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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.

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 monograstric 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

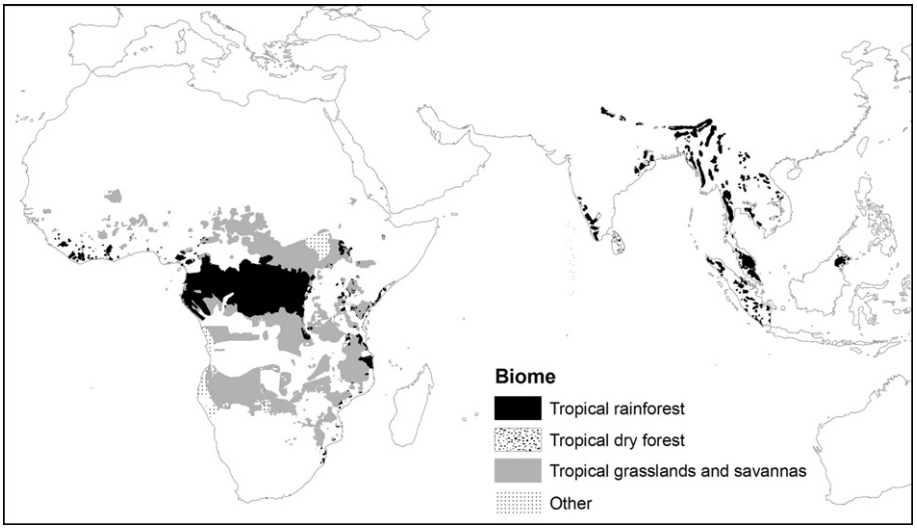

Fig. 1. Current distribution range of African and Asian elephants (source: IUCN Red List). Colors represent major terrestrial habitats as defined by WWF (Olson et al., 2001). Horizontal lines represent Equator and the Tropic of Cancer and Capricorn.