* still exist (Owen-Smith, 1988/9) while two genera (*Elephas* and *Rhinoceros*) remain in Asia. An understanding of large vertebrate-fruit relations in Africa and Asia is thus imperative to both our comprehension of extinct interactions and to the conservation of extant interactions.

The majority of previous African elephant seed dispersal studies have focused on forest elephants. These studies have firmly established elephants as forest gardeners, consuming more seeds from more species than any other taxon of large vertebrate disperser (Campos-Arceiz and Blake, 2011). Of these forest elephant studies two (Feer, 1995 and Blake, 2009) focused on the service forest elephants provide to megafaunal fruit species and identified at least 14 woody species *(e.g. Cola spp*., *Tieghemella heckelii,* and *Balanites wilsoniana)* that they thought relied exclusively on elephants for their dispersal. To my knowledge, the megafaunal fruits of the African savanna have not yet been catalogued. By means of constructing a comprehensive database of all South African tree species, this study attempts to develop a list of purported megafaunal fruit species. In addition, so as to establish the abundance and distribution of the megafaunal component relative to other means of dispersal, a tree dispersal spectrum for South Africa is constructed. The factors that underlie the distribution of megafaunal fruit are also explored. Firstly, the historical spread of elephants relative to that of the megafaunal fruits is compared. The relationship between the distribution of an extant, or recently extirpated megaherbivore and the plants thought to be dispersed by it can only be tested in areas with intact megafaunal populations and a historical record set. Secondly, the distribution of megafaunal fruit along major environmental gradients such as precipitation; soil fertility and temperature, is examined in an attempt to elucidate which factors best predict where they are found. Lastly, the service that terrestrial primates (baboons and hominids) provide megafaunal fruit is explored. The evolution of megafaunal fruit in the African savanna cannot be examined without some consideration of the large primates that have, for millennia, inhabited this continent alongside large vertebrates. Terrestrial primates are unique to Africa and their presence has almost certainly had an effect on the dispersal spectra.

The final part of this study shifts focus from the megafaunal fruit to the savanna elephant that provides the dispersal service. African savanna elephants are thought to be particularly effective seed dispersers (Campos-Arceiz and Blake, 2011). They are found in a wide variety of habitats, including savanna, grassy plains, miombo woodlands and forests, Sahelian scrub, swamps, bushlands and even deserts (IUCN, 2013 and Burnie, 2001). They consume and defecate large quantities of seed (an average of 228 woody plant seeds per defecation - Dudley, 2000), have long gut passage times (up to 53 hours – Davis, 2008) and large home ranges (up to 3000km in the Kalahari Sands, Southern Africa - Conybeare, 1991) potentially allowing for seed dispersal distances over several kilometres. Despite their apparent significance, to my knowledge no study has attempted to quantify the dispersal services provided by African savanna elephants. Using 8 years of elephant movement data coupled with gut passage rates for large fruits, this study presents the first dispersal kernel for the African savanna elephant.

Drivers of the ongoing extinction crisis put large animal species at inordinate risk (Duffy *et al*., 2009). Understanding the magnitude of the service savanna elephants provide megafaunal fruit is essential to plant conservation and to assessing the resilience of the savanna ecosystem to the loss of megaherbivores (Sekar and Sukumar, 2013).

In summary, this thesis examines the seed dispersal spectra of South African trees in general and the megafaunal fruit component in particular. For species with megafaunal fruits, I explored their distribution and abundance in relation to both biotic factors and physical environmental variables. I then studied the services provided to megafaunal fruit by one large vertebrate, the African savanna elephant, so as to provide an indication of the potential effects of the loss of elephants from African landscapes.

The different components of my study and the questions addressed are organised into four chapters as follows:

Chapter 2

In this chapter I explore general dispersal spectra for South African tree species. I wished to know:

- How does the tree dispersal spectrum vary across South African biomes and bioregions?
- If there is variation then is this related to the position of these biomes along major environmental gradients?
- What, if any, are the differences in dispersal spectra between South Africa, Australia and South America?

Chapter 3

Here I consider fruits that appear to be specialised for megaherbivore dispersal. There are too few studies of dispersal of putative megafaunal fruits in the African savannas to identify fruit characteristics from observed interactions of a significant sample of tree species. Instead I used criteria to identify such species developed for South American plant species where the megafauna is extinct. Using the list of South African species with putative 'megafaunal fruits' I explored three hypotheses that might account for their geographic distribution, namely:

- the historical spread of megafauna
- the environmental conditions that support their existence
- the service that elephants and baboons (as a proxy for early humans) provide and how this might have affected their evolution.

I focused on the elephant as the most likely candidate for a megafaunal fruit disperser. However, I also considered baboons as a distinctly African alternative dispersal agent to identify likely overlap.

Chapter 4

In this chapter, I describe the seed shadow created by elephant dispersal to help quantify their potential as long distance dispersal agents. To do so, I combined information from feeding trials conducted on sanctuary elephants with field telemetry data from collared elephants, collected over an 8-year period in Timbavati/KNP.

I wished to know:

- the capacity of elephants to disperse the seeds from different types of megafaunal fruits
- the distances over which they disperse these seeds.

Chapter 5.

In the final chapter I summarise the findings and discuss their relevance for extant populations of megaherbivores in particular elephants, and their megafaunal fruit counterparts. I consider the consequences of elephant extirpation and present a number of research areas that I think deserve consideration.

Chapters are written as discrete units to facilitate publication. Consequently each chapter has its own introduction and literature review resulting in some repetition among chapters. .

CHAPTER 2

The seed dispersal spectrum of South African trees:

distribution patterns and a cross-continental comparison

Introduction

Seed dispersal links the end of the reproductive cycle of adult plants with the establishment of their offspring and so represents a critical process in the life history of plants. Seed dispersal dynamics influence plant processes ranging from the colonisation of new habitats to the maintenance of diversity (Nathan and Muller-Landau, 2000; Wang and Smith, 2002; Thorsen, 2010). The spatial pattern of dispersal thus provides a blueprint upon which biotic communities develop (Schupp and Fuentes, 2000 in Thorsen, 2010). The plant reproductive traits that determine this spatial pattern are under strong selective pressure to maximise fitness and over time, this selection has resulted in the diaspores of numerous seed plants displaying characteristic morphological features that associate them with a particular dispersal method; wings, plumes and balloons with wind-dispersal; elaiosomes with ant-dispersal; fleshy fruit and arils with internal vertebrate-dispersal; hooks, barbs and viscous material with attachment on animal exteriors while explosive fruits are indicative of ballistic-dispersal (van der Pijl 1982; Howe and Smallwood, 1982).

The frequency of these different dispersal adaptations within a plant community is known as the dispersal spectrum (Howe and Smallwood, 1982; Primack, 1987 and Thorsen, 2010). Dispersal spectra are thought to be the result of a complex interplay between plant species attributes such as growth form and height, phylogeny and characteristics of the physical environment in which that plant community occurs (Butler *et al*., 2007). Disentangling the relative contributions of these two attributes sets is difficult and has led to a divergence in findings. One set of authors (Herrera and Pellmyr, 2002; Willson *et al*., 1990 and Thorsen, 2010) examined the dispersal spectra of plant communities, composed of a multitude of growth forms, along major environmental gradients such as precipitation, temperature and soil fertility. These authors found that a number of dispersal mechanisms varied considerably across different environmental regions. In Australia, for example, vertebrate and wind-dispersal increased in frequency along a soil fertility gradient. These authors considered growth form as a contributing factor in determining the dispersal spectra but did not determine it to be of principal importance. In contrast a second set of authors (Hughes *et al*., 1994 and Butler *et al*., 2007) investigated the interaction between dispersal mechanism, plant attributes and the physical environment and have argued that the relationship between physical conditions and the frequency of dispersal mechanism is of little consequence, and the patterns observed result from the indirect influence of plant growth form and seed size. By selecting to examine the dispersal spectra of only trees - here defined as woody perennial plants that typically possess a single stem or trunk (Coates Palgrave, 2002) - this study has essentially, controlled for the influence of plant growth form on dispersal mechanism, allowing for the effect of both phylogeny and the physical environment on the dispersal spectra to be clearly understood.

In southern Africa large latitudinal variation in climate exists, with the northern parts being tropical and the southern parts temperate. In addition, a strong precipitation gradient divides the sub-continent into a xeric western sector and a relatively mesic eastern sector (Rutherford and Westfall, 1986). 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 (Goldblatt, 1978).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. Despite both the presence of steep environmental gradients and the extraordinary diversity of plant species in southern Africa, only two studies have examined the geographical patterns of dispersal. The first, a study, by Knight (1984) attempted to search for broad patterns in the geographical distribution of fruit types in southern African trees. Knight (1984) found that most fruit types tended to cluster along both the latitudinal (tropical-temperate) and longitudinal (xeric –mesic) gradient. Pods and nuts proved the exception, with pods tending to align in only a latitudinal direction and nuts being numerous in both temperate and tropical xeric conditions. Knight (1984) concluded that strategies for dispersal based on morphological attributes are not uniform over the subcontinent. The second study by Milewski and Bond (1982) compared dispersal by ants in two fire-prone sclerophyllous shrubland sites, one in the southwestern Cape and the other in the Barrens in Western Australia. Despite differences in the fauna and flora between continents both were found to have a high incidence of dispersal of diaspores by ants, indicating evolutionary convergence in response to similar physical environments.

Outside of southern Africa, a number of comprehensive seed dispersal spectra studies have been undertaken; in Australia (Willson *et al.,* 1990; Lord *et al*, 1997), New Zealand (Thorsen, 2010) and South America (Griz and Machado, 2001; Ribeiro and Tabarelli, 2002; Aizen and Ezcurra, 1998). These studies have brought to the fore some interesting patterns in dispersal spectra. Firstly, there appears to be a couple of dispersal mechanisms; namely ballistic and attachment that are consistently uncommon. Secondly and with regards to vertebrate dispersal, a widespread association between environmental moisture and the frequency of fleshy fruited species exists. Vertebrate dispersal is very common in tropical rain forests with frequencies typically in excess of 70% and dropping as low as 20%, in dry sclerophyll forest. Lastly, seed size displays a conspicuous global pattern, declining by 2-3 orders of magnitude between the equator and sixty degrees latitude (Moles *et al.*, 2007).

If environmental conditions strongly underlie the distribution of dispersal spectra then one might suspect that similar frequencies of dispersal mechanisms should arise where climates and geomorphology on different continents match (Milewski, 1983). Intercontinental dispersal spectra comparisons have to date paid limited attention to southern Africa. This study attempts to provide the first comprehensive seed dispersal spectra study for southern Africa.

It addresses the following questions: (1) how does the tree dispersal spectrum vary across our South African biomes and bioregions? (2) if there is variation then is this related to the position of these biomes along major environmental gradients? (3) what, if any are the differences in dispersal spectra between South Africa, Australia and South America? (4) what other factors might have played a role in shaping the dispersal spectra observed on these three continents?

Methods

FLORISTIC DATA

In order to produce a dispersal spectrum for South Africa, I compiled a complete database of South African trees (n=1126). This database was constructed primarily from information derived from the 'Trees of Southern Africa' by Coates Palgrave (2002). Coates Palgrave (2002) defined a tree as a woody perennial plant that typically possesses a single stem or trunk, bearing lateral branches at some distance from the ground. The tree database was supplemented with information sourced from three existing databases: the South African National Biodiversity Institute's plant information website, the Royal Botanic Gardens Kew Seed Information Database (SID, 2008) and the JStor Global Plants database (2013), in addition to a collection of other references (see Supplementary Reference List A). The database includes information pertaining to the taxonomy, morphology and ecology of each tree species. In particular, it includes numerous fruit and seed morphological traits. To begin, the fruit of each species was classified as either dry or fleshy. Fleshy fruits were further categorised into two subtypes; berries that contained 1 to many seeds without a hard layer surrounding the seeds or drupes that contained 1 – many (usually 1-2) seeds surrounded by a stony layer. Dry fruits on the other hand were categorised into six subtypes. The first three subtypes are non-dehiscent; the achene – a small single seeded fruit, the samara – a winged achene and the nut – a single seeded fruit with a woody outer layer. The second three subtypes are dehiscent (split open); the follicle which splits on one side, the capsule which splits into several valves and the legume which splits into two valves. Where available the fruit diameter, length and width measurements were recorded. The fruit size was taken to be the largest of these three values in keeping with a study by Almeida-Neto *et al.* (2008). Characteristics of the seed such as the number per fruit, size and colour were also logged. Seed mass estimates were sourced exclusively from the Royal Botanic Gardens Kew Seed Information Database (SID, 2008; and references therein - Supplementary Reference List A). I managed to find seed mass estimates for 560 of the 1126 tree species. In addition, the presence or absence of arils and elaiosomes were documented and where present the colour was specified.

DISPERSAL MECHANISMS

A thorough literature review (Supplementary Reference List A) allowed me to assign the majority of tree species to any one of the following dispersal mechanisms: vertebrate (mammal or bird), wind, ant, ballistic, attachment, water or 'no special' (unassisted). Where the dispersal agent itself was not known, morphological features of the fruit/seed were used to determine the most likely primary dispersal mechanism following a set of parameters set out by Willson *et al.* (1989, 1990) and van der Pijl (1982), and outlined in Table 1.

Table 1: Assignment of dispersal mechanisms based on morphological features of the fruit/seed (adapted from Willson *et al.*, 1989/1990 and van der Pijl, 1982). Morphological features were used to determine the dispersal mechanism when the dispersal agent was unknown.

Assigned Dispersal Mechanism	**Morphological Parameters**
Wind	Fruit or seed has wings, plumes or hairs that will slow the rate of fall
Mammal	Fleshy fruit > 2cm in diameter
Bird	Fleshy fruit <=2cm in diameter. Alternatively it is indicated by the presence of a brightly coloured aril
Ant	Indicated by the presence of an elaiosome (a dull - usually white coloured - fleshy appendage on seeds).
Ballistic	Seed is propelled explosively by a fruit (usually a pod) that opens abruptly or by a lever-like device. Discerned also if the If the pod is said to open with a large crack or if the pods curl into a corkscrew shape.
Attachment	Fruit or seed has hooks, burrs, barbs, sticky hairs or other devices that allow it to adhere to the fur or feathers of a vertebrate.
Water	Buoyant pericarp
No Special	The dispersal agent is unknown and there are no evident morphological features that place it in any of the above categories. Those fruit or seeds that are said to be gravity-dispersed in the literature fall into this category. Some species in this category might be dispersed by large herbivores that eat them along with tree foliage (Foliage-as-Fruit Hypothesis – Janzen, 1983).

DISPERSAL SPECTRA ANALYSES

In order to produce a dispersal spectrum for each of South Africa's biomes, digital distribution data for each tree species was obtained from the National Herbarium Pretoria Computerised Information System (PRECIS). This electronic database system catalogues the details of specimen records from South African herbaria. These location data points were then spatially joined to Mucina and Rutherford's (2006) vegetation map layer through the linking of shape files in ArcGIS (3.1). This resulted in comprehensive species lists across each of Mucina and Rutherford's (2006) vegetation types, bioregions and biomes (Table 2). These species lists were then translated into dispersal spectra across each vegetation unit.

Table 2: Tree species, genera and family counts across the biomes.

Biome	Number of Species	Number of Genera	Number of Families
Fynbos	304	162	64
Succulent Karoo	159	97	51
Nama-Karoo	154	88	47
Grassland	652	280	87
Savanna	847	354	97
Albany Thicket	303	165	67
Indian Ocean Coastal Belt	499	261	81
Forests	395	221	75

In a similar manner, the location data for each tree species was assigned to the degree square in which it occurred allowing for the frequency of each dispersal mechanism to be mapped across grid squares. Dispersal mechanism hot and cold spots were revealed using this approach. Only those grid squares that contained data for 50 or more species were included.

CROSS CONTINENTAL COMPARISON

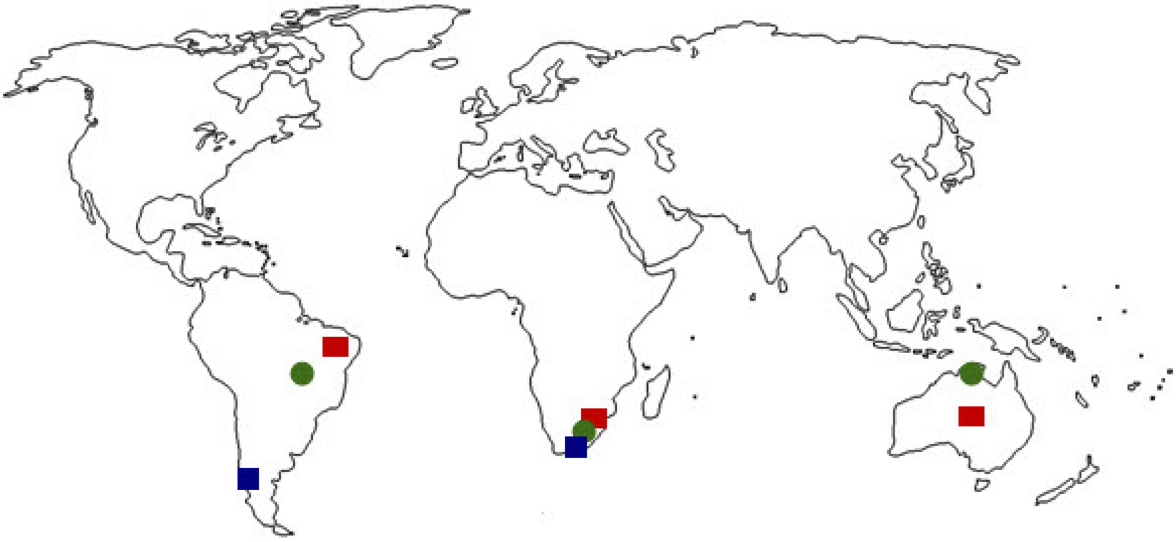


Figure 1: Geographic distribution of dispersal spectra evaluated in this study. Red rectangles = dry forest sites; green circles = moist savanna sites and the blue squares = temperate forest sites.

Cross-continental comparisons were undertaken by matching similar vegetation types in South America and Australia, to those found in South Africa. The vegetation types that were compared fell into three categories; dry forest, moist savanna and temperate forest. In the case of the temperate forests no Australian example was found so only the dispersal spectra of South Africa and South America were compared. The geographical locations of these comparative sites are displayed in Figure 1. For each vegetation type in South America and Australia, comprehensive dispersal spectra studies were sourced. All the South American and Australian seed dispersal spectra studies included all plant forms from herbs through to trees. In all instances, the raw data was sourced from either appendices or the authors themselves and the tree data was extracted so as to ensure compatibility with this study.

Dry Forest

Figure 2: Photographs of the dry forest sites: A) South America: Tropical Dry Forest – the Caatinga in North-Eastern Brazil (Griz and Machado, 2001); B) Africa: Subtropical Dry Forest – Sand Forest (this study); C) Australia: Subtropical Dry Woodland – central Australian woodland and Acacia shrubland (Jurado et al., 1991).

The Caatinga in North-Eastern Brazil was selected as the South American dry forest example (Figure 2 – image A). The Caatinga is a tropical dry forest characterised by considerable year-to-year variability in precipitation. The average annual rainfall for the region varies between 500 and 750 mm, but in parts it can receive as little as 250mm (Sampaio, 1995 in Griz and Machado, 2001). The dispersal spectrum of this region was obtained from a thorough study conducted by Griz and Machado (2001). These authors (Griz and Machado, 2001) assigned the dispersal mode on the basis of fruit morphology following van der Pijl (1982). Those diaspores that did not show any structure indicative of a particular dispersal mode (e.g. elaiosome, edible parts, hairs), and weighed less than 10 mg were classified as wind-dispersed while those that weighed more that 10mg and did not show any structures known to facilitate wind-dispersal were classified as 'no special'.

Sand Forest, situated in the Kwazulu-Natal province on the eastern border of South Africa and extending into Mozambique, was elected as the best example of a South African dry forest (Figure 2 – image B). The mean annual precipitation measured in Sand Forest is 679mm while the mean annual temperature is 21.5°C (Mucina and Rutherford, 2006). The tree species list across all fragments of Sand Forest was derived from both collection records in the Sand Forest obtained from National Herbarium Pretoria Computerised Information System (PRECIS) and supplemented by a tree taxa list produced by Mucina and Rutherford (2006). The dispersal mode was assigned following the method outlined earlier in this chapter (Methods: Dispersal Mechanism).

The subtropical - central Australian woodland and Acacia shrubland was chosen as the Australian dry forest example (Figure 2 – image C). This region has an arid climate with a mean annual rainfall of 263mm, of which 70% falls in summer (Low, 1978 in Jurado *et al*., 1991). In addition, there is high inter-annual variability in precipitation (Lord *et al*., 1997). The average maximum and minimum temperatures are 35°C and 21°C in the hottest month and 19°C and 4°C in the coldest (Low, 1978 in Jurado *et al*., 1991). The dispersal spectrum of this region was obtained from a study conducted by Jurado *et al*. (1991) and represents a near complete inventory of the species in this vegetation type. The authors (Jurado *et al*., 1991) assigned the dispersal mechanism based on the visible fruit structures.

Moist Savanna

Figure 3: Photographs of the moist savanna sites: A) South America: Tropical Cerrado - Fazenda Palmares in Brazil (Ribeiro and Tabarelli, 2002); B) South Africa: Moist Savanna - combination of Andesite Mountain Bushveld, Gauteng Shale Mountain Bushveld and Gold Reef Mountain Bushveld (this study); C) Australia: Arnhem Land Tropical Savanna -Kakadu National Park, Northern Australia (Lord *et al*, 1997).

The Cerrado in Brazil was chosen as the best illustration of a moist South American savanna (Figure 3 – image A). In terms of extent, the Cerrado covers approximately 2 million km^2 - a fifth of the total area of Brazil (Furley and Ratter, 1988 in Ribeiro and Tabarelli, 2002). The Cerrado evolved from forest ancestors from the Late Miocene as C4 grasses began to form a new, flammable biome (Grether *et al*., 2009). The bulk of the cerrado vegetation occurs on poor soils with a mean annual precipitation of ~1500 mm (Nimer, 1979 in Ribeiro and Tabarelli, 2002). The dispersal spectrum of this region was obtained from a study undertaken by Ribeiro and Tabarelli (2002). The seed dispersal mode was assigned based on the morphology of the diaspores. Contrary to this study, Ribeiro and Tabarelli (2002) considered ballistically-dispersed seeds i.e. those that are propelled explosively by a fruit that opens suddenly or by a trip-lever to be wind-dispersed (abiotically-dispersed). Trees in this study were defined as woody plant species with a height greater than 4m and without any branching at ground level.

Three vegetation types within the South African Savanna Biome are considered to be a form of moist savanna; namely Andesite Mountain Bushveld, Gauteng Shale Mountain Bushveld and Gold Reef Mountain Bushveld (Mucina and Rutherford, 2006 – Figure 3 – image B). They all belong to the Central Bushveld Bioregion and are located in northern South Africa, in the Limpopo, North-West and Gauteng provinces (Mucina and Rutherford, 2006). They all receive summer rainfall and are subject to very dry winters. Mean annual precipitation ranges from approximately 550mm to 750mm (Mucina and Rutherford, 2006). The tree species list across all three vegetation types was derived from both collection records obtained from National Herbarium Pretoria Computerised Information System (PRECIS) and from three tree taxa lists produced by Mucina and Rutherford (2006). The dispersal mode was assigned by the method outlined earlier in this chapter.

The Arnhem Land Tropical Savanna in Northern Australia was selected as the Australian moist savanna example (Figure 3 – image C). This region is characterised by a dry monsoonal climate; the majority of the annual rainfall (which can vary from 840 to 2800mm) falls from December to March, while from June to September is typified by an intense drought. The dataset was compiled by J. Egan from Kakadu National Park and supplemented with a species list from Taylor and Dunlop (1985, in Lord *et al*., 1997). Dispersal mode was inferred from external morphological features of the diaspore following the methods of Leishman and Westoby (1994).

Temperate Forest

Figure 4: Photographs of the temperate forest sites: A) South America: Temperate Forest (Southern Chile; Aizen and Ezcurra, 1998); B) South Africa: Southern Afrotemperate Forest (Knysna Forests; this study).

The narrow temperate forest band that extends over much of southern Chile and the eastern slopes of the Patagonian Andes in Argentine is the biome selected to exemplify the temperate forests of South America (Figure 4 – image A). The prevailing climate is wet-temperate with strong oceanic influences (Di Castri and Hajek, 1976 in Aizen and Ezcurra, 1998). Rainfall occurs throughout the year, with a mean annual precipitation of 2090 mm. The dispersal spectrum of this region was obtained from a study conducted by Aizen and Ezcurra (1998) and represents a near complete inventory of the 91 genera in this biome. Dispersal mechanisms were assigned at the genus rather than the species level.

The Southern Afrotemperate Forest is situated along the southern coast of South Africa in the Western Cape and Eastern Cape provinces (Figure 4 – image B). These forests are embedded within temperate biomes such as Fynbos and Grassland (Mucina and Rutherford, 2006). The mean annual precipitation measured in the Southern Afrotemperate Forest is 863mm while the mean annual temperature is 16.7°C (Mucina and Rutherford, 2006). The tree species list across the full extent of the 250km long coastal strip plus other fragments of Southern Afrotemperate Forest was derived from collection records obtained from National Herbarium Pretoria Computerised Information System (PRECIS) and supplemented by a tree taxa list produced by Mucina and Rutherford (2006). The dispersal mode was assigned by the method outlined earlier in this chapter.

Statistics

Differences in the frequency of dispersal mechanisms across similar vegetation types on different continents were analysed by means of chi-squared tables ($\chi2$-test). The criterion for statistical significance was set at the customary $\alpha = 0.05$ (95% confidence).

Results

DISPERSAL SPECTRA ACROSS THE BIOMES

Table 3: The dispersal spectra of trees across South African biomes. Frequency shown in shaded row while non-shaded row shows the actual species count.

Biome Type	Vertebrate % (mammal%; bird %)	Wind %	Water %	Ant %	Ballistic %	Attachment %	No Special%
Indian Ocean Coastal Belt (n=442)	65% (m = 32%, b = 33%)	12%	2%	0%	3%	0%	17%
	288	55	8	1	12	2	76
Desert Biome (n=35)	62% (m = 31%, b = 31%)	23%	0%	0%	0%	3%	11%
	22	8	0	0	0	1	4
Fynbos Biome (n=289)	60% (m = 23%, b = 37%)	19%	1%	3%	1%	1%	16%
	174	56	2	8	2	2	45
Grassland Biome (n=586)	63% (m = 32%, b = 31%)	16%	0%	0%	2%	1%	18%
	367	96	2	1	12	3	105
Nama-Karoo Biome (n=146)	64% (m = 25%, b = 39%)	21%	0%	1%	1%	1%	12%
	93	31	0	2	2	1	17
Savanna Biome (n=756)	62% (m = 34%, b = 28%)	16%	1%	0%	2%	1%	18%
	468	122	7	1	17	4	137
Succulent Karoo Biome (n=154)	53% (m = 23%, b = 31%)	25%	0%	4%	0%	1%	16%
	84	38	0	6	0	2	24
Albany Thicket Biome (n=284)	65% (m = 25%, b = 40%)	17%	0%	1%	1%	1%	15%
	185	47	1	3	3	2	43
Forests (n=354)	65% (m = 29%, b = 36%)	17%	1%	0%	2%	1%	15%
	227	61	2	1	6	3	54

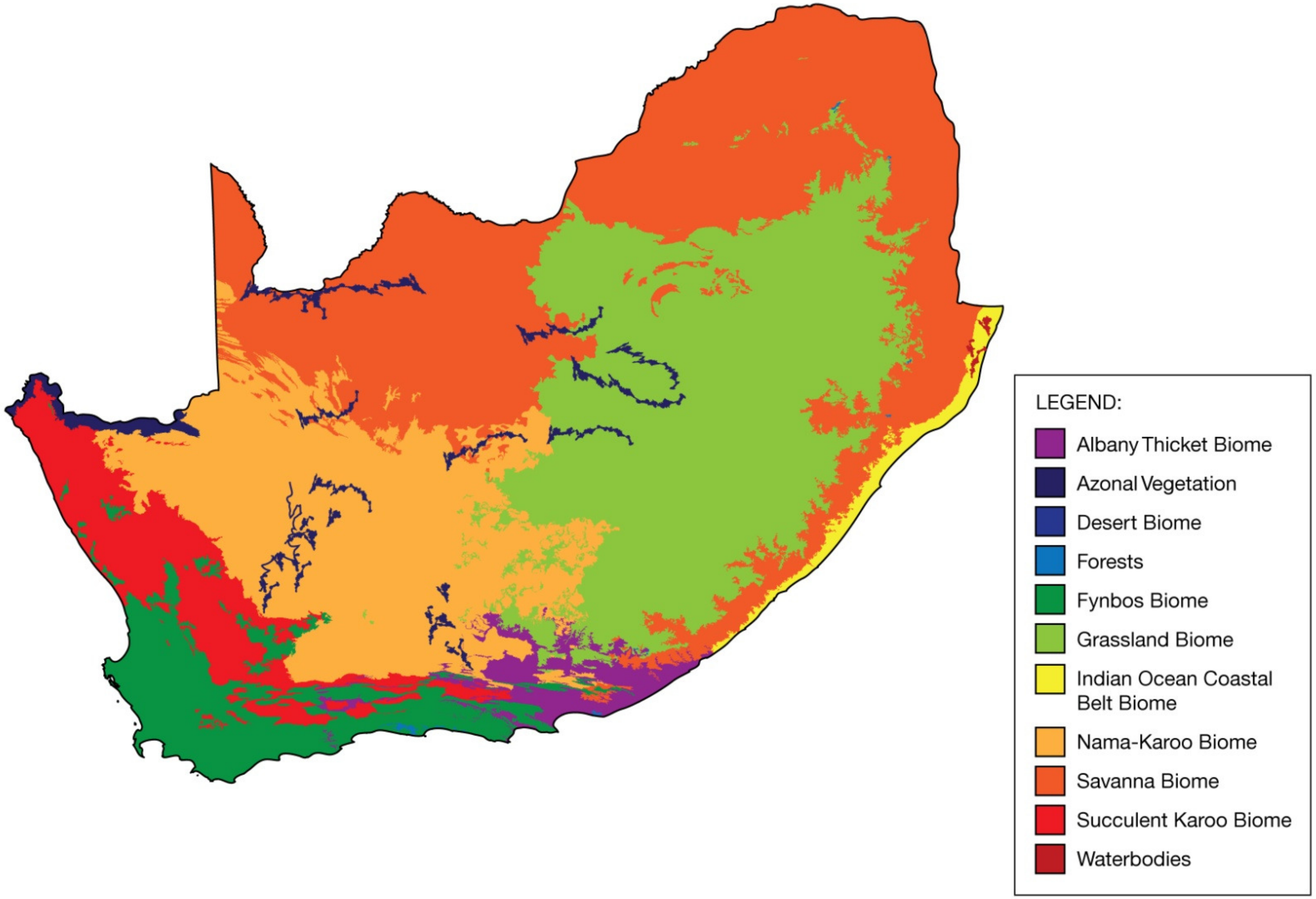


Figure 5: Map of the biomes of South Africa. This map is to be used as a point of reference for the maps that follow.

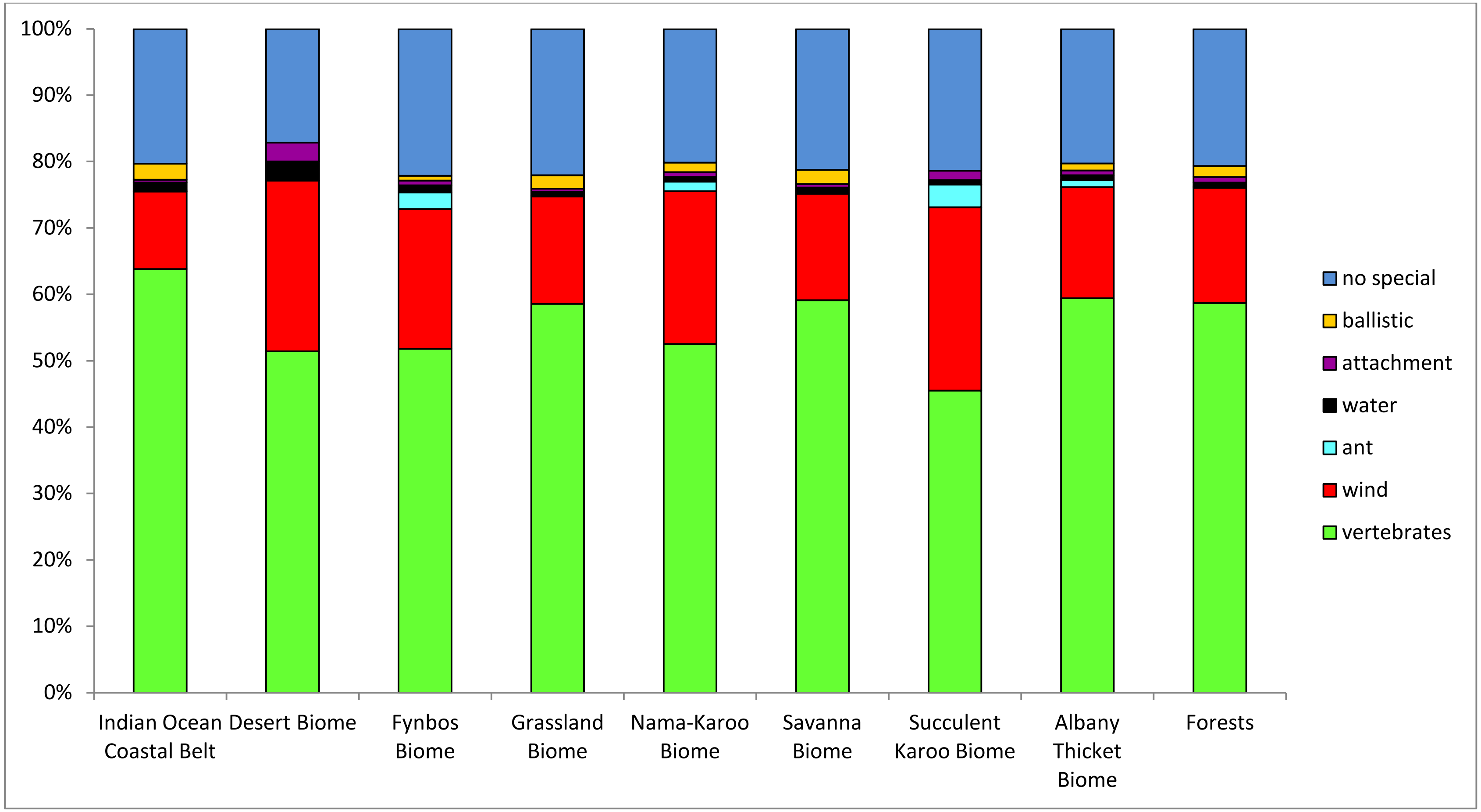
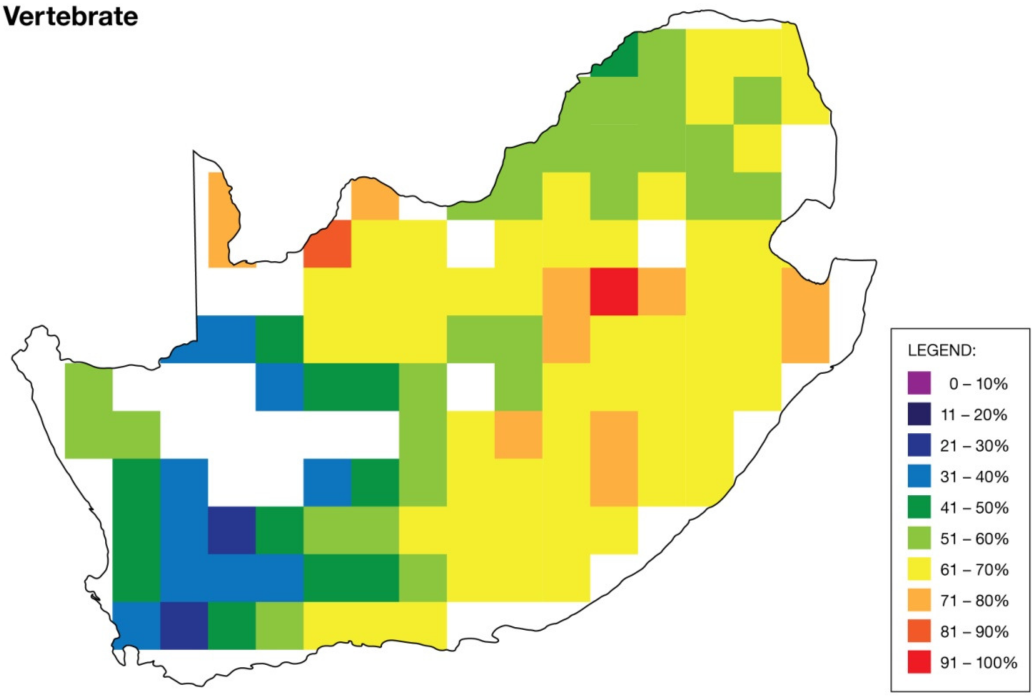


Figure 6: Comparison of dispersal spectra for trees across the South African biomes. Figure based on results in Table 4.


Vertebrate

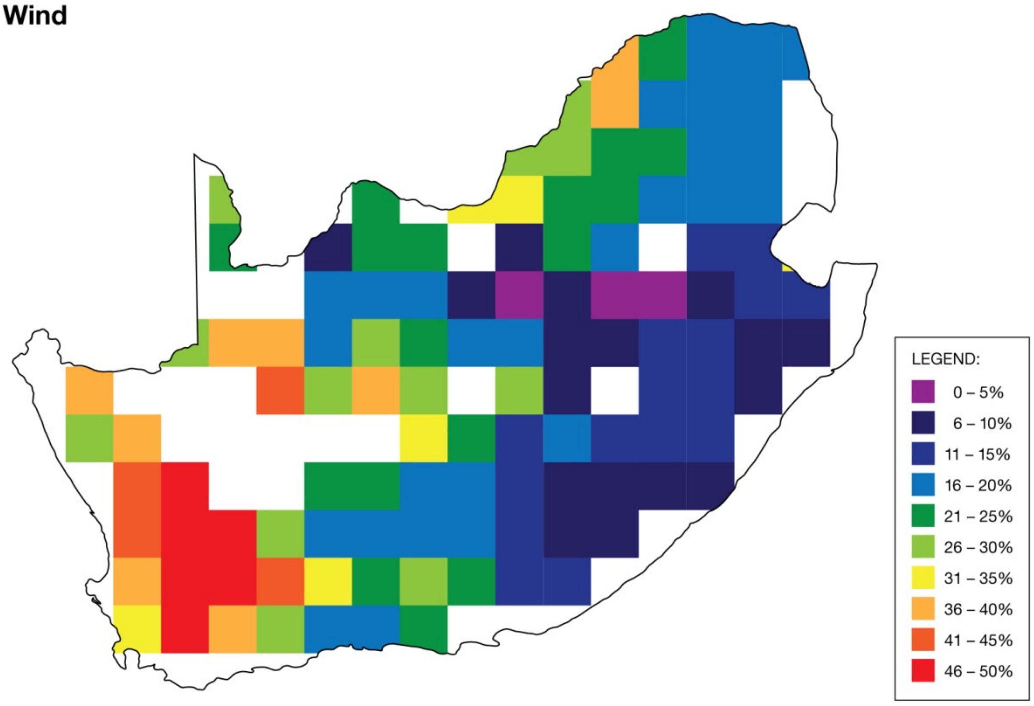
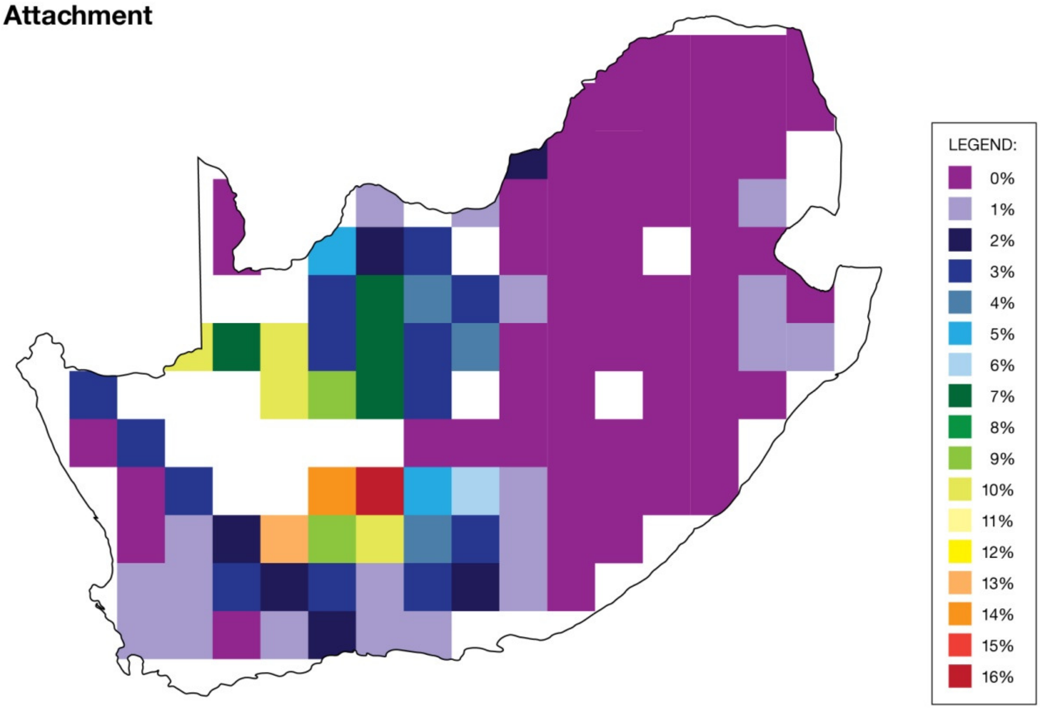

Wind

Figure 7: Geographical spread of the vertebrate and wind dispersal mechanism for southern Africa trees. Dispersal spectra given as a percentage of each degree square. Only those degree squares with greater than 50 species are shown.


Attachment

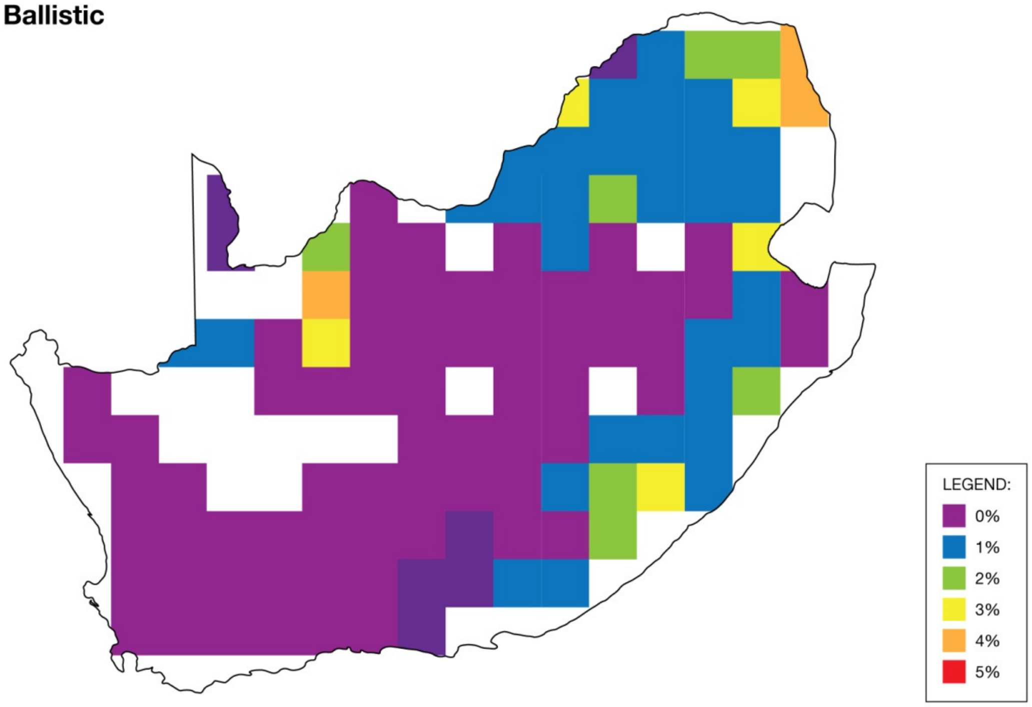

Ballistic

Figure 8: Geographical spread of the attachment and ballistic dispersal mechanism for southern Africa trees. Dispersal spectra given as a percentage of each degree square. Only those degree squares with greater than 50 species are shown.

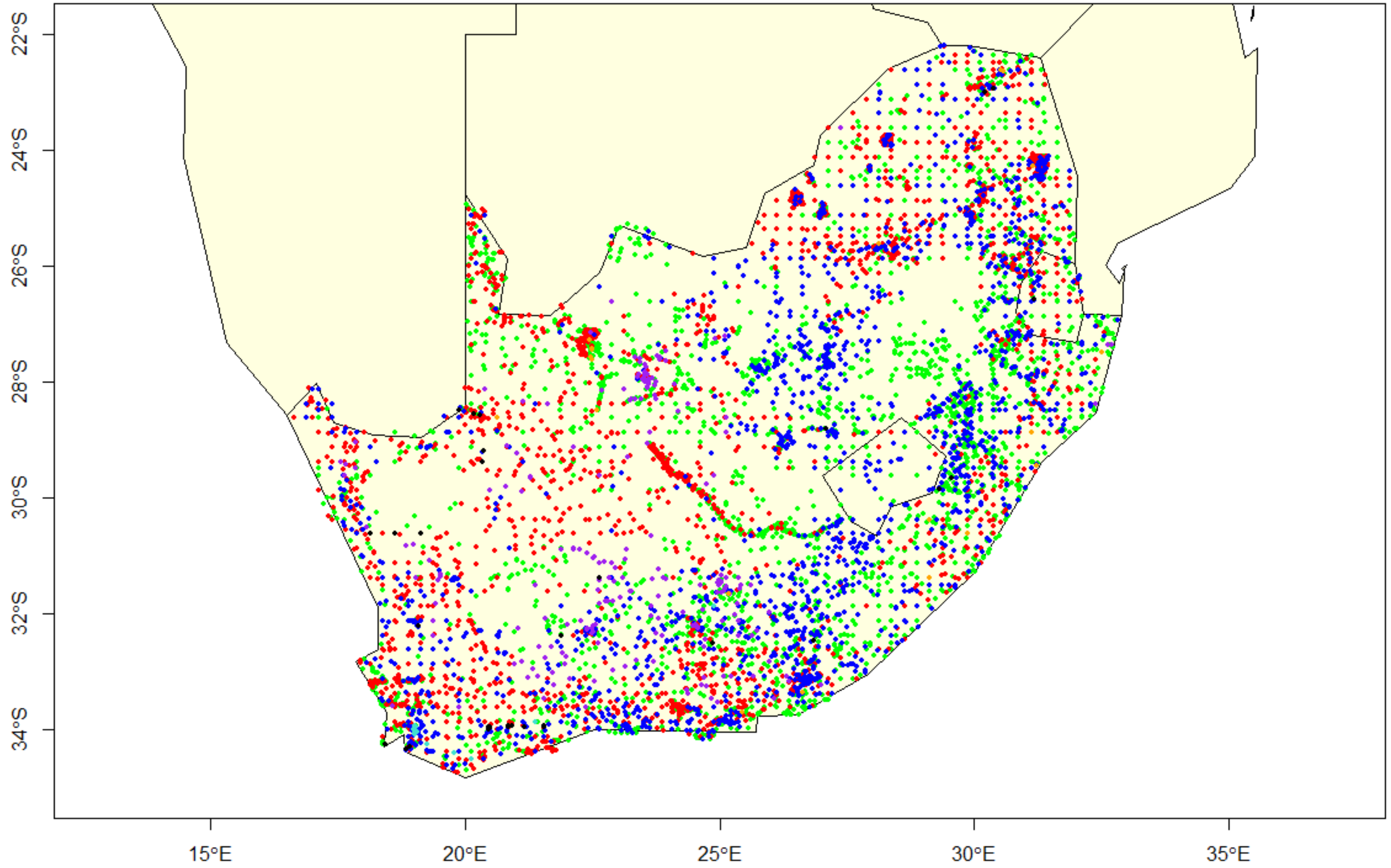


Figure 9: Spatial distribution of the dispersal mechanisms of South Africa tree species. Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. Distribution points north of the border of South Africa were excluded. Dispersal mechanisms colour-coded as follows: vertebrate - green, wind - red, no special - blue, attachment - purple, ant - turquoise, water - black, ballistic – orange.

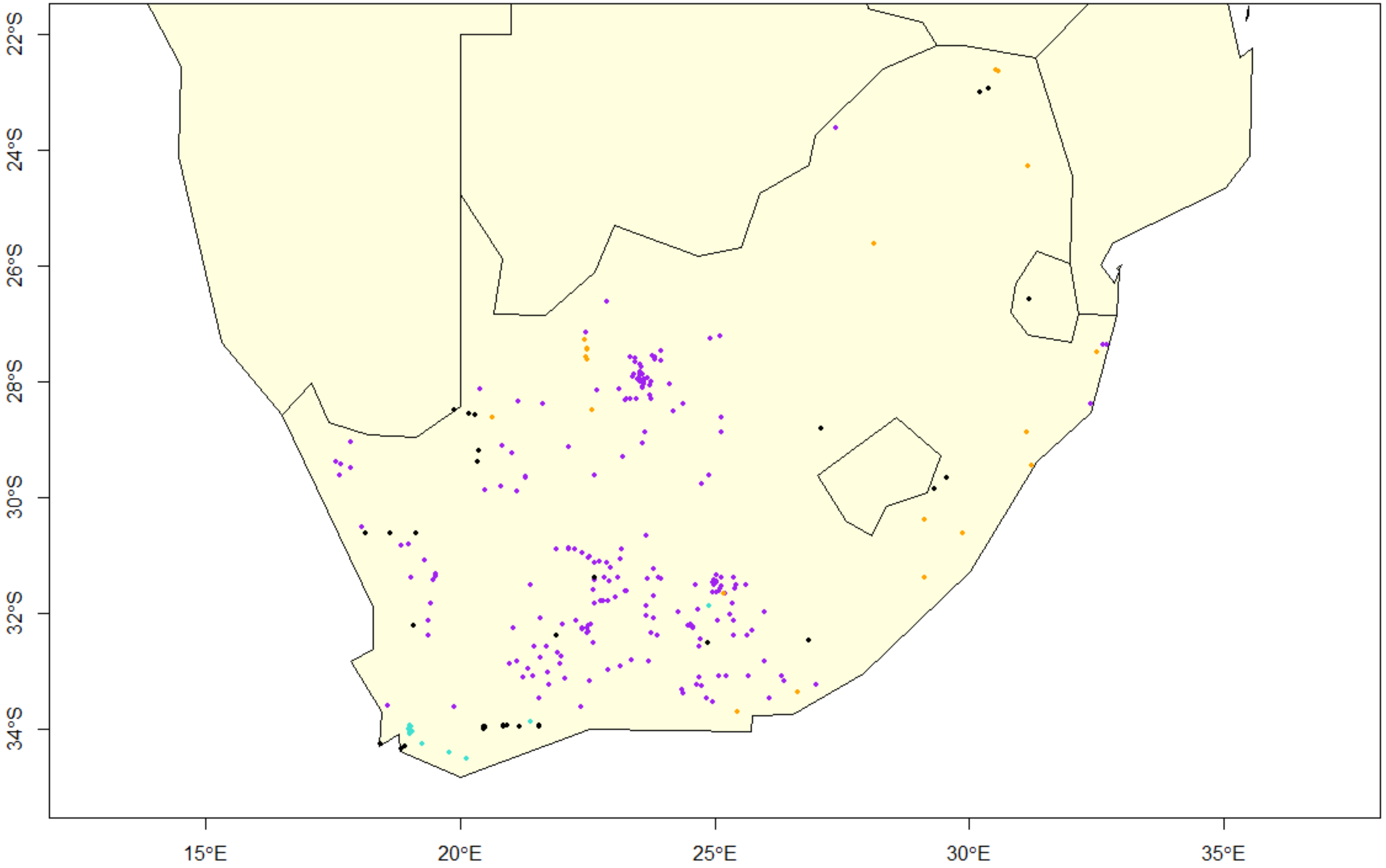


Figure 10: Spatial distribution of the less widespread dispersal mechanisms of South Africa tree species. Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. Distribution points north of the border of South Africa were excluded. Dispersal mechanisms attachment - purple, ant - turquoise, water - black, ballistic – orange.

Vertebrate dispersal of trees is consistently common across all South African biome types. It ranges from 53% in the Succulent Karoo Biome to 65% in three separate biomes; the Indian Ocean Coastal Belt, Albany Thicket and the Forest Biome (Figure 6; Table 4). When examined spatially and at greater resolution, vertebrate dispersal shows both a greater range and a clear trend of increase from west to east (Figure 7) with figures as low as 30% appearing in one degree grid squares in the Fynbos and Succulent Karoo Biome and with figures in excess of 70% appearing in degree squares located in the Savanna, Grassland and Indian Ocean Coastal Belt Biomes.

When dividing vertebrate dispersal into its mammal and bird component, both remain widespread across all biomes. Mammal dispersal ranges from 23% in the Fynbos and Succulent Karoo Biome to 34% in the Savanna Biome. Bird dispersal on the other hand ranges from 28% in the Savanna Biome to 40% in the Albany Thicket Biome (Table 4).

Wind dispersal of trees is the second most common dispersal mechanism after vertebrate dispersal. It varied more widely across the biomes than did vertebrate dispersal, ranging from 12% in the Indian Ocean Coastal Belt to 25% in the Succulent Karoo Biome (Figure 6). When examined in a spatial context, wind dispersal in contrast to vertebrate dispersal shows an increase from east to west (Figure 7) with values <10% being found in grid squares located in the Savanna and Grassland Biome and with values exceeding 40% in the Succulent Karoo and Nama-Karoo Biome.

It is possible that wind dispersal might be somewhat under-represented in this study as small fruit/ seeds that have no obvious morphological adaptation to wind dispersal (and were not known to be wind-dispersed in the literature) were classified as ‘no special’ rather than assuming them to be wind dispersed. This was in keeping with Willson *et al*. (1990) who could find no cut-off seed size below which seeds could be treated as primarily wind dispersed.

Four dispersal mechanisms are consistently uncommon in tree species. The first, ant dispersal, ranges from <1% in the Forest, Desert and Indian Ocean Coastal Belt to 3 and 4% in the Fynbos and Succulent Karoo Biome respectively (Figure 6). Myrmecochory is very common in shrubs found in the Fynbos biome (Bond and Slingsby, 1983) however, as only trees were included in this study, this pattern was not apparent. Outside of the Fynbos

Biome very little research has been undertaken on ant dispersal so accounts in the literature are limited. Also some ant species are known to disperse seeds that lack elaiosomes (Clay, 1983) so one cannot rely solely on the presence of such morphological features to indicate this mode of dispersal.

A second dispersal mechanism, attachment, is consistently rare in tree species (<3%). It represents less that 1.5% in all biomes with the exception of the desert biome where it accounts for 3%. When considered in a spatial context, attachment increases from east to west with values in excess of 10% in grid squares located in the Nama-Karoo and Desert Biome (Figure 8). This study does not take into account fruit/seeds that become sticky when wet (Sθrenson, 1986). Regardless of this, the majority of plant species with adhesive fruits are low-growing; a survey of species bearing adhesive fruits in the Brazilian cerrado showed that 13 out of 14 adhesive species occurred on the ground layer (Gottsberger and Silberbauer-Gottsberger, 1983). Thus it is not surprising that our study of the tree flora returned just a handful of species that attach only to the feet or feathers of birds

Thirdly, ballistic dispersal of tree species ranges from 0% in the Succulent Karoo Biome to 3% in the Indian Ocean Coastal Belt Biome. However, unlike attachment, ballistic dispersal increases from west to east (Figure 8). Ballistic dispersal appears to coincide quite closely with the Indian Ocean Coastal Belt Biome and the Savanna Biome. The large number of dry dehiscent fruit that were classified as ‘no special’ is indicative of the fact that ballistic dispersal has been underestimated in this study. This dispersal mechanism warrants further investigation in an African savanna context.

Lastly, water dispersal appears to be extremely rare (<2%) across all biomes. As would be expected it occurs most often in the Indian Ocean Coastal Belt Biome which is found in a thin strip along the Indian Ocean.

SEED MASS

The median seed mass of tree species declines from low to high latitudes (Figure 11, R^2 value =0.5625).

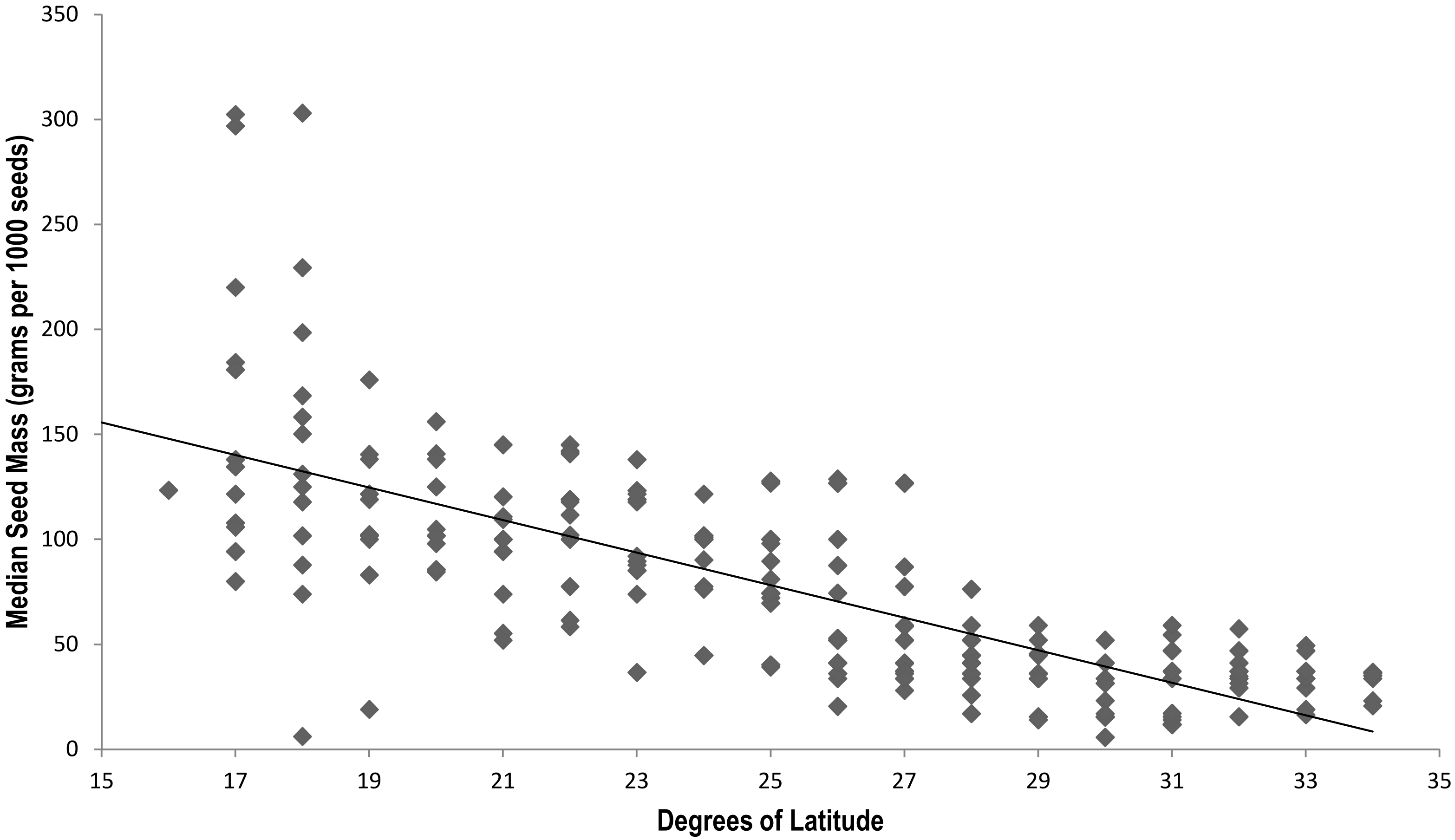


Figure 11: Median seed mass (grams per 1000 seeds) against degrees of latitude. Figure based on the seed mass of 560 South African tree species and their presence or absence in degree squares. The R^2 value =0.5625.

CROSS CONTINENTAL COMPARISON

Physiognomically similar vegetation types across the three southern hemisphere continents (Figure 1) have greatly disparate dispersal spectra. Dry Forests in South Africa have a significantly larger proportion of their tree flora dispersed by vertebrates than the dry woodland in Australia (55% versus only 3% - Table 4; $\chi 2 = 60$, $p < 0.05$, df =2 – Table 5). Additionally, 68% of the Australian dry woodland was made up of fruits that had no morphological adaptation to dispersal. This is in sharp contrast to the 24% and 26% of the South American and Southern African dry woodland tree species that exhibit no morphological adaptation to dispersal (Table 4). Wind dispersal remained fairly constant across the dry forests on all three continents. Ballistic dispersal was found in 12% of the South American dry forest tree species but was entirely absent from both the Southern African and Australian dry forest tree flora (Table 4). Ant dispersal was found in 13% of dry woodland trees in Australia but was absent from the South African and South American dry forest flora.

Dry Forest

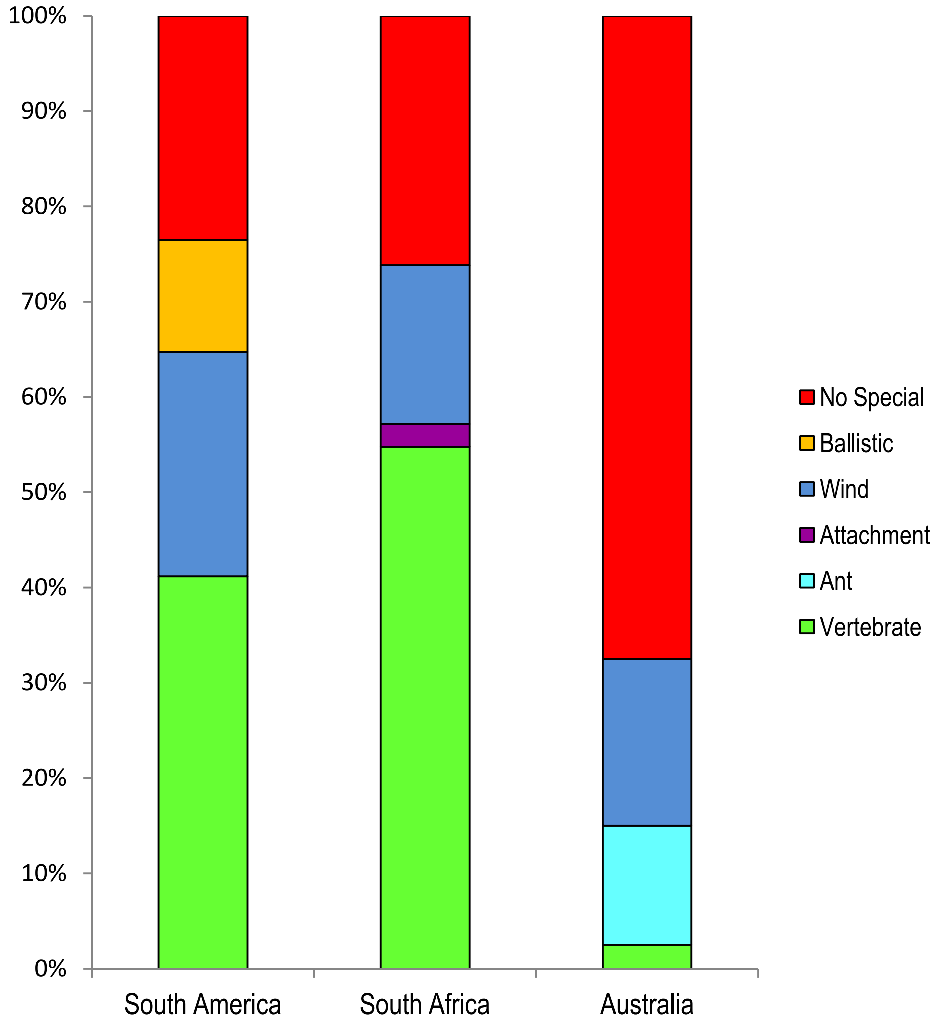


Figure 12: The seed dispersal spectrum in dry forest trees across three continents. South America: Tropical Dry Forest (Caatinga; Griz and Machado, 2001); South Africa - Subtropical Dry Forest (Sand Forest, this study); Australia - Subtropical Dry Woodland (Central Australian woodland and Acacia shrubland; ; Jurado et al., 1991).

Table 4: Number of tree species by dispersal mechanism in three dry forest sites in South America, South Africa and Australia. South America: Tropical Dry Forest (Caatinga; Griz and Machado, 2001); South Africa - Subtropical Dry Forest (Sand Forest, this study); Australia - Subtropical Dry Woodland (Central Australian woodland and Acacia shrubland; Jurado et al., 1991).

Continent	**Vertebrate**	**Ant**	**Attachment**	**Wind**	**Ballistic**	**No Special**
South America (n=17)	7 (41%)	0 (0%)	0 (0%)	4 (24%)	2 (12%)	4 (24%)
South Africa (n=42)	23 (55%)	0 (0%)	1 (2%)	7 (17%)	0 (0%)	11 (26%)
Australia (n=40)	1 (3%)	5 (13%)	0 (0%)	7 (18%)	0 (0%)	27 (68%)

Table 5: Observed versus expected number of dry forest tree species within dispersal mechanism–continent combinations. The dispersal mechanism 'other' is composed of ant, attachment, ballistic and no special as these datasets had cell expected values <5. Chi-squared tests were performed (df = 2).

Vegetation Type	**Vertebrate**	**Wind**	**Other**	**χ2 value**
South America (observed)	7	4	6	0.97
South Africa (expected)	9	3	5	

Vegetation Type	**Vertebrate**	**Wind**	**Other**	**χ2 value**
Australia (observed)	1	7	32	**60**
South Africa (expected)	22	7	11	

The moist savannas across the three southern continents exhibited less disparity in the seed dispersal mechanisms employed than did the dry forests. Vertebrate dispersal is highest in South Africa, where it accounts for 61% of the tree flora. This is followed by 56% in South America and 51% in Australia. Wind dispersal exhibits significant change across the moist savanna; in the Cerrado 43% of species are wind-dispersed, in the moist savanna of South Africa 18% of species are wind-dispersed and in the tropical savanna of Northern Australia only 6% of species are adapted for wind dispersal ($\chi2 = 42$ (South America versus South Africa) and 18 (Australia versus South Africa) $p < 0.05$ for both, df =2 – Table 7). Ant dispersal also shows a conspicuous divergence – 20% of tropical savanna species in Australia are adapted for ant dispersal whereas only 1% of South America cerrado species are ant dispersed (this dispersal mode is completely absent from the moist savanna of South Africa).

Moist Savanna

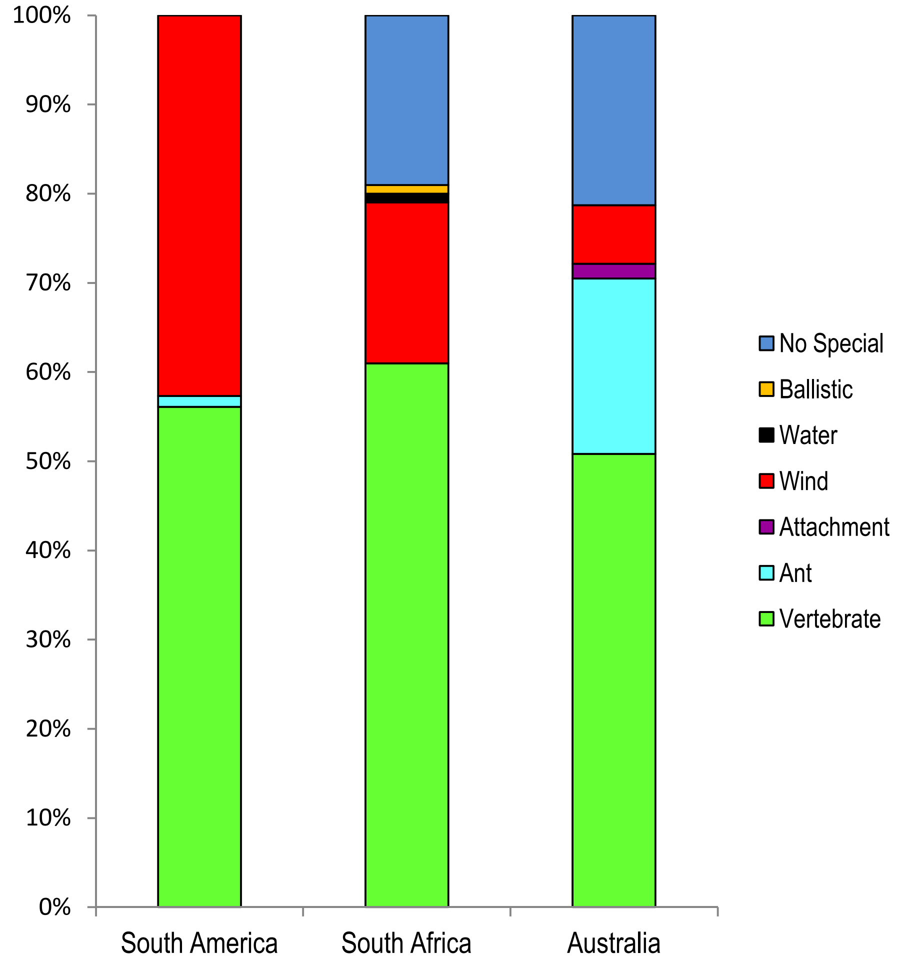


Figure 13: The seed dispersal spectrum in moist savanna trees across three continents. South America: Tropical Savanna (Cerrado; Ribeiro and Tabarelli, 2002); South Africa - Moist Savanna (Andesite Mountain Bushveld, Gauteng Shale Mountain Bushveld and Gold Reef Mountain Bushveld; this study); Australia – Tropical Savanna (Arnhem Land; Lord *et al*, 1997).

Table 6: Number of tree species by dispersal mechanism in three moist savanna sites in South America, South Africa and Australia. South America: Tropical Savanna (Cerrado; Ribeiro and Tabarelli, 2002); South Africa - Moist Savanna (Andesite Mountain Bushveld, Gauteng Shale Mountain Bushveld and Gold Reef Mountain Bushveld; this study); Australia – Tropical Savanna (Arnhem Land; Lord *et al*, 1997).

Continent	**Vertebrate**	**Ant**	**Attachment**	**Wind**	**Water**	**Ballistic**	**No Special**
South America (n=82)	46 (56%)	1 (1%)	0 (0%)	35(43%)	0(0%)	0(0%)	0 (0%)
South Africa (n=205)	125 (61%)	0 (0%)	0 (0%)	37(18%)	2 (1%)	2(1%)	39 (19%)
Australia (n=61)	31 (51%)	12 (20%)	1 (2%)	4(7%)	0 (0%)	0 (0%)	13 (21%)

Table 7: Observed versus expected number of moist savanna tree species within dispersal mechanism –continent combinations. The dispersal mechanism 'other' is composed of ant, attachment, ballistic and no special as these datasets had cell expected values <5. Chi-squared tests were performed (df = 2).

Vegetation Type	Vertebrate	Wind	Other	χ2 value
South America (observed)	46	35	1	**42**
South Africa (expected)	50	15	17	

Vegetation Type	Vertebrate	Wind	Other	χ2 value
Australia (observed)	31	4	26	**18**
South Africa (expected)	37	11	13	

The temperate forests of Chile and South Africa possess dissimilar dispersal spectra (($\chi 2 = 31$, $p<0.05$, $df = 2$ – Table 9). The temperate forests of Southern Chile have 39% of their tree species dispersed by vertebrates while the afrotemperate forests of South Africa have 62% of their tree species dispersed by vertebrates. Similar to the moist savannas of Brazil (Cerrado) the temperate forests of Southern Chile are highly reliant on wind (56%) for the dispersal of their tree species. This differs considerably from the temperate forests of South Africa that are 19% wind dispersed.

Temperate Forest

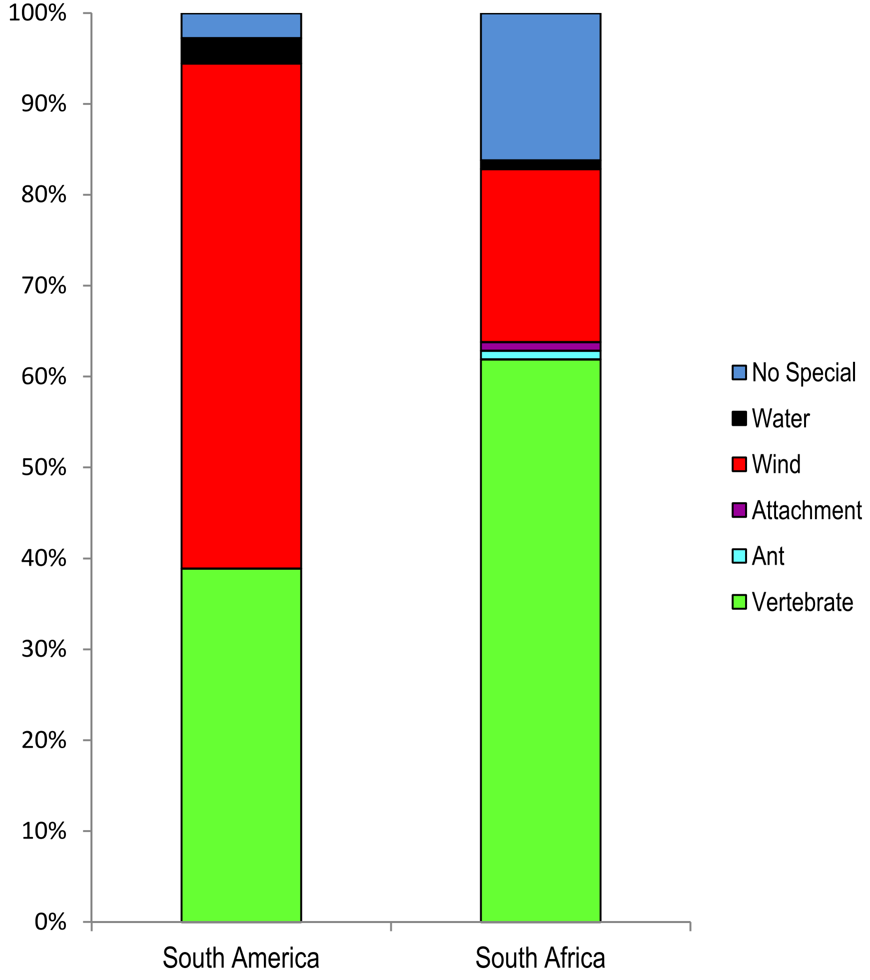


Figure 14: The seed dispersal spectrum in temperate forest trees across three continents. South America: Temperate Forest (Southern Chile; Aizen and Ezcurra, 1998); South Africa: Southern Afrotemperate Forest (Knysna Forests; this study); Australia: Temperate Woodland (New South Wales; Lord *et al*, 1997).

Table 9: Observed versus expected number of temperate forest tree species within dispersal mechanism –continent combinations. The dispersal mechanism 'other' is composed of ant, attachment, ballistic and no special as these datasets had cell expected values <5. Chi-squared tests were performed (df = 2).

Vegetation Type	Vertebrate	Wind	Other	χ2 value
South America (observed)	14	20	2	**31**
South Africa (expected)	22	7	7	

Discussion

DISPERSAL SPECTRA AND GROWTH FORM

This study is restricted to the tree flora of South Africa. Trees represent only 9% of the Southern African flora (Southern Africa: South Africa + Namibia + Botswana – 1700 of 18532 species; Goldblatt, 1978) so in all likelihood they represent a similar fraction of the South African flora. By including only trees this study is limited in its ability to paint a comprehensive picture of the entire dispersal spectrum of South Africa, it does however control for growth form thus allowing for observed differences in dispersal spectra across the country to be attributed to factors other than growth form.

Of the seven dispersal mechanisms employed, three - vertebrate, wind- and 'no special' - were consistently common across the South African biomes while the remaining four – ant, ballistic, attachment and water - were typically rare. This divergence in the frequency with which these dispersal mechanisms occur is characteristic of trees and does not apply to other growth forms with which they co-occur.

Hughes *et al.* (1994) have suggested that in plants there is strong selection to be dispersed at least 1-2 canopy diameters away from the parent. In the case of trees with large canopies this would necessitate the selection of dispersal mechanisms that can achieve distances greater than several meters. Both vertebrate and wind-dispersal produce a strongly leptokurtic distribution of seeds; with many seeds being dropped around the base of the parent plant and a small proportion of seeds being carried many canopy diameters away (Harper, 1977). Owing to the fact that trees tend to be longer-lived and consequently produce fruit over many years, the small subset of the seed crop that is transported a longer distance will likely result in the effective establishment of numerous offspring in safe sites.

In contrast, ants typically disperse seeds 1-2m from their parent plant, with distances of 5m rarely being exceeded (Bond and Slingsby, 1983). Distances attained by ballistic propulsion are constrained by the physical mechanism itself and, like ant-dispersed seeds, rarely surpass a few meters (Willson, 1993; Hughes *et al*., 1994). Thus escape of the 1-2 canopy diameters is far less probable for tree species using ant or ballistic-dispersal.

Escape via longer distance dispersal potentially explains why vertebrate- and wind-dispersal are common in trees and why ant and ballistic dispersal are rare. It does not however account for the infrequency of dispersal via attachment or water, where dispersal vectors are capable of transporting seeds considerable distances. For example, the dispersal of seeds over at least 650km to Macquarie Island is understood to have occurred by adhesion to sea birds (Taylor, 1954). These two dispersal mechanisms are conversely constrained by characteristics of the dispersal vectors themselves. Dispersal via attachment is typically confined to smaller plants due to the availability of dispersal vectors at a suitable height (Guitan and Sanchez, 1992). This premise excludes arboreal mammals that are thought to provide an inferior dispersal service as they are usually more agile and therefore better at finding and removing seeds during grooming (Willson *et al.*, 1990). This trend was first highlighted by Sorenson (1986) who discovered that, in a survey of species with adhesive fruits across 10 floras, 95% were less than 2m in height. Water dispersal, as one might surmise is constrained to those trees that exist in close proximity to rivers or the sea.

With an understanding of the factors that determine the prevalence or scarcity of the different dispersal mechanisms, one can then move on to explore the changes in frequency of these dispersal mechanisms along environmental gradients.

GEOGRAPHICAL AND ENVIRONMENTAL TRENDS

There are two major gradients that divide up Southern Africa. The first is the strong precipitation gradient that separates the subcontinent into a xeric western sector and a relatively mesic eastern sector (Rutherford and Westfall, 1986), while the second is the latitudinal climate gradient that partitions the northern tropical parts from the southern temperate parts.

The two most common dispersal mechanisms, vertebrate and wind, display geographic variation across both these gradients. Vertebrate dispersal is most common in the moist tropical sector of South Africa. The strong association between moisture and vertebrate dispersal has been observed in many previous studies (Gentry, 1982; Almeido-Neto *et al.*, 2008). It has been hypothesised (the 'metabolic costs hypothesis' - Willson *et al.,* 1989) that precipitation may affect the capacity of plants to construct fleshy fruits through both soil nutrients (Milewski, 1986) and soil moisture. The increase in vertebrate dispersal from the lower temperate latitudes to the higher more tropical latitudes is another established association (Fleming *et al.*, 1987). This trend is coupled to the steady decline in seed mass that is evident in this study between 17° and 34°S. According to Hughes *et al.*

(1994) seeds larger than 100mg are likely to be dispersed by vertebrates. Consequently in the tropics, where seeds are 2-3 orders of magnitude larger than their counterparts at high latitudes, vertebrate dispersal is more widespread (Moles *et al.*, 2007).

Within vertebrate dispersal, mammal-dispersal is most common in the Savanna Biome while bird-dispersal is most widespread in the Albany Thicket Biome.

Wind dispersal, in contrast, is most common in the xeric temperate sector of South Africa predominating in the Succulent Karoo, Desert, Nama-Karoo and Fynbos biome. These biomes are dominated by plants of smaller stature that occur at low density and as a result are likely to be exposed to more consistent winds (Howe and Smallwood, 1982). In addition to this, the Succulent Karoo, Desert and Nama-Karoo biome possess depauperate faunal communities relative to other South African biomes (Vernon, 1999). In the absence of sufficient faunal vectors, wind dispersed trees are more likely to be favoured. .

The Fynbos biome, while possessing a richer faunal community, is fire-adapted and contains numerous plant species that are serotinous, that is they retain their seeds in persistent cones or fruits within the canopy. These seeds may be stored for years before being released either after a fire or when the plant itself dies. The majority of serotinous species are adapted for wind dispersal (Bond, 1985). Wind dispersal is likely to be particularly effective in areas that are frequently burnt. Fire rids the canopy and ground of obstacles that hinder the movement of wind and seeds (Hughes *et al*., 1994). Bond (1988) demonstrated that in the post-fire period, fruits of some *Protea* and *Leucadendron* species may be tumbled by wind over 50m. In addition, the thermal drafts associated with fire can result in propagules dispersal.

The rarer dispersal mechanisms (attachment, ant, ballistic and water) also display some conspicuous patterns. Due to the very low frequency of these dispersal mechanisms within South Africa it is probably not reasonable to make assertions along the two major environmental gradients thus these will be discussed in terms of the biomes in which they predominate.

Species that are dispersed by attachment are found almost exclusively in the Desert biome an area that experiences a high variation in both temperature and rainfall. All of the desert-dwelling trees that employ attachment as their means of dispersal (for example: *Acacia borleae, Cadaba aphylla* and *Pisonia aculeata*) have developed a sticky red substance that surrounds the seeds which is thought to adhere to the bills, feet and feathers of birds.

In number terms, ant-dispersed tree species predominate in the Fynbos biome. Tree species dispersed by ants are found in only two families the *Proteaceae* (genus: *Leucadendron, Leucospermum* and *Mimetes*) and the *Papilionoideae* (genus: *Podalyria* and *Virgilia*). All species within the *Leucospermum*, *Mimetes* and *Podalyria* genus are ant dispersed (Lengyel *et al., 2010)*. In these instances, myrmecochory can be considered a feature of these clades. Myrmecochory is a feature of 77 angiosperm families worldwide; in 55 of these families it occurs in over 50% of the species (Lengyel *et al., 2010).* The physiological and energetic costs of developing elaisosomes are thought to be smaller than those associated with the development of fleshy-fruit. This hypothesis is supported by the fact that myrmecochorous plants are more common on infertile soils (Milewski, 1983; Westoby et al., 1990).

Ballistic dispersal appears to coincide quite closely with the Indian Ocean Coastal Belt biome and the Savanna biome. Ballistic dispersal occurs most frequently in the *Acanthaceae* and *Euphorbiaceae* families. A dispersal spectra study undertaken by Griz and Machado (2001) in the Caatinga in Brazil found that all euphorbs within the study area rely on ballistic dispersal through the explosive separation of their mericarps. This suggests that ballistic dispersal might be phylogenetically constrained in the *Euphorbiaceae* family.

Lastly, water dispersal while uncommon throughout South Africa, occurs most often in the Indian Ocean Coastal Belt biome. Water- dispersed diaspores occur across five families namely; *Apocynaceae*, *Avicenniaceae*, *Caesalpinoideae*, *Lecythidaceae* and *Papilionoideae*. Half the species appear to be adapted for fresh-water dispersal, usually within swamp or mangrove environments (for example *Rauvolfia caffra*) while the other half is adapted for oceanic dispersal (for example *Caesalpinia bonduc*) and thus the trees exist on the verge of the tidal zone. It is likely that water dispersal has also been underestimated. Rivers are thought to function as corridors for dispersal and adaptation to dispersal down rivers is likely to have resulted in increased floating capacity in tree species that are associated with river systems (Johansson *et al.*, 1996).

CROSS CONTINENTAL COMPARISON

The large differences in dispersal spectra across the three continents suggest that geographical position and biome type are poor predictors of dispersal mechanism. The underlying variation necessitates the use of a phylogenetic analysis as these differences may be better explained by clade composition and phylogenetic conservatism than by independent selection for these traits based on the environment in which they exist. Across a number of habitat types, seed mass is often a conservative trait between genera or families (Lord *et al*., 1995). Advances in molecular systematics now provide opportunities to test explicit hypotheses regarding the evolutionary transitions between fruit traits (Weiblen *et al*., 2000). Unfortunately, such an analysis is beyond the scope of this study.

CONCLUSION

The differences in the tree dispersal spectra across the South African biomes were not considerable. Wind, vertebrate and ‘no special’ (unassisted) dispersal remain consistently common while ant, ballistic, attachment and water are typically rare. This divergence in the frequency with which these dispersal mechanisms occur is characteristic of trees. Vertebrate dispersal is most common in the moist tropical sector, while wind dispersal occurs most frequently in the xeric temperate sector of South Africa. This trend is likely to be coupled to the steady decline in seed mass I found from the lower to higher latitudes. The rarer dispersal mechanisms; attachment, ant, ballistic and water display characteristic associations with certain biomes; attachment in found most commonly in the desert, in terms of numbers ant dispersal most frequently occurs in the Fynbos Biome, water dispersal is linked to the Indian Ocean Coastal Belt Biome and ballistic dispersal predominates in the Savanna Biome. When comparing physiognomically similar vegetation types across the three southern hemisphere continents marked differences in dispersal spectra are evident. As fruit traits tend to be phylogenetically conserved, these differences are likely to represent evolutionary history constraints. Unfortunately, phylogenetic analyses are beyond the scope of this study but do represent a necessary future addition.

CHAPTER 3

The megafaunal fruit of South Africa:

exploring the factors that underlie their distribution

Introduction

By acting as seed vectors, frugivorous animals play a key role in the ecology and evolution of their food plants (Donatti *et al*, 2007; Herrera, 1995). Frugivores range in size from 5g mistletoe birds (Dicaeidae) to 7,500,000g elephants (Elephantidae). The range and distribution of frugivore sizes is not uniform across ecosystems or geographical regions (Mack, 1993). In light of this, one might suspect that these differences are mirrored in fruit size range and distribution.

Fruit and seed traits dictate both the means by which the seeds are spread from the parent plant, in addition to the likelihood of their subsequent establishment (Levin and Muller-Landau, 2000). The most significant and flexible of these traits is seed size. Seed size can vary 10^5-fold across plant species within the same community (Lord *et al.*, 1995). The potential for seedling establishment is considered to be a positive function of seed size (Levin and Muller-Landau, 2000, Westoby *et al,* 1996). Selection for increasing seed size not surprisingly comes at the cost of other aspects of plant dispersal fitness, in particular seed number. These trade-offs have left biologists (Geritz *et al*., 1999; Ezoe, 1998) theorising that plants invest a similar overall fraction of their resources in dispersal. It thus follows that a plant may place this dispersal investment in a few large, well-protected seeds, or it may adopt a shotgun approach – producing large numbers of small seeds that require very little resource investment.

Another fairly well established seed dispersal trade-off is between seed survivability (function of seed size) and dispersal range. As previously recognised, large seed size confers better seedling competition for safe sites but generally comes at the cost of reduced dispersal ability and thus higher competition with siblings (Ezoe, 1998). Support to this idea was lent by studies such as those by Ezoe (1998), Jordano (1995) and Sakai *et al.* (1998) that found that in the case of wind and bird-dispersed plants, smaller seeds would be transported greater distances from the parent plant but were less likely to survive the establishment phase than were larger seeds. However, when it comes to dispersal by large vertebrates, seed size should be considered relative to the body mass of the vector in question. It has thus been suggested (Guimares *et al*., 2008) that large vertebrate dispersal might prove an exception to the dispersal/survivability trade-off in seed size as large frugivores have the potential to transport considerable seed loads over significant distances.

Fruit that are built for dispersal by large frugivores are often conspicuous in both their size and appearance. The paradoxical existence of such large fruit in the Pacific lowlands of Costa Rica first provoked the attentions of Dan Janzen in the 1970’s. In collaboration with Pleistocene faunal expert Paul Martin they conjectured that these fruit were ecological anachronisms or ‘ghosts of mutualisms past’ that had evolved in the presence of megaherbivores but had remained long after their demise. Janzen and Martin (1982) exemplified the value of adding an important and often-neglected dimension to ecology - the dimension of time (Barlow, 2000).

The global spate of megafaunal extinctions occurred from fifty to one thousand years ago and wiped out large assemblages of giant vertebrates (megaherbivores- animal taxa with a large body mass typically exceeding 1000kg; Owen-Smith, 1988) on almost all continents and island groups, with the exception of Africa and small pockets of South East Asia (Hansen and Galetti, 2009). 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. Why then do these obsolete fruit trees remain? Guimares *et al*. (2008 *sensu* Barlow, 2000) suggest that a broad gradient of reliance on megafauna for dispersal exists (from moderate to extreme anachronisms). Regrettably, the plant fossil record is too incomplete to determine whether the plants more dependent on megafauna, have gone extinct as a result of dispersal failure (Barlow, 2000). The megafaunal fruit that remain are thought to do so as a result of scatter-hoarding rodents, introduced livestock, runoff, flooding, gravity, and human-mediated dispersal (Guimares *et al*., 2008). The loss of dispersal agents has, however, resulted in increasingly clumped spatial patterns, reduced geographic ranges and limited genetic variation in megafaunal fruit trees (Guimares *et al*., 2008).

The large fruit of the Central and West African forests have been studied on a few occasions (Feer, 1995; Blake, 2002) but those of the African savannas appear to have been ignored. In this study I have made the first attempt at compiling a list of the megafaunal fruit tree species of South Africa.

In addition, I explore the patterns underlying their distribution by considering three factors.

The first is the historical spread of elephants. While the African Savanna Elephant (*Loxodonta africana africana)* is not the only megaherbivore present in South Africa, it is the most frugivorous and occurs in densities and areas large enough to mirror extinct megafaunal populations (Prado *et al*, 2001). Elephants are the last survivors of the Proboscidea, an order that originated in Africa some 60 million years ago (Mya) and afterward radiated to all continents with the exception of Australia and Antarctica (Shoshani, 1998). The fossil record of elephants in Africa is patchy (Haynes, 1992). What is known of the fossil history of the Proboscidea is that it was punctuated by a number of adaptive shifts that brought about the mastodonts, gomphotheres, stegodonts and elephants (Carruthers *et al*., 2008). To determine how closely coupled the distribution of our megafaunal fruit trees is to the distribution of the savanna elephant, this study will attempt to develop a picture of their historical spread within South Africa by collating records of elephant skeletal remains, historical sightings, indigenous art and written records left by early European travellers, naturalists and hunters.

The second factor that warrants examination is the environmental conditions that support the existence of megafaunal fruit. To my knowledge, only one study has compared the frequencies of megafaunal fruit across different biomes. This study (Donatti *et al,* 2007) found that the frequency of megafaunal fruits was not constant across two distinct Brazilian ecological communities. In the lowland Atlantic rainforest, 13% of the fleshy-fruited tree species (n = 246) had megafaunal fruit characteristics while in the Pantanal site, the proportion of megafaunal fruit species reached 30% (n =147 species). The authors (Donatti *et al,* 2007) attributed this trend to both the presence of more back-up dispersal agents in the Pantanal and to the frequent flood events that occur there and not in the Atlantic Forest. Flooding is thought to act as a surrogate disperser for megafaunal species (Barlow, 2000; Hunter, 1989).Due to the absence of megafauna the authors were unable to determine whether the divergence in megafaunal fruit frequencies between the two sites was owing to the lack of surrogate dispersal agents or attributable to limits imposed by the abiotic environment. Here, I explore the frequency and reach of megafaunal fruit across the South African biomes and bioregions. In addition I examine their distribution along the following environmental gradients: precipitation; soil fertility and temperature, in an attempt to elucidate which factors best predict where they occur.

The final factor that I explore is the service that elephants and baboons (as a proxy for early humans) provide megafaunal fruit. Unlike the Americas, for example, Africa possesses not only a largely intact megaherbivore community but also large terrestrial primates. These ground-dwelling primates have been able to adapt to the presence of humans and unlike large vertebrates are not threatened by the ongoing extinction crisis (Duffy *et al*., 2009). For this reason one might expect that the fate of megafaunal fruits in Africa is likely to differ from that in the Americas, even if elephants and other large megaherbivores are lost from an area. Understanding the comparative service that elephants and baboons provide megafaunal fruit will help direct management and conservation efforts.

Numerous factors shape the seed dispersal service that elephants and baboons offer. First, owing to their large size and feeding requirements, elephants generally have large home ranges and occur at low densities (Owen-Smith, 1988).For example, elephants in the Kalahari Sands, travel 20 – 50 km or more in daily foraging treks within home ranges of 900 – 3000km (Conybeare, 1991). Baboons, in contrast have home range sizes between 0.75 and 1.1 km^2 and make foraging treks of 0.3 - 2.0 km per day (Bole Valley, Ethiopia; Dunbar and Dunbar 1974). This being said elephants can essentially only move within established park boundaries while the movement of baboons is not curtailed by fences. Secondly, seed gut passage time, which is the time from ingestion to defecation, differs markedly between elephants and baboons. Elephants have been shown to retain seeds for up to 96 hours (this study, chapter 4).To my knowledge, gut passage experiments have not been undertaken for baboons however the gut passage time for chimpanzees is 36-38 hours (Altmann, 1998) so given the difference in size between chimpanzees and baboons it is likely to be approximately 20-30hours. The gut passage time has two major effects on seeds; first and foremost it affects their spatial distribution – longer gut passage time allows for the seed to get further from the parent and secondly it influences their exposure to the acid environment of the digestive tract which has an effect upon the viability and germination potential of the seeds. Thirdly, the characteristics of the fruit that elephants and baboons select differ in some respects. Due to their gape size, elephants consume very large fruit that range in length from 2 – 36cm (Yumoto *et al*., 1995). Specifically, Guimares *et al*., (2008) defined elephant fruits as either large-sized (4-10cm) with one to few large seeds or alternatively very large (>10cm) and multi-seeded. Baboon studies, on the other hand (Kunz and Linsenmair, 2010; Dunbar and Dunbar, 1974) 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 pool. Of significance they found that baboons tended to act as seed predators when fruit were dry and seeds were large and, when feeding on the pulp of fleshy fruits with large seeds, the seeds were usually dropped rather than swallowed (Kunz and Linsenmair, 2010). Medium and large sized fruit with small to medium-sized seeds were in most instances swallowed and effectively dispersed (Kunz and Linsenmair, 2010).

Owing to their smaller body size, gut passage time and ranging distances baboons are unlikely to provide a dispersal service at the same scale as elephants. This being said baboons might offer seeds the advantage of being carried outside of park boundaries, up steep slopes and into rocky areas that might provide safe sites for their establishment. Baboons act as either effective dispersers or potent predators depending on the fruit species in question. Assertions on the seed dispersal service baboons provide are therefore difficult to generalise as a distinctive dispersal syndrome and necessitate each tree species being examined separately.

In summary this study will present a list of proposed megafaunal fruit trees for South Africa and it will explore the pattern underlying the distribution of these megafaunal fruit by addressing three questions: (1) is the distribution of megafaunal fruit coupled to the historical spread of megafauna? (2) is the distribution of megafaunal fruit trees related to their position along major environmental gradients? (3) what service do elephants and baboons (as a proxy for early humans) provide and how has this affected the evolution of megafaunal fruit?

Methods

CLASSIFICATION OF MEGAFAUNAL FRUIT

In order to produce an inclusive list of megafaunal fruit trees, I began by constructing a comprehensive database of all South African trees species (n=1126). This database was built in part from information obtained in the Coates Palgrave (2002) tree reference book. I 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 included only those trees that had a South African tree number. The large number of gaps in the database were filled by an extensive literature review (Supplementary Reference List A) in addition to information sourced from three existing databases: the South African National Biodiversity Institute's plant information website, the Royal Botanic Gardens Kew Seed Information Database (SID, 2008) and the JStor Global Plants database (2013). The result is an extensive tree database that includes information pertaining to the taxonomy, morphology and ecology of each of South Africas tree species. In addition and of relevance to this chapter, multiple fruit and seed traits were recorded. To begin, the fruit of each species was classified as either dry or fleshy. These two fruit types were then further categorised into eight subtypes (see Chapter 2 for more detail). Where available the fruit diameter, length and width measurements were recorded. The fruit size was taken to be the largest of these three values in keeping with a study by Almeida-Neto *et al.* (2008). The 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. Characteristics of the seed such as the number per fruit, size and colour were also logged. Seed mass estimates were sourced exclusively from the Royal Botanic Gardens Kew Seed Information Database (SID, 2008; and references therein - Supplementary Reference List A). The fruiting phenology of the trees was also recorded.

Guimares *et al.*'s (2008) operational definition of megafaunal fruit was then applied across all 1126 tree species. Large fruit (>= 4cm) were tagged and then separated out against two fruit types. The first (Type 1) consisted of fleshy fruit 4-10cm in diameter with up to five large seeds, while the second (Type 2) was made up of either fleshy or dry fruit greater than 10cm in diameter with numerous small seeds. Where dry, Type 2 fruit were also required to be indehiscent. An additional Type 1b category was created for those fleshy fruit that were 3-4cm in diameter but possessed very large seeds (seed mass >5000g per 1000 seeds).

STATISTICS

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

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.

Distribution hot spots of dry and fleshy fruit were identified by eye based on spatial clustering.

HISTORICAL ELEPHANT DISTRIBUTIONS

To establish the historical distribution of the savanna elephant, a database that collated records of elephant skeletal remains, historical sightings, indigenous art and written records left by early European travellers, naturalists and hunters was constructed. In the case of the Northern, Western and Eastern Cape provinces this involved working through the volumes of Skead *et al.* (2007, 2011) and carefully recording every note on historical elephant sightings since 1497. Each sighting was assigned to a geographic sector predefined by Skead (Figure 1). Date details, observer name/s and the elephant herd size was also noted. In the absence of such works for the rest of the country, records were taken directly from a map produced by Ebedes *et al.* (1995). The possibility that the elephant skeletal remains might have been moved from elsewhere was disregarded.

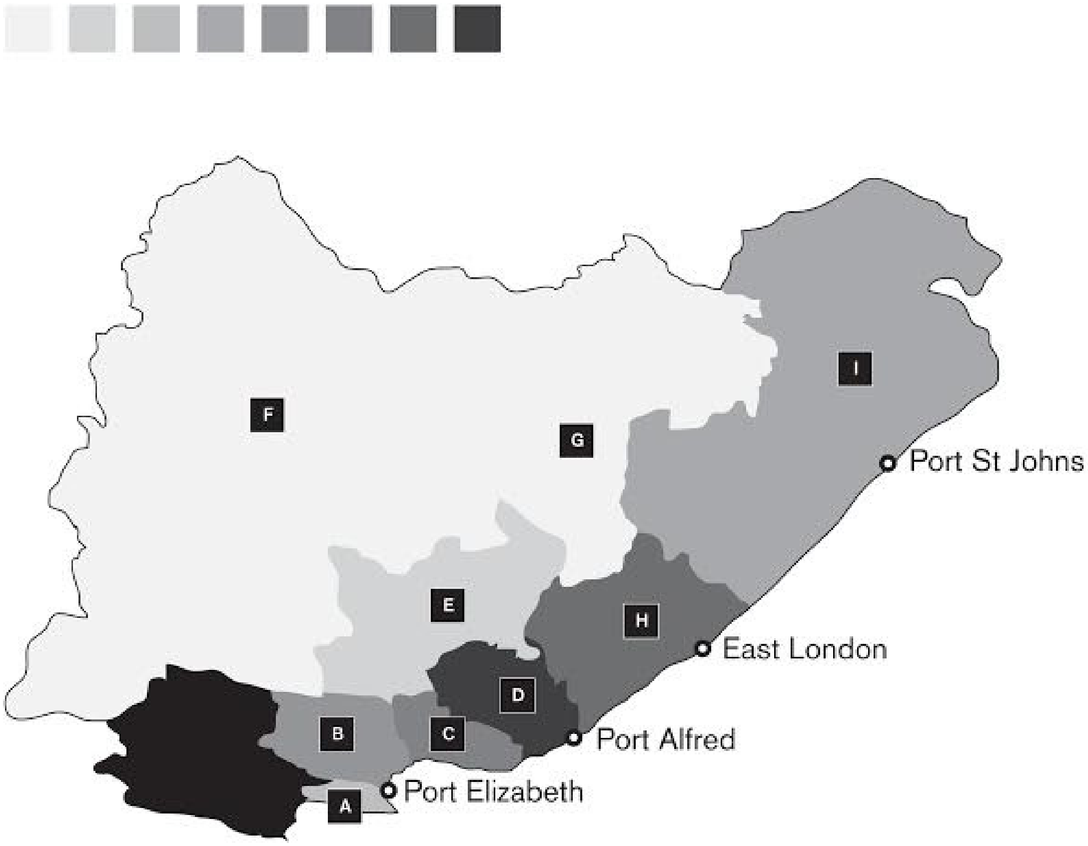


Figure 1: The number of historical elephant sightings by sector in the Eastern Cape. Colour coding represents frequency of incidents per sector (light = few, dark = many). Sectors and number of observations are as follows: A) Gamtoos River to Port Elizabeth: 6; B) Port Elizabeth to the Sundays River (including the Uitenhage and Kirkwood Districts): 10; C) Sundays River to Bushmans River (Alexandria district): 17; D) Bushmans River to the Great Fish River (Albany and Bathurst districts): 38; E) The Sub-coastal Interior (Somerset East, Bedford, Adelaide and Fort Beaufort districts): 4; F) The East Cape Midlands (the Karoo): 0; G) The Border Interior and the North-eastern Cape: 0; H) The Ciskei (Great Fish River to the Great Kei River, and the hinterland): 19; I) The Transkei and East Griqualand (Great Kei River to the Mtamvuna River, and the hinterland): 8. The data was sourced from Skead's (2007) collection of written records left by early European travellers, naturalists and hunters from the 1490s onwards. The sectors follow those outlined by Skead (2007).

ENVIRONMENTAL DATA

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

To explore the environmental gradients underlying the distribution of megafaunal fruit species in the region, the location data points were also spatially joined to climatic data layers sourced from the South African Atlases of Agrohydrology and Climatology (2008); namely mean annual precipitation (MAP), mean annual temperature (MAT), soil fertility, rainfall concentration, rainfall seasonality, CV of annual precipitation. I used a principal component analysis to obtain ordinations of megafaunal fruit distribution according to these climatic predictor variables. The PCA was carried out on a subset of megafaunal trees using the library ade4 of the R package (2005). The sample was determined by cutting a polygon in ARCMAP/ARCGIS software. The climatic variables used are all ordinal values. The sample included 174 megafaunal fruit tree location points in addition to 1473 data points belonging to non-megafaunal tree species. The sample area included the Grassland, Savanna and Nama-Karoo biome.

ELEPHANT AND BABOON DISPERSAL

The dispersal service offered to each of the thirty-one megafaunal fruit species by elephants and baboons was determined by means of an extensive literature review (Supplementary Data: Reference List B). Very little work has been undertaken on seed dispersal in Southern Africa so there are understandable knowledge gaps (Supplementary Data: Table 1). Assumptions based on the dispersal services proffered to morphologically similar species in the same genus in West and/or East Africa were made in a few instances. Baboons were classified as a seed predator when they were found to either consume fruit in their unripe state or when they predated on the seed itself. In addition, where information quantifying the service that elephants offered the megafaunal fruit species was found it was summarised in a second table (Table 5).

Results

THE MEGAFAUNAL FRUIT OF SOUTH AFRICA

Of the 1126 South African tree species, 31 were identified as having megafaunal fruit (Table 1). Thirteen species fitted Guimares *et al.*'s definition of Type 1 fruit. This included two species, *Schinziophyton rautanenii* and *Sclerocarya birrea* fruit (called Type 1b*,* Table 1) that are only 3-4cm in their maximum length but justified inclusion due to their particularly hard and heavy seeds (12500 and 5405g per 1000 seeds respectively). Eighteen species fitted the Type 2 definition; seven of these are fleshy while the remaining eleven are dry fruit (Table 1). A number of fleshy fruit species (n=16) that are 4 to 10cm in maximum length were rejected as megafaunal fruit species on the basis that their fruit contain greater than 5 seeds. The list of these species (Supplementary Data Table 2) includes; *Rothmannia capensis*, *Rothmannia fischeri*, *Strychnos madagascariensis*, *Gardenia cornuta*, *Monodora junodii* and *Solanum aculeastrum,* sizeable fruits that are likely to be noted by their absence.

The majority (54.8%) of megafaunal fruit are found in four families – Mimosoideae (7, 22.6%), Areceae (4, 12.9%), Strychnaceae (3, 9.7%) and Caesalpinoideae (3, 9.7%). In terms of frequency however, megafaunal fruit appear most often in Chrysobalanaceae (1 of 1,100%), Bombacaceae (1 of 1,100%), Arecaceae (4 of 6, 66.7%) and Balanitaceae (2 of 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 35mm in *Sclerocarya birrea* to 450mm (up to a maximum of 900mm) in *Kigelia africana* (Figure 2). The average seed size for Type 1 fruit is 34mm whereas for Type 2 it is 13mm. Seeds of Type 2 fruits are larger than one might have expected; *Strychnos pungens* for example has >5 seeds that are each over 3g in mass (SID, 2008).

Of the megafaunal fruits with data available on their fruit character type; the majority are either drupes (38.5%) or leguminous pods (42.3%) while berries (19.2%) represent the least likely form. With regards to their fruiting phenology no obvious pattern emerges, *Schinziophyton rautanenii* fruits for only one month of the year while three of the palm fruit (*Raphia australis*, *Hyphaene coriacea* and *Hyphaene petersiana)* fruit all year round (Figure 4). Megafaunal fruit are predominantly brown (53.3%), yellow-orange (26.7%) and green (10%) (Table 2, Figure 2 and 5). This is in stark contrast (χ 2 = 265, $p < 0.05$, df = 2, Table 2.2) to smaller vertebrate-dispersed fruit (ornithochores) that are for the most part purple-black (31.7%) and red (24.4%).

Table 1: The megafaunal fruit tree species of South Africa. The fruit are separated into type according to Guimares *et al*. (2008). Type 1 consists of fleshy fruit 4-10cm in diameter with up to five large seeds. A subset to Type 1 (b) was created for those fleshy fruit that were 3-4cm in diameter but possessed very large seeds (seed mass >5000g per 1000 seeds). Type 2 is made up of either fleshy or dry fruit greater than 10cm in diameter 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 (outside parentheses) and the total number of species per family (inside parentheses). With regards to the fruit and seed traits: the fruit size is the maximum dimension (diameter or length); the seed size and seed number was taken from the Jstor Plant Database (2013). The seed mass is given in mass (g) per 1000 seeds and was taken from the Kew Seed Database (2008). Species name as per Coates Palgrave (2006). The changes in the genus *Acacia*, with the exception of *Faidherbia* are not recognised here.

Family	**Megafaunal Species /Family**	**Megafaunal Type**	**Species**	**Fruit Type**	**Size of Fruit (mm)**	**Number of Seeds**	**Size of the Seed (mm)**	**Seed Mass**
Arecaceae	4 (6)	Type I	*Raphia australis*	drupe	90	1	....	....
		Type I	*Hyphaene petersiana*	drupe	50	1	50	21500
		Type I	Hyphaene coriacea	drupe	50	1	50	
		Type I	*Borassus aethiopum**	berry	150	3	....	....
Balanitaceae	2(3)	Type I	*Balanites aegyptiaca*	drupe	50	1	50	1150
		Type I	*Balanites maughamii*	drupe	50	1	50	827
Boraginaceae	1(9)	Type I	*Cordia grandicalyx*	drupe	40	1	....	....
Chrysobalanaceae	1(1)	Type I	*Parinari curatellifolia*	drupe	50	1	27	3315
Papilionoideae	1(56)	Type I	*Cordyla africana*	drupe	80	1-3	32	10000
Sapotaceae	2(15)	Type I	*Mimusops zeyheri*	berry	45	1	18	291
		Type I	*Vitellariopsis marginata*	berry	50	1-2	25	....
Euphorbiaceae	1(75)	Type Ib	*Schinziophyton rautanenii*	drupe	35	1	20	12500
Anacardiaceae	1 (59)	Type Ib	*Sclerocarya birrea*	drupe	35	2-3	15	5405
Rubiaceae	1 (89)	Type II	*Gardenia volkensii*		100	numerous	10	24
Strychnaceae	3 (10)	Type II	*Strychnos cocculoides*	berry	100	numerous	22	476

		Type II	Strychnos spinosa	berry	120	numerous	....	377
		Type II	*Strychnos pungens***	berry	120	numerous	27	3286
Bombacaceae	1(1)	Type II	*Adansonia digitata*		240	numerous	10	478
Bignoniaceae	1(8)	Type II	*Kigelia africana*		675	125	10	125
Capparaceae	1(26)	Type II	*Cladostemon kirkii*		220	numerous	13	....
Mimosoideae	7(67)	Type II dry	*Faidherbia albida*	pod	250	numerous	11	110
		Type II dry	*Acacia erioloba*	pod	130	18	14	251
		Type II dry	*Acacia sieberiana*	pod	210	numerous	12	129
		Type II dry	*Acacia nilotica*	pod	125	numerous	9	127
		Type II dry	*Acacia haematoxylon*	pod	140	numerous	11	500
		Type II dry	*Amblygonocarpus andongensis*	pod	170	numerous	....	....
		Type II dry	*Dichrostachys cinerea*	pod	100	numerous	6	26
Caesalpinoideae	3(33)	Type II dry	*Piliostigma thonningii*	pod	220	numerous	9	138
		Type II dry	*Tamarindus indica*	pod	140	6-12	17	542
		Type II dry	*Cassia abbreviata*	pod	900	numerous	12	357
Papilionoideae	1(56)	Type II dry	*Swartzia madagascariensis*	pod	300	numerous	8	105

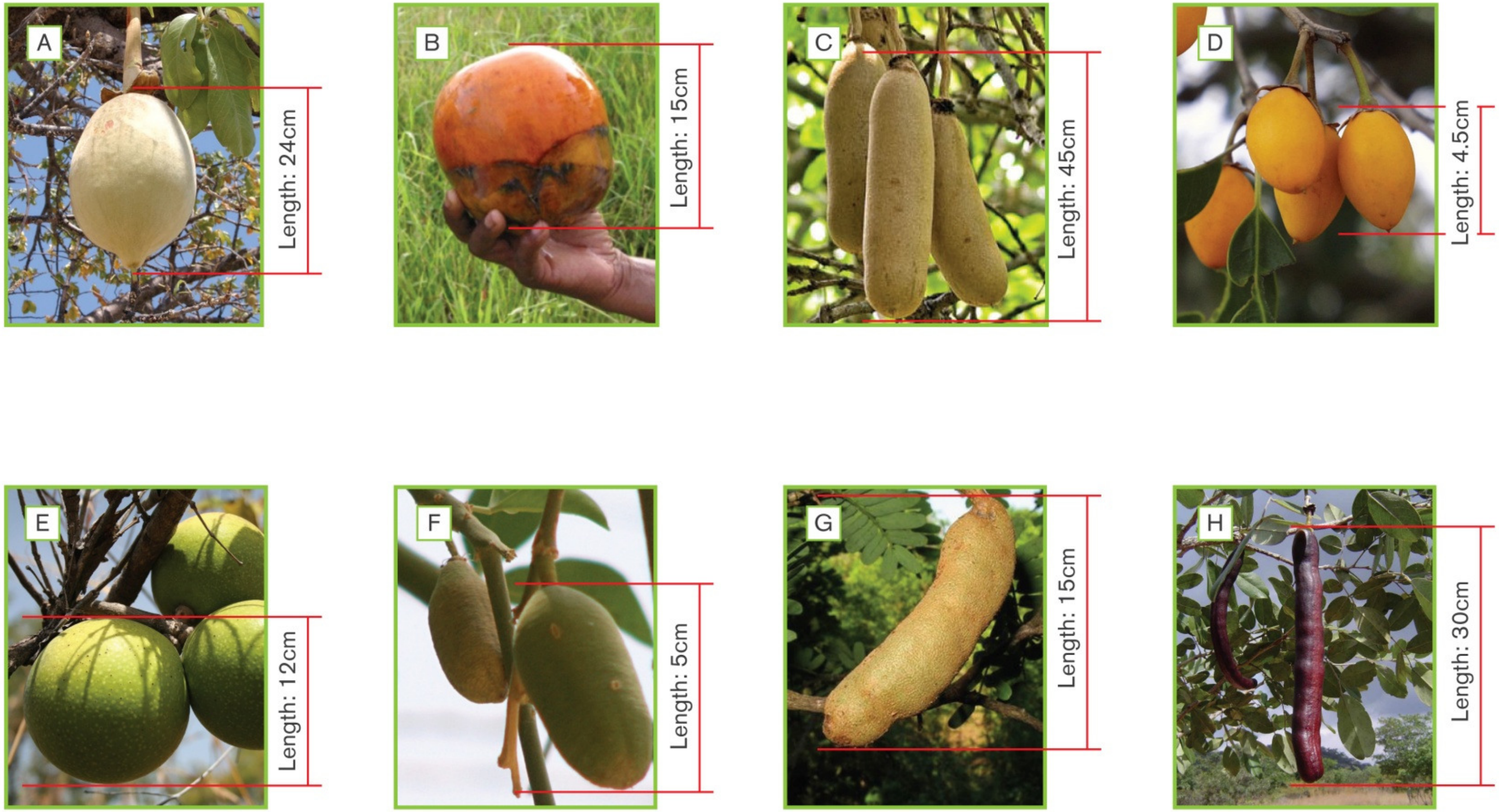


Figure 2: A selection of fleshy and dry fruited megafaunal species from South Africa depicting their size, shape and colour variability. A: *Adansonia digitata*, Bombacaceae; B: *Borassus aethiopum,* Arecaceae; C: *Kigelia africana,* Bignoniaceae; D: *Mimusops zeyheri,* Sapotaceae; E**:** Strychnos spinosa, Strychnaceae; F: *Balanites aegyptiaca*, Balanitaceae; G: *Tamarindus indica*, Caesalpinoideae; H: *Swartzia madagascariensis,* Papilionoideae. Fruit length indicated. See Supplementary Data for photograph references.

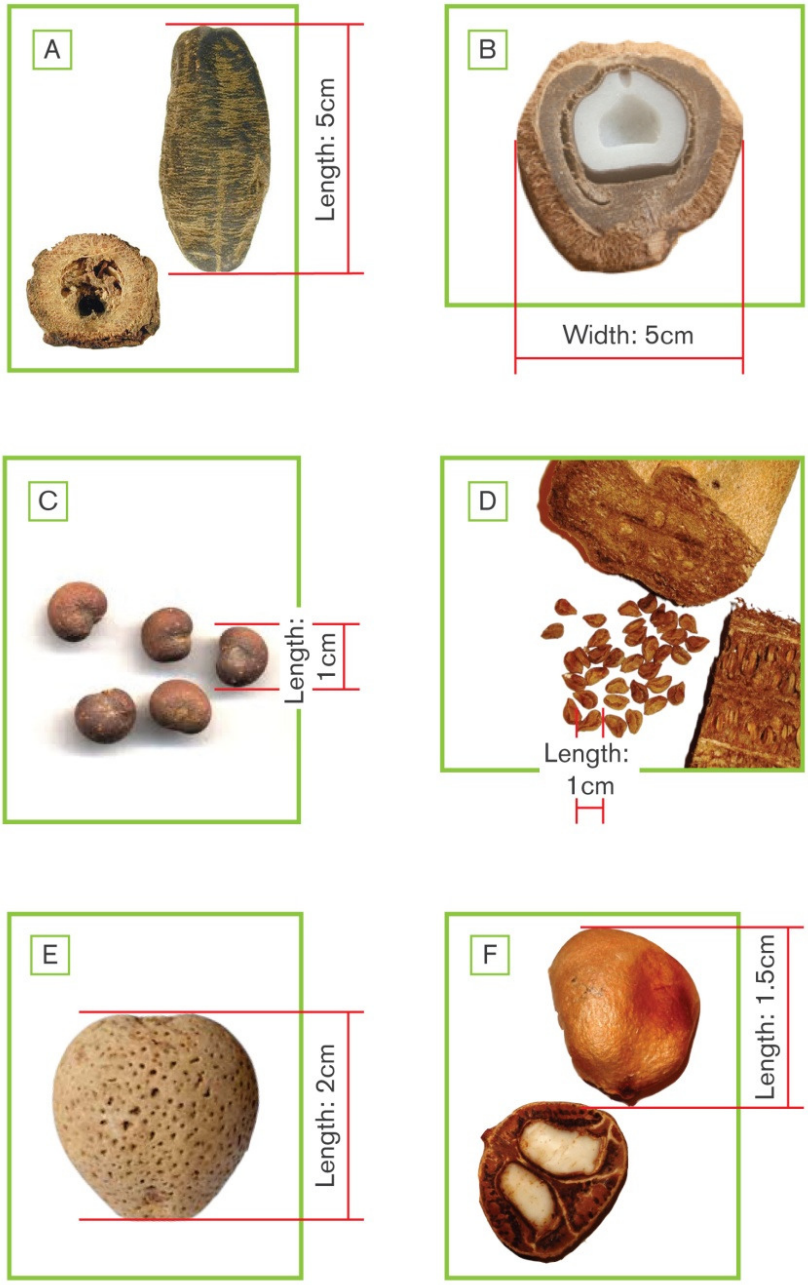


Figure 3: Examples of seeds of megafaunal fruits. A: *Balanites maughamii,* B: *Hyphaene coriacea,* C: *Adansonia digitata, D: Kigelia africana,* E: *Schinziophyton rautanenii,* F: *Sclerocarya birrea*

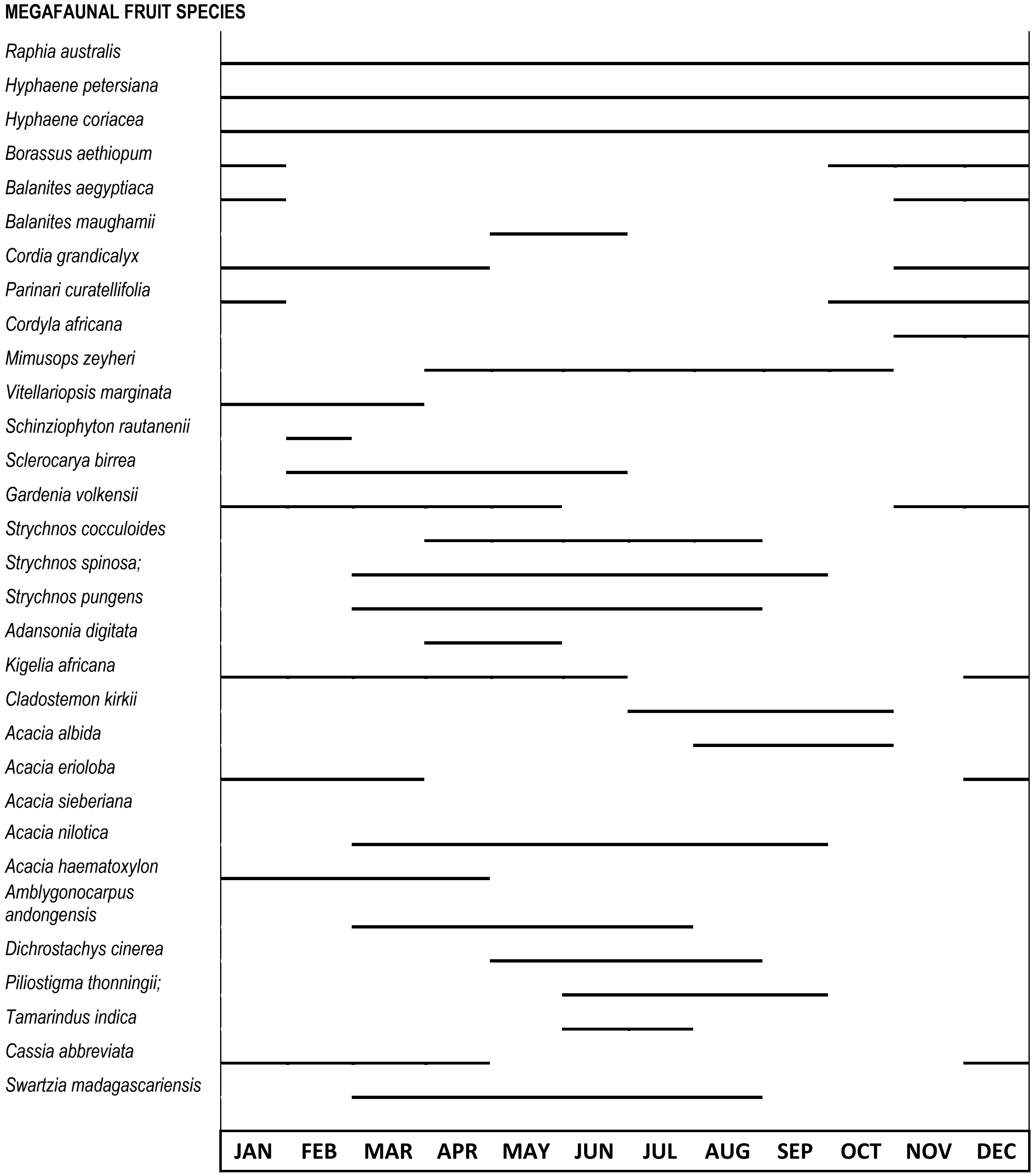


Figure 4: Fruiting phenology of the 31 megafaunal tree species. Basal black lines indicate the months that the species is in fruit.

Table 2.1: Fruit colour in both vertebrate-dispersed (small mammal and bird) versus megafaunal fruits plus result of the chi-squared test (χ 2) where the vertebrate dispersed fruit colours were the expected and the megafaunal fruit colours were the observed (df = 7).

	Brown	**Grey**	**Green**	**Yellow-Orange**	**Others**	**White**	**Red**	**Purple-Black**
Vertebrate (n=536)	112 (20.9%)	2 (0.4%)	20 (3.7%)	88 (16.4%)	11 (2.1%)	2 (0.4%)	131 (24.4%)	170 (31.7%)
Megafaunal (n=30)	16 (53.3%)	2 (6.7%)	3 (10%)	8 (26.7%)	0 (0%)	0 (0%)	1 (3.3%)	0 (0%)

*Fruit colour data was missing for the megafaunal species Ochna glauca.

Table 2.2: Observed versus expected number of species across the dispersal mechanism–colour combinations. Colour categories were combined as some contained cell expected values <5. ‘other’ and ‘white’ were excluded from the analysis. A Chi-squared test was performed (df = 2).

	Brown/Grey/Green	Yellow-Orange	Red/Purple-Black	χ2 value
Vertebrate (expected)	8	5	17	265
Megafaunal (observed)	21	8	1	

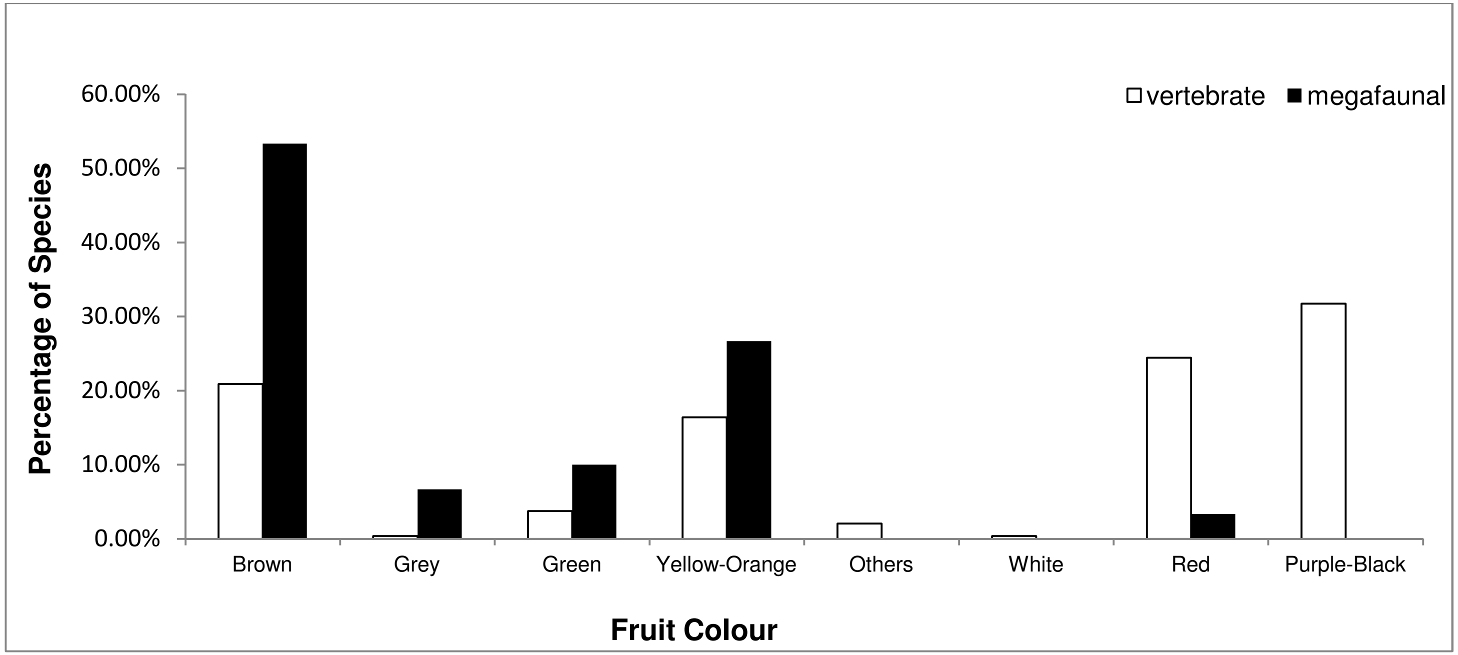


Figure 5: Fruit colour in both vertebrate-dispersed (black bars, n=536) and megafaunal fruits (white bars, n=30).

DISTRIBUTION OF MEGAFAUNAL FRUIT

Megafaunal fruit tree species occur almost exclusively in the northern half of the country (Figure 6.1 – Figure 6.3). 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 hot spot (Figure 7) is located along the north central border of South Africa west of the fleshy fruit hot spot.

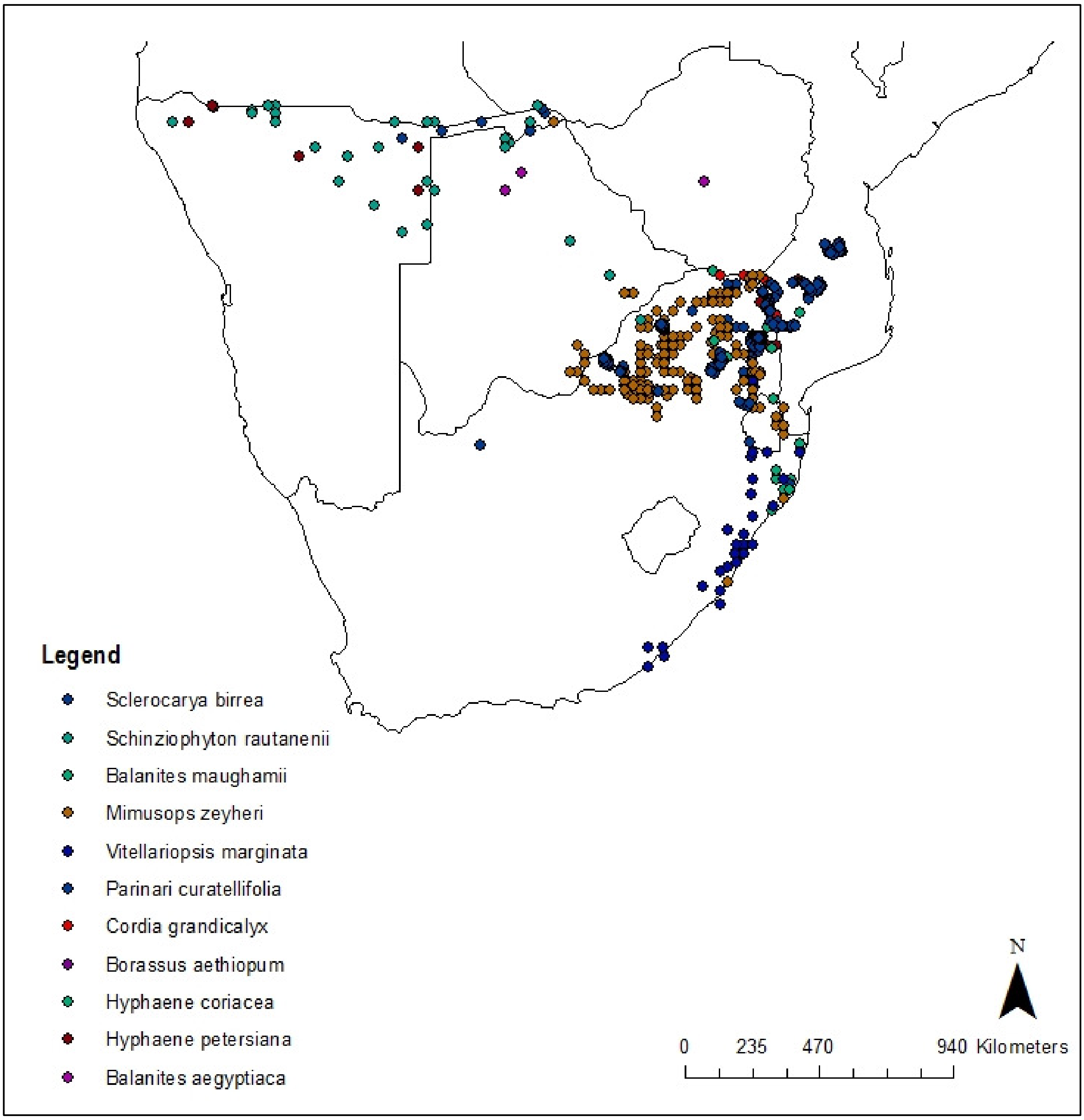


Figure 6.1: Distribution of Type 1 fleshy megafaunal fruit species. Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. Map produced in ArcMap 10.2. Scale shown.

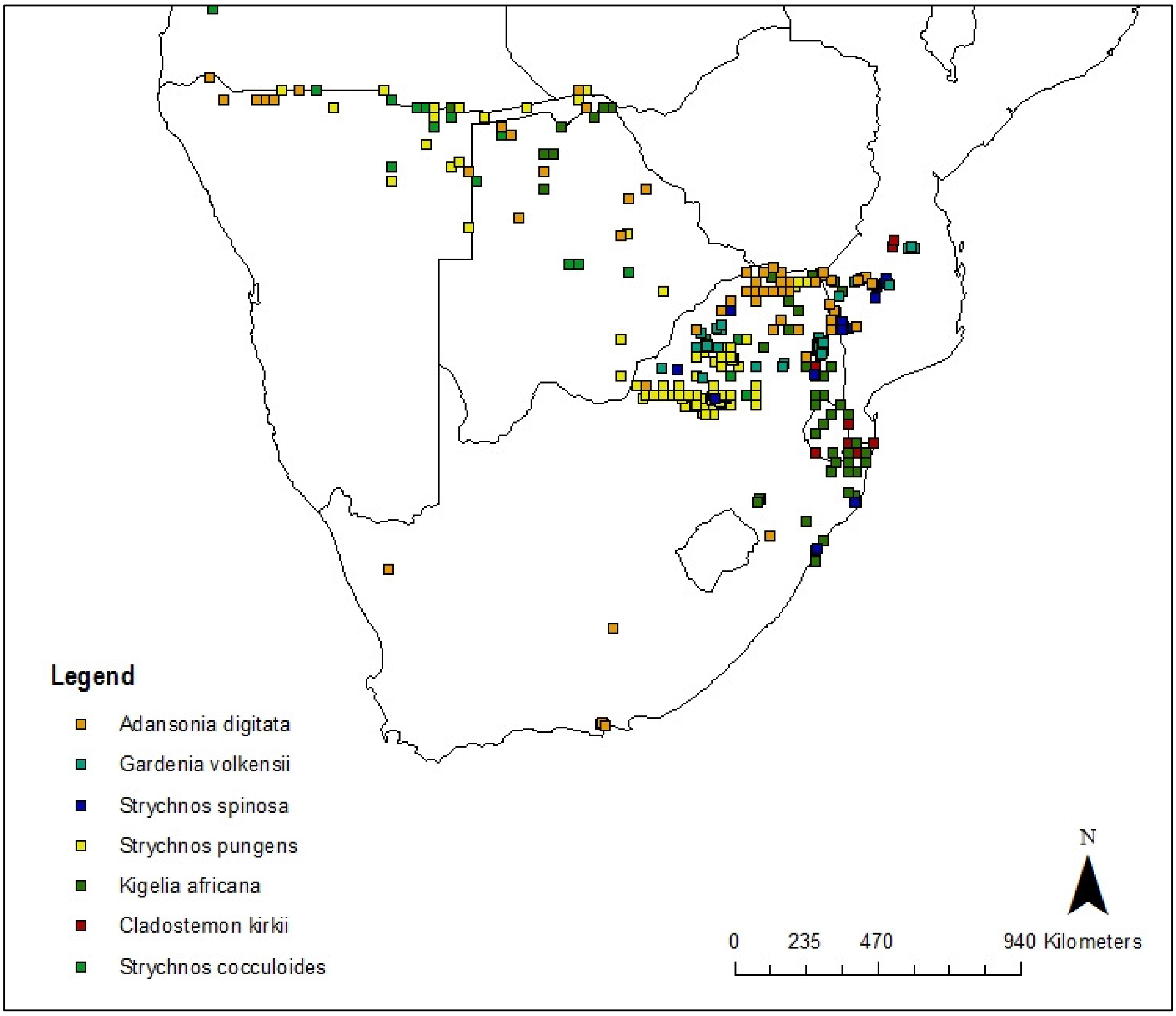


Figure 6.2: Distribution of Type 2 fleshy megafaunal fruit species. Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. Map produced in ArcMap 10.2. Scale shown.

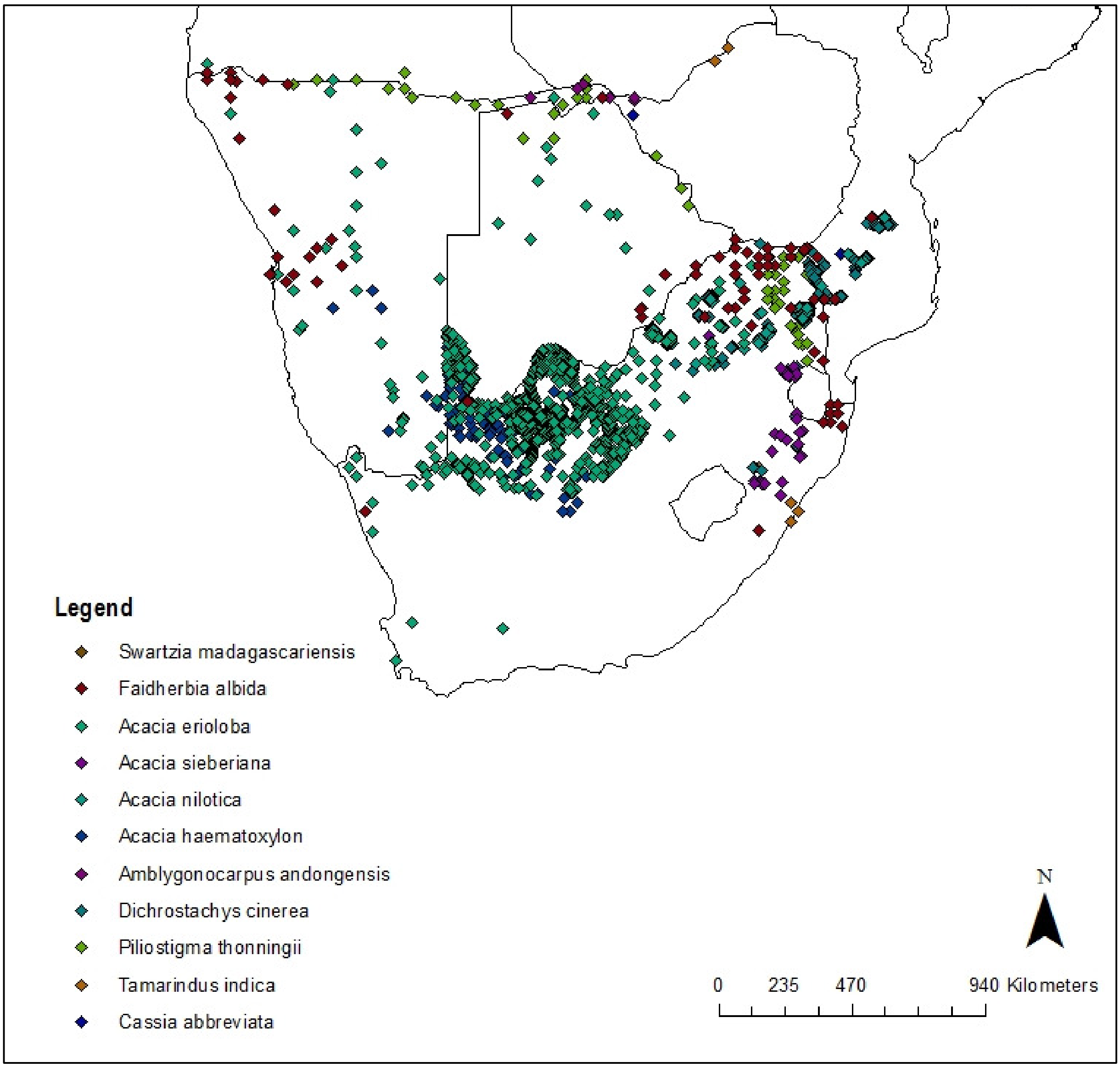


Figure 6.3: Distribution of Type 2 dry megafaunal fruit species. Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. Map produced in ArcMap 10.2. Scale shown.

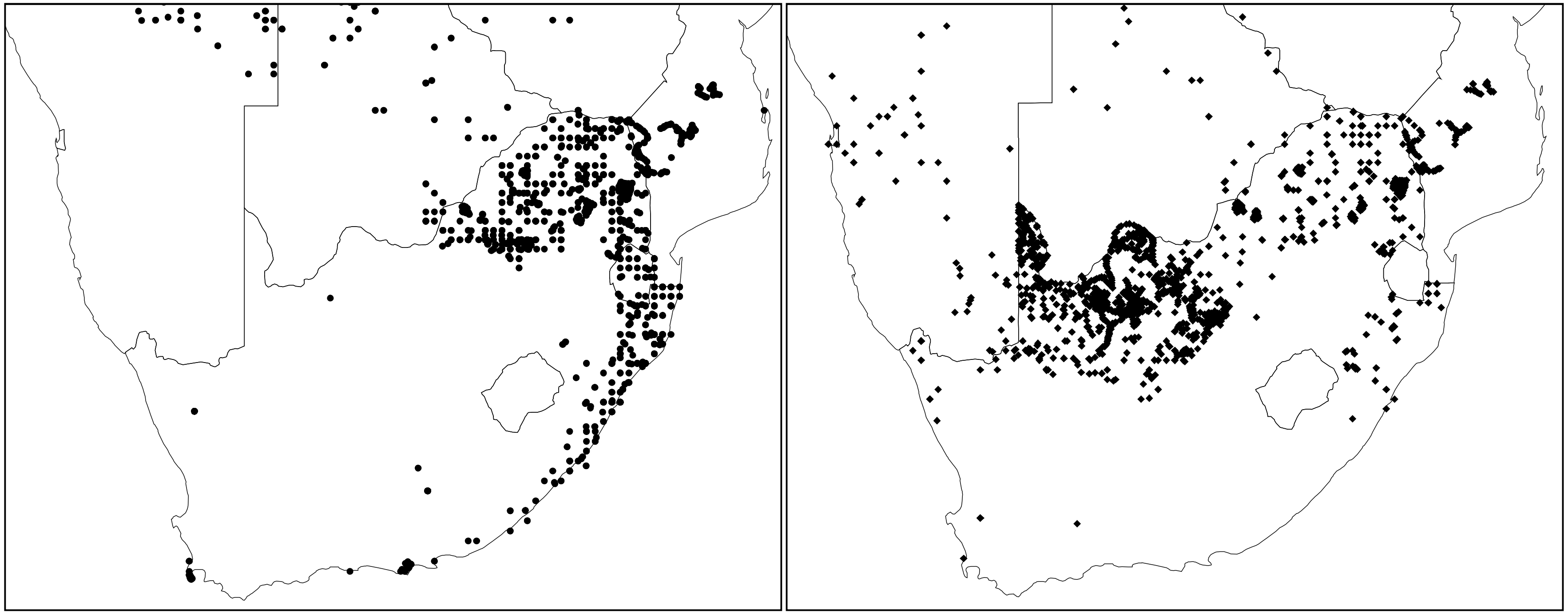


Figure 7: Distribution of fleshy (left) (n = 20) versus dry (right) (n=11) megafaunal fruit. Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database.

THE HISTORICAL SPREAD OF MEGAFAUNA

The historical distribution of elephants in South Africa is indicated in Figure 8. It appears that elephants have at one time or another occurred over much of South Africa. There is a clustering of historical elephant occurrence in the Western and Eastern Cape. 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 reliable historical records. A paucity of incidents occurs in the interior of South Africa but there are nevertheless some records (Figure 8).

Based on Skead's comprehensive synthesis of written records left by early travellers, naturalists and hunters in the Eastern Cape from the 1490s onwards, it appears that elephant numbers have been historically concentrated in the southern coastal belt (Figure 1). The analysis of Skead's record collection additionally indicates the fact that historical elephant herds were particularly large - up to 450 head strong being sighted in the Bushman's River region of the Eastern Cape (Table 3).

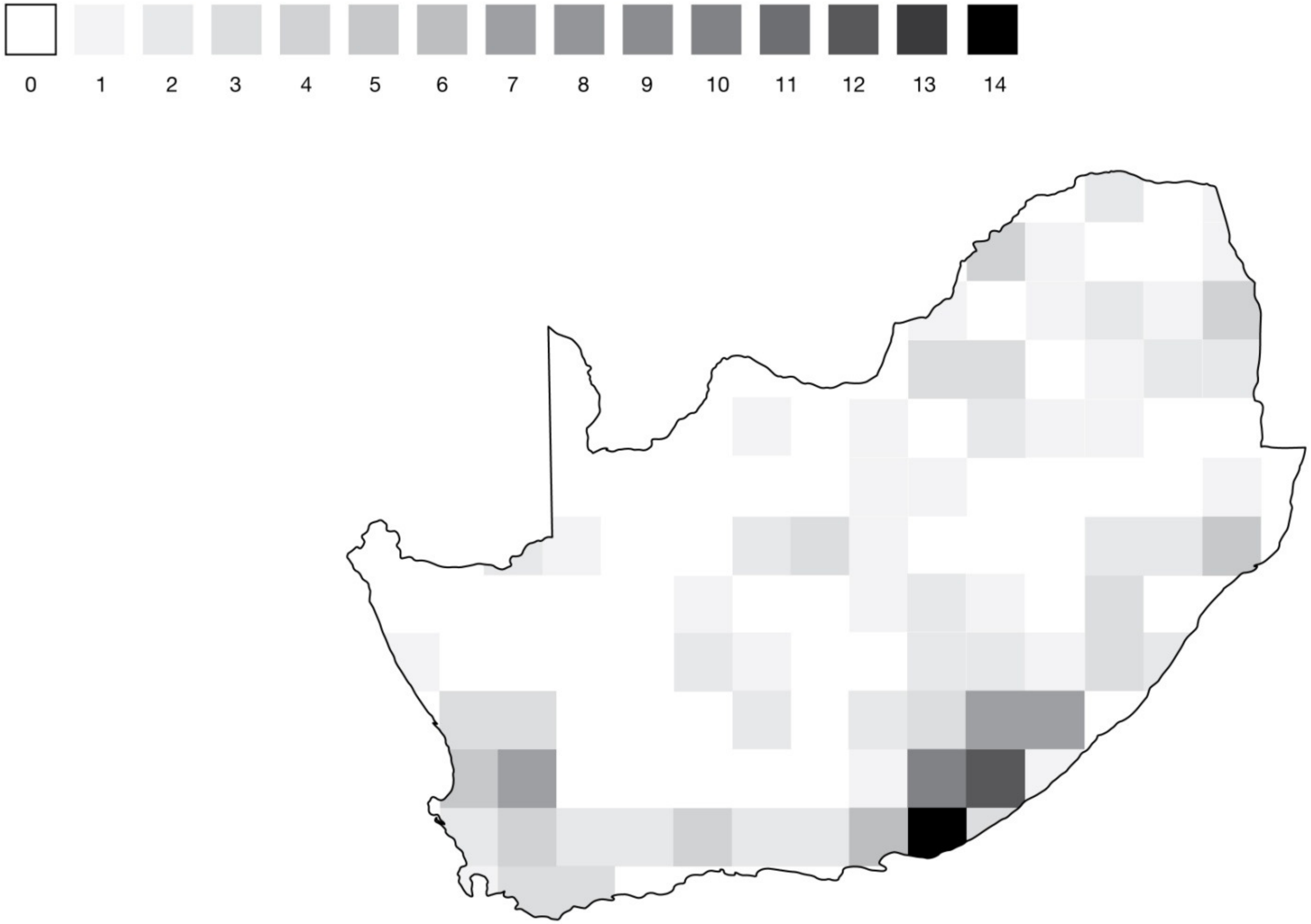


Figure 8: The historical distribution of elephants in South Africa (adapted from Ebedes *et al*., 1995). See key above for a count of elephant occurrences per grid square. Occurrences include finds of elephant skeletal remains, historical sightings and presence of indigenous art depicting elephants.

Table 3: A synthesis of the historical elephant observational data for the Eastern Cape. The data was sourced from Skead's (2007) collection of written records left by early European travellers, naturalists and hunters from the 1490s onwards. The sectors follow those outlined by Skead (2007).

Sector ID	Sector Description	Number of Sightings	Median number of elephants/sighting	Maximum Number of Elephants
A	Gamtoos River to Port Elizabeth	6	5	50
B	Port Elizabeth to the Sundays River (including the Uitenhage and Kirkwood Districts)	10	17.5	160
C	Sundays River to Bushmans River (Alexandria district)	17	50	440
D	Bushmans River to the Great Fish River (Albany and Bathurst districts)	38	40	450
E	The Sub-coastal Interior (Somerset East, Bedford, Adelaide and Fort Beaufort districts)	4	32	53
F	The East Cape Midlands (the Karoo)	0	0	0
G	The Border Interior and the North-eastern Cape	0	0	0
H	The Ciskei (Great Fish River to the Great Kei River, and the hinterland)	19	50	300
I	The Transkei and East Griqualand (Great Kei River to the Mtamvuna River, and the hinterland)	8	15	50

POSITION OF PLANT COMMUNITIES ALONG MAJOR ENVIRONMENTAL GRADIENTS

Megafaunal fruit species distribution is closely correlated with that of the Savanna biome (Figure 9). Of the 31 megafaunal fruit species 29 of them (93.5%) occur, at least in part, in the savanna biome. More specifically, at the level of the bioregion, megafaunal fruit species are most common in the Lowveld Bioregion (23 of 31 – 74.2%), the Central Bushveld Bioregion (18 of 31 – 58.1%) and the Mopane Bioregion (17 of 31 -54.8%). In terms of numbers, megafaunal fruit species are least common in the Albany Thicket (2 of 31 – 6.5%) and in the Desert Biome (2 of 31 – 6.5%). Across the board however, megafaunal fruit species represent a very small proportion of the dispersal spectra in all biomes (1-5%). 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.

The principal component analysis (Figure 10) shows a clustering of megafaunal fruit where the values of temperature average and CV annual precipitation are high.

Table 4: Megafaunal fruit species distributions across biomes and bioregions. The numbers of species are listed in columns. For comparative purposes, the numbers of vertebrate (bar the megafaunal) dispersed species are also listed in columns. The biomes and bioregions are as mapped in Mucina and 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.

BIOME	BIOREGION	VERTEBRATE (All bar megafaunal)	MEGAFAUNAL	% OF MEGAFAUNAL FRUIT (n=31)	TOTAL
Albany Thicket Biome	Albany Thicket	177	2	6%	303
TOTAL		**177 (58%)**	**2 (1%)**	**2 of 31 (6%)**	**303**
Desert Biome	Gariep Desert Bioregion	16	2	6%	34
	Southern Namib Desert Bioregion	7	0	0%	17
TOTAL		**18 (47%)**	**2 (5%)**	**2 of 31 (6%)**	**38**
Fynbos Biome	East Coast Renosterveld Bioregion	65	0	0%	136
	Eastern Fynbos-Renosterveld Bioregion	132	2	6%	244
	Northwest Fynbos Bioregion	38	0	0%	91
	South Coast Fynbos Bioregion	36	0	0%	61
	South Strandveld Bioregion	49	0	0%	82
	Southern Fynbos Bioregion	43	0	0%	90
	Southwest Fynbos Bioregion	66	1	3%	154
	West Coast Renosterveld Bioregion	30	1	3%	78
	West Strandveld Bioregion	27	0	0%	42
	Western Fynbos-Renosterveld Bioregion	52	0	0%	116
TOTAL		**157 (52%)**	**3 (1%)**	**3 of 31 (10%)**	**304**
Grassland Biome	Drakensberg Grassland Bioregion	123	0	0%	204
	Dry Highveld Grassland Bioregion	75	4	13%	136
	Mesic Highveld Grassland Bioregion	291	13	42%	515
	Sub-Escarpment Grassland Bioregion	271	8	26%	473
TOTAL		**361 (55%)**	**15 (2%)**	**15 of 31 (48%)**	**651**
Indian Ocean Coastal Belt	Indian Ocean Coastal Belt	298	11	35%	498
TOTAL		**298 (60%)**	**11 (2%)**	**11 of 31 (35%)**	**498**

Nama-Karoo Biome	Bushmanland Bioregion	35	2	6%	68
	Lower Karoo Bioregion	43	1	3%	83
	Upper Karoo Bioregion	56	3	10%	91
TOTAL		**81 (53%)**	**3 (2%)**	**3 of 31 (10%)**	**154**
Savanna Biome	Central Bushveld Bioregion	295	18	58%	558
	Eastern Kalahari Bushveld Bioregion	45	5	16%	86
	Kalahari Duneveld Bioregion	12	3	10%	29
	Lowveld Bioregion	371	23	74%	644
	Mopane Bioregion	191	17	55%	332
	Sub-Escarpment Savanna Bioregion	277	6	19%	459
TOTAL		**460 (54%)**	**29 (3%)**	**29 of 31 (94%)**	**846**
Succulent Karoo Biome	Karoo Renosterveld Bioregion	19	0	0%	43
	Knersvlakte Bioregion	18	0	0%	47
	Namaqualand Cape Shrublands Bioregion	11	0	0%	17
	Namaqualand Hardeveld Bioregion	25	2	6%	52
	Namaqualand Sandveld Bioregion	16	2	6%	31
	Rainshadow Valley Karoo Bioregion	55	0	0%	118
	Richtersveld Bioregion	15	1	3%	35
	Trans-Escarpment Succulent Karoo Bioregion	16	0	0%	38
TOTAL		**70 (44%)**	**3 (2%)**	**3 of 31 (10%)**	**159**

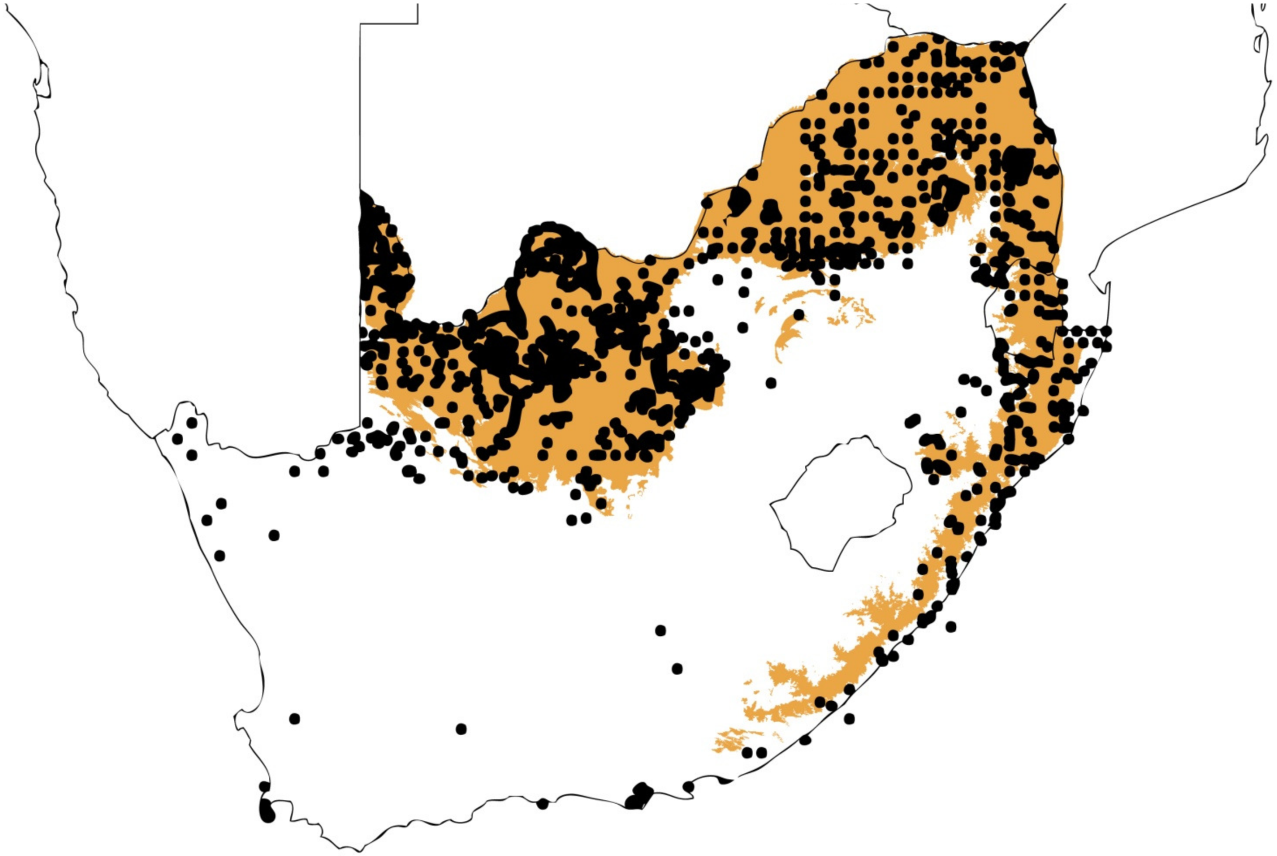
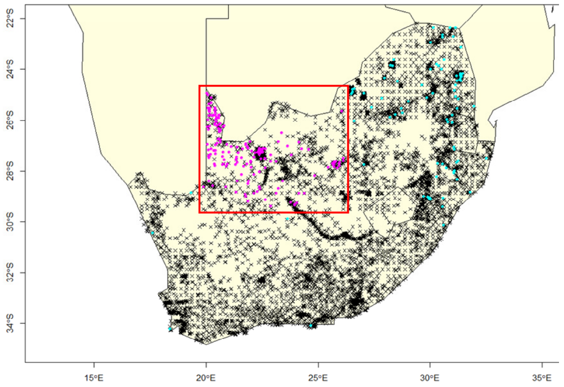


Figure 9: Distribution of all megafaunal fruit (fleshy and dry) relative to the distribution of the Savanna biome (overlaid in orange). Distribution data derived from the National Herbarium Pretoria Computerised Information System (PRECIS) database. The extent of the Savanna biome is given as per Mucina and Rutherford (2006). Distribution points north of the border of South Africa were excluded.



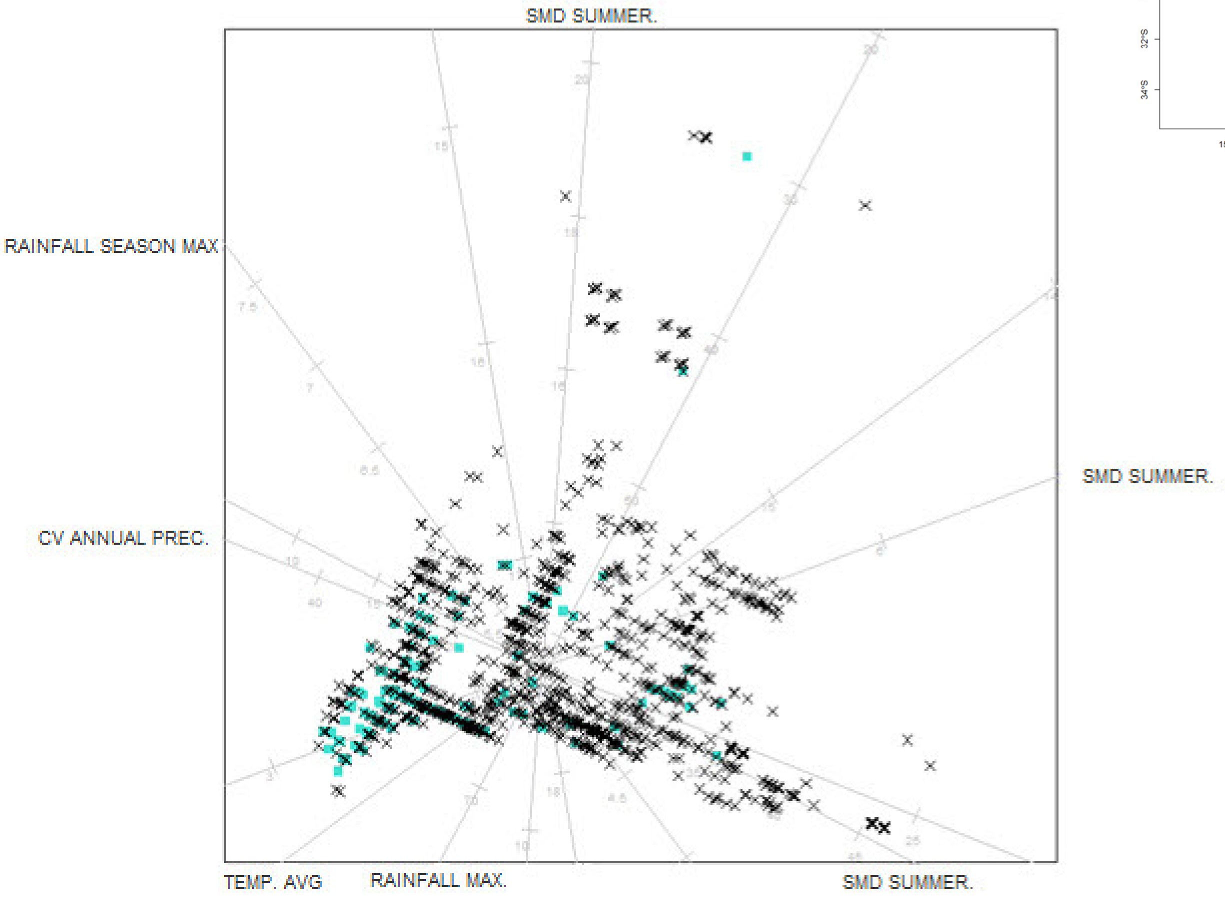


Figure 10: Principal Component Analysis of megafaunal fruit (turquoise squares) versus non-megafaunal (black crosses) distribution against the climatic predictor variables. The data represents a sample area (see area in red box on map) where there are high frequencies of megafaunal fruit.

THE SERVICE THAT ELEPHANTS VERSUS BABOONS PROVIDE THE MEGAFAUNAL FRUIT

A literature review (Supplementary Data: Reference List B) was undertaken to establish the service that savanna elephants provide the 31 megafaunal fruit species identified. It was found that twenty-four megafaunal fruit tree species are known to be dispersed by elephants. In order to better understand the service that elephants provide these fruit, the three studies (Gontier, 2007; Dudley, 2000 and Biru and Bekele, 2012) that dealt with the quantities of seeds transported by savanna elephants were compiled into a table (Table 5).

These studies were conducted over short periods in restricted areas and should thus be treated with some caution. They do however provide us with an appreciation of the sheer quantities of seeds that savanna elephants are capable of moving. This is perhaps best highlighted in the study by Dudley (2000) who found one dung pile containing over 5000 *Acacia erioloba* seeds and another that contained nearly 400 *Schinziophyton rautanenii* seeds (2.8kg worth in dry weight and each approx. 2cm in length – Table 5). In addition to this Dudley (2000) found that on average one elephant in Hwange National Park, Zimbabwe is responsible for transporting approx. 3500 Acacia *erioloba* seeds, 500 *Schinziophyton rautanenii* seeds and 125 *Sclerocarya birrea* seeds per day.

Of the twenty-four megafaunal fruit species consumed by elephants; baboons provide a dispersal service to ten (41.6%), predate on seven (29.2%) and appear to overlook seven (29.2%) of these fruit (Figure 11). These findings are by no means definitive as baboon seed dispersal studies in the savanna have been largely limited to West (Olive baboon - Kunz and Linsenmair, 2010) and East Africa (Yellow baboon - Dunbar and Dunbar, 1974; Barton *et al*., 1993). In Southern Africa studies have only been carried out in the Western Cape (DeVore and Hall, 1965; Davidge, 1978) where megafaunal fruit are scarce and in the Namibian desert (Chacma baboon - Hamilton, 1985).

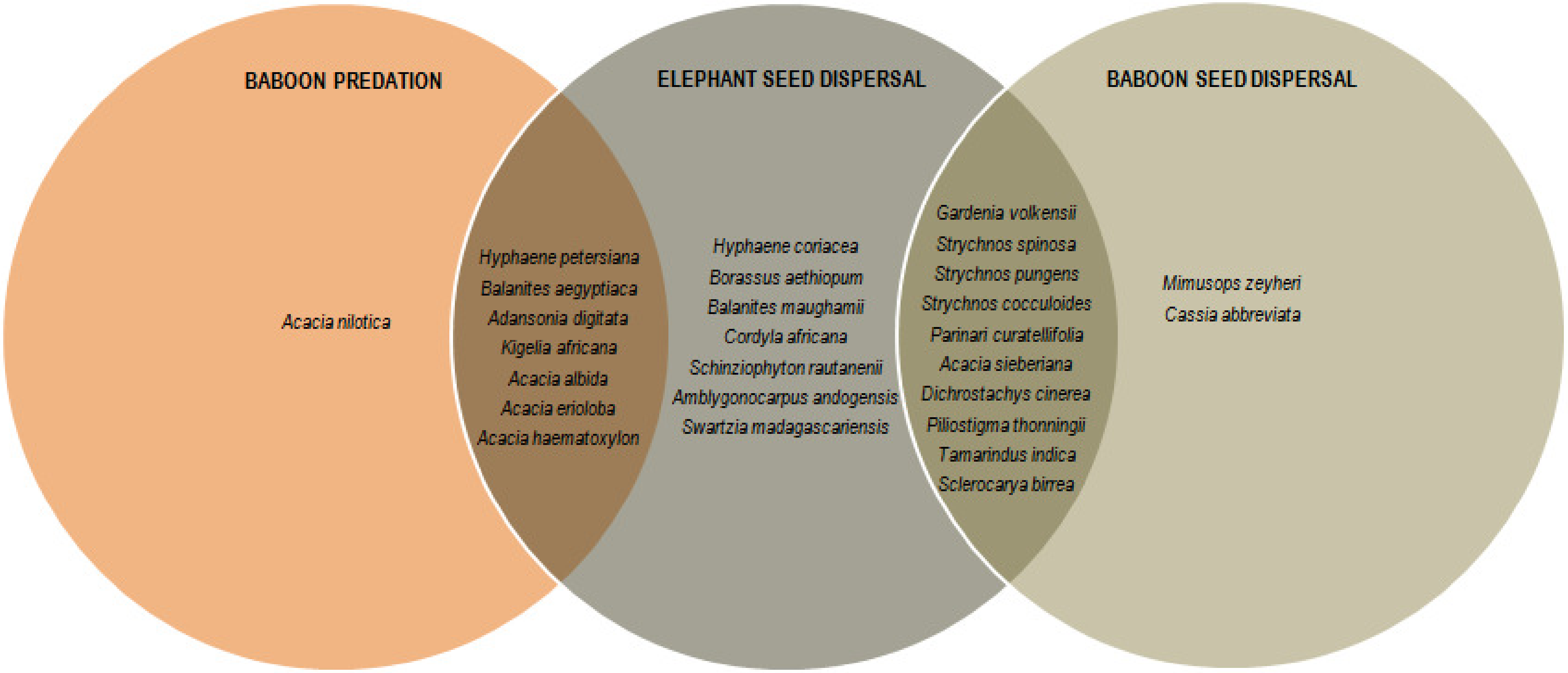


Figure 11: A Venn diagram showing the overlap between elephant seed dispersal and baboon seed dispersal or predation. This is based on Table 1 (Supplementary Data).

Table 5: Frequencies and abundances of seeds of megafaunal fruits found in elephant dung. This data is taken from three separate studies conducted in: a) Tarangire National Park, Tanzania (Gontier, 2007); b) Hwange National Park, Zimbabwe (Dudley, 2000) and c) Babile Elephant Sanctuary, Ethiopia (Biru and Bekele, 2012).

Megafaunal Species	% of dung piles with seeds present	Mean number of seeds per dung pile*	SD	Maximum number of seeds per dung pile	Seed Rain**
Acacia erioloba[b]	54	247	722	5690	3500
Dichrostachyus cinerea[c]	-	60	-	-	
Adansonia digitata[a]	30	3	0.6	-	
Schinziophyton rautanenii[b]	10	4	35	383	500
Sclerocarya birrea[b]	8	2	9	74	125
Balanites aegyptiaca[a]	6	0.3	0.06	-	
Kigelia africana[a]	3	0.1	0.02	-	
Tamarindus indica[a]	3	0.1	0.03	-	

*In a) and c) the mean number of seeds per dung pile was converted from a mean number of seeds per dung bolus by multiplying through by the number of dung boli per dung pile. In a) the value was found to be 2.92 whereas in c) where no such figure was available the figure of 5 found in b) was used.
** Number of seeds transported per elephant per day assumes a defecation rate of 14 dung piles/elephant/day (Dudley, 2000).

Based on the literature review (Supplementary Data: Reference List B) it appears that when dealing with fleshy megafaunal fruit, baboons are likely to be seed dispersers where the seeds are less than 2.8cm in length and where the pulp adheres tightly to the seeds themselves. *Parinari curatellifolia* is 2.7cm and is the largest seed of the megafaunal fruit that, according to a study by Kunz and Linsenmair (2008), baboons swallow intact along with the pulp. *Kigelia africana* seeds on the other hand are only 1cm in length but owing to baboon dexterity are effortlessly separated from the fibrous pulp in which they are dispersed. Where the seed is greater than 2.8cm, baboons tend to prey on the seed itself. These large seeds if not highly toxic are often well protected by a thick shell or endocarp. Baboons are said to have a maximum bite force of up to 600kg (Peters, 1993). *Hyphaene petersiana* which has an incredibly tough endocarp (Peters, 1993) with a required mean bite force of 1804.4 kg - beyond the capacity of baboon jaw strength - is preyed on by baboons while fruits are immature before the endocarp has thickened (Fanshawe 1967; Palmer and Pitman, 1972 in Peters 1993). Alternatively well protected fruit are overlooked by baboons as in the case of *Schinziophyton rautanenii* with a bite force of 656.2kg.

The seeds of the dry megafaunal fruit (Type 2b) are for the most part predated on by baboons (Supplementary Data: Table 1, Figure 11). Whiten *et al.* (1991) describe the dexterous manner in which baboons tear leguminous pods from the tree and using both hands and teeth together slice open the pod and nibble out the seeds. Once inside the baboon's mouth the skins of the seeds are separated and pushed out using their tongue (Whiten et al, 1991). In spite of this, three of the dry megafaunal species (*Dichrostachyus cinerea, Piliostigma thonningii and*

Tamarindus indica) have been found intact in baboon faeces (Kunz and Linsenmair, 2008) but generally in very small numbers. It is likely that some of the seeds that are predated upon are sometimes swallowed accidentally.

Four of the megafaunal fruit species identified in this study – *Raphia australis, Cordia grandicalyx, Vitellariopsis marginata* and *Cladostemon kirkii* - are not known to be dispersed by either elephants or baboons. *Raphia australis* appears to be exclusively dispersed by the threatened Palm-nut vulture (Rushworth and Chittenden, 2004) but the other three species warrant investigation.

Discussion

PATTERNS UNDERLYING THE DISTRIBUTION OF MEGAFAUNAL FRUIT

Authors such as Janzen and Martin (1982), Guimares *et al.* (2008), Campos-Arceiz and Blake (2011) and Donatti *et al. (*2007), who have identified and explored the presence of megafaunal fruit in South America and in Asia; have suggested in numerous studies that the megafaunal fruits of Africa warrant investigation. They hypothesised that in Africa, one was likely to find a greater frequency of megafaunal fruit than elsewhere, given the uninterrupted history of elephants and their predecessors on the continent.

In answer, this study represents the first comprehensive list of megafaunal fruit tree species for South Africa and the first study of its kind for the African savanna landscape at large. The megafaunal fruit trees were identified by means of a framework developed by Guimares *et al.* (2008) and based on fruits consumed by African forest elephants. This framework provided a useful set of starting criteria by which to identify megafaunal fruit tree species. This being said a number of the 16 fruit species that were rejected based on the number of seeds they contain are worthy megafaunal candidates. Members of the *Gardenia* genus are thought to rely on elephants and buffalo for their dispersal – they possess hard endocarps that are impossible to crack open with a hammer (*Gardenia thunbergia*). In addition, *Ficus sansibarica, Strychnos madagascariensis* and both species of *Rothmannia* are consumed by baboons. I would suggest that those fruit greater than 4cm that possess a hard exocarp or endocarp should be considered candidate megafaunal fruits. The framework was also modified at the onset to include large (>10cm in length) dry pods that do not crack open (Type 2b) and have unmistakably evolved alongside large vertebrates. This framework requires more rigorous testing to ascertain its relevance in an African savanna context. This is however beyond the scope of this study.

Of the 1126 tree species found in South Africa, only thirty-one were identified as 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 when one considers that in the only other study to examine the frequency of megafaunal fruits within a plant community, Donatti *et al.*

(2007) found that in two Brazilian sites, 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 megafauna.

Understanding the scarcity of megafaunal fruit in South Africa necessitated a closer look at the species themselves as well as investigating the patterns that underlie their distribution. From a phylogenetic perspective, the megafaunal fruit trees are restricted to a few angiosperm families, most frequently occurring in Chrysobalanaceae, Bombacaceae, Arecaceae and Balanitaceae. These and a number of the 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 (Goldblatt, 1978).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 characterise the Paleotropics 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 elephants and that of megafaunal fruits. In the past - at one time or another - elephants occurred over much of what is now South Africa, including the arid north-western parts. In number terms, elephants look to have had a particular affinity for the coastal and sub-coastal regions of the Eastern Cape and within this region, the majority of historical elephant sightings occurred within the thicket biome (Skead, 2007, 2010). Megafaunal fruit, in contrast, occur in their smallest numbers in the Albany Thicket and Desert Biome.

In terms of geographic distribution, megafaunal fruit tree species in South Africa occur in a narrow northerly band that runs along the edge of the tropics (23° 26' 16" S) and then southwards along the eastern coastline. More specifically, there is a strong correlation between the distribution of megafaunal species and the extent of the savanna biome. The savanna biome is not entirely open; it also includes forest patches that are too small to be considered separately at the biome scale (as mapped by Mucina and Rutherford, 2006). Differences in the distribution of megafaunal fruit across closed forest versus 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 (within the Eastern Kalahari Bushveld Bioregion) while fleshy megafaunal fruits predominate in the wetter eastern savannas (Central Bushveld and Mopane Bioregion) and extending southwards into the Indian Ocean Coastal Belt biome. This pattern further supports the idea that the presence of megafaunal fruit is tightly coupled to their position along major environmental gradients.

Given that the majority of plant species in the South African flora are of temperate origin (Goldblatt, 1978) and that in terms of distribution only the far northern reaches of South Africa occur within the tropics, I would hypothesise that in the hotter and wetter savanna regions north of the South African border one would likely encounter megafaunal fruit with a far greater frequency than was the case in this study. This idea is supported by the fact that the PCA analysis had megafaunal fruit clustering at the higher ends of the precipitation and temperature variables.

THE SERVICE THAT ELEPHANTS AND BABOONS OFFER

Given the continuous history of elephants within the African landscape (Kalb *et al.*, 1996) Janzen and Martin (1982) hypothesised that the potential for co-evolution between fruits and elephants should be higher on this continent than anywhere else. Of the thirty-one megafaunal fruit species identified twenty-four are known elephant fruits. Dudley (2000) hypothesised that four of the species with megafaunal fruits; *Sclerocarya birrea, Adansonia digitata, Schinziophyton rautanenii,* and *Balanites aegyptiaca* were highly reliant on elephants for their effective dispersal. Based on the literature review conducted in this study I would hypothesise that two other species, *Hyphaene coriacea* and *Borassus aethiopum,* are further additions to this list.

It is likely that among the proposed species with megafaunal fruits a 'gradient of reliance' on megafauna for their dispersal exists (Guimares *et al.*, 2008). A combination of factors might contribute to how reliant a plant species is on large vertebrate-dispersal. For example, dry megafaunal fruit while consumed by a suite of other vertebrates might prove highly reliant on megafauna for escaping seed predators (Dinerstein and Wemmer, 1988; Fragoso, 1997). The majority of pods that are consumed after having fallen are typically highly infested by bruchids (Miller, 1993; Gonthier, 2009). Those that are consumed directly from the tree by elephants showed low predation by bruchids in comparison (Miller, 1993). Furthermore, gut passage is thought to kill bruchids at the early stages of infestation when pods are consumed from the ground (Coe and Coe, 1987; Miller and Coe, 1993). More research is required to determine the extent to which each of the megafaunal fruit is dependent upon elephants (or other megafauna) for their dispersal, as this is an important step in understanding the potential consequence of their loss.

The evolution of large fruits in Africa cannot be examined without some consideration of the large primates that have, for millennia, inhabited this continent alongside large vertebrates. There is considerable overlap in the usage of megafaunal fruit by baboons and elephants. Baboons provide an effective seed dispersal service to approximately a third of the megafaunal fruit species but predate on yet another third. A number of factors; fruit type (dry or fleshy), seed size, attachment of pulp and shell strength appear to best predict which seeds are likely to be dispersed and which are likely to be preyed upon. As a seed disperser, baboons are considered to be highly effective; the baboon population in a savanna-forest mosaic in West Africa (145km^2) were responsible for dispersing about 1500 intact seeds d^{-1} km^{-2} (129 seeds>2mm in size; Kunz and Linsenmair, 2010).On the other hand baboons can be consummate seed predators. Baboons prey on the immature seeds of the baobab fruit and according to Venter and Witkowski (2011) are responsible for major (58-85%) crop depletion in areas of cohabitation.

To counter primate seed predation, I would hypothesise that megafaunal fruit are more robustly defended in Africa than on other continents. For one, fruit are more likely to have evolved harder endocarps (shells). This can be measured in terms of bite force. *Schinziophyton rautanenii* for example has an average bite force of 656kg – effectively excluding access to the seed material, by baboons (Peters, 1993). Alternatively fruit may have developed strategies similar to that of *Diospyros mannii* – a West African tree that has succulent fruit that, while immature, are covered by a dense mat of irritant hairs precluding primate predation (Tutin *et al*., 1996).

A number of authors (Donatti *et al,* 2007; Guimares *et al,* 2008) have acknowledged the part that modern humans have played in preventing megafaunal fruit from slipping into extinction and in a number of instances bringing about their widespread cultivation. However, as far as I am aware, the role that early humans played in shaping the current distribution of megafaunal fruit and/or the characteristics of the fruit themselves has not been investigated. Baboons are thought to represent excellent bio-historical as well as functional analogues to early humans (Jolly, 2001). The rationale behind this is two-fold. Firstly, according to Jolly (2001) papionins and homonins are phylogenetically close enough to share many basic attributes by homology yet phylogenetically distant enough that modifications of these attributes would be easily recognised as such (Jolly, 2001). Secondly, and of particular relevance to this study is that unlike the African apes (chimpanzees and gorillas) which have for the majority of their history been predominantly evergreen forest dwellers, baboons have shared open habitats with homonins ever since their respective lineages emerged (Pilbeam, 1972; Jolly, 2001). Chimpanzees colonised Miombo woodland only very recently (Kano, 1972).

In terms of fruit selection and processing, baboons provide a useful proxy for early humans. There are however three inescapable points of divergence. For one, baboons and early humans coexisted in the savanna landscape so there is likely to have been some degree of niche segregation. Secondly, early humans (*Homo habilis* – 2 million years ago; Susman, 1994) began making use of tools so the shells of many of the single seeded species (e.g. *Hyphaene coriacea*) would have posed no obstacle to entry thus making early humans more effective seed predators. Thirdly, owing to their dexterity and intelligence, early humans are believed to have occupied larger home ranges than baboons so their potential to effect long distance dispersal was greater. This long distance dispersal service is well illustrated in a study by Tsy *et al.* (2009) who determined that early humans provided a mobile link between baobab populations on the West and Eastern sides of Africa.

Analyses of the bones and teeth of early humans are unable to differentiate between the types of fruit consumed by baboons and those of early man. It has however been suggested (Milton, 1999) that early *Homo* circumvented the nutritional constraints affecting both apes and baboons by shifting to a relatively low-fibre, high-quality diet. With this in mind it is likely that hominids selected fruits that had a higher pulp to seed ratio. A higher pulp to seed ratio characterises the Type 2 fleshy fruits – the large multi-seeded fruits such as *Strychnos, Rothmannia* and *Gardenia*. Unlike baboons, early *Homo* was probably a 'ripe fruit specialist'. Ripe fruits are higher in sugars and lower in fibre and secondary metabolites (Conklin-Brittain *et al*., 2002). Owing to their superior intelligence it is plausible that homonids were better able to find and exploit ripe fruits than were their savanna counterparts – the baboons – forcing baboons to exploit fruits before ripening. While not universally accepted, most researchers believe that early hominids were inept tree climbers as bipedality is thought to maladapt the hominid skeleton for climbing (DeSilva, 2009). It is therefore likely that fruits that evolved alongside early humans are presented at heights lower then 2m. This is certainly the case in fruits such as *Strychnos, Rothmannia* and *Gardenia.* In outline, a fruit adapted for dispersal by early humans would have non-fibrous, fleshy pulp with multiple seeds and presented within reach. It is possible that the rejected fruits that had too many seeds to fit Type 1 are in fact adapted for dispersal by early humans. The service that early humans would have offered large fruit would not have been curtailed by gut passage time as it is in elephants and baboons as early humans are likely to have carried fruit as they moved.

Conclusion

There are fewer megafaunal fruit trees in South Africa than expected. This looks to be related to the fact that megafaunal fruit are a tropical phenomenon – they largely evolved in the Paleotropics and the abiotic conditions (high precipitation and temperatures) that underpinned their evolution, now limit their distribution. This is best highlighted by the fact that although elephants have historically been found throughout South Africa, megafaunal fruits are not. Megafaunal fruits predominate in the savannas. Savannas in this context of this study includes closed forest patches, which occur in forest/savanna mosaics, and are too small to be considered as a separate biome. Within the savanna biome, as precipitation decreases from east to west there is a switch from fleshy to dry fruits. The framework developed by Guimares *et al.* (2008) was applicable in that it identified fruits that are known to be consumed by elephants and many others that are likely to be. It did however require the addition of a dry multi-seeded fruit type to account for the large dry indehiscent legumes prevalent in a savanna context and known to be an important food source for large herbivores such as the elephant. The majority of the megafaunal fruits identified are known to be dispersed by elephants. The remaining ones are something of an anomaly and require investigation. On the basis of an extensive literature review I suggest the addition of *Hyphaene coriacea* and *Borassus aethiopum* to the list (Dudley, 2002) of four large fruit (*Sclerocarya birrea, Adansonia digitata, Schinziophyton rautanenii,* and *Balanites aegyptiaca)* that are highly reliant on elephants for their effective dispersal. Baboons provide an effective seed dispersal service to approximately a third of the megafaunal fruit species but predate on yet another third. They provide an effective service to seeds that are less than 2.8cm in length where the pulp adheres tightly to the seeds themselves. Beyond this seed upper limit size, baboons usually prey on the seeds themselves. A number of African fruit possess incredibly tough endocarps that put seeds beyond the capacity of baboon jaw strength. In other instances baboons circumvent this defence by consuming the fruit while immature. Early humans, while sharing many attributes of fruit selection and processing with baboons might have deviated on some fronts. Fruits adapted alongside early humans are likely to have a higher pulp to seed ratio, selected when ripe and presented at heights below 2m. Research attention is required in: (1) identifying the megafaunal fruit of the savannas north of the South African border, (2) filling the large knowledge gaps in the feeding ecology of savanna elephants and baboons and (3) assessing the spatial aggregation of megafaunal fruit trees inside reserves that possess intact megaherbivore communities and comparing these with patterns of spatial aggregation outside reserves where megaherbivores have been absent for extended periods.

CHAPTER 4

Bush elephants – long haul seed carriers of the savanna:

the seed dispersal kernel of the African savanna elephant

Introduction

Large terrestrial vertebrates (>1000kg) play a pivotal role in the dispersal of large specialised fruits (megafaunal fruits *sensu* Gautier-Hion *et al.* 1985, Blake *et al.* 2009). However due to a series of extinction events at the end of the Pleistocene (50 to 10 thousand years ago) the large vertebrate communities of Europe, non-tropical Asia, Australia and the Americas vanished in their entirety and with them the dispersal service they offered megafaunal fruit (Martin, 1984; Barlow, 2000). While the era of large vertebrates might have seen its end on most continents, Africa and small patches of tropical Asia remain the exception (Barlow, 2001). Five genera of Africa's megafaunal community (*Ceratotherium, Diceros, Giraffa, Hippopotamus*, and *Loxodonta)* still exist (Owen-Smith, 1988/9) while two genera (*Elephas* and *Rhinoceros*) remain in Asia. An understanding of large vertebrate-fruit relations in Africa and Asia is thus imperative to both our comprehension of extinct interactions and to the conservation of extant interactions.

Of the remaining megafauna in Africa and Asia it is only the African Savanna Elephant (*Loxodonta africana africana)* that occurs in densities and areas large enough to mirror extinct megafaunal populations (Prado *et al*, 2001). This fact, coupled with their established high rate of fruit consumption (Campos-Arceiz and Blake, 2011), made the African Savanna Elephant an excellent subject for a study of the dispersal services supplied by megaherbivores.

The fossil record suggests that elephant-like proboscidean megaherbivores originated in Africa some 60 million years ago and afterward radiated to all continents with the exception of Australia and Antarctica (Shoshani, 1998). Accordingly, one might conclude that given this extended, uninterrupted history of large vertebrates within this continent, the potential for co-evolution between megafaunal fruit and large vertebrates should be higher in Africa than anywhere else (Dudley, 2000). The majority of previous African elephant seed dispersal studies have focused on forest elephants. These studies have firmly established elephants as forest gardeners, consuming more seeds from more species than any other taxon of large vertebrate disperser (Campos-Arceiz and Blake, 2011). Of these forest elephant studies, two (Feer, 1995 and Blake, 2009) focused on the service forest elephants provide to megafaunal fruit species and identified at least 14 woody species *(e.g. Cola* spp., *Tieghemella heckelii,* and *Balanites wilsoniana)* that they thought relied exclusively on elephants for their dispersal. No such study has been undertaken for the African Savanna elephants.

Megafaunal dispersers such as the elephant are important not only because they are capable of processing and swallowing large specialised fruits but also owing to the fact that they can move large numbers of seeds – large and small – over considerable distances (Campos-Arceiz and Blake, 2011). Long distance dispersal is considered to be one of the most important contributors to seed dispersal effectiveness (Clark 1998; Clark et al. 1998; Higgins et al. 2003). It influences large-scale ecological processes, including some of major conservation concern, such as connectivity in fragmented landscapes and range shifts following climate change. Despite this, there are no data on the spatial scale at which the African savanna elephants disperse seeds. It is this spatial distribution of dispersed seeds – the seed shadow - that sets the stage for future demographic processes, such as predation, germination, growth and reproduction (Nathan and Muller-Landau, 2000). African savanna elephants are found in a wide variety of habitats, including savanna, grassy plains, miombo woodlands and forests, Sahelian scrub, swamps, bushlands and even deserts (IUCN, 2013 and Burnie, 2001). They consume and defecate large quantities of seed (an average of 228 woody plant seeds per defecation - Dudley, 2000), have long gut passage times (up to 53 hours – Davis, 2008) and large home ranges (up to 3000km in the Kalahari Sands, Southern Africa - Conybeare, 1991) potentially allowing for seed dispersal distances over several kilometers.

Westcott *et al.* (2005) developed a novel yet practical means of examining the spatial distribution of seeds that, rather than concentrating on the fate of individual seeds, shifts focus to the vertebrate providing the dispersal service. By combining the gut passage rates (time from ingestion to defecation), of the vertebrate in question, with its movement data (speed and direction of movement), one can estimate entire seed shadows (Janzen *et al.*, 1976, Holbrook and Smith, 2000 and Westcott *et al.* 2005). In this study we utilise the Westcott *et al.* (2005) approach and combine information from feeding trials on sanctuary African savanna elephants with movement data for wild individuals to: (1) assess the capacity of elephants to disperse the seeds from different types of megafaunal fruits and (2) estimate the distances over which they disperse these seeds.

Methods

IDENTIFICATION OF MEGAFAUNAL FRUIT PROXIES AND SEED PASSAGE EXPERIMENTS

To quantify seed passage rates through the elephant gut, we conducted a feeding trial at the Elephant Whispers sanctuary situated within the Sandford Conservancy on the banks of the Sabie River in Hazyview, Mpumalanga, South Africa from the 19th to the 23rd March 2012. The sanctuary elephants interact with tour groups in the morning and evening but spend the majority of the day roaming and feeding freely within the Conservancy. Since exposure to indigenous megafaunal fruit is possible within the Conservancy it was necessary to use market fruit varieties in place of the indigenous ones.

Market fruits were selected to represent the two megafaunal fruit types as defined by Guimares *et al* (2008) and applied in Chapter 3 (Table 1). The first type includes fleshy fruits that are 4–10 cm in diameter with up to 5 large seeds (generally >2.0 cm diameter). The mango (*Mangifera indica*) and the peach (*Prunus persica*) were chosen to represent Type 1. The second type includes fleshy/dry fruits that are greater than 10 cm in diameter and have numerous small seeds. The Honeydew Melon (C*ucumis melo*) was selected to represent Type II megafaunal fruits. Fruits were purchased ripe on the day the feeding trial began. Fruit weights and dimensions were recorded. Feeding trials were conducted on four African elephants with body size ranging between 2400 and 6000 kg, including two females and two males.

The fruits were fed to the four elephants in one bout during the regular evening (1700hh) feed. The experimental fruits replaced the regular feed which commonly consists of fruit of an equivalent quantity. The elephants had not previously been exposed to any of these fruit types (*pers. comms.* elephant-keeper, 2012). Following the feed the elephants were led directly to their outdoor enclosures for the duration of the night. Collection of faeces began the following day at 07h00 when the elephants were removed from their individual enclosures to interact with their grooms and to do exercises. Each of the four elephants had a groom that moved with the elephants throughout the day – both during the interaction sessions and during their feeding/roaming time within the Conservancy. Each groom took responsibility for collecting every faeces dropped by their respective elephant. They placed each of the faeces (in its entirety) into a sack/plastic bag and recorded the hour within which the faeces were dropped. Faecal collection thus happened hourly between 07h00 and 1700hh but not during the course of the night. The faeces that were collected in the morning session were assigned a freshness score that placed the time of dropping within the first second or third portion of the night. This score was based on the colour and moisture content of the faeces and was done with input from the grooms. Where the faeces were a mix of boles of varying freshness this was noted and a mean time was assigned. Faeces were thoroughly teased apart by hand; the large seeds were counted and collected while the small (C*ucumis melo)* were assigned a quantity score of present (less than 5), few (5-20) and many (greater than 20). Dung collection and analysis was stopped on day 5.

TELEMETRY AND MOVEMENT ANALYSIS

Telemetry data were obtained from the locations of thirty eight radio-collared wild elephants (27 males, 11 females) in the Timbavati Reserve (part of the Kruger National Park, South Africa) over a period of 8-years (with thanks to the 'Save the Elephants' Foundation). These elephants were fitted with GPS-satellite transmitters. Collars were set to acquire positions at 3, 6, 8 or 12-hour intervals and these positions were transmitted via the ARGOS satellite system. The displacement of individual elephants was estimated across tracking intervals of 12-hour multiples (12- 192 hours). This was achieved by randomly sampling 50-100 different starting points across all movement data for each individual elephant – this ranged between 1 and 8 years (Westcott *et al.*2005). From each of these starting points, the telemetry data series was then moved through until the location closest to the relevant time interval was obtained. The net displacement of the elephant was then calculated as the distance between the first and final GPS position. Time series were non-overlapping and were a minimum of 2 days apart.

SIMULATION MODEL AND DISPERSAL KERNEL ESTIMATION

I designed a stochastic model to simulate the dispersal of seeds ingested by wild savanna elephants. The input data for the model was a simulation of the gut passage regimen of the Type II seeds (*Cucumis melo*) and the telemetry locations of 38 individual elephants (418 001 records). A normal distribution curve (mean=31; SD =15) provided the best fit to the melon gut passage data. This curve allowed for the random generation of gut passage times (~12 000). For each of these simulated gut passage times the model would randomly select an elephant starting location (across any of the 38 elephants) with a time stamp. The model would then move through the ordered elephant co-ordinates until the elapsed time across these co-ordinates equated to or exceeded the gut passage time. Where the gut passage time was overshot the model would calculate the time difference that was sitting in the final elapsed period and perform a rounding calculation. Sensitivity was built in to ensure that the final elapsed period did not represent more than 20% of the total gut passage time. The model then calculated the straight line distance between the starting and final location. These ~12 000 distance measures were then used to produce a dispersal kernel that expresses the probability density of seeds deposited at various distance intervals from the parent tree (see data disc code).

SENSITIVITY ANALYSIS

To estimate the influence of varying the mean of the gut passage curve on seed dispersal patterns, we ran the stochastic model for a simulated gut passage with a mean of 41 hours in addition to another with a mean of 21 hours (SD = 15 across all three simulations).

Results

SEED PASSAGE EXPERIMENTS

The four sanctuary elephants consumed a collective total of 28 mangoes, 40 peaches and 5 melons. With regards to the melon the 5 fruit consumed equated to approximately 2450 melon seeds (Paillan *et al*, 2004). The elephants' interest and subsequent processing of the fruits was highly variable. The first of the mango fruit presented to the elephant were treated differently to those that followed. The seeds of the initial mangoes were cracked open in the mouths' and spat out. The elephant keepers explained that this was common practise where fruits had not been sampled previously. All mango fruit that followed were swallowed in quick succession. The processing of the peaches was difficult to determine. No peach fruit or seeds were spat out. It was however impossible to see if the peach seeds were being bitten down on, in the mouths' of the elephants.

The melons were approximately 20cm in diameter and were handled differently by each elephant. The female elephants rolled the melons underfoot without cracking them open. They then picked them up with their trunk and smashed them against their tusks. This was followed by inserting the melon pieces into their mouths. The one female elephant spat out all the melon she had inserted into her mouth. The other consumed the greater part of one melon but backed away when offered a second. The smaller of the male elephants cracked open the first melon with his trunk but spat out the majority of the melon he placed in his mouth. This elephant also backed away on being offered a second. In contrast the large male consumed three melons in quick succession. This elephant inserted each of the melons into his mouth whole, pursed his lips around them and did not drop a single seed or drop of melon juice.

Seed survival varied greatly across the different fruit types. Of the 28 mango (*Mangifera indica*) fruit that were fed to the elephants, 9 fruit (32%) were recovered intact. Fifteen of the seeds (54%) were recovered as 30 seed halves which were subsequently matched together. The remaining 4 mango seeds (14%) were recovered as stringy fragments. In contrast, only 2 of the 40 peach (*Prunus persica*) seeds (5%) emerged intact. The remainder (95%) were recovered as small fragments (none greater than 20% of the seed surface area).

Although abundance scores prohibit the assignment of an exact seed survival figure to the melon, a more detailed examination of random faeces revealed that the vast majority of seeds (>95% - *personal observation, 2012*) remained intact.

Gut passage curves were produced for the mango (*Mangifera indica*) and the melon (*Cucumis melo*) seeds (Figure 1 and 2). Due to the inadequate sample size of intact peach (*Prunus persica*) seeds no gut passage curve was produced for this fruit.

Mean gut retention time for the mango seeds was 34.7 h (median =30.8 hours). Similarly, the mean gut retention time for the melon seeds was 33.5 h (median = 30.8 h). The difference between the two seed types lay in the gut passage range; mango seeds first appeared 15 hours after ingestion and were present up until 66 hours. In contrast, the melon seeds were evident 7 hours after ingestion and were still present in faeces up until 96 hours (4 days after consumption) – a 43 % greater time radius.

Variation in seed survival was negatively related to average seed weight.

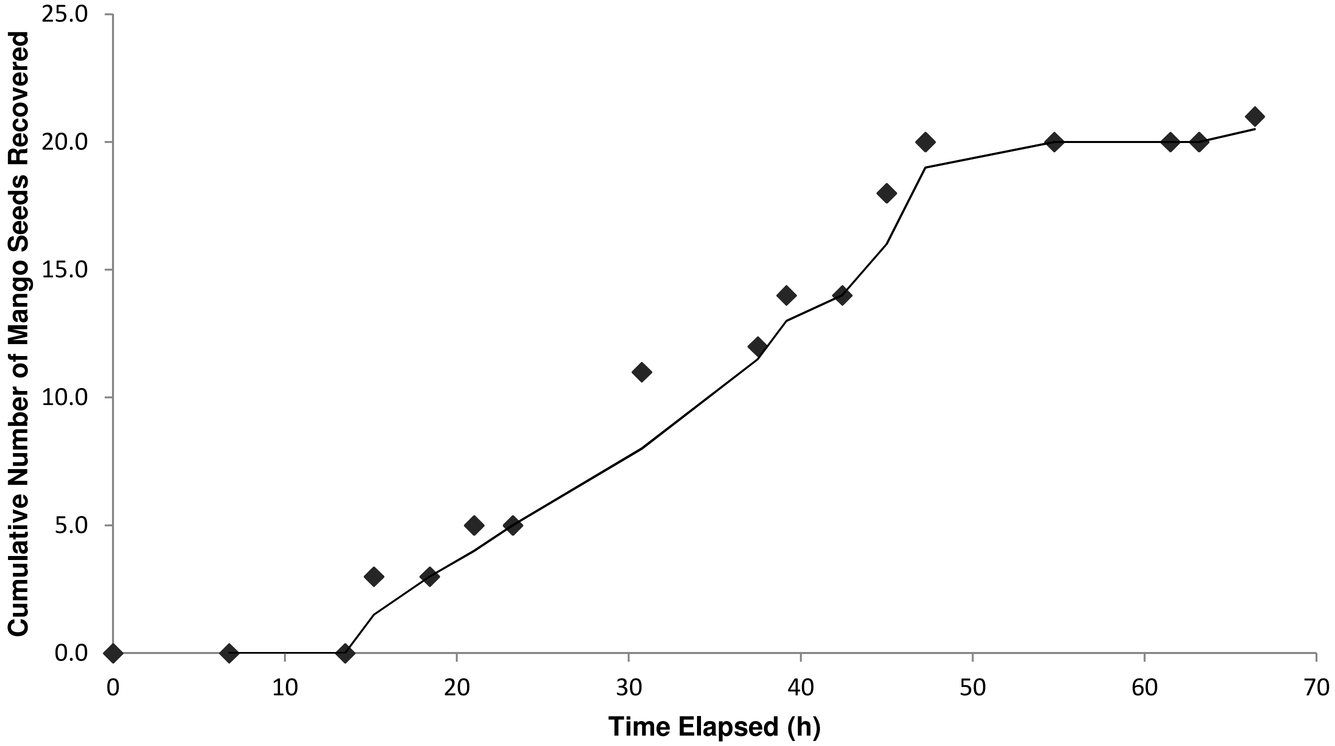


Figure 1: Transit of mango seeds (*Mangifera indica*) through the gut of 4 elephants (2 males, 2 females).

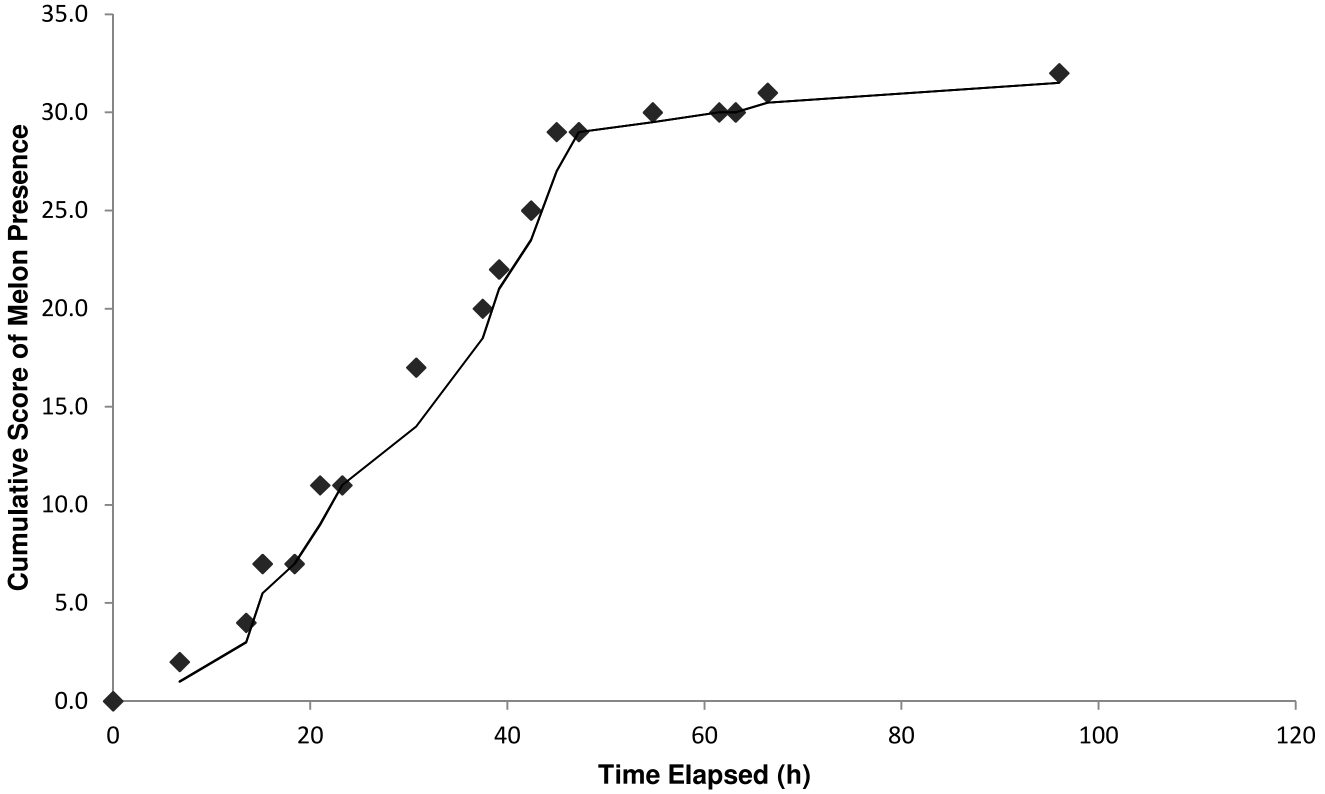


Figure 2: Transit of melon seeds (*Cucumis melo*) through the gut of 2 elephants (1 male, 1 female).

TELEMETRY AND MOVEMENT ANALYSIS

A total of 34 210 displacement events spanning 12 to 192 hours were taken into account. The resulting estimates are likely to be conservative in that they calculate the straight-line distance between the first and last GPS points within the relevant time series.

Distances travelled in a 24-hour period did not have a normal frequency distribution (Shapiro-Wilk goodness-of-fit test $W=0.85$, $p<0.01$; Figure 3), but were strongly leptokurtic (excess kurtosis = 4.18, $n=3120$). The median distance moved per 24-hour period was 2450m while the modal distance was1400m. Sixty percent of the 24-hour movement bouts (1860/3120) resulted in a displacement of >2000 m.

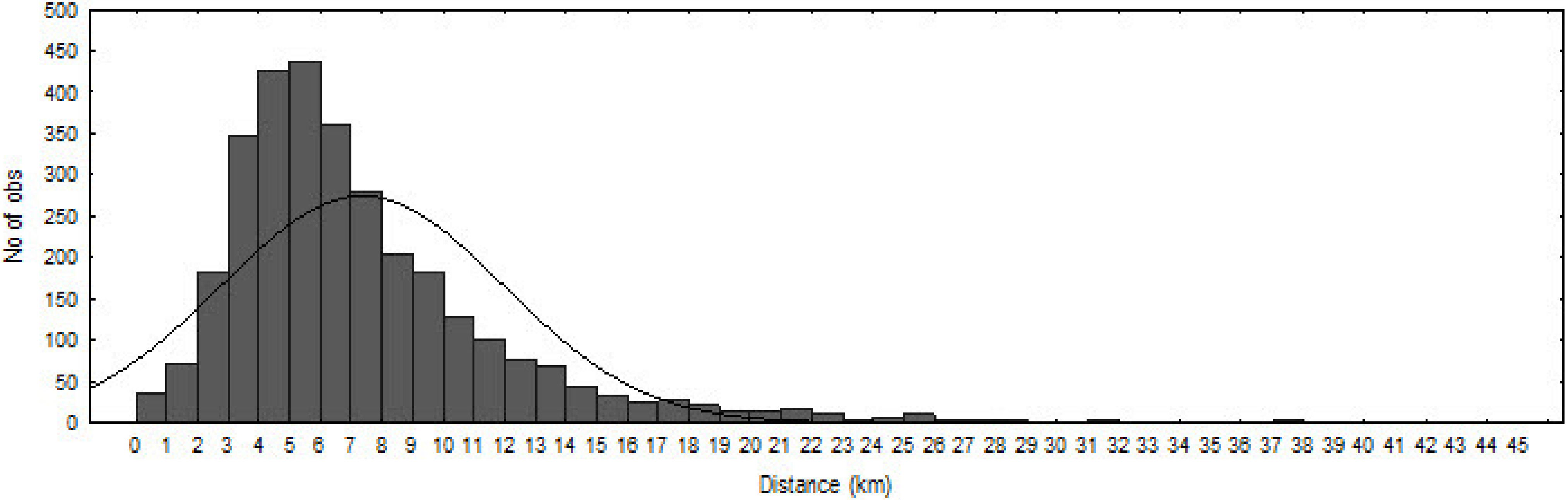


Figure 3: Frequency distribution of distance travelled by 38 elephants (27 males, 11 females) in a 24-hour period.

In order to determine the importance of gut retention to the potential dispersal distance we plotted the median distance travelled over time (Figure 4). Between 168 and 192 hours (7 and 8 days) median distance travelled levels off at approximately 6km. The maximum gut passage time of the mango and melon seeds corresponds to a 3.8km and a 4.4km median dispersal distance (63% and 73% of maximum respectively).

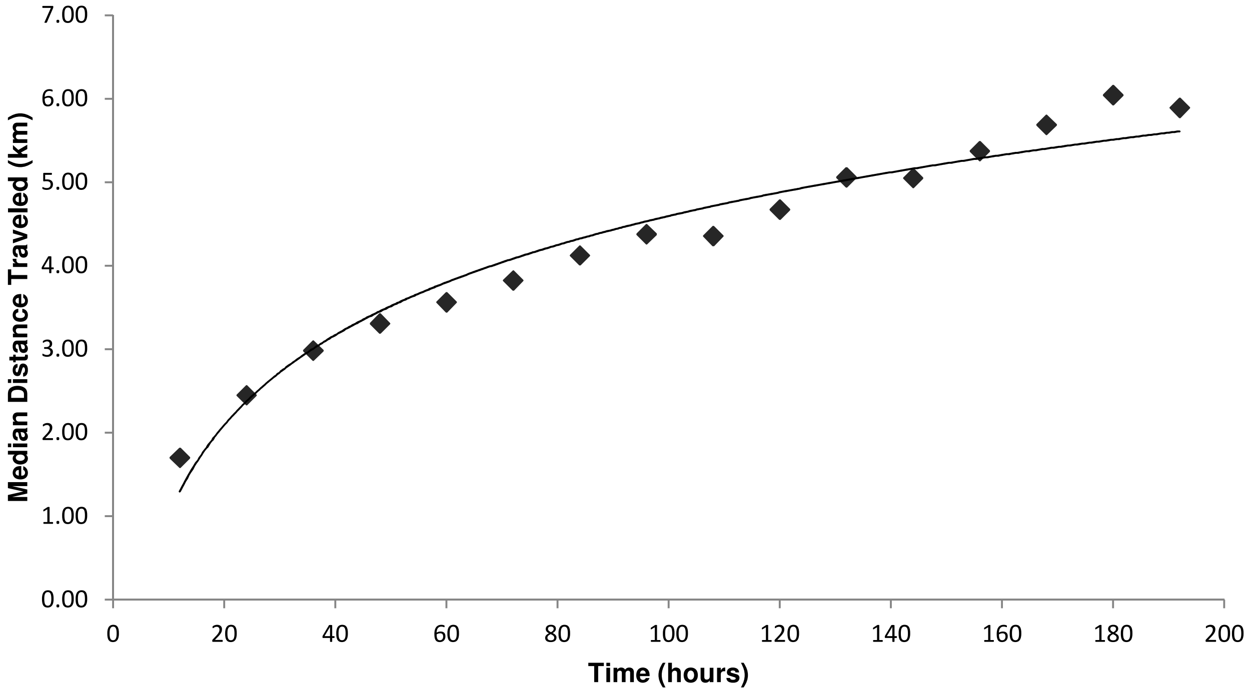


Figure 4: Median distance travelled over time for 38 elephants (27 males, 11 females). The R^2 value is 0.957. The equation of the fitted logarithmic curve is $y = 1.5556\ln(x) - 2.5688$.

It is the maximum dispersal distance that is thought to be one of the most important contributors to seed dispersal success (Nathan *et al.*, 2008). The maximum dispersal distances achieved for each 12-hour time class was expressed in a box and whisker plot (Figure 5). The maximum dispersal distances are consistently 7 (SD=0.01) times that of the 90th percentile value. Accordingly, a small subset of elephant movement events is of a significantly long range. Based on this movement data mango seeds can potentially achieve a maximum dispersal distance of 59km based on their slowest gut passage time while the melon seeds could potentially exceed the 65km distance mark (Figure 5). Maximum dispersal distances appear to reach a ceiling of 70-75km between 108-192 hours (4.5 – 8 days).

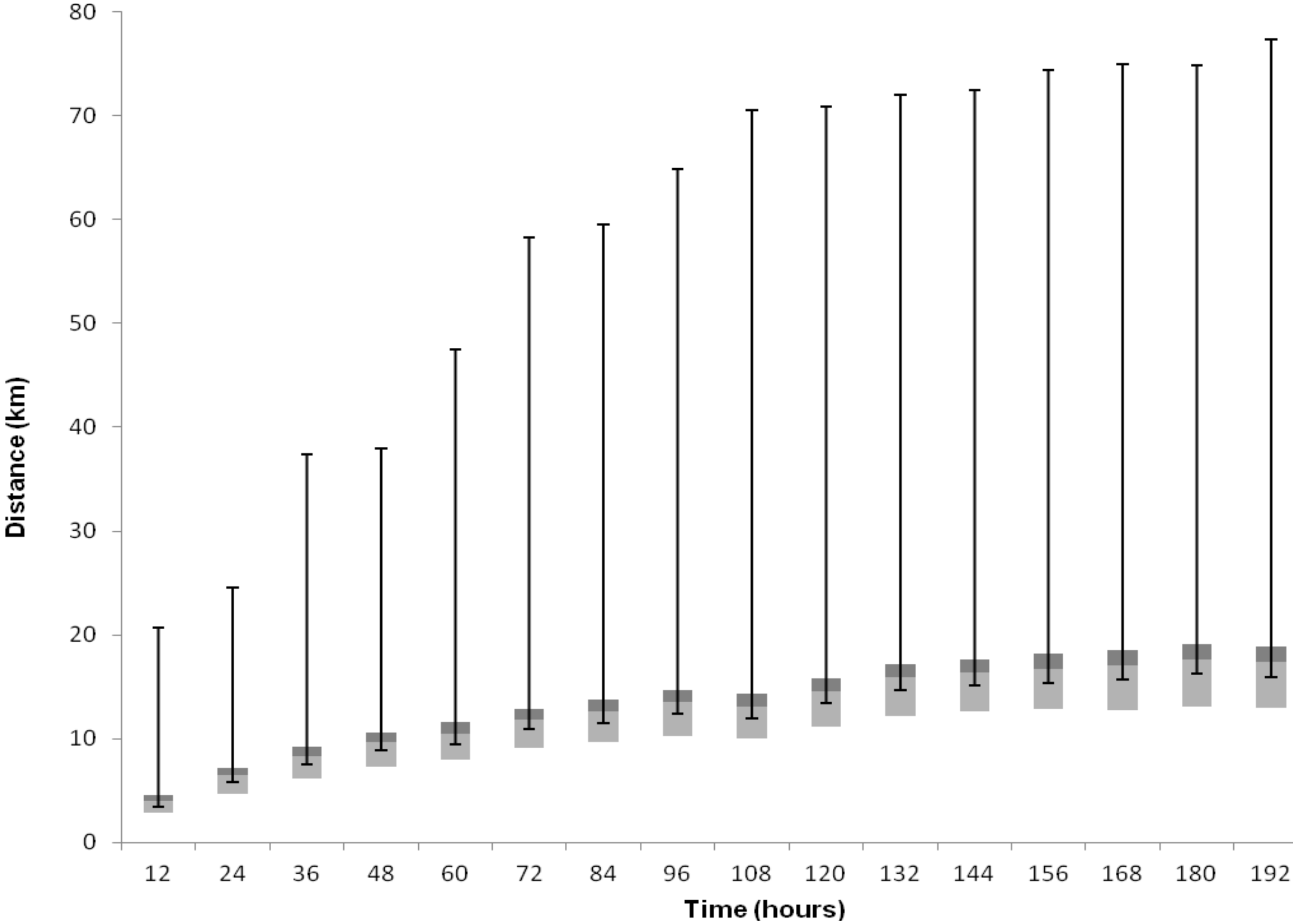


Figure 5: Box and whisker plot of distance across different time intervals. The lower and upper sides of boxes indicate 10th and 90th percentiles. Lines within boxes mark the medians. Whiskers indicate the maximum dispersal distances. Distance travelled for each interval was estimated from data on 50 time series across each of 38 elephants (27 males, 11 females).

The movement data revealed marked sexual dimorphism (Figure 6). A mango seed transported by a male elephant can potentially achieve a dispersal distance of 14km (in 10% of all instances – based on a 90th percentile –Figure 6) whereas the same mango transported by a female elephant can theoretically achieve a dispersal distance of 9km. Similarly, melon seeds consumed by male elephants are expected to be carried in excess of 16km (in 10% of all instances) whereas female elephants are liable to carry the seeds 11km (Figure 6). A seven kilometre dispersal difference separates male and female elephants after 1 week of gut passage time.

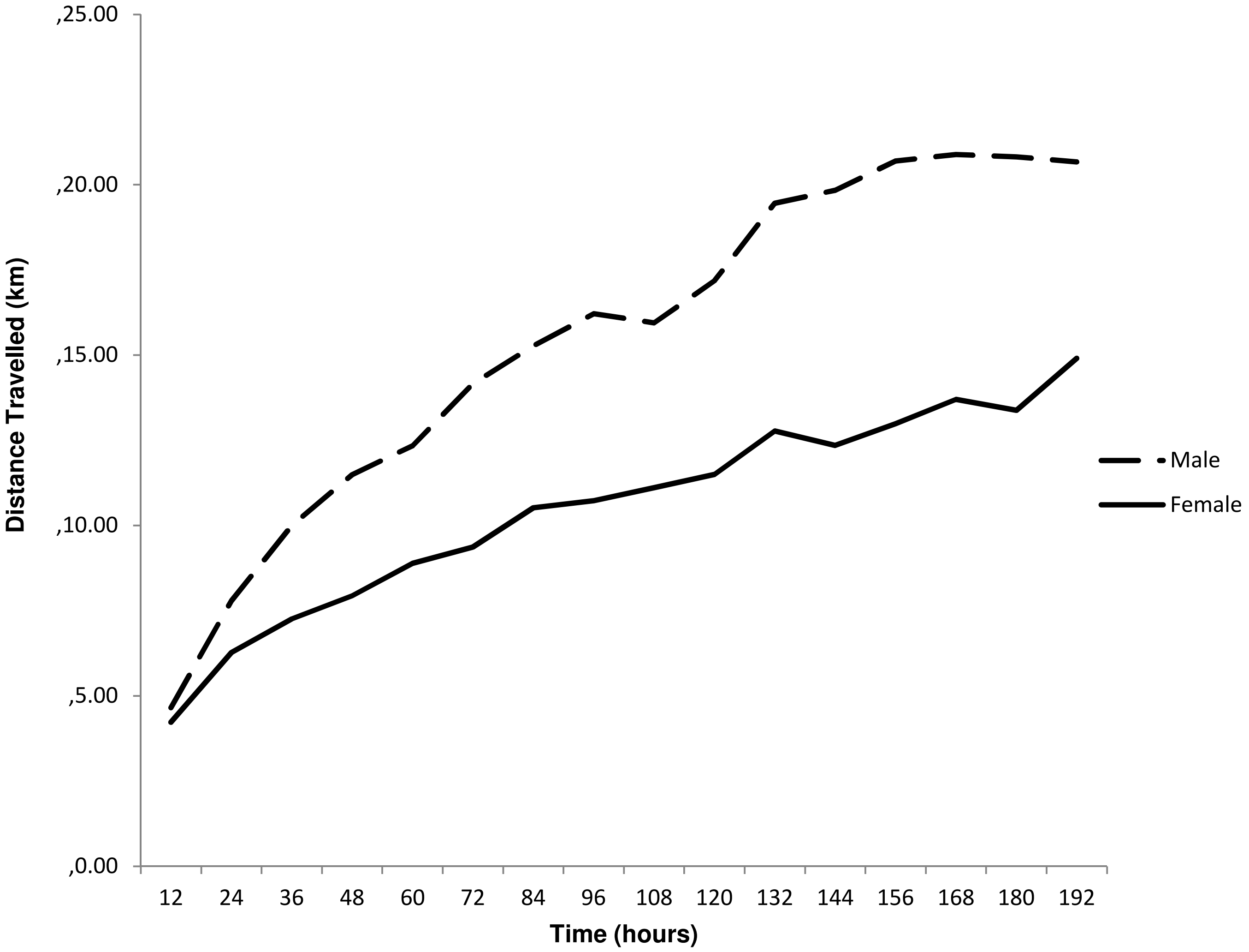


Figure 6: Distance travelled (90% percentile) over time for male and female elephants.

DISPERSAL KERNEL ESTIMATION

Our seed dispersal kernel was highly leptokurtic (Kolmogorov-Smirnov d = 0.17722, $p < 0.01$, Lilliefors $p < 0.01$; Figure 7) and had a fat tail, i.e. dispersal distances did not drop sharply to zero. Our model predicted that 23% (peak dispersal) of seeds were deposited between 1 and 2km from their parent tree. The mean dispersal distance was 3.7 km (Table 1). Distances as vast as 50 km were achieved by a very small seed subset. One percent of seeds were deposited at distances greater than 20km. If one considers that the average African savanna elephant in Hwange National Park, Zimbabwe defecates over 3200 woody plant seeds per day (during the effective dispersal season *138 days* - Dudley, 2000) then the number of seeds likely to reach these distances in excess of 20km is really quite staggering.

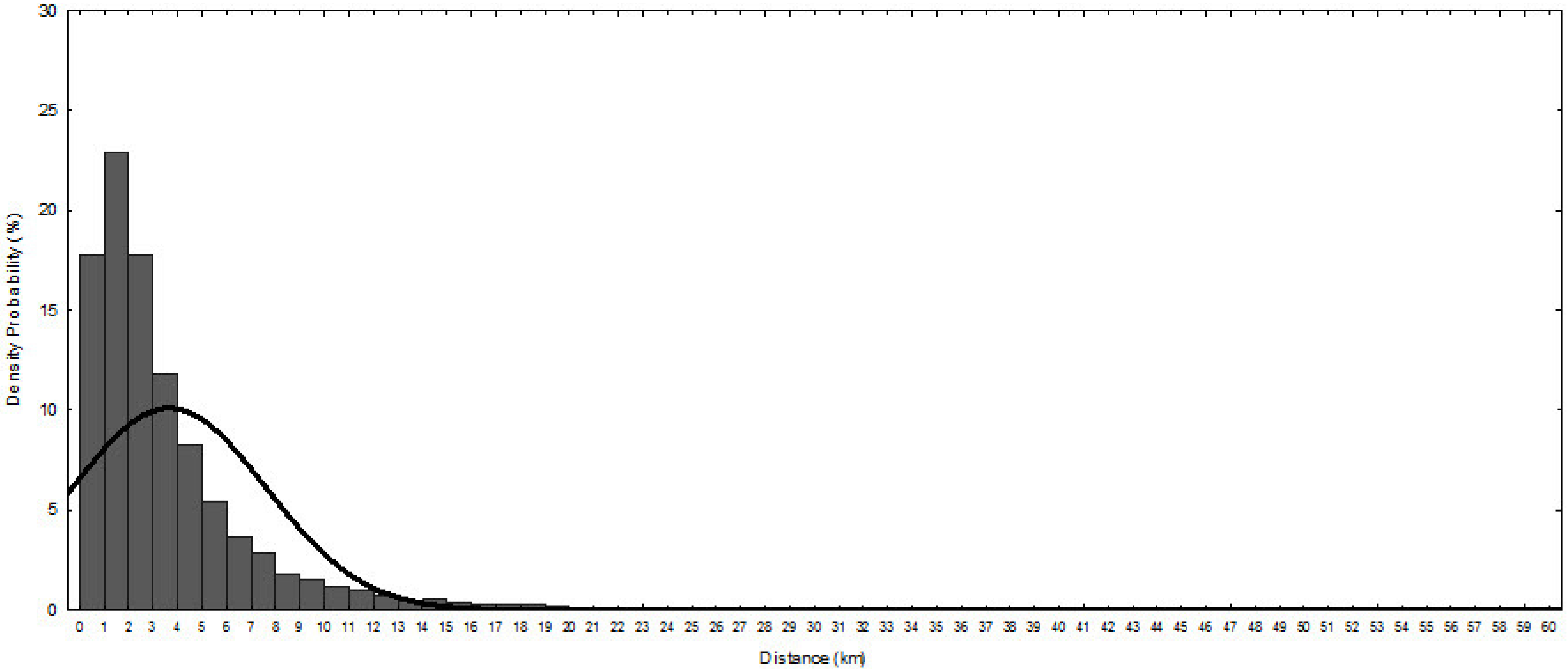


Figure 7: Dispersal kernel produced by African savannah elephants (100.000000*Normal(x, 3.66045085, 3.94806884).

SENSITIVITY ANALYSIS

So as to explore the effect of gut passage rate on the seed deposition densities over distance (dispersal kernel) we modelled gut passage on two hypothetical medians – 21 and 41 hours. The details of the three dispersal kernels are listed below in Table 1 and the curves are shown in Figure 8.

While the addition of an extra 10 hours median gut passage time made little difference to the mean distance a seed is dispersed (extra 500 m) the maximum dispersal distance increased by a 14km margin. In all three dispersal kernels the peak of deposition occurred between 1 and 2 km.

Table 1: Dispersal kernel details for the actual median gut passage rate as well as for two hypothetical median gut passage rates

Median Gut Passage Time	**21 hours (hypothetical)**	**31 hours (actual)**	**41 hours (hypothetical)**
Mean	3.11 km	3.66 km	4.17 km
Median	2.10 km	2.48 km	2.78 km
Standard Deviation	3.36	3.95	4.51
Sample Variance	11.32	15.59	20.30
Kurtosis	16.53	16.19	18.83
Skewness	3.19	3.21	3.33
Minimum	0.006km	0.002 km	0.001 km
Maximum	44.01 km	50.31 km	64.50 km
Count	10066	11020	11248

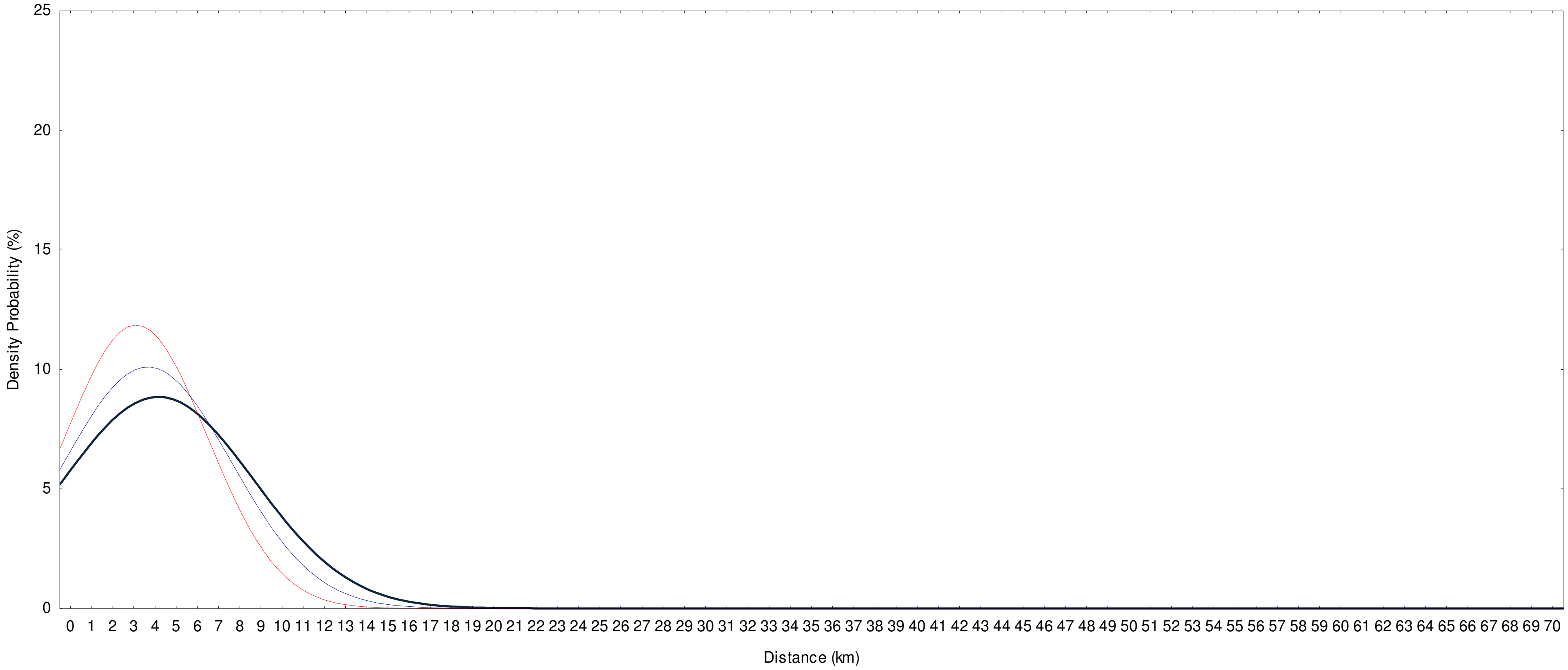


Figure 8: Dispersal kernels produced by African savannah elephants for different median measures (21h (red - hypothetical); 31h (actual in blue) and 41h (dark green - hypothetical).

Discussion

This study provides the first detailed account of the spatial scale at which African savanna elephants disperse seeds. Our results indicate that 50% of seeds are carried over 2500 m and distances up to 65km are achievable in maximum gut passage time. To my knowledge distances of over 60km are unparalleled in the vertebrate seed dispersal literature. Dispersal distances in this range are an order of magnitude greater than the 5-6km maximum dispersal distance achieved by their counterparts – the Asian forest elephants (Campos-Arceiz *et al.,* 2008*)*. Prior to this study the Asian forest elephants, the large-bodied Amazonian characid fish and the *Ceratogymma* hornbills of West Africa were the longest distance seed dispersers of those that had been studied (all dispersing seeds up to 5-7km, Supplementary Data: Table 3).

Perhaps of more relevance is how the dispersal distances of African savanna elephants compare to those provided by sympatric dispersal agents. Sadly little work has been done on African savanna seed dispersal and subsequently the illustration below is based on available studies (Figure 9). Regardless, it is still apparent that the service African savanna elephants afford seeds is highly unique and unlikely to be replicated even as more dispersal agents come under scrutiny. The other large vertebrate (megafauna) that does however warrant the attentions of a seed dispersal study is the African black rhinoceros. Although these animals do not appear to consume great quantities of fruit they are likely to have excessively long seed retention times – the Indian one-horned rhinoceros (*Rhinoceros unicornis*) has a maximum gut passage time of 172 h (7 days - Dinerstein and Wemmer, 1988).

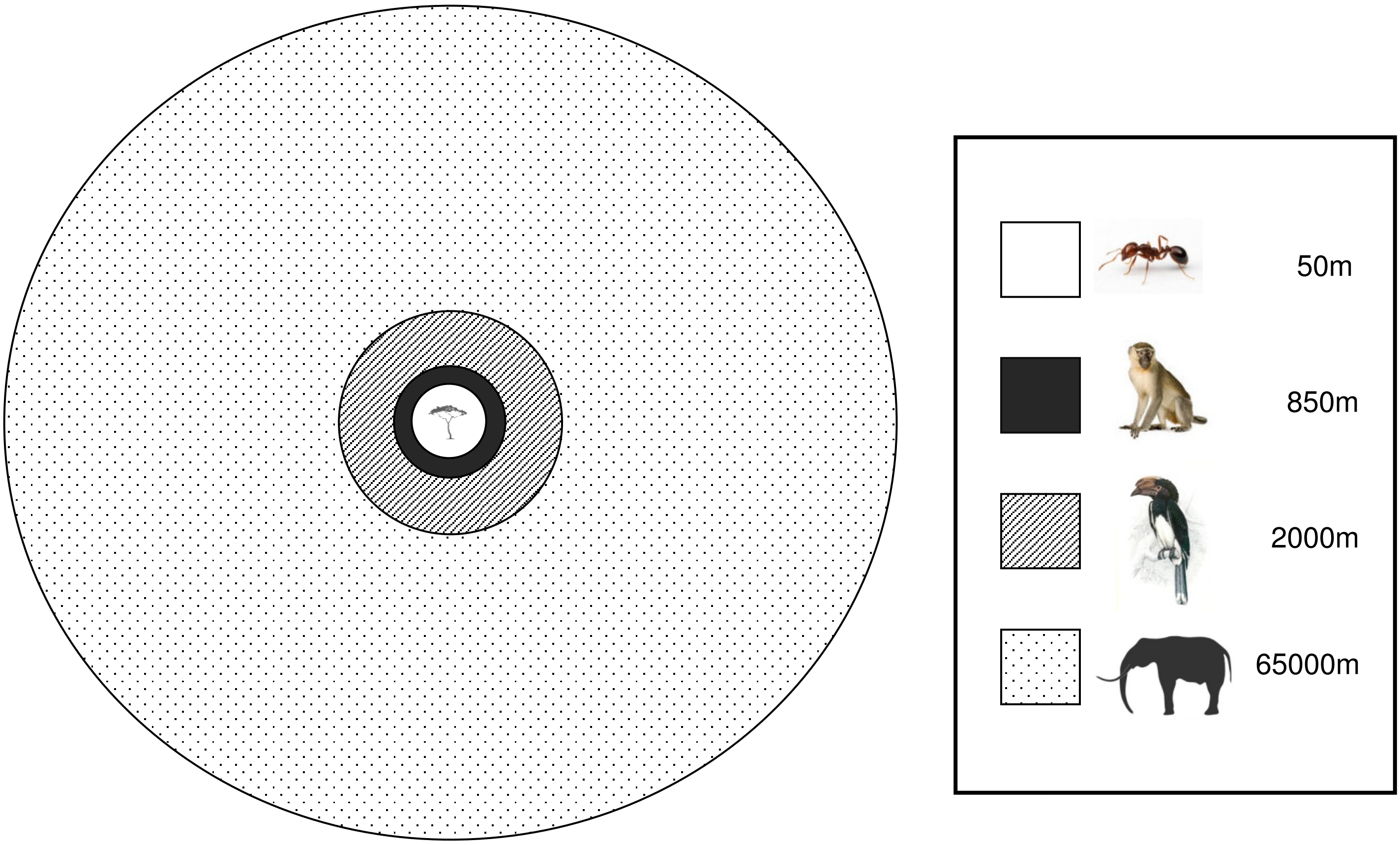


Figure 9: Maximum seed dispersal distances for different disperser functional groups: Trumpeter hornbills - peaks of approx. 500m and tails up to 2 000m; Vervet Monkeys < 850m and Ants < 50m.

The emerging theory in long distance dispersal (LDD) research maintains that the 'standard' dispersal agent i.e. that which is identified by the morphological features of the diaspore, determines the short distance dispersal events but is not responsible for long distance dispersal. Long distance dispersal is thought to be brought about by processes or events that 'break the rules' i.e. nonstandard dispersal events like tropical storms, hurricanes or accidental attachment to a vertebrate (Higgins *et al,* 2003). On the contrary, it appears that African savanna elephants achieve both local and long distance dispersal of large-fruited savanna trees. One percent of seeds are deposited at distances in excess of 20km from the parent tree. Distance figures of this magnitude (1–20km) are in line with those called upon by stochastic migration models in order to explain the rapid migrations seen in the Holocene paleo-records (Clark, 1998; Sauer, 1988; Nathan and Muller-Landau, 2000).

By using the mechanistic framework developed by Westcott *et al.* (2005) we managed to escape a dilemma that frequently plagues dispersal studies – that of scale. In seed rain and genetic seed dispersal studies the dispersal curve will commonly reflect the scale at which the data could be collected. In contrast, when the dispersal agent itself is being tracked it is possible to appreciate the actual scale at which dispersal occurred (Westcott *et al.*, 2005). This is only true however if the timeframe allotted to tracking the dispersal agent is significant enough to allow one to capture both localised and long distance movement events. When one considers that male savanna elephants on occasion make long treks (of >100km at speeds of 1.2km/hr - Henley, 2003) to 'hotspots' (areas with ample water and forage supply - Henley, 2003) it is understandable that months if not years of telemetry data is necessary to capture these extreme long distance dispersal events. As this study employed 1-8 years of movement data from 38 individual elephants (418 001 location points) it is probable that it allowed for the comprehensive characterisation of the long-distance component of the dispersal kernel.

The other constituent of the dispersal kernel is the gut passage curve. Our sanctuary elephants retained mango and melon seeds for a mean gut passage time of 35 and 34 h (median 31hours for both) respectively. This result is in agreement with a previous study by Davis (2008) who recorded a median gut passage time of 37 h. In stark contrast, when looking at the maximum gut passage time, our result for the mango and melon seeds (67 and 96 hours) were considerably longer than those recorded by Davis (53 hours) and by Rees (1982) who estimated food passage time in African savanna elephants to range between 21.4 and 46 h. Our maximum gut passage time for the melon seeds (96 hours) is more line with a gut passage study that was conducted on captive Asian elephants and reported a maximum gut passage time of 114 h – 4.75days- for seeds of one of our megafaunal fruit – *Tamarindus indica*. I investigated the importance of long gut passage time to achieving maximum dispersal distance. I found that in the 4 day (96 hours) maximum gut passage time of melon seeds 73% of maximum median dispersal distance was achieved. Median distance travelled levelled off between 7 and 8 days. This trend held for the maximum potential dispersal distance.

A number of limitations arise from the simplifications necessarily adopted in our study. Firstly, I used a small number of individual elephants in our feeding trial – an inescapable limitation when working with megaherbivores. Anyone who has had the mammoth task of sieving through a day's worth of one elephant's dung will understand this limitation. Secondly, market fruits might not provide reasonable surrogates for our megafaunal fruits. There is likely to be some degree of individual processing however the lack of differences in mean retention time between our two fruit types suggests that these differences might not be conspicuous. Thirdly, this study does not take into account the non-random distribution of fruiting trees or the non-random use of time by elephants. Distant measures in gut passage time were calculated by randomly selecting a starting location. This location might have been occupied by an elephant in the middle of the night in a habitat in which a fruiting tree was unlikely to be found. The effects of elephant behaviour are however averaged out over the model and although important are not likely to significantly alter the magnitude of the dispersal kernel. Fourthly, the model does not consider the effectiveness of dispersal. Dispersal in space is of great consequence but how these seeds survive through time is an equally important question.

African elephants and their ancestors have likely been providing a vehicle for the large-scale movement of megafaunal fruit seeds for millennia. Maintaining their ecological role as a seed disperser may prove to be a significant factor both in the conservation of large-fruited tree diversity within the savannas and in facilitating shifts in biome boundaries in response to global climate change (Woodward 1992, Hulme *et al.* 1996). The consequence of their local extinction on large-fruited tree diversity needs to be urgently explored.

CHAPTER 5

Synthesis

SUMMARY

The focus of this thesis was to firstly construct a list of the megafaunal fruit tree species of South Africa. Secondly, to establish the prevalence of the megafaunal fruit syndrome relative to other means of dispersal in the South African tree flora. Thirdly, it sought to understand the factors that limited the distribution of this syndrome. Lastly, it looked to quantify the dispersal services that the African savanna elephants provide megafaunal fruit.

Using the framework developed by Guimares *et al*., (2008) I identified 31 candidate megafaunal fruit species. As far as I am aware this represents the first comprehensive list of megafaunal fruit tree species for South Africa and the first study to look at the megafaunal fruit of the African savanna landscape at large. These fruit range from the single-seeded *Hyphaene coriacea* that is 5cm in length to the multi-seeded *Kigelia africana* that can reach lengths in excess of 1m. Unexpectedly these megafaunal fruit trees represent only 2.8% of the total tree dispersal spectra and 4% of the vertebrate-dispersed tree species. Megafaunal fruit are predominantly found in tropical tree families. While elephants have historically been found throughout South Africa, megafaunal fruits are not. Their distribution appears to be linked to both high temperature and high rainfall. Using 8 years of elephant movement data coupled with gut passage rates for large fruits I determined the spatial scale at which African savanna elephants disperse seeds. I found that 50% of seeds are carried over 2500 m and distances up to 65km are achievable in maximum gut passage time. Distances such as these are unparalleled in the vertebrate seed dispersal literature and point to the fact that elephants might play a key role in vegetation community dynamics.

Below I explore the importance of long distance dispersal and the consequences of elephant extirpation. I present a number of research areas that I believe deserve consideration.

Is far really better?

I found that elephants carry seeds further than any other vertebrate disperser (other than humans) in our savannas (see Chapter 4). Yet how this translates into the competitive abilities of seeds, the establishment of seedlings and ultimately in the spatial distribution and abundance of plants is a topic that needs to be addressed in a savanna context. As far as I am aware this subject has only been dealt with in two instances, both within a tropical forest context. The first, a study by Seidler and Plotkin (2006) in peninsular Malaysia, compared the dispersal morphologies, fruit sizes, and spatial distributions of 561 tree species. After controlling for phylogeny, they demonstrated that the aggregation pattern of trees in tropical forests is closely linked to the dispersal distances achieved by their diaspores. Ballistically dispersed species were most aggregated while those dispersed by large animals were the least.

The second study, by Blake *et al.* (2009) was particularly pertinent as it looked at patterns of tree aggregation in relation to forest elephant seed dispersal. They classified tree species according to five dispersal syndromes: (a) obligate dispersal by elephants; (b) non-obligate dispersal by elephants; (c) dispersal by other animals; (d) dispersal by wind; and (e) gravity. They found that those trees that relied on elephants for their dispersal (obligate) were the least aggregated suggesting that longer distance dispersal offers seeds a competitive advantage in terms of establishment.

These two studies highlight the role that long distance dispersal plays in placing seeds beyond the damaging reach of Janzen–Connell effects in tropical forests. As far as I know, no study has looked at the spatial aggregation of trees relative to dispersal mechanism within a savanna context. Such a study would provide a baseline that might be revisited following the loss of megaherbivores from an area.

What are the consequences of elephant extirpation?

Large vertebrates, such as elephants are particularly susceptible to eradication by the drivers of the current extinction crisis (Duffy *et al.*, 2009). Despite this we know little of how this imminent loss will affect biodiversity and ecosystem functioning (Corlett, 2013). Elephants might be particularly important in their role as seed disperser. In this study we have demonstrated the extraordinary distances that elephants disperse seeds (see Chapter 4), in addition to identifying several that are likely to be solely reliant upon them (*Adansonia digitata, Schinziophyton rautanenii, Balanites aegyptiaca, Hyphaene coriacea* and *Borassus aethiopum* see Chapter 3).

To better grasp the consequences of elephant extirpation or decline I suggest the following research is given consideration and priority:

1) The construction of a comprehensive list of megafaunal fruit species for both Africa and Asia. Campos-Arceiz and Blake (2011) have already collated the existing studies so there is a foundation from which to begin. Much work is now needed to fill the gaps, particularly in the African savannas. Based on the distribution of the megafaunal fruit within South Africa I suggest that future work identifying megafaunal fruit is focussed in the moister savannas of Southern Africa.
2) In addition to identifying the megafaunal fruit species, it is also important to establish how reliant each of these fruit is on megaherbivores for their dispersal. Species could be classified as moderate, substantial or obligate mutualists (*sensu* Barlow, 2000; Barlow, 2001). An example of an obligate mutualism is that between *Balanites wilsoniana* and the forest elephant. Hundreds of hours of camera footage of *B. wilsoniana*, across numerous individuals revealed that fruits are removed by only forest elephants (Babweteera *et al*., 2007). In Ugandan forests that are devoid of elephants juveniles are only found below parents and the overall population of *B. wilsoniana* is in decline (Babweteera *et al*., 2007). A more moderate mutualism is that between *Dillenia indica*, a large multi-seeded fruit and the Asian forest elephant. In a very recent study in the moist tropical forests of India, Sekar and Sukamar (2013) found that the initial hardness of the fruit was correlated with high elephant visitation. However, if the fruit of *D. indica* was not removed by elephants, it would soften and subsequently become available to smaller frugivores. Understanding these interactions is critical to understanding the megafaunal species most at risk.
3) Identification of backup dispersers. It is critical to determine the extent to which other vertebrates can act as substitutes for megaherbivores and elephants in particular. The presence of large terrestrial

primates in Africa presents an obvious dispersal alternative. In African forests, these primates (gorillas, chimpanzees and bonobos) like megaherbivores, are at high risk of extinction yet in the savannas, baboons have been able to adapt to the presence of humans and unlike megaherbivores are not threatened with extinction. In this study (see Chapter 3) I explored the service that baboons offer the South African megafaunal fruit and found that they provide a highly variable service, acting as either effective dispersers or potent predators. Management of megafaunal fruit trees species in Africa needs to be cognisant of this double role. Baboons, for example prey on the immature seeds of the baobab fruit and according to Venter and Witkowski (2011) are responsible for major (58-85%) crop depletion in areas of cohabitation. In contrast, baboons are known to swallow and disperse intact the seeds of *Parinari curatellifolia (*Kunz and Linsenmair, 2008)*.* Owing to their smaller body size, gut passage time and ranging distances baboons are unlikely to provide a dispersal service at the same scale as elephants. This being said baboons might offer some seeds the advantage of being carried outside of park boundaries, up steep slopes and into rocky areas that might provide safe sites for their establishment. The paradoxical existence of large fruit on the island of Madagascar suggests that primates play a role in the long term persistence of large-fruited trees.

4) Assess the consequences of their loss. Africa is unique in that it provides a testing ground for assessing the consequences of elephant extirpation on megafaunal fruit tree distributions. I suggest that the aggregation of megafaunal trees within protected areas (see Figure 1, with megaherbivores), are compared against the aggregation outside of protected areas where megaherbivores have been absent for extended periods (>100 years). If the megafaunal fruit are highly reliant on elephants for their effective dispersal then outside protected areas one should expect to see clumped tree distributions, in addition to a skewed population structure i.e. more adults than juveniles following Janzen and Martin (1982). Table 1 provides information on the conservation status of the South African megafaunal fruit trees. It includes the number of quarter degree grid squares that each species is found in as a measure of their spread. Those species with limited distribution are likely to be species that are most at risk. Understanding the service that elephants and baboons offer these species should be given priority. In addition I have included a graph that indicates records of each megafaunal fruit tree species inside and outside protected areas. These observations are derived from the PRECIS database (outlined in

Chapter 2 and 3) and may represent sampling bias. They do, however give an indication of which species distribution is largely limited to protected areas, for example *Hyphaene petersiana* – where 90% of observations were made inside protected areas (Figure 1).

Table 1 : Megafaunal species coverage by number of quarter degree squares in which they occur in addition to their Red Data List status.

Family	**Species**	**# of Quarter Degree Grid Squares Occupied**	**Red Data List Status**
Arecaceae	*Raphia australis,*	4	Vulnerable (VU) D2
Arecaceae	*Hyphaene petersiana*	24	Least Concern (LC)
Arecaceae	*Hyphaene coriacea*	13	Least Concern (LC)
Arecaceae	*Borassus aethiopum*	2	Least Concern (LC)
Balanitaceae	*Balanites aegyptiaca*	5	No information available
Balanitaceae	*Balanites maughamii*	14	Decreasing
Boraginaceae	*Cordia grandicalyx*	13	Least Concern (LC)
Chrysobalanaceae	*Parinari curatellifolia*	30	Least Concern (LC)
Papilionoideae	*Cordyla africana*	17	Least Concern (LC)
Sapotaceae	*Mimusops zeyheri*	108	Least Concern (LC)
Sapotaceae	*Vitellariopsis marginata*	30	Least Concern (LC)
Euphorbiaceae	*Schinziophyton rautanenii*	28	Least Concern (LC)
Anacardiaceae	*Sclerocarya birrea*	47	Least Concern (LC)
Strychnaceae	*Strychnos cocculoides*	37	Least Concern (LC)
Rubiaceae	*Gardenia volkensii*	20	Least Concern (LC)
Strychnaceae	*Strychnos spinosa*	20	Least Concern (LC)
Strychnaceae	*Strychnos pungens*	63	Least Concern (LC)
Bombacaceae	*Adansonia digitata*	52	Least Concern (LC)
Bignoniaceae	*Kigelia africana*	53	Least Concern (LC)
Capparaceae	*Cladostemon kirkii*	15	Least Concern (LC)
Mimosoideae	*Acacia albida*	72	Least Concern (LC)
Mimosoideae	*Acacia erioloba*	303	Decreasing
Mimosoideae	*Acacia sieberiana*	21	Least Concern (LC)
Mimosoideae	*Acacia nilotica*	31	Least Concern (LC)
Mimosoideae	*Acacia haematoxylon*	136	Least Concern (LC)
Mimosoideae	*Amblygonocarpus andogensis*	6	No information available
Mimosoideae	*Dichrostachys cinerea*	111	Least Concern (LC)
Caesalpinoideae	*Piliostigma thonningii*	57	Least Concern (LC)
Caesalpinoideae	*Tamarindus indica*	14	No information available
Caesalpinoideae	*Cassia abbreviata*	20	Least Concern (LC)
Papilionoideae	*Swartzia* madagascariensis	unknown	No information available

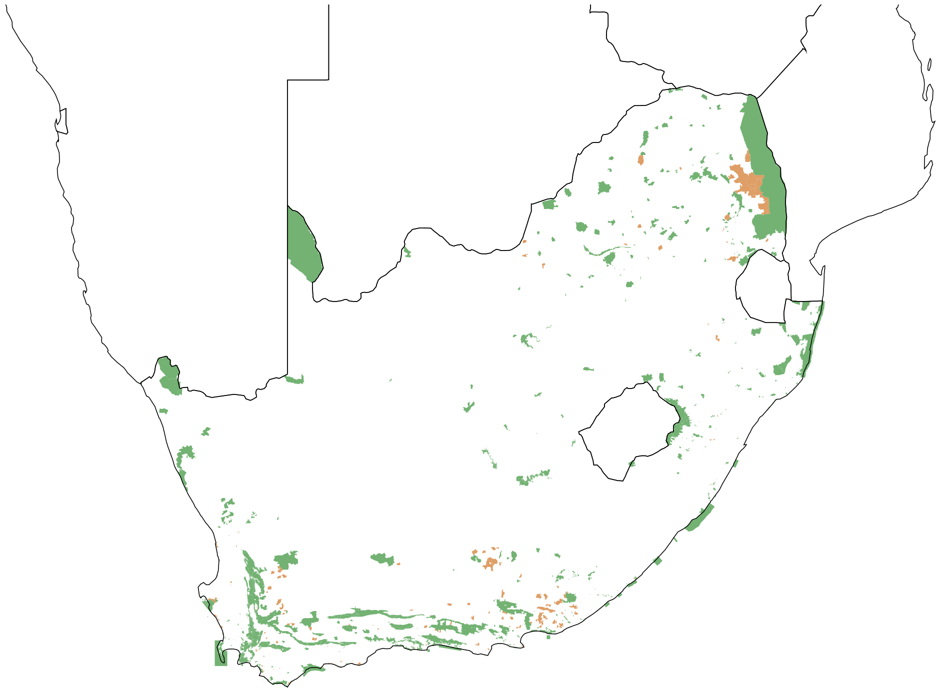


Figure 1: Protected areas in South Africa. The green areas are national parks while the brown areas are private parks or game farms.

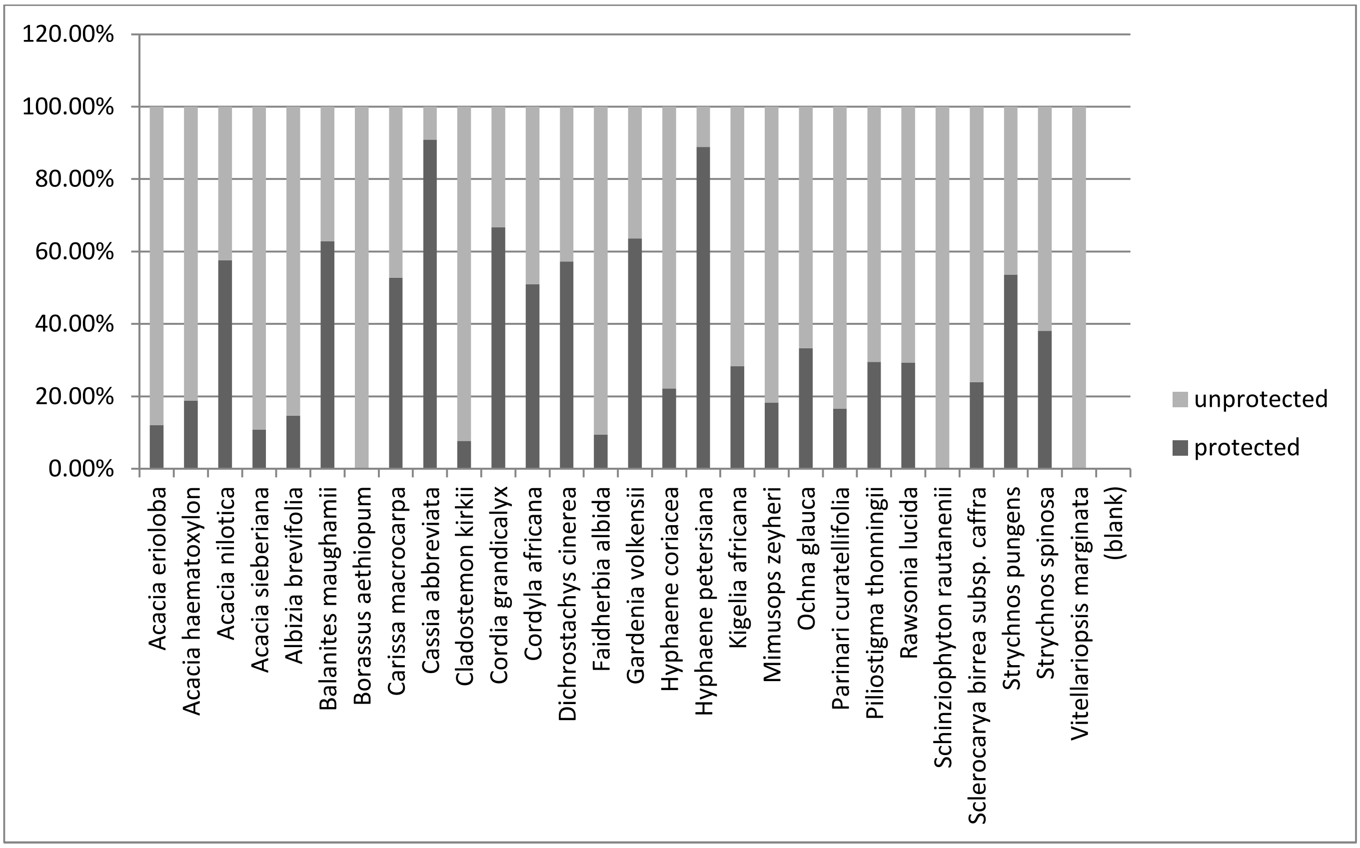


Figure 2: Megafaunal fruit tree species presence in protected versus non-protected areas.

When the service that elephants provide the megafaunal fruit of Africa and Asia is better understood then research should move to understanding the numbers of elephants that are sufficient to maintaining their seed dispersal service. In the meantime, the creation of habitat corridors between protected areas is probably the best way to allow for their continued service to megafaunal fruit trees.

Supplementary Data

Table 1: The dispersal services offered by baboons and elephants to South African megafaunal fruit species. This is based on a thorough literature review of the elephant and baboon seed dispersal literature *(Appendix S2 Ref*erence List). Successfully dispersed: Y= yes; N = no; P =predator and U =unknown. Bite force data is taken from Peters (1993).

Known Dispersal/Predation	Family	Species	Successfully Dispersed by Elephants	Details of Elephant Dispersal	Successfully Dispersed by Baboons	Details of Baboon Dispersal	Bite Force
Dispersed by elephants not by baboon	Arecaceae	*Hyphaene coriacea*	Y	Elephant are known to be very partial to the nuts of the Doum Palm, *Hyphaene coriacea*, in the Northern Frontier Province (Bax and Sheldrick, 1963).	N	Seed Predator: Palm nuts (Hyphaene) are processed more slowly. The hard flaky coat is one edible portion, and as it ripens it hardens, so that each nut must be gnawed for some time (Hamilton *et al*., 1979).	
	Arecaceae	*Borassus aethiopum*	Y	Found intact in elephant dung at Tarangire National Park, Tanzania (Gontier, 2009)	N		
	Balanitaceae	*Balanites maughamii*	A	Assuming that because *B. aegyptiaca* is found intact in elephant dung in the Singida District of Tanganyika Territory/ Hwange National Park that *B. maughamii* is also dispersed by elephants.	N		259-376. Avg 327.9. SSD 43.3
	Papilionoideae	*Cordyla africana*	A	Elephants are exceptionally fond of the fruit. Consequently, the seeds are distributed over a large area (Van Wyk and Van Wyk, 1997 in plantzafrica.com).	U		

	Euphorbiaceae	*Schinziophyton rautanenii*	Y	*Schinziophyton rautanenii* is dispersed by elephant (Bainbridge 1965). The nuts are generally not digested by elephant and are excreted in the dung (Lee, 1973). Found frequently in the dung of elephants in Hwange National Park, Zimbabwe (Dudley, 2000).	U		472-934. AVG 656.2. SD 133.4.
		Amblygonocarpus andogensis	Y	Seeds recovered from elephant dung in a seed dispersal study conducted in Hwange National Park, Zimbabwe (Dudley, 2000).	U		
	Papilionoideae	*Swartzia madagascariensis*	Y	*Swartzia fistuloides* was one of the top 30 fruit species found in the diet of the African forest elephants in the Northern Congo (Blake, 2002).	U		
Dispersed by both elephants and baboons	Rubiaceae	*Gardenia volkensii*	Y	Said to be consumed by elephants (plantzafrica.com)	A	Seeds of *Gardenia cf. aqualla* were found in very small numbers in the faeces of baboons in West Africa (Kunz and Linsemair, 2008).	
	Strychnaceae	*Strychnos cocculoides;* *Strychnos spinosa;* *Strychnos pungens*	A	*Strychnos aculeata* seeds were found in elephant dung collected in Boa National Park, Ghana. Of the 11 species of seed found in the elephant dung, *Strychnos aculeata* was the third most common (Lieberman et al, 1987).	A	*Strynchos sp*. seeds were found intact in baboon faeces in the savanna-forest mosaic of north-eastern Ivory Coast (Kunz and Linsenmair, 2008). McGrew (2010) in a study in West Africa found that baboons ate the pulp of *Strychnos spp.* but carefully spat out the seeds.	
	Chrysobalanaceae	*Parinari curatellifolia*	A	Likely that Parinari are dispersed by elephants. *Parinari excelsa/Parinari montana/Parinari holstii* in West Africa have been identified as megafaunal fruit (Campos-Arceiz and Blake, 2011, Guimares *et al.*, 2008; Feer, 1995).	Y	*Parinari curatellifolia* was the longest intact seed found to be dispersed by the Olive Baboon in the savanna-forest mosaic of West Africa (Kunz and Linsenmair, 2008).	

	Mimosoideae	*Acacia sieberiana*	Y	Seeds recovered from elephant dung in a seed dispersal study conducted in Hwange National Park, Zimbabwe. Dougall and Bogdan (1958) state that the pods are liked by rhinoceros and elephants, and Lamprey (1967) found seedlings of both Acacia albida and *A. sieberiana*, the pods of which are indehiscent, growing in elephant dung in the Lake Manyarra Game Reserve in Tanzania.	Y	Baboons were observed feeding on ripe pods (Majid et al, 2011) in Kibale National Park, Uganda. Seeds said to be poisonous.	
	Mimosoideae	*Dichrostachys cinerea*	Y	*Dichrostachys cinerea* was found in elephant dung in Babile Elephant Sanctuary, Ethiopia (Biru and Bekele, 2012).	Y	Intact seeds (very few) found in baboon faeces collected in a savanna mosaic in West Africa (Ivory Coast) (Kunz and Linsenmair, 2008).	
	Mimosoideae	*Piliostigma thonningii*	Y	Pods are consumed in considerable quantities (Orwa et al, 2009).	Y	Intact seeds (very few) found in baboon faeces collected in a savanna mosaic in West Africa (Ivory Coast) (Kunz and Linsenmair, 2008). Young pods are eaten by baboons during winter months when fresh food is scarce (plantzafrica.com).	AVG 37.5
		Tamarindus indica	Y	Found intact in the dung of elephants monitored in the Tarangire National Park, Tanzania (Gonthier, 2009).	Y	Intact seeds (a large number) found in baboon faeces collected in a savanna mosaic in West Africa (Ivory Coast) (Kunz and Linsenmair, 2008).Seeds of *Tamarindus indica* (Fabaceae) occur with and without the glutinous pulp in baboon faeces. 90.5% of seeds found in baboon faeces remain undamaged.	
	Anacardiaceae	*Sclerocarya birrea*	Y	Elephants (*Loxodonta africana* subsp. *africana*) appear to be the main dispersal agents of marula seeds (Lewis, 1987). Found frequently in the dung of elephants in the Hwange National	Y	Chacma baboons (Papio cynocephalus ursinus) have been observed eating the fermenting fruit and transporting them to new locations (Palmer and Pitman, 1972).	

				Park, Zimbabwe (Dudley, 2000).			
Dispersed by baboons not elephants	Papilionoideae	*Mimusops zeyheri*	N		A	*Mimusops bagshawei* was found in the dung of baboons in Kibale National Park, Uganda (Chapman and Chapman, 1996).	
	Caesalpinoideae	*Cassia abbreviata*	N		Y	Germinating seeds of *Cassia mimosoides* were found in very small quantities in baboon dung in the Shai Hills, Ghana (Lieberman et al, 1979).	
Dispersed by elephants and preyed on by baboons	Arecaceae	*Hyphaene petersiana*	Y	Seeds recovered from elephant dung in a seed dispersal study conducted in Hwange National Park, Zimbabwe. *Hyphaene petersiana* as *H. benguellensis* (Dudley, 2000)	P	Baboons gnaw on immature seed (Fanshawe 1967; Palmer and Pitman, 1972 in Peters 1993).	
	Balanitaceae	*Balanites aegyptiaca*	Y	Found intact in elephant dung in the Singida District of Tanganyika Territory, Tanzania and in Hwange National Park, Zimbabwe (Burrt and Salisbury, 1929; Dudley, 2000).	P	Baboons (*Papio cynocephalus*) obtain seeds from elephant dung and then predate on them (Peters, 1993).	35-86. Avg 55.1. SD 16.8
	Bombacaceae	*Adansonia digitata*	Y	Found frequently in the dung of elephants monitored in the Tarangire National Park, Tanzania (Gonthier, 2009).	P	According to Venter and Witowski (2011) baboons consumed immature baobab fruit. As the seeds are not yet mature they contribute to seed destruction rather than dispersal. Baboons are responsible for major (58-85%) crop depletion. Baboons do not crack baobab seeds that are mature and hard, apparently avoiding damage to their teeth enamel (Sharman 1981).	

	Bignoniaceae	*Kigelia africana*	Y	Found frequently in the dung of elephants monitored in the Tarangire National Park, Tanzania (Gonthier, 2009).	P	Baboons predate on the seeds of the Kigelia when they are ripe (Hamilton *et al.*, 1978). Marais describes the manner in which the individuals of one troop of baboons (Papio ursinus) broke open the hard-shelled fruits of "sausage trees" (*Kigelia pinnata*) with rocks in order to feed on the seeds (Lawick-Goodall *et al*, 1973).
		Acacia albida	Y	Elephants love the seed pods of the apple-ring acacia (*Acacia albida*) (Botany UWC).	P	Baboons reduced fruit production by feeding on unripe fruits and the mass eaten each year was negatively correlated with rainfall (Dunham, 1990).
		Acacia erioloba	Y	*Acacia erioloba* pods may constitute a key nutritional resource for elephant populations inhabiting the Kalahari Sands landscapes of southern central Africa (Dudley, 1999).	P	Baboons (Dunham, 1990) consume unripe Acacia pods
		Acacia haematoxylon	A	A. erioloba is a polyploid of A. haematoxylon (Coe. 1998). Assuming the same re dispersal	P	
Preyed on by baboons not dispersed by elephants		*Acacia nilotica*	U	Eaten by a variety of ungulates but can find no evidence of seeds of *Acacia nilotica* in the dung of elephants.	P	Pods heavily processed. Pods are torn from the tree and using both hands and teeth together sliced open and the seeds nibbled out: within the mouth the skins of the seeds are separated and pushed out using the tongue (Whiten et al, 1991).
Neither elephants nor baboons are	Arecaceae	*Raphia australis*	N		N	
	Boraginaceae	*Cordia grandicalyx*	U		U	

known dispersal agents	Sapotaceae	*Vitellariopsis marginata*	N	N	
	Capparaceae	*Cladostemon kirkii*	U	U	Baboons were seen eating the fruit of *Cladostemon kirkii* in Namaso Bay in Malawi (1984).

Table 2: List of fleshy fruited species (4-10cm in maximum length) that were rejected from the megafaunal list on the basis that their fruit contained more than 5 seeds.

Monodora junodii
Ormocarpum trichocarpum
Maerua caffra
Aeschynomene nodulosa
Brabejum stellatifolium
Erythrophysa alata
Gardenia cornuta
Gardenia ternifolia
Ficus sansibarica
Rothmannia capensis
Rothmannia fischeri
Oncoba spinosa
Thilachium africanum
Solanum aculeastrum
Strychnos madagascariensis
Strychnos gerrardii

Table 3: Comparison between known dispersal kernel studies (references in Reference List A0

Animal Category	**Disperser Species**	**Plant Species**	**Location**	**Mean Dispersal Distance**	**Maximum Dispersal Distance**	**Details of Data and Model**
Birds	*Myadestes melanops; Phainoptila melanoxantha; Semnornis frantzii*	*Phytolacca rivinoides, Witheringia solanacea; Witheringia coccoloboides*	Monteverde Cloud Forest Reserve, Costa Rica	Enormous variation between individuals of the same species.	**370m**; **570m** and **220m** respectively	Matrix modelling using gut retention times from feeding trials and movement patterns from radio-telemetry data.
Birds	*Ceratogymna cylindricus; Ceratogymna atrata* (hornbills)	8 species	Dja Reserve, Cameroon	Small seeds: C. cylindricus =1127; C. atrata = 1422. Large Seeds: C. cylindricus =1947; C. atrata = 1620. Seed diameter ranged from 1-14mm.	*C. cylindricus* =**3558m**; C. atrata = **6919m**	Matrix modeling using gut retention times from feeding trials and movement patterns from radiotelemetry data.
Monkey	*Cebus capucinus* (white faced capuchin monkey)	Not specific	Barro Colorado Island, Panama	150m (highest probability of seed dispersal ranging between 100 m and 200 m)	**844m**	Direct observations of individual monkeys, along with a gut retention time of 100 minutes, which was the time at which captive individuals defecated 75% of the seeds they consumed of various species.
Flightless Bird	*Casuarius casuarius* (cassowary)	11 species	Queensland, Australia	239m	Maximum dispersal distances ranged from **324m** for *Elaeocarpus largiflorens spp. largiflorens* to **1473m** for *Ficus crassipes.*	Matrix modelling using gut retention times from feeding trials and movement patterns from radiotelemetry data.

Monkey	*Ateles paniscus* (spider monkey)	*Virola calophylla*	Manu National park, Peru	245m (if only dispersed seeds are considered)	**1500m** (dispersal curve maximum)	Simulation model based on movement pattern data (direct follows of foraging individuals).
Tortoise	*Chelonoidis denticulata* (tortoise)	a mixture of seeds, including *Jacaratia spinosa* and *Genipa americana*	Pará, Brazil	dry season: 174.1 m; rainy season: 276.7 m	**1210m** (in 12 days gut passage time)	Matrix modeling using gut retention times from feeding trials and movement patterns from radiotelemetry data and "spool-and-line-tracked" individuals.
Elephants	*Elephas maximus* (Asian elephant)	*Tamarindus indica*	Myanmar and Sri Lanka	1988 m	**5772 m**	Matrix modeling using gut retention times from feeding trials and movement patterns from radiotelemetry data.

Birds	Turacos *(Musophagidae): Corythaeola Cristata (Great Blue Turaco); Musophaga johnstoni (Ruwenzori Turaco); Tauraco schuettii (Black-billed Turaco)*	6 tree species	Nyungwe Forest Reserve, Rwanda	Seeds with short retention time: 119 - 229 m; seeds with a long retention time: 156-304 m	Not given	Gut retention times came from feeding trials conducted on captured Ruwenzori Turacos. Dispersal distances were estimated based on observations of the number of trees visited.
Tapir	Tapirus indicus (Malayan tapirs)	Nine plant species representing a broad range of fruit and seed traits occurring in the habitat of Malayan tapirs	Krau Wildlife Reserve, Malaysia	917–1287m	**3289 m**	Matrix modelling using gut retention times from feeding trials and movement patterns from radiotelemetry data.
Fish	Colossoma macropomum (Large bodied Characid)	Duroia duckei (Rubiaceae; tree), Cecropia latiloba (Urticaceae; pioneer tree), Cayaponia cruegeri (liana) and Cayaponia tubulosa (Cucurbitaceae; liana), and Annona muricata (Annonaceae; tree)	Pacaya-Samiria National Reserve, Peru	337–552 m	**5495 m**	Matrix modeling using gut retention times from feeding trials and movement patterns from radiotelemetry data.

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Available on data disc.

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