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Seed dispersal potential of Asian Elephants

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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* Linn, 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.

Key words: Dillenia indica, Elephas maximus, seed germination, survival analysis, Thailand

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 (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 Jr. 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 Jr. 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 et al. (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 hours and a maximum of 5 hours 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.

2.2 Study species

Dillenia indica Linn. is an evergreen tree species of the family Dilleniaceae found throughout South and Southeast Asia, including the natural habitats of the Asian elephants (Van Steenis 1948; Abdille et al. 2005; Sekar and Sukumar 2013). The tree can grow up to 30 m in height (Van Steenis 1948; Gardner et al. 2000). Its fruits are large, around 10 cm in diameter, with many small seeds of about 6 mm in length that are protected by a hard mesocarp (Van Steenis 1948; Abdille et al. 2005; Sekar and Sukumar 2013). No significant arboreal frugivores were observed for *D. indica;* rodents as well as rhesus macaques (*Macaca mulatta*) are generally unable to access the seeds but some bovids (e.g. gaur *Bos gaurus*) can consume the fruits and seeds (Sekar and Sukumar 2013; Sekar et al. 2015). However, some individuals have difficulties dealing with the hardness of the mesocarp and elephants were found to eat more than twice as many fruits as the wild and domestic bovids combined (Sekar and Sukumar 2013). As the species is often found at watersides, it is not clear how much it relies on elephants relative to water for its seed dispersal (Van Steenis 1948; Datta and Rawat 2008; Sekar and Sukumar 2013).

2.3 Feeding trials

We selected six female elephants for our feeding trials, ranging in age from 6 to 35 years and in body weight from 2.9 to 3.5 tons. All elephants were born in captivity with the exception of the oldest one, for which no data were available. Elephants were seasonally allowed to range in a nearby forest with some restrictions, but not at the time of our experiments. Their normal diet of mainly grasses and various other feeds (e.g. bamboo, sugarcane, bananas) was maintained during the feeding trials. The animals were regularly checked by the foundation’s veterinarian and were in good health. We offered the animals ripe *D. indica* fruits ad libitum. The elephants were fed one at a time to facilitate a detailed monitoring of their defecation time and to ensure enough manpower was available to retrieve all the dung and seeds. Before being fed to the elephants, the fruits were weighed and the number of seeds they contained estimated based on a regression model of seed number vs weight of control fruits (Campos-Arceiz et al. 2012). We monitored the elephants throughout the day and sieved the collected dung through a 2-mm wire mesh with water hoses. In the evenings, elephants were brought to a barn or to resting grounds. We collected the dung defecated in the nighttime in the early morning and assigned all seeds retrieved the mean time between when we stopped and resumed monitoring. We then dried the collected seeds and stored them in labeled paper envelopes for planting within one week of their collection date. We stopped dung collection when no further seeds were found in the dung over the course of at least 12 consecutive hours.

2.4 Germination trials

We counted seeds extracted from elephant dung and planted them in 2l pots with commercial potting soil at a nursery shaded with shadow nets. Five seeds were planted per pot and pots were regularly watered. We sequentially planted the seeds retrieved from the different study animals to minimize any potential negative effects of prolonged seed storage time on their germination ability. As the gut passage time (GPT) as well as the deposition of seeds in dung can impact seed survival and seedling growth (Lewis 1987; Nchanji and Plumptre 2001; Cochrane 2003; Campos-Arceiz et al. 2008b; Campos-Arceiz and Blake 2011) we included the two treatments ‘GPT’ and ‘dung’ in our germination experiments. For the GPT treatment, we assigned the seeds to different GPT categories to assess the effect of GPT on the germination rate or time to germination. We selected four categories: one for control and three GPT categories, according to the time of peak seed retrieval and whether the levels of seed loads in the dung piles were increasing or decreasing. The four categories were delineated as follows (*i*) control: fresh and non-ingested control seeds, (*ii*) short: all seeds retrieved within 30 h of GPT ($GPT \leq 30$ h; $n = 1878$), (*iii*) medium: all seeds retrieved after 30 h but within 48 h ($30h < GPT \leq 48$ h; $n = 3797$), and (*iv*) long: all seeds retrieved after 48 h ($GPT > 48$ h; $n = 581$). For each of the six elephants, we planted a total of 200 seeds, 150 divided into the three GPT categories plus 50 fresh and non-ingested control seeds. In aggregate, 1200 seeds were planted. A total of 300 seeds were planted for the first GPT category plus another 300 seeds for the control treatment. We planted 410 seeds for the second GPT period while for the last GPT category, only 190 seeds were available due to the fast digestion of some elephants. Half of all the seeds planted in each of the three GPT categories were planted in pot soil only and the other half in combination with elephant dung. For the latter, the lower half of the pot was filled with pot soil and the upper half was filled with elephant dung, in which the seeds were placed. Germination and appearance of the first true leaves were monitored at least three times per week for a period of six months. We stopped monitoring 45 days after the last seed in a pot had germinated and no further germination event had occurred.

In addition to the single seed germination experiments, we planted two sets of whole fruits in two subsequent years. In the first year, we half-buried the fruits but recorded no germination success. In the second year we simply placed another 20 fruits on the ground, but unfortunately the experiment was interrupted by heavy rains and flooding before any germination event might have taken place. We therefore excluded this part of the experiments from all analyses.

2.5 Statistical data analysis

As we could not definitively declare the remaining non-germinated seeds as dead, we used survival analysis to calculate the germination rate as a function of time (Allison 1995; Hosmer and Lemeshow 1999). An important feature of the seed germination data is that the germination times are right-censored due to termination of the experiment before some seeds might still have germinated. For the latter, the exact germination time, thus, remains unknown and they are generally more likely to be censored. As a result, we used the censored and uncensored germination times, with the time in days from planting a seed to the date of germination of the seed as the response variable. We first estimated the distribution function of the seed germination times, i.e., the germination time distribution function (GTDF), and used this function to describe the germination times of the seeds subjected to the different treatments. When evaluated at time *t* the GTDF yields the probability that a given seed from the population of experimental seeds will have a germination time that exceeds *t*. This can be expressed succinctly as

$$G(t) = Pr\,(T > t) \tag{1}$$

where $G(t)$ is the germination distribution function (GTDF) and T is the germination time of a randomly selected seed. We computed nonparametric estimates of the germination distribution function by both the product-limit and life-table methods, also commonly called the Kaplan-Meier and actuarial methods, respectively, in the SAS LIFETEST procedure (SAS Institute 2016). We also computed the closely related function, the cumulative distribution function (CDF):

$$F(t) = 1 - G(t) \tag{2}$$

We further computed the probability density function (PDF) of the germination time, defined as the derivative of $F(t)$, and denoted as $f(t)$ and the hazard function $h(t)$ defined as

$$h(t) = f(t) / G(t). \tag{3}$$

We compared different germination time curves to determine whether the populations of seeds subjected to different treatments had identical GTDF functions. To do this, we used nonparametric *k*-sample tests based on weighted comparisons of the estimated hazard rate of the individual populations under the null and alternative hypotheses, where *k* denotes the number of different treatment groups being compared. We conducted several statistical tests, differing in their weight functions, comprising the log-rank test, Wilcoxon test, Tarone-Ware test, Peto-Peto test, modified Peto-Peto test, and Fleming-Harrington G_ρ family of tests. In the Wilcoxon test for homogeneity, pairs of the germination time functions were compared using the multiple-comparison method and the P-values for the paired tests (raw P-values) adjusted for multiplicity using simulation adjustment (simulated P-values). We performed log-rank and Wilcoxon test, respectively, to test the significance of the association of the germination variable with covariates (category of seeds, dung treatment and planting date of seeds). These tests were conducted by pooling over any defined strata, thereby adjusting for the stratum variables, and were carried out using the SAS LIFEREG procedure (SAS Institute 2016).

If T_i is a random variable denoting the germination time and C_{i1}, D_{i2}, and t_{i3} are covariates denoting the gut passage time category (0,1,2,3), dung treatment (0= without dung, 1= with dung) and planting date (0, 6, 13, 20, 27, 33 days from the start of the experiment) for the i^{th} seed in the sample, then the model for the association between the germination time and the three covariates fitted by the LIFEREG procedure is

$$Log_e (T_i) = \beta_0 + \beta_{i,1,0}\, C_{i,1,0} + \beta_{i,1,1}\, C_{i,1,1} + \beta_{i,1,2}\, C_{i,1,2} + \beta_{i,1,3}\, C_{i,1,3} + \beta_{i,2,0}\, D_{i,2,0} + \beta_{i,2,1}\, D_{i,2,1} + \beta_7\, t_{i,3} + \sigma\varepsilon_i \tag{4}$$

where ε_i is a random error term and the βs and σ (scale) are parameters to be estimated. The log transformation of T_i ensures that the predicted values of T are positive regardless of the values of the covariates or their regression coefficients.

3. Results

The number of fruits consumed by individual elephants during the feeding trials averaged 15.2 ± 6.2 ($n = 76$) and ranged between 8 and 25. The mean weight of a single fruit was 427.6 ± 75.4 g ($n = 188$) whereas the average number of seeds per fruit was 168.9 ± 63.5 ($n = 112$). A total of 6253 ingested seeds were retrieved from the dung of five elephants over the entire course of the feeding trials. For the sixth elephant we could not ensure a continuous monitoring and therefore excluded this data set from survival rate calculations. The average seed survival rate for five elephants was 79%, based on estimated numbers of seeds per fruit. However, the regression of the number of seeds against the weight of control fruits suggested a weak relationship ($r^2 = 0.12$, $P = 0.000$) albeit highly statistically significant and based on an approach used by other studies (Campos-Arceiz et al. 2012; Sekar et al. 2015). This implies that the reliability of the estimated survival rates of the ingested fruit seeds during their passage through the elephant gut (this should not be confused with the germination rate of the planted experimental seeds) was relatively low. The low reliability arises from the uncertainty associated with the total number of seeds in the ingested fruits estimated from the regression relationship.

The mean (±1 SD) GPT was 35.3 (± 9.3) h, with a mean minimum of 20 (± 2.1) h and a mean maximum of 72 (± 8.6) h. Of the 1200 seeds planted across all the experimental treatments, 68% germinated and 96% of those that germinated developed first leaves over the course of the seven-month monitoring period. Until the censoring time at 167 days (plus 45 days monitoring without germination event), 61% of control seeds germinated, 69% for short GPT, 67% for medium GPT, and 80% for long GPT, respectively. The mean germination success of seed loads from different elephants was 70% or 105 (± 18.9) seeds per animal. The remaining non-germinated seeds were censored (supplementary data 1). The germination time curves for the four GPT categories (including the control), varied significantly in their expected mean times to germination ($Z = 7.77$; SE = 24052.94; $P < 0.0001$; Fig 2, supplementary data 2) except for categories 1 and 2 that were similar ($\chi^2 = 0.4$, $P = 0.9091$, supplementary data 3). Germination times were significantly longer for the control (80%), short (29%), and medium (26%) categories, than for the long GPT category (Table 1; Fig. 2). Similarly, control seeds had longer expected germination times than seeds in the short ($Z = 5.24$; SE = 0.0642; $P < 0.0001$), medium ($Z = 5.96$; SE = 0.0603; $P < 0.0001$) and long ($Z = 8.16$; SE = 0.0720; $P < 0.0001$; Fig. 2, supplementary data 4) GPT categories. Dung treatment (yes, no) and planting date (0, 6, 13, 20, 27, 33 days from the start of the experiment) had highly significant associations with germination time as shown by the nonparametric Wilcoxon and log-rank tests (P < 0.0001; supplementary data 5 and 6). Results of the LIFEREG procedure of SAS (SAS Institute 2016) provided evidence that GPT (χ^2 = 72.6, $P < 0.0001$), dung treatment (χ^2 = 62.5, $P < 0.0001$) and date of planting (χ^2= 140.9, $P < 0.0001$) strongly influenced germination time (supplementary data 7). The parameter estimates of the regression coefficients showed that the expected germination time is [100 × (1 - $e^{-0.3567}$)] = 30% significantly longer for seeds treated with dung than for the untreated seeds (Table 1, Fig.3). The same applies to the median (or any other percentile) time to germination.

The percent increase in the expected germination time for each one unit increase in the planting date is expressed as [100 × ($e^{0.02505}$ - 1)] = 2.54%. This implies that each additional day that passes before the seeds are planted is associated with a 2.54% increase in the expected time to germination, given that the other covariates are held constant. This temporal influence on germination was likely due to the changing climatic conditions over seven months, with longer dry periods in between.

4. Discussion

4.1 Faster germination time for elephant-ingested seeds

In addition to the study of Sekar et al. (2015) in India, we used a larger sample size of elephants and experimentally evaluated the influence of elephant dung itself on seed germination. Furthermore, we propose and apply a different approach to analyzing germination data by using statistical methods for survival analysis to reduce the potential bias associated with censoring the time to germination of seeds. Our results show that *D. indica* benefits from being eaten, although it does not solely depend on elephants for germination (i.e., a large number of seeds also germinate without being eaten). Surviving post-germination is yet another challenge and the faster germination time for seeds ingested by elephants can be expected to be beneficial if it substantially reduces the risk of seed destruction by post dispersal predators (Schupp 1993; Traveset and Verdú 2002; Cochrane 2003). The environmental conditions of the establishing site as well as the type of seed dormancy additionally influence germination speed (Crawley 2000; Traveset and Verdú 2002). Elephant dung has so far been found to provide neutral or beneficial environmental conditions in the form of nutrients, humidity and protection from predation (Campos-Arceiz and Blake 2011). Surprisingly, we found that *D. indica* seeds planted with dung had a longer germination time than seeds planted without dung, which might have been due to the limited pot size and no interaction with surrounding soils and fauna. In natural conditions, the intraspecific competition of large amounts of seeds deposited in the same dung pile might reduce seedling success (Lewis 1987; Campos-Arceiz and Blake 2011). The seed load naturally depends on how many fruits the elephants consumed, which, in our study differed across individuals, with 25 fruits being the maximum amount eaten. Sekar et al. (2015) observed individual differences across elephants, ranging from 7 to 52 fruits of *D. indica* being eaten. Generally, for elephants in natural habitats it is well documented that *D. indica* is a welcome addition to their usual diet (Campos-Arceiz et al. 2008a; Datta and Rawat 2008; Sekar and Sukumar 2013), and the elephants in our study seem to conform with this observation.

4.2 Germination success increases with gut passage time

We found that *D. indica* seeds that had the longest gut passage time had the highest germination success. The gut passage can have positive, negative or neutral effects on seed viability (Campos-Arceiz and Blake 2011). In our study, ingested *D. indica* seeds, regardless of their GPT category, had a higher germination rate compared to non-ingested control seeds. One challenge in seed germination experiments is that observation time is often limited and potential later germination events might be missed. Several studies have addressed this challenge by testing whether the remaining non-germinated seeds contained a viable or a rotten embryo (e.g. Chapman et al. 1992; Nchanji and Plumptre 2003; Campos-Arceiz et al. 2008b) and/or by continuing monitoring until a certain time after the last seed has germinated (Campos-Arceiz et al. 2012; Sekar et al. 2015; our study). The risk of bias remains due to the potential censoring of data and wrongly pronouncing potentially viable seeds as non-viable. We used survival analysis to minimize both potential sources of bias (Allison 1995). The proportion of germinated seeds as a function of time allowed the comparison of germination success among the different categories at any given point in time until the censoring date and provided information on the category-specific speed of germination.

4.3 Large dispersal distances through elephants

Apart from the faster germination of ingested seeds, another benefit for *D. indica* from the seeds consumed by elephants might be the seed dispersal distances and their impacts on the seed shadow (the distribution of viable seeds around their source; Janzen 1971; Willson and Traveset 2000). Asian elephants have home ranges of 50 - 1000 km^2, reflecting the large area across which they can alter or maintain plant composition in ecosystems (Sukumar 1989; Campos-Arceiz et al. 2008b; Sukumar 2006). The seed dispersal distance by elephants varies with the size of the plant seed consumed, with larger seeds taking more time to pass through the digestive system (Powell 1997). *Dillenia indica* seeds (~6 mm in size) are relatively small and, hence, remain in the digestive tract for a rather short time period; their maximum GPT of 72 h we found is much shorter than the maximum GPT of 114 h, reported for tamarind seeds (*T. indica*), which are about twice as large in size (Campos-Arceiz et al. 2008b). Mean dispersal distances for the latter were found to be about 1-2 km in Myanmar and Sri Lanka, depending on the season (Campos-Arceiz et al. 2008b), while Sekar et al. (2015) recorded mean dispersal distances of about 3.5 km for *D. indica*, *Artocarpus chaplasha*, and *Careya arborea* in India. Tamarind seeds were negatively affected by the retention time in the gut (Campos-Arceiz et al. 2008b). In contrast, *D. indica* seeds in our study profited: the longest GPTs and, therefore, the largest potential dispersal distance had the highest germination success. Hence, our findings highlight *D. indica*´s high adaption to and potential benefit from megafaunal dispersers.

4.4 Other potential means of seed dispersal

With decreasing numbers of elephants and other megaherbivores as seed dispersers, plants have to rely on alternative means of dispersal such as livestock, humans or water, which has been reported for *D. indica* (Van Steenis 1948; Donatti et al. 2007; Datta and Rawat 2008; Guimarães Jr. et al. 2008, Sekar et al. 2015). This might not apply for areas with longer dry periods, where smaller animals might contribute to seed dispersal (Sekar and Sukumar 2013). Elephants remove significantly more fruits than other animals such as bovids, macaques and rodents but all of these species were able to access the seeds once the mesocarp had softened (Sekar and Sukumar 2013). While removal does not necessarily lead to dispersal, rodents, for example, are known to store seeds, thereby sometimes contributing to dispersal (Forget et al. 2002; Hulme 2002; Vander Wall 2002). Also macaques can serve as effective seed dispersers but in several cases have negative impacts on germination and viability of some species depending on the temporal context (Albert et al. 2013; Tsuji 2014). Domestic bovids, on the other hand, are able to disperse a great number of seeds for some species as well, but do not reach the seed dispersal capacity of elephants (Sekar et al. 2015).

4.5 Conclusion and conservation implications

In times of climate change, a large dispersal area might become increasingly important as it might help in buffering off potential population losses due to adverse environmental conditions (Corlett and Westcott 2013). However, due to increasingly intensive land use and destruction of ecologically important forests, movements of large mammals are becoming increasingly impeded with the result that their seed dispersal potential might either rapidly decline or even disappear altogether. Large-seeded plant species in particular are at a greater risk of being negatively affected by selective logging and hunting as large seed-dispersing frugivores are often the first animals to vanish from disturbed forests (Markl et al. 2012). Plant species experiencing the loss of their main seed dispersing animal agents might suffer collapses in their recruitment and regeneration cycles (Guimarães Jr. et al. 2008; Blake et al. 2009). Likely consequences will be increased clustering of tree populations and lower dispersal distances with associated reductions in the overall geographic range as well as losses in genetic variation (Cramer et al. 2007; Guimarães Jr. et al. 2008; Terborgh et al. 2008; Markl et al. 2012; Pérez-Méndez et al. 2015). Changes in species composition are to be expected with particularly severe ecological shrinkage in isolated ecosystems (Hansen and Galetti 2009; Markl et al. 2012).

Our results show that *D. indica* does not solely depend on but seems to benefit from being eaten by elephants as ingested seeds were significantly more likely to germinate and to do so earlier than non-ingested control seeds. With this study we contribute to the understanding of the effects of Asian elephants' frugivory which has been much less researched than that of African ones (Campos-Arceiz and Blake 2011). While we still know relatively little about elephant seed dispersal, particularly in Asia, it is clear that elephants hold key functions in forest ecosystems. The megaherbivores shape ecosystems through their high food intake and by destroying vegetation through trampling or breaking, thereby acting as filters on tree recruitment and shifting balances of herbaceous and woody plants (Bakker et al. 2016; Malhi et al. 2016; Terborgh et al. 2016). They are likely helping to avert exceeding redundancy while maintaining plant diversity and thus further decline or local loss of elephants and other large herbivores would likely favor abiotically-dispersed species, leading to simpler plant communities (Blake et al. 2009; Campos-Arceiz and Blake 2011). The disappearance of elephants could further trigger cascading effects for overall system functioning through alterations in habitat and trophic structures, leading to changes in abundance or even extinction of other animal species down to potential deterioration of carbon storage and disturbances of nutrient cycles (Wolf et al. 2013; Bello et al. 2015; Malhi et al. 2016). Hence, their stringent protection will not only benefit the pachyderms themselves but also aid in conserving the habitat for a broad range of plant and other animal species, and ultimately sustaining the services such forests provide also for humankind.

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Author contributions

FKH., ACT., TS., CS. conceived and designed the study. FKH performed the experiments with the support of JER. JOO, FKH, JMB analyzed the data. FKH, ACT, JOO wrote the manuscript; other co-authors provided important editorial input.

Compliance with ethical standards

Conflict of Interest: The authors declare that they have no conflict of interest.

Statement of human and animal rights

All applicable institutional and/or national guidelines for the care and use of animals were followed.

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Table 1. Maximum likelihood parameter estimates for the model relating germination time to the gut passage time (GPT) categories (control, short, medium, long), dung treatment (yes, no) and date of planting seeds. The null hypothesis is that all the coefficients are 0. *exp(β)* is the estimated ratio of the expected (mean) germination times. CL= 95% confidence limits.

Parameter	***Level***	***exp (β)***	***SE***	***Lower CL***	***Upper CL***	χ^2	***P***
Intercept		4.021	0.067	3.891	4.152	3662.7	< 0.0001
GPT	Control	0.588	0.072	0.447	0.729	66.6	< 0.0001
	Short	0.251	0.071	0.112	0.391	12.4	0.0004
	Medium	0.229	0.068	0.095	0.363	11.3	0.0008
	Long	0.000					
Dung	Yes	-0.357	0.045	-0.445	-0.268	62.5	< 0.0001
	No	0.000					
Date		0.025	0.002	0.021	0.029	140.9	< 0.0001
Scale		0.746	0.020	0.708	0.786		

List of Figures

Figure 1. Mean proportion (red line) and 95% confidence band (green shaded area) of germinated seeds across all categories as a function of time to germination. Germination rate =1- proportion of non-germinated seeds. The vertical dashed lines mark the beginning of germination and the right-censoring date, respectively. Monitoring of seeds was continued for 45 days after the date of the last germination event.

Figure 2. The proportion of germinated seeds as a function of time for the control group (not ingested) and the three gut passage time (GPT) treatment groups (short: GPT $\leq$ 30 h, medium: 30 h $<$ GPT $\leq$ 48 h, long: GPT $>$ 48 h) and the pointwise 95% confidence bands. Germination rate =1- proportion of non-germinated seeds.

Figure 3. The proportion of germinated seeds as a function of time since planting in days for the seeds planted with dung and without dung and the 95% pointwise confidence bands. Germination rate =1- proportion of non-germinated seeds.

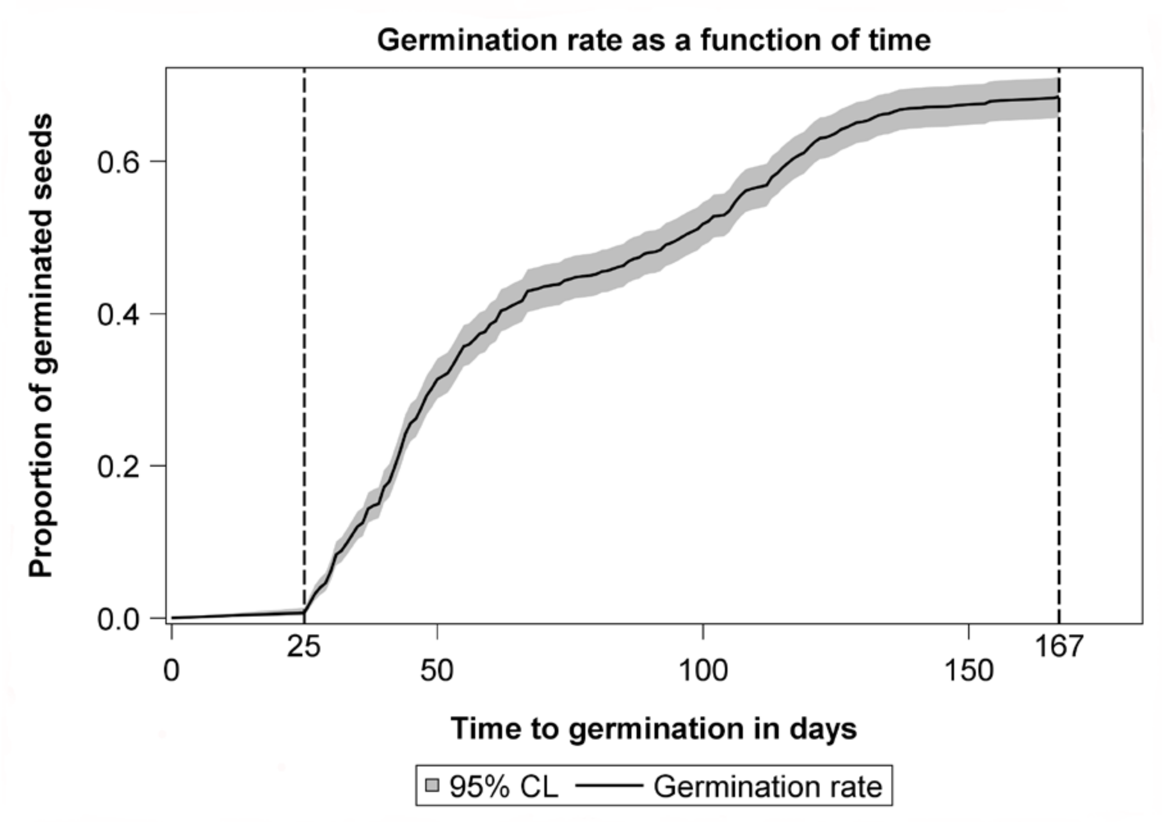
Germination rate as a function of time
Proportion of germinated seeds
0.0
0.2
0.4
0.6
0
25
50
100
150
167
Time to germination in days
95% CL
Germination rate

Figure 1

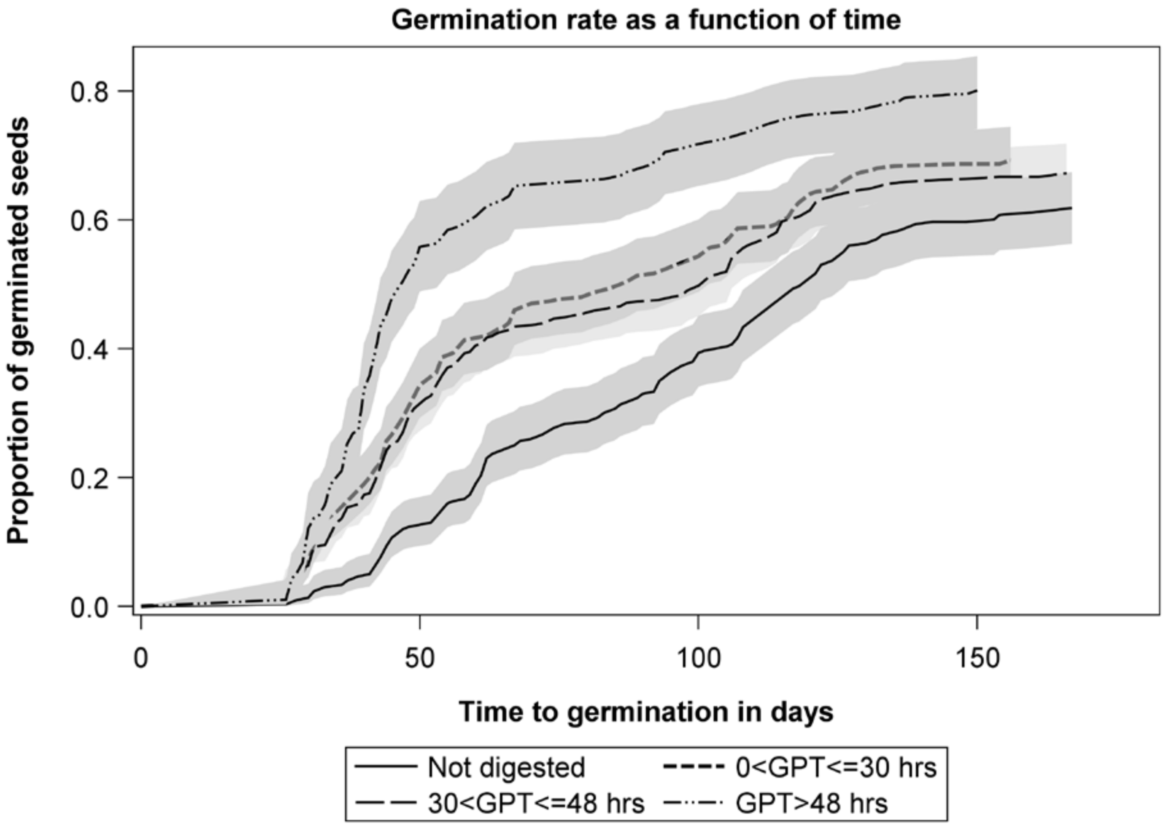
Germination rate as a function of time
Proportion of germinated seeds
0.0
0.2
0.4
0.6
0.8
0
50
100
150
Time to germination in days
Not digested
0<GPT<=30 hrs
30<GPT<=48 hrs
GPT>48 hrs

Figure 2

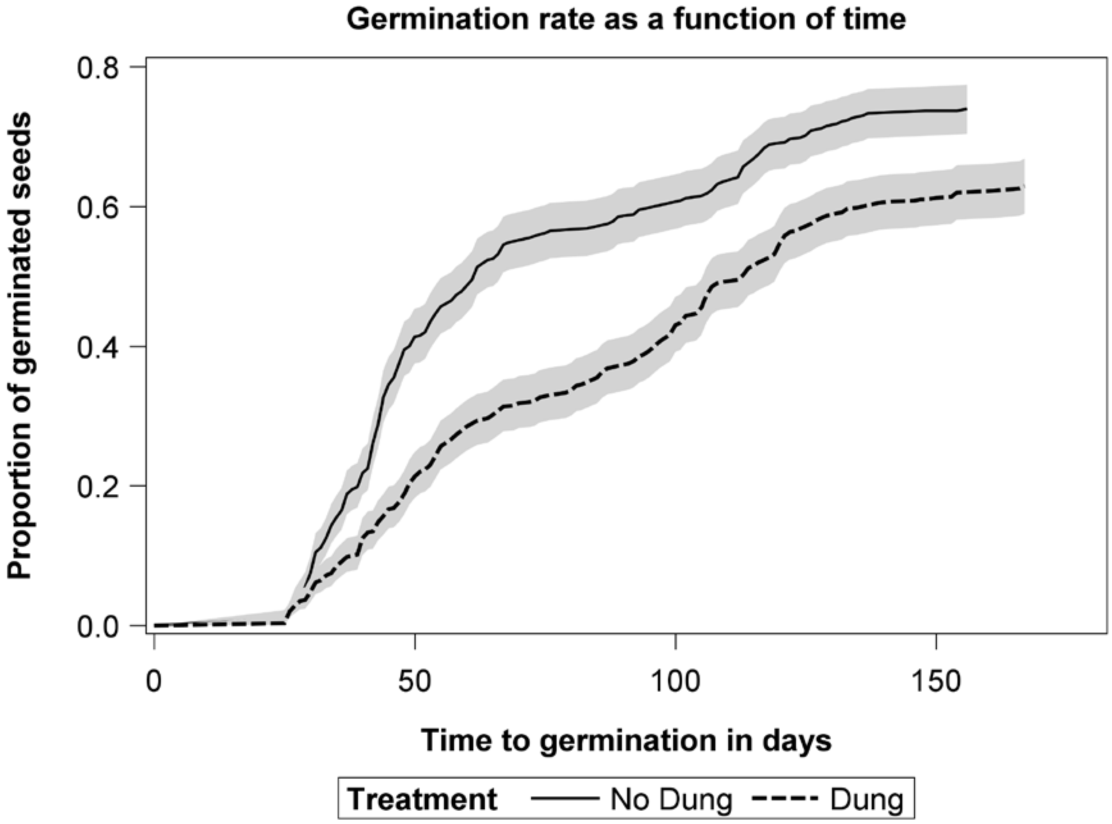
Germination rate as a function of time
Proportion of germinated seeds
0.0
0.2
0.4
0.6
0.8
0
50
100
150
Time to germination in days
Treatment
No Dung
Dung

Figure 3