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Seed dispersal potential of Asian elephants

Franziska K. Harich [a, *], Anna C. Treydte [a, 1], Joseph O. Ogutu [b], John E. Roberts [c], Chution Savini [d], Jan M. Bauer [e, 2], Tommaso Savini [f]

[a] Department of Agroecology in the Tropics and Subtropics, University of Hohenheim, Garbenstr. 13, 70593 Stuttgart, Germany
[b] Biostatistics Unit, University of Hohenheim, Fruwirthstr. 23, 70593 Stuttgart, Germany
[c] Golden Triangle Asian Elephant Foundation, 229 Moo 1, Chiang Saen, Chiang Rai 57150, Thailand
[d] International College for Sustainability Studies, Srinakharinwirot University, 114 Sukhumvit 23, Wattana, Bangkok 10110, Thailand
[e] Institute for Health Care & Public Management, University of Hohenheim, Fruwirthstr. 48, Kavaliershaus 4, 70593 Stuttgart, Germany
[f] Conservation Ecology Program, King Mongkut's University of Technology Thonburi, 49 Soi Tienthalay 25, Bangkhuntien-Chaithalay Road, Thakham, Bangkhuntien, Bangkok 10150, Thailand

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ABSTRACT

Elephants, the largest terrestrial mega-herbivores, play an important ecological role in maintaining forest ecosystem diversity. While several plant species strongly rely on African elephants (*Loxodonta africana; L. cyclotis*) as seed dispersers, little is known about the dispersal potential of Asian elephants (*Elephas maximus*). We examined the effects of elephant fruit consumption on potential seed dispersal using the example of a tree species with mega-faunal characteristics, *Dillenia indica* L., in Thailand. We conducted feeding trials with Asian elephants to quantify seed survival and gut passage times (GPT). In total, 1200 ingested and non-ingested control seeds were planted in soil and in elephant dung to quantify differences in germination rates in terms of GPT and dung treatment. We used survival analysis as a novel approach to account for the right-censored nature of the data obtained from germination experiments. The average seed survival rate was 79% and the mean GPT was 35 h. The minimum and maximum GPT were 20 h and 72 h, respectively. Ingested seeds were significantly more likely to germinate and to do so earlier than non-ingested control seeds ($P = 0.0002$). Seeds with the longest GPT displayed the highest germination success over time. Unexpectedly, seeds planted with dung had longer germination times than those planted without. We conclude that *D. indica* does not solely depend on but benefits from dispersal by elephants. The declining numbers of these mega-faunal seed dispersers might, therefore, have long-term negative consequences for the recruitment and dispersal dynamics of populations of certain tree species.

1. Introduction

With ongoing forest fragmentation and losses, the seed dispersal of some tropical plants is becoming increasingly hampered as populations of large seed dispersal agents are declining and their movements are being restricted (Corlett, 2002). This is of concern for overall forest diversity as the dispersal of seeds away from the parent organism is an essential strategy used by plants to find suitable establishment sites of reduced competition, herbivore or pathogen attacks (Howe and Smallwood, 1982; Harms et al., 2000; Willson and Traveset, 2000; Corlett, 2014). Dispersal mechanisms include abiotic drivers such as wind or water and biotic dispersal modes such as endo- or epizoochory, with vertebrates as dispersal agents (van der Pijl, 1972; Burrows, 1986; Murray, 1986; Fleming and Kress, 2011). A broad range of different animal species can serve as seed dispersers, including birds, bats, rodents, carnivores, primates and terrestrial herbivores (Howe, 1986; Stiles, 2000; Corlett, 2014). Provided the seeds can survive the consumption process, frugivorous animals, particularly the large-sized animals, can disperse seeds over wide distances

* Corresponding author.
E-mail addresses: harich@uni-hohenheim.de, f.harich@gmx.de (F.K. Harich), anna@treydte.com (A.C. Treydte), jogutu2007@gmail.com (J.O. Ogutu), jroberts@anantara.com (J.E. Roberts), chutionsavini@gmail.com (C. Savini), janmbauer@gmail.com (J.M. Bauer), tommasosavini@gmail.com (T. Savini).
[1] Present address. Department of Biodiversity Conservation and Ecosystem Management, Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania.
[2] Present address. Department of Intercultural Communication and Management, Copenhagen Business School, Porcelænshaven 18A, 2000 Frederiksberg, Denmark.

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(Seidler and Plotkin, 2006). Among large herbivores, elephants are noteworthy in playing a prominent role in maintaining tree diversity in forest ecosystems. With a diet comprising more than 350 different plant species, African forest elephants (*Loxodonta cyclotis*) consume the broadest spectrum of fruits of all extant elephant species (Blake, 2002) while Asian elephants (*Elephas maximus*) reportedly forage on around 100 different plant species (Sukumar 1989; Chen et al., 2006; Campos-Arceiz et al., 2008a; Baskaran et al., 2010; Campos-Arceiz and Blake, 2011).

Hence, the range of plant species consumed by elephants varies greatly across geographic regions as do their daily travel and, therefore, potential seed dispersal distances (Sukumar 1989). Forest elephants in Ivory Coast have been reported to cover 1–15 km/day, for an average of about 6 km/day (Theuerkauf and Ellenberg, 2000) whilst in northern Congo their travel distance varied between 2 and 22 km/day (Blake, 2002). However, the actual distances over which elephants can disperse seeds can be much larger, especially for large seeds, which can take several days to pass through the digestive tract (Powell, 1997). Notably, travel and dispersal distances of up to 57 km over a period of three days have been recorded for elephants in the Congo (Blake et al., 2009). The maximum dispersal distance for Asian elephants varies with geographical conditions and can range from an estimated 4–6 km in Myanmar and 46–54 km in India, with 50% and >80% of seeds being dispersed over 1 km distances from their origins, respectively (Campos-Arceiz et al., 2008b; Sekar et al., 2015). This implies that both African and Asian elephants could potentially disperse seeds over distances as large as 54–57 km. In tropical forests such distances are much larger than the maximum dispersal distances of other seed dispersers. Distances can be more than seven times longer than the maximum dispersal distance for black-casqued hornbills (*Ceratogymna atrata*) in West Africa and about 43 times longer than the maximum recorded dispersal distance for gibbons (*Hylobates mulleri x agilis*) in Borneo (Holbrook and Smith, 2000; McConkey, 2000). Asian elephants might, therefore, rank among the most important long-distance seed dispersal agents in Asia (Campos-Arceiz et al., 2008b).

Some trees have even adapted to this mode of dispersal, the so-called "megafaunal-syndrome" (Janzen and Martin, 1982; Guimarães et al., 2008; Blake et al., 2009; Campos-Arceiz and Blake, 2011). Dispersal syndrome refers to a general set of characteristics of fruits and seed traits which are associated with a particular mode of dispersal, e.g. the evolvement of large fruits and seeds that attract megafauna as consumers and dispersers (van der Pijl, 1972; Janzen and Martin, 1982; Howe, 1985; Campos-Arceiz and Blake, 2011). Several plants such as *Balanites wilsoniana*, *Sacoglottis gabonensis*, *Irvingia gabonensis* and *Panda oleosa* likely rely exclusively on African forest elephants as seed dispersal agents for spatial distribution, increased germination success and reduced germination time with associated reduced exposure to seed predators (White, 1994; Cochrane, 2003; Babweteera et al., 2007; Blake et al., 2009; Campos-Arceiz and Blake, 2011). In contrast, no such obligate seed dispersal mutualism has been recorded for Asian elephants thus far and they seem to disperse fewer seeds from fewer tree species than their African forest elephant counterparts. This view might however be biased due to the overall poorer knowledge of Asian elephant nutritional ecology (Corlett, 1998; Kitamura et al., 2007; Campos-Arceiz and Blake, 2011; Corlett, 2014). While the passage of seeds through the gut of an African elephant generally enhances germination probability, there is little comparable data for the Asian elephant. One experimental study that explored the influence of gut passage on seed germination in the Asian elephant was disturbed too early to draw firm conclusions (Kitamura et al., 2007) whilst a second study found negative effects for tamarind (*Tamarindus indica*) seeds after ingestion (Campos-Arceiz et al., 2008b). In the face of declining numbers of large mammals in Southeast Asia (Ripple et al., 2015), more insights into their importance for the dispersal of seeds of different tree species are necessary to assess threats to forest ecosystems. Results from Africa showed that the loss of elephants (and other large frugivores) negatively affects the recruitment of animal-dispersed tree species, thereby fostering the development of species-poor tree communities with abiotic dispersal modes (Blake et al., 2009). Animal-dispersed tree populations in contrast will likely face increased clustering, contraction of their geographic ranges and reduction in genetic variation if the numbers of their dispersal agents decline or vanish altogether (Cramer et al., 2007; Guimarães et al., 2008; Terborgh et al., 2008; Markl et al., 2012; Pérez-Méndez et al., 2015).

Also in Southeast Asia, defaunated forests are very likely to face declines in tree diversity over time (Brodie et al., 2009; Harrison et al., 2013; Caughlin et al., 2014). Large frugivores like tapirs (*Tapirus indicus*) can be effective dispersers for small-seeded plants but seem to be only limited substitutes for megafaunal seed dispersers (Campos-Arceiz et al., 2012). Even so, few detailed studies have experimentally tested the impacts of Asian elephant fruit consumption on seed dispersal efficiency and studies of their frugivory and seed dispersal potential are still rare (Campos-Arceiz and Blake, 2011; Corlett, 2014). However, Sekar et al. (2015) recently assessed the potential of domestic bovids as replacements for elephant seed dispersal in India and Sekar and Sukumar (2013) investigated the ecology of *Dillenia indica*, which is known to be eaten by elephants.

We expand upon the studies of Sekar and Sukumar (2013) and Sekar et al. (2015) by using *Dillenia indica* as an exemplary megafaunal syndrome species to empirically (*i*) establish whether and to what extent the seeds survive gut passage, (*ii*) assess if the seeds that have passed through the elephant gut have a higher average germination rate than control seeds that have not, (*iii*) assess the effects of planting ingested and control seeds with or without elephant dung, and (*iv*) quantify the degree to which the gut passage time (GPT) affects the viability of seeds. With this study we also aim to highlight the importance of seed dispersal for overall forest diversity and general biodiversity conservation in the context of land-use changes.

2. Materials and methods

2.1. Study site

The feeding and germination experiment was conducted in northern Thailand, in cooperation with the Golden Triangle Asian Elephant Foundation (GTAEF), located in the border area between Thailand, Myanmar and Laos (UNODC, 2006; Chin, 2009). The annual precipitation is about 1550–1650 mm with a peak from June to September and a dry season from December to March. The average daily temperature ranges from 25.8 °C to 27.7 °C (unpublished GTAEF records). The natural vegetation of Northern Thailand is characterized by a mosaic of evergreen and deciduous forest patches (Gardner et al., 2000). Elephants of the foundation are ex-street begging elephants rescued to a forest environment in Northern Thailand. They are partly kept in disturbed natural forest remnants, partly on grasslands in the floodplains of the Ruak river, a tributary to the Mekong river, and partly in open barns. The animals are sometimes used for touristic activities like riding and bathing, for an approximate average of 3.5 h and a maximum of 5 h per day. For most of the remaining time, elephants are allowed to roam in the forest or grassland, but are restricted by up to 30 m long chains in the night.