Original article

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

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\begin{abstract}
As the largest frugivores on Earth, elephants have unique ecological properties. Found in deserts, savannas, 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, defeating 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 catastrophically 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.
\end{abstract}

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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
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 gomphotheres 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 km² (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 km² 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

![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.
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/km², with density strongly correlated with the local availability of *Tieghemella heckli* 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
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.

![Graph showing frugivory percentage in Asian, forest, and savanna elephants](image)

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

### 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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Country</th>
<th>Site</th>
<th>Lat (°)</th>
<th>Rain (mm yr⁻¹)</th>
<th>N dung piles sampled</th>
<th>% Containing seeds</th>
<th># spp</th>
<th># Tree species</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>AFE</td>
<td>Ivory Coast</td>
<td>Tai</td>
<td>6</td>
<td>1650</td>
<td>42</td>
<td>37</td>
<td></td>
<td></td>
<td>Alexandre (1978)</td>
</tr>
<tr>
<td>AFE</td>
<td>Ivory Coast</td>
<td>Tai</td>
<td>6</td>
<td>1650</td>
<td>44</td>
<td>44</td>
<td></td>
<td></td>
<td>Merz (1981)</td>
</tr>
<tr>
<td>AFE</td>
<td>Ghana</td>
<td>Bia</td>
<td>6</td>
<td>1500</td>
<td>93</td>
<td>35</td>
<td>35</td>
<td></td>
<td>Short (1981)</td>
</tr>
<tr>
<td>AFE</td>
<td>Gabon</td>
<td>IRET</td>
<td>0</td>
<td>1755</td>
<td>99</td>
<td>32</td>
<td>30</td>
<td></td>
<td>Gautier-Hion et al. (1985), Feer (1995)</td>
</tr>
<tr>
<td>Ghana</td>
<td>Bia</td>
<td>6</td>
<td>1500</td>
<td>31</td>
<td>100</td>
<td>11</td>
<td></td>
<td></td>
<td>Lieberman et al. (1987)</td>
</tr>
<tr>
<td>Cameroon</td>
<td>Santchou</td>
<td>5</td>
<td>1750</td>
<td>250</td>
<td>65</td>
<td>22</td>
<td>20</td>
<td></td>
<td>Tchamba and Sene (1993)</td>
</tr>
<tr>
<td>Gabon</td>
<td>Lope</td>
<td>0</td>
<td>1536</td>
<td>311</td>
<td>82</td>
<td>72</td>
<td>54</td>
<td></td>
<td>White et al. (1993)</td>
</tr>
<tr>
<td>Zaire</td>
<td>Kahuji-Biega</td>
<td>1</td>
<td>1990</td>
<td>203</td>
<td>14</td>
<td>14</td>
<td></td>
<td></td>
<td>Yumoto et al. (1995)</td>
</tr>
<tr>
<td>Gabon</td>
<td>Loango</td>
<td>2</td>
<td>2363</td>
<td>220</td>
<td>92.3</td>
<td>49</td>
<td></td>
<td></td>
<td>Morgan and Lee (2007)</td>
</tr>
<tr>
<td>Rep Congo</td>
<td>Ndoki</td>
<td>2</td>
<td>1422</td>
<td>855</td>
<td>94</td>
<td>96</td>
<td>73</td>
<td></td>
<td>Blake et al. (2009)</td>
</tr>
</tbody>
</table>

| AFE    | Tanzania | Singida | 5       |                |                      |                   |       |               | Burtt and Salisbury (1929) |
| Kenya  | Shima Hills | 4 | 1151     | 233            | 90.5                 | 221               |       |               | Engel (2000) |
| Kenya  | Arabuko-Sokoke | 3  | 1000     | 736            | 64.5                 | 42                 |       |               | Muoria et al. (2001) |
| Tanzania | Tarangire | 3     | 620      | 66             |                      |                   |       |               | Gonthier (2009) |

|  | AFE    | Tanzania | Singida | 5       |                |                      |                   |       |               | Burtt and Salisbury (1929) |
| Thailand | Khao Yai | 14      | 2270     | 2249         |                      |                   |       |               | 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                 | 44    |               | 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) |

3.6 1927.2 463.3 89.3 42.5 38.9

3.6 853.3 355.6 78.3 53.2 15.3

6.8 1963.0 721.6 61.85 26.6 8.6
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 Ollariaeae 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, Omphalocarpum, 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 megafloral 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, Balanitaceae, Sapotaceae and Anacardiaceae all produce a pungent aroma that even humans can smell 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 “megafloral 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
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 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

4. Traveling through and with elephants among others.

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

### Table 2

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

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

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 Wenmer, 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.
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 vampirinus (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 Sclerocarya caffra (Lewis, 1987) and Balanites wilsoneiana (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 bolus 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 bolus. 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 wilsoneiana 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

### Table 4

<table>
<thead>
<tr>
<th>Elephant taxon</th>
<th>Plant species</th>
<th>Seed survival (%)</th>
<th>Mean GPT (km)</th>
<th>Max. GPT (km)</th>
<th>Study duration</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>ASE Zimbabwe</td>
<td>Acacia erioloba</td>
<td>11.5</td>
<td>30.5</td>
<td>36</td>
<td>367</td>
<td>Dudley (1999)</td>
</tr>
<tr>
<td>AE Sri Lanka</td>
<td>Cucumis melo</td>
<td>20.2</td>
<td>72</td>
<td>72</td>
<td>72</td>
<td>Weerasinghe et al. (1999)</td>
</tr>
<tr>
<td>AFE Rep Congo</td>
<td>Tamarindus indica</td>
<td>75.1</td>
<td>39.5</td>
<td>113.8</td>
<td>140</td>
<td>Campos-Arceiz et al. (2008b)</td>
</tr>
</tbody>
</table>

### Table 5

<table>
<thead>
<tr>
<th>Elephant Taxon</th>
<th>Country</th>
<th>Mean displacement (km)</th>
<th>Max. displacement (km)</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>ASE Zimbabwe</td>
<td>–</td>
<td>30</td>
<td></td>
<td>Dudley, 1999</td>
</tr>
<tr>
<td>AFE Ivory Coast</td>
<td>8.5</td>
<td>12</td>
<td></td>
<td>Theuerkauf et al., 2000</td>
</tr>
<tr>
<td>Rep Congo</td>
<td>3.5</td>
<td>57</td>
<td></td>
<td>Blake et al., 2009</td>
</tr>
<tr>
<td>AE Sri Lanka</td>
<td>1.2</td>
<td>6</td>
<td></td>
<td>Campos-Arceiz et al., 2008b</td>
</tr>
</tbody>
</table>
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/km²/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/km²/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 wisoniana; Table 3) and can be reliable dispersers, consuming up to one fourth of Balanites wisoniana 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 wisoniana 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 un-picked with elephants in the species consumed and dispersed in Asian 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 overlapped 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 Ginnaryadi, 2010). Conservation complexity is exacerbated given the high value humans put on elephants and elephant products, and thus politics, 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 Ntiamo-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 proboscisians 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.jactao.2011.01.014.

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