Original article

Megagardeners of the forest − the role of elephants in seed dispersal

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ABSTRACT

As the largest frugivores on Earth, elephants have unique ecological properties. Found in deserts, savannahs, and forests, they are the last remnants of a diverse lineage. Among the three currently recognized forms, African forest elephants are the most frugivorous, followed by Asian and African savannah elephants, although their role as seed dispersers is variable and context-dependent. African forest elephants may consume more seeds from more species than any other taxon of large vertebrate dispersers, defecating them over long distances in viable conditions into nutrient-rich and protective dung. In short, elephants are forest gardeners. The signature of elephant dispersal is evident in the spatial distribution of trees suggesting that elephants maintain tree diversity and retain low redundancy in seed dispersal systems. Large numbers of forest elephants ranging over large areas may be essential for ecosystem function. The loss of elephants will have important negative consequences for the ecological trajectories of some plant species and whole ecological communities, yet the conservation status of forest elephants is catastrophic in Asia and rapidly becoming so in Africa due to hunting and other conflicts with people. In this paper we review the current knowledge of elephants as seed dispersers, discuss the ecological consequences of their decline, and suggest priority areas for research and conservation action.

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1. Introduction

In 1986, Daniel Janzen published a paper entitled "*Mice, big mammals, and seeds: it matters who defecates what where*" (Janzen, 1986). Fourteen years later, Howe and Miriti's (2000) paper, "*No question: seed dispersal matters*" reviewed the seminal paper of Harms et al. (2000) who definitively answered the long-standing question of whether or not seed dispersal enhances the diversity of tropical forest − it does! These papers aptly summarize what a huge scientific literature has revealed: that seed dispersal mechanisms are a critical component of plant life histories, which ultimately shape the structure, composition, and function of ecosystems around the world. More recently the profound importance of long distance dispersal has been demonstrated, including rare dispersal events (e.g. Trakhtenbrot et al., 2005; Nathan et al., 2008). In the tropics and sub-tropics a majority of tree species rely on animal dispersal (Howe and Smallwood, 1982; Fleming et al., 1987) and animal body size, ecological niche, diet and ranging patterns determine the dispersal potential, competitive balance, and survival fate of hundreds of billions of seeds every year. As the largest terrestrial animals, elephants provide an excellent example of the "large, generalist herbivore". The body size of elephants, their overwhelming contribution to total vertebrate biomass within communities (White, 1994), and catholic, often highly frugivorous, diet make them particularly formidable dispersers of seeds.

Here we provide a first review of the current literature on the ecological role of elephants as seed dispersers. We discuss the seed dispersal abilities of the three extant taxa of elephants across their current distribution on the basis of their respective diet, ranging behavior and the effects of ingestion and deposition patterns on seed germination and establishment. We evaluate the likely consequences of elephant disappearance; and conclude with a discussion of future research needs and priority conservation actions to ensure that elephants may continue to fulfill their ecosystem role in representative ecological settings.

1.1. Extant and extinct elephant taxa, geographical distribution, and major habitats occupied

Elephants are the last survivors of the Proboscidea, an Order that originated in Africa some 60 million years ago (Mya) and

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subsequently radiated to all continents except Australia and Antarctica (Shoshani, 1998). Proboscidean diversity flourished between the Miocene (24–5 Mya) and the Pliocene (5 to 2 Mya) and declined sharply toward the end of the Pleistocene (2 Mya to ~12,000 BP; Sukumar, 2003). Late Pleistocene/early Holocene proboscidean extinctions were largely driven by human hunting (Surovell et al., 2005) and include the mammoths in Eurasia and North America, stegodons in Asia, mastodons in North America, and gomphoteres in South America (Shoshani, 1998; Sukumar, 2003; Corlett, 2010).

Current taxonomy recognizes two extant species of elephant, the African elephant (*Loxodonta africana*) and the Asian elephant (*Elephas maximus*). Within African elephants, strong morphological, behavioural, ecological and genetic differences exist between African forest (*L. a. cyclotis*) and savannah (*L. a. africana*) elephants, and their taxonomic status remains debated (Roca et al., 2001; Eggert et al., 2002; Debruyne, 2005; Johnson et al., 2007; Rohland et al., 2010). Here, we treat them as separate taxa on ecological grounds following Blake and Hedges (2004), who suggested that African forest elephants and Asian elephants living in forests are more ecologically equivalent than African forest and savannah elephants.

A remarkable feature of elephants is their once widespread distribution, and the recent contraction thereof due to human pressure. Populations of African elephants once ranged from the Mediterranean to the Cape of Good Hope (Barnes, 1999), while today they have an estimated range of over 3.3 million km^2 (22% of the continent) and populations in 37 countries; their range is highly fragmented (Blanc et al., 2007). Asian elephants had a historical range that included West Asia, the Indian subcontinent, Southeast Asia (including Sumatra, Java, and probably Borneo), and China as far North as the Yangtze river (Sukumar, 2003). Today, Asian elephant range is highly fragmented, and occupies less than 0.5 million km^2 in 13 counties (Blake and Hedges, 2004; Choudhury et al., 2008; Fig. 1), mostly in small highly restricted pockets of habitat. Current elephant population estimates are 470,000–690,000 in Africa (Blanc et al., 2007) and 25,000–45,000 in Asia (Blake and Hedges, 2004), though in both cases these figures are best guesses.

Elephants can occur across a wide array of environmental conditions, existing in six (perhaps up to 9) of the 14 major terrestrial habitats (biomes) on Earth (Olson et al., 2001; Fig. 1). African elephants occur mostly in tropical rain forest and tropical grasslands and savannahs, and to a lesser extent in flooded tropical grasslands, montane areas, and desert and xeric areas. Asian elephants, on the other hand, occur mostly in tropical moist and in tropical dry broadleaf forests (Fig. 1). It is inevitable thus that elephants show very different ecological responses (e.g. diet composition, movement patterns, social behavior) and play hugely variable roles as seed dispersers in different environments, both between and within elephant taxa.

1.2. The food habits and ranging behavior of a megaherbivore

The huge body size allows elephants to overcome some of the predation pressures faced by smaller animals, but makes them slaves of their stomachs. For example, a wild adult Asian elephant may spend up to 18 h per day feeding, consuming some 150 kg of food (Vancuylenberg, 1977).

As monogastric hindgut fermenters, elephants are rather poor at dealing with defensive toxins produced by plants (Clauss et al., 2003) – a problem they can reduce by increasing food diversity, thus reducing intake of each particular toxin. The diet of elephants can be highly diverse, though this depends on the diversity and composition (nutrients and secondary compounds) of the plants available. African savannah elephants in arid Namibia eat just 33 plant species, while in Uganda they consume over 200 species. In the Ndoki forest of Congo, forest elephants eat at least 500 plant species (Blake, 2002), the highest known dietary diversity of any mammal. Asian elephants often consume *ca.* 100 plant species (e.g. McKay, 1973; Sukumar, 1990; Chen et al., 2006; Campos-Arceiz et al., 2008a). Fruit is also an important component of elephants diet (e.g. Alexandre, 1978; Short, 1981; White et al., 1993; Blake, 2002; Campos-Arceiz et al., 2008a). Unlike most frugivores, their large mouth and gape means that elephant feeding is not limited by the size of fruits or seeds.

Body size and feeding requirements mean that elephants generally have large home ranges and occur at low densities (Owen-Smith, 1988), in step with the body mass-home range continuum across terrestrial mammals (Fig. 2). Among elephant taxa, it is difficult to compare home range size because of the often overwhelming effects of human pressure on ranging (Blake et al., 2009) and because there have been few detailed studies of movements of Asian elephants. It is likely that Asian elephants have the smallest home ranges, followed by African forest elephants and
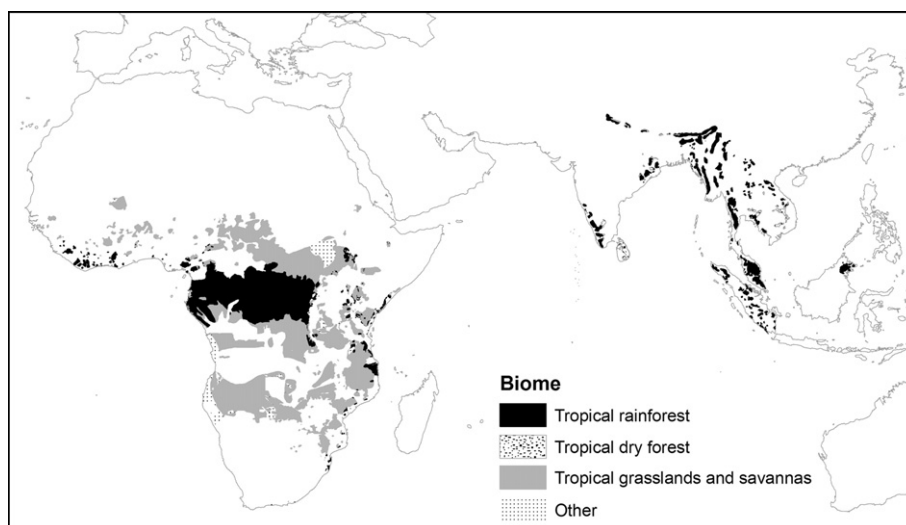

Biome
- ■ Tropical rainforest
- ▨ Tropical dry forest
- ▨ Tropical grasslands and savannas
- ▨ Other

Fig. 1. Current distribution range of African and Asian elephants (source: IUCN Red List). Colors represent major terrestrial habitats as defined by WWF (Olson et al., 2001). Horizontal lines represent Equator and the Tropic of Cancer and Capricorn.
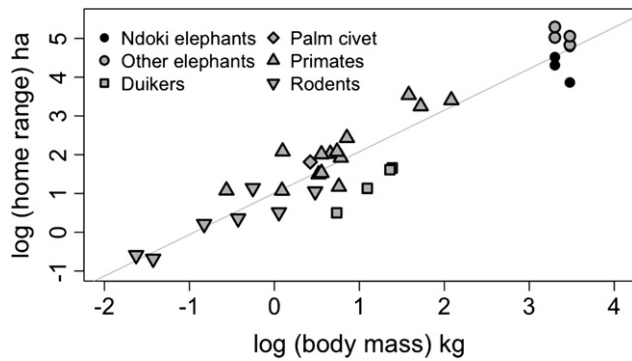
Fig. 2. Body size to home range relationships for selected mammalian forest seed dispersers in the Congo Basin (figure from Blake et al., 2009).

finally African savannah elephants, with desert-adapted elephants in Mali having the largest minimum convex polygon (MCP) ranges of all at up to 35,000 km^2 (Blake et al., 2003).

All these factors – large food requirements, broad dietary breadth, large gape size, and extensive home ranges – shape the seed dispersal functions of elephants.

2. Reliability of seed removal and diversity of plants dispersed by elephants

2.1. Reliability of seed removal

Seed dispersal reliability (the likelihood of a particular seed to be removed by the disperser) is a key component of animals' seed dispersal effectiveness. This is particularly important in the case of dispersers that, like elephants, occur at low densities and can take many months to cover their home ranges (Fernando et al., 2008). However assessing fruit removal rate is particularly difficult for elephants since they may pay only occasional visits to a given fruiting plant, but a single visit can have a huge impact on fruit removal.

The available data on elephant seed dispersal reliability comes from studies on the relationship between elephants and the tree *Balanites wilsoniana* conducted in Kibale National Park, Uganda. In 4455 h of camera trapping Babweteera et al. (2007) recorded 62 elephant-visits (i.e. a mean of one elephant-visit every three days per tree). Also in Kibale, Cochrane (2003) monitored the fate of fruits from 50 *B. wilsoniana* trees. She found that elephants visited almost half of the focal trees (46.0%, $n = 50$) and dispersed as many as 26.3% ($n = 3697$) of all the fruits marked. Most fruits not dispersed by elephants were consumed by predators (57.9%) or rotted (12.9%, $n = 3697$; Cochrane, 2003). *B. wilsoniana* seems to be a highly preferred food item for Kibale elephants, meaning that these high values of seed removal rate cannot necessarily be extrapolated to many other fruit species dispersed by elephants.

2.2. Elephant fruit-foraging efficiency

Reliability and the efficient exploitation of forest fruits (always a temporally and spatially-clumped resource) by elephants may depend on their ability to predict when and where fruits are likely to be available. Elephants are among the most intelligent animals (Hart et al., 2008) and can process complex spatio-temporal information. They keep track and predict the location of other members in their group (McComb et al., 2001; Bates et al., 2008), are aware of the expected onset of rains in locations up to 200 km away (Viljoen, 1989), and can remember where to find food and water in case of an extreme drought, even decades after having

last visited these sites (Foley, 2002). Other intelligent animals such as chimpanzees (*Pan troglodytes*) use euclidean cognitive maps that allow them to remember when and where they can find particular resources in the forest and navigate to them directly without the need to use landmark references (Normand and Boesch, 2009).

African forest elephants seem to use spatio-temporal memory to exploit fruit resources. Short (1983) found that elephant density in Bia National Park (Ghana) varied seasonally between 0.13 and 0.44 ind/km^2, with density strongly correlated with the local availability of *Tieghemella hecklii* and *Parinari excelsa* fruits. Similarly, elephant densities increase sharply in a restricted area of the Lopé Reserve (Gabon) during the fruiting period of *Sacoglottis gabonensis* (White, 1994). White (1994) assumed that elephants were moving outside their normal home ranges into the high fruit area.

Elephants may also improve their foraging efficiency by following permanent trails created by repeated movements to and from dependable resources. Blake and Inkamba-Nkulu (2004) found that in Nouabalé-Ndoki National Park (Congo) elephants move in straight lines between large fruiting trees using permanent trails and that the density of elephant trails is positively correlated with the density of trees with fruits eaten by elephants. Permanent trail intersections are characterized by higher than expected abundance of fruit trees. In Kibale (Uganda), Wing and Buss (1970) noted that all adult trees of *Balanites wilsoniana* were connected by a network of elephant trails. Trails may therefore represent a form of societal spatial memory.

3. Diversity of plants dispersed by elephants

3.1. Diversity of seeds dispersed at a given site

The diversity of plant species dispersed is an important component of the community-level effectiveness of a seed disperser (Dennis and Westcott, 2006). Due to the difficulty to directly observe fruit removal by elephants, the diversity of seeds dispersed is generally quantified based on the contents of dung (Table 1). In the available literature we found more studies using this method with African forest elephants (11 studies) than for savannah (6) or Asian elephants (5). Overall the percentage of dung samples containing seeds and fruit fragments, the number of species, and the number of woody plant species was higher in African forest elephants than in African savannah and Asian elephants (Table 1). In all studies of African forest and savannah elephants, at least 65% of dung piles contained some seeds, while in the tropical moist forests of Khao Yai (Thailand) only 21% of dung piles contained seeds (Kitamura et al., 2007). Similarly, African forest elephants always dispersed 14 or more woody species (trees or shrubs; $n = 8$ studies) while in Asia only one study found elephants to disperse more than ten woody species ($n = 5$ studies; Table 1).

We conducted analyses using generalized linear models (GLM) to assess the effect of different factors on the diversity of plants dispersed by elephants. In the analyses we included (a) elephant taxon (factor with three levels), (b) latitude (absolute value in degrees), (c) rainfall (mm), (d) the interaction between latitude and rainfall, and (e) sampling effort (number of dung samples inspected) as explanatory variables while (a) the proportion of samples containing seeds or fruits, (b) the number of species found, or (c) the number of tree species were used as response variables. The percentage of samples containing seeds was arcsin transformed and analyzed with a normal distribution of the error. The remaining two models were analyzed using a Poisson distribution of the error. The proportion of dung samples containing seeds was not affected by elephant taxon (Fig. 3a) or any of the other factors tested. The number of species and the number of tree species were

Table 1
Diversity of seeds found in elephant dung. AFE: African forest elephant; ASE: African savannah elephant; AE: Asian elephant; See A1 on OSM for a complete list of the references in the table.

Ele Taxon	Country	Site	Lat (±°)	Rain (mm yr^{-1})	N dung piles sampled	% Containing seeds	# spp	# Tree species	Ref.
AFE	Ivory Coast	Tai	6	1650			42	37	Alexandre (1978)
	Ivory Coast	Tai	6	1650	72		44	44	Merz (1981)
	Ghana	Bia	6	1500	190	93	35	35	Short (1981)
	Gabon	IRET	0	1755	104	99	32	30	Gautier-Hion et al. (1985), Feer (1995)
	Ghana	Bia	6	1500	31	100	11		Lieberman et al. (1987)
	Cameroon	Santchou	5	1750	250	65	22	20	Tchamba and Seme (1993)
	Gabon	Lope	0	1536	311	82	72	54	White et al. (1993)
	Zaire	Kahuzi-Biega	1	1990	203		14	14	Yumoto et al. (1995)
	Cameroon	Banyang-Mbo	6	4083	2387		50	43	Nchanji and Plumptre (2003)
	Gabon	Loango	2	2363	220	92.3	49		Morgan and Lee (2007)
	Rep Congo	Ndoki	2	1422	855	94	96	73	Blake et al. (2009)
			3.6	1927.2	463.3	89.3	42.5	38.9	
ASE	Tanzania	Singida	5				12	12	Burtt and Salisbury (1929)
	Kenya	Shimba Hills	4	1151	233	90.5	221		Engel (2000)
	Zaire	Ruindi & Lulimbi			414		5		Brahmachary (1995)
	Zimbabwe	Hwange	19	650	329	80	28	28	Dudley (2000)
	Kenya	Arabuko-Sokoke	3	1000	736	64.5	42		Muoria et al. (2001)
	Tanzania	Tarangire	3	620	66		11	6	Gonthier (2009)
			6.8	855.3	355.6	78.3	53.2	15.3	
AE	Thailand	Khao Yai	14	2270	2249		9	9	Kitamura et al. (2002)
	Thailand	Khao Yai	14	2270	701	21.1	7	7	Kitamura et al. (2007)
	Sri Lanka	NW	8	1375	145	74	44	7	Samansiri and Weerakon (2007)
	Vietnam	Cat Tien	11	2400	34	58.8	4	2	Varma et al. (2008)
	Sri Lanka	SE	7	1500	479	93.5	69	18	Campos-Arceiz (2009)
			10.8	1963.0	721.6	61.85	26.6	8.6	

significantly affected by elephant taxon (with forest elephants always having a higher effect size than African savannah or Asian elephants; Fig. 3b,c), the rainfall * latitude interaction and the number of dung piles inspected (with a positive effect; see Tables S1 and S2 in OSM). Our results show that African forest elephants are more frugivorous and disperse more seeds than African savannah and Asian elephants, that elephant populations near the equator tend to disperse a higher diversity of plants and seeds and that the effect of the distance to the Equator is mediated by environmental factors such as precipitation. Besides pointing to the taxonomic and geographic differences in elephant diet and dispersal capacity, our analysis stresses the need to use large sample sizes of dung piles, across seasons and geography, to obtain reliable results.

The differences in the level of frugivory between forest and savannah elephants in Africa are understandable based on differences in plant and fruit diversity in their respective habitats, however the low level of frugivory found in Asian elephants is surprising. Possible reasons for this include: (a) proboscideans have inhabited Asia for about 23 Mya compared with 60 Mya in Africa, and Asian plants might have had less time to adapt to them as dispersers; (b) in Africa, elephants occur over a much broader band straddling either side of the Equator (where plant diversity, importance of trees as growth habit, animal-mediated seed dispersal, and seed sizes are higher; Moles et al., 2007); (c) Asian tropical forests are dominated by wind-dispersed dipterocarps rather than trees with fruits specifically evolved for animal dispersal as is the case in African forests; and finally (d) current knowledge may be heavily biased toward understanding African elephant diet compared to Asian elephants, since there have been far fewer studies on frugivory of Asian elephants than for African forest elephants, and those available have often been at relatively high latitudes (>10 degrees) or in highly human-dominated dry tropical forest environments.
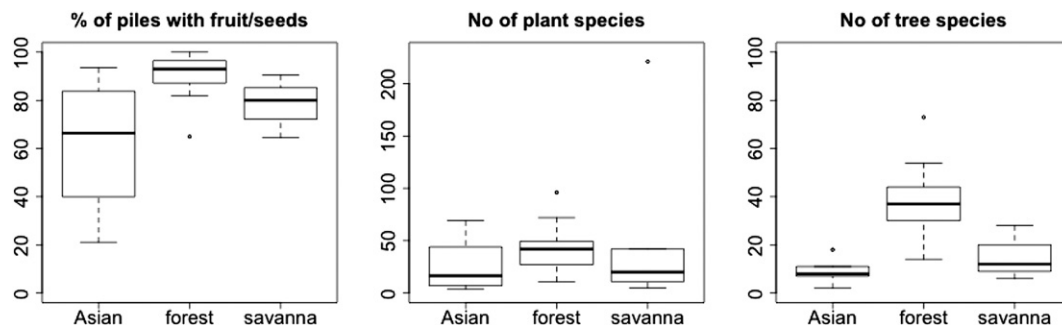

Fig. 3. Presence of seeds, number of species, and number of tree species in the dung of Asian, African forest, and African savannah elephants.

3.2. Plants that elephants disperse

Elephants may disperse a large variety of plant species at a given site, however the total number of species dispersed by elephants globally has not been published. We assessed this by compiling published information and some non-published sources (see A2 in OSM for the complete list of references used) on the fruits that elephants consume or seeds they disperse across research sites. We identified 451 species, from 268 genera in 73 families. African elephants disperse seeds from at least 335 species and 213 genera in 65 families, while Asian elephants are known to disperse 122 species from 92 genera in 39 families. This list is likely to increase as more studies are conducted, especially in Asia.

The dominant families of plants dispersed include Fabaceae (52 species), Malvaceae (33), Sapotaceae (30), Poaceae (25), Moraceae (23), and Euphorbiaceae (22) with more than 20 species dispersed for each family (Fig. 4). With the exception of the Fabaceae and Poaceae, there is little overlap in the species dispersed by elephants in Africa and Asia (Fig. 4). Among those families with five or more species, Chrysobalanaceae, Acanthaceae, Compositaceae, and Ola-caeae have been described as dispersed by elephants only in Africa (so far), while Dilleniaceae is exclusive to Asia (Fig. 4). By genera, *Ficus* (15 species) is the most common, followed by *Grewia* (10), *Strychnos* (9), *Diospyros* (8), and *Solanum* (8). Among genera, there is more continent-level specificity (e.g. *Chrysophyllum*, *Omphalo-carpum*, *Gambeya*, *Manilkara*, *Dillenia*, and *Panicum*; Fig. 4)

3.3. Characteristics of fruits consumed by elephants

Alexandre (1978) used the fruit and seed traits of 37 tree species to classify elephant-dispersed plants into four broad categories (Table 2). Feer (1995) followed the same classification, which was later used by Guimaraes et al. (2008) to characterize neotropical

megafaunal-syndrome plants. Yumoto et al. (1995) describe the fruits eaten by elephants in Kahuzi-Biega National Park (DR of Congo) as including mostly brown–green–yellow fruits, a range of fruit lengths of 2.1–35.3 cm, and sugar concentrations of 4.5–37%. In Khao Yai (Thailand), Asian elephants consume 10 species ranging 2.6–8.1 cm in length, most of them with hard seeds, and all but two of yellow color (the remaining two being red and brown; Kitamura et al., 2002, 2007).

During the day, elephants have a dichromatic vision — very similar to that of deuteranope color-blind people — and cannot distinguish red from green and orange from yellow (Yokoyama et al., 2005). It is not surprising thus that most of the fruits they consume are "unattractive" — as described by Alexandre (1978) — and in the range of green, yellow, and brown. Elephants however have a very sensitive olfactory capacity and it is expectable that they rely on this sense to find fruits in the forest floor. Indeed all the fruits consumed by elephants in Khao Yai emit a sweet aroma perceivable by people (Kitamura et al., 2007). In African forests, fruits of many species including those in the Irvingiaceae, Balani-taceae, Sapotaceae and Anacardiaceae all produce a pungent aroma that even humans can spell from a considerable distance (S. Blake, pers. obs.).

3.4. The need to be eaten — obligate seed dispersal relationships

Among seed dispersal mutualisms, generalism seems to be the rule (e.g. Bascompte et al., 2006) and obligate relationships are rare in nature. However, they have been suggested to occur for a number of species dispersed by elephants. They all involve plant species that fit into the so-called "megafaunal-syndrome" i.e. plants with very large fruits and seeds that may have evolved to attract the megafauna to consume and (often exclusively) disperse them (Janzen and Martin, 1982; Guimaraes et al., 2008). Obligate
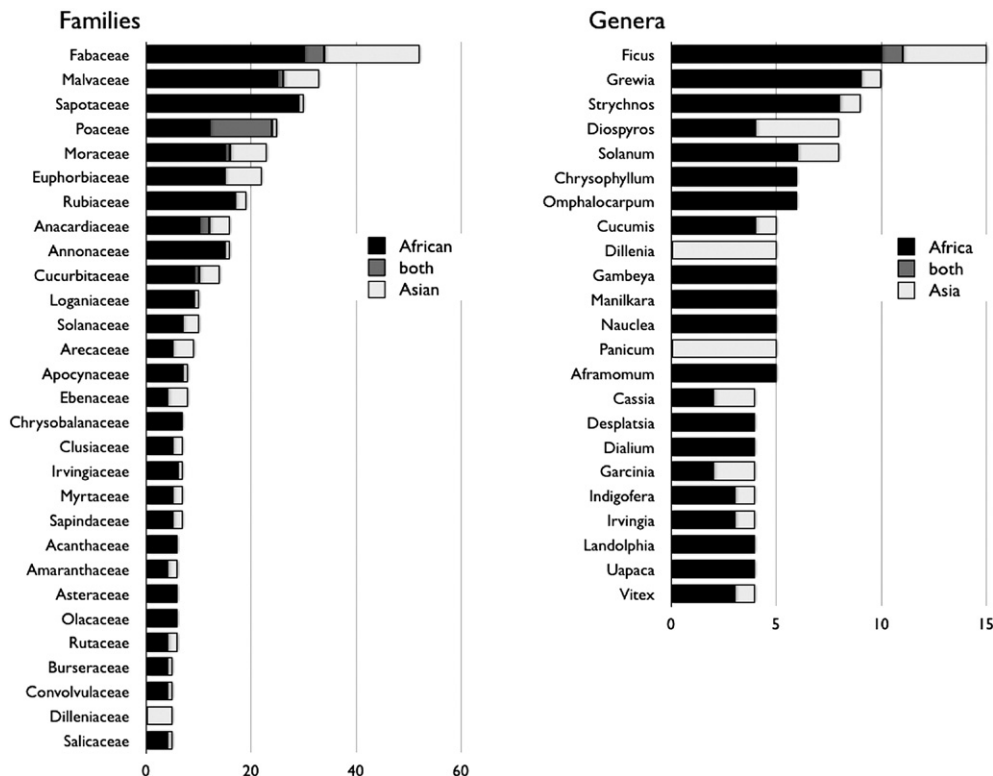

Fig. 4. Families and Genera known to be dispersed by African and Asian elephants.

Table 2
Characteristics of fruits consumed by elephants (following Alexandre, 1978).

Type	Species type	Size	Seed characteristics	Pulp characteristics	External appearance	Germination
I	Parinari holstii	4–10 cm	Few (1–5) hard (woody)	Soft juicy or dry fibrous, odorant, red	Unattractive, greenish	Slow
II	Pentadesma butyracea	>10 cm	Many and soft	Abundant, soft, flagrant, yellowish	Unattractive, brownish	Fast
III	Samanea dinklagei	Large	Small	More or less flagrant		Requires scarification
IV	Other fruits consumed by elephants for which elephants are not prime dispersers					

relationships between plants and elephants have obvious implications for forest ecology and conservation — if the density of elephants is reduced or populations are lost, megafaunal plants may lose their competitive advantage and be replaced by other less able competitors.

All plant species thought to be dispersed solely by elephants are found in Africa (Table 3). Alexandre (1978) mentions 30 species only known to be dispersed by elephants in Tai NP (Ivory Coast); although it is unlikely that elephants are the only disperser for all of them. Feer (1995) found that wild forest duikers in Africa did not disperse seeds larger than 2.2 cm in length, though captive duikers did regurgitate larger seeds. Blake et al. (2009) describe up to 13 species dispersed only or predominantly by elephants in the Ndoki forest (Congo). While there is no published evidence of any plant species being exclusively dispersed by Asian elephants, this is most likely a consequence of the poorer knowledge of their feeding ecology rather than the lack of such relationships. Asian plants that might rely on elephants as primary animal dispersal agent include *Borassus flabelifer*, *Feronia limonia*, and a number of *Mangifera* spp., among others.

4. Traveling through and with elephants – from fruit removal to seed deposition

4.1. Seed survival to gut passage

When elephants eat fruits, some seeds are defecated intact while others might be destroyed – chewed in the mouth or digested in the guts. The probability of a seed to survive mouth and gut treatment will vary with the characteristics of seeds (e.g. size, hardness, protection offered by pulp). Seed survival to gut passage can be estimated in controlled feeding trials, in which elephants are fed a known amount of seeds and surviving seeds are later retrieved from dung and counted. We are aware of just two published estimates of seed survival to elephant gut passage (Table 4). *Acacia erioloba* seeds consumed by African savannah elephants showed a high mortality, with less than 12% survival (Dudley, 1999), although this experiment might have been interrupted too early to accurately estimate seed survival. Tamarind seeds ingested by Asian elephants showed much higher survival (75%; Campos-Arceiz et al., 2008b), although a separate experiment comparing 12 native and introduced plants from Sri Lanka showed that the range of survival varies largely between species (A.R. Larrinaga, pers. comm.).

4.2. Seed gut passage time

The time from ingestion to defecation – or seed gut passage time (GPT) – has two main effects on seeds: (1) the exposure time to the acid environment of elephant digestive tract may alter the viability and germination capacity of seeds; and (2) it is one of the main determinants of the spatial pattern of seed dispersal. Seed GPT data can also be estimated in feeding trials, in which the time of ingestion is known and the time of defecation of each seed is recorded. Dudley (1999) estimated mean and maximum GPT values of 30.5 and 36 h for *Acacia erioloba* seeds consumed by African savanna elephants. This again might be an underestimation, since the experiment (apparently) only lasted 36 h (Dudley, 1999). Mean and maximum GPT of tamarind seeds ingested by Asian elephants were much longer: 40 h and 5 days, respectively (Campos-Arceiz et al., 2008b; Table 4). Such seed GPT are much longer than those of co-occurring smaller seed dispersers such as bulbuls (range 5–159 min; Weir and Corlett, 2007), hornbills (e.g. 2.6–5.7 h; Holbrook and Smith, 2000), palm civets (mean = 2.6 h; Nakashima and Sukor, 2010), and black bears (median = 15.2–19.7 h; Koike et al., 2011); but comparable to those of primates like macaques (mean = 37–54 h, max = 109 h; Tsuji et al., 2010) and gorillas (mean = 47.3 h, max = 130 h; Remis, 2000); and shorter than many herbivores with smaller size and similar digestive systems, such as equids (mean = 50–70 h; Cosyns et al., 2005) and rhinoceroses (peak 64–88 h, max = 172 h; Dinerstein and Wemmer, 1988).

4.3. Elephant movements while carrying seeds and spatial scale of dispersal

In endozoochory, dispersal distance depends on seed gut passage time and the movement of the disperser during this period. Combining information from seed retention times and elephant displacement curves it is possible to estimate one-dimensional dispersal kernels. Campos-Arceiz et al. (2008b) used movement data from three elephants in southeastern Sri Lanka and three in central Myanmar and found mean dispersal distances of 1–2 km and maximum dispersal distances of 6 km. Mean and maximum dispersal distances varied moderately among regions and seasons.

Table 3
Obligate seed dispersal mutualisms. AFE: African forest elephant; ASE: African savannah elephant.

Ele Taxon	Country	Site	# Species dispersed	Species	Ref
ASE	Zambia	Lupande	1	*Sclerocarya caffra*	Lewis, 1987
	Uganda	Kibale	1	*Balanites wilsoniana*	Chapman et al., 1992; Cochrane, 2003; Babweteera et al., 2007
AFE	Ivory Coast	Tai	30		Alexandre, 1978
	Gabon	Lope	1	*Sacoglottis gabonensis* *Autranella congolensis* *Balanites wilsoniana* *Detarium macrocarpum* *Drypetes gossweileri* *Irvingia gabonensis* *Irvingia grandifolia* *Irvingia robur*	White, 1994
	Rep Congo	Ndoki	13	*Klainedoxa gabonensis* *Mammea africana* *Maranthes* sp. *Omphalocarpum elatum* *Panda oleosa* *Tridesmostemon omphalocarpoides*	Blake et al., 2009

Table 4
Seed survival and retention time estimated in feeding trials with elephants. ASE: African savannah elephant; AE: Asian elephant.

Elephant taxon	Plant species	Seed survival (%)	Mean GPT	Max. GPT	Study duration	Ref.
ASE	*Acacia erioloba*	11.5	30.5	36	36?	Dudley (1999)
AE	*Cucumis melo*		20.2	72	72	Weerasinghe et al. (1999)
	Tamarindus indica	75.1	39.5	113.8	140	Campos-Arceiz et al. (2008b)

These analyses were conducted with a small sample size (6 elephants) and short temporal data (6 weeks in each of two seasons) but still are likely to reflect the regular dispersal pattern provided by elephants in these environments. Elephants moved (and thus dispersed seeds) over short distances relative to their movement potential yet these distances are high compared with sympatric animal dispersers (Campos-Arceiz et al., 2008b). In Central Africa, in the moist tropical forests of Ndoki (Congo) Blake et al. (2009) used data from four collared elephants and estimated that 88% of dispersed seeds are moved >1 km from the parent, while a full 14% of large seeds are transported >10 km. The maximum dispersal distance recorded was 57 km. These distances dwarf dispersal distances of other animal dispersers in central African forests (Blake et al., 2009). Other authors have ventured to estimate probable dispersal distances based on rough estimates of seed retention times and movement rates (Table 5).

There are other animals capable of dispersing seeds over long distances such as Southeast Asian flying foxes *Pteropus vampirus* (Epstein et al., 2009), smaller African fruit bats (Richter and Cumming, 2008), neotropical guacharos *Steatornis caripensis*, and to a lesser extent hornbills, fruit pigeons, and some migratory birds (see Corlett, 2009 and references therein). But few can match the distances over which elephants travel, and these animals will only disperse tiny seeds (e.g. fruit bats when flying long distances) or different species to those dispersed by elephants (e.g. hornbills). Forest rhinos in Asia, other large terrestrial herbivores, carnivores, and apes may disperse some of the same fruit species as elephants (i.e. seeds from large-fruited or -seeded plants) over long distances, but such events are likely to be rare (Corlett, 2009; Koike et al., 2011).

5. From defecation to germination

5.1. Effect of elephant gut passage, dung, and clumping on germination

Passing through the gut of an elephant can have different effects on the viability and germination of seeds. Some megafaunal-syndrome plants have developed large seeds protected with a thick testa (large seeds are more prone to predation) that benefit from going through elephant guts in that gastric acids scarify the seeds and break dormancy, thus stimulating germination. This might be the case with the seeds of *Sclerocarva caffra* (Lewis, 1987) and

Table 5
Estimated dispersal distances provided by elephants. AFE: African forest elephant; ASE: African savannah elephant; AE: Asian elephant.

Elephant Taxon	Country	Mean displacement (km)	Max. displacement (km)	Ref.
AfSE	Zimbabwe	–	30	Dudley, 1999
AFE	Ivory Coast	8.5	12	Theuerkauf et al., 2000
	Rep Congo	3.5	57	Blake et al., 2009
AE	Sri Lanka	1.2	6	Campos-Arceiz et al., 2008b

Balanites wilsoniana (Chapman et al., 1992; Cochrane, 2003). In the available studies, consumption by African elephants generally resulted in a highly improved probability of germination for seeds whereas consumption by Asian elephants had milder effects, sometimes positive, sometimes negative, often neutral (Fig. 5a). This is likely to be a consequence of the plant species studied (often elephant-specialists in African but not in Asian studies). Passage through elephant guts reduced the time to germination of seeds, especially in the case of African elephants (Fig. 5b). In one study, GPT was found to have a negative impact on seed viability – the longer the time seeds spend in the gut the lower the chance of germination (Campos-Arceiz et al., 2008b).

Elephants deposit seeds inside a mass of moist, fertilized substrate – the dung pile. Dung can provide beneficial conditions in terms of protection from predation, humidity for germination, and nutrient availability for seedling growth. Indeed, Lewis (1987) showed that the germination of seeds of *Sclerocarya caffra* retrieved from elephant dung and experimentally placed into elephant dung *boli* tripled that of others planted directly on soil. In contrast, Nchanji and Plumptre (2003) compared germination of elephant-ingested seeds of 14 different plants in elephant dung vs. forest soil and found no difference in overall germination, although the germination time of seeds in elephant dung was generally shorter. Overall, although little data is available, deposition in dung seems to have a neutral or positive effect upon seed germination (Fig. 5c).

Elephants tend to defecate seeds in large clumps – an effect that is likely to result in mortality due to competition between close-neighboring, sibling seedlings. Lewis (1987) also tested the effect of clumping by experimentally putting a range of 1–11 seeds of *Sclerocarya caffra* in dung *boli*. He found that after five months, the initial positive correlation between the number of seeds in a dung bolus and the number of shoots was lost and a slightly negative effect on seedling growth was incurred, most likely as a result of competition. Since elephants can defecate thousands of seeds in a single deposition, more studies are necessary to understand the effect of clumping on seedling fate, and its variation by plant species and environmental conditions.

5.2. Post-dispersal seed predation and secondary dispersal

Clumping has a potential effect on two other processes that have not been properly studied with elephants: post-dispersal predation and secondary dispersal. Cochrane (2003) found that a high percentage (57.9%, $n = 3697$) of seeds of *Balanites wilsoniana* not dispersed by elephants ended up consumed by predators, but do seeds deposited in elephant dung suffer similar predation? Numerous animals forage in elephant dung piles, most likely to consume seeds and the abundant invertebrate fauna in it (Dudley, 2000; Campos-Arceiz, 2009). Magliocca et al. (2003) found that sitatungas (*Tragelaphus spekei*) and red river hogs (*Potamochoerus porcus*) regularly foraged on elephant dung piles in forest clearings of the Republic of Congo. They assumed that sitatungas and pigs were consuming seeds defecated by elephants and therefore acting as seed predators (Magliocca et al., 2003). Feer (1995) also suggested post-dispersal seed predation by red river hogs and
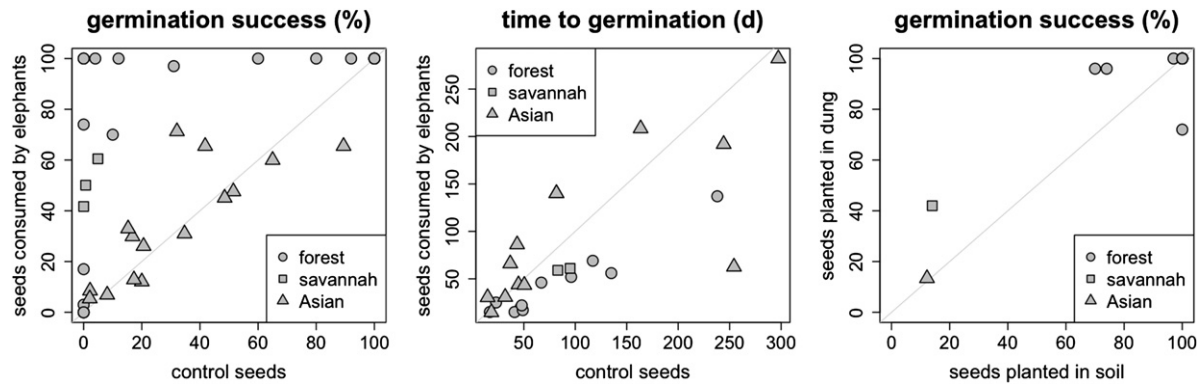
Fig. 5. Effects of elephant ingestion and dung deposition on seed germination. (a) effect of ingestion by elephants on the probability of germination of seeds; (b) effect of ingestion on germination time; (c) effect of deposition in dung on the probability of germination. We plotted available data in each case, comparing the value of treatment and control seeds. Values above the central transversal line indicate an increase in the effect by the treatment and values under the line a decrease. Data from: Alexandre, 1978; Lewis, 1987; Lieberman et al., 1987; Chapman et al., 1992; Cochrane, 2003; Nchanji and Plumptre, 2003; Kitamura et al., 2007; Campos-Arceiz et al., 2008b; Larrinaga et al. unpublished.

rodents — though we find it likely that some of these may also act as secondary seed dispersers. Given the importance of these processes on forest dynamics and the almost complete lack of data, studies addressing secondary seed predation and dispersal from elephant dung are badly needed.

6. Elephant signature — spatial consequences of seed dispersal by elephants

If seed dispersal really matters to the population dynamics of plants, its effects should be reflected in the competitive abilities of seeds and seedlings and ultimately in the spatial distribution and abundance of plants (Harms et al., 2000). Early observations showed that for many tropical trees, few or no seeds and seedlings germinate and survive under the parent tree, due to the density-dependent mortality caused by seed and seedling predators and pathogens, observations that were formalised into the ubiquitous Janzen–Connell Hypothesis (Janzen, 1970; Connell, 1971). This theory has since been supported by numerous studies (Schupp, 1992; Hansen et al., 2008), refined to include impacts on kin competition (Howe and Smallwood, 1982), and shown to promote species diversity in tropical forests (Harms et al., 2000). Plant species either need dispersal mechanisms that take their seeds out of range of density-dependent mortality effects (they escape in space) or mast fruiting strategies, which saturate seed and seedling predators and pathogens (they escape in time). On a larger spatial scale, long distance dispersal by plants promotes colonization of vacant areas and ecological succession (Fragoso et al., 2003; Trakhtenbrot et al., 2005), enhances connectivity in fragmented landscapes and migration rates (e.g. as a response to global warming), and can even have detrimental effects promoting the spread of animal-dispersed invasive plants.

Seidler and Plotkin (2006) demonstrated that the aggregation pattern of trees in tropical forests closely tracks dispersal distance, with ballistically dispersed species most aggregated and large-animal dispersed species least aggregated. Animal-dispersed plant species are usually dispersed by a suite of dispersers, thus it is generally difficult to assess the influence of each disperser species on the pattern of plant distribution, however the existence of narrow mutualisms between elephants and certain plant species may make it possible to test the influence of elephants on distribution pattern of those species.

Lewis (1987) suspected that elephants were the only dispersers of *Sclerocarya caffra* in Luangwa Valley (Zambia) but found that trees of this species were highly clumped, with clump locations

highly correlated with deep and well-drained soils rather than elephant distribution in the area. He concluded that elephants were not responsible of the final pattern of distribution of the plant (Lewis, 1987). Babweteera et al. (2007), after proving that elephants were the only removers of *Balanites wilsoniana* seeds in Uganda, compared the distribution of juvenile *B. wilsoniana* in areas with and without elephants. Only in the forest with elephants they found *B. wilsoniana* juveniles away from adult trees (Babweteera et al., 2007), showing that the loss of elephants impacts the spatial dynamics of this species.

In the most comprehensive study to date, Blake et al. (2009) 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. From their analysis of the spatial patterns of 5667 trees of from at least 163 species they found evidence to support that elephant dispersal overcomes strong Janzen–Connell effects for the obligate category. Trees dispersed solely by elephants showed *increasing* aggregation at spatial scales up to 200 m (Blake et al., 2009). At a landscape scale (up to 67 km linear distance) dispersal syndrome predicted tree similarity decay in space, with obligate elephant dispersed species being essentially randomly distributed while similarity of all other syndromes decayed in space, with rate of decay tracking dispersal syndrome from gravity to non-obligate. They concluded that African forest elephants tip the competitive balance in favour of the species-rich large animal dispersed species.

7. Megagardeners of the forest — summary

7.1. Importance of elephants as seed dispersers and differences among taxa

We have shown that elephants are important dispersers of seeds in all environments in which they occur; however their degree of importance varies across habitats, taxa, and continents. Importance is defined here as a combination of factors including: a) the diversity of plant species dispersed, b) their reliability and number of seeds dispersed, c) the distances over which those seeds are dispersed, d) the germination potential of dispersed seeds, and e) the suitability of the site where seeds are deposited for germination (Howe and Smallwood, 1982; Schupp, 1993; Howe and Miriti, 2000). An additional consideration is the functional redundancy with other seed dispersers — i.e. to what extent elephant seed

dispersal functions might be fulfilled by other dispersers in the absence of elephants.

African forest elephants seem to be one of the most effective seed dispersal agents in the tropics. They disperse large amounts of seeds (as many as 346 seeds/km^2/day in Ndoki; Blake et al., 2009) from a high diversity of plants (average = 42.5 species per site; Table 1), particularly trees (average = 39 species per site; Table 1), and are the exclusive or near-exclusive disperser of a considerable number of plant species (Table 3). Moreover, African forest elephants disperse seeds over unprecedented distances compared to other vertebrate dispersers with measurable impacts on spatial distribution of dispersed species (Blake et al., 2009). Ingestion by African forest elephants has neutral or positive effects on the germination probability of seeds and it accelerates the germination process (Fig. 5).

African savannah elephants have been less studied. Like African forest elephants, they also disperse large amounts of seeds (e.g. 2054 seeds/km^2/day in Hwange National Park; (Dudley, 2000), generally from a lower diversity of plants (but see data from Shimba Hills (Engel, 2000) in Table 1) and trees (15 species per site; Table 1). African savannah elephants are also involved in some highly-specialized seed dispersal mutualisms (e.g. *Balanites wilsoniana*; Table 3) and can be reliable dispersers, consuming up to one fourth of *Balanites wilsoniana* seeds in Kibale NP (Uganda; Cochrane, 2003). Among all elephant taxa, savannah elephants from arid and semi-arid environments are likely to provide the longest seed dispersal distances (e.g. elephants in Namibia and Mali frequently travel more than 50 km in 24 hours; Viljoen, 1989; Blake et al., 2003). Consumption by African savannah elephants also tends to have a positive effect on seed germination (Fig. 5). Indeed, in Kibale, 57% of *Balanites wilsoniana* ingested by elephants germinate compared to just 3% for seeds collected from under the parent tree (Chapman et al., 1992).

Data for Asian elephants is more fragmentary, making it difficult to assess their role in seed dispersal processes. Asian elephants appear to disperse seeds less frequently, and from a lower diversity of plants (particularly trees: almost five times fewer species) than African forest elephants (Table 1). Asian elephants also disperse seeds over several kilometers although distances are much shorter than those described for African forest elephants, which might reflect a bias toward the study of Asian elephant movements in highly fragmented landscapes; (Campos-Arceiz et al., 2008b; Blake et al., 2008). Asian elephants mild mouth and gut treatment means that a high proportion of the seeds they ingest are defecated in viable conditions (Campos-Arceiz et al., 2008b) and can subsequently germinate similarly or better than non-ingested seeds (Fig. 5a). There are no publications to date documenting the existence of obligate seed dispersal mutualism for Asian elephants, although a number of plant (mostly tree) species are likely candidates. Studies in the forests of Malaysia and Indonesia will likely be instrumental to advance our understanding of their importance as seed dispersers.

7.2. Consequences of elephant decline

Given the massive losses in elephant numbers and range over the last several millennia (Sukumar, 2003) and especially in recent decades (Michelmore et al., 1994; Barnes et al., 1995; Blake and Hedges, 2004; Blake et al., 2007), it is important to understand the consequences of elephant decline or loss for forest ecosystem dynamics. Janzen and Martin (1982) speculated on the impact of the loss of the Gomphotheres from the South American continent some 10,000 years ago, suggesting this would have had a huge impact on the abundance and spatial distribution of plants adapted to their dispersal, the so-called megafaunal fruits. This idea has been revisited by several authors, from open critique (Howe, 1985) to strong support and refinement (Guimaraes et al., 2008).

The main limitations to evaluating the consequences of elephant disappearance are (1) the absence of baseline information to compare the demography of elephant-dispersed fruits with and without elephants, and (2) the long generation times of tropical trees which will obscure all but the most dramatic of impacts, a fact ignored by Hawthorne and Parren (2000) who, not surprisingly, failed to find an impact of elephant loss on Ghanaian forests. The most compelling study to date on consequences of elephant loss is that of Blake et al. (2009), whose results imply that elephant loss will dramatically arrest the recruitment of obligate elephant dispersed species and reduce the competitive viability of non-obligate species, thus favouring the species-poor abiotically dispersed tree community.

An important question is to what extent other vertebrates can 'take up the slack' left by the decline or disappearance of elephants. Regional patterns of frugivore diversity in tropical forests reveal that Asian forests contain lower diversity than those of Africa and the Neotropics (Fleming et al., 1987). Of particular note is the species density of primates in African rainforests, which is over 3 times higher than elsewhere (Fleming et al., 1987). Today's un-hunted African rainforests are replete with frugivores over 5 kg, many of which eat and disperse the same species as African forest elephants (e.g. Gautier-Hion et al., 1985). In the absence of elephants, these frugivores would continue to provide some dispersal service to most of elephant-dispersed plants. Species that are exclusively or primarily dispersed by African forest elephants (Table 3), however, would fail to be effectively dispersed (Cochrane, 2003; Babweteera et al., 2007; Blake et al., 2009). In African savannahs, where the number of animal-dispersed plant species is few, the extant browsing megafauna (giraffe, black rhino, ostriches) may go some way to replace elephant dispersal. At any rate, and because current defaunation results in simultaneous and dramatic declines in entire guilds of large-bodied vertebrates, the numbers of potential replacement dispersers will also be seriously depleted. In Asian forests, frugivory is not as common or widespread as it is in African forests, and while many primates and ungulates do consume fruits and disperse seeds, there is a large proportion of them that are predominantly folivorous. Hence, the frugivore community is relatively species poor, with seed predators abundant. Orang-utans and Asian rhinoceroses may once have over-lapped with elephants in the species consumed and dispersed in Southeast Asia but given the range shrinkage and dire situation of orang-utan and rhinoceros populations, it is highly unlikely that they would ever provide any ecological replacement to declining Asian elephants. While many species in Africa and a few in Asia share considerable dietary overlap with elephants, few can compete with the spatial scale over which elephants disperse seed (Dudley, 2000; Campos-Arceiz et al., 2008b; Blake et al., 2009; Corlett, 2009).

In summary, the local reduction or disappearance of elephant populations will result in (a) a limited set of (highly-specialized) plant species being poorly dispersed or not dispersed at all; and (b) many species being dispersed in lower quantities and especially at shorter distances — though perhaps in a more scattered pattern. The expected result is a simplification of the community-level interaction network, an increase in the vulnerability of ecosystem function, and changes in the demography and distribution of a considerable number of plant species. Defaunation will ultimately tip the competitive balance toward favouring the species-poor guild of abiotically-dispersed species, a notion supported by work on the loss of smaller-bodied dispersers (Terborgh et al., 2008).

7.3. Conservation needs

Conservation needs of elephants across their range at first appear bewilderingly complex (Blake and Hedges, 2004). In many African savannah ecosystems, adequate protection and hard boundaries have led to what is often perceived as an over-abundance of elephants (Barnes, 1983). Management more often than not involves measures to control numbers through socially acceptable combinations of translocations, sterilization, and culling (van Aarde et al., 2006; Whyte et al., 2003). In Central African forests and savannahs the opposite is true and elephants are swiftly being eradicated due to illegal killing (Blake et al., 2007). In west Africa, once vast populations of both savannah and forest elephants are now restricted to a few small populations of often fewer than 100 individuals, in islands of habitat surrounded by human infrastructure (Barnes, 1999). In Asia, the situation is critical; the number of wild elephants is not known but probably less than 30,000 mostly in small restricted areas (Blake and Hedges, 2004). Human elephant conflict is rife, and the growth of the human population and rate of habitat loss means that this will only increase in the coming years (Hoare and du Toit, 1999; Hedges and Giunaryadi, 2010). Conservation complexity is exacerbated given the high value humans put on elephants and elephant products, and thus emotion, rather than technical expertise drives management. A strong lobby may stop culling in South Africa, while another promotes international trade in ivory to China where illegal ivory is already on sale for $1000/kg.

The complexity of conservation however boils down to the ability to control two simple factors: stopping illegal killing and providing adequate space for elephants to fulfill their ecological role in viable populations (Stephenson and Ntiamoa-Baidu, 2010). Unfortunately, management policy and practice has been incredibly ineffective in achieving either of these goals. In the context of this paper, which is primarily concerned with the seed dispersal role of elephants, two management questions are most pertinent: 1) where do nations and the international community want functional ecosystems to survive with their full complement of native species, and 2) how many elephants ranging over how much land are sufficient to provide their necessary ecosystem services and maintain viable populations. Until these strategic questions are agreed upon and supported by scientific studies, conservation will most likely continue in a piecemeal and ineffective manner. Effective law enforcement in terms of controlling illegal killing and respecting land use classifications is the only short-term solution, and we are generally failing on both counts within the majority of elephant range on both continents (Wasser et al., 2010).

7.4. Future research priorities

Given the ecological importance of elephants, there are surprisingly few studies that address their ecosystem role as seed dispersal agents, compared to, for example, primates and birds. The field is largely wide-open for investigation. We suggest a combination of pure and applied research necessary to better understand elephant seed dispersal systems, and to improve management in those ecosystems where elephants occur and where they once occurred. The following are some priority areas of future research and consideration:

1. We still have a poor understanding of obligate elephant-plant dispersal relationships, which need to be defined and clarified. Which species require elephant dispersal to flourish?
2. What are the unique characteristics of elephant seed shadows that will be lost in the absence of elephants?

3. What are the impacts of elephant population growth and decline on populations of other seed dispersers and what does this mean for plant recruitment?
4. How many elephants are sufficient to maintain the functionality of their seed dispersal role. This is particularly important as elephant range inevitably shrinks into island protected areas and habitat fragments. At what point do the impacts of elephant density (browsing and trampling) become detrimental to the very species they otherwise effectively disperse?
5. Can assisted dispersal (e.g. McLachlan et al., 2007) substitute for elephants in areas where they have become locally extinct, and what are the management steps necessary to maintain tree population viability?
6. Should we re-wild the Neotropics, and other regions where proboscidians once lived, with pachyderm substitutes from Africa and/or Asia (e.g. Donlan et al., 2005)?

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.actao.2011.01.014.

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